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The influence of nutrient and water availability on carbohydrate storage in loblolly pine

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Abstract

We quantified the effects of nutrient and water availability on monthly whole-tree carbohydrate budgets and determined allocation patterns of storage carbohydrates in loblolly pine (*Pinus taeda*) to test site resource impacts on internal carbon (C) storage. A factorial combination of two nutrient and two irrigation treatments were imposed on a 7-year-old loblolly pine stand in the Sandhills of North Carolina. Monthly collections of foliage, branch, stem, bark, and root tissues were made and total non-structural carbohydrate analyses were performed on samples collected in years 3 and 4 after treatment initiation. Seasonal fluxes of carbohydrates reflected the hypothesized use and storage patterns. Starch concentrations peaked in the spring in all tissues measured; however, minimum concentrations in aboveground tissue occurred in late winter while minimum concentrations in below ground tissue occurred in late fall. Increased nutrient availability generally decreased starch concentrations in current year tissue, while increasing starch in 1-year-old woody tissue. Irrigation treatments did not significantly impact carbohydrate flux. The greatest capacity for starch storage was in below ground tissue, accounting for as much as 400 kg C/ha per year, and more than 65% of the total stored starch C pool. The absolute amount of C stored as starch was significantly increased with increased nutrient availability, however, its relative contribution to the total annual C budget was not changed. Published by Elsevier Science B.V.

Keywords: Nutrient and water availability; Carbohydrate storage; Loblolly pine

1. Introduction

Carbohydrate storage serves to buffer the tree during periods of low C gain relative to C use. Excess sugars accumulate as non-structural starch when C production exceeds growth demands, and conversely provide a buffer when consumption is greater than current production (Ericsson, 1978). Starch acts as both a long-term and short-term storage polysaccharide in plants. It is accumulated during active photosynthesis and then mobilized and exported as sucrose for respiration. Differences in starch concentrations could indicate different rates of production, or shifts in allocation.

Conifers accumulate non-structural carbohydrates in needles prior to bud-break, and mobilize them during the initiation of shoot growth (Kozlowski and Winget, 1964; Kozlowski and Keller, 1966; Krueger and Trappe, 1967; Ericsson, 1978, 1979, 1980; Deans and Ford, 1986; Webb and Kilpatrick, 1993). A decrease in starch content reflects the sink strength of the tree in relation to the production of current

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photosynthate in the early growing season. A starch deficit aboveground will likely lead to a decline in productivity.

Carbohydrate contents of stems and needles within species follow similar cyclic patterns. An early study by Reines and Bamping (1962) and a more recent study by Birk and Matson (1986), showed this annual cycle in loblolly pine foliage, with fluctuating levels of insoluble, or starch, fractions that followed those of the soluble component by approximately 2 months. The insoluble fractions reached a quantitative peak in March, followed by a decline until November and December. Krueger and Trappe (1967) documented a somewhat different temporal pattern in concentration of total sugars and starch in seedling roots and tops during winter months. They found that sugars increased in concentration starting in November, reached a peak nearly three times the lowest (summer) concentrations, then decreased steadily to a low level in May. Starch concentrations decreased during the winter sugar buildup then increased rapidly in March to a mid-April peak. Physiological differences between mature trees and seedlings may explain some of these differences.

The degree to which environmental stresses and management practices impact internal carbohydrate distribution is of increasing concern as global climate change scenarios are explored and plantation management intensifies. Several studies have documented decreases in starch reserves and subsequent growth when pine trees were exposed to ozone (Meier et al., 1990; Anderson et al., 1995). Other studies with elevated CO_2 treatments have generally produced increased starch concentrations in pine needles (Maier, personal communication; Ludovici, unpublished data).

The mechanics by which site resources affect seasonal patterns of starch accumulation are of particular interest, as management practices shift toward increasing fertilizer use and silvicultural intensity. Work by Meyer and Spittstoesser (1971), Etter (1972), and Matson and Waring (1984) have shown that starch reserves accumulate to higher levels in plants grown in nutrient deficient soils, presumably because without adequate nutrients, growth and maintenance demands on carbohydrates are less than production. However, Birk and Matson (1986) found that fertilization treatments increased starch reserves in needles. Understanding management impacts on C storage pools can lead to improved long-term productivity.

The three primary objectives for this study were to (1) examine starch concentrations in all tissues and determine if treatments affected concentrations or seasonal patterns, (2) quantify starch storage capacity and the plant component distribution of capacity by treatment, and (3) compare treatment effects on stored starch as a percentage of annual production.

2. Materials and methods

2.1. Study outline

The Southeast Tree Research and Education Site (SETRES) was established in 1992 in the Georgia-Carolina Sandhills, in Scotland County, NC (35°N latitude, 79°W longitude). A mix of 10 one-half sib families of loblolly Piedmont selections had been hand-planted on a 2 m × 3 m spacing in March 1985 after felling of the previous natural longleaf pine (*Pinus palustris* Mill.) stand. The soil was an infertile excessively well-drained, sandy, siliceous, thermic psammentic Hapludult soil of the Wakulla series, and had an available water holding capacity of 16–20 cm (8–10%) in the upper 2 m of the profile. Annual precipitation averaged 1210 mm but extended droughts occur during the growing season. Mean annual temperature in the region was 17 °C with the coldest monthly daytime average temperatures in January (0.5 °C) and the warmest in July (32.9 °C).

The experimental design was a factorial combination of two nutrition treatments (no fertilization or fertilization to optimum foliar levels) and two irrigation treatments (no irrigation or irrigation to 40% available moisture) replicated in four randomized complete blocks (Albaugh et al., 1998). Each treatment plot was 0.25 ha and includes a 0.09 ha measurement plot, with 10 m buffer strips between plots. Complete control of non-pine vegetation had been maintained in all plots since 1992 through a combination of mechanical and chemical (glyphosate) methods.

2.2. Sample collection

Tissue samples were collected monthly from April 1995 through June 1996. All samples were placed on

dry ice in the field to stop enzymatic activity, and stored at −20 °C until being freeze-dried. Samples were later ground in a Wiley mill, to pass through as 20 mesh screen, and sub-sampled for analyses.

Seven fully elongated fascicles were collected from each of four crown positions from seven trees per treatment plot. Foliage for these analyses was collected from the 1994 first flush cohort growing on a 1993 first flush branch, and from the 1995 first flush cohort on a 1994 first flush branch, after the new foliage had elongated (June or July).

Stem and branch material were collected from five dominant or co-dominant trees in each treatment plot. A secondary branch growing on a primary branch located in the upper third of the crown was removed and the unfoliated portion of branch was collected. Ten cores (4.3 mm diameter × 2 cm length) were collected from each tree for stem and bark samples. Using an increment borer, cores were taken in a spiral around the stem with a range in collection points of 0.2–2.5 m from the ground. Cores were separated into bark, current year and previous year tissues.

Root samples were collected from five cores (15 cm × 15 cm) in each treatment plot. Roots were sifted from the soil before live roots were separated into four size classes (<2, 2–5, 5–15 and >15 mm diameter). Fine roots were defined as <2 mm in diameter, and coarse roots represent those 2–15 mm in diameter. Loss on ignition analysis of root samples provided a correction factor for soil in each sample.

2.3. Carbon budgets

Carbohydrate analyses were performed following the enzymatic assay of Schoeneberger et al. (1992), as modified from Jones et al. (1977). Approximately 25 mg of the ground samples were extracted with 80% ethanol at 80 °C for 3 min, mixed and centrifuged. The supernatant (soluble sugars) and pellet (starch) were kept at <0 °C until analysis. The sample pellet was incubated first with KOH, then, digested with an amyloglucosidase solution. The resulting sugar units were quantified with a hexose assay mix and expressed as mg glucose/g dry tissue. Quality control measures included use of an in-house standard tissue with every sample set, and 15% sample replication. Replicability levels of 5% about the mean were used for within and between run variability.

Biomass production values for 1995 were from Albaugh et al. (1998) with a modification to include an estimate of bark production (Metz and Wells, 1965). Root biomass estimates were generated from the methods in Albaugh et al. (1998). Carbon budgets for tissue production utilized archived data sets of tissue analyses for carbon content. Average carbon concentrations used for these calculations were foliage 50%, branch 48%, bark 48%, stem 48%, tap root 44%, coarse roots 44%, and fine roots 42% (Ludovici, unpublished data).

The difference between maximum and minimum starch concentration during the year, was used as an estimate for the starch buffering capacity (Table 1) of each tissue by main effect treatment combination. Starch buffering capacity is a gross approximation of the capacity of any tissue to supply starch. Tap root tissues were not analyzed, and were assigned a starch buffering capacity of 200 mg glucose/g tissue, to emulate properties of the similar coarse root material. The total potential for any tissue to store starch was deemed the starch storage capacity (Table 2) and was calculated as the product of mean end of 1995 biomass estimates (Albaugh et al., 1998) and the average starch buffering capacity for that current year tissue. The amount of C available from stored starch was calculated using the chemical formula for glucose, the final breakdown product in starch analyses. Because carbohydrates are reported as mg glucose/g tissue and glucose is 40% C, carbon stored as starch could be easily calculated from starch storage capacity values.

Table 1
Starch buffering capacity (mg glucose/g tissue), calculated as the difference between maximum and minimum starch concentrations, for each main effect treatment combination, and each tissue type sampled from April 1995 through June 1996

Tissue type	Control	Irrigated	Fertilized	Irrigated and fertilized
Foliage	94	84	66	67
Branch	65	67	61	74
Bark	35	38	43	36
Stem	18	20	19	21
Tap[a]	200	200	200	200
Coarse	191	227	232	209
Fine	130	149	130	140

[a] Using estimated buffering capacity.

Table 2
Annual starch storage capacity in kg/ha and allocation (%) by main effect treatment combination and tissue type sampled from April 1995 through June 1996

Tissue type	Control	Irrigated	Fertilized	Irrigated and fertilized
Foliage	244 (11)	244 (8)	330 (9)	389 (9)
Branch	254 (11)	268 (9)	451 (12)	599 (13)
Bark	53 (2)	74 (3)	141 (4)	133 (3)
Stem	110 (5)	156 (5)	249 (7)	311 (7)
Tap[a]	620 (28)	646 (22)	1434 (39)	1527 (34)
Coarse	821 (37)	1266 (44)	916 (25)	1364 (33)
Fine	140 (6)	242 (8)	146 (4)	151 (3)
Total	2242	2896	3667	4474

[a] Using estimated buffering capacity.

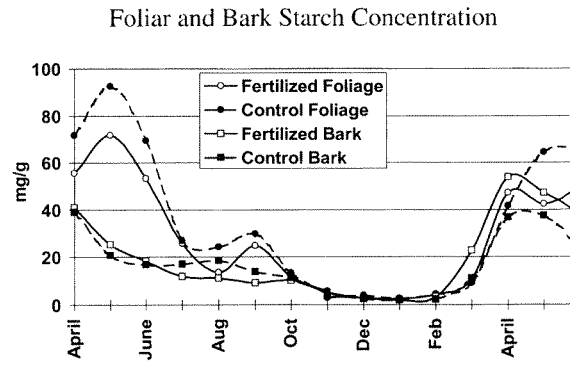

Fig. 1. Foliar and bark starch concentrations for fertilized and non-fertilized trees at SETRES (April 1995–June 1996).

2.4. Statistical analyses

The study was implemented as a 2×2 factorial, randomized complete block. Effects of nutrition level and irrigation on starch concentration were tested for each monthly collection and each tissue, using two-way analyses of variance (ANOVA) for a randomized complete block design (Statistical Analysis System, 1988 (Proc GLM)). Inspection of residuals and normal probability plots ensured data conformed to the assumptions of ANOVA, and when necessary, data were log-transformed to normalize variances across treatments (Sokal and Rohlf, 1995). Treatment effects were considered significant if $P < 0.05$.

3. Results

3.1. Carbohydrate fluxes in individual tissues

Foliar starch concentrations in current year foliage exhibited seasonal fluxes as hypothesized (Fig. 1), with fertilized trees having significantly lower starch concentrations than non-fertilized trees during the growing season (Table 3). Foliar starch concentrations were less than 1% throughout the winter months (November–February), and began a rapid increase as bud break occurred. Foliar starch increased throughout the period of needle elongation, reaching a peak of 9% in control treatments, in May, followed by a decline through the summer and fall.

Branch tissue starch concentrations were also lower in fertilized trees than in non-fertilized trees during the 1995 season, but that pattern reversed and showed a significant increase in starch concentration in fertilized branch tissue during 1996 (Fig. 2). Starch concentrations peaked in April or May at 7.1% and gradually decreased to 0.2% in January (Fig. 2). Branch starch concentrations were similar in magnitude to those in foliage and displayed similar seasonal fluxes, with values below 1% during the winter then increasing steadily during the spring. Branch tissue starch was occasionally increased by the irrigation treatment (Table 3).

Bark starch concentrations were significantly impacted by fertilization treatment (Table 3), with

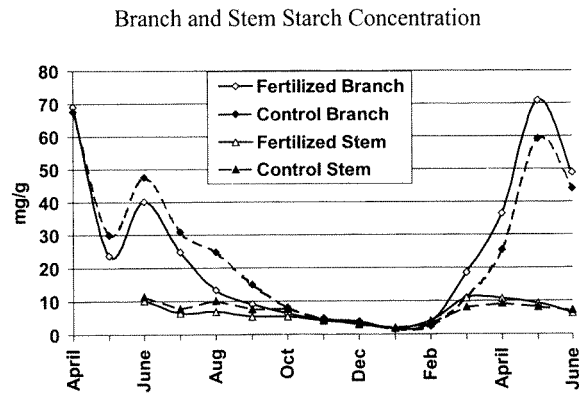

Fig. 2. Branch and stem starch concentrations for fertilized and non-fertilized trees at SETRES (April 1995–June 1996).

Table 3
ANOVA results of the 2 × 2 factorial design with irrigation and fertilization main effect treatments, presented as $P > F$-values, for starch concentrations for each loblolly pine tissue

Date	Main effect treatment	Needle	Branch	Bark	Stem	Coarse roots	Fine roots
April 1995	Irrigated		0.015	0.693		0.892	0.067
	Fertilized		0.614	0.639		0.442	0.267
	Irrigated and fertilized		0.069	0.173		0.618	0.216
May 1995	Irrigated		0.733	0.351		0.063	0.356
	Fertilized		0.011	0.120		0.019	0.020
	Irrigated and fertilized		0.368	0.664		0.551	0.026
June 1995	Irrigated		0.104	0.548	0.136	0.575	0.564
	Fertilized		0.060	0.652	0.238	0.098	0.078
	Irrigated and fertilized		0.541	0.731	0.304	0.669	0.592
July 1995	Irrigated	0.462	0.289	0.266	0.142	0.010	0.010
	Fertilized	0.031	0.095	0.047	0.117	0.115	0.423
	Irrigated and fertilized	0.565	0.356	0.795	0.626	0.990	0.566
August 1995	Irrigated	0.241	0.020	0.089	0.224	0.416	0.513
	Fertilized	0.001	0.001	0.014	0.050	0.114	0.471
	Irrigated and fertilized	0.498	0.724	0.808	0.392	0.492	0.688
September 1995	Irrigated	0.368	0.501	0.016	0.139	0.924	0.263
	Fertilized	0.239	0.029	0.010	0.027	0.005	0.040
	Irrigated and fertilized	0.267	0.267	0.901	0.371	0.566	0.834
October 1995	Irrigated	0.796	0.514	0.270	0.505	0.266	0.768
	Fertilized	0.432	0.205	0.562	0.005	0.150	0.877
	Irrigated and fertilized	0.731	0.255	0.407	0.202	0.429	0.558
November 1995	Irrigated	0.611	0.549	0.474	0.650	0.677	0.161
	Fertilized	0.458	0.106	0.907	0.447	0.002	0.005
	Irrigated and fertilized	0.864	0.894	0.077	0.110	0.824	0.173
December 1995	Irrigated	0.759	0.730	0.262	0.271	0.081	0.697
	Fertilized	0.028	0.905	0.164	0.615	0.013	0.404
	Irrigated and fertilized	0.720	0.613	0.123	0.087	0.608	0.454
January 1996	Irrigated	0.635	0.199	0.803	0.373	0.422	0.083
	Fertilized	0.916	0.063	0.772	0.378	0.129	0.089
	Irrigated and fertilized	0.777	0.987	0.416	0.378	0.797	0.799
February 1996	Irrigated	0.306	0.984	0.341	0.419	0.802	0.465
	Fertilized	0.602	0.001	0.003	0.003	0.510	0.954
	Irrigated and fertilized	0.904	0.458	0.655	0.725	0.709	0.773
March 1996	Irrigated	0.114	0.587	0.057	0.393	0.308	0.616
	Fertilized	0.043	0.002	0.000	0.017	0.680	0.316
	Irrigated and fertilized	0.421	0.972	0.090	0.796	0.929	0.673
April 1996	Irrigated	0.925	0.227	0.894	0.317	0.597	0.434
	Fertilized	0.021	0.001	0.001	0.015	0.363	0.201
	Irrigated and fertilized	0.368	0.565	0.735	0.233	0.662	0.144
May 1996	Irrigated	0.801	0.476	0.966	0.450	0.992	0.448
	Fertilized	0.007	0.025	0.083	0.304	0.094	0.099
	Irrigated and fertilized	0.507	0.123	0.009	0.971	0.370	0.634
June 1996	Irrigated	0.411	0.094	0.853	0.052	0.514	0.295
	Fertilized	0.062	0.204	0.008	0.279	0.358	0.666
	Irrigated and fertilized	0.685	0.091	0.144	0.811	0.815	0.057

fertilized trees exhibiting lower concentrations in the months of July, August and September, and higher concentrations the following spring (Fig. 1). Seasonal fluctuations in bark starch concentrations were similar to, but of lesser magnitude than in branch tissue, with a peak of 5.4% in April and values below 1% through the winter.

Stem starch concentrations were significantly lower in fertilized trees during the late summer months of August, September and October, and higher in February, March and April (Table 3). Starch concentrations in current year stem tissue reached their maximum in the spring and minimum in January, but were always less than 1.2% (Fig. 2).

Coarse roots starch concentrations were significantly reduced in fertilized treatments compared with controls (Table 3), but seasonal fluxes in coarse root starch were more dynamic than those for other tissues, regardless of the treatment (Fig. 3). Starch concentrations in coarse roots began to increase in October, after bud set, and increased until bud break in the spring. Peak concentrations of 22% in April 1995 and 16% in May 1996 were measured in the control treatments. Minimum starch concentrations occurred in October, and never fell below 2%.

Fine root starch concentrations were significantly lower in fertilized treatment plots in the fall (Table 3) and were generally not impacted by irrigation treatments. Fine root starch concentrations mirrored the seasonal pattern detected in coarse roots, with peaks of 15.3% in April 1995 and 12% in April 1996 and a minimum of 1% in October (Fig. 3).

Starch concentrations were always greatest in roots compared to other tissues (Fig. 4). Root starch concentrations were as much as 300% higher than in branches, the next most concentrated tissue. Comparison of the seasonal fluxes of starch showed that there are also differences in when the increases began, and peaks of different tissue types occurred. Build-up or recharge of carbohydrates stored as starches, began in the fall in belowground tissues, but did not begin until spring in aboveground tissues (Fig. 4).

3.2. Starch storage budgets

Starch buffering capacity was much lower in above ground tissues than belowground tissues (Table 1), and was, on an average unaffected by treatment in all tissues. The lone exception was in foliage storage starch buffering capacity, which decreased with increasing nutrient availability. Starch storage and allocation to aboveground tissues generally followed patterns of biomass production, with increasing absolute quantities in fertilized treatments, and relative distribution between aboveground tissues not affected by treatments (Table 2). Foliar tissue accounted for 12% of the standing biomass and as much as 11% of starch storage. Branch and bark tissues combined contributed 25% of the standing biomass, but a maximum of only 16% of the starch storage capacity, while stem tissue, which comprised 33% of the standing biomass allocation, accounted for less than 7% of the storage starch allocation (Table 2). Tap roots, which comprised a small proportion

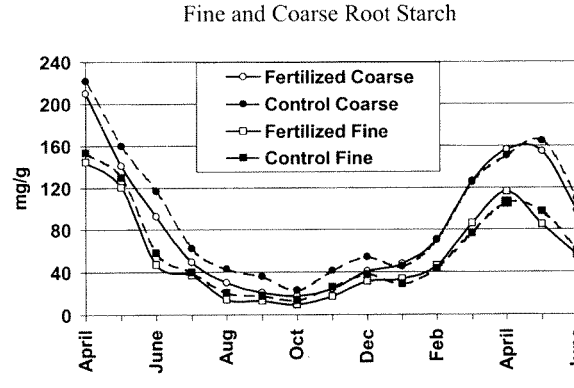

Fig. 3. Fine and coarse root starch concentrations for fertilized and non-fertilized trees at SETRES (April 1995–June 1996).

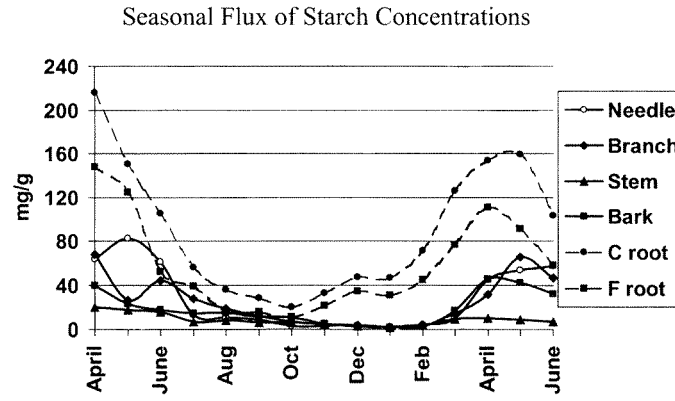

Fig. 4. Average starch concentrations, across fertilization and irrigation treatment, by tissue at SETRES (April 1995–June 1996).

(less than 17%) of the total biomass, showed substantially increased estimates of starch storage with fertilization, and contributed as much as 39% of the total estimated starch storage (Table 2). Coarse root starch storage accounted for the largest proportion of storage capacity comprising 25–44% of the total storage budget. Absolute coarse root biomass (Albaugh et al., 1995) and starch storage were increased by fertilization treatments, but the proportional contribution to the total budgets were decreased slightly. Fertilization treatments decreased fine root biomass and its proportional allocation to both total biomass and the annual starch storage capacity by 50%. Regardless of stand management regime, belowground tissues combined, accounted for more than 68% of the estimated starch storage capacity (Table 2).

Total carbon needed for 1995 production estimates was 5176 kg C/ha per year in the control treatment, 6670 kg C/ha per year in irrigated plot, 10,233 kg C/ha per year in fertilized plots and 12,169 kg C/ha per year in irrigated and fertilized plots. Calculated carbon stored as starch was as low as 897 kg C/ha in the control treatment, and as high as 1790 kg C/ha in the irrigated plus fertilized treatment, with intermediate values of 1158 and 1467 kg C/ha calculated for the irrigated and fertilized treatments, respectively (Fig. 5). The percentage of carbon needed for annual production, which can be provided by internal starch storage, was quantified as 17% in the control treatment, 17% in the irrigated treatment, 14% in the fertilized treatment and 15% in the irrigated and fertilized treatment.

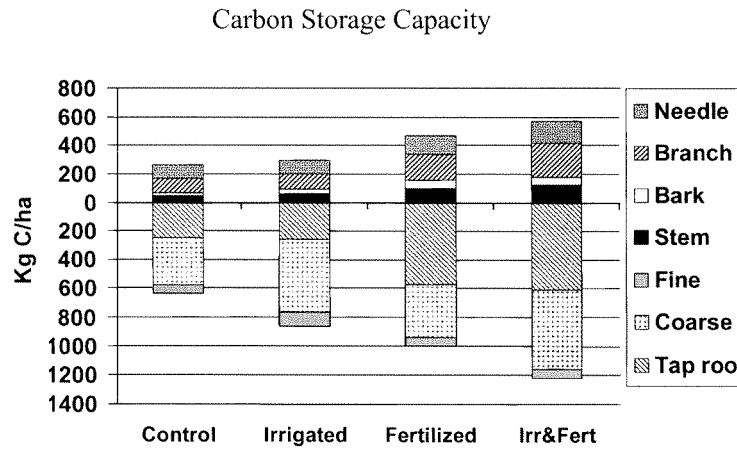

Fig. 5. Carbon storage in individual tissues for the 1995 growing season, by fertilization and irrigation treatment combination at SETRES.

4. Discussion

Other researchers have documented evidence of varying starch concentrations in plants, but none have quantified its contribution to the annual whole-tree carbon budget, or explored how starch allocation in multiple pine tissues are impacted by nutrient and water availability. In this experiment, starch concentrations were six times more likely to be impacted by site fertility than water availability treatment. Starch concentrations themselves were also more indicative of treatment differences during the later summer (July–September), than any other period. These responses varied by tissue, as significant differences in starch concentration occurred in the late summer and spring in aboveground tissues, and during the dormant season in belowground tissues.

In this study, fertilization treatments decreased growing season starch concentrations in all tissues; however, higher starch concentrations were measured in fertilized tissues during the following spring. Birk and Matson (1986) also found that starch concentrations during the growing season were lower in current foliage from high fertility sites than low fertility sites. They defined a positive relationship between starch and nitrogen concentrations during the dormant season, while the relationship was negative during the growing season. The magnitude and direction of the change in starch reserves, with the onset of growth following the dormant season, may indicate nutrient limitations in loblolly pine and potential growth responses to fertilization. They also observed that fertilization increased starch reserves in current needles at the end of the growing season (0.7 versus 1.4%), and the rate of starch mobilization during the initiation of needle growth. They concluded that carbon reserves accumulated during the growing season in mature 1-year-old needles on control sites indicated lower sink strength under low nutrient conditions. The lower growing season storage we measured, followed by the increased storage during the spring recharge period, supports the idea that storage may be restricted by nutrient availability and use, but that positive fertilizer effects are seen in the long-term growth response to early and increased resource availability.

All tissues displayed seasonal fluctuations in starch concentrations, but the timing of maximum and minimum concentrations varied with tissue type. Generally, starch concentrations peaked in the spring and remained low during the dormant season. Examination of all our tissue types on the same graph (Fig. 4), clearly demonstrates that below ground recharge (carbon storage) starts in October, while aboveground accumulations do not begin until February or March. Adams et al. (1986) also reported that low root starch concentrations occurred in autumn and that foliar starch concentrations were lowest in winter. In our study, stem tissue had peak concentrations in March, followed by bark and fine root starch peaks in April, coarse root and branch peaks in April or May, and foliar starch peak concentrations in May or June. This progression was not unexpected, and supports the hypothesis that starches accumulate in woody tissue during later winter and early spring, when foliar sink strengths remain low. Fertilization treatments also significantly increased springtime starch concentrations in woody tissues, indicating the early advantage those trees have in producing and accumulating carbon. As day length and photosynthetic production of assimilates increase, starch concentrations progressively increase in tissues nearer to the source of carbohydrate production. Our results support that sugars produced during the dormant season are moved belowground and that excess sugars produced in the spring are stored in, and readily available to, aboveground tissue.

Peak concentrations of starch were much higher in roots than in aboveground tissue, indicating their propensity to function as carbon storage units. Peak starch concentrations in root tissues were 300–2200% greater than in foliar or stem tissue, respectively. Deans and Ford (1977) reported starch levels in 9-year-old Sitka spruce roots that were of the same magnitude that we measured; however, Adams et al. (1986) later reported much lower magnitude of starch fluctuations than in either study (maximum of 17%, minimum of 2%), perhaps because their coarse roots were elutriated and oven dried. Hallgren et al. (1991) found that, compared to fine roots, the starch and sugar concentrations of coarse roots were nearly twice as great, but those tissues had also been oven-dried and had concentrations of 5–10%. We found that roots were able to accumulate significant quantities of carbon as starch throughout the dormant season.

The absolute starch contents were greater in fertilized treatments than in control treatments, even though those concentrations were lower, because of the increased biomass production. These results were not unexpected, and bring to question the importance of relative allocation patterns of starch storage in response to management treatments. We concluded that the allometry of mean allocation of starch to above- and belowground tissues was not affected by treatment; and that approximately 30% of the relative starch was in aboveground tissues, while 70% was in belowground tissues. Our results indicate that absolute values of starch storage are clearly dependent on management treatment; however, relative allocation patterns aboveground and belowground, and the percent contribution of stored starch to the annual carbon budget, are not. However, fertilization treatments did alter relative starch allocation between belowground components by decreasing relative contributions from coarse and fine roots.

This stand of trees was 10 years old and had been receiving irrigation and fertilization treatments for three growing seasons. Our results indicate that 20–30% of the biomass was in root tissue, which contributed 70% of the C storage, suggesting a highly efficient system for maintaining aboveground biomass. Because allometry of loblolly pine trees shifts aboveground with increasing physiologic age, and presuming starch concentrations remain the same in a given tissue type, then relative proportion of root storage starch to the total carbon storage budget would decrease with stand age. Absolute quantities of starch would however continue to increase in proportion to stand productivity or growth rate. If fertilization further decreases belowground biomass or starch concentration within a tissue, the smaller buffering capacity in younger and faster growing stands, compared with older stands, may leave younger stands more at risk for stresses. Certainly, any shift in storage allocation and growth costs will have important biological implications for long-term survival.

Understanding the seasonal fluxes of carbohydrates within a tree will lead to improved management practices. While irrigation treatments rarely affected soluble sugar or starch concentrations in any tissue. Fertilizer applications in winter could enhance root production and coincide with increased starch production and storage. Knowing that starch accumulation in aboveground tissue occurs in March through June, suggests that late season pruning and thinning would facilitate maximum carbon recharge from those tissues. Branch starch contents suggest the best time to prune is when concentrations are lowest, in October or January. Root disturbances, which result from heavy equipment, would also be best timed for late summer or early fall to maximize starch utilization and storage in root tissues. Removal of coarse roots and woody tissues decreases the C storage capacity and may put trees at risk the following year.

These findings indicate the importance of dormant season photosynthesis in building starch reserves, and the important role belowground tissue has in carbon storage and thus long-term productivity. There is tremendous storage capacity, which can impact increased growth potential and reserves to overcome stresses, drought, extreme temperatures, pests and natural disasters. In our study, stored starch accounted for 15–19% of C needed for annual production, and more than 70% of starch storage was in belowground tissue. It is important to note that these estimates are minimum, because they represent the annual net change. Within a day and during the season, stored starch may be even more important.

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