Stand-Scale Correspondence in Empirical and Simulated Labile Carbohydrates in Loblolly Pine

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ABSTRACT. As investment into intensive forestry increases, the potential trade-offs between productivity and sustainability should be scrutinized. Because of their important role in internal carbon (C) budgets, labile C pools may provide a measure of the potential ability of trees and stands to respond to stress. We modified the process model BIOMASS to examine daily C budgets of midrotation nonfertilized and fertilized loblolly pine stands. We tested whether the absolute difference between daily simulated net canopy assimilation (GPP minus maintenance respiration) and our empirical estimates of production, or daily gross carbon balance, mimics the labile carbohydrate C pool. We compared this labile pool surrogate to independent, empirical analyses of total nonstructural (starch and soluble sugars) carbohydrates from an individual whole-tree analysis scaled to the stand level.

Of particular interest, the simulated daily gross C balance indicated periods of carbon deficit during the growing season that lasted from 1 to 40 days. Simulated daily net C balance was met from labile C storage during these periods. Fertilized plots had similar time-period trends as the control plots, but exhibited a twofold increase in C assimilation and use. Simulated and empirical estimates of the labile carbohydrate pools displayed similar seasonal trends, although their correspondence depended on the time of year. Simulations indicated a winter/early spring "recharge" period; concentrations peaked at -50 and -60 mg C g biomass-l in control and fertilized plots, respectively, in 1995. The overall correlation between predicted and empirical estimates was low to moderate ($r = 0.51$). The best agreement was with the empirical data from April through June as concentrations declined; however, predicted minimum concentrations (15 and 5 mg C g biomass-l in control and fertilized plots, respectively) were lower, and obtained earlier in the year than the empirical data (-20 mg C mg biomass-l). These analyses quantify the strong extent that loblolly pine exhibits a buffered capacity to balance the C budget when current photosynthesis occasionally cannot meet daily C requirements. Further development of our approach may lead to a tool for analyzing potential risks associated with intensive forest management. FOR. SCI. 47(1):60–68.

Key Words: Fertilization, labile carbohydrate, loblolly pine, process modeling.

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L ABILECARBOHYDRATESSERVEAS animportantcarbon buffer that contributes to the growth and survival of coniferous forest species. Conifers accumulate nonstructural carbohydrates (NSC) in needles prior to budbreak and mobilize them during the initiation of shoot growth (Kozlowski and Keller 1966, Ericsson 1979, Birk and Matson 1986, Webb and Kilpatrick 1993). The accumulation (sink) and mobilization (source) of NSC are processes that likely enable consistent growth activity during optimal growing periods, ensuring seasonal C balance. Because of their important role in internal C budgets, labile C pools may provide a measure of the potential ability of trees and stands to respond to stress.

Forest management practices have the potential to manipulate the patterns and magnitude of labile C pools. We are now well aware of the direct impacts of improved nutrition, on nutrient poor sites, on loblolly pine growth and development (Vose and Allen 1988, Schultz 1997, Albaugh et al. 1998). Operational fertilization as a forest management tool in loblolly pine is increasing rapidly: industrial fertilization increased from 18,000 ha per year in 1988, to 390,000 ha in 1998 (NCSFNC 1999). Although improved nutrition clearly increases growth, it is unclear what impacts, if any, fertilization may have on labile C pool dynamics.

Empirical studies, such as the labile C studies cited above, typically examine point-in-time estimates. However, this approach does not permit study of process-level relationships. Conversely, process models are useful because they integrate many processes over space and time scales that are otherwise very difficult or impossible to examine empirically (Jarvis 1995, Johnsen et al. 2000). Together, empirical and simulation comparisons help to refocus research efforts, and they lead to greater understanding of process-based functional relationships. Ultimately, process models may be useful for making strategic forest management decisions.

As investment into intensive loblolly pine forestry increases, the potential trade-offs between productivity and sustainability will need to be scrutinized. Here, we examine a potential tool and approach toward this end. The importance of seasonal starch reserves has long been known (Schimper 1903), but the extent that daily or monthly reserves influence growth in loblolly pine has not been documented. Results from a modeling exercise, as well as past tree carbohydrate research, led Sampson et al. (1997) to propose that loblolly pine stands exhibit a strong temporal surplus-buffered C budget whereby, occasionally, photosynthate from photosynthesis cannot meet C requirements for growth and for construction and maintenance respiration. Essentially, "surplus" periods buffer daily "deficit" periods. In this article, we test whether the difference between simulated net canopy assimilation (GPP minus maintenance respiration) and our empirical estimates of growth corresponds to a labile C pool; we compare model results with empirical data collected from tissue digests from individual whole-tree analyses that were scaled to the stand level. We applied the process model BIOMASS (McMurtrie and Landsberg 1992) written for loblolly pine (Sampson et al. 1996), and modified for these analyses, to control and fertilized treatments of an intermediate-aged loblolly pine stand.

Methods

Study Site

This study is part of a comprehensive investigation of the influence of soil nutrient and moisture availability on the ecophysiology of plantation loblolly pine (*Pinus taeda* L.) at SETRES (Southeast Tree Research and Education Site, Scotland County, NC). The study was established in 1992 in the Georgia-Carolina Sandhills, in Scotland County, NC (~35°N Lat., ~79°W Long.) on an infertile, excessively well-drained sandy, siliceous, thermic psammentic Hapludult soil of the Wakulla series. A mix of 10 one-half sib families of loblolly Piedmont selections had been hand planted on a 2 m x 3 m spacing in March 1983 after felling of the previous natural longleaf pine (*Pinus palustris* Mill.) stand. Annual precipitation averages 1,210 mm, but extended droughts occur during the growing season. Mean annual temperature in the region is 17°C with the coldest temperatures in January (0.5°C) and the warmest in July (33°C).

Treatments consisted of a 2 x 2 factorial combination of nutrition (optimum nutrition and no addition) and moisture (ambient and well watered) treatments replicated four times. For the optimum nutrition treatment, N was applied annually in an attempt to achieve a foliar N concentration of 1.3% with other macro- and micronutrients in balance; control foliar N was approximately 0.9%. Fertilization treatment goals have been achieved (Albaugh et al. 1998). Treatment plots were 0.25 ha in size (50 x 50 m), encompassing 30 x 30 m measurement plots with 10 m buffer strips between plots. Complete control of nonpine vegetation in the treatment plot has been maintained since 1992 through a combination of mechanical and chemical (glyphosate) methods. Nutrient treatments have been maintained since March 1992, and irrigation treatments have been functional since April 1993. A detailed description of site nutrition management as well as stand summary statistics may be found in Albaugh et al. (1998).

Empirical Carbohydrate Analyses

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 subsampled for analyses.

Seven fully elongated fascicles were collected from each of four crown positions from seven trees per treatment plot. Foliage was collected from the 1994 first flush cohort growing on a 1993 first flush branch, and from the 1994 first flush cohort growing on a 1992 first flush branch. Foliage was collected from the 1995 first flush cohort on a 1994 first flush branch, and the 1995 first flush cohort collected from a 1993 first flush branch, after the new foliage had elongated (June or July).

Stem and branch material were collected from five dominant or codominant trees in each treatment plot. A secondary

branch growing on a primary branch located in the mid- to upper third of the crown was removed, and the nonfoliated portion of branch was collected. Ten cores (4.3 mm diameter x 2 cm long) 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 to 2.5 m from the ground. Cores were separated into bark, current year, and previous year tissues.

Root samples were collected from 5 cores (15 cm x 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 later defined as <2 mm in diameter, and coarse roots represent those >15 mm in diameter. Loss on ignition analysis of root samples provided a correction factor for soil in each sample.

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. All sugars were broken down enzymatically for analyses, and labile C was quantified as the pool of starch and soluble sugars. Soluble glucose and sucrose (as well as trehalose, mannose, xylose, etc.) were considered a bulk sugar pool, and individual sugars were not quantified separately.

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) but were adjusted from more detailed analyses of root depth distribution (Kress et al. unpublished). 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). These %C values were calculated from C analyses of individual tissue types.

Process Simulations

We modified the process model BIOMASS version 13.0 (adapted for loblolly pine) (Sampson et al. 1996), to examine in more detail the carbon (C) budget of loblolly pine trees and stands. This adaptation of BIOMASS (version 14.0) compares empirical estimates of productivity with simulated net canopy assimilation directly. Version 14.0 of BIOMASS utilizes the input structure found in previous versions of BIOMASS (e.g. McMurtrie and Landsberg 1992). However, while previous versions used the empirical data for monthly comparisons, we altered the model to compare C budget outputs on a daily basis. This modification did not alter how total carbon gain was estimated but does modify the frequency it is tracked. Adapting the model for a daily time-step

required inclusion of explicit C storage while monthly budgets in previous versions used implicit C storage.

We used BIOMASS version 14.0 to examine C budgets by comparing empirical estimates of daily changes in standing mass (converted to C units), considered as an estimate of tissue production, to model estimates of net canopy assimilation. This structure enabled us to test whether the difference between net canopy assimilation and our production estimate represents the labile C pool. In this version, residual C enters labile storage when daily net assimilate exceeds daily requirements as estimated by the empirical data. Removal of C from the labile pool is used to balance the difference between daily net assimilate and use when growth exceeds the daily estimate of net available assimilation.

Model Development

Standing biomass is input into the model at the start of the simulation for 25 periods throughout the simulation run for fine and coarse roots, and 20 periods for stems, branches, and foliage biomass. The difference in standing mass from time T to time $T+1$ is considered an estimate of production. Tissue senescence occurs when daily changes in standing biomass are negative between time T and time $T+1$.

We estimate tissue-specific construction respiration cost (R_C) from the production estimates. Tissue R_C rates are from Chung and Barnes (1977). Daily estimates of production and R_C are compared to daily estimates of net assimilate. If production and R_C are less than net assimilate, they are subtracted with the balance going to labile storage. If production and R_C exceed net assimilate, the difference is removed from storage to meet the estimated use. Any C removed from storage and used in tissue production has an associated R_C cost (Amthor 1989).

Labile C storage follows a fixed hierarchy, with storage following: fine roots > foliage > coarse roots > branches > stems. Removal of C from storage, however, differs from this pattern. Labile C allocated to fine root storage can only be removed from the fine root pool for fine root production (Sune Linder, pers. comm.). Otherwise, the hierarchy remains foliage > coarse roots > branches > stems. While we recognize that this hierarchy lacks direct support from empirical data, the order of the hierarchy was conceived to mimic a conceptual source-sink relationship. In addition, the order (other than the fine root storage dynamics) would not affect model outputs; mass balance is maintained in this model. Maximum storage capacity was estimated from the empirical data set and is determined as a proportion of standing mass for each tissue. Maximum storage capacity on a mass basis was 10% for foliage tissue, 5% fine roots, 9% stems, and 5% branches. Coarse roots, including tap, may store 65% of the starch storage on a mass basis. The stem and branch carbohydrate storage estimates (and roughly, the temporal magnitudes) are comparable to those found for slash pine (*P. elliottii* Engelm.) stands of Florida (Gholz and Cropper 1991) and for Monterey pine stands from Australia (Cranswick et al. 1987) for similar ages and treatments. The initial labile C pool for each treatment was defined prior to simulations; please see "simulations conducted" below for details. Simulations are conducted under the assumption of

mass balance; labile C storage cannot exceed maximum, nor deplete below zero and, if these conditions are met, error warnings are posted rendering new runs necessary.

We incorporated new algorithms into the model to utilize current information from the site including equations to estimate maximum, potential photosynthesis (*Amax*), and tissue maintenance respiration (R_M). The model calculated *Amax* as a linear function of tissue nitrogen content (g N m^{-2}). Empirical data suggest that the relationship between *Amax* and tissue nitrogen content varied with time of year and age of foliage (Maier et al. 2000), therefore, separate equations were used for April through September and October through March for calculations of *Amax.* Parameter estimates for photosynthetic quantum efficiency (Q) were obtained by fitting a nonrectangular hyperbola to observed light response curves for 1-yr-old and current year foliage at four different times during the year. BIOMASS, then, uses *Amax* to calculate daily C gain as responses to light, air temperature, vapor pressure deficit, and soil water.

We modeled foliage respiration as a function of air temperature (Maier 2000) using site-specific temperature response curves (Maier 2000). Separate equations, roughly corresponding to winter, spring, summer and fall seasons, were used to reflect seasonal differences in basal respiration and Q_{10} values; the Q_{10} for foliage respiration ranged from 1.6 to 2.1. Because empirical estimates of foliage respiration were unresponsive to leaf nitrogen (Maier 2000), we used similar equations within the model to estimate foliage respiration for control and fertilized stands. Equations to simulate stem and branch tissue respiration were based on a relationship developed by Maier (2000) following procedures in Maier et al. (1998) where maintenance respiration is proportional to tissue nitrogen content corrected for temperature. In the model, air temperature was used as a surrogate for tissue temperature. Base temperature for calculation of Q_{10} was 0°C, and basal respiration was a linear function of tissue nitrogen content. Empirical estimates of fine root (<2 mm diameter) respiration rates were a function of soil temperature with a $Q_{10} = 2$ (Maier 2000). There were no allowances for fine root nitrogen content; thus, stand fine root respiration was strictly a function of fine root biomass. Base temperature for calculation of the Q_{10} for fine roots was 0°C. And, coarse root tissue respiration was estimated from standing mass as found in BIOMASS (McMurtrie and Landsberg 1992). Although only minimum and maximum temperatures are utilized, the rate-temperature (*T*) function varies diurnally similar to previous versions of BIOMASS (McMurtrie and Landsberg 1992). The model uses a sinusoidal function to estimate the daily trend in ambient air temperature, assuming the minimum temperature occurs at dawn and average temperature (minimum plus maximum *T/2*) at sunset, and a linear trend in *T* from sunset until the minimum temperature the following day.

Model *Parameterization* and Calibration

Biomass production was estimated from monthly or bimonthly changes in tissue mass for stems, branches, and fine and coarse roots and from LAI for foliage production. We used the 1995-1996 temporal progression in standing mass

from empirical investigations and destructive harvests to estimate biomass production for stems, branches, and fine and coarse roots from SETRES for control and fertilized treatments (Maier et al. 1998). Periodic standing biomass was estimated for each tissue component by using bimonthly (or less) measures of growth phenology, and production estimates from pre- and post-growing season surveys for stem, branch, and coarse roots. Fine root biomass was estimated from sequential coring methods (Kress, unpublished data, Mignano 1995).

Foliage biomass production was estimated from leaf area index (LAI) converted to mass units using an estimate of specific leaf area (30.5 cm^2 g^{-2})(Albaugh, unpublished data, Althoff 1994). Loblolly pine typically carries two foliage cohorts during most of the calendar year (Albaugh et al. 1998). To characterize foliage dynamics for the 1995-1996 simulation, foliage biomass of four cohorts (1993, 1994, 1995, 1996) was required. We assumed that the foliage mass at minimum LAI represented foliage production from the previous growing season. We were thus able to assign production for each foliage cohort. The difference in mass between the yearly production estimate and total foliage mass at maximum LAI of the year the cohort was produced yielded an estimate of foliage mass of the previous year's foliage cohort. We used needle litterfall to estimate LAI (Sampson and Allen, unpublished). While this approach characterizes changes in the pool, and not flux changes in foliage development and senescence, we would expect that this approach underestimates foliage production. However, we observed similar foliage cohort production estimates as those observed from destructive harvests (Albaugh et al. 1998).

Several parameter estimates were updated from those used in previous model versions (e.g., Sampson and Allen 1998, 1999). Namely, herein we assumed a 2 m soil profile, with a 25 cm surface profile; the parameters for soil available water were estimated from Abrahamson et al. (1998). Maximum stomatal conductance was estimated from Ewers (1999). For these simulations we used the light response model (canopy assimilation) and the stomatal model of McMurtrie et al. (1990) (stomatal conductance) found in BIOMASS (McMurtrie and Landsberg 1992).

Simulations

We simulated the carbon pools and fluxes for control and fertilized treatments for 1995 through 1996 at SETRES. Initial labile C pools for both treatments at the start of the 1995 year were set using iterative simulations to obtain labile carbohydrate concentrations (mg C g biomass-') comparable to those observed in the separate, empirical investigation corresponding to the first sample date (i.e., day of year 105, or April 15, 1995). Carbon fluxes were simulated for two consecutive years; labile C storage at the end of 1995 determined the initial starting values for the 1996 simulation year. Meteorological input data for these simulations used the minimum requirements for BIOMASS: shortwave radiation, minimum and maximum daily temperatures, and precipitation. These data were obtained from an on-site met station. Note that our simulation and empirical analyses were not

aimed toward assessing diurnal C dynamics. We specifically examined: (1) the simulated daily photosynthetic contribution to the gross carbon budget [net canopy assimilation (carbon available for partitioning) minus the empirical estimate of all-tissue production (plus R_C)]; (2) the temporal (seasonal) change in stored labile C (i.e., our labile C pool), converted to concentration estimates compared to the independent, tree level analyses of total nonstructural carbohydrates (starch and sugars-see above) scaled to the stand level; and (3) a one-to-one comparison of these concentration estimates. Stand summary statistics can be found in Albaugh et al. (1998). For graphical comparisons, simulation outputs were truncated in 1996 to correspond with the last sample collection of the empirical data.

Results

Simulated gross primary productivity (GPP) was 8.56 Mg C ha^{-1} in 1995 for control plots and 17.58 Mg C ha^{-1} in fertilized plots (Table 1). Maintenance respiration (R_M) accounted for, roughly, 40% of GPP in both treatments in 1995. Our estimates of net primary productivity (plus construction respiration, R_C) were slightly less than the model estimate of net canopy assimilation (Table 1).

The temporal patterns in the carbon budget, illustrated here as the daily gross carbon balance (net canopy assimilation minus growth and R_C), depicted seasonal differences in daily C supply from photosynthesis as compared to the empirical estimate of C use (Figure la and lb). The dynamic time course in carbon balance indicated periods of both positive and negative C days associated with daily differences in gross photosynthesis, autotrophic respiration (R_M), and the empirical estimate of tissue production. Noticeable are broad periods where C used in growth far exceeded C supply from daily net canopy assimilation (e.g. ~ day of year 95 to 220). Fertilized plots had similar trends, although the absolute amount of carbon was twice that as the control plots (Figure lb). Seasonal patterns in daily C supply in relation to the empirical estimates of the requirements for growth extended into 1996 with similar deficits beginning in April.

Simulated labile C pools corresponded reasonably well to those estimated from the empirical analyses for April through June 1995, but during other periods of the year there was less correspondence between the two approaches (Figure 2). Labile carbohydrate concentration (starch plus sugars) for the empirical estimates were highest in April (49 and 50.4 mg
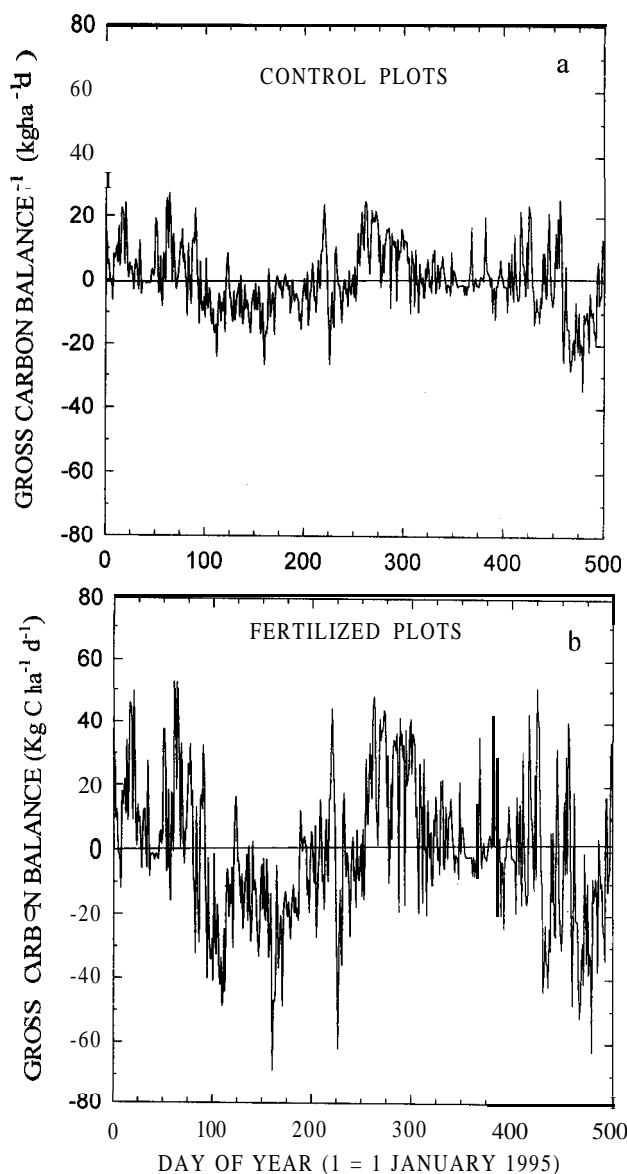

Figure 1. Simulated, daily gross carbon balance (daily net canopy assimilation minus the empirical estimate of all-tissue production, plus construction respiration) for intermediate-aged loblolly pine stand during 1995 and early 1996 for control (A) and fertilized (B) plots.

C g biomass' in control and fertilized plots, respectively), with rapid diminishment observed in the pools through August (Figure 2a and 2b). Simulated labile C pools had similar patterns for control and fertilized plots: minimum concentrations were lower, obtained earlier in the year than the empirical data indicated, and they reached higher levels later in the year (Figure 2a and 2b). And, while the magnitude of the difference was substantial during the summer and early autumn periods, during much of the year the simulated estimates were within, or close to, one standard deviation of the empirical estimate. Moreover, and more importantly, there were consistent trends in the temporal patterns observed between predicted and empirical estimates. Specifically, the early season draw-down of the labile C pools was followed by an increase to a brief stabilization of the pool in autumn prior to a "recharge" period starting in early winter (Figure 2a and 2b).

Table 1. The 1995 carbon budget (**Mg C ha^{-1} $year^{-1}$**) for an intermediate-aged loblolly pine stand for control and fertilized treatments at SETRES (Southeast Tree Research and Education Site). GPP, R_M, R_C; and simulated net canopy assimilation are outputs from BIOMASS, the empirical estimate of NPP is derived from estimates of initial and final standing biomass as from Albaugh (1998).

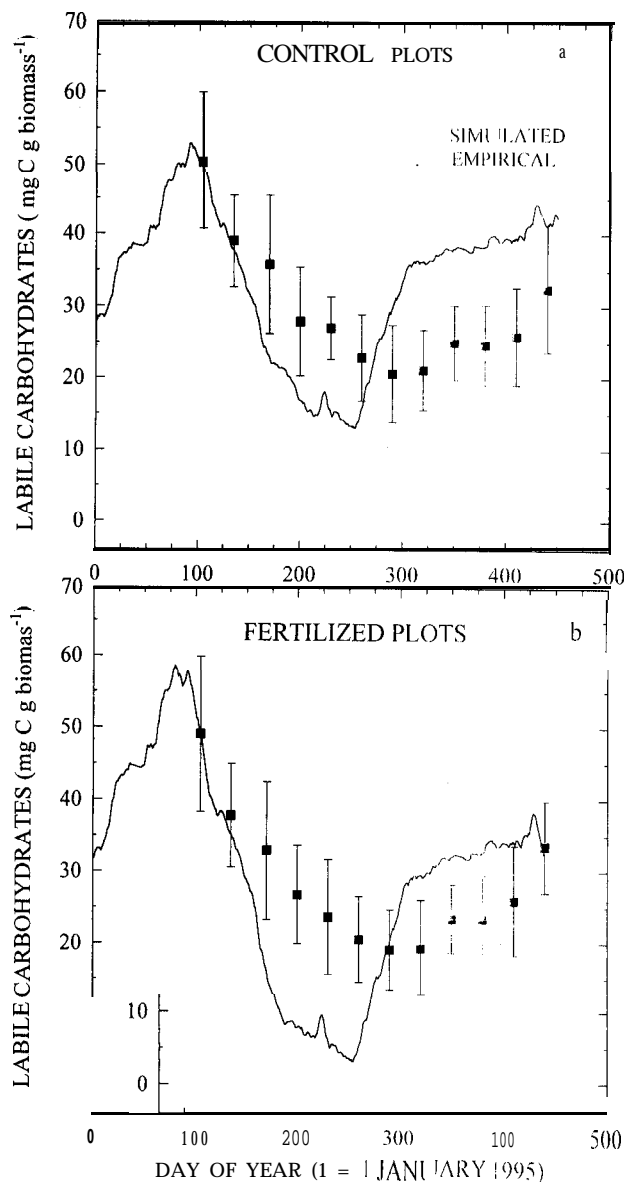| Estimate	Control	Fertilized
GPP	8.56	17.58
Maintenance respiration (R_M)	3.46	6.99
Construction respiration (R_C)	0.56	1.20
Empirical estimate of NPP (plus R_C)	4.71	10.17
Simulated net canopy assimilation	5.11	10.59

Figure 2. Comparison of simulated (line) versus empirical (symbol) estimates of labile, nonstructural carbohydrates for intermediate-aged loblolly pine stands for 1995 and early 1996 for control (A) and fertilized (B) plots. Error bars denote one standard deviation of the mean for the empirical estimates.

A one-to-one comparison of the simulated versus the empirical labile C pool estimates (Figure 3) demonstrated a low to moderate correlation (for standard correlation: $r = 0.51$, $P = 0.0117$, for regression forced through the origin: $r = 0.93$, $P = 0.05$). The poorer fit at lower concentrations corresponded to the midsummer growth periods.

Discussion

We hypothesized that we could predict labile C pools as the difference between modeled net C assimilation and empirically derived structural biomass production. Overall, it appears that our approach has merit. In both fertilized and nonfertilized treatments, modeled seasonal patterns of labile C pools corresponded reasonably with empirical estimates, especially with regard to the temporal patterns observed.
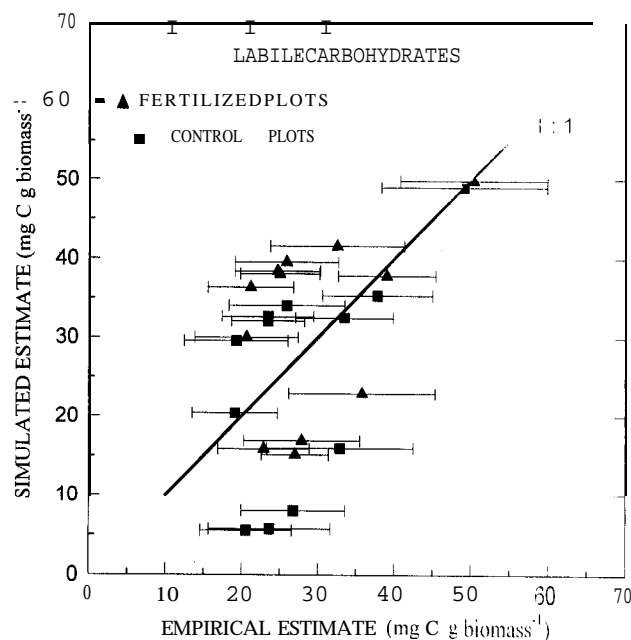

Figure 3. A scatterplot depicting the relationship between the empirical estimates of labile, nonstructural carbohydrates with the simulated estimates for intermediate-aged loblolly pine stands during 1995 and early 1996 for control (squares) and fertilized (triangle) plots. Data points reflect midmonth dates representing monthly means from the empirical analysis.

The distribution of random and systematic error, and propagation, can influence model outputs. Net canopy assimilation was predicted using the process model BIOMASS 14.0 and parameterized from physiological investigations conducted at SETRES (Ewers et al. 1999, Maier et al. 1998). Thus, net C assimilation (gain) estimates are subject to errors associated with the parameter estimates, exaggerated by scaling, as well as the extent that the model structure correctly simulated the system. Growth estimates are from empirical data. Initial and final biomass was estimated by applying site-specific allometric equations to individual tree height and dbh estimates, and growth progression was estimated using phenology measures, LAI progression, and sequential soil core data; all were subject to sampling error. Assuming sampling errors for biomass estimates and model parameters have both positive and negative impacts on estimates of growth and C gain, and the distributions of the sign of these errors are random, the correspondence, both qualitatively and quantitatively, of modeled and empirical estimates represents an overall assessment of the model structure. The overall moderate correlation ($r = 0.5$ 1) between predicted and observed data, and particularly the reasonable simulation of seasonal patterns in labile C pools, indicates we have succeeded in simulating the basic elements of the stands C dynamics. Thus, given the potential for error propagation from the aggregation of a series of modeled physiological processes overlaid on empirical estimates of growth (also made with error), this analysis indicates the structure of the model is sound, at least for loblolly pine on our particular site.

Clearly, additional improvements are required. Underestimation of labile carbohydrate concentrations in midsummer, and overestimation later in the year may be, in part, attributed to one or more factors associated with the

"improvements" made in this version. Probable differences in *Amax* within the canopy as influenced by nitrogen profiles have not yet been incorporated, and a more rigorous validation of the maintenance respiration equations may be required. Soil nutrition directly impacts several important processes incorporated in the model. First, fertilization can increase net photosynthetic (P,) rates. The impacts of fertilization on P_n of loblolly pine have not been consistent in the literature. For instance, while Samuelson (2000) showed N fertilization increased P_n of greenhouse-grown loblolly pine seedlings, she found no impact of fertigation on P_n of field-grown saplings (Samuelson 1998); however, the latter work was conducted on a site where even the control plots were of very high fertility. Even at one research site, SETRES, fertilization effects on P_n have not been consistent from investigator to investigator or from date to date. In our parameterization we used two equations to represent the relationship between P_n and foliar N concentration; N concentration appears to have minimal impact on P_n in the active growth season and highly influences it during the rest of the year (Maier, unpublished) and this trend has been repeated in a more recent study (Gough 2000). Our assignment of two different response curves over the year represents our current best, albeit overly simple, representation but clearly constitutes a weak point in parameterization and calibration.

In addition to impacting *P,,* fertilization at SETRES has been shown to reduce stomatal conductance in studies assessing whole-tree sap flow (Ewers et al 1999) and instantaneous gas exchange (Murthy et al. 1997). Fertilization also directly impacts tissue respiration rates (Maier 1998) and standing fine root biomass (Albaugh et al. 1998). Although cosine corrected light extinction coefficients were not influenced at SETRES (Sampson and Allen 1998), fertilization has approximately doubled stand leaf area (Albaugh et al. 1998); dramatically increased solar radiation reaches the forest floor under control versus the fertilized stands (Sampson and Allen 1998) impacting temperatures at the forest floor. The above examples indicate the range of profound and subtle impacts that nutrition has on physiological responses, as well as the potential difficulty in adequately incorporating them into a process model (Landsberg et al. 2001, Johnsen et al. 2001).

The selection of labile C content starting values also impacted the correspondence between predicted and observed estimates. We faced a dilemma in the choice of what the initial labile C pools should be for this modeling exercise; the model requires an initial estimate, and only direct empirical evidence (that we do not have) could verify our starting values. Different starting values influenced predicted values particularly for the initial sampling dates, although they had little impact on the predicted seasonal patterns. We choose to match values for the data obtained from the first sampling date of the empirical analyses. However, we would have had more confidence had we actually had empirically derived starting values.

The temporal pattern in simulated labile C pools can be explained by season-specific processes that are essentially required to buffer the system against short-term fluctuations in the local climate. Favorable growing conditions in late winter and early spring coupled with little or no aboveground growth and low respiration enables surplus C for storage. Carbon costs during this period include allocation to belowground pools. Initiation of aboveground growth reduces surplus C into late spring and, with the onset of the new foliage cohort development, and the exponential requirements for C from R_M and R_C, results in a window where daily C requirements exceed C supply from instantaneous assimilation (Figure 1 a and 1 b). For the observed rapid growth rates during this period, daily requirements would have to be met by both daily net assimilate as well as supplies of C from storage. Recharge of labile C pools is due to both the seasonal decrease in C allocation to growth (both structural C and R_C), and reduced R_M costs as temperatures declined after the summer months.

Our analyses differ from previous work in that we have assessed the contribution of labile C to whole tree/stand carbon budgets; i.e., we sampled and estimated C pools in all tree organs from large trees. Using the difference between the empirical growth observations and simulated net canopy assimilation (Figure 1), we calculated the contribution of labile C to the total yearly C requirements. In these analyses C supplied from storage accounted for over 16% of the net available C for growth and growth maintenance in the control plots in 1995. For fertilized plots the annual supplement from labile carbohydrate was more than 20% of the net yearly budget in 1995. Thus, these analyses further support the contention that labile carbon buffers daily whole-tree C budgets on days of carbon gain deficit, and that this capacity contributes to the ability of the species to maintain high growth rates (Sampson et al. 1997).

Seasonal fluctuations in the labile C pool have been empirically examined and modeled in other studies. Cropper and Gholz (1993) found sinusoidal seasonal patterns of labile (nonstructural starch) C pools in slash pine. Our modeled seasonal patterns correspond to what they reported for field sampling and slash pine simulations. Although they do not differentiate between periods of daily C surplus or deficit, clear periods of C storage and removal are apparent. Cropper and Gholz (1993) hypothesized that the dynamics of the labile pool can be attributed to the balance between daily net assimilation and the outputs of respiration and growth.

The contribution of labile C would be especially important during periods of rapid needle growth and elongation. Chung and Barnes (1980) found an increased percentage of photosynthate allocated to storage for soluble sugars plus starch in current needles of loblolly pine during the months of May through mid-July (roughly day-of-year 151 to 196). Allocation to storage declined immediately following peak mid-July levels (Chung and Barnes 1980). Cranswick et al. (1987) found yearly fluctuations in sucrose and starch, where sucrose concentrations of 1-yr-old foliage exhibited declines from June into August, with a slight increase through November for Monterey pine *(P. radiata).* It is apparent that without a labile C buffer during short-term C deficit periods, leaf area expansion would likely be suppressed. Decreased leaf growth would accrue further "opportunity costs" as reduced leaf area subsequently decreases integrated canopy photosynthesis

and, accordingly, decreases total yearly production. As such, labile C may be particularly important for multiple flushing species such as loblolly pine. Labile C reserves may permit loblolly pine to respond positively to treatments such as fertilization (Vose 1988, Albaugh et al. 1998) even though mid-summer C gain can be depressed due to soil and air water deficits, and high temperatures (Teskey et al. 1987, Ellsworth 2000). In addition, positive C gain over much of the nongrowing season would be important for recharging the labile C pool; mid-winter P_N of loblolly pine, although not well studied, may be an important component of yield (Ellsworth 2000, Gough 2000, Martin 2000, Maier, unpublished data).

The use of BIOMASS for this analysis does not imply that we consider it the best tool available for such analyses. BIOMASS was originally developed for use with *Pinus radiata,* requires data inputs of intermediate complexity, and was easily modified for *Pinus taeda* due to the ecophysiological similarities between the two species. SETRES is a long-term manipulative field experiment (Albaugh et al. 1998), and the parameterization and calibration of BIOMASS was central to its design and initial field investigations. Thus, our modification and utilization of BIOMASS for this analysis was an extension of previous efforts. Overall, our results indicate that the basic approach to assessing labile C pools is reasonable, although not of sufficient accuracy for making management decisions. Further efforts to develop models to assess risks of labile C depletion should carefully consider initial model selection and/or development. A sensitivity analysis, preferably using multiple models, to assess the appropriate time-scale, and the relative complexity of data input to use for this type of analysis, might prove fruitful.

Ultimately, it will be desirable to evaluate labile carbon pools in multiple scenario analyses. For example, while fertilization can increase growth rate, are there conditions where fertilized trees are more at risk to succumb to biotic and abiotic stress? Thus, the impacts of midsummer droughts, increased vapor pressure deficit, foliage loss, and so on, could then be assessed. Although, this modeling exercise contributes toward this end, the current model structure overlays process model estimates of net carbon gain over empirical estimates of growth. Predictive scenario analyses will require both net C gain and growth to be modeled. Such risk analyses will become increasingly more important as plantation management continues to become more intensive.

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APPENDIX A

Table 1. Key parameters used in the process model BIOMASS version 14.0 for control and fertilized plots at SETRES (Southeast Tree Research and Education Site) for the start of simulations (1995).

Parameter estimate	Control	Fertilized	Units
Standing biomass			
Stems	10.118	16.403	Mg biomass ha^{-1}
Branches	3.882	7.437	"
Coarse roots	4.347	9.027	"
Fine roots	1.082	1.0	"
Foliage (+1 cohort)	2.70	5.11	"
Foliage (+2 cohort)	0.26	0.2	
Specific leaf area	30.5	30.5	$cm^2\ g^{-1}$ (projected)
Initial and (peak) LAI	0.91 (1.21)	1.62 (2.36)	$m^2\ m^{-2}$ proj.
Initial available water	180	180	m m
Rooting depth	2	2	M
Canopy light extinction (G)	0.5	0.5	Unitless
Quantum efficiency	0.054	0.068	mole C mole PAR
Maximum conductance	0.240	0.240	mole m^{-2} (one-sided) s^{-1}