Agricultural and Forest Meteorology 149 (2009) 1531–1540

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Whole-ecosystem labile carbon production in a north temperate deciduous forest

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ARTICLE INFO

Article history:
Received 15 January 2009
Received in revised form 17 April 2009
Accepted 21 April 2009

Keywords:
Labile carbon
Non-structural carbohydrates
Net primary production (NPP)
Net ecosystem production (NEP)
Respiration
Ecosystem
Carbon cycle
Photosynthesis

ABSTRACT

Labile carbon (C), which is principally comprised of non-structural carbohydrates, is an essential intermediary between C assimilation and structural growth in deciduous forests. We developed a new approach that combined meteorological and biometric C cycling data for a mixed deciduous forest in Michigan, USA, to provide novel estimates of whole-ecosystem labile C production and reallocation to structural net primary production (NPP). We substantiated inferred seasonal patterns of labile C production and reallocation to structural NPP with measurements of *Populus grandidentata* and *Quercus rubra* wood non-structural carbohydrate concentration and mass over two years. Our analysis showed that 55% of annual net canopy C assimilate (A_c) was first allocated to labile C production rather than to immediate structural NPP. Labile C produced during the latter half of summer later supported dormant-season structural growth and respiration, with 34% of structural NPP in a given year requiring labile C stored during previous years. Seasonal changes in wood non-structural carbohydrate concentration and mass generally corroborated inferred temporal patterns of whole-ecosystem labile C production and reallocation to structural NPP. Our findings confirm that disparities can arise between same-year meteorological and biometric net ecosystem production when meteorologically measured C assimilation and biometrically measured growth are asynchronous because of temporary photosynthate allocation to labile C storage. We conclude that a broader understanding of labile C production and reallocation at the ecosystem scale is important to interpreting lagged canopy C cycling and structural growth processes.

1. Introduction

High-quality meteorological and biometric carbon (C) cycling datasets are allowing new insights into the allocation of assimilated C to forest C pools (Barford et al., 2001; Gough et al., 2008b). One product of assimilated C that has not been quantified for a whole ecosystem is labile C, which can be stored and later applied to plant structural growth during leaf-off and periods of depressed photosynthesis (Hoch and Korner, 2005; Hoch et al., 2003) or allocated directly or following storage to root exudates that support microbial symbiont metabolism and growth (Carbone et al., 2007; Keel et al., 2006; Phillips and Fahey, 2005). Plant-level studies show that considerable quantities of labile C accumulate in tissues when the supply of photosynthate exceeds the C requirement for current structural growth and that labile C, comprised of non-structural carbohydrates, lipids, and sugar alcohols, is later remobilized when photosynthate C supply is insufficient to support structural growth (Barbaroux et al., 2003; Korner, 2003; Landhausser and Lieffers, 2003; Wong et al., 2003). In deciduous species, this temporary allocation of photosynthate to labile C can prompt a significant lag of months to years between C assimilation and allocation to structural growth (Hoch et al., 2003; Kagawa et al., 2006a,b; Keel et al., 2006). Although plant-scale studies indicate that labile C is an important intermediary between C assimilation and structural growth, the relationship of labile C to these C cycling processes at the ecosystem-scale remains unclear.

The allocation of photosynthate to labile C rather than to immediate structural growth and, subsequently, the reallocation of labile C to structural growth during periods of depressed photosynthesis are hypothesized to cause poor correspondence between short-term rates of canopy C assimilation and structural growth in deciduous forests (Barford et al., 2001; Ehman et al., 2002; Gough et al., 2008b) and wetland ecosystems (Rocha and Goulden, 2008). Canopy C assimilation and forest structural

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doi:10.1016/j.agrformet.2009.04.006

growth could diverge if labile C buffers structural growth against environmental constraints that immediately and more acutely reduce photosynthesis. Photosynthesis often adjusts immediately to environmental conditions, while structural growth may be correlated with environmental conditions occurring weeks to years earlier (Arneth et al., 1998; Chen et al., 2002; Loescher et al., 2003; Orwig and Abrams, 1997; Wofsy et al., 1993). Remobilization of labile C to sustain structural growth during periods of depressed photosynthesis might explain why tree-ring increment is sometimes poorly correlated with current climate and canopy C assimilation (Rocha et al., 2006). The allocation of photosynthate to labile C storage rather than to immediate structural growth also may be why meteorological based estimates of net ecosystem production (NEP), which incorporate canopy C fluxes, showed poor agreement with same-year biometric estimates of NEP derived partly from structural growth measurements, but converged after several years (Barford et al., 2001; Gough et al., 2008b). At our study site, a 1-year lag was observed between canopy C assimilation estimated from meteorological data and net primary production (NPP) derived from biometric estimates of structural growth (Gough et al., 2008b). Similarly, Rocha and Goulden (2008) reported high correspondence of prior-year summer meteorological measurements of GPP and current-year biometric estimates of NPP in a freshwater marsh, suggesting that late season photosynthetic C allocation to overwinter labile C storage fueled structural growth the following spring. In the current study, we test the hypothesis that an offset between annual meteorological and biometric NEP at our site, first reported by Gough et al. (2008b), was partly caused by the initial allocation of assimilated C to labile C production rather than to immediate structural growth. Identifying the role that labile C plays in reconciling short-term canopy and structural growth C cycling processes may improve C cycling models, which increasingly rely on aggregated biometric and meteorological estimates of NEP for parameterization and validation (Kucharik et al., 2006; Kucharik and Twine, 2007; Law et al., 2003; Luo, 2003; Luyssaert et al., 2007; Randerson et al., 2002).

Here, we introduce a new approach for quantifying whole-ecosystem labile C production and reallocation to structural growth from combined high-quality meteorological and biometric data (Gough et al., 2008b). The premise of our novel method is that labile C production equals net C assimilation (C supply) minus structural net primary production (C demand) when C supply exceeds demand and, conversely, that the quantity of labile C required for structural growth is equal to structural NPP minus net C assimilation when C demand exceeds current photosynthate supply (Hoch et al., 2003; Sampson et al., 2001). We inferred whole-ecosystem labile C production and its subsequent contribution to structural NPP by quantifying the temporal imbalance between C supplied by daily canopy net C assimilation, the sum of meteorological net ecosystem CO_2 exchange and heterotrophic respiration (Gough et al., 2008b), and C demand for current structural growth, estimated from daily biometric structural NPP. Although we focus on the labile C contribution to plant structural growth at the ecosystem scale, it is important to note that labile C has multiple fates, including temporary storage before reallocation to plant structural growth or, instead, allocation to root exudates that supply soil heterotrophs with substrate C (Keel et al., 2006). We also employed standard tissue analyses of non-structural carbohydrates, the primary component of the labile C pool (Hoch et al., 2003), to substantiate that seasonal amplitudes in wood non-structural carbohydrate concentration and mass correspond with inferred estimates of labile C production and reallocation to structural NPP.

2. Materials and methods

2.1. Study site

Our study was conducted at the University of Michigan Biological Station in northern lower Michigan, USA (45°35.5′N, 84°43′W). The study site lies on the northeastern side of an interlobate moraine, the slope of which gently decreases from SW to NE draining into nearby Douglas Lake. Soils are primarily excessively drained sand of the Rubicon-East Lake series. Average annual (1942–2003) temperature is 5.5 °C and precipitation 817 mm.

The dominant ecosystem is a secondary successional mixed northern hardwood forest that naturally regenerated following clearcut harvesting and fire in the early 20th century (Gough et al., 2007). The forest canopy averages 22 m in height. Dominant canopy species include *Populus grandidentata* Michx. (bigtooth aspen) and *Populus tremuloides* Michx. (trembling aspen), which together comprise over 40% of the basal area, *Quercus rubra* L. (northern red oak), *Betula papyrifera* Marsh. (paper birch), *Fagus grandifolia* Ehrh. (American beech), *Acer saccharum* Marsh. (sugar maple), *Acer rubrum* L. (red maple), and *Pinus strobus* L. (white pine). The understory primarily consists of *Pteridium aqulinium* (bracken fern) and saplings of the canopy species.

2.2. Meteorological and biometric carbon cycling parameters

We estimated daily total net primary production of structural C mass contained in live wood, leaves, fruit, and branches, and fine roots for aspen (*P. grandidentata*) and oak (*Q. rubra*) individually and for the entire forest from 2001 to 2003 and 2005 to 2006. We did not calculate daily structural NPP in 2004 because high temporal resolution live wood dry mass production data were not available. To derive whole-ecosystem daily structural NPP our general approach was to first estimate the daily production of structural C mass for each tissue by multiplying daily tissue dry mass production, estimated empirically or from modeling, by a constant fraction of structural C contained in the dry mass of each respective tissue. The fraction of dry tissue that is structural C was calculated for aspen and oak trees at our site by subtracting the mean non-structural carbohydrate C fraction of dry tissue mass (Section 2.4) from the total C fraction of each dry tissue quantified using elemental analysis. Structural C at our site comprised 48%, 44%, and 41% of dry mass of wood, leaf/fruit/branch, and fine roots, respectively.

Specifically, daily above- and belowground dry wood mass production was estimated as the increase in wood mass from one measurement date to the next using site and species specific allometric equations relating bole diameter (D) to aboveground wood dry mass (M_A) (Gough et al., 2008b), and from equations relating belowground wood dry mass (M_B) to M_A (Cairns et al., 1997). During the growing season weekly to biweekly D was recorded for 190 trees with $D \geq 10$ cm using band dendrometers. Daily structural wood C production (p_W) was inferred from the linear increment of $M_A + M_B$ between two measurement dates multiplied by a structural C fraction of dry mass of 0.48. Annual structural wood C production (P_W) was the annual increment of $M_A + M_B$ times 0.48.

Daily leaf, fruit, and branch structural C production ($p_{L,F,B}$) was calculated by multiplying annual leaf, fruit, and fine branch dry mass production ($PD_{L,F,B}$) estimated from litter traps placed on the forest floor (area = 0.264 m^2, $n = 20$) by the daily fraction of annual vegetation area production calculated from twice weekly (during leaf expansion) to monthly measurements of vegetation area index (I) and by a structural C fraction of dry mass of 0.44

(Gough et al., 2008b):

$$p_{L,F,B} = PD_{L,F,B} \times \frac{(I_{t+1} - I_t)}{(I_{max} - I_0)} \times 0.44 \quad (1)$$

where $I_{t+1} - I_t$ is vegetation area production between two measurement dates, I_{max} is maximum I, and I_0 is minimum I. Daily leaf, fruit, and fine branch structural C production between measurement dates was estimated using linear interpolation. Annual structural C production ($P_{L,F,B}$) was the annual sum of $p_{L,F,B}$. Daily fine root structural C production (p_{FR}) was the product of daily fine root turnover estimated from daily mean soil temperature (T_S, 7.5 cm) and standing fine root dry mass (M_{FR}) (Gough et al., 2008b) multiplied by a structural C fraction of dry mass of 0.41:

$$p_{FR} = [0.0113 + 0.035T_S/365] \times [M_{FR} \times 0.41] \quad (2)$$

Annual fine root structural C production (P_{FR}) was the annual sum of p_{FR}. We sampled M_{FR} in 2000 and 2003 to a depth of 80 cm using soil cores (1700 cm^3 $sample^{-1}$, $n = 30$). Daily net primary production of structural C mass ($NPP_{ST,D}$) was:

$$NPP_{ST,D} = p_{L,F,B} + p_{FR} + p_W \quad (3)$$

We estimated daily A_c from meteorological estimates of daily net ecosystem CO_2 exchange (NEE_D) between forest and atmosphere, and chamber based measurements of whole soil and heterotrophic respiration (Gough et al., 2008b). Detailed meteorological tower instrumentation, specifications, and methods are described by Schmid et al. (2003). A 46 m tower equipped with eddy-covariance systems provided continuous measurements of 3-D turbulent velocity fluctuations and eddy-covariance fluxes of momentum (sonic anemometers; CSAT-3, Campbell Scientific, Inc.) and CO_2 fluxes as hourly averages (infrared gas analyzer; LI-6262 or LI-7000 from 2005; LI-COR Inc.; Lincoln, NE). CO_2 fluxes are subject to quality control, including outlier rejection, and a friction velocity $u_* \leq 0.35$ m s^{-1} criterion to discard values obtained under low turbulence conditions where the change of CO_2 storage in the canopy air space could be important. NEE_D was the 24-h sum of hourly NEE. Other climate measurements included photosynthetic photon flux density (PPFD) above the canopy using PPFD sensors (LI-190SZ, LI-COR Inc., Lincoln, NE, USA), soil temperature (T_S) at 7.5 cm depth in three locations near the base of the meteorological tower using type E thermocouples, and volumetric soil water content (θ_S) recorded to a depth of 30 cm at four locations using CS615 or CS616 soil moisture probes (Campbell Scientific, Inc., Logan, UT, USA).

Methods used to estimate daily heterotrophic respiration (R_H) are described by Gough et al. (2007, 2008b). Briefly, we measured instantaneous soil respiration (r_S) from 1998 through 2006 in 31 locations using a LI-COR LI-6400 equipped with a LI-6400-09 soil CO_2 flux chamber (LI-COR Inc.). We modeled r_S separately for three seasons as a function of T_S using a 2-parameter exponential function with an additive log-linear or linear θ_S function. Continuous mean hourly r_S was estimated from T_S and θ_S data and was summed over 24 h to determine daily soil respiration (R_S). We determined the contribution of heterotrophic respiration to total soil respiration using the component integration method (Hanson et al., 2000), in which instantaneous heterotrophic soil respiration (r_H) was quantified from laboratory incubated root-free O-horizon and mineral soils (Gough et al., 2008b). The fraction of r_S attributed to heterotrophs at 20 °C (f_h) was calculated as r_H/r_S.

Daily A_c, expressed using parameters in our calculations, was (Gough et al., 2008b):

$$A_c = NEE_D + (|R_S| f_h) = NEE_D + |R_H| \quad (4)$$

where positive NEE_D indicates net C uptake by the forest. Note that A_c also equals gross primary production (GPP) minus autotrophic respiration (R_A), where NEE = GPP − $|R_H|$ − $|R_A|$, or the net quantity of C assimilated that is available for allocation to structural growth or labile C production. Annual meteorological NEP was NEE_D summed over 1 year. Annual biometric NEP was the annual sum of daily NPP less annual R_H (Gough et al., 2008b).

2.3. Labile C production and requirement for structural growth and respiration

We estimated the quantity of assimilated C allocated to whole-ecosystem labile C production (P_{LC}) as the difference between concurrent photosynthetic C supply and C demand for structural growth (Fig. 1A; Hoch et al., 2003). When A_c, or photosynthetic supply, exceeded current demands for daily structural NPP, or $NPP_{ST,D}$, annual P_{LC} was:

$$P_{LC} = \sum (A_c - NPP_{ST,D}), \quad \text{when } A_c > NPP_{ST,D} \quad (5)$$

where P_{LC} is production of a common pool of labile C that can be stored prior to reallocation to plant structural growth or respiration, or is available for allocation to root exudates immediately or following storage.

The quantity of annual structural NPP that required stored labile C (NPP_S) was estimated as the summed C requirement for $NPP_{ST,D}$ that was not met by current A_c:

$$NPP_S = \sum (NPP_{ST,D} - A_c), \quad \text{when } A_c < NPP_{ST,D} \quad (6)$$

Autotrophic respiration requiring labile C during the dormant (non-photosynthetic) period was:

$$R_A = NEE_D + |R_H|, \quad \text{when } A_c = 0 \quad (7)$$

where Eq. (7) is valid when GPP or canopy C assimilation is zero and NEE = GPP − $|R_H|$ − $|R_A|$.

2.4. Plant tissue non-structural carbohydrate analysis

We collected branch, bole, and coarse root tissues approximately monthly during the 2005 and 2006 growing seasons for analysis of non-structural carbohydrates. Due to the destructive nature of sampling, we sequentially collected tissue from three different replicate sets of canopy dominant aspen ($n = 3$) and oak ($n = 3$) trees, with a period of overlapping collection when transitioning from one set to the next. Aspen and oak were selected because they were the dominant diffuse-porous and ring-porous species, respectively, in the UMBS forest. Current-year branch tissues were collected from the mid-outer tree canopy using a shotgun. Bole and coarse root tissues were extracted to a radial depth of up to 4 cm using a 5 mm diameter increment corer. Coarse roots (>10 cm in diameter) were sampled 15–30 cm from the base of the tree and at a soil depth of ~10 cm. Bole samples were collected at 1.4 m (breast) height. To minimize diurnal variability in non-structural carbohydrate mass, samples were collected between the hours of 12:00 and 4:00 p.m. (Dickson and Larson, 1981). Tissue samples were placed on ice in 20 ml glass scintillation vials upon collection, and later stored at −80 °C until lyophilized.

We quantified soluble starch and sugars in woody tissues using standard methods (Jones et al., 1977). Bark and xylem from coarse roots, boles, and branches were separated and, for course roots and boles, the remaining core segmented into 1 cm increments prior to being ground for 3 min with a ball mill. Soluble sugars (sucrose, glucose, and fructose) were extracted from 25 mg of tissue with 80% ethanol (5 ml) at 80° C for 5 min. Extracts were centrifuged and the supernatants pooled; a 2 ml aliquot was removed and

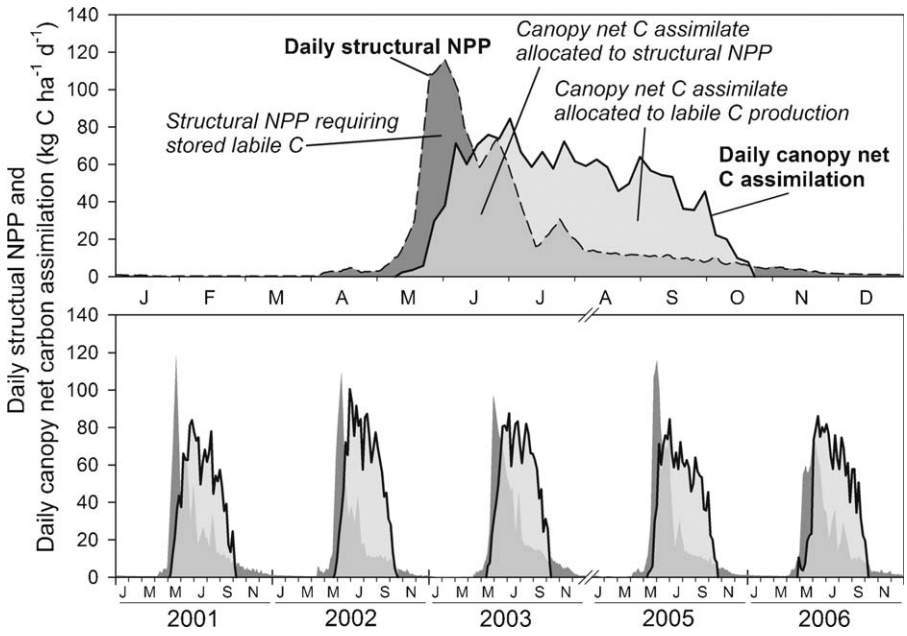

Fig. 1. Seasonal patterns of labile carbon (C) production and structural net primary production (NPP) requiring labile C inferred from the temporal imbalance between daily structural NPP and canopy net C assimilation for 2005 (A) and 2001–2003, 2005–2006 (B). For illustrative purposes, 5-day structural NPP and canopy net C assimilation means are shown.

dried using a vacuum evaporator. Dried extract was resuspended with 3 ml deionized water and 40 mg polyvinylpolypyrrolidone and spun down using a centrifuge. A 0.5 ml aliquot was colorimetrically assayed for soluble sugars according to Jones et al. (1977) and modified for use on aspen tissues (Curtis et al., 2000). Soluble sugar recovery was >95%.

To quantify starch, tissue pellets already extracted for soluble sugars were resuspended using 1 ml of 0.2N KOH and incubated at 80 °C for 25 min. KOH was neutralized by adding 0.2 ml of 1N acetic acid. Starch was hydrolyzed to glucose with α-amyloglucosidase solution (pH 7.05) at 55 °C for 1.5 h and assayed according to Jones et al. (1977). Starch recovery was >95%. Total sample non-structural carbohydrate concentration was the sum of soluble sugars and starch averaged across xylem and phloem. Non-structural carbohydrate mass was converted to C mass using a fraction of 0.41 g C g^{-1} dry weight for soluble sugars and 0.44 g C g^{-1} dry weight for starch (Hoch et al., 2003) and expressed as the concentration of dry tissue mass.

2.5. Bole and coarse root non-structural carbohydrate mass

We estimated ecosystem non-structural carbohydrate mass of oak and aspen boles and coarse roots (diameter >2 mm) by multiplying the fraction of tissue non-structural carbohydrate C by the species-specific ecosystem mass of bole and coarse root wood. To estimate average whole bole and coarse root non-structural carbohydrate concentrations, we first modeled starch and glucose concentration as a function of radial tissue depth for every sampling date. The concentration of non-structural carbohydrate at depths not sampled (>4 cm) was estimated through extrapolation using either a linear or power function. The appropriate function for aspen and oak tissues was selected based on published relationships of radial depth and tissue non-structural carbohydrate concentrations for diffuse-porous (e.g., aspen) and ring-porous (e.g., oak) species (Hoch et al., 2003). Incremental radial tissue non-structural carbohydrate concentrations were weighted by area and integrated across depths to calculate average whole bole and coarse root non-structural carbohydrate concentrations. Average whole bole and coarse root non-structural carbohydrate concentrations were estimated for aspen and oak with a mean radial depth of 14 cm ($n = 16$) and 12 cm ($n = 73$), respectively, reflecting the mean bole radius determined through field surveys of diameter (1.4 m height, D) in a 1.1 ha plot. Ecosystem oak and aspen bole and coarse root mass was estimated from field surveys of D and allometric equations relating bole mass to D, and coarse root mass to bole mass (Gough et al., 2008b). The quantity of ecosystem non-structural carbohydrate C contained in oak and aspen boles and coarse roots was the product of respective tissue non-structural carbohydrate C fractions and corresponding dry mass. The seasonal amplitude of aspen and oak non-structural carbohydrate mass, hereafter referred to as non-structural carbohydrate mass depletion, was the difference between maximum dormant season and minimum succeeding spring/summer bole plus coarse root non-structural carbohydrate mass (Hoch et al., 2003). Standard errors estimated from across-replicate variances were scaled linearly to the ecosystem.

2.6. Statistical analyses

We used ANOVA with repeated measures to analyze differences in non-structural carbohydrate concentrations across time, species, and tissue types. Tissue non-structural carbohydrate concentrations observations were square root transformed prior to statistical analyses to correct for non-normal distribution. In 2006, where overlap occurred between second and third cohorts differences were tested using a two-sample t-test; no significant difference between cohorts was found in either species across tissue types ($P > 0.05$). Tissue non-structural carbohydrate concentrations were compared among dates and tissues using Tukey's HSD ($\alpha = 0.05$). Standard errors for estimates of non-structural carbohydrate concentrations, and mass and production parameters were estimated as the quadrature sum of between-sample variances and variances of predicted values when derived from equations. Statistical analyses were conducted using JMP 7.0 or SAS 8.0 statistical software (SAS Institute, Cary NC, USA).

Table 1
Net canopy carbon (C) assimilate allocated to whole-ecosystem net primary production of structural C mass or the production of labile C, and annual structural NPP and dormant-season autotrophic respiration requiring labile C, 2001-2003, 2005–2006 (kg ha^{-1} year^{-1} ± 1 S.E.).

	2001	2002	2003	2005	2006	Mean
Net canopy C assimilate allocated to structural NPP	3579 (1159)	2810 (1963)	4126 (1343)	3769 (1367)	3875 (1349)	3632 (1436)
Net canopy C assimilate allocated to labile C production	3976 (885)	5424 (1694)	4084 (989)	4147 (977)	4237 (1058)	4374 (1121)
Structural NPP requiring labile C	2051 (353)	1975 (365)	1758 (426)	2030 (448)	1646 (350)	1892 (389)
Autotrophic respiration requiring labile C	1529 (550)	1426 (998)	1740 (593)	1560 (431)	1222 (488)	1495 (610)

3. Results

3.1. Labile C production and reallocation to structural growth and respiration

The temporal imbalance between whole-ecosystem C assimilation and structural growth at our site indicate that a substantial quantity of C fixed by the canopy was allocated to labile C production, and also that a considerable fraction of plant structural growth and respiration require stored labile C. An abrupt rise in daily structural NPP occurred prior to the photosynthetic period during all years, with forest structural growth peaking in early June and then declining rapidly through mid-summer (Fig. 1B). Canopy net C assimilation was sustained at comparatively high rates throughout the latter half of summer resulting in photosynthetic C supply substantially exceeding demands for daily structural NPP during this period. The late season imbalance between C supply and demand indicates that an average of 55% of annual A_c was allocated to labile C production, with the remainder applied to structural NPP during the early photosynthetic period (Table 1). The fraction of annual A_c allocated to labile C production was very similar for all years (50–53%) except 2002, which was considerably higher (66%). Structural growth relied heavily on previously stored labile C, with 34% of annual structural NPP requiring labile C. Dormant-season autotrophic respiration required an average of 1495 kg C ha^{-1} year^{-1} of stored labile C (Table 1).

Net primary production of structural C mass was constrained by the partitioning of assimilated C to structural growth and labile C storage. Current-year structural NPP was negatively correlated with current-year labile C production ($P = 0.02$, Fig. 2A). This relationship was primarily due to anomalously high A_c allocation to labile C production and, conversely, low C assimilate allocation to structural NPP in 2002. Current-year structural NPP was not significantly related to prior-year labile C production ($P = 0.24$, Fig. 2B).

3.2. Meteorological and biometric annual net ecosystem production

We evaluated 8-year trends in annual meteorological and biometric NEP to determine if interannual variation in labile C production and reallocation to structural growth, and thus a lag between canopy photosynthesis and structural growth, affect the convergence of these two estimates of annual C storage. Agreement between same-year meteorological and biometric NEP was poor during the first 4 years of measurements, but improved considerably thereafter (Fig. 3). A steep decline in meteorological NEP in 2001 preceded that of biometric NEP in

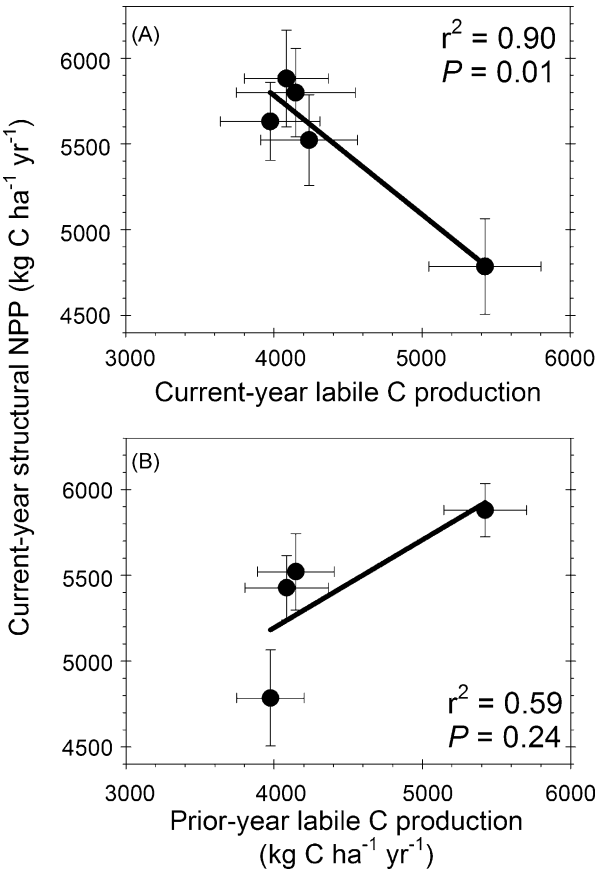

Fig. 2. The relationship between current-year net primary production of structural carbon (C) mass and current- (A) and prior-year (B) non-structural carbohydrate production. For illustrative clarity, value ± 1/4 S.E.

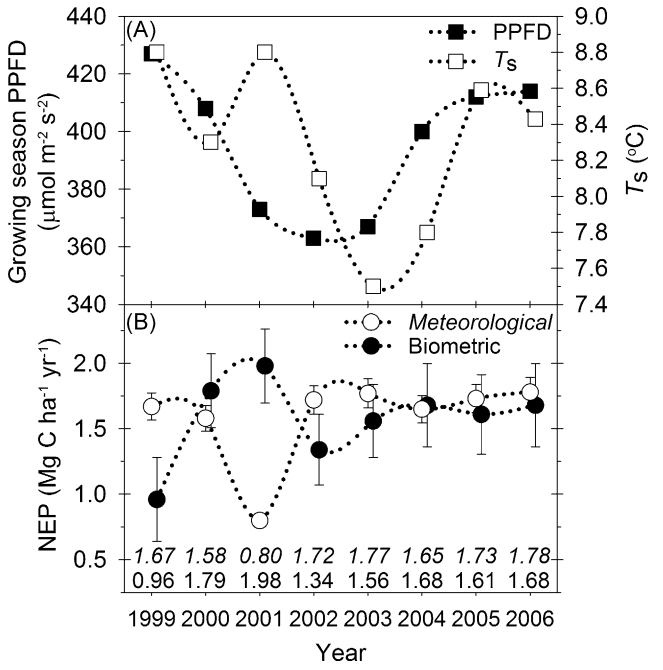

Fig. 3. Annual net ecosystem production (NEP) estimated from meteorological and biometric data and climate drivers, 1999–2006. Mean growing season (May–September) photosynthetic photon flux density (PPFD) and soil temperature (T_S, 7.5 cm) are shown (A) with NEP estimated using meteorological and biometric approaches (B). Meteorological and biometric NEP estimates are in italicized and plain text, respectively. For illustrative clarity, value ± 1/2 S.E.

2002 and coincided with low growing season PPFD and high average annual T_S. Divergence of annual meteorological and biometric NEP in 2001 corresponded with typical patterns of labile C production and reallocation to structural growth and preceded anomalous partitioning of canopy photosynthate to labile C or structural growth in 2002 (Table 1). Eight-year average annual NEP estimated using meteorological and biometric methods was 1.59 and 1.58 Mg C ha^{-1} year^{-1}, respectively, with same-year NEP estimated using the approaches differing by 2–148%. Estimates of meteorological and biometric NEP varied interannually by up to 106% and 122%, respectively.

3.3. Aspen and oak tissue non-structural carbohydrate concentrations

Non-structural carbohydrate concentrations varied by tissue type, species, and over time (Fig. 4A and B). In aspen, branch non-structural carbohydrate concentrations, which averaged 6.9% over sampling dates, were consistently higher than those of boles (1%) or coarse roots (2.5%). Oak tissue non-structural carbohydrate concentrations were significantly higher than in aspen, with mean values over time of 10.6%, 12.5%, and 3.3% in branches, boles, and coarse roots, respectively. Seasonal variation in non-structural carbohydrate concentrations were observed in all aspen and oak tissue types and generally corresponded with dynamic periods of whole-ecosystem labile C production and reallocation to structural NPP and autotrophic respiration. In aspen, non-structural carbohydrate concentrations in all tissue types declined leading up to the period of labile C production and then increased to a maximum in mid- to late summer. Oak bole and coarse root non-structural carbohydrate concentrations exhibited a similar but more pronounced response, dropping rapidly leading up to labile C production and then increasing until the non-structural carbohydrate production period ended. Oak branch tissue, however, showed an opposite trend during the period of labile C production, with non-structural carbohydrate concentrations increasing, especially in 2006, prior to and during early labile C production and then declining during late summer. Tissue non-structural carbohydrate concentrations generally declined during the dormant season.

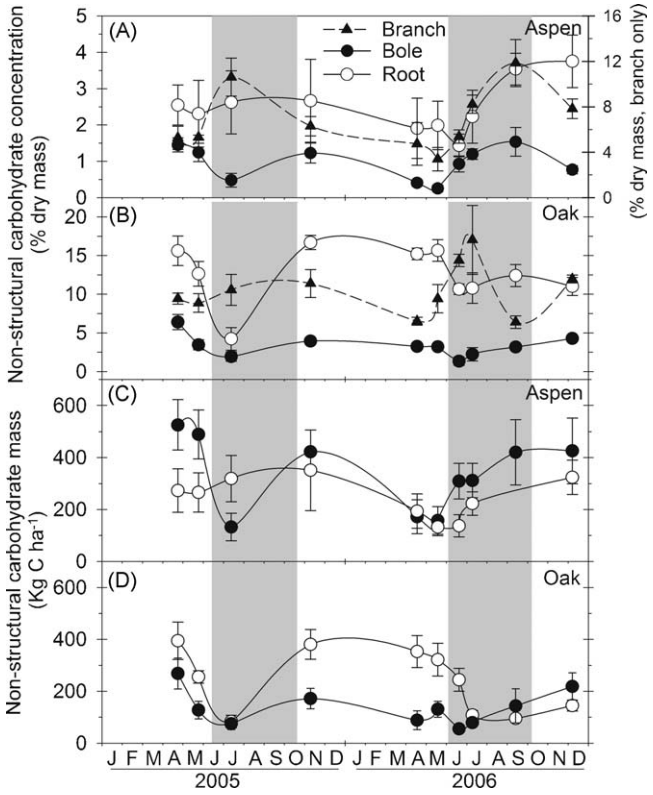

Fig. 4. Seasonal non-structural carbohydrate dynamics of aspen and oak wood, 2005–2006. Tissue non-structural carbohydrate concentrations for aspen (A) and oak (B) branches, boles, and coarse roots are presented together with ecosystem non-structural carbohydrate mass of aspen (C) and oak (D) boles and coarse roots (mean ± 1 S.E.). Grey shaded area is the period of whole-ecosystem labile C production derived from Fig. 1. Note scale difference between panels A and B.

3.4. Aspen and oak non-structural carbohydrate mass and net primary production of structural C mass

Seasonal patterns in aspen and oak bole and coarse root non-structural carbohydrate mass were similar to those for tissue non-structural carbohydrate concentrations. Aspen generally stored more non-structural carbohydrates in boles while oak stored more labile C in coarse roots. Non-structural carbohydrate C mass in aspen boles was more dynamic than in coarse roots across time (Fig. 4C). In contrast, oak coarse roots stored >2 times more non-structural carbohydrates than boles during the 2005–2006 dormant period (Fig. 4D). Both species exhibited a seasonal depletion in non-structural carbohydrate mass from boles and coarse roots during the early Spring and Summer, followed by a refilling period in the late summer that coincided with whole-ecosystem labile C production. Although ecosystem aspen bole and coarse root mass was 3.6 times greater than that of oak, non-structural carbohydrate mass was similar for the two species due to much higher non-structural carbohydrate concentrations in oak. Total (bole + coarse root) ecosystem non-structural carbohydrate mass for aspen varied from 290 kg C ha^{-1} in mid-summer to 800 kg C ha^{-1} during dormancy. Total oak non-structural carbohydrate mass varied more than 4-fold, from 160 to 660 kg C ha^{-1}.

Spring non-structural carbohydrate mass depletion was comparable in magnitude to the production of individual structural C mass pools (Table 2), reinforcing our inferred whole-ecosystem observations that a considerable quantity of labile C is remobilized to support early season structural growth. Branches were not included in non-structural carbohydrate mass depletion estimates because seasonal patterns, especially in oak, showed increasing non-structural carbohydrate concentrations in the spring, suggesting that branches accumulate labile C remobilized from other woody tissues prior to leaf-out. Spring non-structural carbohydrate mass depletion was similar for the two species, varying from 347 to 504 kg C ha^{-1}. These values were comparable to the annual C invested in leaf, fruit, and branch structural C production in aspen and in the structural C production of all tissue types individually in oak.

Table 2
Spring wood NSC mass depletion (kg C ha^{-1}) and annual net primary production of structural C mass (kg C ha^{-1} year^{-1}) for aspen and oak tissues, 2005 and 2006 (value ± 1 S.E.).

	Aspen		Oak	
	2005	2006	2005	2006
Spring non-structural carbohydrate mass depletion	347 (37)	483 (128)	504 (85)	365 (63)
Wood structural NPP	885 (25)	1001 (28)	393 (52)	473 (63)
Leaf, fruit, branch structural NPP	369 (41)	308 (37)	824 (130)[a]	302 (53)[a]
Fine root structural NPP	662 (130)	761 (149)	307 (60)	359 (70)
Total structural NPP	1916 (139)	2070 (156)	1524 (152)	1134 (108)

[a] Fruit comprised 628 and 60 kg C ha^{-1} in 2005 and 2006, respectively.

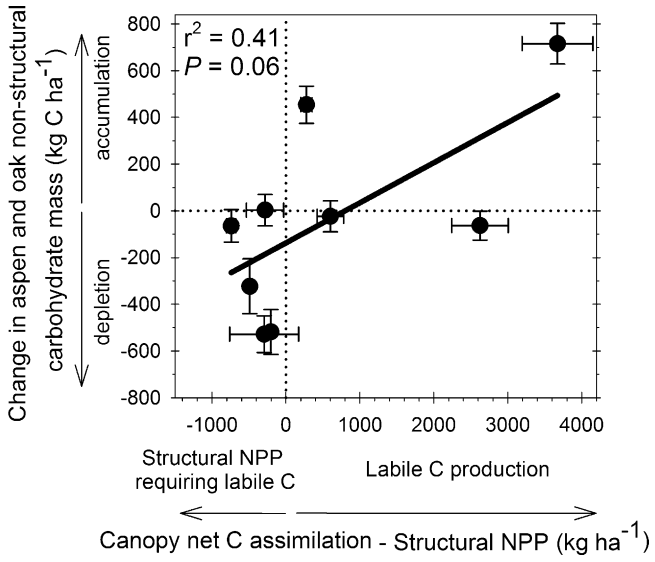

Fig. 5. Correspondence of between-measurement changes in aspen and oak non-structural carbohydrate mass (*y*-axis), and overlapping whole-ecosystem structural net primary production (NPP) requiring stored labile carbon (C) and photosynthate allocation to labile C production (*x*-axis) inferred from summed daily differences between net canopy carbon assimilation and daily structural NPP (Eqs. (5) and (6)). Values are for periods between dates illustrated in Fig. 4. For illustrative clarity, value ± 1/4 S.E.

3.5. Correspondence of measured non-structural carbohydrates and inferred labile C parameters

Seasonal patterns of labile C production and reallocation to structural growth generally corresponded with depletion and accumulation cycles of wood non-structural carbohydrate concentrations and mass in aspen and oak. We observed a positive relationship between inferred whole-ecosystem labile C production and the quantity of structural NPP that required stored labile C, and changes in aspen and oak non-structural carbohydrate mass between measurement dates ($P = 0.06$, Fig. 5).

4. Discussion

To our knowledge, we report the first whole-ecosystem analysis of labile C production and requirement for structural NPP and autotrophic respiration. Our results show that a considerable quantity of C taken up by our deciduous forest was allocated to labile C production before being reallocated to plant structural growth or respiration. The imbalance between structural NPP and A_c was substantial during late summer, with over half of the net C assimilated annually allocated to labile C production. Structural growth relied heavily on stored labile C that accumulated during the latter half of summer in previous years, requiring labile C for over a third of annual structural NPP. Dependence of spring structural growth on C assimilated during previous years is supported by plant-scale isotope labeling studies (Helle and Schleser, 2004; Kagawa et al., 2006a,b; Keel et al., 2006). Although no other estimates of annual labile C production are available, our estimate of structural NPP requiring labile C is similar to 20-30% for a mature *Fagus sylvatica* forest (Skomarkova et al., 2006) and somewhat higher than 20% for a loblolly pine plantation that had photosynthetic capabilities year-round (Gough et al., 2004; Sampson et al., 2001). Two lines of evidence provide some validation of our labile C production estimates. First, annual labile C production was similar to demands for plant structural growth and respiration outside of the photosynthetic period. Our estimates of labile C production averaged only 21% higher than the quantity of labile C required to fuel dormant-season structural NPP and autotrophic respiration. It is possible that this apparent surplus labile C was allocated to pools that we did not quantify. For example, our estimate of surplus labile C production that exceeded the requirement for plant structural growth and respiration is similar in magnitude to the fraction of whole-ecosystem net photosynthate allocated to rhizosphere C (i.e., root exudates and/or mycorrhizae) in a New Hampshire forest (14%) (Fahey et al., 2005) and photosynthate allocated to rhizosphere C in two northern hardwood species (5.9–12.3%) (Phillips and Fahey, 2005). Second, seasonal patterns of labile C production and reallocation generally corresponded with depletion and accumulation cycles of woody tissue non-structural carbohydrate concentrations and mass in aspen and oak.

Our results support hypotheses that same-year meteorological and biometric estimates of NEP may diverge when assimilated C is diverted away from structural growth and instead invested in labile C production and, additionally, when stored labile C supplements structural growth during periods of low C assimilation (Barford et al., 2001; Ehman et al., 2002; Gough et al., 2008b; Rocha and Goulden, 2008). However, we note that this conclusion is based primarily on a single year (2002) in which unusually high allocation of assimilated C to labile C production corresponded with low structural NPP. We previously hypothesized that a 1-year offset between annual A_c and total in 2001 and 2002 was caused by low labile C production in 2001, when meteorological NEP reached an 8-year minimum, thereby resulting in an insufficient supply of labile C for spring structural growth in 2002 (Gough et al., 2008b). In the present study, we found that prior-year labile C production was weakly related to current-year structural NPP, possibly because our limited 4-year dataset was insufficient to detect a significant statistical relationship or because the existing pool of labile C was adequate to sustain spring structural growth even when labile C production was reduced temporarily. Plant-scale studies indicate that the quantity of C stored in labile C is often in excess of that required for spring structural growth (Hoch et al., 2003; Korner, 2003) and that spring structural growth, although primarily reliant on labile C produced during the previous year, utilizes labile C produced several years earlier (Keel et al., 2006). The presence of a large, fluid reservoir of labile C also could explain why structural growth at our site was less sensitive to climate than was C assimilation. Biometric NEP did not exhibit the same negative response as meteorological NEP in 2001 to low growing season PPFD and high T_S, climate parameters known to constrain C assimilation in our forest (Gough et al., 2008a,b). Labile C mobilized to supplement structural growth may have partially buffered structural NPP from a steep climate-driven decline, thereby attenuating the response of biometric NEP to annual climate constraints that affected meteorological NEP. Labile C supplemented structural growth when C assimilation was insufficient in a managed pine forest (Sampson et al., 2001). Importantly, our results further support our previous hypothesis (Gough et al., 2008b) that same-year meteorological and biometric NEP may be equally valid estimates of annual C storage, but that these independent approaches measure C cycling processes with different sensitivities to annual climate.

Non-structural carbohydrate dynamics in aspen and oak wood support our inferred whole-ecosystem labile C trends and confirm a high reliance of structural growth on labile C. Although we observed differences in tissue non-structural carbohydrate concentrations between aspen and oak, both species displayed considerable seasonal variation in wood non-structural carbohydrate mass that generally corresponded with inferred labile C production and reallocation. Total structural growth of aspen and oak tissues paralleled the quantity of non-structural carbohydrate mass depletion in the spring, suggesting that structural growth

was partly constrained by the amount of non-structural carbohydrate mass reallocated to developing tissues. Our estimates of seasonal non-structural carbohydrate mass depletion were similar in magnitude to leaf structural C mass production in aspen and also individual wood, leaf/fruit/branch, and fine root structural C mass production in oak, and they compare well with those for deciduous species in a Swiss temperate forest (Hoch et al., 2003). We observed higher oak wood non-structural carbohydrate mass depletion in 2005 when acorn production was high, which is in contrast to the results of Korner (2003), who reported no relationship between changes in branch non-structural carbohydrate concentrations with masting. Although large species differences in labile C production and reallocation may obscure whole-ecosystem labile C patterns, in our forest near synchronization of non-structural carbohydrate dynamics in aspen and oak, which comprised two-thirds of standing live wood C mass, may explain why we were able to detect moderate correspondence between measured wood non-structural carbohydrates and inferred whole-ecosystem labile C dynamics. Many plant species exhibit diverse seasonal amplitudes of tissue non-structural carbohydrate concentrations, suggesting that there is considerable variation in the quantity of photosynthate allocated to labile C production and also in the reliance of structural growth on stored labile C (Barbaroux et al., 2003; Hoch et al., 2003; Palacio et al., 2007).

While seasonal labile C dynamics are well-documented at tissue and plant scales, climate and genetic constraints on interannual variation of labile C pools and fluxes are poorly understood (Hoch et al., 2003). Our independent tissue and whole-ecosystem analyses suggest that year-to-year variation in labile C dynamics may be coupled with climate and genetic constraints that mediate the timing of structural growth initiation and termination in relation to photosynthetic C uptake. In our forest, spring depletion of non-structural carbohydrate mass coincided with a high labile C requirement for structural NPP, while non-structural carbohydrate accrual during late summer occurred when structural growth effectively terminated and canopy net C assimilation persisted. Non-structural carbohydrate concentrations in boles and branches of temperate deciduous and conifer trees generally decrease during bud break and increase following leaf-out (Hoch et al., 2003; Korner, 2003; Wong et al., 2003). Similar to our study, periods of labile C accumulation and depletion in loblolly pine corresponded with climate and phenologic driven changes in the balance between photosynthesis and structural growth. Climate together with genetically controlled phenological differences among species largely constrains the temporal imbalance between C supply and demand for structural growth, and may affect labile C production and reallocation patterns among ecosystems (Baldocchi et al., 2005; Hoch et al., 2003; Piao et al., 2007; Sampson et al., 2001).

Inferred estimates of whole-ecosystem labile C production and reallocation were made with a relatively high degree of uncertainty. We quantified the principal errors of daily structural NPP, heterotrophic respiration, and NEE, parameters that were used to derive estimates of labile C production and reallocation to structural NPP (Eqs. (5) and (6)). Errors for daily structural NPP and heterotrophic respiration accounted for inter-sample variation and the uncertainty of models used to predict fine root NPP and soil respiration (Gough et al., 2008b). Daily NEE error was a function of gap-filling frequency and duration (Richardson and Hollinger, 2007). Because whole-ecosystem labile C production and reallocation estimates were derived from meteorological and biometric C cycling data, errors were compounding. For example, labile C production was calculated by subtracting daily structural NPP from A_c, the latter of which is the sum of NEE and heterotrophic respiration. Uncertainty for labile C production thus was the quadrature sum of independent errors for daily NEE, heterotrophic respiration, and structural NPP, producing a standard error that averaged 40% of the 5-year mean. Systematic biases in meteorological C fluxes associated with low turbulence conditions and ecosystem heterogeneity, and biases in biometric C fluxes caused by systematic sampling (e.g., daytime soil respiration measurements only) were not quantified, but long-term convergence of meteorological and biometric NEP suggests either that both methods produce valid results or that both are uniformly biased (Gough et al., 2008b). Additional studies of whole-ecosystem labile C dynamics are necessary to further validate the absolute magnitudes of these estimates.

Other sources of uncertainty in inferred and direct labile C parameter estimates could not be readily quantified. We did not account for seasonal changes in wood density which affect the intra-annual distribution of wood mass production in some species (Skomarkova et al., 2006) or short-term changes in bole diameter caused by modulating plant water status that could confound estimates of wood structural NPP. However, a 24-h assessment of aspen bole diameter conducted in July 2008 detected no discernable change (April Chiriboga, unpublished data). Our estimates of labile C production only considered photosynthate allocation to structural NPP and respiration, and could be inflated if C was immediately allocated in significant quantities to volatile organic compounds, root exudates, or microbial symbionts. Although these pools are thought to be small relative to plant structural and labile C pools, their contribution to most forest C budgets is not known (Andrews et al., 1999; Fahey et al., 2005; Qualls et al., 2002; Sandnes et al., 2005). Also, while our tissue analyses emphasized non-structural carbohydrates, labile C pools additionally may contain lipids and sugar alcohols (Hoch and Korner, 2005; Hoch et al., 2003). However, lipids only were detectible in the wood of two of six deciduous species and probably were minimally reallocated to structural growth in a temperate deciduous-conifer forest (Hoch et al., 2003). In scaling tissue non-structural carbohydrate concentrations to mass in aspen and oak wood, we performed limited sampling across radial depths (to 4 cm) and along the bole and coarse root surface. Non-structural carbohydrate concentration varied significantly along bole and coarse root surfaces in mature oak and beech trees, generally increasing with height or depth (Barbaroux et al., 2003). We did not include branches in our scaled estimates of non-structural carbohydrate mass because seasonal trends in non-structural carbohydrate concentrations were opposite of those in boles and coarse roots in oak, suggesting that branch non-structural carbohydrate accumulation prior to leaf-out may be caused by the remobilization of carbohydrates from other woody tissues. Branches of mature oak and beech trees had high non-structural carbohydrate concentrations, but low whole-tree non-structural carbohydrate mass compared with boles and coarse roots due to biomass differences among organs (Barbaroux et al., 2003). Despite this high uncertainty, seasonal changes in wood non-structural carbohydrate concentrations and mass generally corroborated inferred whole-ecosystem labile C dynamics.

5. Conclusions

Labile C produced during the latter half of summer in our deciduous forest played a critical role in later fueling dormant-season respiration and spring structural growth. Half of A_c was temporarily allocated to labile C production before remobilization to structural NPP or respiration. Whole-ecosystem and wood labile C dynamics in our deciduous forest are supported by tissue and whole-tree studies that indicate a high reliance of early season structural growth on stored labile C (Kagawa et al., 2006a,b; Keel et al., 2006).

Our results have important implications for comparative analyses of meteorological and biometric estimates of NEP, and for studies linking climate and tree ring growth. Late season allocation of photosynthate to labile C production rather than to current structural NPP together with the reliance of early season structural growth on stored labile C indicate that photosynthesis and structural growth in our forest are at times temporally offset. This pattern of labile C production and reallocation was similar during most years examined, but our results show that meteorological and biometric NEP may diverge when there is high annual variability in the partitioning of assimilated C to structural NPP and labile C production and when stored non-structural carbohydrates buffer structural growth against climate conditions that reduce A_c. Further investigation is required to determine if labile C production and reallocation to structural growth are similarly important to other ecosystem C budgets, and to elucidate constraints on interannual variation in labile C production and its reallocation. Variation among species and plant communities in canopy duration and physiology, and in seasonal amplitudes of non-structural carbohydrate concentrations suggest that substantial differences may exist across ecosystems in the timing and magnitude of labile C production and in the reliance of structural growth on stored labile C when A_c is depressed.

Acknowledgements

This research was supported by the U.S. Department of Energy's Office of Science (BER) through the Midwestern Regional Center of the National Institute for Global Environmental Change under Cooperative Agreements No. DE-FC03-90ER610100, the Midwestern Regional Center of the National Institute for Climatic Change Research at Michigan Technological University, under Award No. DE-FC02-06ER64158, and USDA Forest Service Award No. 06-JV-11242300-145. We acknowledge the University of Michigan Biological Station for facilities and material support. We thank two anonymous reviewers for their excellent suggestions.

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