

The role of harvest residue in rotation cycle carbon balance in loblolly pine plantations. Respiration partitioning approach

ASKO NOORMETS*, STEVE G. McNULTY†, JEAN-CHRISTOPHE DOMEQ*‡, MICHAEL GAVAZZI†, GE SUN† and JOHN S. KING*

*Department of Forestry and Environmental Resources, North Carolina State University, Campus Box 7260, 920 Main Campus Drive, Ste 300 Raleigh, NC 27695, USA, †Eastern Forest Environmental Threat Assessment Center, USDA Forest Service EFETAC Raleigh, 920 Main Campus Drive, Ste 300 Raleigh, NC 27606, USA, ‡Bordeaux Sciences Agro, University of Bordeaux, UMR 1220 TCEM ENITA/INRA, F-33175, Gradignan France

Abstract

Timber harvests remove a significant portion of ecosystem carbon. While some of the wood products moved off-site may last past the harvest cycle of the particular forest crop, the effect of the episodic disturbances on long-term on-site carbon sequestration is unclear. The current study presents a 25 year carbon budget estimate for a typical commercial loblolly pine plantation in North Carolina, USA, spanning the entire rotation cycle. We use a chronosequence approach, based on 5 years of data from two adjacent loblolly pine plantations. We found that while the ecosystem is very productive (GEP up to $2900 \text{ g m}^{-2} \text{ yr}^{-1}$, NEE at maturity about $900 \text{ g C m}^{-2} \text{ yr}^{-1}$), the production of detritus does not offset the loss of soil C through heterotrophic respiration (R_H) on an annual basis. The input of dead roots at harvest may offset the losses, but there remain significant uncertainties about both the size and decomposition dynamics of this pool. The pulse of detritus produced at harvest resulted in a more than 60% increase in R_H . Contrary to expectations, the peak of R_H in relation to soil respiration (SR) did not occur immediately after the harvest disturbance, but in years 3 and 4, suggesting that a pool of roots may have remained alive for the first few years. On the other hand, the pulse of aboveground R_H from coarse woody debris lasted only 2 years. The postharvest increase in R_H was offset by a decrease in autotrophic respiration such that the total ecosystem respiration changed little. The observed flux rates show that even though the soil C pool may not necessarily decrease in the long-term, old soil C is definitely an active component in the site C cycle, contributing about 25–30% of the R_H over the rotation cycle.

Keywords: chronosequence, coarse woody debris, detritus, harvesting, heterotrophic respiration, loblolly pine, managed forest, soil carbon

Received 2 April 2012 and accepted 30 May 2012

Introduction

Increasing global population and expanding land use mean that an ever greater percentage of human needs for wood products are being met by managed forests. Currently, about 7% of world's forests are plantations and 57% are secondary forests recovering from anthropogenic disturbance (FAO, 2010). From 2000 to 2005, the rate of increase in the area of planted forests was $2\% \text{ yr}^{-1}$ and is accelerating (FAO, 2009). However, it is unclear, whether or how the contribution of forests to global C cycling may change with their transition from natural to managed state (Piao *et al.*, 2009; Stinson *et al.*, 2011). The increased frequency of disturbance makes for a very dynamic and rapidly changing biogeochemical exchange, to the point where age-related variability

may be the predominant source of spatial variation (Desai *et al.*, 2008), and comparable in magnitude with environmental variability. There are significant changes in forest structural and functional traits as related to age (Noormets *et al.*, 2006, 2007), which have been recognized as having far greater influence on forest productivity and CO_2 exchange than climate (King *et al.*, 1999; Pregitzer & Euskirchen, 2004; Magnani *et al.*, 2007).

Although plantation forests are efficient in biomass production, the effects of increased frequency of disturbance (including site preparation, fertilization, vegetation control, thinning and harvest) on detritus decomposition and soil C balance remain poorly understood. For example, Yanai *et al.* (2003) outlined how major national syntheses since mid-1990s ultimately have relied on the classic study by Covington (1981), which reported 20% loss of mineral soil C following harvest. More recent measurements of soil C have been

Correspondence: Asko Noormets, tel. +1 919 515 7040, fax +1 919 513 2978, e-mail: anoormets@gmail.com

much more equivocal about the negative effect of harvesting on the soil C pool (summarized by Yanai *et al.*, 2003). Although there have been a number of studies that report postharvest increases in soil CO₂ efflux, few have been able to define the exact source (but see Diochon *et al.*, 2009; Mallik & Hu, 1997; Moroni *et al.*, 2007). Even though there are several chronosequence studies reporting higher soil CO₂ emissions following harvest, in broader syntheses, these patterns disappear among reports of no harvest effect (Johnson & Curtis, 2001; Subke *et al.*, 2006; Amiro *et al.*, 2010). The lack of consistent response is usually attributed to compensating changes in autotrophic and heterotrophic contributions as proposed by Toland & Zak (1994). In most cases, the phenomenon has often been attributed to higher soil temperature and moisture (e.g., Edwards & Ross-Todd, 1983; Gordon *et al.*, 1987; Yanai *et al.*, 2003; Hagemann *et al.*, 2010). Yet, it remains largely unclear to what extent changes in microclimate, increased organic matter availability, physical disturbance, or priming of old soil C contribute to this increase.

If increased mineralization of soil C is a common phenomenon in postharvest forests, it has significant implications for site C balance. In some cases, it has been demonstrated that the increase in soil CO₂ production occurs in deeper, mineral soil layers (Mallik & Hu, 1997; Moroni *et al.*, 2007; Diochon *et al.*, 2009). In others, specific logging practices have been associated with leaching of nutrients from the soil profile (Tyree *et al.*, 2009; O'hehir & Nambiar, 2010). This, in turn, could lead to a progressive decline in forest productivity over multiple rotation cycles (Gough *et al.*, 2008a). While the loss of soil C and nutrients is potentially reversible, the recovery is a much slower process. For example, in restored prairies, the plant C and N pools (above- and belowground) reached levels similar to native prairies in a few decades, whereas soil organic C and total N recovered on a century timescale (Matamala *et al.*, 2008).

The replenishment of soil C stocks in tree plantations through detritus is highly episodic, following the rotation cycle. With limited information on the decomposition and stabilization dynamics of organic debris in general (Harmon *et al.*, 1986), data on the dynamics of harvest residue in managed forests and the effects of different site preparation techniques are even harder to come by (but see Hagemann *et al.*, 2010; Moroni *et al.*, 2009; Takagi *et al.*, 2009). As there may not be a stoichiometric balance among different C pools in intensively managed forests, the fluxes between them are also continuously adjusting. Upscaling such a system in space and time presents significant additional uncertainties. Compared with other C pools, understanding of the dynamic of woody detritus is very limited, yet essential

to understanding the role of managed and disturbed forests in the regional C cycle. The goal of the current study was to assess the role of harvest-generated detritus and heterotrophic respiration (R_H) in the rotation cycle C balance. An earlier analysis of one of our study sites suggested a consistent loss of soil C as R_H exceeded new inputs through detritus (Noormets *et al.*, 2010). The current study re-evaluated that conclusion using independent measurements and chronosequence upscaling. We assessed the decomposition dynamics of postharvest debris and coarse woody debris using measurements in two different-aged loblolly pine (*Pinus taeda* L.) stands over a 5 year period. Given that the sites are located on C-rich organic soils, we hypothesized that the increase in R_H due to the physical disturbance of the harvest and preplanting site preparation techniques would exceed the decline in R_A due to the death of root systems.

Materials and methods

Study sites

This study was carried out in two loblolly pine (*Pinus taeda* L.) plantations, registered in FLUXNET database as US-NC1 and US-NC2. US-NC1 was harvested just prior to the start of measurements in early 2004 and planted with 2 year old loblolly pine seedlings in early 2005, and US-NC2 was 13 years old at the start of the measurements in 2005, having been planted in 1992. Ecosystem carbon pools and CO₂ fluxes were measured over a 5 year period (2005–2009). Although the different site indices (88 and 66, respectively) may confound the chronosequence analysis (Peichl *et al.*, 2010), we use space-for-time substitution to estimate the integrated rotation cycle carbon balance in commercially managed loblolly pine plantations typical to the region.

The study area is located in the lower coastal plain in North Carolina, USA, at 35°48' N 76°40' W. The area is flat, <5 m above sea level, with ground water depth of 0.5–1.0 m during the dormant season. The mean (1971–2000) annual precipitation is 1320 mm, mean temperature in July is 26.6 °C, and in January 6.4 °C. The study period spanned two consecutive drought years (2007 and 2008), which had annual rainfall 60% and 45% lower than the long-term mean, respectively. The drought affected the carbon fluxes of interest, but was inconsequential for evaluating the age-related changes in the fluxes following harvest. While soils are fluvial in origin at both sites, the Cape Fear series soil at US-NC1 has slightly higher water-holding capacity and a surface loam layer, whereas the Belhaven series soil at US-NC2 has a muck layer. The carbon content is 203 and 635 t C ha⁻¹, and 16.3 and 20.7 t N ha⁻¹ in the top 1 m at US-NC1 and US-NC2, respectively. Both sites were bedded before planting with about 5 m row spacing, and received standard vegetation control. Trees were planted originally at 1435 and 1913 trees ha⁻¹ (tph) at US-NC1 and US-NC2, respectively, but at the time of measurement, the stem densities were 1046 and 670 tph. As no additional

vegetation control was applied after planting, the ground cover at US-NC1 was dominated by annuals and shrubs in years 1–3 (*Solidago* spp., *Eupatorium capillofolium*, *Erechtites hieracifolia* and *Smilax rotundifolia*). Total aboveground understory biomass was 300 g C m⁻² in year 1, and 510 g C m⁻² in year 3 (Table 1). Pine aboveground biomass was 60 g C m⁻² in year 3 and 271 g C m⁻² in year 4, when it reached canopy closure. The mid-rotation stand US-NC2 had a maximum projected leaf area index (LAI) during the growing season of 3.9–4.3 m² m⁻² and decreased to 2.4–2.8 m² m⁻² in winter, partly due to leaf fall of subdominant and understory *Acer rubrum*. LAI was measured on four of the 13 vegetation survey plots (described below) using a LAI-2000 Plant Canopy Analyzer (Licor Inc., Lincoln, NE, USA). Although the estimates were not adjusted for clumping, it is unlikely to affect the following analysis as the canopy was closed, and the LAI measurements were carried out on the same plots throughout the study, allowing for interannual comparison. Furthermore, the litterfall-based estimate of peak LAI in 2006 (as the sum of litterfall in 2006 and 2007) was similar to the optical estimate (3.87 vs. 4.0 m² m⁻²). More details of US-NC2 can be found in Noormets *et al.* (2010). We do not have the exact fertilizer application history for these stands, but operational silvicultural prescriptions for this region call for 28–50 kg N and P ha⁻¹ at the time of planting, and 140–195 kg ha⁻¹ N and 28 kg ha⁻¹ P at mid-rotation (Allen & Campbell, 1988; Allen *et al.*, 1990).

To estimate the postharvest slash and root biomass at US-NC1, we conducted a vegetation survey in 2008 at a nearby mixed bottomland hardwood forest, very similar to the vegetation at US-NC1 prior to the harvest in 2004. This third site was located 31 km from the loblolly pine stands, at Bull Neck Swamp, NC (35.95N, -76.42W). The belowground biomass at this 70 year old stand was 12% higher than at US-NC2 (Table 1). Extrapolating the observed biomass trends to the age of the typical 25 year rotation cycle suggests that root biomass in a 25 year loblolly pine plantation would be about 55% higher than in the mature mixed bottomland hardwood stand at US-NC1.

Biometric measurements

Carbon storage was quantified for all major pools, including stemwood, foliage, belowground woody biomass, understory, coarse and fine woody debris (CWD and FWD, respectively), the O-horizon, and soil. The standing biomass in aboveground and belowground woody tissues was estimated from species-specific allometric relationships (Wells *et al.*, 1975; Flowers, 1978; Swindel *et al.*, 1982; Clark *et al.*, 1985; Stucky *et al.*, 1999; Miller *et al.*, 2006), based on tree height and/or diameter at breast height (DBH, 1.4 m above ground level). These measurements were made in 13 14 m diameter Tier-3-type vegetation survey plots (Wofsy & Harriss, 2002), located throughout the 0.25 (US-NC1) and 1 km² (US-NC2) study area. All trees with DBH >2.5 cm were tagged, identified to species and re-measured every winter for changes in diameter and height. Site-specific biometric equations were developed for young loblolly pine at US-NC1 ($N_{AG} = 49$, $N_{BG} = 31$), devil's walking stick (*Aralia spinosa*; $N_{AG} = 16$, $N_{BG} = 4$), winged sumac (*Rhus copallinum*; $N_{AG} = 5$, $N_{BG} = 3$), and pawpaw (*Asimina*

triloba; $N_{AG} = 5$, $N_{BG} = 3$). Understory biomass was sampled on 10 1 m² plots in 2005 and 2007 in US-NC1, and on ten 18.6 m² plots in 2007 and 2008 in US-NC2. The biomass was separated into live and dead, herbaceous, and woody components. The dry weight of the understory vegetation was measured after drying for 48 h (or until constant weight for woody samples) at 65 °C.

Leaf area index was measured at US-NC2 using an LAI-2000 (LiCor, Lincoln, NE, USA). Measurements were taken throughout the year from five points (center and four cardinal directions 7 m from each plot center) on the four centrally located vegetation plots. At US-NC1, the open and low canopy precluded reliable application of optical methods until 2009. Therefore, leaf area index was estimated from litterfall and specific leaf weight data. Leaf fall was measured with three 0.18 m² litter traps on each plot. The litter was collected every 90 days during spring and summer, and monthly during fall and early winter. The samples were separated into needles, leaves, twigs, and reproductive litter, and oven-dried to constant mass at 65 °C. Dried samples were weighed immediately upon removal from the oven, subsampled, and ground for elemental analysis. Coarse woody debris biomass was estimated on 13 plots in 2005 and 2006 and on 25 plots from 2007 on, laid out on a grid across the study area. Each plot had two perpendicular 40 m transects, originating from the center of the plot. The direction of the first transect was determined with a random number generator. All pieces of CWD larger than 7.6 cm in diameter at the intersection with the transect were identified to species when possible (and to hardwood or softwood when species identification was not possible), and the diameter and decay class were recorded (FIA, 2007). Snags (dead standing trees) in the vegetation plots were also included in this pool. The C content of CWD was determined in 2008 for loblolly pine and seven hardwood species based on three samples of each collected from the site. The decay rate reduction factors were based on Waddell (2002). Forest floor was sampled in the mid-rotation stand four times a year. There was considerable variation both among plots and between the measurements times, with a coefficient of variation for the latter of 10–18%. Fine roots were collected from soil cores cut out of four soil pits adjacent to the four centrally located vegetation plots. Soil pits were dug into the bed midway between two dominant trees, and soil cores were collected from each horizon on two perpendicular soil pit walls. Roots were removed prior to drying the samples at 65 °C for 48 h. Soil samples were then ground to a fine powder, re-dried for 24 h, and weighed for C and N analysis on a PerkinElmer 2400 elemental analyzer (Perkin Elmer, Watham, MA, USA). All biomass estimates were converted to carbon units using a carbon content of 49%, based on repeated site-specific destructive sampling of stem, branch, and leaf samples, analyzed between 2006 and 2009. The resulting biomass and productivity estimates were slightly lower than those reported earlier (Noormets *et al.*, 2010) where we used an average C content of 53%, based on Birdsey (1992).

Biomass pools at the time of harvest were estimated by linearly extrapolating all pool sizes from the mid-rotation out to the harvest age of 25 years. The annually estimated pool

Table 1 Biomass pools ($t C ha^{-1}$) at two loblolly pine (US-NC1, US-NC2), a native mixed bottomland hardwood (BN) and a projected harvest-age loblolly pine stand (LP25)

Year & years since harvest	US-NC1					US-NC2					LP25			BN		
	2005	2006	2007	2008	2009	2004	2005	2006	2007	2008	2009	2017	2017	2008	2008	
1	2	3	4	5	12	13	14	15	16	17	25	25	70	70	70	
Component																
AG woody	0.03 ± 0	0.32 ± 0.03	1.64 ± 0.15	3.8 ± 0.31	9.0 ± 0.63	35.2 ± 2.7	39.9 ± 3.1	45.4 ± 3.5	53.3 ± 4.8	58.9 ± 5.2	63.9 ± 5.8	112.0	112.0	52.9 ± 7.3	52.9 ± 7.3	52.9 ± 7.3
Leaves	0.03 ± 0	0.24 ± 0.02	1.06 ± 0.1	1.4 ± 0.12	2.7 ± 0.2	2.1 ± 0.2	2.4 ± 0.2	2.7 ± 0.2	3.2 ± 0.3	3.5 ± 0.3	3.8 ± 0.4	6.6	6.6	1.2 ± 0.2	1.2 ± 0.2	1.2 ± 0.2
Coarse roots	0.01 ± 0	0.12 ± 0.01	0.53 ± 0.05	1.3 ± 0.11	2.3 ± 0.18	9.3 ± 0.7	10.5 ± 0.8	12.0 ± 0.9	14.0 ± 1.3	15.5 ± 1.4	16.7 ± 1.5	29.6	29.6	19.0 ± 8.2	19.0 ± 8.2	19.0 ± 8.2
Fine roots	n/a	n/a	n/a	n/a	n/a	2.1	2.5	2.8	3.3	3.4	3.5	6.0	6.0	~3.8	~3.8	~3.8
Coarse woody debris (CWD)	23.9*	12.6 ± 1.8	6.8 ± 1.8	~5.6	4.4 ± 0.9	n/a	2.9 ± 1.2	~2.9	2.9 ± 0.49	4.3 ± 0.74	4.1 ± 0.8	3.7	3.7	n/a	n/a	n/a
Forest floor	n/a	n/a	n/a	n/a	<6.6‡	n/a	9.9 ± 1.8	9.4 ± 0.9	10.0 ± 1.1	13.5 ± 2.4	11.3 ± 1.9	~16.0§	~16.0§	n/a	n/a	n/a
AG slash¶	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	29.7	29.7	13.5	13.5	13.5
Understory**	3.0 ± 0.5	~4.1	5.1 ± 0.4	n/a	>1.1††	n/a	n/a	n/a	0.93 ± 0.14	0.70 ± 0.12	~0.66‡‡	~0.7	~0.7	~7	~7	~7
Harvest residue§§	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	60.0	60.0	39.5	39.5	39.5

Mean ± SE. ~ indicates interpolated/extrapolated values; n/a, indicates data not available; AG, aboveground. Sites: US-NC1 – early-rotation loblolly pine plantation, US-NC2 – mid-rotation loblolly pine plantation, LP25 – pool sizes at US-NC2 extrapolated out to 25 years, which is the typical harvest age in the region, BN – Bull Neck Swamp, a bottomland hardwood forest very similar in age and species composition to the stand at US-NC1 prior to conversion to a pine plantation.

*CWD in the following year + R_{CWD} * 2 / 0.8 (accounting for fractionation and microbial carbon use).

†CWD in the following year + R_{CWD} * 3.5 (the ratio of mass loss and R_{CWD} from temperature relationships in year 2).

‡6.6 ± 0.35 $t C ha^{-1}$ in 6/28/2011.

§Estimated by extending the trendline for forest floor estimates from 2005–2011 to 2017.

¶Aboveground slash = 0.25*(AG woody + Leaves).

**Includes woody and non-woody groundcover and shrubs.

††1.1 ± 0.2 $t C ha^{-1}$ in 07/28/2010.

‡‡0.62 ± 0.25 $t C ha^{-1}$ in 07/27/2010.

§§Harvest residue = AG slash + Coarse roots + Understory.

sizes using allometric relationships of diameter at breast height and height with time were linear over the 5 year observation period, with $R^2 > 0.985$ for all observed pools (total, aboveground woody, stem, root and leaf biomass). Harvest residue or slash was estimated as the difference between estimated pool sizes at the time of harvest (LP25 and BN in Table 1) and harvesting efficiency in southern pines (Clark *et al.*, 2004). Total annual belowground allocation (BGA) was calculated as the sum of leaf, fine, and coarse root production, and branchfall.

CO₂ flux measurements

Eddy covariance. Ecosystem exchange of CO₂ was measured with an open-path eddy covariance system consisting of LI-7500 infrared gas analyzer (Licor, Lincoln, NE, USA), CSAT-3 sonic anemometer (Campbell Scientific (CSI), Logan, UT, USA), and CR5000 datalogger (CSI). US-NC2 had a CO₂ profile sampler based on a LI-820 infrared gas analyzer (Licor), with air intakes at 0.05×, 0.2×, 0.6× and 0.9× of canopy height (Noormets *et al.*, 2006, 2007) for estimating CO₂ storage in the canopy air space. US-NC1 did not have a similar system as the canopy was open and all the flux was expected to be accounted for by turbulent exchange. The eddy covariance systems were mounted at 6 m at US-NC1 until February 2008 and at 11.6 m from August 2008 onward. At US-NC2, the instruments were mounted at 22.5 m throughout the study. The distance from the instrument tower to the nearest edge of the stand of interest was 250 m at US-NC1 and 440 m at US-NC2. In the predominant wind directions, the fetch distances were 350 and >450 m, with the ratio of uniform fetch to measurement height ($z_m = z - d$, where z is sensor height and d is zero-plane displacement) 39–89 at US-NC1 and 32–39 at US-NC2. US-NC2 was surrounded by stands of similar age and species composition, whereas US-NC1 bordered with a similar stand in the east, but was surrounded by taller mature pine stands in the other directions. The 30 min mean fluxes of CO₂ were computed as the covariance of vertical wind speed and the concentration of CO₂, using the EC_Processor software package (<http://www4.ncsu.edu/~anoorme/ECP/>; Noormets *et al.*, 2006, 2007), and data quality control and gapfilling were performed as reported earlier (Noormets *et al.*, 2010).

Additional micrometeorological parameters measured above canopy included air temperature (Ta, HMP45AC, Vaisala, Finland), photosynthetically active radiation (PAR, LI-190, Licor Inc.), net radiation (Rn, CNR-1, Kipp & Zonen, Delft, the Netherlands), and precipitation (P, TE-525, Campbell Scientific Inc. (CSI), Logan, UT, USA). The PAR measurements were corrected for sensor drift based on annual comparisons against Ameriflux standard sensor (PARLITE, Kipp & Zonen), and assuming a linear drift. Soil temperature (Ts) was measured at depths of 5 and 10 cm with CS107 (CSI) temperature probe, soil volumetric water content (VWC) was averaged through the top 30 cm using a vertically inserted CS616 time domain reflectometer (CSI), and the depth of GWT was monitored using pressure water level data logger (Infinites, Port Orange, FL, USA).

Soil respiration. Soil respiration was measured biweekly on four central vegetation survey plots at each site. Each plot included six 20 cm diameter soil respiration collars (10 cm diameter until 2008), which were measured with LI-8100 soil respiration system (Licor) and 8100-103 (8100-102 until 2008) survey chamber. At each measurement, soil temperature (at 5 and 10 cm) and moisture (top 20 cm) were recorded adjacent to each collar with HI 98501 (Hanna Instruments, Woonsocket, RI) handheld thermometer and CS620 HydroSense water content sensor (CSI). Continuous automated measurements of SR were conducted at the instrument tower starting 2005 at US-NC2 and 2008 at US-NC1. We used a LI-8100 soil respiration system with 8100-104 long-term chamber (at US-NC2 8100-101 until 2008). Continuous measurements of soil temperature at a 5 cm depth were made at the central instrument tower using CS107 thermistors (CSI), and at each of the SR plots using HOBO U12-008 datalogger, and four TMC6 temperature probes (Onset Computer, Pocasset, MA, USA) per plot. The respiration rates in individual collars varied as a function of distance from trees, with the within-plot variability exceeding that among the plots (Noormets *et al.*, 2010). Upscaling to annual scale was conducted on per-collar basis using empirical relationships with temperature and moisture using both the automatic and survey chamber measurements, weighting the collars in proportion to stand-wide area distribution of distance to the nearest tree (Noormets *et al.*, 2010). Heterotrophic respiration (R_{H+}) was estimated from annual SR using the global relationships reported by Bond-Lamberty *et al.* (2004)

Respiration of coarse woody debris. Respiration from coarse woody debris (R_{CWD}) was measured in 2007–2008 in eight permanently installed PVC collars using LI-8100 soil respiration system and 8100-102 survey chamber. Substrate temperature was measured with HI 98501 thermometer and substrate moisture was assessed on qualitative scale based on visual appearance and time since last rainfall. The level of decay of the substrate was evaluated periodically according to Harmon *et al.* (1986). The decay classes exhibited distinctly different decay rates and different sensitivity to environmental conditions. However, given the final sample size per decay class ($n = 66–73$ in different years), we were able to develop temperature response functions for decay classes two and three. Although measurements were also conducted on logs belonging to decay class four, we had to exclude 70% of the data due to suspected leaks during measurements due to decreasing substrate integrity and high porosity. As the result, the estimates of base respiration and temperature sensitivity were poorly defined in this decay class.

The annual fluxes of CWD respiration were estimated with two different approaches. First, the chamber measurements of CO₂ efflux from CWD were regressed with the temperature of CWD, grouped by different decay class, and scaled up using a non-linear regression model based on estimated CWD temperature, which in turn was estimated based on the relationship between CWD and soil temperature over a 4 year period. The upscaled estimates were further weighted by the ratio of CWD projected area (A_{CWD}) to plot area (A) as in Eqn (1).

$$R_{\text{CWD}}^{\text{p}} = R_{\text{CWD}} \frac{A_{\text{CWD}}}{A} \quad (1)$$

For years when R_{CWD} measurements were not conducted (2005, 2006, 2009), the fluxes were estimated using the temperature response model established for 2007. Given that from July of 2007 through June of 2009 the sites experienced severe drought (Noormets *et al.*, 2010; Domec *et al.*, 2012b), we considered the parameterization for 2007 to better represent the moister years than that for 2008. Second, the change rate of CWD mass was converted into units of CO_2 emitted by adjusting annual mass loss ($M_{\text{CWD},t+1} - M_{\text{CWD},t}$) for (i) microbial C use (growth efficiency of 20%; Epron *et al.*, 2006; Ngao *et al.*, 2005) that would contribute to loss of CWD, but not to observed CO_2 production, and (ii) fragmentation, which has been estimated to be comparable in magnitude to the rate of mineralization (Harmon *et al.*, 1986). Sometimes, fragmentation may start with a lag of a few years (see Harmon *et al.*, 1986), but in the current study, the measured CO_2 emission rates were adjusted from year 1. Annual mass change was estimated from the amount and decay class (DC) of CWD present (FIA, 2007).

$$R_{\text{CWD}}^{\text{M}_{\text{CWD}}} = \frac{0.8}{2} (M_{\text{CWD},t+1} - M_{\text{CWD},t}) \quad (2a)$$

where

$$M_{\text{CWD}} = \sum_{\text{DC}=1}^S M_{\text{CWD}}^{\text{DC}} \quad (2b)$$

Missing from these estimates is the explicit accounting for the decay of harvest residue or slash, which consists of foliage, bark, branches and small stems.

Data processing and gapfilling

Gaps in eddy covariance fluxes and soil respiration were filled with non-linear regression models as described previously (Noormets *et al.*, 2010). In February, 2008, the tower at US-NC1 was damaged in a storm and flux measurements did not resume until July. The 22 week data gap was filled by comparing three different methods and averaging the output of (i) daily interpolated values between 2007 and 2009, and (ii) gapfilling model estimates fitted to the rest of the year. The difference between these estimates was $65 \text{ g C m}^{-2} \text{ yr}^{-1}$. An estimate using a 2nd-order Fourier transform (Richardson & Hollinger, 2007) was not used in the averaging because the seasonality of NEE was distorted due to no data being available during the spring transition. Even though the estimates from the two preferred methods were similar, it has been estimated that a weeklong data gap could translate into an additional uncertainty of up to 30 g C m^{-2} (Richardson & Hollinger, 2007), which, in the worst case, would add $660 \text{ g C m}^{-2} \text{ yr}^{-1}$ to our annual flux uncertainty in 2008.

Partitioning respiration

Partitioning ecosystem respiration (ER) to above- and below-ground heterotrophic (R_{HSoil}) and autotrophic (R_{A}) components was based on several assumptions. We hypothesized

that the global relationship in $R_{\text{HSoil}}:\text{SR}$ ratio described by Bond-Lamberty *et al.* (2004) would not hold in the young regenerating forest. Following a harvest, there would be a large pool of coarse roots that would gradually die and become a substrate for microbial decomposition. At one extreme, one could speculate that most of SR would originate from heterotrophic processes. However, this scenario did not hold up in the mass balance analysis, when all respiration fluxes were constrained at the ecosystem level by ER. The harvested site was also rapidly colonized by annuals and shrubs, which probably contributed to at least some autotrophic activity below ground. Thus, we consider the global model ($R_{\text{HSoil-BL}}$) and SR as the two boundaries between which true R_{HSoil} probably fell. As the vegetation and new root systems developed, R_{HSoil} probably shifted closer to $R_{\text{HSoil-BL}}$. To further constrain R_{HSoil} , we estimated R_{A} as (1) the difference between GEP and biometric estimates of net primary production (NPP), or (2) 50% of gross ecosystem production (GEP), which is the global mean (Waring *et al.*, 1998), although we recognize that $R_{\text{A}}:\text{GEP}$ ratio may not be constant (DeLucia *et al.*, 2007; Piao *et al.*, 2010).

$$R_{\text{A1}} = \text{GEP} - \text{NPP} \quad (3a)$$

$$R_{\text{A2}} = 0.5\text{GEP} \quad (3b)$$

$$R_{\text{HSoil}_i} = \text{ER} - R_{\text{CWD}} - R_{\text{A}_i} \quad (3c)$$

To close the carbon budget for $R_{\text{HSoil-BL}}$, R_{A} was estimated as the residual: $R_{\text{A-BL}} = \text{ER} - R_{\text{CWD}} - R_{\text{HSoil-BL}}$.

Harvest losses

In managed forests, the C cycle is open and a significant fraction of assimilated carbon leaves the site at harvest. The exact amount of removal depends on species, and the market demand for different wood products, which, in turn, may vary regionally and in time. In this study, we used a removal rate of 87% of stemwood, which has been reported for slash pine in similar climate (Clark *et al.*, 2004). Given the allocation patterns in loblolly pine, this removal rate is equivalent to 75% of aboveground biomass, falling between the alternative estimates of 54% and 80% of overall aboveground biomass as reported by Gower *et al.* (2006) and Yanai *et al.* (2003). Clearly, closing the carbon balance depends on the correct estimation of harvest exports, but unfortunately, these estimates are not well constrained. Although we do not consider the fate of harvested biomass further, it is worth mentioning that it is estimated that only about 28% of the harvested wood ends up in final products, with the rest being lost in milling and transportation (Ingerson, 2009).

Results

Biomass

Following the clear-cut harvest of a mixed native hardwood stand in 2004, site US-NC1 was estimated to have approximately $2390\text{--}2850 \text{ g C m}^{-2}$ in CWD and nearly as much in dead fine and coarse roots (Table 1). As we

did not measure the diameters of trees in the preharvest forest, we can only estimate the range of belowground dead biomass from other similar stands in the region. The Bull Neck Swamp site, 31 km from US-NC1, that had similar vegetation composition and age compared to US-NC1 before harvest, had $1900 \pm 820 \text{ g C m}^{-2}$ (mean \pm SD) in coarse roots, which would ultimately all die and begin to decay within a few years following the harvest. Based on the aboveground biomass estimates for the same site, and assuming 87% harvest removal of stemwood (Clark *et al.*, 2004), the initial amount of aboveground slash was estimated at 1720 g C m^{-2} , consistent with the range of observed CWD. New 2 year old seedlings were planted in 2005, but the biomass at the site was dominated by herbaceous and woody groundcover through the first 3 years (Table 1). However, by year 5, pine leaf area and productivity had reached levels comparable to the mid-rotation stand US-NC2, with about 275 g C m^{-2} in foliage biomass. The canopy still had a significant understory component, particularly in the first part of the growing season when water availability was higher, discussed in more detail elsewhere (Domec *et al.*, 2012a). Also, by year 5, CWD and understory biomass had declined to levels comparable to those observed at US-NC2 (Table 1).

The harvesting and subsequent site preparation destroyed the forest floor in the young stand, and partly mixed it with the topsoil. Forest floor measurements resumed only 7 years after harvest, by which time forest floor had recovered to about half of that in the mid-rotation stand (Table 1). In the mid-rotation stand, there was a slight increasing trend in forest floor mass (Table 1), but it seemed sensitive to interannual variability in weather (data not shown). There was a distinct cycle of alternating phases of forest floor accumulation and loss, but among years, the timing of these phases shifted significantly, with the timing of leaf fall affected both by natural processes of aging and storms (data not shown).

Ecosystem-level CO_2 exchange

US-NC1 was a strong source of C to the atmosphere immediately following the harvest, owing to the harvest residue, large pool of dead roots and disturbance of the top soil. The site respired 2127 ± 35 (mean \pm gap-filling uncertainty) $\text{g C m}^{-2} \text{ yr}^{-1}$ in the first year, of which nearly 80% originated from soil ($1727 \pm 45 \text{ g C m}^{-2} \text{ yr}^{-1}$). The rate of decomposition of the dead organic matter slowed in subsequent years, but some of the decline in SR was compensated for by increasing aboveground respiration, first from the understory, but increasingly from the pines, as well. Although ER

decreased to about $1650 \text{ g C m}^{-2} \text{ yr}^{-1}$ in years 3 and 4 following the harvest (Fig. 1b), it was largely attributable to a decrease in R_A due to drought-induced reductions in GEP (Noormets *et al.*, 2010) rather than to a decline in R_H . As an average over the 5 year observation period, annual ER did not significantly differ between the early- and mid-rotation stands, whereas SR and $R_{\text{HSoil-BG}}$ declined.

Gross ecosystem productivity also recovered rapidly after harvest due to no weed control. The ground cover assimilated $1290 \pm 40 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the first year following the harvest, and $1625 \pm \text{xx} \text{ g C m}^{-2} \text{ yr}^{-1}$ in the second year. Pine photosynthesis was not directly measured, but pine leaf mass contributed only 0.02 and 1.5% to total site canopy (mass-based, based on destructive harvest) in 2005 and 2006, respectively (14% in 2007 and 57% in 2008). The declines in GEP in 2007 and 2008 are attributable to severe droughts during these years (Fig. 1b; Domec *et al.*, 2012a; Noormets *et al.*, 2010). The drought years prolonged the postharvest source phase and suppressed carbon uptake over the

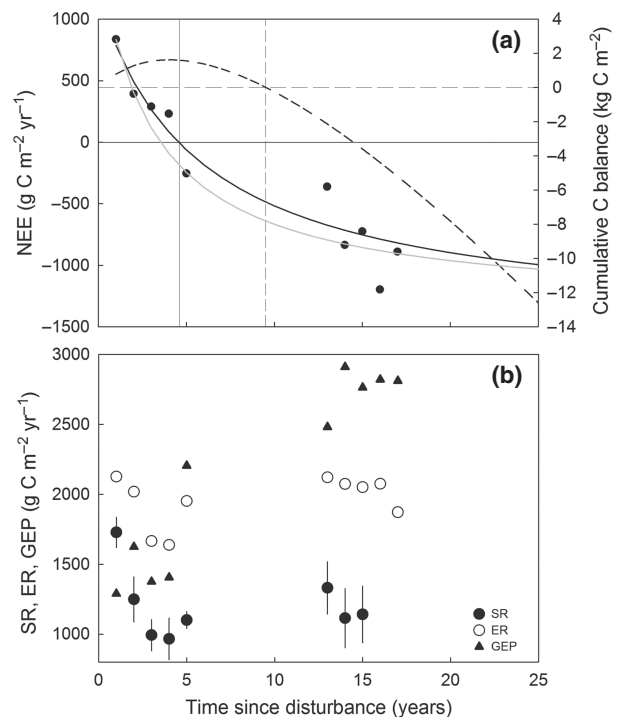


Fig. 1 Main ecosystem carbon fluxes over 5 years in two loblolly pine plantations of different age. (a) Annual and cumulative net ecosystem exchange (NEE) of CO_2 , with black line indicating a rectangular hyperbola model, fitted to all the measurements, the black dashed line marks cumulative carbon balance, and the gray line is a rectangular hyperbola fitted to non-drought-year data. (b) Ecosystem respiration (ER), soil respiration (SR), and gross ecosystem production (GEP). SR = Mean \pm SD of five plots.

entire chronosequence (black vs. gray line on Fig. 1a). The early-rotation site US-NC1 became a C sink by year 5, sequestering about $250 \pm 15 \text{ g C m}^{-2} \text{ yr}^{-1}$, whereas without the drought, the transition from C source to sink may have occurred a year earlier. However, a detailed evaluation of drought effects and other interannual variability separate from age-related changes is beyond the scope of the current study. The average rate of annual sequestration at the mid-rotation stand US-NC2 was $800 \text{ g C m}^{-2} \text{ yr}^{-1}$, but individual years varied widely, ranging from 360 to $1195 \text{ g C m}^{-2} \text{ yr}^{-1}$.

CWD respiration

The two methods for estimating CWD loss rate were relatively consistent with each other (Fig. 2b), with the main losses occurring in the first 2–3 years and declining to levels comparable to the mid-rotation stand ($\approx 20 \text{ g C m}^{-2} \text{ yr}^{-1}$) by year 4. The gapfilling uncertainty of chamber measurements was 21–23% for decay class two and 10–11% for decay class three, and the difference between the two methods (chamber measure-

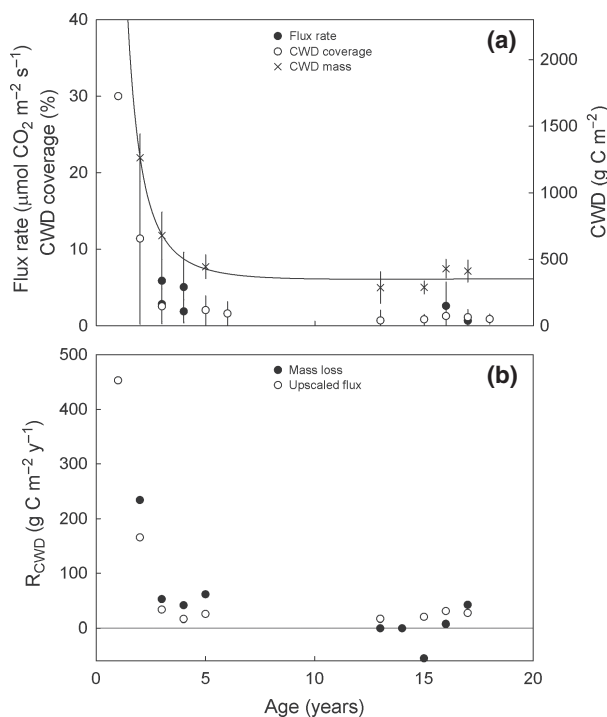


Fig. 2 Coarse woody debris (CWD) decomposition (R_{CWD} ; rates for decay classes 2 and 3 are shown), CWD areal coverage, and total CWD biomass (a), and the derived area-normalized R_{CWD} derived from CWD loss rate and from upscaled CO_2 emission rates (b). The fluxes are presented as estimates of CO_2 emissions. See Methods for further details and assumptions.

ments and interannual mass loss) of estimated R_{CWD} was 68, 19, 21, and $36 \text{ g C m}^{-2} \text{ yr}^{-1}$ in years 2–5, respectively ($\text{CV} = 24\text{--}62\%$; Fig. 2b). The main changes in the site-level losses were driven by the decrease in CWD mass and areal coverage, whereas the CO_2 evolution rate per unit CWD area changed much less (Fig. 2a). Therefore, the temperature-adjusted decay-class-specific decay rates were applied throughout the study period within each site. The mass-based estimates of R_{CWD} were negative in some years, and were attributed to (i) measurement uncertainty in years 3 and 4 at US-NC1, and (ii) storm-related episodes of snag fall-over, which increased the CWD present in 2007 and 2008 over the preceding years at US-NC2. The cumulative loss of CWD was about 2020 g C m^{-2} , most of it in the first 4 years beyond which the CWD inputs and losses were balanced. The integrated R_{CWD} over the first 4 years was estimated at 781 and 668 g C m^{-2} from the mass loss and flux upscaling approach, respectively (Fig. 2b).

Autotrophic respiration and partitioning ER

The two data-based estimates of autotrophic respiration were consistent with the residual estimate. As hypothesized, the methods diverged more in the young than the mid-rotation stand. While $R_{\text{A-BL}}$ increased with age in the young stand similar to R_{A1} and R_{A2} (Eqns 3a and b), it was about 40% higher (Fig. 3). The interannual variability was greater using the biometric estimate (R_{A1}), possibly due to temporal lags between assimilation and growth, and interannual variability in allocation to storage and root growth.

Heterotrophic soil respiration was estimated as the residual (Eqn 3c) and could be used to assess the

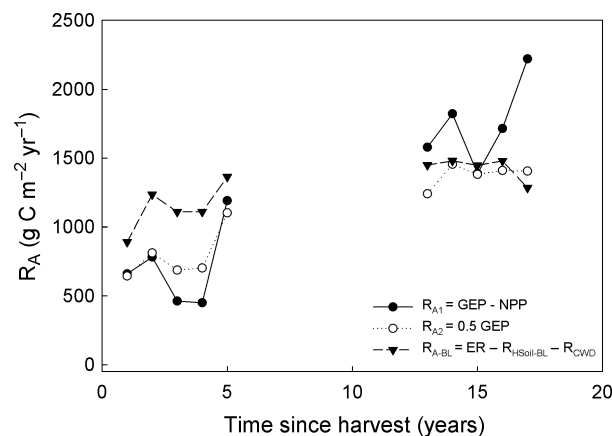


Fig. 3 Alternative estimates of autotrophic respiration (R_{A}) in two loblolly pine stands. Years 1–5 come from US-NC1, years 13–17 from US-NC2.

internal consistency of the partitioning methods. However, unlike in comparisons of R_{CWD} with CWD mass loss data, for partitioning ER R_{CWD} is the observed CO_2 production rate, not adjusted for microbial C use and fragmentation. Given that the biometric and statistical estimates of R_{HSoil} are independent of SR measurements, their ratio offers an assessment of internal consistency. As a 5 year average, the two data-based estimates of R_{HSoil} did not differ from the estimate of the global model ($R_{HSoil-BL}$), and were about 50% of SR (Fig. 4). However, in the early rotation stand, both data-based estimates of R_{HSoil} diverged significantly from the global model and while they were consistent in 3 years out of the 5 year observation period, during severe droughts, the biometric estimates exceed SR, implying internal inconsistency. However, the temporal dynamic was very similar with the statistical method. Overall, even by the 5th year of measurements, the heterotrophic component of soil CO_2 efflux remained higher in the early-rotation than the mid-rotation stand, whereas the CWD pool aboveground had declined to the level seen in the mid-rotation stand (Fig. 5).

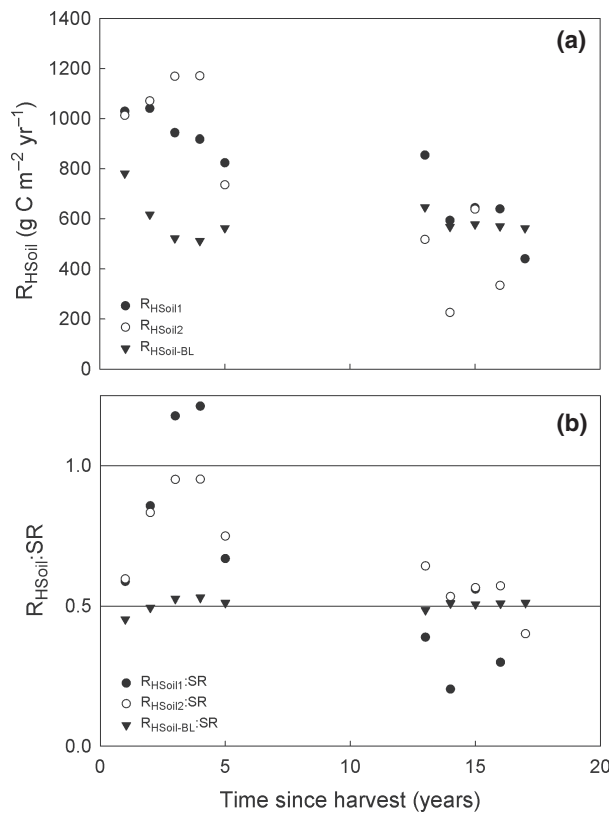


Fig. 4 Belowground heterotrophic respiration (R_{HSoil} ; see Eqn 3a–c) from three different approaches and its ratio to total soil respiration (SR) in two loblolly pine stands. Years 1–5 come from US-NC1, years 13–17 from US-NC2.

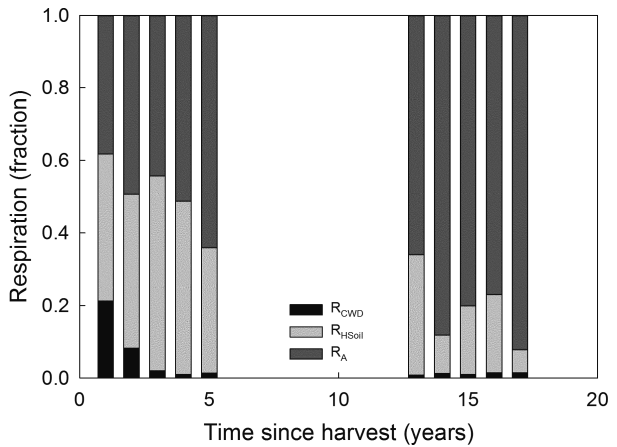


Fig. 5 Partitioning of total ecosystem respiration in two loblolly pine plantations. Years 1–5 come from US-NC1, years 13–17 from US-NC2. R_A is the average of biometric and global estimates (R_{A1} and R_{A2} , see Methods), R_{HSoil} is estimated as the residual.

Given the different pool sizes after the harvest of mixed hardwood and loblolly pine stands, it is possible that R_{Htotal} ($R_{HSoil} + R_{CWD}$) would have been slightly higher than observed here, had the early rotation site been established as a second rotation of pine. On one hand, there would have been more logging slash and root biomass (Table 1). Conversely, CWD and R_{CWD} would probably have been lower, but over the rotation cycle, its contribution to ecosystem C balance was small compared with R_{Htotal} . Although we re-checked the allometric equations for different ages of loblolly pine and are confident about the productivity estimates of different pools, we are less sure about harvest removal, and other related changes.

CWD production and BGA

New CWD production occurred only in the mid-rotation stand US-NC2, whereas in the early rotation stand, CWD production was zero. Even when trees died, their size was well below the CWD threshold. At US-NC2, CWD production was highly variable among plots and years, with the mean annual tree death rates ranging 0–2.3%, and the fall-over rate of snags ranging 0–63%. Given the proportionality of this estimate to standing biomass and the aggrading nature of the stand, the 5 year mean CWD production rate was estimated at 7–12 $g C m^{-2} yr^{-1}$ based on the snag production and fall-over rates, and about 30 $g m^{-2} yr^{-1}$ based on consecutive CWD surveys.

CWD production at the time of harvest is difficult to constrain accurately, partly because of the non-biological processes involved, as well as because of

associated disturbances of remaining pools. Based on biometric estimates of various pool sizes in (i) loblolly pine plantation at harvest age, and (ii) a mixed bottomland hardwood forest similar to what was at US-NC1 prior to planting, we estimated that aboveground woody harvest residue was 2970 or 1350 g C m⁻², respectively, and the total dead organic matter produced in a harvest was 6000 or 3950 g C m⁻², respectively (Table 1). Given the estimated slash in the harvest-age forests, the estimated CWD pool of 2390–2850 g C m⁻² immediately following the harvest may be an overestimate as it should be smaller than the slash pool. However, it is also possible that a smaller fraction than the assumed 87% of stemwood was removed from the site.

Discussion

Uncertainties

This study was an attempt to evaluate rotation cycle carbon balance using an unreplicated pair of loblolly pine stands. As such, it is vulnerable to the weaknesses typically associated with chronosequence studies, including site matching, representativeness, and changes in environmental conditions and management practices over time (Yanai *et al.*, 2003; Howard *et al.*, 2004). It has been suggested that matching sites by site index would ameliorate some of the problems (Peichl *et al.*, 2010). In the current study, the early-rotation site US-NC1 had a higher site index than the mid-rotation site US-NC2 (88 and 66, respectively). As a result, the combination of sites as in this study may represent net ecosystem carbon balance intermediate to those with internally consistent site indices as the rate of recovery may currently have been overestimated, whereas the fluxes at later stages may have been underestimated. It remains unclear whether the difference in site indices is primarily due to soil properties, the 25 ppm increase in atmospheric CO₂ between the two harvests, or the fact that the two sites have been under intensive silvicultural management for different period of time (see Methods). Other factors that may not necessarily have contributed to the site mismatch, but nevertheless were poorly constrained or unquantified, include other C transformation pathways (leaching, CH₄, and VOC emissions), the amount and decomposition dynamics of fine logging slash, and photodegradation. However, these fluxes are assumed to be minor in their contribution to total site C balance, and insignificant across the rotation cycle. On the other hand, even though the decomposition of fine woody debris may be faster than that of CWD (Mattson *et al.*, 1987; Chambers *et al.*, 2000) and it may not contribute to rotation cycle C balance, it may play a role

by priming soil C mineralization (Smolander *et al.*, 2010). Although the difference between the mass loss and flux upscaling estimates of R_{CWD} was smaller than the expected uncertainty of either method, the fact that upscaled chamber fluxes were consistently lower than CWD mass loss could also be attributable to three methodological biases. First, CO₂ emissions from the ends of decaying CWD exceed the lateral flux rates because of lower resistance to diffusion alongside the xylem vessels than across them (Forrester & Mladenoff, personal communication). As we measured R_{CWD} in the traditional way, with collars mounted on the upward facing side of the fallen logs, an underestimate is possible. Second, it is also possible that our sampling, which was restricted to decay classes two and three, was biased for not including the more advanced decay classes four and five. This could have been exaggerated by presumably greater fragmentation of these decay classes. And finally, it is possible that fragmentation may have been greater than the assumed equivalence with mineralization as the CWD was disturbed during the harvest and subsequent site preparation. The importance of photodegradation in the current study was discounted on account of reports of it being limited in mesic environments (Smith *et al.*, 2010). Yet, if it did occur, photodegradation would have inflated the decomposition rates of highly lignified tissues more (CWD, Austin & Ballare, 2010) and inflated R_{CWD} estimates in the first few years following the harvest. The rotation cycle carbon balance is also affected by assumptions made in extrapolations of various pool sizes to the time of harvest. We used linear extrapolation of all major biomass pools, based on the consistent trends across both stands (Table 1). This may be counter-intuitive, as there are limits to leaf area and fine root biomass, but given the observed trends, saturation points could not be detected. In case the leaf and fine roots pools and respective detritus inputs at harvest are overestimated, the extent of soil C loss would be underestimated.

Nevertheless, as the different independent estimates of forest rotation cycle C balance are consistent with one another, and the respiration budget was closed to within 10 ± 5%, we conclude that the main conclusions drawn in this study are robust. Yet, C transformations in the early years of recovery from stand-replacing disturbance need to be better constrained, particularly as they have disproportionate influence on long-term C balance of the stand.

Biomass

The biomass pools and estimates of NPP at US-NC2 reported here are slightly smaller than reported

previously (Noormets *et al.*, 2010), mainly because of adjustments in biomass C content (49 vs. 53%; see Methods). In addition, we re-checked the carbon content of hardwood species, and switched from hardwood allometric equations based on diameter at breast height (DBH) and height to those based only on DBH. Combined, these changes resulted in increased biomass estimates for American holly (*Ilex opaca*) and lower estimates for red maple (*Acer rubrum*), compared with initial estimates. However, most of the changes in total above- and belowground biomass pools were attributable to pine biomass, because of the overwhelming predominance of this species over hardwoods.

The sizes of the major biomass pools at the two sites exhibited roughly linear increase with time except for the first 2 years at US-NC1 (Table 1). We used this linearity to estimate the sizes of these major pools by extending the observed growth rate at the mid-rotation stand out to 25 years, finding that the total standing biomass at that age might be about 154 t C ha^{-1} (Table 1). However, if we consider the vegetation that was at US-NC1 prior to this planting (i.e. mixed bottomland hardwood forest), the estimated standing biomass at maturity was 52.9 t C ha^{-1} , based on assessment from a nearby stand with similar site characteristics. The harvest residue generated by clearcutting each of these forests would be 58 or 33 t C ha^{-1} , respectively, with 62 and 75% of it belowground. The estimates of postharvest CWD of $23.9\text{--}28.5 \text{ t ha}^{-1}$ are closer to the expected residue from the bottomland hardwood harvest. With fine logging residue that was not quantified, and the large uncertainties about CWD estimates (discussed below), we can consider these estimates consistent with one another.

A large proportion (approximately 10–15%) of total ecosystem carbon is in the forest floor (Table 1), and the harvest-related dynamics of this pool may alter carbon transfer from aboveground to belowground pools. A classic study by Covington (1981) indicated a 50% decline of forest floor over a 20 year period following harvest. Although some hypotheses have been put forward that might explain the long-lasting impact of harvesting (Aber *et al.*, 1982), the generality of this finding has later been called into question because subsequent studies have not observed comparable trends, nor have models been able to explain such a pattern (Yanai *et al.*, 2003). However, some loss of forest floor is expected, probably enhanced by the mixing of forest floor with mineral soil (Yanai *et al.*, 2003). In this study, forest floor was not quantified during the early years following the harvest because of the severe disturbance, where mixing of slash with mineral soil and subsequent bedding destroyed a clearly defined forest floor. In year 7 after the harvest, new forest floor had formed

and was slightly more than half of that in the mid-rotation stand. Assuming litter additions and turnover rates similar to the mid-rotation stand, the 7 year time-point fit on the same trend-line that characterizes the change in that stand, consistent with earlier observations of constant rate of forest floor accumulation (Gholz & Fisher, 1982). For integrated rotation cycle carbon balance, the dynamics of forest floor *per se* are not important if it recovers, but the effect that this disturbance has on mineral soil carbon cycling and new carbon transfer from above- to belowground pools could be important. For example, microbial biomass and activity have been reported to increase proportionally with slash addition (Tisdale, 2008).

Fluxes

The carbon fluxes at the two plantations were large, with NEE ranging from $+840$ to $-1200 \text{ g C m}^{-2} \text{ yr}^{-1}$ at different stages of the rotation cycle. The integrated CO_2 exchange over 25 year rotation cycle (area under the dashed curve on Fig. 1a) is projected to be about 126 t C ha^{-1} . Although we did not measure ecosystem fluxes in the mixed bottomland hardwood forest, the mean tree age (about 70 years) and total standing biomass (Table 1) suggest that the NPP of this forest must be about fivefold lower. With an 87% stemwood removal rate for pines (Clark *et al.*, 2004) and 54% AG biomass removal rate for hardwoods (Gower *et al.*, 2006), the postharvest slash at the site is estimated at 57.6 and 43.2 t C ha^{-1} , respectively.

It took about 4.5 years to become a net sink of C (without a severe drought that occurred in 2007–2008, it may have been as fast as 3.5 years, Fig. 1a), and about 9.5 years for the plantation to regain C lost in the harvest-related disturbance. While the removal and subsequent recovery of leaf area after harvest resulted in proportional change in GEP, there was practically no change in ER (Fig. 1b). Yet, the contribution of different components changed significantly (Figs 1–5) as discussed below. Overall, the dynamics and mechanisms of flux recovery were strongly affected by the rapid colonization of the site by annuals and shrubs, consistent with Takagi *et al.* (2009).

The large year-to-year changes at each site were in part attributable to the aggrading canopy in the young stand but also to large extremes in precipitation (Domec *et al.*, 2010; Noormets *et al.*, 2010). The effect of the 100 year drought in 2007–2008 (Noormets *et al.*, 2010) affected both GEP and ER, but was more pronounced on GEP. We did observe the hypothesized increase in R_{H} , both in above- and below-ground, but contrary to our hypothesis, this increase was roughly in balance with the decline in R_{A} , similar to the report of

Toland & Zak (1994). This is likely attributable to the rather high R_A at our mid-rotation stand (about 70%; Fig. 5), all the more so on the organic soils (Subke *et al.*, 2006). However, given the relatively high fine root length density and deep profile (Domec *et al.*, 2012a), the observed breakdown of SR is not unreasonable. The total increase in SR was short-lived compared with earlier studies where higher postharvest SR was reported (Gordon *et al.*, 1987; Idol *et al.*, 2000; Noormets *et al.*, 2006, 2007), with only the first 2 years exhibiting higher emissions.

CWD dynamics

Changes in the CWD pool and turnover represent a key effect of harvest, yet both inputs to and outputs from this pool remain poorly quantified in relation to other fluxes. In the current study, the CWD pool seemed to be in steady state between ages 5 and 20 years, at about 300–400 g C m⁻² (Table 1). Mean CWD production rate in the mid-rotation stand, estimated from snag production and fallover rate, was 21.3 ± 7.0 g C m⁻² yr⁻¹ (mean \pm SD). This is similar to the mean of 0.4 t DW ha⁻¹ yr⁻¹ reported for 20 year old stands at Hubbard Brook Ecosystem Study (Tritton, 1980; as cited by Harmon *et al.*, 1986), but about 5- to 20-fold lower than in mature natural forest stands of the Pacific Northwest (Sollins, 1982; Harmon *et al.*, 1986; Spies *et al.*, 1988), Northeast USA (Siccama *et al.*, 2007), slash pine in Florida (Clark *et al.*, 2004), and mixed hardwood stand at Coweeta Hydrologic Laboratory in North Carolina (Mattson *et al.*, 1987). This difference between the sites in this study and those previously reported could, in part, be due to the vigorous growth, low tree density and low mortality in the mid-rotation stand. Dead trees contributed only about 12% of all CWD inputs (ranging from 0 to 33%), compared to 61% in the old-growth sites in Pacific Northwest (Harmon *et al.*, 1986). However, the proportion of CWD and litterfall in total dead organic matter production was similar in the current study and that reported in literature (e.g., Sollins, 1982; Harmon & Hua, 1991), about 5–20%. It is important to note, however, that the interannual variation of CWD production from both snag fallover and branchfall was very high (5 year CV = 145%) and associated with storms.

Mean R_{CWD} (including both mineralization and fragmentation) was estimated at 41.5 ± 13.4 g C m⁻² yr⁻¹ (mean \pm SD) at age 3 and 4, and 18.8 ± 5.2 g C m⁻² yr⁻¹ for years 13–19 (overall 26.3 ± 13.8 g C m⁻² yr⁻¹). Even though R_{CWD} was 5- to 10-fold higher than the baseline in the first 2 years following the harvest, it was still less than half of the heterotrophic contribution from soil (Figs 2b and 4a). The base rate of R_{CWD} was similar to that reported for jack pine stands

in Canada (Howard *et al.*, 2004), higher than in black spruce forest (Hagemann *et al.*, 2010), but lower than in a mixed hardwood forest at Coweeta Hydrologic Laboratory (Mattson *et al.*, 1987), which is climatically most similar to the current study. While the CWD pool and its decomposition rate were lower than those in many natural old-growth forests (references above), the decay constant ($k = 0.06$) was similar to those reported for a range of species (Harmon *et al.*, 1986; Mattson *et al.*, 1987; $k = 0.015 \dots 0.26$), and in line with the global model based on mean annual temperature developed by Chambers *et al.* (2000). The similarity of inputs to and losses from the CWD pool (18.8 vs. 21.3 g C m⁻² yr⁻¹) suggests that at least in mass terms, CWD is not a big contributor to soil C pools. It is unknown whether branchfall, which was threefold greater than CWD input, contributed more or less to the soil C pool. Given that the ratio of fragmentation to mineralization is greater in fine woody debris than in CWD (Mattson *et al.*, 1987; Chambers *et al.*, 2000), the proportion of the material stabilized and incorporated into soil C pools may also differ from CWD.

As the chamber-based R_{CWD} measurements were conducted primarily in 2007 and 2008, the two driest years of the measurement period, a question arises whether the same upscaling relationships with temperature and moisture would apply in other years. It is broadly recognized that moisture, ground contact, and colonization by fungi are key factors affecting CWD decomposition (Mattson *et al.*, 1987; Yanai *et al.*, 2003; Hagemann *et al.*, 2010). However, we did not see any evidence of clear moisture response, which lends more confidence in the upscaled annual values. Furthermore, the mass loss data are consistent with the chamber estimates (Fig. 2b). Yet, despite our best attempts to independently estimate R_{CWD} , several of the assumptions that were made in the upscaling remain untested. These include the rate of fragmentation, microbial C use efficiency, sampling bias (see Methods), the amount of logging residue generated during harvest, the amount of slash mixed into soil, and a potential lag between harvest and start of fragmentation. Although the exact R_{CWD} in the first year is uncertain, the independent estimates based on mass loss and on upscaled fluxes are consistent with one another, suggesting that R_{CWD} was higher in the first than in subsequent years, and that the assumptions made were broadly plausible (including the assumption of no lag before the start of decomposition).

Partitioning respiration

Given the several conservative relationships between ecosystem fluxes, like R_A : GEP (Waring *et al.*, 1998)

and R_H :SR (Bond-Lamberty *et al.*, 2004), there are multiple ways of attempting to partition ER short of measuring all components directly. Each approach is associated with its own assumptions and uncertainties. In the current study, we reasoned that harvesting is more likely to offset the proportionality between R_{Hsoil} and SR than the R_A and GEP. Nevertheless, the biometric and allometric estimates of R_A (see Methods) were not identical. They were more consistent in the mid- than early-rotation stand, implying that the assumptions made about allocation patterns were more closely followed in the former. Their differences are attributable to buffering effects from storage and belowground allocation. As biometric NPP estimates are blind to interannual differences in belowground allocation, the use of stored carbohydrates from the previous year for current year growth may contribute to partial decoupling between assimilation and productivity (Barford *et al.*, 2001; Gough *et al.*, 2008b). In conifers, the decoupling may be even greater due to the multi-year lifespan of leaves, which could introduce even longer and multilayered lag effects. Furthermore, the R_{A1} :GEP ratio did exhibit a significant increase with age (R_{A1} :GEP = $0.39 + 0.016Age$). Yet, the interannual differences in the three R_A estimates were similar, suggesting that the environmental factors affected most ecosystem carbon fluxes, from GEP to R_H . The mean R_{A1} :GEP ratio in the mid-rotation stand was 0.63 ± 0.1 , higher than the global mean of 0.5 used in R_{A2} (Eqn 3b), and also higher than our earlier estimate of 0.55 ± 0.03 , based on $R_A = ER - 0.5SR$ (Noormets *et al.*, 2010).

The last step of partitioning ER involves estimating R_{Hsoil} as the residual term. Figure 4a shows that R_{Hsoil} in the early rotation stand had increased by about $2/3$ over the baseline levels in the mid-rotation stand. The flux- and productivity-based estimates differed during the dry years of 2007 and 2008, probably due to the drought-related changes in allocation (including growth:storage ratio) patterns, but overall, both showed a more gradual decline in R_{Hsoil} than was observed in R_{CWD} (Figs 2b and 4a). This could be attributed to the gradual dying of coarse roots, which could well take multiple years, especially in root-sprouting species (in current study, root sprouting contributed minimally to the returning ground cover). As the disturbance-related transient respiration pulses are very poorly understood, this is a significant distinction. Although the different sensitivity of decomposition of different C pools to environmental drivers is well recognized (e.g., Toland & Zak, 1994), above- and belowground R_H are typically still treated as a homogeneous component (summarized by Pregitzer & Euskirchen, 2004). As the information is accumulating about different temporal dynamics

and environmental sensitivities of various processes, decomposition models can increasingly take advantage of it, although challenges remain about collecting the relevant field data.

As mentioned, the stimulation of R_{Hsoil} by harvest is reported with regularity in individual chronosequence studies; most synthesis and meta-analysis studies fail to detect a consistent effect (Johnson & Curtis, 2001; Yanai *et al.*, 2003; Subke *et al.*, 2006; Amiro *et al.*, 2010). Furthermore, in some studies, the effect may have been obscured by possible site mismatch in the chronosequence (e.g., Law *et al.*, 2003). In addition to sites where reductions in R_A completely offset any increases in R_{Hsoil} , it is possible that variable recovery time confounds the signal in regional analyses (Piao *et al.*, 2010). Given the brevity of the respiration spike on one hand and the possible lag after harvest on the other, it is possible that such transient events get lost either in the timing of measurements or in the averaging protocols of meta-analyses when different developmental stages are averaged together. Yet, as both stimulation and no stimulation of SR have been reported from different latitudes and soil types, no ready explanation associated with climatic or priming differences seems apparent. We hypothesized that if the input of harvest residue serves as a priming agent (Kuzuyakov *et al.*, 2000), the increase in R_{Hsoil} should be more pronounced in organic soils or in environments favoring rapid decomposition. However, the current evidence of spatial patterns of stimulation does not bear it out.

The ratio of R_{Hsoil} to SR in the mid-rotation stand (0.33 ± 0.14) was similar to that reported for other pines (Ewel *et al.*, 1987; Ryan *et al.*, 1996; Schäfer *et al.*, 2003), but significantly higher (0.64 ± 0.17) and very dynamic in the early-rotation stand (Fig. 4b). While R_{Hsoil} decreased in absolute magnitude, its portion of SR peaked in years 3 and 4 (a 100 year drought in 2007–2008, Noormets *et al.*, 2010), suggesting contrasting sensitivity to drought between R_A and R_{Hsoil} . While the complete discussion of the drivers of interannual differences is beyond the scope of the current study, this difference between R_A and R_{Hsoil} dynamics is pronounced. The heterotrophic respiration ($R_{Htotal} = R_{Hsoil} + R_{CWD}$) fraction of ER was significantly lower in the current study than the average estimated for disturbed forests in general (Amiro *et al.*, 2010; 60% vs. 90%; Fig. 5).

Long-term carbon sequestration

Extrapolating NEE out to 25 years and integrating the area under the curve, we estimate that about 12,525 g C m⁻² would be sequestered over the 25 year rotation cycle (Fig. 1). Upon subtracting the amount of

stemwood that would likely be harvested from the stand (8895 g C m^{-2}), the input to the ecosystem would be 3630 g C m^{-2} , which would partly decay over the subsequent rotation cycle and partly contribute to the replenishment of soil C. Although we do not know which plant C pools are preferentially incorporated to soil pool, it is intuitive that root carbon buried deeper in the soil may take longer to mineralize than surface litter. Yet, the literature on coarse root decomposition suggests that this pool has decay rates similar to aboveground CWD, with decay constants of about 0.13–0.16 (King *et al.*, 1997; Ludovici *et al.*, 2002; Miller *et al.*, 2006; Garrett *et al.*, 2008). This is consistent with our calculations based on estimated belowground biomass and observed SR. Thus, by the end of the 25 year rotation cycle, over 96% of coarse roots would have decayed, and only 100–200 g C m^{-2} might remain of all harvest residue. Whether this, indeed, enters the long-term soil C pool is unclear. On annual basis, the losses of C from soil (R_{HSoil}) exceeded inputs (total belowground allocation, BGA) by $95 \pm 155 \text{ g C m}^{-2} \text{ yr}^{-1}$ (mean \pm SD; see also Noormets *et al.*, 2010) in the mid-rotation stage (years 13–17), and by 380–800 $\text{g C m}^{-2} \text{ yr}^{-1}$ in the first 5 years following the harvest (Fig. 6). The rotation cycle average soil C deficit was estimated at 124–267 $\text{g C m}^{-2} \text{ yr}^{-1}$, depending on the R_A estimates used. With as big annual deficits as the estimated 25 year surplus (and it being positive by definition, given the exponential decay function used), it is unclear if soil C pool may be growing or shrinking. Even if soil C losses are offset by the input of harvest residue, maintaining the SR at observed levels requires that soil

C be part of the cycle. We estimate that about 5.5% of the soil C pool of about 41.4 kg C m^{-2} (top 1 m) would have to mineralize over the 25 year rotation cycle, given the observed ER and SR. Although we do not know the exact origin of respired C, our conclusion fits the observation of Diochon *et al.* (2009), that harvesting can trigger the loss of deep soil C.

It is evident that replenishing soil C pool is critically dependent on the pulse of dead carbon inputs at harvest time. Furthermore, as the aboveground harvest residue disappears in only a few years, the inputs must be proportionally larger from dead roots. However, much about the decomposition dynamics of coarse roots remains unknown. For example, in contrast with the similar decay constants reported in the previous paragraph, Ludovici *et al.* (2002) found that coarse roots may persist for decades, possibly by staying alive well past the harvest of the aboveground part. Given that they also observed faster decay of dried than fresh roots (Ludovici & Kress, 2006), it is possible that the experimentally determined decay constants (based on dried samples) may be biased high.

Our current study suggests that there is a fine balance between the soil C pool and harvest residue, which determines the long-term site C balance. In this light, recent efforts to convert harvest residue to bioenergy production or other 'green' purposes are likely to accelerate the decline of old soil C and may undermine the sustainability of site productivity. As the area of loblolly pine plantations is projected to expand rapidly over the next 15 years (Zhang & Polyakov, 2010), the implications on soil C resources may be significant. While we need to be cautious when extrapolating our findings to other areas, because the drained peat soils at our study site may be more vulnerable to decomposition than most, the potential sensitivity of soil and detritus C stocks to additional harvest removals was also highlighted in the recent modeling study using Fluxnet-Canada data (Grant *et al.*, 2010). At all sites, long-term exports must be kept in balance with inputs. While specific recommendations have been made to increase soil C sequestration in forests through targeted management practices (Jandl *et al.*, 2007), they may not always be compatible with the timber production mission of intensive forestry. For example, maintaining high productivity in a mixed species stand while minimizing disturbance and extending rotation length seems difficult to accomplish in a single stand.

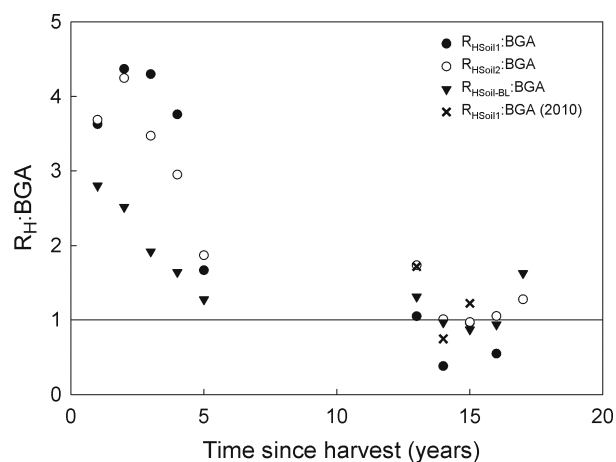


Fig. 6 The ratio of annual soil carbon losses (R_{HSoil}) to inputs (BGA) in two loblolly pine plantations. Years 1–5 come from US-NC1, years 13–17 from US-NC2. BGA includes leaf, fine and coarse root production and branchfall. Crosses represent values based on earlier NPP estimates (Noormets *et al.*, 2010) using higher biomass carbon content.

Acknowledgements

This work was supported primarily by USDA FS EFETAC cooperative agreements 03-CA-11330147-073 and 04-CA-11330147-238, and partly by DOE-NICCR award 08-SC-NICCR-1072, DOI

Southeast Climate Science Center award G10AC00624, DOE-TES award 11-DE-SC-0006700 and USDA NIFA award 2011-68002-30185. Johnny Boggs and Emrys Treasure helped with field data collection, and Chris Maier offered helpful insight into CWD and harvest residue decay dynamics. The work was conducted on the lands of Weyerhaeuser Corporation, which provided generous logistical support. In particular, we appreciate the help of Dr. Jami Nettles, Cliff Tyson, Joe Bergman, and Dr. Robert Campbell.

References

- Aber JD, Melillo JM, Federer CA (1982) Predicting the effects of rotation length, harvest intensity, and fertilization on fiber yield from northern hardwood forests in New England. *Forest Science*, **28**, 31–45.
- Allen HL, Campbell RG (1988) Wet site pine management in the southeastern United States. In: *Management, use, and Value of Wetlands. The Ecology and Management of Wetlands*, Vol 2, (eds Hook DD, Mckee WH Jr, Smith HK, Gregory J, Burrell VG Jr, Devoe MR, Sojka RE, Gilbert S, Banks R, Stolzy LH, Brooks C, Matthews TE, Shear TH), pp. 173–184. Timber Press, Portland, OR.
- Allen HL, Dougherty PM, Campbell RG (1990) Manipulation of water and nutrients — practice and opportunity in Southern U.S. pine forests. *Forest Ecology and Management*, **30**, 437–453.
- Amiro BD, Barr AG, Barr JG *et al.* (2010) Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research G. Biogeosciences*, **115**, G00K02, doi: 10.1029/2010JG001390.
- Austin AT, Ballare CL (2010) Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of The National Academy of Sciences of The United States of America*, **107**, 4618–4622.
- Barford CC, Wofsy SC, Goulden ML *et al.* (2001) Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Science*, **294**, 1688–1691.
- Birdsey RA (1992) *Carbon Storage and Accumulation in United States Forest Ecosystems*. GTR-WO-59. USDA Forest Service, Washington DC.
- Bond-Lamberty B, Wang C, Gower ST (2004) A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology*, **10**, 1756–1766.
- Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.
- Clark A, Phillips DR, Frederick DJ (1985) *Weight, Volume, and Physical Properties of Major Hardwood Species in the Gulf and Atlantic Coastal Plains*. Research Paper SE-250. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Clark KL, Gholz HL, Castro MS (2004) Carbon dynamics along a chronosequence of slash pine plantations in north Florida. *Ecological Applications*, **14**, 1154–1171.
- Covington WW (1981) Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology*, **62**, 41–48.
- DeLucia EH, Drake JE, Thomas RB, Gonzalez-Meler M (2007) Forest carbon use efficiency: is respiration a constant fraction of gross primary production? *Global Change Biology*, **13**, 1157–1167.
- Desai AR, Noormets A, Bolstad PV *et al.* (2008) Influence of vegetation and seasonal forcing on carbon dioxide fluxes across the Upper Midwest, USA: implications for regional scaling. *Agricultural and Forest Meteorology*, **148**, 288–308.
- Diochon A, Kellman L, Beltrami H (2009) Looking deeper: an investigation of soil carbon losses following harvesting from a managed northeastern red spruce (*Picea rubens* Sarg.) forest chronosequence. *Forest Ecology and Management*, **257**, 413–420.
- Domec JC, King JS, Noormets A, Treasure EA, Gavazzi MJ, Sun G, McNulty SG (2010) Hydraulic redistribution of soil water affects whole stand evapotranspiration and net ecosystem carbon exchange. *New Phytologist*, **187**, 171–183.
- Domec JC, Ogee J, Noormets A *et al.* (2012a) Interactive effects of nocturnal transpiration and climate change on the root hydraulic redistribution and carbon and water budgets of Southern United States pine plantations. *Tree Physiology*, **32**, 707–723.
- Domec JC, Sun G, Noormets A *et al.* (2012b) Water flux components and their responses to drought in two intensively managed coastal plain loblolly pine forests: method comparisons. *Forest Science*, In press.
- Edwards NT, Ross-Todd BM (1983) Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residue removal. *Soil Science Society of America Journal*, **47**, 1014–1021.
- Epron D, Nouvellon Y, Deleporte P *et al.* (2006) Soil carbon balance in a clonal *Eucalyptus* plantation in Congo: effects of logging on carbon inputs and soil CO₂ efflux. *Global Change Biology*, **12**, 1021–1031.
- Ewel KC, Cropper WP, Gholz HL (1987) Soil Co₂ evolution in Florida slash pine plantations. 2. Importance of root respiration. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **17**, 330–333.
- FAO (2009) *State of the World's Forests 2009*. Food and Agriculture Organization of the United Nations, Rome.
- FAO (2010) *Global Forest Resources Assessment 2010: Progress Towards Sustainable Forest Management*. Food and Agriculture Organization of the United Nations, Rome.
- FIA (2007) *Phase 3 Field Guide – Down Woody Materials, Version 4.0*. (ed Service UF) USDA Forest Service, Arlington, VA.
- Flowers WR (1978) *Individual Tree Weight and Volume Equations for Site Prepared Loblolly Pine Plantations in the Coastal Plain of the Carolinas, Georgia, and North Florida*. Master of Science, University of Georgia, Athens.
- Garrett LG, Oliver GR, Pearce SH, Davis MR (2008) Decomposition of *Pinus radiata* coarse woody debris in New Zealand. *Forest Ecology and Management*, **255**, 3839–3845.
- Gholz HL, Fisher RF (1982) Organic-matter production and distribution in slash pine (*Pinus Elliottii*) plantations. *Ecology*, **63**, 1827–1839.
- Gordon AM, Schlentner RE, Cleve KV (1987) Seasonal patterns of soil respiration and CO₂ evolution following harvesting in the white spruce forests of interior Alaska. *Canadian Journal of Forest Research*, **17**, 304–310.
- Gough CM, Vogel CS, Schmid HP, Curtis PS (2008a) Controls on annual forest carbon storage: lessons from the past and predictions for the future. *BioScience*, **58**, 609–622.
- Gough CM, Vogel CS, Schmid HP, Su HB, Curtis PS (2008b) Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agricultural and Forest Meteorology*, **148**, 158–170.
- Gower ST, Mckeon-Ruediger A, Reitter A *et al.* (2006) *Following the Paper Trail. The Impact of Magazine and Dimensional Lumber Production on Greenhouse gas Emissions: A Case Study*. The Heinz Center, Washington, DC.
- Grant RF, Barr AG, Black TA, Margolis HA, Mccaughy JH, Trofymow JA (2010) Net ecosystem productivity of temperate and boreal forests after clearcutting—a Fluxnet-Canada measurement and modelling synthesis. *Tellus Series B-Chemical and Physical Meteorology*, **62**, 475–496.
- Hagemann U, Moroni MT, Gleissner J, Makeschin F (2010) Disturbance history influences downed woody debris and soil respiration. *Forest Ecology and Management*, **260**, 1762–1772.
- Harmon ME, Hua C (1991) Coarse woody debris dynamics in 2 old-growth ecosystems - comparing a deciduous forest in China and a conifer forest in Oregon. *BioScience*, **41**, 604–610.
- Harmon ME, Franklin JF, Swanson FJ *et al.* (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**, 133–302.
- Howard EA, Gower ST, Foley JT, Kucharik CJ (2004) Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. *Global Change Biology*, **10**, 1267–1284.
- Idol TW, Pope PE, Ponder F (2000) Fine root dynamics across a chronosequence of upland temperate deciduous forests. *Forest Ecology and Management*, **127**, 153–167.
- Ingerson A (2009) *Wood Products and Carbon Storage: Can Increased Production Help Solve the Climate Crisis?* The Wilderness Society, Washington, DC.
- Jandl R, Lindner M, Vesterdal L *et al.* (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma*, **137**, 253–268.
- Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management*, **140**, 227–238.
- King JS, Allen HL, Dougherty P, Strain BR (1997) Decomposition of roots in loblolly pine: effects of nutrient and water availability and root size class on mass loss and nutrient dynamics. *Plant and Soil*, **195**, 171–184.
- King JS, Albaugh TJ, Allen HL, Kress LW (1999) Stand-level allometry in *Pinus taeda* as affected by irrigation and fertilization. *Tree Physiology*, **19**, 769–778.
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biology & Biochemistry*, **32**, 1485–1498.
- Law BE, Sun OJ, Campbell J, Van Tuyl S, Thornton PE (2003) Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biology*, **9**, 510–524.
- Ludovici KH, Kress LW (2006) Decomposition and nutrient release from fresh and dried pine roots under two fertilizer regimes. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **36**, 105–111.
- Ludovici KH, Zarnoch SJ, Richter DD (2002) Modeling in-situ pine root decomposition using data from a 60-year chronosequence. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **32**, 1675–1684.

- Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–850.
- Mallik AU, Hu D (1997) Soil respiration following site preparation treatments in boreal mixedwood forest. *Forest Ecology and Management*, **97**, 265–275.
- Matamala R, Jastrow JD, Miller RM, Garten CT (2008) Temporal changes in C and N stocks of restored prairie: implications for C sequestration strategies. *Ecological Applications*, **18**, 1470–1488.
- Mattson KG, Swank WT, Waide JB (1987) Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **17**, 712–721.
- Miller AT, Allen HL, Maier CA (2006) Quantifying the coarse-root biomass of intensively managed loblolly pine plantations. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **36**, 12–22.
- Moroni MT, Carter PQ, Strickland DW, Makeshin F, Parkinson DR, Kahnt L (2007) Effect of forest harvesting biomass and respiration in and slash piling on microbial Newfoundland boreal forests. *Canadian Journal of Soil Science*, **87**, 455–458.
- Moroni MT, Carter PQ, Ryan Daj (2009) Harvesting and slash piling affect soil respiration, soil temperature, and soil moisture regimes in Newfoundland boreal forests. *Canadian Journal of Soil Science*, **89**, 343–355.
- Ngao J, Epron D, Brechet C, Granier A (2005) Estimating the contribution of leaf litter decomposition to soil CO₂ efflux in a beech forest using ¹³C-depleted litter. *Global Change Biology*, **11**, 1768–1776.
- Noormets A, Ewers BE, Sun G, Mackay DS, Zheng D, McNulty SG, Chen J (2006) Water and carbon cycles in heterogeneous landscapes: an ecosystem perspective. In: *Ecology of Hierarchical Landscapes: From Theory to Application*, (eds Chen J, Saunders SC, Brosowski KD, Crow TR), pp. 89–123. Nova Publishers, New York.
- Noormets A, Chen J, Crow TR (2007) Age-dependent changes in ecosystem carbon fluxes in managed forests in northern Wisconsin, USA. *Ecosystems*, **10**, 187–203.
- Noormets A, Gavazzi MJ, McNulty SG, Domec JC, Sun G, King J, Chen J (2010) Response of carbon fluxes to drought in a coastal plain loblolly pine forest. *Global Change Biology*, **16**, 272–287.
- O'hehir JF, Nambiar EKS (2010) Productivity of three successive rotations of *P. radiata* plantations in South Australia over a century. *Forest Ecology and Management*, **259**, 1857–1869.
- Peichl M, Arain MA, Brodeur JJ (2010) Age effects on carbon fluxes in temperate pine forests. *Agricultural and Forest Meteorology*, **150**, 1090–1101.
- Piao S, Ciais P, Friedlingstein P, De Noblet-Ducoudré N, Cadule P, Viovy N, Wang T (2009) Spatiotemporal patterns of terrestrial carbon cycle during the 20th century. *Global Biogeochemical Cycle*, **23**, GB4026.
- Piao SL, Luysaert S, Ciais P *et al.* (2010) Forest annual carbon cost: a global-scale analysis of autotrophic respiration. *Ecology*, **91**, 652–661.
- Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology*, **10**, 2052–2077.
- Richardson AD, Hollinger DY (2007) A method to estimate the additional uncertainty in gap-filled NEE resulting from long gaps in the CO₂ flux record. *Agricultural and Forest Meteorology*, **147**, 199–208.
- Ryan MG, Hubbard RM, Pongracic S, Raison RJ, Mcmurtrie RE (1996) Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology*, **16**, 333–343.
- Schäfer KVR, Oren R, Ellsworth DS *et al.* (2003) Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology*, **9**, 1378–1400.
- Siccama TG, Fahey TJ, Johnson CE *et al.* (2007) Population and biomass dynamics of trees in a northern hardwood forest at Hubbard Brook. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **37**, 737–749.
- Smith WK, Gao W, Steltzer H, Wallenstein MD, Tree R (2010) Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. *Global Change Biology*, **16**, 484–495.
- Smolander A, Kitunen V, Tamminen P, Kukkola M (2010) Removal of logging residue in Norway spruce thinning stands: long-term changes in organic layer properties. *Soil Biology & Biochemistry*, **42**, 1222–1228.
- Sollins P (1982) Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **12**, 18–28.
- Spies TA, Franklin JF, Thomas TB (1988) Coarse woody debris in Douglas-Fir forests of Western Oregon and Washington. *Ecology*, **69**, 1689–1702.
- Stinson G, Kurz WA, Smyth CE *et al.* (2011) An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. *Global Change Biology*, **17**, 2227–2244.
- Stucky JM, Patti HD, Shear TH (1999) Regression equations for estimating *Ilex opaca* biomass components. *Castanea - The Journal of the Southern Appalachian Botanical Society*, **64**, 350–354.
- Subke JA, Inglisma I, Cotrufo MF (2006) Trends and methodological impacts in soil CO₂ efflux partitioning: a meta-analytical review. *Global Change Biology*, **12**, 921–943.
- Swindel BF, Conde LF, Smith JE, Hollis CA (1982) Green weight of major tree species in the north Florida pine flatlands. *Southern Journal of Applied Forestry*, **6**, 74–78.
- Takagi K, Fukuzawa K, Liang N *et al.* (2009) Change in CO₂ balance under a series of forestry activities in a cool-temperate mixed forest with dense undergrowth. *Global Change Biology*, **15**, 1275–1288.
- Tisdale JL (2008) *Quantifying the Effects of Organic Residues on Soil Nitrogen and Phosphorus Availability*. Unpublished MS North Carolina State University, Raleigh.
- Toland DE, Zak DR (1994) Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. *Canadian Journal of Forest Research*, **24**, 1711–1716.
- Tritton LM (1980) *Dead Wood in the Northern Hardwood Forest Ecosystem*. Unpublished PhD Yale University, New Haven, CT.
- Tyree MC, Seiler JR, Maier CA, Johnsen KH (2009) *Pinus taeda* clones and soil nutrient availability: effects of soil organic matter incorporation and fertilization on biomass partitioning and leaf physiology. *Tree Physiology*, **29**, 1117–1131.
- Waddell KL (2002) Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecological Indicators*, **1**, 139–153.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology*, **18**, 129–134.
- Wells C, Jorgensen J, Burnette C (1975) *Biomass and Mineral Elements in a Thinned Loblolly Pine Plantation at age 16*. Research Paper SE-126. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Wofsy SC, Harriss RC (2002) The North American Carbon Program (NACP). In: *Report of the U.S. Interagency Carbon Cycle Science Program*, U.S. Global Change Research Program, pp. 62, Washington, DC, USA.
- Yanai RD, Currie WS, Goodale CL (2003) Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. *Ecosystems*, **6**, 197–212.
- Zhang DW, Polyakov M (2010) The geographical distribution of plantation forests and land resources potentially available for pine plantations in the U.S. South. *Biomass & Bioenergy*, **34**, 1643–1654.