

Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance

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Abstract

We used estimates of autotrophic respiration (R_A), net primary productivity (NPP) and soil CO_2 evolution (S_{ff}), to develop component carbon budgets for 12-year-old loblolly pine plantations during the fifth year of a fertilization and irrigation experiment. Annual carbon use in R_A was 7.5, 9.0, 15.0, and 15.1 Mg C ha^{-1} in control (C), irrigated (I), fertilized (F) and irrigated and fertilized (IF) treatments, respectively. Foliage, fine root and perennial woody tissue (stem, branch, coarse and taproot) respiration accounted for, respectively, 37%, 24%, and 39% of R_A in C and I treatments and 38%, 12% and 50% of R_A in F and IF treatments. Annual gross primary production ($\text{GPP} = \text{NPP} + R_A$) ranged from 13.1 to 26.6 Mg C ha^{-1} . The I, F, and IF treatments resulted in a 21, 94, and 103% increase in GPP, respectively, compared to the C treatment. Despite large treatment differences in NPP, R_A , and carbon allocation, carbon use efficiency ($\text{CUE} = \text{NPP}/\text{GPP}$) averaged 0.42 and was unaffected by manipulating site resources.

Ecosystem respiration (R_E), the sum of S_{ff} and above ground R_A , ranged from 12.8 to 20.2 $\text{Mg C ha}^{-1}\text{yr}^{-1}$. S_{ff} contributed the largest proportion of R_E , but the relative importance of S_{ff} decreased from 0.63 in C treatments to 0.47 in IF treatments because of increased aboveground R_A . Aboveground woody tissue R_A was 15% of R_E in C and I treatments compared to 25% of R_E in F and IF treatments. Net ecosystem productivity ($\text{NEP} = \text{GPP} - R_E$) was roughly 0 in the C and I treatments and 6.4 $\text{Mg C ha}^{-1}\text{yr}^{-1}$ in F and IF treatments, indicating that non-fertilized treatments were neither a source nor a sink for atmospheric carbon while fertilized treatments were carbon sinks. In these young stands, NEP is tightly linked to NPP; increased ecosystem carbon storage results mainly from an increase in foliage and perennial woody biomass.

Keywords: carbon budget, ecosystem respiration, gross primary productivity, growth respiration, maintenance respiration, net ecosystem productivity, net primary productivity, pine plantation, *Pinus taeda* L., soil CO_2 evolution

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Introduction

Forests in the northern hemisphere may function as large sinks for atmospheric carbon (Cias *et al.*, 1995; Schimel, 1995; Houghton *et al.*, 1998; Tan *et al.*, 1998). Advances in micrometeorological methods for measuring energy and mass exchange over forest canopies have allowed relatively robust estimates of forest net

ecosystem productivity (NEP) (e.g. Wofsy *et al.*, 1993; Baldocchi *et al.*, 1996). These studies show that annual NEP is relatively small, an order of magnitude less than its component fluxes: photosynthesis and ecosystem respiration (Clark *et al.*, 1999; Curtis *et al.* 2002). Because these two processes respond differently to forest disturbance, small changes in either may have a significant impact on NEP. Ecosystem respiration (R_E), the sum of autotrophic (R_A), and heterotrophic (R_H) respiration, plays a major role in determining whether a forest functions as a source or sink for atmospheric

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carbon (Ryan *et al.*, 1994; Goulden *et al.*, 1996, 1998; Law *et al.*, 1999, 2001; Granier *et al.*, 2000; Valentini *et al.*, 2000; Falge *et al.*, 2002). Micrometeorological techniques, however, do not allow for partitioning of the underlying components, such as photosynthesis, carbon allocation, tissue respiration, and soil CO₂ evolution (root respiration and R_H) that together compose ecosystem carbon cycling (Rayment and Jarvis, 1997). Component studies provide a means for understanding whole system behavior and to determine how forest ecosystems respond to environmental change and forest management activities.

Plantation forests, because of their relatively simple structure, are useful for studying the relationships between component respiration and ecosystem carbon exchange. In addition, managed plantations are increasingly becoming a significant part of the landscape and our understanding of how species selection and silvicultural treatments affect biological growth potential, carbon cycling, and sequestration is still relatively poor. Gladstone and Ledig (1990) hypothesized that plantation forests may sequester atmospheric carbon at a higher rate and more efficiently than natural forests and, thus, may be an effective strategy for partially offsetting net carbon emissions to the atmosphere (Vitousek, 1991; Kursten and Burschel, 1993; US DOE, 1999). Fast growing plantation forests may also be one way to quickly turn highly degraded sites into carbon sinks. For example, intensive management will likely increase stand NEP largely by increasing net primary productivity (NPP) (Johnsen *et al.*, 2001).

Loblolly pine (*Pinus taeda* L.) is an important commercial species in North America with over 18 million hectares of natural and planted forest from east Texas and Oklahoma to Virginia (Schultz, 1997). These forests are potentially some of the most productive forests in the United States and thus will likely be important on a regional and national scale for mitigating anthropogenic CO₂ emissions (Johnsen *et al.*, 2001). Many of these forests grow on sites with moderate to poor soil fertility, which may limit their potential for C sequestration. Because of its economic importance and its plasticity with respect to forest management, numerous studies have been conducted to discern how climate, genetics, and resource availability affect growth, ecology, and ecophysiology of loblolly pine (Kinerson *et al.*, 1974; Teskey *et al.*, 1987; Vose and Allen 1988; Albaugh *et al.*, 1998; Ellsworth 2000; Samuelson *et al.*, 2001, 2003; Will *et al.*, 2001; Retzlaf *et al.*, 2001, see Schultz 1997). Fertilization of nutrient-deficient loblolly pine plantations leads to increased stand leaf area and stem biomass (Vose and Allen, 1988; Albaugh *et al.*, 1998), a shift in carbon allocation from belowground to aboveground tissues (Albaugh *et al.*, 1998; Retzlaf *et al.*,

2001) and an increase in production efficiency (biomass or volume increment/leaf area) (Vose and Allen, 1988; Albaugh *et al.*, 1998; Jokela and Martin, 2000). On sites of very low native nutrient supply, fertilization increases photosynthetic rates (Murthy *et al.*, 1996; Zhang *et al.*, 1997; Maier *et al.*, 2002), although these effects are minor (or ephemeral) relative to large increases in leaf area. Interestingly, predicted increases in growth of loblolly pine forest from elevated CO₂ (DeLucia *et al.*, 1999) will likely be tempered by low native nutrient supply (Groninger *et al.*, 1999; Oren *et al.*, 2001). While fertilization clearly increases aboveground productivity (Allen *et al.*, 2001), less is known about how altering resource availability changes stand carbon dynamics. Improved nutrition increases specific respiration rates of perennial woody tissue (Maier *et al.*, 1998; Maier, 2001), but generally has no effect on specific respiration of foliage or fine roots (Maier, 2000). Application of fertilizer in established loblolly pine plantations appears to suppress soil CO₂ evolution (Maier and Kress, 2000; Butnor *et al.*, 2003); however, the mechanisms involved are unclear. A system-level analysis of all system components is required to ascertain the effects of site fertility, management and climate on carbon sequestration in intensively managed loblolly pine forests.

In this paper, we develop annual carbon budgets for mid-rotation (12 years old) loblolly pine stands using measurements of growth and empirically derived functions of tissue-specific respiration and soil CO₂ evolution (Maier *et al.*, 1998; Maier, 2000; Maier and Kress, 2000; Maier, 2001). The objectives were to (1) determine how resource availability and tissue nutrient status alter the components of autotrophic and ecosystem respiration, (2) scale tissue level respiration and growth to estimate annual gross primary productivity (GPP) and net ecosystem productivity (NEP), and (3) determine if resource availability alters the ratio of NPP/GPP (carbon use efficiency; CUE).

Materials and methods

Site description

The study site is a loblolly pine plantation located at the Southeast Tree Research and Education Site (SETRES), 17 km north of Laurinburg, NC (34°54'20"N, 79°29'0.3"W). Site elevation is 13.7 m and the topography is flat. The soils are a sandy, silicious, thermic psammentic hapludult (Wakulla series, USDA Soil Classification System) and are typically nutrient poor and well drained. Available soil moisture at field capacity is 18–20 cm in top 2 m profile (≈9%). The climate is mild with mean annual, summer, and winter

air temperatures of 17 °C, 26 °C, and 9 °C, respectively. Long-term mean annual rainfall is 1210 mm, evenly distributed throughout the year. The stand consists of a mix of 10 improved North Carolina Piedmont loblolly pine families planted in 1985 after the harvest of the previous natural longleaf pine (*Pinus palustris* Mill.) stand. Seedlings were planted at 2.65 × 3 m spacing at a density of 1260 trees per hectare.

Experimental design

In 1992, at the beginning of the eighth growing season, a 2 × 2 factorial study using a combination of nutrition (no addition and optimum nutrition) and water (no addition and well watered) was begun. Treatments were control (C), irrigated (I), fertilized (F) and irrigated and fertilized (IF) replicated four times. Treatment plots were 50 × 50 m (0.25 ha) with interior sampling plots of 30 × 30 m. Treatment objectives were to maintain foliage in fertilized treatments at optimum nutrition and soil in the irrigated treatments at a minimum of 40% of available soil moisture in the top 50 cm profile (≅ 3.5%). The nutrition treatment began in the spring 1992 and irrigation began in spring 1993. Irrigation was suspended during the dormant season (late November–February). To achieve optimum nutrition, fertilizer was applied annually to maintain foliar nitrogen concentrations ([N]) near 1.3% with other macro- and micro-

nutrients in balance; control foliar [N] was about 0.9% (Murthy *et al.*, 1996; Albaugh *et al.*, 1998). Albaugh *et al.* (1998) provides a detailed description of treatment application, monitoring and efficacy. All non-pine vegetation was eliminated using a combination of chemical (glyphosate) and mechanical methods. The forest floor was primarily pine litter.

Stand characteristics

Through December 1996, fertilized treatments received a total of 586 kg N, 145 kg P, 337 kg K, 168 kg Ca, 146 kg Mg, 209 kg S, and 3.9 kg B per hectare (Albaugh *et al.*, 1998, 2003). At this time, height, diameter, basal area, and leaf area were all significantly greater in the fertilized plots (Table 1). Fertilized treatments (F and IF) had nearly twice the standing biomass carbon in foliage, stem, branch, taproot, and coarse lateral root pools than did non-fertilized treatments (C and I). There was no significant treatment difference in fine root biomass. In all treatments, stem tissue was the largest single reservoir for carbon containing about 45% of the standing carbon biomass while fine roots was less than 6% of total stand carbon. Aboveground (73%) and belowground (27%) carbon distribution was similar between treatments. Fertilization caused a shift in the relative carbon distribution among belowground components. Fine root biomass comprised 20–23% of

Table 1 Stand characteristics and carbon content in standing biomass in 1996 for 12-year-old loblolly pine plantations at SETRES

Treatment	Control	Irrigated	Fertilized	Irr + fert	SE
DBH (cm)	10.92	11.39	14.23	14.97	0.16
Height (m)	6.68	7.18	8.45	8.94	0.08
Density (stems ha ⁻¹)	1156	1189	1200	1144	44
Basal area (m ² ha ⁻¹)	11.6	12.8	20.3	21.5	0.30
Litterfall (Mg C ha ⁻¹)	1.1	1.4	2.4	2.7	
<i>Leaf area index</i>					
January	0.98	1.08	1.90	2.15	
August	1.36	1.57	2.68	3.06	
<i>Component (Mg C ha⁻¹)</i>					
Foliage	1.53	1.90	3.01	3.59	0.15
Branches	2.71	3.12	5.44	6.19	0.35
Stems	7.28	8.42	13.25	14.97	0.75
Taproot	2.10	2.31	5.18	5.6	0.23
Coarse root*	1.22	1.49	2.33	1.95	0.08
Fine root*	0.84	1.13	0.97	0.96	0.7
Total aboveground	11.52	13.44	21.7	24.75	
Total belowground	4.16	4.93	8.48	8.51	
Total	15.68	18.37	30.18	33.26	

All values are for December except for leaf area index (projected), which is for January and August. SE is the combined standard error.

*Fine and coarse root carbon biomass values are for the top 200 cm of soil. The coarse root pools are lateral coarse roots excluding the taproot.

SETRES, Southeast Tree Research and Education Site.

belowground biomass in the C and I treatments compared to 11% in the F and IF treatments, while biomass in taproots increased from 47% to 50% in C and I treatments to greater than 60% in F and IF treatments.

Stand carbon budget

Annual carbon budgets were developed for the 12-year-old stands in 1996 using a component analysis method similar to that described by Ryan (1991). This approach relies on scaling-up of measurements made on samples of different tissues to estimate whole tree or stand carbon use (Ågren *et al.*, 1980; Linder and Troeng, 1981; Linder and Axelsson, 1982; Ryan *et al.*, 1996; Ryan *et al.*, 1997). In our study, daily carbon use in growth and respiration were calculated for each tissue component and then summed to estimate stand :

$$GPP = \sum (NPP_i + R_{Ti}), \quad (1)$$

where NPP and R_T are net primary production and total respiration (growth and maintenance), respectively for tissue component i (foliage, branches, stems, fine roots, coarse lateral roots, and taproots). Component biomass was estimated for each measurement plot with treatment-specific allometric equations based on tree stem dimensional measurements. Albaugh *et al.* (1998) describe the destructive sampling procedures and development of allometric equations. Annual NPP for branch, stem, taproot, and coarse lateral root components was estimated as the difference between initial and final biomass. Annual NPP for foliage was the total foliage biomass for the 1996 cohort. Biomass on any particular day was the sum of initial biomass plus the estimated growth through that date. Daily foliage biomass was estimated from annual production and seasonal changes in relative foliage elongation and abscission. Fine (≤ 2 mm) and coarse lateral root live and dead biomass (> 2 mm) was measured from

monthly cores 15 cm diameter and 15 cm depth (4–5 per plot) (Maier and Kress, 2000). Fine and coarse lateral root biomass was scaled to a 200 cm depth using treatment-specific scalars (Maier and Kress, 2000). Fine root production was estimated using the Fairly and Alexander (1985) decision matrix. Carbon mass was assumed to be 50% of biomass.

Respiratory carbon use was based on the functional model of respiration (McCree, 1970; Amthor 1989, 2000) where respiration is partitioned into a growth and maintenance component:

$$R_T = r_g(dW/dt) + r_m W, \quad (2)$$

where R_T is the total respiration, r_g is the growth coefficient, dW/dt is the tissue growth measured as the change in biomass with time, r_m is the maintenance coefficient, and W is the tissue biomass. Growth respiration (R_G) is the product $r_g * (dW/dt)$ and maintenance respiration (R_M) is the product $r_m * W$. The above equations were applied to each tissue component using specific tissue response functions and biomass measurements. Daily estimates for each tissue were summed to obtain annual respiration.

Maintenance respiration is strongly affected by temperature and in some cases by the nutritional status of the tissue (Maier *et al.*, 1998). There were significant tissue differences in wintertime specific respiration rates at SETRES (Table 2). Foliage had the highest rates followed by fine roots (< 2 mm), branches, coarse lateral roots, and stems (Maier, 2000). Fine root respiration rates were 5–10 times greater than stem respiration rates. Specific respiration rates of branches, stems, and coarse roots were significantly greater in the fertilized than in the non-fertilized treatments. In contrast, fertilization had no effect on specific respiration rates of foliage or fine roots. Since R_M is strongly temperature dependent, the maintenance term was calculated by

$$R_{Mi} = W_i R_B e^{k(T - T_B)}, \quad (3)$$

Table 2 Typical wintertime R_M rates at 20 °C for loblolly pine tissues at SETRES

Treatment	Foliage	Branch	Stem	Coarse roots	Fine roots
Control	3.75 (0.30)	0.18 (0.01)	0.09 (0.01)	0.84 (0.11)	2.21 (0.12)
Irrigated	NA	0.21 (0.01)	0.12 (0.01)	NA	NA
Fertilized	3.75 (0.23)	0.23 (0.02)	0.18 (0.03)	1.34 (0.18)	1.65 (0.23)
Irr + fert	NA	0.27 (0.02)	0.18 (0.01)	NA	NA

All values are $\mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$. Numbers in parentheses are treatment standard errors. NA, not available; SETRES, Southeast Tree Research and Education Site.

where R_M is the maintenance respiration for each tissue component i , R_B is the mean tissue maintenance respiration at a base temperature (e.g. 0°C or 20°C), W_i is the stand tissue biomass or nitrogen content ($[N] \times \text{biomass}$; Barnes and Hole, 1978; Maier *et al.*, 1998; Amthor, 2000; Maier, 2000, 2001), k is the tissue-specific temperature coefficient for response to temperature, T is the average daily tissue temperature, and T_B is the base temperature. Parameter estimates for Eqn (3) are given in Appendix 1. Branch and taproot R_M were calculated using stem tissue parameters and appropriate tissue temperature and nitrogen values. Tissue R_G was calculated as a fixed proportion of daily biomass production assuming a construction cost of 0.24 for stems (Maier, 2001, Appendix 1), branches and taproot, and 0.25 for foliage, fine and coarse lateral roots (Amthor, 1989).

Air, soil (5 cm depth), stem, and branch temperature were continuously measured as part of the site environmental monitoring. Foliage and root temperature were assumed to equal air and soil temperature, respectively. Daily tissue $[N]$ for branches, stems, and coarse lateral roots were estimated by linear interpolation between monthly measurements. Because of large diurnal changes in air and aboveground woody tissue temperature, foliage, branch, and stem R_M were calculated on an hourly basis and then summed for a daily rate. Daily taproot, coarse, and fine root R_M was calculated from average daily soil temperature. Foliar R_M during the day was assumed to be 0.6 times night respiration rate (Kirschbaum and Farquhar, 1984).

Ecosystem respiration (R_E) represents the total carbon loss from the system and includes heterotrophic respiration (R_H). Because R_H is difficult to measure, we estimated R_E by

$$R_E = R_{A,ag} + S_{ff}, \quad (4)$$

where $R_{A,ag}$ is aboveground autotrophic respiration, the sum of foliage, branch and stem respiration, and S_{ff} is soil surface CO_2 efflux which includes root respiration and R_H from surface litter, soil necromass, and mineral soil. Soil CO_2 evolution rates were estimated from daily average soil temperature (5 cm) and soil moisture using

$$S_{ff} = (m \cdot \theta_s \cdot R_{max}) / ((m \cdot \theta_s) + R_{max}) \cdot Q^{T/10}, \quad (5)$$

where θ_s is volumetric soil water content, T is soil temperature, m is the rate of change in S_{ff} with θ_s , R_{max} is maximum S_{ff} when $\theta_s = 100\%$, and Q is the rate of change in S_{ff} with a 10°C change in soil temperature (Maier and Kress, 2000). Parameter estimates for Eqn (5) are given in Appendix 1. Daily soil moisture was estimated by linear interpolation between measured

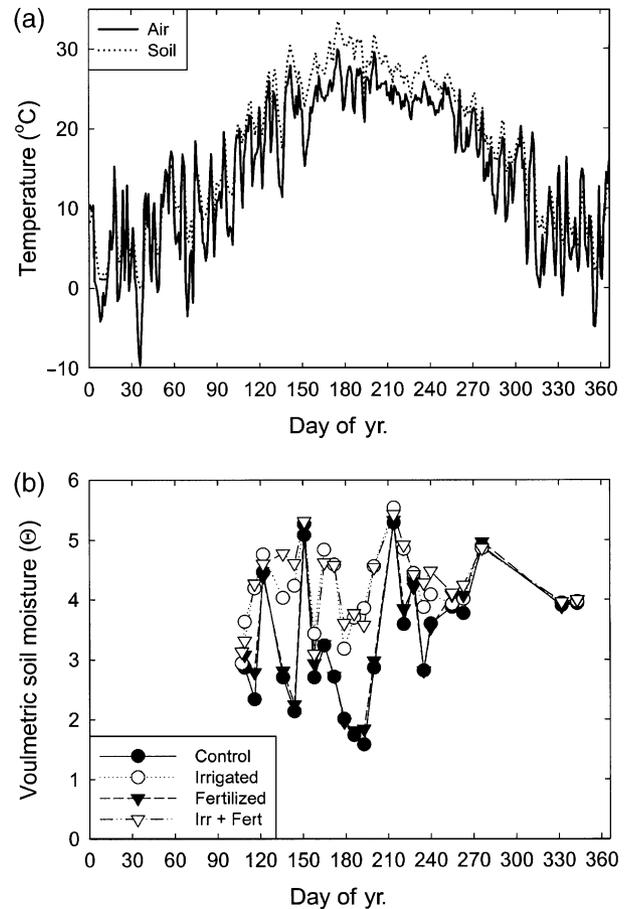


Fig. 1 Seasonal variation in (a) daily mean air and soil (5 cm) temperature and (b) mean treatment volumetric soil moisture in the top 50 cm in 1996 at SETRES.

values (Fig. 1b). Net ecosystem productivity (NEP) is the total carbon flux into or out of the stand:

$$\text{NEP} = \text{GPP} - R_E. \quad (6)$$

In Eqn (6), a negative NEP would indicate a net loss of carbon from the system.

Statistical analysis

Individual plot estimates of NPP, R_A , GPP, S_{ff} , R_E , and NEP were generated from plot specific measures of biomass, tissue $[N]$, temperature, and soil moisture. Treatment effects of fertilization, irrigation, and fertilization plus irrigation were determined using a randomized complete block analysis of variance (SAS Institute Inc. 1988). Main or interactive effects of treatments were considered significant at $\alpha = 0.05$. Tukey's studentized range test at $\alpha = 0.05$ was used to separate treatment means.

Results

Environmental conditions

Average daily air temperatures ranged from below freezing during the winter to around 30 °C in the summer months. Long periods below freezing were rare. Soil temperatures at 5 cm were less variable than air temperature and were never below 0 °C (Fig. 1a). Soil temperature was similar between treatments, although, during the summer months, soil temperature in the fertilized treatments could be 2–4 °C cooler than non-fertilized treatments (data not shown). Total rainfall was 100 cm. Irrigated plots received an additional 40 cm from irrigation during the growing season (days 100–250). Volumetric water content in the irrigated plots remained above 3% during this time (Fig. 1b). In contrast, θ was below 2.5% in the non-irrigated stands for parts of April, May and from mid-June through most of July (days 160–200). Significant rainfall in early August increased θ to above 5% in all treatments; θ remained at or above 3% for the remainder of the year.

Component NPP

Irrigation and fertilization resulted in a significant increase in total NPP (Table 3). On an annual basis, total NPP was 5.6, 6.8, 10.3, and 11.2 Mg C ha⁻¹, respectively, in the C, I, F, and IF treatments (Table 4). Compared to C treatments, I treatment increased NPP by 22% while F treatment increased NPP by 86%. The combined IF treatment was additive (no interaction) increasing NPP by 102%. In C and I treatments, 64–67% of NPP was allocated aboveground compared to 69% and 75%, respectively, in F and IF treatments. Fertilization resulted in a relative decrease in carbon allocation to fine roots and an increase in allocation to foliage stems and taproots. Fine root NPP was 27% of total NPP in C treatments compared to only 13% of NPP in IF treatments.

R_A

Treatment differences in biomass and NPP were generally reflected in stand R_A . Because of increased biomass

and NPP, fertilized stands had 84% more R_A (Tables 3 and 4) than non-fertilized stands. Total foliage respiration ($R_T = R_M + R_G$) used 34–38% of stand R_A (Fig. 2) in all treatments and was the single largest component of the autotrophic carbon budget. Fine root R_T was the second largest component of stand R_A in the C and I treatments followed by a similar contribution from stem, branch, and coarse lateral root respiration. In contrast, both stem and branch R_T equaled or exceeded fine root R_T in the F and IF treatments. In addition, carbon use in coarse lateral roots and taproots were proportionally higher in the fertilized treatments. Taproot R_T was the smallest component of stand R_A in all treatments.

The relative importance of component respiration varied seasonally. Foliage R_T was always the largest respiratory component (Fig. 3) accounting for 30–55% of stand R_A (Fig. 4). The relative magnitude of foliage R_T decreased in mid-spring and again in early autumn coinciding with increased stem R_T . During these periods, aboveground woody tissue respiration (stem + branch) exceeded foliage R_T and was the largest component of aboveground respiration ($R_{A,ag}$). Stem R_T was bimodal peaking in the spring (DOY 90–125) and in the fall (DOY 280) (Fig. 3), reflecting changes in seasonal stem growth rate and tissue [N] (data not shown). In C treatments, fine root R_T accounted for 15–25% of stand R_A and was the second largest respiratory component except during the spring when stem R_T was similar in magnitude. In contrast, fine root R_T was always less than 15% of stand R_A in the IF treatment (Figs 3 and 4).

S_{ff} and R_E

Fertilization alone had no effect on annual S_{ff} (Tables 3 and 4). However, there was a significant irrigation effect and fertilization by irrigation treatment interaction (Table 3). The increase of S_{ff} attributed to irrigation was greater in the non-fertilized plots than in the fertilized plots. The effect of irrigation was limited to the summer months. There were little treatment differences in S_{ff} during the fall, winter, and early spring, but during the summer, higher soil moisture significantly increased S_{ff} in the irrigated treatments (Fig. 5).

Table 3 Statistical summary (probability > *F*) of treatment effects on annual carbon use in net primary productivity (NPP), autotrophic respiration (R_A), gross primary productivity (GPP), soil CO₂ evolution (S_{ff}), ecosystem respiration (R_E) and net ecosystem productivity (NEP)

Variable	NPP	R_A	GPP	S_{ff}	R_E	NEP
Fertilizer	<0.001	0.001	<0.001	0.651	<0.001	<0.001
Irrigation	0.024	0.221	0.095	<0.001	0.004	0.770
Fertilizer × irrigation	0.695	0.393	0.489	<0.001	0.257	0.570

Table 4 Annual carbon budget in 1996 for 12-year-old loblolly pine plantations subjected to supplemental moisture and nutrient treatments

Parameter	Control	Irrigated	Fertilized	Irr + fert	SE
Foliage production	1.51	1.88	2.90	3.58	
R_G	0.38	0.47	0.72	0.90	
R_M	2.41	2.99	4.48	4.91	
Branch production	0.56	0.71	1.05	1.23	
R_G	0.13	0.17	0.25	0.29	
R_M	0.86	0.94	1.88	1.99	
Stem production	1.50	1.94	3.11	3.59	
R_G	0.36	0.47	0.75	0.86	
R_M	0.60	0.69	1.82	1.84	
NPP _{ag}	3.57	4.53	7.06	8.40	
$R_{G,ag}$	0.87	1.11	1.72	2.05	
$R_{M,ag}$	3.87	4.62	8.18	8.74	
Total $R_{A,ag}$	4.74	5.73	9.90	10.79	
Fine root production	1.50	1.64	1.93	1.50	
R_G	0.38	0.41	0.48	0.38	
R_M	1.47	1.71	1.68	1.48	
Coarse root production	0.15	0.22	0.37	0.31	
R_G	0.04	0.06	0.09	0.08	
R_M	0.68	0.82	1.99	1.61	
Taproot production	0.34	0.41	0.96	1.03	
R_G	0.08	0.10	0.23	0.25	
R_M	0.18	0.21	0.81	0.81	
NPP _{bg}	1.99	2.27	3.26	2.84	
$R_{G, bg}$	0.50	0.57	0.80	0.71	
$R_{M, bg}$	2.33	2.74	4.48	3.90	
Total $R_{A, bg}$	2.83	3.31	5.28	4.61	
Total production (NPP)	5.56	6.80	10.32	11.24	0.40
Total R_A	7.57	9.04	15.18	15.40	0.66
GPP (NPP + R_A)	13.13	15.84	25.50	26.64	1.05
Soil CO ₂ evolution (S_{ff})	8.11	10.38	9.26	9.38	0.15
$R_E(S_{ff} + R_{A, ag})$	12.85	16.11	19.16	20.17	0.55
NEP (GPP - R_E)	0.28	-0.27	6.34	6.47	0.55
CUE (NPP/GPP)	0.42	0.43	0.41	0.42	

Carbon was partitioned into production (NPP), maintenance (R_M) and growth (R_G) respiration. All values are in Mg C ha⁻¹ yr⁻¹ (except carbon use efficiency (CUE)). SE is the combined standard error.

On an annual basis, R_E ($R_{A, ag} + S_{ff}$) ranged from 12.9 in C treatments to 20.2 Mg C ha⁻¹ in IF treatments (Table 4). Soil CO₂ evolution accounted for the largest portion of R_E in all treatments, however, the relative contribution differed between treatments. In the C and I treatments, S_{ff} comprised about 64% of R_E with 22% and 15% coming from foliage and aboveground woody tissue (stem + branch), respectively. In the F and IF treatments, S_{ff} was roughly 48% of R_E and the balance equally partitioned between foliage and woody tissue (Fig. 6).

GPP and NEP

The annual carbon budget by tissue component for each treatment is given in Table 4. Gross primary

productivity (GPP) the sum of total NPP and R_A was 13.1 and 15.8 Mg C ha⁻¹ yr⁻¹ in the C and I treatments, respectively, vs. 25.5 in F and 26.6 Mg C ha⁻¹ yr⁻¹ in IF treatments. The I, F, and IF treatments resulted in a 21%, 94%, and 103% increase in GPP, respectively, over the C treatments. Autotrophic respiration consumed about 58% of GPP in all treatments. Maintenance respiration ranged from 6.2 to 12.6 Mg C ha⁻¹ yr⁻¹ accounting for about 82% of R_A and 47% of GPP.

Treatment differences in nutrient availability altered carbon allocation patterns particularly between above- and belowground tissues. In non-fertilized treatments, about 36% of GPP was allocated belowground compared to 33% and 28% for F and IF treatments, respectively. This difference is the result of a shift in NPP from below- to aboveground plant parts and due

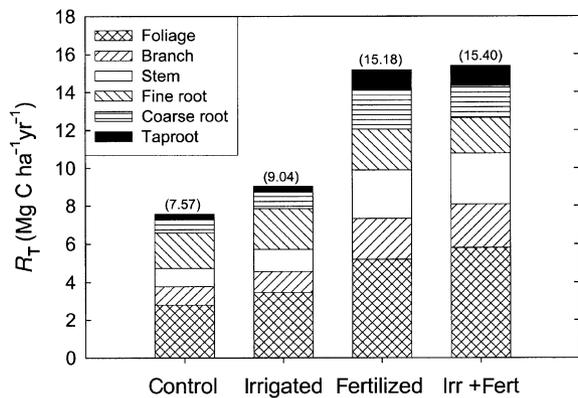


Fig. 2 Mean annual carbon flux from total respiration (R_T) (maintenance plus growth respiration) by tissue component in 12-year-old loblolly pine plantations. Values were generated using Eqns (2) and (3).

to an increase in stem and branch R_M in fertilized treatments. Stem NPP and R_T was 19% of GPP in C treatments compared to 24% of GPP in IF treatments, while fine root NPP and R_T decreased from 26% of GPP in C treatments to 13% in IF treatments. While fertilization had a large impact on the magnitude of NPP, R_A , GPP, and the relative allocation of carbon to biomass components, there was no significant treatment effect on stand CUE, which averaged 0.42 for all treatments.

Ecosystem respiration was roughly equal to GPP in the C and I treatments. Thus, net ecosystem production ($NEP = GPP - R_E$) was close to zero, indicating on an annual basis, these stands were neither a net carbon source nor sink for atmospheric carbon. In contrast, GPP was much larger than R_E in F and IF treatments indicating these stands were currently functioning as a carbon sink sequestering approximately 6.4 Mg C ha^{-1} annually.

Discussion

Potential problems with component analysis

The greatest uncertainty in the component carbon budget is the estimate of belowground carbon allocation for root production and root maintenance and growth respiration. While fine root biomass is a relatively small portion of the standing mass, annual production and turnover represents 14–25% of the forest carbon budget (Landsberg and Gower, 1997). Unfortunately, estimating fine root production is notoriously difficult and results are heavily dependent on methodology (Hendricks *et al.*, 1993). For example, in our stands sequential coring on a monthly time step showed that fine root biomass and production were significantly lower in fertilized

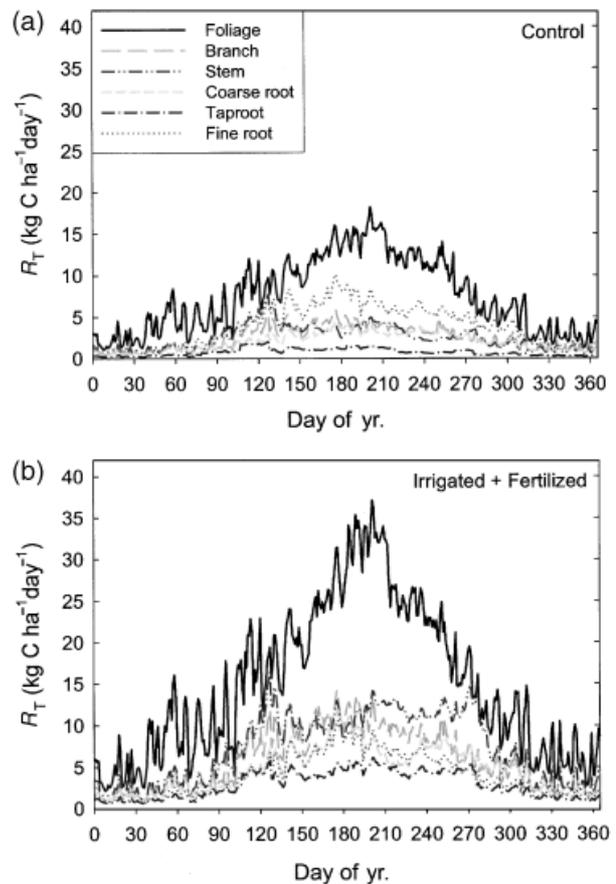


Fig. 3 Seasonal variation in daily total respiration (R_T) by tissue component in (a) control and (b) irrigated and fertilized 12-year-old loblolly pine plantations. Values were generated using Eqns (2) and (3).

stands during the first 4 years of treatment (1992–1995) (Albaugh *et al.*, 1998). These results are consistent with those found in other pine ecosystems (Gower *et al.*, 1992, 1994; Haynes and Gower, 1995; Ryan *et al.*, 1996) using a similar sampling approach. However, periodic coring may miss ephemeral roots if growth pulses exceed sampling events (Nadelhoffer *et al.*, 1985; Santantonio and Grace, 1987) and underestimate fine root production. King *et al.* (2002) measured fine root growth using minirhizotrons in our stands in 1996 and found that fertilization increased fine root production ($\cong 108\%$), suggesting that fine root production and turnover are positively correlated with nutrient availability (Nadelhoffer *et al.*, 1985; Nadelhoffer and Raich, 1992; Hendricks *et al.*, 1993).

Soil $[\text{CO}_2]$ may have a significant impact on fine root R_M . We derived our equations of fine root R_M from measurements made at ambient air $[\text{CO}_2]$ rather than soil $[\text{CO}_2]$ (Maier, 2000). Several recent studies (Qi *et al.*, 1994; Clinton and Vose, 1999; McDowell *et al.*, 1999)

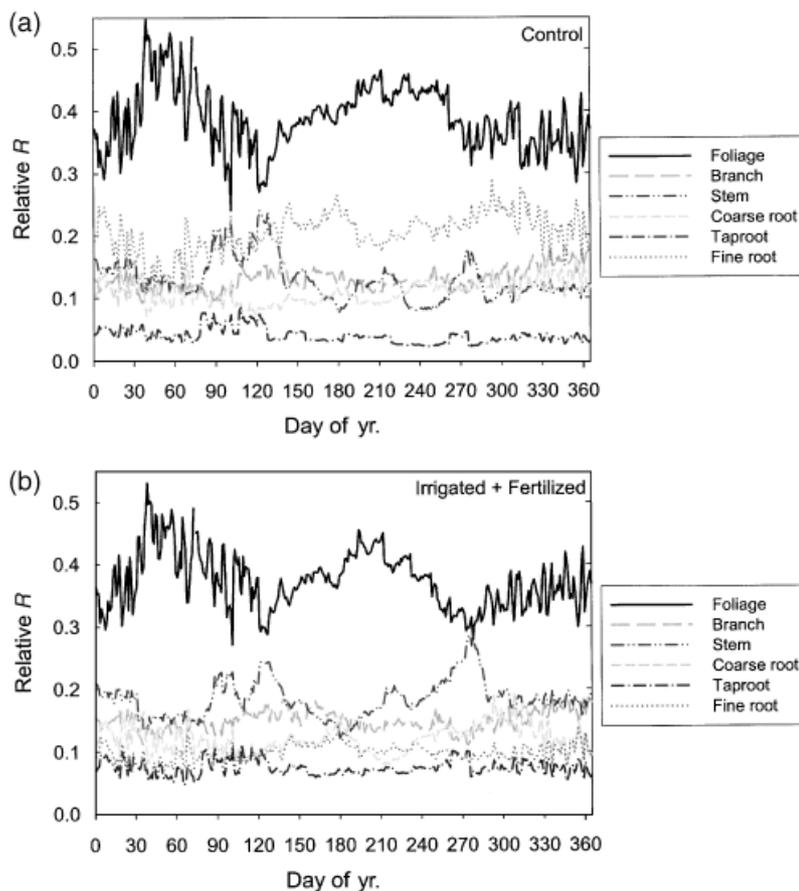


Fig. 4 Comparison of the relative magnitude in total respiration (R_T) by tissue component between (a) control and (b) irrigated and fertilized 12-year-old loblolly pine plantations.

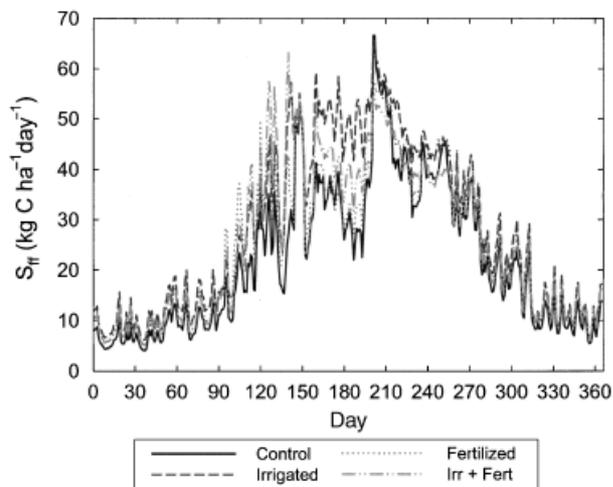


Fig. 5 Seasonal variation in the mean treatment soil CO_2 evolution (S_H) in 1996. Values were estimated using Eqn (5).

found that high soil CO_2 concentration inhibits fine root respiration rates. On the other hand, Burton and Pregitzer (2002) found that measurement $[\text{CO}_2]$ had

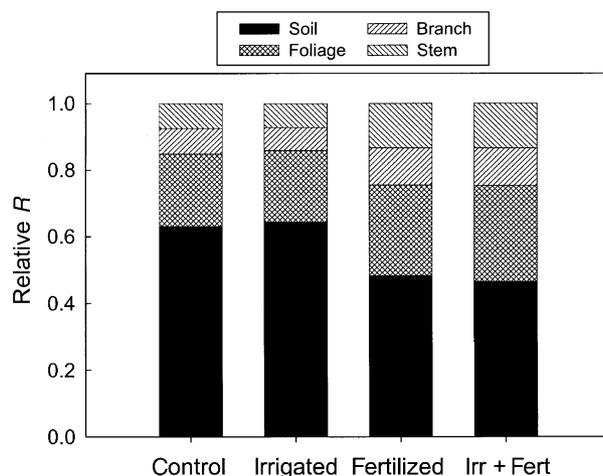


Fig. 6 Fraction of ecosystem respiration (R_E) generated from soil and aboveground components.

little affect on *in situ* measurement of root respiration in a number of tree species. In our study, if carbon allocation to fine root respiration is reduced by 65% to

account for soil [CO₂] effects, then total belowground carbon allocation is only 55% of the present values.

The mature tissue approach for partitioning respiration into R_M and R_G assumes that these processes are fundamentally independent with respect to carbon use (Amthor, 1989, 2000). In forest trees, this view is likely overly simplistic. Maintenance respiration of mature foliage (Teskey *et al.*, 1984, Brooks *et al.*, 1991) and stems (Sprugel, 1990; Lavigne and Ryan, 1997; Maier, 2001) varies seasonally, spatially and with growth rate of the tree. In addition, the mature tissue approach assumes that wintertime measurements of respiration reflect R_M at other times of the year and ignores short-term (seasonal) temperature acclimation. We used a growth coefficient of 0.25 (Penning de Vries, 1975) to estimate fine root R_G . This value probably reflects the growth coefficient for woody tissues such as stem and taproots (Maier 2001); however, it may grossly underestimate R_G for fine roots that typically have much higher nutrient concentrations. McDowell *et al.* (1999) estimated a construction coefficient for fine roots of 0.68 in western hemlock.

Seasonal and annual carbon budget

After 4 years of irrigation and 5 years of fertilization, annual GPP in the irrigated and fertilized treatments (26.6 Mg C ha⁻¹) was twice that in the controls (13.1 Mg C ha⁻¹). These values are considerably lower than that reported for a 16-year-old loblolly pine plantation (41 Mg C ha⁻¹ yr⁻¹, Kinerson *et al.*, 1977); however, GPP in C treatments was close to that for a 23-year-old *Pinus elliotii* Engelm. plantation in Florida (11.0 Mg C ha⁻¹ yr⁻¹, Cropper and Gholz, 1993). Autotrophic respiration consumed more than 58% of GPP similar to that reported for other conifers (Ryan *et al.*, 1994, 1997; Law *et al.*, 1999) and shows that autotrophic respiration is one of the largest components of the forest carbon budget. Foliage respiration was always the largest single component of stand R_A . This is generally the case in developing conifer forests (Ryan *et al.*, 1994). Fine root respiration was the second largest component of stand R_A in the non-fertilized treatments, however, because of increased growth in fertilized treatments, stem and branch R_T exceeded fine root R_T . Unlike in other conifers (Cropper and Gholz, 1991; Ryan *et al.*, 1994, 1996), tissue nitrogen concentration had no effect on foliage or fine root respiration (Maier 2000) perhaps because the range in [N] in these stands was small. Therefore, differences between treatments were due to fertilization effects on biomass and accretion patterns. On the other hand, stem, branch, and coarse root respiration were correlated with tissue nitrogen (Maier *et al.*, 1998; Maier, 2000). The seasonal trend in stem R_T was bimodal with peaks in the spring and late summer

that reflect increases in stem radial growth and changes in tissue [N] (Maier, 2001). Combined stem and branch R_T equaled or exceeded foliage respiration during the spring and fall.

Fertilization, in general, appears to increase carbon partitioning to perennial tissues (stem, branch, taproots, and coarse roots) and decreases partitioning to ephemeral fine roots (Linder and Axelsson, 1982; Cannell, 1985; Ryan *et al.*, 1996). This is a typical response for loblolly pine (Albaugh *et al.*, 1998; King *et al.*, 1999; Samuelson *et al.*, 2000; Retzlaff *et al.*, 2001). Partitioning of GPP, which includes carbon use in respiration, is similar. The relative carbon partitioning for production and respiration for aboveground/belowground components ranged from 63/37 in C treatments to 72/28 in the IF treatments. Ryan *et al.* (1996) found similar results for 20-year-old *P. radiata* plantations.

The relative belowground carbon allocation in this study (28–36%) is in the range reported for other coniferous forests. Ryan *et al.* (1996) estimated that belowground carbon allocation was 42% and 22% of GPP, respectively, in non-fertilized and fertilized *Pinus radiata* D. Don plantations. In *Pinus ponderosa* Laws., Law *et al.* (1999) reported a much higher belowground carbon partitioning (61%) in a multi-aged stand, and Williams *et al.* (1997) reported that belowground carbon allocation ranged between 21% and 51% for a number of sites. These studies, however, estimate belowground carbon allocation using a mass balance approach (Raich and Nadelhoffer, 1989) where carbon allocated to belowground to support root growth and respiration is calculated as the difference between soil CO₂ evolution and aboveground litterfall. This approach assumes that litter input and root biomass stocks as well as mineral soil carbon are temporally stable (i.e. 1 year). Giardina and Ryan (2002) modified the approach to account for dynamic carbon pools that occur in developing stands. Using their procedure, we estimated an annual belowground carbon allocation of 8.5, 11.5, 9.9, and 9.8 Mg C ha⁻¹ for the C, I, F, and IF treatments, respectively. These values are about twice that estimated for non-fertilized treatments and 17–34% higher than fertilized treatments (Table 4). Some of this discrepancy may be due to our underestimating of fine root production. Although, the ratio of S_{ff} : litterfall, 7.4, 7.4, 3.9, and 3.5 for C, I, F, and IF treatments, respectively, falls within the range reported for a number of young (<45 years old) forest ecosystems (Davidson *et al.*, 2002).

CUE

There was no treatment effect on stand CUE despite a two-fold increase in NPP indicating that increased

stand respiration with increased nutrient availability is closely linked to higher growth rates (Ryan *et al.*, 1996). Our estimate of CUE (0.42) is similar to that reported for a mixed-aged *P. ponderosa* forest (0.45, Law *et al.*, 1999), but lower than a 14-year-old *P. taeda* plantation (0.50, Kinerson *et al.*, 1977) and an 8-year-old *P. radiata* plantation (0.54, Arneth *et al.*, 1998). CUEs are lower in boreal coniferous forests (0.34–0.36, Ryan *et al.*, 1997). Aboveground CUE (0.43) was also similar to 20-year-old *P. radiata* stands (Ryan *et al.*, 1996). The fact that our estimates of CUE closely match that reported for other forest gives confidence that the respiration estimates and scaling techniques are reasonably accurate.

Waring *et al.* (1998) summarized the annual carbon budgets for 12 stands across a range of forest types and found that the ratio of NPP:GPP (i.e. CUE) averaged 0.47 (range 0.40–0.52) and hypothesized that NPP is a constant fraction of GPP. The constancy of this ratio is a simplifying assumption in the stand growth model 3-PG (Landsberg and Waring, 1997). The idea that NPP is a constant fraction of GPP is based on the assumption that growth, photosynthesis, and respiration are tightly linked (Amthor, 1989), and thus, a decrease or increase in net assimilation due to a change in resource availability will be followed by concomitant change in respiration and tissue growth (Ryan *et al.*, 1996). However, because of the dynamic changes in stand structure and tissue physiology a constant CUE over the course of stand development may be an over simplification (Medlyn *et al.*, 1999; Mäkelä and Valentine, 2001). Net primary productivity typically declines after canopy closure in even-aged stands (Gower *et al.*, 1995). This decline has been attributed to: (1) an increase in the ratio of respiring wood to foliage or (2) a direct or indirect reduction in the specific rate of photosynthesis from either nutritional limitations (Murty *et al.*, 1996) or increased stem hydraulic resistance (Ryan and Waring, 1992; Hubbard *et al.*, 1999). A decrease in the specific rate of photosynthesis would not necessarily lead to a decrease in CUE if specific woody tissue respiration decreases with stand age and sapwood mass (Lavigne *et al.*, 1996; Lavigne and Ryan, 1997). However, a constant CUE would not occur if the ratio of respiration to photosynthesis increases with stand age. An increase in respiration/photosynthesis ratio was considered the prime factor decreasing NPP (and CUE) in balsam fir (Hunt *et al.*, 1999) and Scots pine (Mäkelä and Valentine, 2001). In our stands, growth efficiency (biomass production/leaf area) has not changed with stand age (8–16 years) (Albaugh *et al.*, 2003), thus, it is unlikely that CUE has changed. Since intensively managed loblolly pine plantations are grown in short rotations of 20–30

years, a constant CUE may not be an unreasonable assumption for developing carbon inventories of these systems.

R_E

Our estimates of annual soil CO₂ evolution (8.1–10.4 Mg C ha⁻¹) are similar to other mid-rotation loblolly pine plantations (Andrews and Schlesinger, 2001; Butnor *et al.*, 2003). These rates accounted for 47–66% of R_E . Soil CO₂ evolution is generally 50% or more of R_E in temperate (Law *et al.*, 1999; Xu *et al.*, 2001) and boreal conifer forests (Lavigne *et al.*, 1997) in North America and Europe (Janssens *et al.*, 2001). Fertilization had no effect on S_{ff} , but irrigation increased S_{ff} compared to non-irrigated treatments when soil water was low and there was a strong treatment interaction. These effects are likely mediated through heterotrophic metabolism, since neither treatment had a significant effect on fine root R_M (Maier and Kress, 2000). We did not measure R_H directly but estimated it as the difference between soil CO₂ evolution and root respiration ($R_H = S_{ff} - R_{A,bg}$, Table 4). On an annual basis, R_H was higher in the C (5.3 Mg C ha⁻¹) and I (7.1 Mg C ha⁻¹) treatments than in the F (4.0 Mg C ha⁻¹) and IF (4.8 Mg C ha⁻¹) treatments. Root respiration comprised roughly a third of S_{ff} in non-fertilized treatments, thus in these stands R_H was the single largest component of R_E . In contrast, root respiration in fertilized treatments was half of S_{ff} and $R_{A,ag}$ was the most important component of R_E . The effects of fertilization on S_{ff} and heterotrophic metabolism are unclear. Li (2000) found that the fertilization had no impact on soil microbial biomass or population diversity at SETRES. However, fertilization can cause a decrease in mycorrhizal infection (Gardina and Ryan, 2002) and thus affect metabolism of belowground carbon (Rygiewicz and Anderson, 1994). Butnor *et al.*, (2003) found that recent fertilization with urea suppressed S_{ff} in 18-year-old loblolly forests. Understanding heterotrophic carbon metabolism is important for estimating ecosystem carbon use efficiency (CUE_E). CUE_E can be defined as

$$CUE_E = (NPP + \Delta S_C) / (GPP + R_H),$$

where ΔS_C is the change in mineral soil carbon content. If S_C does not change over short periods (i.e. a year) and since NPP/GPP is conservative, then CUE_E was greater in fertilized treatments (0.35) than in non-fertilized treatments (0.30). This example illustrates that R_H is an important component of the ecosystem carbon and budget and may determine the long-term potential for site carbon storage (Landsberg and Gower, 1997).

NEP

Based on component analysis, non-fertilized treatments after 12 years of stand development were neither a source nor a sink for atmospheric CO₂, while fertilized treatments were clearly sequestering carbon (6.4 Mg C ha⁻¹ yr⁻¹). We should note that all competing vegetation was eliminated on our study plots. An understory of wiregrass (*Aristida stricta*) and woody shrubs and trees is typical for these sites before crown closure. While other vegetation will compete with the pine for site resources and reduce pine productivity, including carbon storage and flux from these components would likely have made the non-fertilized stands a net carbon sink. There are few studies with which to compare component analysis of NEP. Lai *et al.* (2002) used a combination of model simulations and field measurements to estimate NEP in a non-fertilized and fertilized 8-year-old loblolly pine plantation on a site adjacent to ours (i.e. similar soils). While their stands were younger, they were planted at a higher density and had similar peak leaf area and aboveground woody biomass to our stands. Their analysis showed that the non-fertilized stand was functioning as weak source of carbon to the atmosphere (-1.06 Mg C ha⁻¹), while the fertilized stand was a slight sink (1.27 Mg C ha⁻¹). Our estimate of NEP for the fertilized stands compare favorably with eddy covariance measurements for young managed pine plantations (5.4–6.5 Mg C ha⁻¹ yr⁻¹ *P. taeda*, Law *et al.*, 2002; 5.0 and 7.2 Mg C ha⁻¹ yr⁻¹ *P. radiata*, Arneeth *et al.* 1998; 7.4 Mg C ha⁻¹ yr⁻¹ *P. elliotii*, Clark *et al.*, 1999). However, eddy covariance may underestimate nighttime respiration when atmospheric turbulence is low (Baldocchi *et al.*, 1997; Lavigne *et al.*, 1997; Janssens *et al.*, 2001).

Net ecosystem productivity should theoretically reach a maximum near canopy closure when the foliage/woody biomass ratio is highest (Gower *et al.*, 1994). The canopy in the fertilized stands was nearly closed with a LAI of 3.5. Thus, NEP of 6–7 Mg C ha⁻¹ yr⁻¹ may represent the maximum for these stands. In our stands, NEP was tightly linked to NPP and increased carbon storage resulted mainly from an increase in stem, taproot, and coarse root biomass. Four years of fertilization slightly increased mineral soil carbon content in the top 15 cm (non-fertilized = 12.0 ± 0.28 mg g⁻¹; fertilized = 13.7 ± 0.42 mg g⁻¹) (Maier and Kress 2000). However, rapid decomposition of short-lived tissues (i.e. foliage and fine roots) contributes very little carbon to the refractory soil humic materials (Schlesinger 1990). High rates of soil CO₂ evolution combined with frequent disturbance from harvesting will likely limit significant accumulation of

mineral soil C in these systems (Richter *et al.*, 1999). Most belowground carbon accumulation during stand development is the result of accretion of coarse woody laterals and taproots (Richter *et al.*, 1995). Additionally, because dead woody laterals and taproots decompose very slowly, long-term carbon storage over multiple rotations is tied to the accumulation of belowground coarse woody debris (Johnsen *et al.*, 2001). Taproots and large lateral roots can persist for 50 or more years after harvest (Van Lear *et al.*, 1995, Ludovici *et al.*, 2002) providing zones of enhanced fertility and soil moisture that will impact stand productivity for many years (Van Lear *et al.*, 2000).

Conclusions

Manipulation of site resources had a significant impact on stand NPP, GPP, R_A, R_E, and NEP. Autotrophic respiration was greater than 50% of GPP in all treatments of which, maintenance respiration was the largest component (≈82%). CUE was conservative (0.42) therefore; the proportion of assimilated carbon used for maintenance and construction respiration was similar between treatments. Soil CO₂ evolution was the largest component of R_E. Irrigation increased S_{ff} most likely though increased R_H. At age 12, NEP in non-fertilized treatments was roughly zero indicating these stands were still not a sink for atmospheric carbon. In contrast, positive NEP (6.4 Mg C ha⁻¹ yr⁻¹) in the fertilized stands shows that these stands were functioning as strong carbon sinks. We conclude that (1) on nutrient poor soils, site carbon balance recovers very slowly after disturbance (e.g. harvesting and site preparation) and (2) increasing productivity through management of site resources will likely result in an overall increase in carbon sequestration in loblolly pine plantations.

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Appendix 1. Equations for predicting component maintenance respiration (R_M), growth respiration (R_G) and soil CO₂ evolution (S_{ff}).

Woody tissue

Woody tissue maintenance (R_M) and growth (R_G) respiration were estimated from monthly measurements of tissue CO₂ efflux (Maier, 2000; 2001; Maier *et al.*, 1998). The mature tissue method (Amthor 1989, 2000) was used to partition measured CO₂ efflux into R_M and R_G components. This approach assumes that respiration during the dormant season (December–February), when growth is minimal, represents primarily R_M . Tissue R_M was calculated as a function of tissue temperature and nitrogen content using the following:

$$\tau R_{Mi} = (b_0 + b_1 * W_i) * e^{k * T},$$

where $R_{Mi} = \mu\text{mol CO}_2 \text{ s}^{-1}$, W_i = component nitrogen content (moles), $T = ^\circ\text{C}$, τ is a scaling factor.

Stem, branch and taproot: $b_0 = -0.000109$; $b_1 = 0.590$;
 $k = 0.069$.

Coarse root: $b_0 = 0.001333$; $b_1 = 0.994$;
 $k = 0.067$.

During the growing season, R_G was estimated as the difference between the measured respiration rate and estimated R_M . The growth coefficient (r_g) was calcu-

lated as the slope of the relationship between R_G and stem growth (Maier, 2001).

Fine roots and foliage

Fine root and foliage R_M were estimated using an approach similar to that used for woody tissue. Fine root R_M was measured on excavated fine roots during dormant season (Maier 2000). For foliage, respiration measurements were made on fully expanded needles four times during the year (Maier, 2000). Tissue R_M was calculated as a function of tissue temperature and carbon mass using the following:

$$\tau R_{Mi} = b_0 * W_i * e^{k * T},$$

where $R_{Mi} = \mu\text{mol CO}_2 \text{ s}^{-1}$, W_i = component carbon mass (kg), $T = ^\circ\text{C}$, τ is a scaling factor.

Fine roots: $b_0 = 0.3750$; $k = 0.070$.

Foliage

(Nov–Jan) $b_0 = 0.0630$; $k = 0.072$.

(Feb–Apr) $b_0 = 0.1026$; $k = 0.069$.

(May–Jul) $b_0 = 0.1237$; $k = 0.045$.

(Aug–Oct) $b_0 = 0.0550$; $k = 0.065$.

Soil CO₂ evolution

Seasonal patterns of soil CO₂ evolution (S_{ff}) were estimated from monthly measurements of soil CO₂ evolution, soil temperature, and moisture (Maier and Kress, 2000). The seasonal pattern of S_{ff} was modeled using an equation adapted from Hanson *et al.* (1993):

$$\tau S_{ff} = (m * \theta_s^m * R_{\max}) / ((m * \theta_s) + R_{\max}) * Q^{T/10}$$

where $S_{ff} = \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, θ_s = volumetric soil water; Q = rate change in S_{ff} with 10 °C increase in soil temperature; R_{\max} is maximum S_{ff} , τ is a scaling factor.

Control: $m = 0.187$; $R_{\max} = 1.289$; $Q_{10} = 2.37$.

Irrigated: $m = 0.307$; $R_{\max} = 1.195$; $Q_{10} = 2.25$.

Fertilized: $m = 0.278$; $R_{\max} = 1.088$; $Q_{10} = 2.40$.

Irr + fert: $m = 0.197$; $R_{\max} = 2.268$; $Q_{10} = 2.19$.