Ecological Applications, 14(4), 2004, pp. 1154–1171
© 2004 by the Ecological Society of America

CARBON DYNAMICS ALONG A CHRONOSEQUENCE OF SLASH PINE PLANTATIONS IN NORTH FLORIDA

KENNETH L. CLARK,[1,3] HENRY L. GHOLZ,[1,4] AND MARK S. CASTRO[2]

[1]*School of Forest Resources and Conservation, University of Florida, P.O. Box 110410, Gainesville, Florida 32611 USA*
[2]*University of Maryland, Center for Environmental Science, Appalachian Laboratory, Frostburg, Maryland 21532 USA*

Abstract. To determine factors controlling the carbon dynamics of an intensively managed landscape, we measured net CO_2 exchange with the atmosphere using eddy covariance and soil CO_2 fluxes using static chambers along a chronosequence of slash pine (*Pinus elliottii* var. *elliottii*) plantations consisting of a recent clearcut, a mid-rotation (10-yr-old) stand, and a rotation-aged (24-yr-old) stand. Daytime net ecosystem exchange of CO_2 (NEE_{day}) at the clearcut was not significantly different than zero during the growing season of the first year following harvest and reached levels that were ~40% of those at the older stands during the second growing season. NEE_{day} was similar at the mid-rotation and rotation-aged sites, reflecting the similar leaf areas of these stands. Nighttime net ecosystem exchange of CO_2 (NEE_{night}) was an exponential function of air or soil temperature at all sites. However, low decomposition rates of litter and flooding of the site following harvest likely constrained NEE_{night} at the clearcut, and drought affected rates at the mid-rotation site. Annual net ecosystem exchange of CO_2 (NEE_{yr}) was estimated at -1269 and -882 g $C \cdot m^{-2} \cdot yr^{-1}$ at the clearcut, and 576 and 603 g $C \cdot m^{-2} \cdot yr^{-1}$ at the mid-rotation stand in 1998 and 1999, respectively. For comparison, NEE_{yr} was 741 and 610 g $C \cdot m^{-2} \cdot yr^{-1}$ at the rotation-aged stand in 1996 and 1997, respectively. In contrast, annual ecosystem respiration (R_{eco}) was similar in magnitude at all sites during all years. Although R_{eco} is similar in magnitude, NEE_{yr} is highly dynamic across this intensively managed landscape, with a maximum range of ~2000 g $C \cdot m^{-2} \cdot yr^{-1}$. This range exceeds that across all the sites in both the Ameriflux and Euroflux networks and illustrates the need to include the range of stand ages and disturbance histories in landscape- to regional-scale flux estimates.

Key words: carbon cycle; eddy covariance; Florida, USA; management cycle; net carbon exchange; slash pine plantation.

INTRODUCTION

Fire and hurricane damage have historically been the major large-scale, intense disturbances to forest ecosystems in the southeast United States (Myers and Ewel 1990). Recently, forest management has assumed this role. For example, managed, even-aged pine flatwoods are now the most extensive forest ecosystem in North Florida, comprising ~70% of the forested landscape. Stands are typically harvested on a rotation interval of 15–25 years. Mechanized harvesting is usually stem-only, and the residual branches, foliage, and understory are "raked" into slash piles and left to decompose or are burned. Shortly after harvest, sites are bedded, which mixes much of the remaining fine litter into the soil and also exposes bare soil. Sites are then allowed to lie fallow for up to a year, during which time native understory vegetation regenerates (unless, as in some cases, herbicides are applied). Trees are typically planted at harvest density following a second bedding treatment. These intensively managed stands occur within a matrix of older pine stands, cypress swamps that are managed at longer return intervals, and lakes.

Carbon (C) balances of these intensively managed landscapes are highly dynamic. During and immediately following harvesting, leaf area and biomass are minimal, detrital mass is large, and net CO_2 exchange with the atmosphere (NEE) is likely dominated by heterotrophic respiration. If detrital inputs decompose rapidly, the sum of heterotrophic and autotrophic respiration, termed ecosystem respiration (R_{eco}), may exceed pre-disturbance levels and result in a large release of CO_2 to the atmosphere. In contrast, young, aggrading pine stands can accumulate C at high rates, often exceeding 500 g $C \cdot m^{-2} \cdot yr^{-1}$ in stemwood increment alone (Jokela and Martin 2000, FAO 2001*a*, Oren et al. 2001). For example, using eddy covariance to estimate whole-ecosystem CO_2 exchange, Lai et al. (2002) reported that a 17-yr-old loblolly pine (*Pinus taeda*) plantation accumulated 605 g $C \cdot m^{-2} \cdot yr^{-1}$, and Clark et al. (1999) reported that a late-rotation slash pine (*P. elliottii* var. *elliottii*) plantation accumulated 740 and 610

Manuscript received 5 December 2002; revised 6 July 2003; accepted 8 September 2003; final version received 29 October 2003. Corresponding Editor: M. L. Goulden.

[3] Present address: USDA Forest Service, Northeastern Research Station, 501 Four Mile Road, New Lisbon, New Jersey 08064 USA. E-mail: kennethclark@fs.fed.us

[4] Present address: Division of Environmental Biology 635.01, National Science Foundation, 4201 Wilson Boulevard, Arlington, Virginia 22230 USA.

g $C \cdot m^{-2} \cdot yr^{-1}$ over two consecutive years. Increments in detritus, mainly fine litter in managed stands, can add substantial amounts to total C accumulation in unburned forests, because pine litter decomposes relatively slowly (Gholz et al. 2000).

The magnitude of C loss following harvest, timing of the switch between "source" and "sink" during the reorganization phase of regeneration (sensu Borman and Likens 1979), and duration and magnitude of the C sink determine the long-term C balance of these landscapes. Although plantation forestry is an increasingly important land use across the southeastern Coastal Plain, few estimates exist to evaluate the C dynamics of these intensively managed systems. Using a C mass balance approach across a 35-yr chronosequence of 21 different slash pine plantations in North Florida, Gholz and Fisher (1982) inferred that net ecosystem production was -742 g $C \cdot m^{-2} \cdot yr^{-1}$ during the first year following harvest, neutral at approximately 3 yr, and peaked at 484 g $C \cdot m^{-2} \cdot yr^{-1}$ 11 yr following harvest. Thornton et al. (2002) used the Biome-BioGeochemical Cycles (BGC) model to simulate C dynamics of a number of conifer forests after clearcutting and predicted that C loss following harvest of a slash pine plantation in North Florida reached -522 g $\cdot m^{-2} \cdot yr^{-1}$, C balance was neutral at 5 yr, and the maximum C accumulation rate was 351 g $C \cdot m^{-2} \cdot yr^{-1}$ 10 yr following harvest. Although both the chronosequence and modeling approaches have been extensively used to evaluate the short- and long-term C balance of these ecosystems (see also Ewel and Gholz [1991], Cropper and Gholz [1993]), we lack independent, direct measurements to evaluate their predictions. In addition, an understanding of the factors controlling net CO_2 exchange in these forests through management cycles is key to evaluating the sustainability of a number of management practices, where trade-offs exist between the timing and type of harvest, the use of understory control, vegetation and soil C storage, soil nutrient status, and the conservation value of converting native forest to pine plantations.

Our objective was to use eddy covariance to evaluate the empirical model of rotation-length C dynamics in managed slash pine stands proposed by Gholz and Fisher (1982) and later simulated by Ewel and Gholz (1991), Cropper and Gholz (1993), and Thornton et al. (2002), in terms of the magnitude and duration of C loss following harvest and the magnitude and timing of the maximum C sink. While the empirical model was primarily descriptive, further modeling, field measurements, and analysis allow us to determine the major factors controlling net CO_2 exchange with the atmosphere and soil CO_2 fluxes at a range of time steps. We used a chronosequence consisting of a recent clearcut, two mid-rotation (9- to 11-yr-old) stands, and a rotation-aged stand (23- to 25-yr-old) to test the hypotheses that (1) rates of daytime net CO_2 exchange are directly related to leaf area and thus parallel vegetation recovery following harvesting and disturbance at the clearcut, (2) nighttime net CO_2 exchange rates are similar among stands along the chronosequence, because heterotrophic respiration is largely controlled by litter quality, which is low in slash pine flatwoods, and (3) annual net CO_2 exchange peaks as early as the time of crown closure (8 yr following replanting in Gholz and Fisher [1982]), and then decreases with increases in respiring biomass in older stands.

Methods and Materials

Study sites

Study sites were established 15 km northeast of Gainesville, Alachua County, Florida, USA (29°44′ N, 82°9′30″ W). Long-term (1955–2000) mean January and July temperatures were 14°C and 27°C, respectively (NCDC 2001). Mean monthly minimum and maximum temperatures throughout the study period (January 1998 to December 1999) ranged from 5.9°C to 19.5°C and from 21.5°C to 32.9°C for January and July, respectively. Long-term mean annual rainfall for Gainesville was 1332 mm, and annual precipitation in 1997, 1998, and 1999 was 1391, 1247, and 942 mm, respectively. Soils of the sites are ultic alaquods (sandy, siliceous, thermic) that are poorly drained and low in organic matter and available nutrients. The distributions of discontinuous subsurface spodic (organic) and argillic (clay) horizons range between 30 and 70 cm and between 100 and 200 cm depth, respectively (Gaston et al. 1990).

The 85-ha clearcut site was previously dominated by a 25-yr-old (in 1997) plantation of *Pinus elliottii* var. *elliottii* Englm. established on industry land and managed for pulpwood production (Clark et al. 1999). Following stem-only harvest of this stand (May 1997 to January 1998), woody residue was raked into piles, and the site was bedded twice (June and November 1998). Mixed genotype seedlings were then planted at harvest density during December 1998 and January 1999 (Table 1). Other common species included *Ilex glabra* (L.) A. Gray, *Serenoa repens* (W. Bartram) Small, *Myrica cerifera* L., *Lyonia* spp., *Lachnanthes caroliniana* (Lam.) Dandy, *Rubus* spp., grasses, and sedges. The site was not fertilized during the study. The water table fluctuated from the surface to ~1.3 m depth during our study.

The mid-rotation sites were also slash pine plantations on industry land, established in 1989 and 1990. Two sites were used because the first stand was damaged by wildfire in June 1998, after which measurements were moved to a second stand nearby. The soils and management histories were indistinguishable between the two sites, so all data were pooled for analysis and referred to collectively as the "mid-rotation site" below. Trees had been planted at harvest densities, following similar harvest and site preparation (Table 1). Understory vegetation consisted of native species reestablished naturally after site preparation, primarily

TABLE 1. Structural characteristics for the clearcut, mid-rotation, and rotation-aged stands established 15 km northeast of Gainesville, Alachua County, Florida, USA.

Parameter	Clearcut	Mid-rotation	Rotation-aged†
Years since harvest	0–2	10–12	24–26
Stem density (no. stems/ha)	0	2084 ± 132	1301 ± 81
Stand height (m)	0.3–1.0	9.9 ± 1.3	19.2 ± 1.0
Stem diameter at 1.3 m (cm)	0	9.8 ± 0.4	17.4 ± 0.2
Basal area (m^2/ha)	0	16.4 ± 0.7	31.4 ± 1.4
Leaf area index (m^2/m^2)	0.1–3.0	3.1–5.1	4.0–6.5

Notes: Sample sizes are 20–30 plots (0.5 and 1.0 m^2) at the clearcut and four plots (625 m^2 each) for the mid-rotation and rotation-aged sites. Values are means ± 1 SD.

† From Clark et al. (1999).

Serenoa repens, *Ilex glabra*, and *Myrica cerifera*. Other common species included *Gelsemium sempervirens* (L.) Saint-Hilaire, *Vaccinium* spp., and *Galusaccia* spp. Minimum fetch from the towers was ~800 m, and both stands were surrounded by other slash pine plantations between 5 and 25 years in age. The water table fluctuated from the surface to below 2.7 m depth during our study.

The rotation-aged stand formerly at our clearcut site had been planted at harvest density in 1973, following similar harvest and site preparation (Table 1). Understory vegetation consisted of native species reestablished naturally after site preparation, primarily *Serenoa repens*, *Ilex glabra*, and *Myrica cerifera*, grasses, and herbs. Minimum fetch from the tower was ~800 m. This site was also surrounded by other slash pine plantations between 10 and 25 years in age. Details of this site and previous flux measurements are in Clark et al. (1999) and Gholz and Clark (2002).

Eddy covariance measurements

Net ecosystem exchange (NEE) of CO_2 was estimated using a closed-path eddy covariance system composed of a three-dimensional sonic anemometer (R3A, Gill Instruments, Lymington, UK), a closed-path infrared gas analyzer (LI-6262, LI-COR, Lincoln, Nebraska, USA), a 30 m long, 0.4 cm inner diameter teflon-coated tube and a small air pump, and a lap-top PC running RCOM software (Moncrieff et al. 1997, Clark et al. 1999, Gholz and Clark 2002). Sonic anemometers were mounted 4 m above the canopy at all sites. The inlet of the tube was placed between the upper and lower sensors of the sonic anemometer, and air was drawn through the LI-6262 at a rate of 5.0 to 6.0 L/min, using a mass flow controller (Tylan General, Torrance, California, USA) or calibrated rotometers to regulate flowrates. The mean lag time from the tube inlet on the tower to the LI-6262 at the base was 5–7.5 s for all sites. The LI-6262 was calibrated frequently (every 1–2 d) using CO_2 tanks that were traceable to primary standards. Coordinate rotation of the raw sonic anemometer signals was used to obtain turbulence statistics perpendicular to the local streamline. The maximum values for the covariance between turbulence and CO_2 concentrations were compared to a 200-s digital recursive mean to calculate instantaneous fluxes (Katul et al. 1999). Net CO_2 exchange was then calculated at half-hour intervals. Fluxes were corrected for frequency attenuation of scalar concentrations down the sampling tube and non-ideal frequency response of the LI-6262 using transfer functions (Moncrieff et al. 1997). Barometric pressure data were then used to calculate fluxes at ambient atmospheric pressure. Half-hourly changes in CO_2 concentration at the height of the sampling inlet were used to estimate the flux associated with the change in storage of CO_2 in the air column beneath the inlet at the clearcut (4 m^3), and either this method or a profile system with inlets at 2, 5, and 10 m height were used to estimate CO_2 storage at the mid-rotation site. We used the sign convention that positive values of NEE were from the atmosphere to the ecosystem.

Flux data were collected on 209 and 273 days at the clearcut and mid-rotation site, respectively. Flux data were rejected when collected during periods with measurable rainfall, when 30-min periods were incomplete, or when condensation was observed in the sampling lines, resulting in a total of 7472 and 9827 half-hourly values for the clearcut and mid-rotation site, respectively. Previous research indicated that the sum of sensible, latent, and soil heat fluxes accounted for a mean of 90% and 86% of net radiation measured at the clearcut and mid-rotation site, respectively (Gholz and Clark 2002). Soil heat fluxes were not measured at the rotation-aged site, but sensible and latent heat fluxes together accounted for a mean of 75% of net radiation.

For the analyses presented here, only daytime and nighttime data collected during periods when the canopy was well coupled with the atmosphere were used (e.g., Goulden et al. 1996*b*, Falge et al. 2001). We estimated well-coupled conditions by plotting nighttime NEE (NEE_{night}) vs. friction velocity, u^*, for values of air temperature binned in 2°C increments, and used the mean u^* values where NEE_{night} had reached an asymptote. Resultant u^* thresholds were 0.1 m/s at the clearcut and 0.2 m/s at the mid-rotation and rotation-aged stands. Of the half-hourly values measured, 49.4% and 52.1% occurred above these u^* thresholds at the clearcut and the mid-rotation site, respectively.

Soil CO_2 measurements

Soil CO_2 fluxes were measured at eight permanent locations at each site (two in each biomass census plot at the clearcut and two in each tree census plot at the forested sites). Static chambers (29 cm diameter, 10 cm tall, ~6605 cm^3) were placed over anchors fixed in the forest floor for 20 min, and air in the headspace was sampled with 20-mL nylon syringes at 0, 5, 10, 15, and 20 min. Soil CO_2 fluxes were sampled three times from each chamber during a 24-h sampling period: early morning, midday, and early evening. Syringe samples were analyzed for CO_2 using a Shimadzu 8A gas chromatograph (Shimadzu, Columbia, Maryland, USA) equipped with a flame ionization detector. Gas standards (Scott Specialty Gases, Plumsteadville, Pennsylvania, USA) that bracketed sample concentrations were analyzed with samples. Litter temperature and soil temperature (5 cm depth) were measured at each chamber at the beginning and end of each 20-min sampling period using Omega (Stamford, Connecticut, USA) or Fisher Scientific (Pittsburgh, Pennsylvania, USA) dial thermometers. Soil water content at 0–10 cm depth was estimated from soil cores that were placed in soil cans. Soil samples in cans were weighed, dried at 60°C, and weighed again to calculate soil water content. Soil CO_2 measurements were made approximately once every two months at each site and encompassed the range of soil temperatures and moisture conditions.

Meteorological measurements

Incident shortwave radiation (LI-200; LI-COR), photosynthetic photon flux density (PPFD) (LI-190; LI-COR), net radiation (Q7; Radiation and Energy Balance Systems, Seattle, Washington, USA), air temperature and relative humidity (HMP 23 UT; Vaisala, Helsinki, Finland; mounted in a Stevens enclosure), windspeed and direction (12-002; R. M. Young, Traverse City, Michigan, USA), and precipitation (TI-525; Texas Electronics, Dallas, Texas, USA) were measured on the towers at all sites. Soil temperatures were measured at 5 cm depth (ES-060, Omnidata International, Logan, Utah, USA), and soil heat flux was measured using heat flux plates (HFT-3.1, Radiation and Energy Balance Systems) buried at 10 cm depth at the clearcut and the mid-rotation age sites. Meteorological data were recorded with automated data loggers (Easy Logger EL824-GP; Omnidata). Water table depth was measured with a Stevens water depth gauge (F-68; Leupold and Stevens, Beaverton, Oregon, USA) at each site. Soil water content measurements were made at regular intervals throughout the sampling period. Barometric pressure data were obtained from the Gainesville Regional Airport, within ~6–10 km of the sites.

Net ecosystem exchange, ecosystem respiration, and soil respiration

Annual estimates of NEE require continuous values of half-hourly CO_2 exchange. To estimate daytime net CO_2 exchange (NEE_{day}) for periods when we did not have measurements, we fit a rectangular hyperbola to the relationship between PPFD and NEE_{day} (Ruimy et al. 1995):

$$NEE_{day} = \frac{\alpha PPFD F_{max}}{\alpha PPFD + F_{max}} - R \quad (1)$$

where α is the apparent quantum yield ($dF_{CO2}/dPPFD$ at PPFD = 0), F_{max} is the net CO_2 exchange at light saturation, and R is the mean net CO_2 exchange at PPFD = 0. To estimate nighttime net CO_2 exchange (NEE_{night}), half-hourly net exchange rates were regressed on air or soil temperature using an exponential function with the following form:

$$NEE_{night} = a \exp(bT) \quad (2)$$

where a and b are regression coefficients and T is the mean half-hourly air or soil temperature. SigmaPlot 5.0 Regression Wizard software (SPSS, Chicago, Illinois, USA) was used to estimate parameters in Eqs. 1 and 2. We then used modeled data calculated from the continuous meteorological data for periods when we did not have measured fluxes to estimate annual NEE for each site. Annual R_{eco} was calculated for each site using continuous half-hourly air or soil temperature and Eq. 2, and modeled values were again used to estimate nighttime net CO_2 exchange for periods when we did not have measured fluxes. Similarly, annual soil respiration was calculated for all three sites using continuous half-hourly soil temperature and a function similar to Eq. 2 calculated from soil CO_2 measurements. We had less continuous soil temperature data from sites, due to harvesting of the rotation-aged site in 1997 and the wildfire at the first mid-rotation site in 1998. Therefore, we calculated annual soil CO_2 fluxes for 1998 and 1999 at the clearcut, but only for 1999 at the mid-rotation site, and only for 1996 at the rotation-aged site. We used ± 1 SE of the value of each parameter in Eqs. 1 and 2 to evaluate the sensitivity of annual estimates to modeled values. We also evaluated different threshold values of u^* (± 0.05 m/s), slight errors in the measurement of PPFD (± 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and temperature ($\pm 0.5$°C) on modeled values used in annual estimates.

"Summer and fall" was defined as May through October and "winter and spring" as November through April. These periods roughly correspond to a growing and a dormant season, because slash pine holds two age classes of foliage through the summer and fall, but only one in the winter and spring (Gholz et al. 1991*b*). Understory leaf area is also reduced in the winter and early spring, because perennial herbs die back in the winter, and a number of shrubs are deciduous. However, substantial photosynthesis (Teskey et al. 1994) and net C exchange (Clark et al. 1999) can occur during winter and spring.

Biomass and litterfall measurements

Stem removal during the harvesting of the clearcut site was estimated as the difference between the total stand biomass estimated in 1997 (Clark et al. 1999) and the sum of residual material in 20 0.5-m^2 plots (fine litter) and four 100-m^2 plots (coarse wood) measured before litter "raking" and the first bedding treatment. Aboveground biomass accumulation at the clearcut was estimated using clip plots (0.5 m^2 or 1.0 m^2) at 3, 6, 12, and 24 mo following harvest. Plots (n = 20–30) were located randomly within the vicinity of the meteorological tower. Samples were separated into grasses, herbs, shrubs, and palms, dried at 60°C, and weighed. A leaf area meter (Delta T Devices, Burwell, Cambridge, UK) and fresh samples that were then dried at 60°C and weighed were used to develop equations to estimate leaf area of each group from dry mass at the clearcut.

Tree inventories and measurements of diameter at 1.3 m (dbh, in centimeters) and height (in meters) were conducted annually in four 625-m^2 plots at the mid-rotation and rotation-aged sites (Table 1). Tree biomass and growth increments were estimated from allometric relationships based on destructive harvest of 35 trees from the mid-rotation site and published allometric relationships for the rotation-aged site (Gholz et al. 1991*b*). Understory biomass at the mid-rotation and rotation-aged sites was estimated from census data in each plot using allometric relationships based on various plant dimensions (Gholz et al. 1999; H. L. Gholz and K. L. Clark, *personal observations*). Fine litterfall was collected monthly from 10 1-m^2 traps at random locations in two of the four measurement plots at the mid-rotation and rotation-aged sites. Forest floor mass (five 0.1-m^2 samples per plot) and coarse woody debris were sampled in each plot at the end of the study. Values obtained from a CNS analyzer (Carlo Erba, Milan, Italy) and mass loss on ignition at 550°C (H. L. Gholz and K. L. Clark, *personal observations*) was used to convert biomass to C mass.

Comparison to empirical chronosequence model

Gholz and Fisher (1982) sampled biomass, forest floor, and soil C pools along a chronosequence of stands ranging from recent clearcuts to 35-yr-old stands to infer rates of C accumulation in slash pine plantations following harvest. We extrapolated annual net ecosystem productivity (NEP) from their data and compared these to annual NEE estimates obtained here. Carbon pools in biomass and forest floor were also compared to those obtained in our study. The original study noted much lower stem density for the oldest (35-yr-old) stands, but not a correspondingly higher mass of coarse woody debris. This led us to conclude that the oldest stands had in fact been planted at a lower density, so that for this retrospective analysis we truncated the original chronosequence at 27 yr (similar to the approach used by Thornton et al. [2002]).

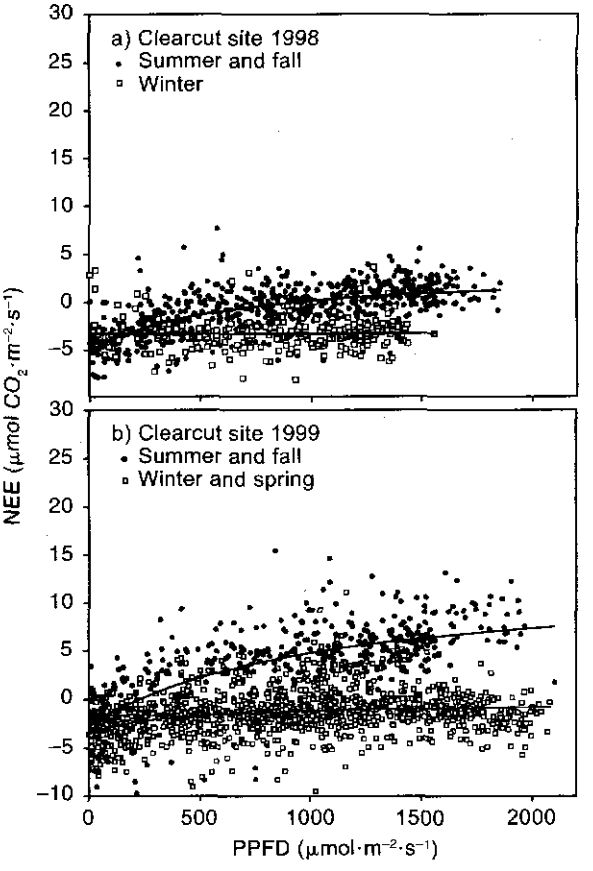

FIG. 1. Daytime net CO_2 exchange (NEE) as a function of photosynthetic photon flux density (PPFD) at the clearcut site during the (a) first year following harvest and (b) second year following harvest. Study sites were established 15 km northeast of Gainesville, Alachua County, Florida, USA. Regression equations and statistics are given in Table 2.

RESULTS

Net CO_2 exchange

During the growing season (summer and fall 1998) of the first year following harvest at the clearcut, daytime net CO_2 exchange (NEE_{day}) was often positive, but only weakly related to PPFD (Fig. 1a, closed circles; Table 2). Daytime exchange rates were reduced to much less than zero following the second bedding treatment, tree planting, and the first hard freezes at the end of November and early December 1998, which reduced leaf area index (LAI) substantially (Fig. 1a, open squares). NEE_{day} remained below zero throughout the winter and spring of the second year following harvest and then became a strong curvilinear function of PPFD during the second growing season (Fig. 1b, closed circles). Mean maximum rates of NEE_{day} at this time reached 6.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ at 1500 μmol PPFD $\cdot m^{-2} \cdot s^{-1}$. Daytime exchange rates were again re-

TABLE 2. Equation parameters and statistics for daytime net CO_2 exchange (NEE_{day}) as a function of photosynthetically active radiation along the chronosequence.

Site and sampling period	α	F_{max}	R	n	r^2	P
Clearcut						
1998 summer and fall	0.014 ± 0.003	8.437 ± 0.475	−5.076 ± 0.345	612	0.45	<0.0001
1998 winter†	0.001 ± 0.001	···	−4.469 ± 0.329	283	0.02	0.0083
1999 summer and fall	0.011 ± 0.002	17.643 ± 2.584	−2.392 ± 0.421	534	0.47	<0.0001
1999 winter and spring	0.009 ± 0.004	3.170 ± 0.342	−3.468 ± 0.324	1123	0.08	<0.0001
Mid-rotation						
Winter and spring						
VPD < 2 kPa	0.050 ± 0.005	24.691 ± 0.603	−3.757 ± 0.530	1203	0.63	<0.0001
VPD ≥ 2 kPa	0.015 ± 0.009	23.756 ± 7.579	−0.356 ± 2.419	116	0.41	<0.0001
Spring/summer drought						
VPD < 2 kPa	0.035 ± 0.003	29.108 ± 0.883	−5.078 ± 0.451	1046	0.71	<0.0001
VPD ≥ 2 kPa	0.018 ± 0.004	22.428 ± 1.571	−3.418 ± 1.024	716	0.41	<0.0001
Summer and fall						
VPD < 2 kPa	0.078 ± 0.011	33.967 ± 1.101	−7.631 ± 1.080	507	0.67	<0.0001
VPD ≥ 2 kPa	0.045 ± 0.029	27.156 ± 3.130	−6.094 ± 4.915	167	0.35	<0.0001
Rotation-aged‡						
Summer and fall	0.044 ± 0.005	26.537 ± 1.329	−4.616 ± 1.163	218	0.70	<0.0001
Winter and spring	0.038 ± 0.005	29.280 ± 1.809	−3.044 ± 0.552	353	0.78	<0.0001

Notes: Data were fit to Eq. 1: $NEE_{day} = [\alpha\ PPFD\ F_{max}/(\alpha\ PPFD + F_{max})] - R$. Parameter definitions: α, apparent quantum yield at PPFD = 0; PPFD, photosynthetic photon flux density; F_{max}, net CO_2 exchange at light saturation; R, mean net CO_2 exchange at PPFD = 0; VPD, vapor pressure deficit. Parameter values are reported as means ± 1 SE. P values are for overall model fit.

† Equation with the form $\alpha \times PPFD + R$.

‡ These data have been published previously in Clark et al. (1999).

duced considerably following the first hard freezes at the end of November and early December 1999 (Fig. 1b, open squares). Mean Bowen ratios (sensible heat flux/latent heat flux) rarely exceeded 0.72, indicating that little drought stress occurred throughout the study (Gholz and Clark 2002).

In contrast to the clearcut, NEE_{day} at the mid-rotation and rotation-aged sites were strong curvilinear functions of PPFD throughout the measurement periods (Fig. 2, Table 2). Although parameters relating daytime net CO_2 exchange to PPFD were significantly different during summer and winter periods at the mid-rotation site ($t = 2.82$ for α, $t = 3.04$ for F_{max}, $t = 5.51$ for R; df = 3753, $P < 0.01$ for all comparisons), minimal seasonality was observed for instantaneous rates of net CO_2 exchange during the daytime. Mean maximum rates of NEE_{day} at 1500 μmol PPFD·m^{-2}·s^{-1} reached 14.7 μmol CO_2·m^{-2}·s^{-1} in the summer and 14.5 μmol CO_2·m^{-2}·s^{-1} in the winter. Reduced rates of NEE_{day} were observed during all seasons when vapor pressure deficit (VPD) was >2 kPa, but model parameters were significantly lower only during periods of drought when the water table was below 2.7 m depth in spring 1999 ($t = 4.86$ for α, $t = 5.44$ for F_{max}, $t = 2.25$ for R; df = 1760, $P < 0.01$ for comparisons of α and F_{max}, and $P < 0.05$ for R; Fig. 2b, open squares; Table 2). Mean maximum rates reached only 9.1 μmol CO_2·m^{-2}·s^{-1} at 1500 μmol PPFD·m^{-2}·s^{-1} during these periods. Reduced latent energy flux relative to sensible heat was also observed, with mean Bowen ratios of 0.5 in the summer and fall and >0.83 during spring 1999 (Gholz and Clark 2002).

At the rotation-aged site, parameters relating half-hourly NEE_{day} to PPFD were similar for summer and winter periods, and little seasonality was observed at the same light levels (Clark et al. 1999; Table 2). The water table depth ranged from 0.2 to 1.3 m from the surface, indicating that little drought stress occurred throughout the measurement period (May 1995 to April 1997).

Nighttime net CO_2 exchange (NEE_{night}) was an exponential function of air and soil temperatures during well-coupled conditions at all sites ($u^* > 0.1$ m/s at the clearcut and $u^* > 0.2$ m/s at the mid-rotation and rotation-aged sites; Table 3). However, soil water status apparently affected NEE_{night} at both the clearcut and the mid-rotation site at some time during our study. At the clearcut, NEE_{night} was only a weak function of air or soil temperature when the site was flooded during the growing season of the first year following harvest (Fig. 3, closed circles) and then became a much stronger function of temperature when the soil was drier during the winter of 1998 and throughout the second year following harvest (Fig. 3, open squares; Table 3). Parameters used to model NEE_{night} as a function of air temperature differed between the two sample periods ($t = 5.91$ for a, $t = 8.57$ for b; df = 1140, $P < 0.01$ for both comparisons), and mean nighttime net CO_2 exchange at an air temperature of 20°C was calculated at −4.5 and −5.7 μmol CO_2·m^{-2}·s^{-1} during flooded

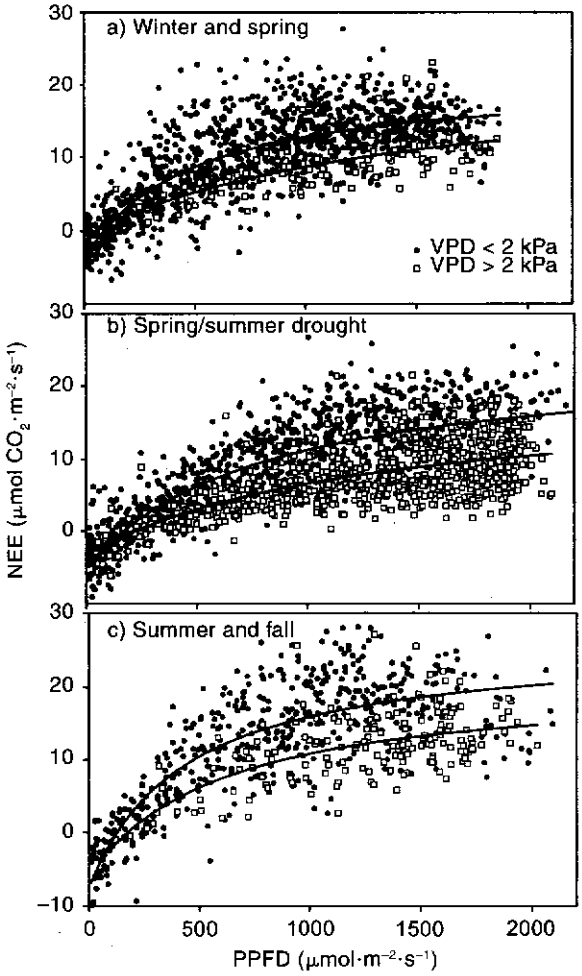

FIG. 2. Daytime net CO_2 exchange (NEE) as a function of photosynthetic photon flux density (PPFD) at the mid-rotation-aged sites during (a) winter and spring, (b) spring to early summer drought, and (c) summer and fall. Regression equations and statistics are given in Table 2. VPD is the vapor pressure deficit.

and relatively dry conditions, respectively. Slightly higher Q_{10} values resulted when NEE_{night} was modeled as a function of soil temperature when compared to air temperature during both sampling periods (Table 3).

Under well-mixed conditions at the mid-rotation site, NEE_{night} was a stronger function of air or soil temperature during relatively wet conditions in 1998 and in the summer and fall of 1999 (Fig. 4, closed circles) than during drier periods in late winter and spring of 1999 (Fig. 4, open squares; Table 3). Parameters used to model NEE_{night} as a function of air temperature differed between the two periods ($t = 3.31$ for *a*, $t = 6.86$ for *b*; df = 1337, $P < 0.01$ for both comparisons; Table 3), and mean NEE_{night} calculated at an air temperature of 20°C was −5.5 and −4.4 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ during wet and relatively dry periods, respectively. Eqs. relating NEE_{night} to soil temperature at 5 cm depth at the mid-rotation site also resulted in slightly higher Q_{10} values when compared to those using air temperatures during both sampling periods (Table 3).

Parameters used to model the relationship between NEE_{night} and air temperature were significantly different when dry conditions at the clearcut were compared to wet conditions at the mid-rotation site (the more typical situations; $t = 1.92$, $P < 0.1$ for *a*, $t = 2.86$, $P < 0.01$ for *b*; df = 1586 for both comparisons; Table 3). However, mean NEE_{night} was similar across a range of temperatures; mean rates were −5.7 vs. −5.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ at an air temperature of 20°C and −7.5 vs. −6.7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ at an air temperature of 25°C at the clearcut and the mid-rotation site, respectively. Interestingly, parameters relating NEE_{night} to air temperature or soil temperature were similar for flooded conditions at the clearcut and dry conditions at the mid-rotation site.

At the rotation-aged site, NEE_{night} was also a significant function of air and soil temperature (Table 3; Clark et al. 1999). All measurements were made during relatively moist soil conditions.

Soil CO_2 flux

Soil CO_2 fluxes were a similar exponential function of soil temperature across all three sites when all data were pooled within each site (Fig. 5, Table 4). Mean rates at a soil temperature of 20°C were −2.5, −2.4, and −2.7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ at the clearcut, mid-rotation, and rotation-aged sites, respectively. However, midday soil heat flux was 3–5 times greater, and mean daytime soil temperature was 2°–3°C higher at the clearcut during the summer of the first year following harvest when compared to the mid-rotation site. As a result, integrated daytime soil CO_2 fluxes were greater at the clearcut when compared to the other two sites. At night, soil temperatures were similar among sites, and calculated half-hourly soil CO_2 fluxes represented a mean of 69.5 ± 29.0% (mean ± 1 SD, $n = 1142$), 68.1 ± 31.6% ($n = 1350$), and 71.9 ± 32.4% ($n = 274$) of NEE_{night} measured at the clearcut, mid-rotation, and rotation-aged sites, respectively. Increased vegetation cover reduced soil heat fluxes at the clearcut during the second year following harvest, and daytime soil temperatures were only slightly higher than those at the mid-rotation site. Consequently, daytime soil CO_2 fluxes were lower at the clearcut during the second year following harvest. Drought conditions also apparently affected soil CO_2 fluxes at the mid-rotation site in 1999. For example, calculated soil respiration represented 71.1 ± 31.6% of measured half-hourly NEE_{night} in 1998, while during dryer periods in 1999, the proportion was 60.6 ± 30.4%. Spatial variability of soil CO_2 fluxes was greatest at the clearcut and least at the rotation-aged site (Table 4).

Annual ecosystem carbon balance and partitioning

Annual NEE (NEE_{yr}) was negative during the first two years following harvest at the clearcut; estimates

TABLE 3. Equation parameters and statistics for nighttime net CO_2 exchange (NEE_{night}) as a function of air or soil temperature along the chronosequence.

Site and sampling period	Temperature (T)	a	b	n	r^2	P	Q_{10}
Clearcut							
First year, flooded	air	3.178 ± 0.276	0.023 ± 0.004	279	0.11	<0.0001	1.3
First year, flooded	soil	2.190 ± 0.343	0.036 ± 0.007	279	0.10	<0.0001	1.4
First and second years, dry	air	1.991 ± 0.126	0.053 ± 0.003	863	0.34	<0.0001	1.7
First and second years, dry	soil	0.762 ± 0.091	0.087 ± 0.005	863	0.36	<0.0001	2.4
Mid-rotation							
Wet conditions	air	2.273 ± 0.168	0.043 ± 0.004	725	0.20	<0.0001	1.6
Wet conditions	soil	1.287 ± 0.305	0.070 ± 0.010	725	0.18	<0.0001	2.0
Dry conditions	air	2.878 ± 0.198	0.019 ± 0.003	614	0.06	<0.001	1.2
Dry conditions	soil	1.775 ± 0.222	0.049 ± 0.007	614	0.05	<0.001	1.6
Rotation-aged†							
Pooled	air	1.509 ± 1.001	0.058 ± 0.003	477	0.36	<0.0001	2.0
Pooled	soil	0.737 ± 0.127	0.083 ± 0.008	259	0.27	<0.0001	2.3

Notes: Data were fit to Eq. 2: $NEE_{night} = a \exp(bT)$. Parameter definitions: a and b, regression coefficients; T, mean half-hourly air or soil temperature. Parameter values are reported as means ± 1 SE. P values are for overall model fit. Q_{10} values were calculated for 15°–25°C.

† These data have been published previously in Clark et al. (1999).

were −1269 g $C \cdot m^{-2} \cdot yr^{-1}$ during the first year and −882 g $C \cdot m^{-2} \cdot yr^{-1}$ during the second year (Table 5). NEE_{yr} was estimated at 576 and 603 g $C \cdot m^{-2} \cdot yr^{-1}$ at the mid-rotation site in 1998 and 1999, respectively. For comparison, NEE_{yr} was previously reported as 741 and 610 g $C \cdot m^{-2} \cdot yr^{-1}$ at the rotation-aged site in 1996 and 1997, respectively (Table 5; Clark et al. 1999). NEE_{yr} was sensitive to different parameters in Eq. 1 used to "fill in" missing daytime fluxes at each site. Using ±1 SE of the mean parameter values individually, maximum deviations from NEE_{yr} calculated using mean parameter values were 10.5%, 21.2%, and 31.5% at the clearcut, mid-rotation, and rotation-aged sites, respectively (Table 5). Potential errors in the measurement of PPFD of ±25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ led to maximum deviations of 2.0%, 14.6%, and 12.1% from NEE_{yr} estimates at the clearcut, mid-rotation, and rotation-aged sites, respectively (Table 5).

A greater number of modeled values were used to calculate nighttime fluxes in the estimation of NEE_{yr}, because low windspeed conditions prevailed throughout the night during the study. Estimates were equally sensitive to both parameters in Eq. 2 used to calculate missing nighttime fluxes, with a maximum deviation of 10.7% from NEE_{yr} calculated using mean parameter values for the mid-rotation site in 1998 (Table 6). Re-

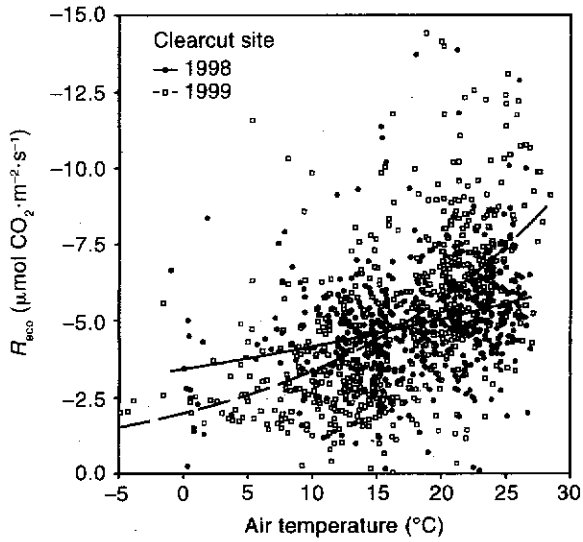

FIG. 3. Ecosystem respiration (R_{eco}; nighttime net CO_2 exchange) as a function of air temperature at the clearcut site when mean half-hourly $u^* > 0.1$ m/s (u^* is friction velocity). Regression equations and statistics are given in Table 3.

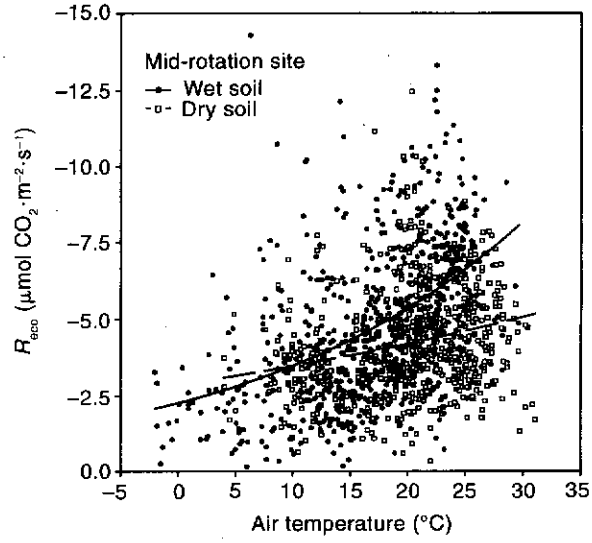

FIG. 4. Ecosystem respiration (R_{eco}; nighttime net CO_2 exchange) as a function of air temperature at the mid-rotation-aged sites when mean half-hourly $u^* > 0.2$ m/s. Regression equations and statistics are given in Table 3.

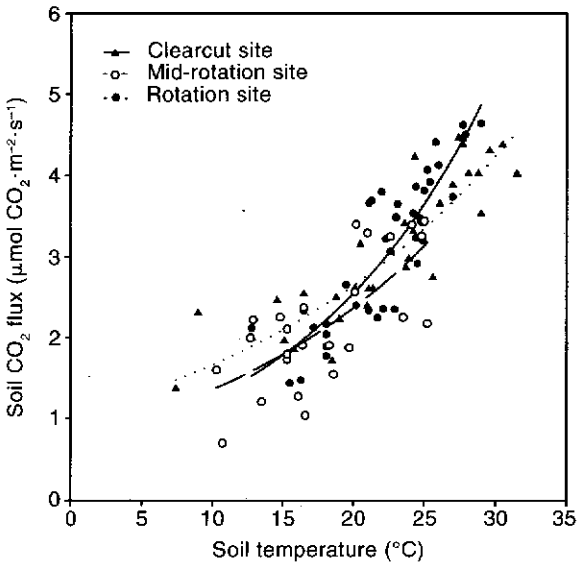

FIG. 5. Soil CO_2 flux as a function of soil temperature at the clearcut, mid-rotation, and rotation-aged sites. Regression equations and statistics are given in Table 4.

duction of the value of the u^* threshold (to 0.05 m/s at the clearcut and 0.15 m/s at the mid-rotation and rotation-aged sites) led to the inclusion of values of NEE_{night} where coupling between the stands and the atmosphere was marginal and resulted in a maximum deviation of −21.0% from calculated NEE_{yr} at the clearcut in 1999. Potential errors in the measurement of air temperature of ±0.5°C resulted in maximum deviations of 3.1%, 3.1%, and 3.9% from NEE_{yr} at the clearcut, mid-rotation, and rotation-aged sites, respectively (Table 6).

Estimated R_{eco} was similar in magnitude at all three sites during all years (Table 7). For example, the maximum difference between annual R_{eco} estimates was 480 g C/m², 23% of the mean estimate for all sites and years measured. Annual R_{eco} estimates were equally sensitive to the parameters in Eq. 2 used to calculate missing nighttime fluxes (Table 7), with a maximum deviation of 10.1% from the estimate calculated using mean parameter values for the mid-rotation site in 1998. Reduction of the value of the u^* threshold resulted in a maximum deviation of 10.7% at the clearcut in 1998. Potential errors in the measurement of air temperature of ±0.5°C resulted in maximum deviations of 2.6%, 2.1%, and 3.0% from annual R_{eco} estimates at the clearcut, mid-rotation, and rotation-aged sites, respectively (Table 7).

Annual soil respiration (R_{soil}) represented only 58.8% and 46.7% of estimated ecosystem respiration at the clearcut in 1998 and 1999 (Table 8); possible explanations for this are discussed below. As expected, R_{soil} accounted for a smaller proportion of ecosystem respiration during the second year when compared to the first year following harvest at the clearcut, corresponding to an increase in aboveground biomass and leaf area and decreases in soil heat fluxes and daytime soil temperatures. At the mid-rotation site, R_{soil} represented 50.3% of estimated R_{eco} in 1998 (using data collected during the first half of the year), and 47.5% during the relatively dry conditions of 1999. R_{soil} was 52.9% of R_{eco} at the rotation-aged site in 1996. Sensitivity analyses using ±1 SE of parameter values and ±0.5°C of the half-hourly soil temperature data suggested that slight errors in the estimation of soil temperature contributed little variability to annual soil CO_2 flux estimates (Table 8).

Removal and accumulation of biomass and litter

Aboveground residual material was 4666 g C/m² at the clearcut following harvesting, composed of 59.6% fine litter, 36.9% coarse litter, and 3.5% residual large stems (Table 9). We assumed that the residual coarse root mass was similar to that in the previous rotation-aged stand and calculated total residual C mass at 6002 g/m² in early 1998. Using the estimated total C mass for the rotation-aged stand (Table 9; foliar biomass estimated at 559 g/m²; calculated from Clark et al. [1999]), C loss during harvest was calculated at 5423 g C/m², ~47.5% of total preharvest C mass in vegetation. Stem removal during harvest was calculated as 87.4% of the original C mass in stems.

Grasses dominated the accumulation of biomass and leaf area at the clearcut during the first and second years following harvest (Table 10). Initially, woody biomass accumulation by shrubs was relatively rapid, but site preparation in November 1998 reduced woody species and palm biomass substantially. Aboveground biomass accumulation reached 116 g C/m² for grasses and 185

TABLE 4. Means and ranges of coefficient of variation for soil CO_2 flux (R_{soil}; n = 8 sampling chambers at each site), and equation parameters, statistics, and Q_{10} values for R_{soil} as a function of soil temperature at 5-cm depth along the chronosequence.

Site	CV (%)		a	b	n	r^2	P	Q_{10}
	Mean	Range						
Clearcut	54	44–69	1.038 ± 0.126	0.047 ± 0.005	31	0.78	<0.0001	1.6
Mid-rotation	35	23–44	0.770 ± 0.188	0.056 ± 0.012	24	0.49	<0.0001	1.8
Rotation-aged	27	15–35	0.606 ± 0.099	0.072 ± 0.007	38	0.77	<0.0001	2.1

Notes: Data were fit to Eq. 2 with the form $R_{soil} = a \exp(bT)$. Parameter values are reported as means ± 1 SE. P values are for overall model fit. Q_{10} values were calculated for 15°–25°C.

TABLE 5. Annual net ecosystem exchange of CO_2 (NEE_{yr}), sensitivity analyses for daytime net CO_2 exchange parameters in Eq. 1, and error analysis for photosynthetic photon flux density (PPFD) levels along the chronosequence.

Site and year	NEE_{yr} ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Percentage deviation (maximum values)†			
		α	F_{max}	R	PPFD
Clearcut					
1998	−1268.5	3.1	1.4	4.8	1.3
1999	−882.2	10.5	3.8	7.9	2.0
Mid-rotation					
1998	575.9	19.2	6.2	21.2	14.6
1999	603.1	14.1	4.5	15.2	10.0
Rotation-aged‡					
1996	740.5	26.4	9.4	22.7	9.6
1997	610.0	31.5	10.7	27.5	12.1

Notes: Worst-case-scenario maximum deviation from the value calculated using mean parameter values is shown as a percentage of NEE_{yr}. For an explanation of the parameters, see Table 2.

† Values reported for α, F_{max}, and R are percentage deviations from NEE_{yr} for ± 1 SE variation of the parameter in the column head; values reported for PPFD are percentage deviations from NEE_{yr} for ±25 μmol variation of PPFD from the mean value.

‡ These data previously published in Clark et al. (1999).

g C/m² for all aboveground biomass two years following harvest (Table 10). Calculated LAI reached a maximum of 3.0 two years following harvest, approximately 59% and 46% of maximum values at the mid-rotation and rotation-aged sites, respectively.

The mid-rotation site had lower foliar biomass and foliage production than the rotation-aged site, as estimated by the amount of foliar litterfall; foliar litterfall was 174 ± 39 and 191 ± 48.6 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1998 and 1999 (mean ± SD) at the mid-rotation site vs. 288.1 ± 35.1 and 271.0 ± 33.1 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1995 and 1996 at the rotation-aged site, respectively. LAI had a seasonal minimum and maximum of 3.1 and 5.1 and 4.0 and 6.5 at the mid-rotation and rotation-aged stands, respectively (Table 1). Accumulation of living biomass and litter on the forest floor at the mid-rotation site was estimated at 555 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1999, slightly less than the NEE value of 603 g $C \cdot m^{-2} \cdot yr^{-1}$ estimated from the eddy covariance data (Table 11). Accumulation of biomass and litter at the rotation-aged site was estimated at 745 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1996, similar to the value of 741 g $C \cdot m^{-2} \cdot yr^{-1}$ estimated using eddy covariance data (Clark et al. 1999; Table 11).

DISCUSSION

The chronosequence sampled here spanned a typical harvest rotation, and harvest and replanting activities were consistent with intensive management practices

TABLE 6. Annual net ecosystem exchange of CO_2 (NEE_{yr}), sensitivity analyses for nighttime net CO_2 exchange parameters in Eq. 2, the threshold value of mean half-hourly friction velocity (u^*), and error analysis for nighttime air temperature measurements along the chronosequence.

Site and year	NEE_{yr} ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Percentage deviation (maximum values)†			
		a	b	u^*	Nighttime air temperature
Clearcut					
1998	−1268.5	5.1	4.4	6.9	0.8
1999	−882.2	6.0	5.3	21.0	3.1
Mid-rotation					
1998	575.9	10.4	10.7	4.3	3.1
1999	603.1	9.2	9.3	3.7	2.5
Rotation-aged					
1996	740.5	7.2	6.2	1.8	3.2
1997	610.0	9.0	7.8	1.6	3.9

Notes: Worst-case-scenario maximum deviation from the value calculated using mean parameter values is shown as a percentage of NEE_{yr}.

† Values reported for a and b are percentage deviations from NEE_{yr} for ± 1 SE variation of the parameter in the column head; values reported for u^* are percentage deviations from NEE_{yr} for ±0.05 m/s variation of u^* around the mean value; values of nighttime air temperature are percentage deviations from NEE_{yr} for ±5°C variation of T around the mean value.

TABLE 7. Ecosystem respiration (R_{eco}), sensitivity analyses for net CO_2 exchange parameters in Eq. 2, the threshold value of mean half-hourly friction velocity (u), and error analysis for air temperature measurements along the chronosequence.

Site and year	R_{eco} (g C·m^{-2}·yr^{-1})	Percentage deviation (maximum values)†			
		a	b	u^*	Air temperature
Clearcut					
1998	1974.4	8.2	8.9	10.7	1.3
1999	2386.6	6.1	7.1	8.0	2.6
Mid-rotation					
1998	2346.0	7.2	10.1	2.1	2.1
1999	2001.6	6.9	8.5	3.1	1.8
Rotation-aged					
1996	1955.9	6.7	7.0	3.0	2.9
1997	1907.1	6.7	7.0	2.9	3.0

Notes: Worst-case-scenario maximum deviation from the value calculated using mean parameter values is shown as a percentage of R_{eco}.

† Values reported for a and b are percentage deviations from R_{eco} for ±1 SE variation of the parameter in the column head; values reported for u^* are percentage deviations from R_{eco} for ±0.05 m/s variation of u^* around the mean value; values reported for air temperature are percentage deviations from R_{eco} for ±5°C variation of T around the mean value.

used throughout the region. A potential limitation in our study was the use of two mid-rotation stands, because the first site was damaged by wildfire in June 1998. However, both stands had similar annual foliar litterfall (t = 0.71, df = 8) and annual total litterfall (t = 1.16, df = 8). Both stands had similar light compensation points (128 vs. 140 μmol PPFD·m^{-2}·s^{-1}), and mean NEE_{day} at 1500 μmol PPFD·m^{-2}·s^{-1} was within 1 μmol CO_2·m^{-2}·s^{-1} during both summer and winter periods. Parameters used to model NEE_{night} in Eq. 2 were similar among the two sites when data for wet and dry periods were pooled (t = 0.86 for a, t = 1.93 for b; df = 1337). Annual NEE estimates for each site differed by less than 5%.

Net CO_2 exchange

Daytime NEE was strongly regulated by leaf area at the clearcut. Substantial leaf area and biomass had accumulated before the first bedding treatment in June 1998, primarily due to resprouting by shrubs and palms and regeneration of grasses and herbs. Consequently, mean NEE_{day} was greater than zero at light levels above 1000 μmol PPFD·m^{-2}·s^{-1} within 6 mo of the end of harvest activities. When the second site preparation occurred in November 1998, leaf area was reduced by ~65%, and mean daytime fluxes at 1500 μmol PPFD·m^{-2}·s^{-1} were reduced immediately by 3–5 μmol CO_2·m^{-2}·s^{-1}. Frost further reduced NEE_{day} because it resulted in considerable mortality of grasses and pe-

TABLE 8. Annual soil CO_2 flux (R_{soil}) calculated using parameters in Table 4 and continuous soil temperature at 5-cm depth along the chronosequence.

Site and year	R_{soil} (g C·m^{-2}·yr^{-1})	Percentage deviation (maximum values)†			$\%R_{eco}$
		a	b	Soil temperature	
Clearcut					
1998	1161.7	12.1	12.4	2.4	58.5
1999	1114.8	12.1	11.9	2.4	46.7
Mid-rotation					
1999	951.6	23.3	27.1	2.7	47.5
Rotation					
1996	1035.2	15.3	14.4	3.4	52.9

Notes: Worst-case-scenario maximum deviation from the value calculated using mean parameter values and the portion of ecosystem respiration (R_{eco}) attributed to R_{soil} are shown as percentages.

† Values reported for a and b are percentage deviations from R_{soil} for ±1 SE variation of the parameter in the column head; values reported for soil temperature are percentage deviations from R_{soil} for ±0.5°C variation of T around the mean value.

TABLE 9. Distribution of carbon (g C/m²; mean ± 1 SD) at the clearcut (early 1998), mid-rotation (1999), and rotation-aged (1996) sites.

Component	Clearcut	Mid-rotation	Rotation-aged†
Pinus elliottii			
Branches and twigs	0	288.0 ± 20.4	537.1 ± 40.5
Stems	0	1643.6 ± 131.1	6206.4 ± 315.9
Coarse roots	1336.4 ± 68.0‡	353.9 ± 28.2	1336.4 ± 68.0
Total wood	0	1997.5 ± 159.3	8079.9 ± 423.2
Understory	45.2 ± 18.7	287.9 ± 174.1	190.8 ± 95.4
Forest floor and coarse wood	4666.1 ± 1760.4	1080.2 ± 382.8	2596.0 ± 651.8
Total	6047.7	5651.1	10 866.7

Notes: Biomass was estimated in 20 0.5-m² plots at the clearcut and four 625-m² plots at the mid-rotation and rotation-aged plots. The forest floor was sampled in 20 0.5-m² plots at the clearcut and 20 0.1-m² plots at the mid-rotation and rotation-aged stands.

† From Clark et al. (1999).

‡ Dead coarse-root mass was assumed to be the same as live coarse-root biomass at the rotation-aged stand.

rennial herbs, which composed most of the leaf area at that time. Further disturbance occurred during tree planting in December 1998 and January 1999, yet mean NEE_{day} had recovered to 6 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ by the growing season of the second year following harvest, ~40% of mean maximum rates at 1500 μmol $\cdot m^{-2} \cdot s^{-1}$ at the older sites. Daytime rates remained at these levels until frost again resulted in mortality of grasses and perennial herbs in December 1999.

Little seasonality in daytime net CO_2 exchange was observed at the closed-canopy sites when VPD < 2 kPa, suggesting that lower LAI and rates of net assimilation are compensated for by reduced R_{eco} during winter and spring (see also Clark et al. [1999]). In contrast, at the same level of incident radiation, latent heat fluxes were significantly greater in summer and fall than in winter and spring at both sites, corresponding with seasonal increases in LAI (Table 1; Gholz and Clark 2002).

When VPD < 2 kPa, NEE_{day} at the mid-rotation site was similar to that previously measured at the rotation-aged site for a given value of PPFD (Clark et al. 1999). Peak leaf area and annual needle litterfall were lower at the mid-rotation site than at the rotation-aged site, but respiring biomass was also lower (Ryan et al. 1994). Leaf area and needle litterfall values for the mid-rotation and rotation-aged sites are similar to those in nearby plantations of similar ages, where LAI had a seasonal minimum and maximum of 3.7 and 6.5, and needle litterfall ranged from 160 to 283 g $C \cdot m^{-2} \cdot yr^{-1}$ (Gholz et al. 1991*b*, Jokela and Martin 2000).

Drought conditions were experienced in spring 1999 and resulted in periods of reduced stomatal conductance, lower latent heat fluxes relative to sensible heat, and a significant reduction in NEE_{day} in response to high VPD during the late morning and early afternoon, particularly at the mid-rotation site (Gholz and Clark 2002). Reduced NEE_{day} during drought stress is consistent with results reported from other pine-dominated stands under similar conditions (Arneth et al. 1998, Anthoni et al. 1999, Law et al. 2001*a*). For example, mean NEE_{day} was reduced from 11 to 7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ during summer drought in a 6-yr-old ponderosa pine (*P. ponderosa*) plantation in California (Law et al. 2001*a*), and extended periods of near-zero NEE_{day} occurred during an extreme summer drought in a ponderosa pine stand in central Oregon (Anthoni et al. 1999). Drought conditions intensified through 2000 and resulted in extended periods of very low NEE_{day} throughout the late morning and afternoon during the spring months (G. Starr, K. L. Clark, T. A. Martin, and H. L. Gholz, *unpublished data*).

During most sampling periods, NEE_{night} under well-mixed conditions was an exponential function of air or soil temperature at all sites. Similar relationships have

TABLE 10. Aboveground biomass (mean ± 1 SE) and leaf area index (LAI) at the clearcut site following harvest in June–November 1997.

Time since harvest (mo)	Aboveground biomass of components (g C/m²)				LAI (m²/m²)
	Grass	Herbs and shrubs	Palms	Total	
3	27.4 ± 17.2	16.7 ± 15.0	1.1 ± 0.8	45.2 ± 18.7	0.7
6	19.8 ± 8.2	16.4 ± 9.0	47.1 ± 9.4	83.3 ± 13.1	0.8
12	43.5 ± 7.7	18.5 ± 12.8	···	62.0 ± 17.9	1.0
24	116.2 ± 27.4	77.8 ± 40.1	···	184.8 ± 17.2	3.0

Note: Biomass was estimated using clip plots of 0.5–1.0 m².

† Plots were sampled 1 mo following site preparation (bedding) and tree planting, which disturbed ~65% of the total area and removed most of the palms.

TABLE 11. Annual carbon accumulation rates (g C·m^{-2}·yr^{-1}; mean ± 1 SE) for the mid-rotation (1999) and rotation-aged (1996) sites based on mensurational mass balance measurements.

Component	Mid-rotation	Rotation-aged†
Pinus elliottii		
Foliage	31.9 ± 5.5	0
Branches and twigs	44.5 ± 5.7	39.3 ± 2.6
Stems	211.6 ± 31.2	303.1 ± 11.8
Coarse roots	57.6 ± 8.5	65.7 ± 2.5
Total wood	313.7 ± 45.4	410.1 ± 16.8
Understory‡	0	0
Forest floor and coarse wood§	209.5 ± 35.0	335.0 ± 107.3
Total‖	555.1	745.1

† From Clark et al. (1999).
‡ Understory biomass is assumed to be in steady state (Gholz and Fisher 1982).
§ Includes tree mortality.
‖ Assumes that soil C remains constant on an annual basis.

been reported for other forest ecosystems, although Q_{10} values for our data from the clearcut and mid-rotation sites are relatively low compared to estimates for other sites (2.1 to 3.5; Goulden et al. 1996*b*, Lavigne et al. 1997, Law et al. 1999, Lai et al. 2002).

We expected that the poor litter quality of slash pine would be the major factor controlling increased rates of heterotrophic respiration and therefore initial rates of NEE_{night} and soil respiration at the clearcut. Rates of mass loss from foliage and fine roots of slash pine range between 15% and 18% per year (Gholz et al. 1985*b*, 2000), a result of relatively low N and P concentrations and high concentrations of lignin and polyphenols. Even in the absence of retranslocation, N and P concentrations are low in pine foliage, ranging from 8.0 to 12.0 mg N/g. However, the dynamics of microbial populations and site hydrology are highly interactive. Reduced leaf area also resulted in lower rates of interception loss and transpiration and led to prolonged flooding at the clearcut during periods of abundant rainfall early in the study. Anoxic soil conditions likely resulted in reduced rates of heterotrophic respiration during the first year following harvest, particularly during the summer wet season, despite the fact that soil temperatures were relatively high. The weak relationship between nighttime net CO_2 exchange and air or soil temperature during this time stands in contrast to the relatively strong relationship observed later during drier soil conditions. A similar response was observed for soil CO_2 fluxes at the clearcut, where the Q_{10} for soil CO_2 flux was 1.6 compared to 2.1 at the previous rotation-aged stand on the same site. Therefore, both poor litter quality and soil water status constrained soil respiration by reducing the rate of heterotrophic respiration. As a result, R_{eco} was similar among sites, although differences in detrital mass, canopy cover, soil heat flux, and peak soil temperatures were large.

Soil water status also apparently constrained ecosystem respiration at the mid-rotation site. We observed differences in the relationship between nighttime net CO_2 exchange and air or soil temperature during periods of low soil moisture when the water table was below 2.7 m depth when compared to wetter conditions, and summed nighttime net CO_2 fluxes were lower during periods of drought stress. Goulden et al. (1996*a*) and Anthoni et al. (1999) also reported that ecosystem respiration was lower and thus NEE_{yr} greater when soils were relatively dry, due to drought effects on soil microbial populations that apparently reduced rates of heterotrophic respiration. Lower rates of net assimilation could also constrain labile C supply to fine roots, reducing fine root respiration (Ewel et al. 1987*b*, Janssens et al. 2001).

Soil CO_2 flux

Mean soil CO_2 fluxes were an exponential function of soil temperature at all sites, and temperature explained 78% and 77% of the variation in mean fluxes at the clearcut and rotation-aged sites. At the mid-rotation site, however, temperature explained only 49% of the variability in soil CO_2 flux, and partial decoupling of soil temperature and CO_2 flux was likely due to drought effects on heterotrophic and autotrophic respiration. Previous measurements in a 9-yr-old and a 29-yr-old slash pine plantation indicated that soil CO_2 flux was strongly related to soil temperature (r^2 = 0.89 and 0.75, respectively; Ewel et al. 1987*a*), but was also affected by soil moisture levels; soil CO_2 fluxes were lower than predicted when the 29-yr-old site was flooded. Ewel et al. (1987*b*) suggested that reduced root respiration was likely, because root respiration represented 51–63% of soil CO_2 flux, and rates of litter and SOM decomposition are relatively insensitive to soil water status. Independent soil chamber measurements made at the rotation-aged site by Fang et al. (1998) also showed a strong dependence on soil temperature; 90% of the variability in soil CO_2 flux could be accounted for by the variation in soil temperature when soil moisture was not limiting.

Using a larger number of sampling locations (n = 20), Fang et al. (1998) reported that the CV of soil CO_2 flux was ~55% at the rotation-aged site, greater than

the value of 27% reported here. They indicated that soil CO_2 flux was substantially greater beneath palmetto in the understory, which had higher root biomass than other sample locations on the forest floor, and this contributed to relatively high spatial variability.

Our Q_{10} values for soil CO_2 fluxes were within the range of those reported in earlier studies in slash pine plantations (1.9–2.5; Ewel et al. 1987*a*, Fang et al. 1998), but are at the low end of the range of 1.4–3.9 reported in studies in other forest ecosystems (Davidson et al. 1998, Law et al. 1999, Andrews and Schlesinger 2001, Xu and Qi 2001). A number of other investigations have shown that the relationship between soil CO_2 flux and temperature is modulated by soil moisture levels (Bowden et al. 1998, Davidson et al. 1998, Xu and Qi 2001). For example, Xu and Qi (2001) reported a Q_{10} of 1.4 for soil CO_2 flux when soil moisture was <14% of saturation and 1.8 when soil moisture was >14% saturation in an 8-yr-old ponderosa pine plantation. When soil CO_2 flux is compared to nighttime ecosystem respiration at the closed-canopy sites, our values are within the range of those reported from other forest ecosystems, where soil CO_2 flux was 48–77% of ecosystem respiration (Lavigne et al. 1997, Law et al. 1999, 2001*b*).

Annual ecosystem carbon balance and partitioning

The clearcut was a greater source of C during the second year following harvest than was calculated from the data in Gholz and Fisher (1982), with estimates of −883 vs. −550 g $C \cdot m^{-2} \cdot yr^{-1}$ for the eddy covariance data and empirical model, respectively. Although we did not observe positive NEE_{yr} at the clearcut, it is likely that rates recover to positive values within 3–4 years following harvesting, coincident with the rapid biomass accumulation by pine saplings. This result is consistent with the empirical model of Gholz and Fisher (1982), who indicated that NEP becomes positive after 3–4 years following harvest, although Thornton et al. (2002) predicted that NEP would not be positive until five years using the Biome-BGC model.

Estimated NEE_{yr} at the mid-rotation site in 1998 and 1999 was 109.3% and 114.4% of that estimated in the original empirical model, where NEP peaked at 527 ± 105 g $C \cdot m^{-2} \cdot yr^{-1}$ (mean ± 1 SE) 14 yr following harvest. Thornton et al. (2002) estimated that NEE averaged 380 ± 55 g $C \cdot m^{-2} \cdot yr^{-1}$ at the mid-rotation site in 1998 and 1999, representing only 66% and 63% of NEE_{yr} estimated using eddy covariance. Interestingly, the Biome-BGC model also underestimated NEE at a 17-yr-old loblolly pine plantation by 31% over the same period.

NEE_{yr} at the rotation-aged site was considerably greater than that estimated for a 26-yr-old stand in the original chronosequence of Gholz and Fisher (1982; ~363 ± 90 g $C \cdot m^{-2} \cdot yr^{-1}$). Both the mid-rotation and rotation-aged sites sampled here were similar (within ±1 SE) to those of similar ages along the original chronosequence in terms of needle mass, stem wood, and understory biomass. N concentrations in both first and second year foliage at the rotation-aged stand sampled here were similar to those at the 26-yr-old stands in the original chronosequence (1.0 ± 0.1 and 0.9 ± 0.1% N vs. 1.0 and 0.9% N, respectively; Gholz et al. 1985*a*). However, the rotation-aged stand had greater forest floor mass than those in the original chronosequence, which likely could be attributed to greater fine litterfall flux. Increased foliage dynamics at the rotation-aged stand could partially account for the difference between eddy covariance data and the original modeled estimates of NEE_{yr}. Although results differed somewhat over time scales of half-hourly to monthly, NEE_{yr} simulated using the process-based Slash Pine Model version 2 (SPM2) matched estimated NEE for the rotation-aged site closely; simulated values were 693 and 648 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1996 and 1997, respectively (Cropper 2000, Clark et al. 2001).

NEE_{yr} values for the mid-rotation and rotation-aged stands were at the high end of the range of estimates for forests in North America and Europe, but similar to those estimated for a 17-yr-old loblolly pine (*P. taeda*) plantation in North Carolina (605 g $C \cdot m^{-2} \cdot yr^{-1}$; Lai et al. 2002) and a number of other plantations dominated by coniferous species at temperate latitudes (Table 12; FLUXNET compilation, Valentini et al. 2000, Janssens et al. 2001). Substantial C accumulation occurs during the winter at both of our closed-canopy stands, and this pattern has been noted in other temperate coniferous forests that do not experience a substantial number of frost days (Anthoni et al. 1999, Hollinger et al. 1999, Lai et al. 2002).

R_{eco} estimates were similar for the clearcut, mid-rotation, and rotation-aged sites. Our values for the closed-canopy stands were within the range obtained using simulation models. Ewel and Gholz (1991) estimated R_{eco} at 2600 g $C \cdot m^{-2} \cdot yr^{-1}$ for a 29-yr-old slash pine plantation, ~87% of simulated gross primary production (GPP). In a dry year simulation (837 mm), ecosystem respiration was only slightly less at 2580 g $C \cdot m^{-2} \cdot yr^{-1}$ and represented >100% of simulated GPP. R_{eco} estimated for the mid-rotation site using the Biome-BGC model averaged 1800 g $C \cdot m^{-2} \cdot yr^{-1}$, ~77% and 90% of our estimated values for 1998 and 1999, respectively (Thornton et al. 2002). Estimates for a 17-yr-old stand of loblolly pine in North Carolina averaged 63.8% and 68.6% of those for our mid-rotation and rotation-aged sites, respectively (Lai et al. 2002). Mean air temperature at the North Carolina site was similar in the summer (27°C), but considerably lower in the winter (7.6° vs. 14°C) when compared to the Florida sites, which may account for this difference between stands 6.5° apart in latitude.

Sensitivity analyses using ±1 SE of parameter values, calculated CVs, and 0.5°C of the half-hourly soil temperature data indicated that spatial variability contributed greater uncertainty to annual soil CO_2 flux es-

TABLE 12. Net ecosystem exchange of CO_2 (NEE), ecosystem respiration (R_{eco}), gross ecosystem production (GEP), and the percentage of GEP released by ecosystem respiration for selected forests.

Site	Stand age (yr)	NEE (g C·m^{-2}·yr^{-1})	R_{eco} (g C·m^{-2}·yr^{-1})	GEP (g C·m^{-2}·yr^{-1})	R_{eco}/GEP (%)
Pine plantations					
Florida, clearcut†	1	−1269	1974	705	280.0
	2	−882	2386	1504	158.6
Florida, mid-rotaton†	10	576	2346	2922	80.3
	11	603	2002	2605	76.9
Florida, rotation-aged‡	24	741	1956	2695	72.6
	25	610	1907	2517	75.8
Duke Forest, loblolly pine§	17	605	1342	1808	74.2
Naturally regenerated stands					
Florida, longleaf/slash‖	60	178	1581	1759	89.9
Florida, cypress pond‡	80	84	1426	1510	94.0
	80	37	1504	1541	97.6
Oregon, ponderosa pine¶	14	0	835	835	100.0
Ponderosa pine#	250	300	1014	1314	77.2
Euroflux sites††	various	270	1100	1380	80.0

† This study.
‡ Clark et al. (1999), this study.
§ Lai et al. (2002).
‖ Powell (2002).
¶ Law et al. (2001*b*).
# Anthoni et al. (1999), Law et al. (2001*b*).
†† Janssens et al. (2001), mean of Euroflux sites.

timates than slight errors in the estimation of soil temperature at all sites. Parameters used to model soil CO_2 flux and thus the annual estimate were most variable at the mid-rotation age site, likely a reflection that the water table dropped relatively rapidly throughout late 1998 and 1999.

We expected that R_{soil} would represent a substantial fraction of R_{eco} at the clearcut, and as aboveground biomass accumulated, the proportion of R_{eco} attributed to belowground processes would decrease over time. However, soil CO_2 fluxes were only 58.1% and 45.4% of estimated R_{eco} at the clearcut in 1998 and 1999, respectively. We underestimated soil CO_2 flux at this site because we did not measure soil fluxes from coarse woody debris piles and/or the soil beneath them. In contrast to the soil flux chambers, CO_2 flux from coarse woody debris piles was sampled within the footprint of the eddy flux measurements. Assuming that all the residual wood and coarse litter raked into piles decomposed at a rate similar to that for coarse wood as reported by Gholz et al. (1991*a*), we calculated that an additional 320.5 and 266.0 g C·m^{-2}·yr^{-1} was released from the soil surface in 1998 and 1999, respectively. Total soil + detrital fluxes would then increase to 75.1% and 57.9% of R_{eco} at the clearcut, respectively. We also may have underestimated soil CO_2 flux at the clearcut because it was necessary to remove herbaceous biomass from inside the sampling rings more frequently there so as not to include aboveground plant respiration. Root respiration contributes >50% to soil respiration in older slash pine stands (Ewel et al. 1987*b*), but the contribution of root respiration to soil CO_2 flux in recently harvested stands is unknown. It is also possible that herbaceous biomass has a higher respiration rate than pine foliage, because herbaceous biomass has a higher N content and higher respiration rates per unit leaf area than slash pine foliage.

Estimated annual R_{soil} at the closed-canopy sites are consistent with previous results using both dynamic (infrared gas analyzer [IRGA]) and static (soda lime) techniques in similar slash pine plantations. Ewel et al. (1987*a*) reported that R_{soil} was 850 and 1300 g C·m^{-2}·yr^{-1} in 9- and 29-year-old slash pine plantations, respectively, spanning our estimates for the mid- and rotation-aged sites. Our soil fluxes at the rotation-aged site are also consistent with modeling activities; measured soil flux averaged 84% of annual soil CO_2 flux estimated for a 29-yr-old stand (1230 g C·m^{-2}·yr^{-1}; Ewel and Gholz 1991). Ewel and Gholz (1991) estimated that soil CO_2 fluxes represented 46% of R_{eco} for a 29-yr-old slash pine stand, which compares favorably with measurements at the closed-canopy stands reported here. The proportion of R_{eco} due to soil CO_2 fluxes for the closed-canopy stands was at the low end of the range of 56–77% reported from other sites (Lavigne et al. 1997, Law et al. 1999, 2001*b*, Xu et al. 2001).

We estimated gross ecosystem production (GEP) for the three sites by summing NEE_{yr} and R_{eco} (e.g., Janssens et al. 2001). Despite the minimal biomass of woody vegetation, estimated GEP was 705 and 1505 g C·m^{-2}·yr^{-1} at the clearcut during the first and second years following harvest. Estimated GEP at the clearcut in 1999 averaged 54% and 58% of rates estimated at the mid-rotation and rotation-aged sites, respectively. Values estimated for the rotation-aged site in 1996 and

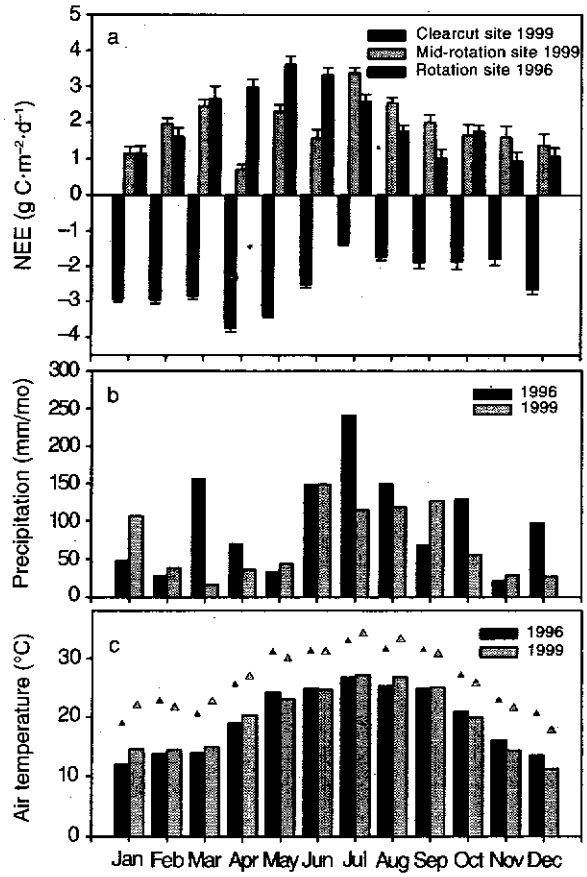

FIG. 6. (a) Daily net CO_2 exchange (NEE; means ± 1 SE) at the clearcut, mid-rotation, and rotation-aged sites. (b) Monthly precipitation in 1996 and 1999. (c) Mean daily air temperature (bars) and mean maximum daily air temperature (triangles) by month in 1996 and 1999.

1997 were similar to those estimated for the mid-rotation-aged site in 1999, with all estimates within the range of simulated GPP estimates of 2950 g $C \cdot m^{-2} \cdot yr^{-1}$ during a year with normal rainfall and 2240 g $C \cdot m^{-2} \cdot yr^{-1}$ during a dry year reported by Ewel and Gholz (1991) for a 29-yr-old pine flatwood site. As stands age, the proportion of R_{eco} to GEP initially decreases rapidly, then slowly increases (Table 12). Canopy LAI increases rapidly in these stands and then stabilizes at a relatively young age (Gholz and Fisher 1982). With increasing stand age, R_{eco} increases slowly relative to GEP, resulting in progressively lower values of NEE in older pine flatwoods (Powell 2002) and natural cypress ecosystems (Clark et al. 1999, Table 12).

Our results argue that NEE_{day} and GEP, and thus annual NEE, are strongly controlled by herbaceous LAI and not necessarily by the presence of live woody vegetation in forest ecosystems recovering from disturbance. However, this pattern is also modulated by climate variability. For example, reduced rates of mean daily NEE during spring 1999 at the mid-rotation site contrast strongly with mean daily NEE at the rotation-aged site during periods of abundant moisture in spring 1996, while warm and extremely cloudy conditions in September 1996 resulted in very low rates at the rotation-aged site (Fig. 6).

Intense disturbances such as clearcutting lead to a highly dynamic landscape in terms of C fluxes. Our range of NEE_{yr} along this chronosequence (~2000 g $C \cdot m^{-2} \cdot yr^{-1}$) is considerably larger than the range of estimates reported across all the sites of the AmeriFlux (−419 to 739 g $C \cdot m^{-2} \cdot yr^{-1}$) and Euroflux (−90 to 736 g $C \cdot m^{-2} \cdot yr^{-1}$) networks combined (FLUXNET compilation, Valentini et al. 2000). This highlights the importance of including a range of stand ages and management histories as well as multiple years of data to accurately assess long-term C fluxes from the ecosystem to regional scales.

Quantifying the effects of disturbance is clearly key to estimating potential differences in C fluxes resulting from current land use patterns when compared to those that may have occurred across this same landscape in the past or might in the future. In this century, natural, fire-controlled flatwood forests dominated by longleaf pine (*Pinus palustris*) have largely been replaced by intensively managed stands of slash pine. Currently, we have little data to estimate how C balances for intensively managed stands differ from those of natural longleaf pine flatwoods. However, the carbon dynamics of these intensively managed plantations may contrast strongly to those of natural ecosystems at the stand level. Estimates from older sites (~80–90 years old) in this landscape indicate that they are long-term sinks for C (naturally regenerated pine and cypress pond sites in Table 12), albeit at lower annual rates than those reported here for the even-aged plantations. In addition, the fire regime characterizing this landscape has changed, because the current long return interval/high intensity wildfire regime contrasts strongly with the fast return/low intensity regime that is hypothesized to have occurred in historic forests. At the landscape scale, however, intense management likely results in greater variability in C fluxes, but averaged at this scale, C fluxes may be suprisingly similar to those that characterized natural forests.

The general pattern of C dynamics reported here may be applicable to other intensively managed landscapes outside of the southeastern coastal plain. Intensively managed plantations currently comprise an estimated 124 Mha worldwide and are projected to increase to up to 234 Mha by 2050 (FAO 2001*b*). Many of these stands are composed of various species of pines (*Pinus radiata*, planted as an exotic in Australia, New Zealand, and Chile; *P. sylvestris*, native to Europe, Scandinavia, and Siberia; and *P. taeda* and *P. elliottii* var. *elliottii*, both native to the southeastern United States, but also widely planted throughout the tropics) and are typically managed on an even-aged basis. A range of stand ages often occur within the same landscape, similar to the pattern characterizing the southeastern coastal plain.

Climate will likely modulate patterns of C dynamics of these intensively managed stands, with the switch from C source to sink and the timing of the maximum sink occurring later in regions with shorter growing seasons or experiencing significant seasonal drought (Law et al. 2001*b*, Thornton et al. 2002).

ACKNOWLEDGMENTS

We thank Jose Luis Hierro, Dan and Angela Golub, Cajun Sun, Helga Soares, Steven Smitherman, and Robert Hamlin for assistance during the project. We thank the Jefferson-Smerfit Corporation and the Rayonier Corporation for allowing access to the sites. Two anonymous reviewers improved the manuscript. This research was supported by the Office of Science (BER), U.S. Department of Energy, through the Southeastern Regional Center of the National Institute for Global Environmental Change under Cooperative Agreement No. DE-FC03-90ER61010. This is Florida Agricultural Experiment Station, Journal Series No. R-09931.

LITERATURE CITED

Andrews, J. A., and W. H. Schlesinger. 2001. Soil CO_2 dynamics in a temperate forest with experimental CO_2 enrichment. Global Biogeochemical Cycles **15**:149–162.

Anthoni, P. M., B. E. Law, and M. H. Unsworth. 1999. Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. Agricultural and Forest Meteorology **95**: 151–168.

Arneth, A., F. M. Kelliher, T. M. McSeveny, and B. N. Byers. 1998. Fluxes of carbon and water in a *Pinus radiata* forest subject to soil water deficit. Australian Journal of Plant Physiology **25**:557–570.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.

Bowden, R. D., K. M. Newkirk, and G. M. Rullo. 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. Soil Biology and Biochemistry **30**:1591–1597.

Clark, K. L., W. P. Cropper, Jr., and H. L. Gholz. 2001. Evaluation of modeled carbon fluxes for a slash pine ecosystem: SPM2 simulations compared to eddy flux measurements. Forest Science **47**:1–8.

Clark, K. L., H. L. Gholz, J. B. Moncrieff, F. Cropley, and H. W. Loescher. 1999. Environmental controls over net exchanges of carbon dioxide from contrasting Florida ecosystems. Ecological Applications **9**:936–948.

Cropper, W. P., Jr. 2000. SPM2: a simulation model for slash pine (*Pinus elliottii*) forests. Forest Ecology and Management **126**:201–212.

Cropper, W. P., Jr., and H. L. Gholz. 1993. Simulation of the carbon dynamics of a Florida slash pine plantation. Ecological Modeling **66**:213–249.

Davidson, E. A., E. Belk, and R. D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology **4**:217–227.

Ewel, K. C., W. P. Cropper, Jr., and H. L. Gholz. 1987*a*. Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. Canadian Journal of Forest Research **17**:325–329.

Ewel, K. C., W. P. Cropper, Jr., and H. L. Gholz. 1987*b*. Soil CO_2 evolution in Florida slash pine plantations. II. Importance of root respiration. Canadian Journal of Forest Research **17**:330–333.

Ewel, K. C., and H. L. Gholz. 1991. A simulation model of the role of belowground dynamics in a Florida pine plantation. Forest Science **37**:397–438.

Falge, E., et al. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agricultural and Forest Meteorology **107**:43–69.

Fang, C., J. B. Moncrieff, H. L. Gholz, and K. L. Clark. 1998. Soil CO_2 efflux and its spatial variation in a Florida slash pine plantation. Plant and Soil **205**:135–146.

FAO [Food and Agriculture Organization]. 2001*a*. Mean annual volume increment of selected industrial forest plantation species. Working paper FP/1. Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO. 2001*b*. Future production from forest plantations. Working paper FP/13. Food and Agriculture Organization of the United Nations, Rome, Italy.

Gaston, L., P. Nkedi-Kizza, G. Sawka, and P. S. Rao. 1990. Spatial variability of morphological properties at a Florida flatwood site. Soil Science Society of America Journal **54**: 527–533.

Gholz, H. L., and K. L. Clark. 2002. Energy exchange across a chronosequence of slash pine forests in North Florida. Agricultural and Forest Meteorology **112**:87–102.

Gholz, H. L., and R. F. Fisher. 1982. Organic matter production and distribution in slash pine plantation ecosystems. Ecology **63**:1827–1839.

Gholz, H. L., R. F. Fisher, and W. L. Pritchett. 1985*a*. Nutrient dynamics in slash pine plantation ecosystems. Ecology **66**: 647–659.

Gholz, H. L., D. N. Guerin, and W. P. Cropper, Jr. 1999. Phenology and productivity of saw palmetto (*Serenoa repens*) in a north Florida slash pine plantation. Canadian Journal of Forest Research **29**:1248–1253.

Gholz, H. L., L. M. Krazynski, and B. G. Volk. 1991*a*. Disappearance and compressability of buried pine wood in a warm temperate soil environment. Ecological Applications **1**:85–88.

Gholz, H. L., C. S. Perry, W. P. Cropper, Jr., and L. C. Hendry. 1985*b*. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. Forest Science **31**:463–478.

Gholz, H. L., S. A. Vogel, W. P. Cropper, Jr., K. McKelvey, K. C. Ewel, R. O. Teskey, and P. J. Curran. 1991*b*. Dynamics of canopy structure and light interception in *Pinus elliottii* stands, North Florida. Ecological Monographs **61**: 33–51.

Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology **6**:751–765.

Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. C. Wofsy. 1996*a*. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science **271**:1576–1579.

Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. C. Wofsy. 1996*b*. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biology **2**:169–182.

Hollinger, D. Y., S. M. Goltz, E. A. Davidson, J. T. Lee, K. Tu, and H. T. Valentine. 1999. Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. Global Change Biology **5**:891–902.

Janssens, A. I., et al. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology **7**:269–278.

Jokela, E. J., and T. A. Martin. 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Canadian Journal of Forest Research **30**:1511–1524.

Katul, G. G., et al. 1999. Spatial variability of turbulent fluxes in the roughness sublayer of an even-aged pine forest. Boundary Layer Meteorology **93**:1–28.

Lai, C.-T., G. Katul, J. Butnor, D. Ellsworth, and R. Oren. 2002. Modelling night-time ecosystem respiration by a constrained source optimization method. Global Change Biology **8**:124–141.

Lavigne, M. B., et al. 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. Journal of Geophysical Research **102**: 28977–28985.

Law, B. E., A. H. Goldstein, P. M. Anthoni, M. H. Unsworth, J. A. Panek, M. R. Bauer, J. M. Fracheboud, and N. Hultman. 2001*a*. CO_2 and water vapor exchange by young and old ponderosa pine ecosystems during a drought year. Tree Physiology **21**:299–308.

Law, B. E., M. G. Ryan, and P. M. Anthoni. 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biology **5**:169–182.

Law, B. E., P. E. Thornton, J. Irvine, P. M. Anthoni, and S. Van Tuyl. 2001*b*. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biology **7**:755–777.

Moncrieff, J. B., J. M. Massheder, A. Verhoeh, J. Elbers, B. Heusinkveld, S. Scott, H. de Bruin, P. Kabat, and P. J. Jarvis. 1997. A system to measure surface fluxes of energy, momentum and carbon dioxide. Journal of Hydrology **188–189**:589–611.

Myers, R. L., and J. J. Ewel, editors. 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

NCDC [National Climatic Data Center]. 2001. Climatic data, Gainesville Regional Airport, Gainesville, Florida. National Oceanic and Atmospheric Administration, Asheville, North Carolina, USA.

Oren, R., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maier, K. V. R. Schafer, H. McCarthy, G. Hendrey, S. G. McNulty, and G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature **411**:469–472.

Powell, T. 2002. Carbon, water and energy exchange for a mature, naturally regenerated pine forest in North Central Florida. Thesis. University of Florida, Gainesville, Florida, USA.

Ruimy, A., P. G. Jarvis, D. D. Baldocchi, and B. Saugier. 1995. CO_2 fluxes over plant canopies and solar radiation: a review. Advances in Ecological Research **26**:1–68.

Ryan, M. G., S. Linder, J. M. Vose, and R. M. Hubbard. 1994. Dark respiration in pines. Ecological Bulletins (Copenhagen) **43**:50–63.

Teskey, R. O., H. L. Gholz, and W. P. Cropper, Jr. 1994. Influence of climate and fertilization on net photosynthesis of mature slash pine. Tree Physiology **14**:1215–1227.

Thornton, P. E., et al. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agricultural and Forest Meteorology **113**:185–222.

Valentini, R., et al. 2000. Respiration as the main determinant of carbon balance in European forests. Nature **404**: 861–865.

Xu, M., T. DeBiase, Y. Qi, A. Goldstein, and Z. Liu. 2001. Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. Tree Physiology **21**:309–318.

Xu, M., and Y. Qi. 2001. Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Global Change Biology **7**:667–677.