

Response of carbon fluxes to drought in a coastal plain loblolly pine forest

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Abstract

Full accounting of ecosystem carbon (C) pools and fluxes in coastal plain ecosystems remains less studied compared with upland systems, even though the C stocks in these systems may be up to an order of magnitude higher, making them a potentially important component in regional C cycle. Here, we report C pools and CO₂ exchange rates during three hydrologically contrasting years (i.e. 2005–2007) in a coastal plain loblolly pine plantation in North Carolina, USA. The daily temperatures were similar among the study years and to the long-term (1971–2000) average, whereas the amount and timing of precipitation differed significantly. Precipitation was the largest in 2005 (147 mm above normal), intermediate in 2006 (48 mm below) and lowest in 2007 (486 mm below normal). The forest was a strong C sink during all years, sequestering 361 ± 67 (2005), 835 ± 55 (2006) and 724 ± 55 (2007) $\text{g C m}^{-2} \text{yr}^{-1}$ according to eddy covariance measurements of net ecosystem CO₂ exchange (NEE). The interannual differences in NEE were traced to drought-induced declines in canopy and whole tree hydraulic conductances, which declined with growing precipitation deficit and decreasing soil volumetric water content (VWC). In contrast, the interannual differences were small in gross ecosystem productivity (GEP) and ecosystem respiration (ER), both seemingly insensitive to drought. However, the drought sensitivity of GEP was masked by higher leaf area index and higher photosynthetically active radiation during the dry year. Normalizing GEP by these factors enhanced interannual differences, but there were no signs of suppressed GEP at low VWC during any given year. Although ER was very consistent across the 3 years, and not suppressed by low VWC, the total respiratory cost as a fraction of net primary production increased with annual precipitation and the contribution of heterotrophic respiration (R_h) was significantly higher during the wettest year, exceeding new litter inputs by 58%. Although the difference was smaller during the other 2 years (R_h : litterfall ratio was 1.05 in 2006 and 1.10 in 2007), the soils lost about $109 \text{ g C m}^{-2} \text{yr}^{-1}$, outlining their potential vulnerability to decomposition, and pointing to potential management considerations to protect existing soil C stocks.

Keywords: canopy conductance, carbon budget, drained coastal plain forest, ecosystem productivity, ecosystem respiration, heterotrophic respiration, litterfall

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Introduction

Coastal plain forests remain one of the few undercharacterized ecosystems in the otherwise dense Ameriflux

network of eddy covariance sites (Hargrove & Hoffman, 2005; <http://public.ornl.gov/ameriflux/>). Carbon (C) fluxes in coastal plain forests are expected to differ from upland forests because of contrasting hydrologic regime, soil type and climate. In the tropics, forests on drained peatland have been found to be about 25% more productive than upland forests in a similar climate (Hirano *et al.*, 2007). While not all coastal plain soils are rich in organic matter, many of them have C

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densities up to an order of magnitude higher than upland soils (Johnson & Kern, 2003). And even on sandy soils, intensively managed commercial forests show net productivity up to four times higher than naturally regenerated stands (Powell *et al.*, 2008). Therefore, despite limited range, the coastal plain forests may contribute significantly to the regional and continental C cycle. Furthermore, our earlier work has demonstrated that for accurate regional upscaling, the C fluxes of smaller and functionally different land cover units must be known, and that reliance solely on predominant land cover classes may not be justified (Desai *et al.*, 2008).

The organically rich soils also tend to have higher (sometimes up to 50-fold) nitrogen concentration (<http://soils.usda.gov>), which is a likely contributor to high productivity levels often observed in these soils (Reich *et al.*, 1997). However, high availability of nitrogen also promotes decomposition, thus probably accelerating the loss of the organic material in the soil (Khan *et al.*, 2007). If this occurs, these soils may be vulnerable to self-propagating cycle of decomposition. While the biological effects can be overridden by extreme events like fires (Poulter *et al.*, 2006), understanding the processes that control the base exchange rates is still essential, especially as increasing temperature and associated higher evapotranspiration are projected to lower the ground water table (GWT) and increase soil organic matter decomposition in peatlands (Ise *et al.*, 2008). Yet, quantitative understanding of these processes is only beginning to emerge, as the C cycle in these ecosystems has not been comprehensively characterized (but see Trettin & Jurgensen, 2003).

In this study, we report on 3 years of C fluxes from a 15-year old loblolly pine (*Pinus taeda*) plantation in coastal North Carolina, USA. The contrasting precipitation regime during these years, including a moderate El Niño in 2006–2007 (National Weather Service Climate Prediction Center, <http://www.cpc.noaa.gov/index.php>), provided insight into the impact of extreme variations in precipitation on ecosystem C exchange. Projections for the intensification of the hydrologic cycle (Huntington, 2006) and pole-ward movement of jet streams (Archer & Caldeira, 2008) suggest that interannual differences in precipitation dynamics may become increasingly more significant as a driver of ecosystem processes in the region. The goals of the current study were: (i) characterize the C pools and fluxes of the lower coastal plain forest, and (ii) characterize the sources of interannual variability in the fluxes, including sensitivity to the severe drought in 2007. Given the high proportion of total ecosystem C contained in soil, we hypothesized that soil respiration (SR) and particularly heterotrophic respiration (R_H)

would constitute a significant fraction of total ecosystem CO_2 efflux. We also hypothesized that SR would be limited by soil aeration instead of moisture and that SR would be negatively related to the latter.

Materials and methods

Site description

The study site is a loblolly pine (*P. taeda* L.) plantation, located at 35°48'N 76°40'W, on the lower coastal plain of North Carolina, USA. The area is flat, <5 m above sea level, on deep Belhaven series histosol (loamy mixed dysic thermic terric Haplosaprists). The soil C concentration is 26% and N concentration 1.0%, the Oi (litter) horizon was 38 ± 7 mm (mean \pm SD) deep, and the Oe (duff) horizon 14 ± 5 mm. The area is classified as Mid-Atlantic flatwoods (US EPA, http://www.epa.gov/wed/pages/ecoregions/ncsc_eco.htm), and belongs to the outer coastal plain mixed forest province (Bailey, 1995). The study area was clearcut and ditched in the late 19th to early 20th century and farmed briefly before turning it to commercial timber production. The plantations in the area are typically supplemented with 28–50 kg N ha⁻¹ and as much P at the time of planting, and 140–195 kg ha⁻¹ N and 28 kg ha⁻¹ P at mid-rotation.

The mean (1971–2000) annual precipitation is 1320 mm, mean temperature in July is 26.6 °C, and in January 6.4 °C. The canopy height was 11.9 m (2005), 12.8 m (2006) and 14.1 m (2007), and the maximum projected leaf area index (LAI) during the growing season was 3.9 (2005), 4.0 (2006) and 4.3 (2007) m² m⁻². In winter, LAI decreased to 2.4–2.8 m² m⁻², mostly due to leaf fall of subdominant and understory *Acer rubrum*. LAI was measured on four of the 13 vegetation survey plots (described below) with a LAI-2000 Plant Canopy Analyzer (Licor Inc., Lincoln, NE, USA). Although the estimates are not adjusted for clumping, it is unlikely to affect the following analysis as the canopy was closed, and the LAI measurements were carried out on the same plots throughout the study, allowing for interannual comparison. Furthermore, the litterfall-based estimate of peak LAI in 2006 (as the sum of litterfall in 2006 and 2007) was similar to the optical estimate (3.87 vs. 4.0 m² m⁻²).

C pools

C storage was quantified in all the major pools, including the stemwood, foliage and belowground biomass for the major canopy and understory species, plus woody groundcover, coarse woody material (CWM), the O-horizon and soil. The standing biomass in aboveground and belowground woody tissues was estimated

from species-specific allometric relationships (Flowers, 1978; Swindel *et al.*, 1982; Clark *et al.*, 1985; Tew *et al.*, 1986; Stucky *et al.*, 1999; Jenkins *et al.*, 2004), based on tree height and diameter at breast height (DBH, 1.4 m). These measurements were made in thirteen 14-m diameter Tier-3-type vegetation survey plots (Wofsy & Harriss, 2002), located throughout the 1 km² study area. All trees with DBH >2.5 cm were tagged, identified to species and remeasured every winter for changes in diameter.

Leaf fall was measured with three 0.18 m² litter traps on each plot. The litter was collected every 60 days during spring and summer, and every 2 weeks during fall and early winter. The samples were separated into needles, leaves, twigs, and reproductive litter, and oven dried at 65 °C for 24 h. Dried samples were weighed immediately upon removal from the oven, subsampled and ground for elemental analysis. The CWM biomass was estimated on 25 plots laid out on 5 × 5 grid across the study area. Each plot had two perpendicular 40-m transects, originating from the center of the plot. The direction of the first transect was determined with a random declination generator. All pieces of CWM larger than 7.6 cm in diameter at the intersection with the transect were identified to species, and the diameter and decay class were recorded (FIA, 2007). Snags (dead standing trees) in the vegetation plots were also included in this pool. The C content of CWM was determined according to Birdsey (1992), and the decay rate reduction factors were based on Waddell (2002). Soil cores of 5 cm diameter and 20 cm deep were dried at 65 °C for 48 h, sieved to remove roots, ground to a fine powder, re-dried for 24 h, and weighed for C and N analysis on a PerkinElmer 2400 (Perkin Elmer, Waltham, MA, USA) elemental analyzer.

Biometric estimation of net ecosystem productivity

Net primary productivity (NPP_B) of the ecosystem was calculated from the annual changes in above- and belowground live biomass, plus leaf fall, fine root production and branch fall (Table 1). Since understory biomass and soil C were measured only in the last year, these pools were assumed to be relatively constant through the years and omitted from NPP_B calculations. Fine root biomass was estimated as a fraction of woody root biomass, assuming a ratio of 0.22 between these pools based on the relationship with mean annual temperature at five forest sites in eastern US as reported by Curtis *et al.* (2002), and a turnover of 0.21 yr⁻¹ according to Matamala *et al.* (2003). These estimates were compared with those assuming fixed ratio between fine and woody root productivity (Curtis *et al.*, 2002), and were found to result in comparable estimates. Net ecosystem productivity (NEP_B) was calcu-

lated as NPP_B minus $R_{h,v}$, and change in CWM (Curtis *et al.*, 2002). In addition to the reported biomass estimates following Flowers' (1978) equations (Table 1), we also calculated estimates using Tew *et al.*'s (1986) and Jenkins *et al.*'s (2004) equations (not shown). Owing to differences in the geographic specificity of the initial studies, the biomass estimates were consistently higher using Jenkins' equations compared with the equations of Flowers and Tew. However, for all equations, NEP_B estimates were within 15–25% of each other, and the standard errors of the mean NEP_B estimates from different methods overlapped. We chose to use Flowers' equations because they were developed for sites closest to our study area. Heterotrophic respiration was estimated as 50% of SR in NEP_B calculations, following Curtis *et al.* (2002).

Microclimate and eddy covariance measurements

The following micrometeorological parameters were measured above canopy: air temperature (Ta, HMP45AC, Vaisala, Finland), photosynthetically active radiation (PAR, LI-190, Licor Inc.), net radiation (Rn, CNR-1, Kipp & Zonen, Delft, the Netherlands) and precipitation (P, TE-525, Campbell Scientific Inc., (CSI), Logan, UT, USA). The PAR measurements were corrected for sensor drift based on annual comparisons against Ameriflux standard sensor (PARLITE, Kipp & Zonen), and assuming linear drift. Soil temperature (T_s) was measured at 5 and 20 cm with CS107 (CSI) temperature probe, soil moisture profile was measured with Sentek EnviroSCAN (Sentek Sensor Technologies, Stepney, Australia), soil volumetric water content (VWC) was averaged through the top 30 cm using a vertically inserted CS616 time domain reflectometer (CSI), and the depth of GWT was monitored with pressure water level data logger (Infinites, Port Orange, FL, USA).

The turbulent exchange of CO₂ between the forest canopy and atmosphere was measured throughout 2005, 2006 and 2007 using eddy covariance. The 23 m instrument tower was located in the middle of the 1 km² stand. The distance to the nearest road was 450 m (26 × measurement height of 18 m). The stand was surrounded in most directions by uniform canopy with similar species and age composition, that extended a uniform fetch to 900–1300 m (50–70 × measurement height). The turbulent flux showed no directional variability, suggesting that the fetch was sufficient for periods when other quality control criteria were met. The tower was instrumented with a LI-7500 open-path infrared gas analyzer (Licor Inc.), a CSAT3 3-dimensional sonic anemometer (CSI), and a CR5000 data logger (CSI). The 30-minute mean fluxes of CO₂ were computed as the covariance of vertical wind speed and

Table 1 Carbon pools and fluxes

		2004	2005	2006	2007
Eddy covariance and chamber-based fluxes ($\text{gC m}^{-2} \text{yr}^{-1}$)					
A	NEE	na	-361 ± 67	-835 ± 55	-724 ± 55
B	ER	na	2121	2074	2051
C	GEP	na	2482	2911	2764
D	SR	na	1331 ± 374 (24)	1114 ± 422 (24)	1141 ± 404 (24)
E	$R_h = 0.5 \times D$	na	667	558	571
F	$R_a = B - E$	na	1454	1516	1480
G	$\text{NPP}_E = C - F$	na	967	1344	1232
	$-NEE : \text{NPP}_E$	na	0.37	0.62	0.59
	SR : ER	na	0.63	0.54	0.56
Pools (Mg C ha^{-1})					
H	Aboveground woody biomass	40.1 ± 11.1 (10)	46.6 ± 13.2 (10)	52.9 ± 15.2 (10)	61.3 ± 18.2 (10)
I	Belowground woody biomass	9.7 ± 2.7 (10)	11.3 ± 3.2 (10)	12.8 ± 3.7 (10)	14.8 ± 4.4 (10)
J	Fine root biomass = $0.22^* \times I$	2.13	2.49	2.82	3.26
K	Understory	na	na	na	1.5 ± 0.7 (13)
L	CWM	na	2.9 ± 4.3 (13)	na	3.5 ± 3.3 (13)
M	Branchfall	na	na	0.6 ± 0.6 (13)	0.5 ± 0.3 (13)
N	Leaf litter fall	na	3.1 ± 0.5 (13)	4.1 ± 0.7 (13)	4.0 ± 0.6 (10)
O	Soil	na	na	na	414 ± 38 (4)
P	Litterfall = $M + N + 0.21^\dagger \times J$	na	$4.2 \pm 1.8^\ddagger$	5.3 ± 1.7 (13)	5.2 ± 1.8 (10)
Biometric fluxes ($\text{gC m}^{-2} \text{yr}^{-1}$)					
Q	$\text{NPP}_B = dH + dI + 0.21^\dagger \times J + M + N$	na	1232 ± 367 (10) ‡	1302 ± 391 (10)	1549 ± 537 (10)
R	$\text{NEP}_B = Q - E - dL$	na	564 ± 332 (10) $^\ddagger, \S$	743 ± 315 (10) \S	977 ± 472 (10) \S
S	$\text{NEP}_B : \text{NPP}_B$	na	0.46	0.57	0.63
	$-NEE : \text{NEP}_B$	na	0.64	1.12	0.74

Biometric fluxes derived as in Curtis *et al.* (2002). The error estimates are cumulative gapfilling uncertainty (ΣU) across all gapfilled periods for NEE, and standard deviation for SR, C pools, NPP_B and NEP_B . The number of plots is given in parentheses.

*Estimated based on the relationship of the ratio of fine root to woody root biomass with mean annual temperature across five forests in eastern US, as reported by Curtis *et al.* (2002).

† Average turnover of loblolly pine roots <2 mm in diameter (Matamala *et al.*, 2003).

‡ Branchfall data estimated as the mean of 2006 and 2007.

\S dL estimated as the mean annual change from 2005 to 2007.

NEE, net ecosystem CO_2 exchange; ER, ecosystem respiration; GEP, gross ecosystem productivity; SR, soil respiration; R_h , heterotrophic respiration; NPP, Net primary productivity; CWM, coarse woody material.

the concentration of CO_2 , using the EC_PROCESSOR software package (<http://www4.ncsu.edu/~anoorme/ECP/>). The algorithm uses the formulation of Leuning (2004) in the planar fit coordinate system (Wilczak *et al.*, 2001), which was defined from the entire year's mean wind data. The turbulent fluxes were adjusted for fluctuations in air density (Webb *et al.*, 1980). Sonic temperatures were corrected for changes in humidity and pressure (Schotanus *et al.*, 1983). The 30-minute fluxes were corrected for the warming of IRGA according to Burba *et al.* (2008). Net ecosystem exchange of CO_2 (NEE) was calculated as the sum of turbulent flux and change in CO_2 storage in the canopy air space. CO_2 storage was estimated as the mean rate change in CO_2 concentration, measured at four heights (about $0.05 \times$, $0.2 \times$, $0.6 \times$ and $0.9 \times$ of canopy height) in the canopy air column (Noormets *et al.*, 2007).

Daily maximum canopy conductance ($g_{c-\max}$; m s^{-1}) to water vapor was estimated as (Morris *et al.*, 1998; Anthoni *et al.*, 2002):

$$g_{c-\max} = \frac{pER_w}{\rho VPD R_d}, \quad (1)$$

where p is atmospheric pressure (kPa), E is evapotranspiration ($\text{kg m}^{-2} \text{s}^{-1}$), ρ is air density (kg m^{-3}), VPD is vapor pressure deficit (kPa) and R_d and R_w are universal gas constants for dry air and water vapor, respectively. Based on the observation that the rate change in stomatal conductance in response to VPD is related to stomatal opening at a given VPD level (Oren *et al.*, 1999), we used the mean $g_{c-\max}$ at $VPD = 1.5 \pm 0.1$ kPa ($g_{c1.5}$) as a seasonal indicator of moisture stress.

Quality control and gapfilling of eddy covariance data

Data quality was judged by atmospheric stability and flux stationarity (Foken & Wichura, 1996) during periods of well-developed turbulence (Goulden *et al.*, 1996) as reported previously (Noormets *et al.*, 2007, 2008b). Following the quality screening, the remaining data coverage was 42% (2005), 47% (2006) and 49% (2007), with gaps caused primarily by periods of dew and precipitation, and poorly developed turbulence ($u^* < 0.20$, determined for the site, data not shown). The latter often co-occurred with very stable or very unstable atmospheric conditions. The gaps were filled with a dynamic parameter model (Moffat *et al.*, 2007; Noormets *et al.*, 2007), where the respiration model was parameterized first using only the night-time data, and once daytime respiration estimates were available, gaps in daytime NEE were filled. The performance of the gapfilling model was typical of network-wide standards (data not shown). A recent comprehensive comparison of commonly used gapfilling methods (Moffat *et al.*, 2007), of which our method was a part, showed that across methods, there remains about 3–5% random error at 30-minute level, that is more related to the sampling error of the turbulent exchange than to model properties. A comparison of gapfilling with CarboEurope standardized gapfilling tool (<http://gaia.agraria.unitus.it/database/eddyproc/>) yielded annual NEE estimates within 8–15% of those reported here (depending on year). Additionally, ecosystem respiration (ER) and gross ecosystem productivity (GEP) differed by 3% from the estimates reported here. The interannual differences far exceeded differences between gapfilling methods.

Gapfilling uncertainty (U , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was estimated from the model residuals (ϵ , measured-modeled) according to Flanagan & Johnson (2005) and Aurela *et al.* (2002):

$$U = \sqrt{\frac{\sum_{i=1}^n \epsilon^2}{n^2 - n}}, \quad (2)$$

where n is the number of observations. The seasonal mean uncertainties were about 13% for night-time gaps (range 6–34%) and 11% for daytime gaps (range 8–21%). When applied to all gapfilled periods, these uncertainties amounted to 55–67 $\text{g C m}^{-2} \text{ yr}^{-1}$ (Table 1).

SR

SR was measured continuously near the instrument tower and bi-weekly in four of the 13 vegetation survey plots using a portable infrared gas analyzer (LI-8100 (Licor Inc.) with 8100-101 automatic long-term chamber and 8100-102 survey chamber, respectively, and permanently installed PVC collars. Each plot had six perma-

nently installed PVC collars. Soil temperature and moisture at 5 and 10 cm depths were measured at the time of SR measurements. Upscaling to the annual scale was carried out using both the automatic and survey chamber measurements, using the empirical relationships between SR and soil temperature and moisture (Noormets *et al.*, 2008a). Continuous measurements of soil temperature at a 10 cm depth were made at the central instrument tower using CS107 thermistors (CSI), and at each of the SR plots using HOBO H8 datalogger, and four TMC6 temperature probes (Onset Computer Corporation, Pocasset, MA, USA) per plot. There were large and consistent differences among collars, and the annual estimates are presented as means of collar-specific upscaling to the entire year ($n = 4 \times 6 = 24$). The base respiration and temperature sensitivity (not shown) were defined much better for individual collars than for plots, and the variability among collars within a plot exceeded that among the plots. Furthermore, collars within 1.5 m from trees had consistently about 40% higher SR than collars further away. When scaling up to stand level, we weighed the measurements closer to the trees two times more heavily than those further away because two-thirds of the total stand ground area is located within 1.5 m from a tree and one-third is within 1.5–2.5 m.

Tree hydraulic conductance

Whole tree hydraulic conductance (K_{tree}) was calculated from the diel variation in leaf water potential and tree transpiration (Loustau *et al.*, 1998). Leaf water potentials were measured from dawn to mid-afternoon with a pressure chamber (PMS, Albany, OR, USA). Measurements were made biweekly from May to October and then once a month in November and December of 2007. Tree transpiration (E) was determined from trunk sap flux measured in six healthy trees. Stem sap flux measurements were made at 1.4 m above the ground at four different radial trunk positions using 10 mm heat dissipation sensors (James *et al.*, 2002; Domec *et al.*, 2006), modified after Granier (1987). Thirty-minute average temperature difference data were computed and stored in a data logger (CR10, CSI). The sensor signal was converted to sap flux density (J_S in $\text{kg m}^{-2} \text{ s}^{-1}$) according to Granier (1987), assuming that natural temperature gradients between sensors are small (Lundblad *et al.*, 2001) and accounting for the effects of non-zero night-time fluxes on the signal baseline (Oishi *et al.*, 2008). Sapwood depth and bark thickness were measured from 16 surrounding felled trees as well as from tree cores taken from eight trees. The total sapwood area from the site was estimated from the relationship between measured sapwood area and DBH, combined

with stand-level inventory of DBH at the site. Using sapwood area and LAI, J_S was scaled and converted to a tree-scale average transpiration per unit leaf area (E , in $\text{kg m}^{-2} \text{s}^{-1}$). For this specific site, further details of sap-flow methodology and results are given by Domec *et al.* (2009).

Statistical analysis

The comparison of microclimatic conditions between years was analyzed with repeated measures ANOVA (PROC MIXED in SAS), using day of year as the repeated measure. The effect of VWC on GEP and NEE was calculated similarly, but with PAR as the repeated measure. The significance of least squares differences among years was calculated with a multiple range test using Kramer's (1956) approximation for unbalanced samples.

Results

Microclimate

The three study years (2005–2007) were similar in terms of air temperature (T_a), but differed significantly in the amount and timing of precipitation (Fig. 1). Soil temperature (T_s) did not significantly differ on an annual scale, but the main growing season (May–September) was 1.3 and 0.8 °C warmer in 2005 than in 2006 and 2007 ($P < 0.0001$ and 0.05, respectively; data not shown). The increase in T_a in the spring was slower during the study than the long-term average, with about a 15-day lag. The cooling phase, from July through the end of the year, closely mirrored the long-term mean. The precipitation (P), soil VWC and GWT were all tightly coupled (Fig. 1) because of the high water table. Compared with the long-term mean, precipitation in recent years has shifted from relatively uniformly distributed to drier winters and wetter summers (Fig. 1b). Consequently, all three study years exhibited consistent rainfall deficit at the beginning of the year which recovered by the start of the growing season. In 2005, the annual cumulative rainfall exceeded the long-term mean by about 150 mm, largely due to intense rains in late summer and fall. In contrast, 2007 had lower than average rainfall throughout the year, and the cumulative precipitation deficit amounted to nearly 500 mm yr^{-1} . Year 2006 had annual rainfall similar to the long-term mean (1320 mm). While the total P during the growing season was very similar between 2005 and 2006, the individual rain events were about twice as frequent, but half the size in 2006 compared with 2005 (Fig. 1b). The contrast in P between the 2 years was largest from May through September, when 51% of total

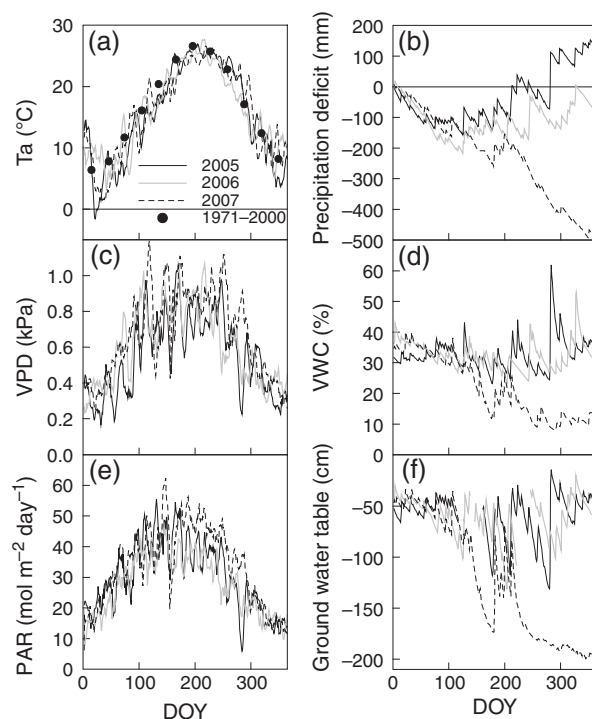


Fig. 1 The annual course of daily mean air temperature (T_a) and 30-year (1971–2000) monthly mean air temperature, precipitation deficit compared with the 30-year mean, vapor pressure deficit (VPD), soil volumetric water content (VWC), daily total photosynthetically active radiation (PAR) and the depth of ground water table (GWT) during 3 years at a loblolly pine plantation in the lower coastal plain in North Carolina, USA. The T_a , VPD and PAR are presented as 7-day running means to improve readability. The statistics presented in the text are based on actual daily data.

rainfall (732 mm) came in events $> 50 \text{ mm d}^{-1}$ in 2005, whereas in 2006 only 25% (of total of 744 mm) fell in such large events. A detectable increase in VWC ($> 1\%$ in the top 30 cm) required about 15 mm of rain over 3 days, and such events were separated by an average of 7.1 days in 2005, 4.8 days in 2006, and 12.2 days in 2007. The severe precipitation deficit in 2007 was reflected in significantly lower VWC (11%, $P < 0.0001$) compared with 2005 and 2006. For the entire year, the difference averaged 11% (in absolute terms), but during the peak drought in the fall, the VWC was over 20% lower in 2007 than in 2005 or 2006. From May through September, VPD was about 125 and 100 Pa higher in 2007 than in 2005 and 2006, respectively ($P < 0.001$ and 0.01, respectively; Fig. 1c), despite the limited differences in air temperature. The PAR was higher in 2007 (with the weighted mean of 34_A mol d^{-1}), than in 2005 (30.5_{AB}) or 2006 (27.6_B ; different letters mark significant differences at $P < 0.05$). The differences were particularly pronounced from June through September (Fig. 1e), but

were significant across the entire year ($P < 0.05$). The interannual differences in VPD seemed more related to soil moisture availability than radiation. Including VWC as a covariate in the ANOVA removed any differences from among the years (778_A, 791_A and 761_A Pa in 2005, 2006 and 2007, respectively), suggesting proportional compensation. However, normalizing VPD by PAR showed that relative to radiative forcing VPD was unexplainably high in 2007, and low in 2006.

Ecosystem C fluxes

Based on allometric estimates the forest sequestered 602 ± 332 (2005; mean \pm SD across 10 plots), 781 ± 315 (2006) and 1020 ± 472 (2007) $\text{g C m}^{-2} \text{yr}^{-1}$, whereas eddy covariance-based estimates were 361 ± 67 (2005; mean \pm gapfilling uncertainty), 835 ± 55 (2006) and 724 ± 55 (2007) $\text{g C m}^{-2} \text{yr}^{-1}$ (Table 1). The relatively high biomass increment is the result of year-round canopy and favorable climatic conditions rather than high instantaneous assimilation rates. The peak GEP was $12\text{--}13 \text{ g C m}^{-2} \text{day}^{-1}$, balanced by equally high ER of $8\text{--}10 \text{ g C m}^{-2} \text{day}^{-1}$. As a result, the peak NEE was $3\text{--}5 \text{ g C m}^{-2} \text{day}^{-1}$. The interannual differences in NEE were reflected in the GEP totals, whereas ER was very consistent among years (Fig. 2). In contrast, annual SR was significantly higher and contributed 63% of ER in 2005, compared with 54% and 56% in 2006 and 2007, respectively (Table 1). Across all years, NEE consistently peaked in April and May, as the increase in GEP in June and July was smaller than the increase in

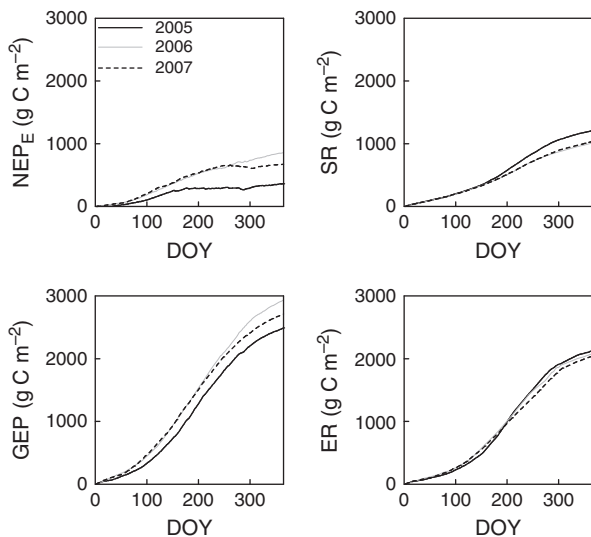


Fig. 2 Cumulative net ecosystem exchange of CO_2 (NEE), gross ecosystem productivity (GEP), soil respiration (SR) and ecosystem respiration (ER) during 3 years at a loblolly pine plantation in the lower coastal plain in North Carolina, USA.

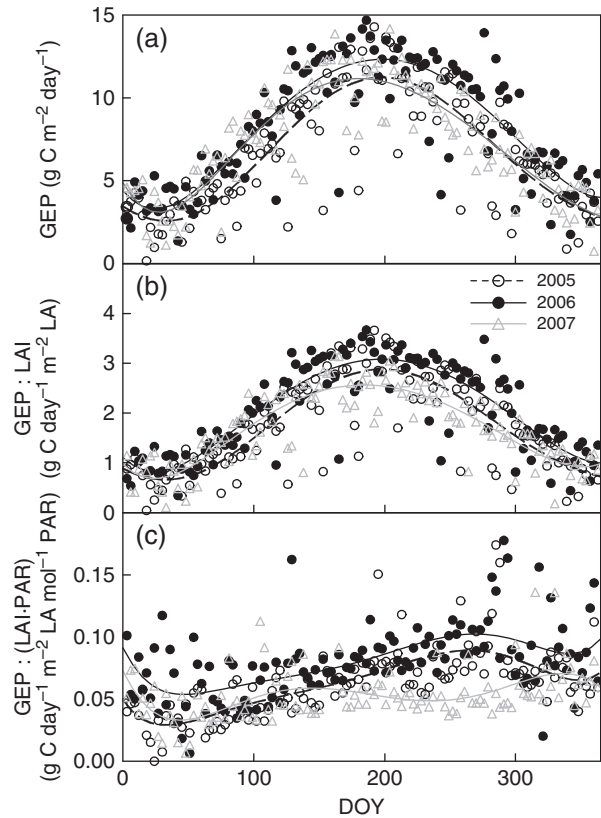


Fig. 3 Daily gross ecosystem productivity (GEP, a), GEP normalized by annual peak leaf area index [GEP:LAI, b, $\text{g C d}^{-1} \text{m}^{-2} \text{leaf area (LA)}$], and by peak LAI and daily photosynthetically active radiation [GEP:(LAI \times PAR), c] during 3 years at a loblolly pine plantation in the lower coastal plain in North Carolina, USA. Data is thinned $3 \times$ for improved readability (i.e. only every third day is shown). The lines are best-fit sixth-degree polynomials.

ER. The net exchange declined to near C neutral at about DOY 180 (in 2005) and DOY 250 (in 2007). However, rains in September and October (especially in 2006) relieved some of the summer moisture deficit, and C uptake continued throughout the year.

The interannual differences in GEP were enhanced when normalized by LAI, and especially when normalized by PAR and LAI (Fig. 3). Using these normalizations, 2006 emerged as the most productive year and 2007 the least. Although consistent and statistically significant, the differences in daily total GEP were small. Given that 2007 had the highest PAR, normalizing by it suppressed GEP disproportionately to other years. Whereas in 2005 and 2006 the PAR-normalized GEP increased throughout the growing season as the new cohort of leaves matured and their photosynthetic capacity increased, in 2007 the LAI- and PAR-normalized GEP peaked in May (around DOY 130).

Variability of GEP and ER with VWC

The relationship between VWC and GEP was neither statistically significant during a given year nor consistent among years. The VWC effects and differences among years were similar but more pronounced on the basis of LAI-normalized GEP than direct daily GEP, so only the former is presented here. In 2005, the lowest GEP occurred during the highest VWC (Fig. 4) and the VWC-related suppression of GEP increased with PAR. However, the data in this VWC class originated almost exclusively from early May, when leaves were not fully matured. During other years, the VWC effect on GEP increased at lower PAR levels, but was only marginally significant ($P < 0.1$; Fig. 4). Importantly, there was no sign of suppressed GEP during low VWC conditions. In 2005 and 2007, light use efficiency (α) decreased with decreasing VWC (0.05 ± 0.004 and $0.03 \pm 0.007 \text{ mol CO}_2 \text{ mol}^{-1} \text{ PAR}^{-1} \text{ VWC}$ in 2005

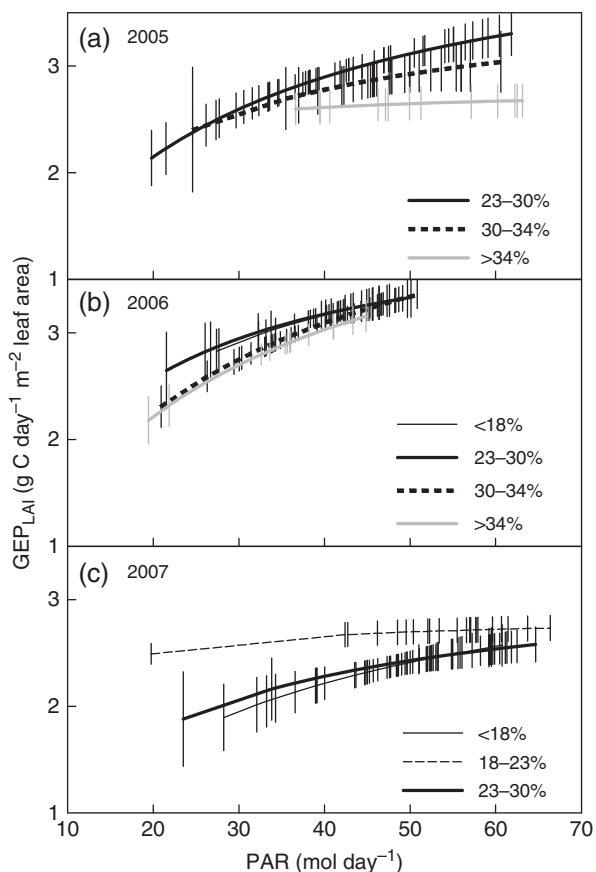


Fig. 4 The response of LAI-normalized gross ecosystem productivity (GEP_{LAI}) to photosynthetically active radiation (PAR) during different soil moisture conditions during the months of May through October of 3 years in the lower coastal plain in North Carolina, USA. The data are the means and 95% confidence intervals of fitted data (actual data points not shown for clarity) for different soil moisture classes.

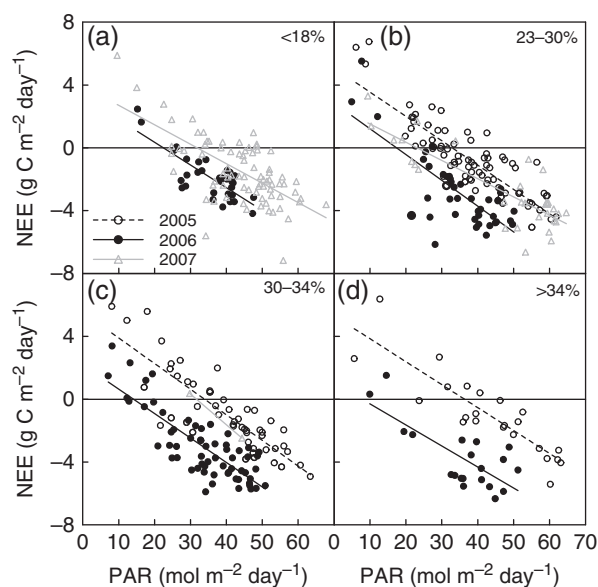


Fig. 5 The response of net ecosystem exchange of CO_2 (NEE) to photosynthetically active radiation (PAR) during the months of May through October in 3 years at different soil moisture conditions. Each panel represents a different soil moisture class. Since daily mean VWC of 18–23% occurred only in 2007, interannual comparison is not possible and this moisture class is not shown. The Pearson correlation coefficient indicated that daily PAR explained about 82% (range 66–88%) of variation in daily NEE for any given VWC class during a given year.

and 2007, respectively, $P < 0.0001$, data not shown). However, there were compensating trends in maximum photosynthetic capacity (P_{max} ; estimated as a parameter of rectangular hyperbola), which offset the effect of α and suppressed the VWC effects on daily GEP. In 2006, when GEP was significantly higher than in the other years ($P < 0.0001$), the trends in α and P_{max} with VWC were opposite, possibly signifying super-optimal VWC.

ER was highest at intermediate VWC levels and decreased in both drier and wetter conditions (not shown). However, the temperature sensitivity of ER did not exhibit a consistent response to VWC. As low VWC usually coincided with high T_a (and T_s), the temperature effects partly masked the VWC effects. Interannual differences in ER were detectable only during the driest soil conditions (VWC < 18%), when ER in 2007 was lower than in 2006. During higher VWC, all years fell on the same temperature response curve and any differences in ER could be explained by differences in temperature (data not shown).

While the interannual differences in the NEE PAR response were clear (Fig. 5), the VWC effect on this response (NEE vs. PAR) was smaller. Nevertheless, the intercept (proxy for daytime respiration) and compensation point increased as the soil became drier (Fig. 6). Interestingly, the absolute value of these parameters, as

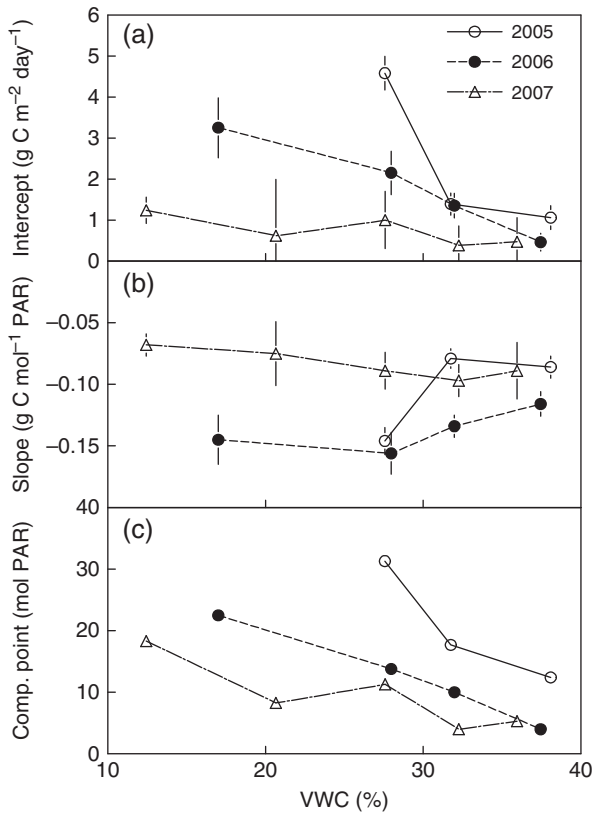


Fig. 6 The parameters of NEE light response (Fig. 6) as a function of soil moisture conditions. The data are modeled parameters estimates and the standard error of the estimate. VWC is the mean of the particular VWC class (<18, 18–23, 23–30, 30–34 and >34%).

well as the rate of change with VWC was lower in 2007 than in 2006 or 2005. Even though no significant differences were detected in ER among years, the lower intercept and compensation point, that suggest lower daytime respiration, rank in the same order as the annual total ER (Table 1). The slope of the daily NEE-PAR relationship (ecosystem level light use efficiency) was greater in 2006 than in 2005 or 2007, and higher at intermediate than at low or high VWC.

Variability of g_{c-max} with VPD

Daily maximum canopy conductance (g_{c-max}) declined with VPD at $VPD > 1$, and leveled off at 12–13 $mm\ s^{-1}$ during periods of sufficient soil moisture. However, when VWC was below 20% (equivalent to 50% of total extractable moisture at this site), as it was in June and from mid-August until the end of the year in 2007 (Fig. 1), g_{c-max} declined progressively with increasing VPD to as low as 5 $mm\ s^{-1}$ (not shown). The g_{c-max} -VPD relationship did not significantly differ between 2005 and 2006, whereas in 2007 g_{c-max} was lower and more

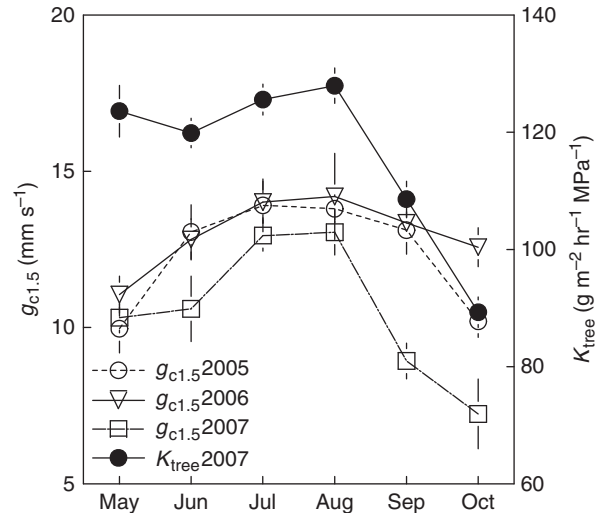


Fig. 7 The seasonal dynamics of VPD-normalized canopy conductance ($g_{c1.5}$, canopy conductance at VPD = 1.5 kPa) and whole tree hydraulic conductance (K_{tree}).

sensitive to high VPD than during the other years at similar VPD. Indications of moisture stress were seen both in VPD-normalized canopy conductance ($g_{c1.5}$), as well as whole tree hydraulic conductance (Fig. 7). The decline in g_{c-max} on the seasonal scale was more pronounced as a function of precipitation deficit (Fig. 8a) than VWC (not shown), and was accompanied by corresponding decrease in NEE (Fig. 8b). In 2006 and 2007, g_{c-max} decreased about 2.5 $mm\ s^{-1}$ for every 100 mm increase in the rainfall deficit. In 2005 the deficit was small, and any effect on g_{c-max} was not detectable. The magnitude of NEE, in turn, declined by 7.5_B (2005), 5.9_B (2006) and 11.3_A (2007) $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ per 10 $mm\ s^{-1}$ decline in g_{c-max} . At any given g_{c-max} , NEE was about 2.4 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ less negative in 2005 than in 2006 or 2007 ($P < 0.0001$; Fig. 8).

Discussion

Productivity and sources of uncertainty

The loblolly pine plantation was a strong C sink, accumulating 360–835 $g\ C\ m^{-2}\ yr^{-1}$ during the 3 years of study (Table 1). While not measured in current study, losses of C in the form of CH_4 or dissolved organic compounds are likely to contribute about 100- to 1000-fold less. For example, CH_4 emissions from similar forested *Sphagnum* peatlands remain under 3.5 $g\ m^{-2}\ yr^{-1}$ (Bridgman *et al.*, 2006), and loss of dissolved organic C at our study site has been found to be even smaller (0.01 $g\ m^{-2}\ yr^{-1}$ (Amatya *et al.*, 1998). Compared with native forests in the SE US coastal plain, the NPP_B at our current study site is in the upper end of

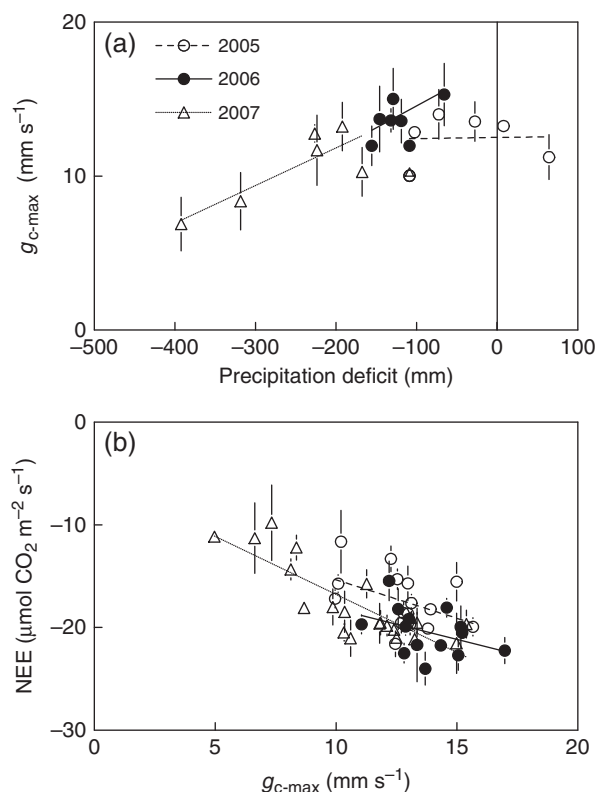


Fig. 8 Monthly mean of the daily maximum canopy conductance (g_{c-max}) as a function of monthly cumulative precipitation deficit (a) and daily total net ecosystem exchange of CO₂ (NEE) as a function of g_{c-max} from May through October during 3 years.

the range of 477–1117 $g\ C\ m^{-2}\ yr^{-1}$ (Meronigal *et al.*, 1997; Ozalp *et al.*, 2007). It is important to note that in terms of hydrologic regime and average groundwater depth, the current site falls on the dry end of the range of floodplain forests characterized by Meronigal *et al.* (1997). They showed that NPP was highest with groundwater depth at about 50–80 cm (which is where the current study site falls), and decreased at both higher and lower depths. The net productivity of our study site was also similar to intensively managed *Pinus pinaster* (in LeBray, France) and *Pinus elliotii* (in Florida, USA) stands, but had 25–80% higher GEP and 25–160% higher ER (Clark *et al.*, 1999; Berbigier *et al.*, 2001). The GEP and ER reported in current study were more similar (+25%) to those at the *P. pinaster* stand in LeBray, France, which is, like our current study site, located on about 60 cm of organic soil layered over sand with high GWT (Berbigier *et al.*, 2001). The *P. elliotii* stand, on the other hand, is located on well-drained sand, and very limited organic horizon, the accumulation of which is suppressed by regular low-intensity fires typical to that ecosystem (Clark *et al.*, 1999). Following the site differences in the organic layer, the relative con-

tribution of SR to ER was also lower in the *P. elliotii* stand compared with the other two.

Biometric estimates put the annual C gain at 600–1020 $g\ C\ m^{-2}\ yr^{-1}$. Owing to incomplete measurements of all C pools, there are uncertainties associated with these estimates. The biggest of these is probably fine root productivity, which was estimated based on literature (Matamala & Schlesinger, 2000; Curtis *et al.*, 2002; Matamala *et al.*, 2003), but variability in belowground allocation, branchfall and CWM decomposition may also contribute (Table 1). Even though the assumption of fine root biomass being a certain fraction (22%) of woody root biomass (as estimated based on the relationship of this ratio with mean annual temperature across five forests in eastern US; Curtis *et al.*, 2002) resulted in fine root biomass estimates similar to those reported for an upland loblolly pine plantation (Matamala & Schlesinger, 2000), questions remain. Indeed, the resulting BNPP : NPP ratio of 0.17 is higher than the 0.06 reported by Matamala & Schlesinger (2000). It may be possible that despite the allometric equations having been developed very near to the current study location, the consistent 24% belowground allocation (Fowler *et al.*, 1988) may not have been appropriate at the current study site. On broad scale, belowground allocation is thought to decrease with productivity (Palmroth *et al.*, 2006), but whether it also applies to interannual variability, is not yet known.

The unaccounted for variability in belowground allocation and use of stored carbohydrates for spring-time growth and leaf development are the likely causes behind the variable differences between the eddy covariance and biometric estimates of NEP. Such partial decoupling of current year weather and observed growth has been reported previously. For example, Gough *et al.* (2008) and Barford *et al.* (2001) have shown that individual years could differ substantially in terms of biometric and eddy covariance-based NEP estimates, but over several years the methods converged. Furthermore, Braswell *et al.* (1997) detected a 1- to 3-year lag between temperature and normalized difference vegetation index (NDVI) anomalies and a 1.5- to 2.5-year lag with atmospheric CO₂ concentration anomalies on the global scale.

Given these indications of overestimated BNPP, it could be questioned if the 24% belowground allocation in the biometric equations is accurate. It should also be noted that while this percentage is low compared with upland pine forests (Mokany *et al.*, 2006; King *et al.*, 2007), it was actually the highest among the biometric models developed for loblolly pine in this area (Flowers, 1978; Tew *et al.*, 1986; Jenkins *et al.*, 2004). On the other hand, if we estimate BNPP as 6% of total NPP as observed by Matamala & Schlesinger (2000), the result-

ing NEP_B estimates would come to 418 (2005), 612 (2006) and 801 (2007) $gC\ m^{-2}\ yr^{-1}$, and the total ($-NEE$): NEP_B ratio over the 3-year study period would equal 1.05. In reality, the $BNPP:NPP$ ratio would probably fall somewhere in between the 0.06 and 0.17 estimates used here.

Comparison with other ecosystems

Compared with Duke Forest, a similar-aged loblolly pine plantation in similar climate but on upland soils, the NEE was similar, but both GEP and ER were 20–23% higher in current study (Schäfer *et al.*, 2003; Oren *et al.*, 2006; Stoy *et al.*, 2006). Although there are limited studies that would allow paired comparison of upland and lowland ecosystems, Hirano *et al.* (2007) reported comparable differences between a drained tropical peatland forest in Indonesia and upland forests in the Amazon, both of which were exposed to similar climatic conditions. They observed 22–31% higher annual ER at the peatland site than reported for the Amazonian upland forests (Saleska *et al.*, 2003; Goulden *et al.*, 2004).

Compared with other coastal forests, total ecosystem C at our study site (nearly $500\ tC\ ha^{-1}$; Table 1) far exceeds the average estimates for the coastal oak-pine, loblolly-shortleaf pine, oak-gum-cypress, and longleaf-slash pine forests of $163\text{--}260\ tC\ ha^{-1}$ (Heath *et al.*, 2003). Given the organic soil, favorable C:N ratio, good moisture availability, and high T_s , we expected a high SR:ER ratio. Surprisingly, however, SR was only 54–63% of ER (Table 1), which is similar to that found in a 56-year old Douglas fir stand in the Pacific coast of Canada (Jassal *et al.*, 2007), but lower than the 75–80% reported for Duke Forest (Juang *et al.*, 2006; Stoy *et al.*, 2006). Although there is no reason to doubt the differences between the two sites, the recent advances in measurement methodology (Bain *et al.*, 2005) have lead to more conservative SR estimates, implying that the different methodologies may have contributed to the observed difference between the current study and the data from Duke Forest. Given that ER did not statistically differ between the years, whereas SR was significantly higher in 2005 than 2006 and 2007 (Table 1), the difference in SR:ER ratio is also statistically significant. Usually, the contribution of SR to ER decreases during drought as soil microbes become moisture limited (e.g. Clark *et al.*, 2004). In current study, this held for 2005 and 2007, whereas the lower SR (and SR:ER) in 2006 was not attributable to low VWC.

Sensitivity of C fluxes to drought

The interannual variability was most striking in P, but was also seen in PAR and VPD. The corresponding

differences in NEE correlated better with those in GEP than ER (Table 1), but neither exhibited a drought-related suppression at low VWC. Although the effect of VWC on daily NEE was not statistically significant, the parameters of the NEE PAR response exhibited distinct interannual and VWC-related trends. However, the interannual contrasts and intra-annual trends with VWC were contrary to one another – daytime respiration (intercept, Fig. 6a) and compensation point were the lowest during the dry year, but decreased with increasing VWC during a given year. We hypothesize that the lower sensitivity of the intercept and compensation point to VWC during the drier years were related to lower stomatal conductance, which affected GEP and the amount of carbohydrate substrates available for respiration (Högberg *et al.*, 2001, 2008; Noormets *et al.*, 2008b). This hypothesis is supported by the suppressed g_{c-max} and K_{tree} under drought conditions (Fig. 7), as well as by the earlier decline of GEP in September and October (DOY 245–305) in 2007 compared with 2005. This pattern is not depicted by the simple polynomial fitted in Fig. 4, but is apparent in daily values. The temporal dynamics of K_{tree} suggests that xylem elements lost part of their hydraulic efficiency during drought conditions (Fig. 7), probably because of cavitation-induced loss of conductivity (Tyree & Sperry, 1989), lending support to the hypothesized physiological limitation of GEP under moisture stress.

However, the interannual differences in moisture limitation of GEP were partially confounded by differences in LAI and PAR. Daily GEP did not respond to the drought in 2007 until DOY 250, when the precipitation deficit exceeded $-250\ mm$ (Figs 1 and 2). The moisture limitation became more apparent upon normalizing GEP per unit leaf area and PAR. The normalized GEP saturated by DOY 130 (Fig. 3), suggesting that the second flush of leaves that emerged in July was less efficient than the existing foliage and its contribution to the overall plant C budget was limited. While the drought in June probably suppressed the gas exchange rates of all leaves, the adverse effect on the development of new leaves was likely greater than that on the exchange rates of existing foliage (Noormets *et al.*, 2008b). However, as seen above, the contribution of environmental differences among the years and those of physiological responses to these factors may have been of comparable importance. The direct effects of VWC on GEP, ER, and ER temperature-sensitivity were not statistically significant, but the individual effects combined so that at the NEE level, sensitivity to both VWC and VPD was statistically significant (Figs 6 and 8). Furthermore, across years the ER: NEP_B ratio seemed tightly coupled to precipitation (Fig. 9). This, along with the similarly good relationship with

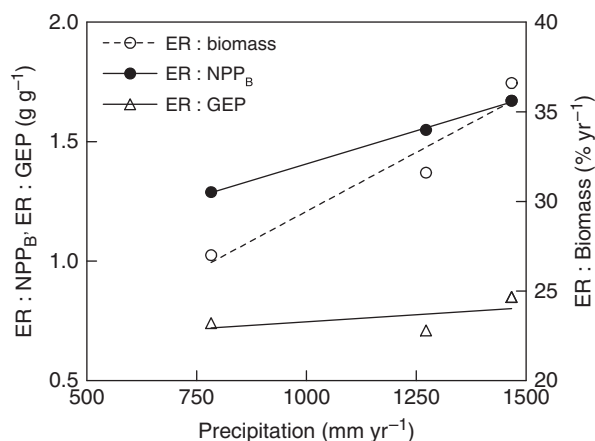


Fig. 9 Respiratory carbon losses as a function of annual precipitation, normalized by standing biomass, NPP_B and GEP.

ER : Biomass ratio and a relatively weak relationship with ER : GEP ratio suggests that the interannual variation in ER may have been mediated by carbohydrate availability for R_h , whereas R_a (and by extension, growth) may have been less restricted by drought conditions.

Despite these responses to P, the dynamics of g_{c-max} suggest that the moisture limitation manifested more strongly through high evaporative demand (VPD) than through limitations in supply (i.e. VWC). However, the effect was greatest during low VWC (Figs 1 and 7). The strong VPD sensitivity of NEE observed in current study is similar to that reported for an intensively managed *Pinus elliottii* stand in Florida (Powell *et al.*, 2008). In contrast to current study, however, both GEP and ER responded to drought in *P. elliottii*, conserving annual NEE. Whether GEP is the primary source of interannual variations in NEE in our current ecosystem remains to be seen. Some published studies have reported greater interannual variation in GEP than ER (e.g. Barr *et al.*, 2002), but they are outnumbered by studies showing the opposite pattern (e.g. Goulden *et al.*, 1998; Lee *et al.*, 1999; Law *et al.*, 2000; Pilegaard *et al.*, 2001; Arain *et al.*, 2002; Morgenstern *et al.*, 2004). Sometimes, simultaneous changes in GEP and ER may offset each other, and stabilize NEE (Richardson *et al.*, 2007; Powell *et al.*, 2008), but in the current study the opposite seems to have occurred.

Soil C balance

The lack of direct VWC-limitation of ER at our study site stands in stark contrast with most other published studies (e.g. Krishnan *et al.*, 2006; Jassal *et al.*, 2007; Reichstein *et al.*, 2007; Noormets *et al.*, 2008a). Although the interannual differences in ER were limited, there were indications of changing contribution of compo-

nent fluxes to ER, with SR : ER (and thus $R_h : R_a$) ratio being higher during the wettest year (Table 1). This observation corroborates our earlier hypothesis that the drought conditions may have suppressed R_h more than R_a , based on the interannual differences in the ER : NPP_B ratio as a function of precipitation. Yet, during any given year, the relationship between $R_h : R_a$ ratio and VWC was not well defined (data not shown), being particularly noisy in 2006 when VWC varied the least.

While R_h was modest (but comparable to other systems; Berbigier *et al.*, 2001; Gough *et al.*, 2008), and the litter inputs (Table 1) were in the middle of the 313–680 $g\ m^{-2}\ yr^{-1}$ range reported for a number of coastal SE US forests (Megonigal *et al.*, 1997; Ozalp *et al.*, 2007 and references therein), litter inputs were 37% (2005), 5% (2006) and 9% (2007) lower than R_h . Given that the R_h estimate is a conservative one ($0.5 \times SR$), it is unlikely that the estimated soil C loss is exaggerated. Furthermore, given that both overly wet and overly dry years had higher $R_h : litterfall$ ratio, it seems the only conditions when the soil at this site would acquire C would be during the most productive years with high litter input, overall highlighting the vulnerability of soil C stocks in this ecosystem.

With about 22% higher R_h than the litter input across the 3 years, the soil lost about 109 $g\ C\ m^{-2}\ yr^{-1}$, which is close to double the average loss of soil C from all nonpermafrost peatlands in the conterminous US (about 60 $g\ C\ m^{-2}\ yr^{-1}$; Bridgman *et al.*, 2006). As the loss of SOC from peatlands is usually associated with the intensity of disturbance, and can range from 33 to 800 (up to 1500) $g\ C\ m^{-2}\ yr^{-1}$ (Silvola, 1988; Trettin *et al.*, 1996; Trettin & Jurgensen, 2003), the current study site could be considered as little to moderately disturbed. However, it is not clear how much of this loss can be attributed to draining and other management practices. More rigorous measurements of the individual components of ER are required to increase the confidence in the partitioning estimates and identify the primary substrates. Currently, the uncertainty about turbulent fluxes is on the order of 30–50 $g\ C\ m^{-2}\ yr^{-1}$ (Hollinger & Richardson, 2005; Papale *et al.*, 2006; Richardson *et al.*, 2006; Moffat *et al.*, 2007; Noormets *et al.*, 2008b), and therefore reading any significance into interannual differences in R_h borders on the margins of error. While the assumptions made in deriving R_h are conservative, these estimates need to be verified through direct measurements.

Conclusions

The loblolly pine plantation in the lower coastal plain of North Carolina, USA, acted as a strong C sink, sequestering 360–835 $g\ C\ m^{-2}\ yr^{-1}$ through the 3 years of

study. The interannual differences were greater in GEP than ER, and were attributable to variation in precipitation dynamics, with indirect effects on incident PAR. Even though the GWT was generally high, there were indications of moisture limitation on C sequestration, including (i) sensitivity of g_{c-max} to VPD at low VWC (<50% of total extractable water), and (ii) decreasing plant hydraulic conductivity K_{tree} during drought. The mediation of moisture limitation through evaporative demand (VPD) rather than limiting supply (VWC) contrasts with earlier analyses of ecosystem responses in drier upland areas. Overall, our data suggest that the drought suppressed GEP, and indirectly R_h , whereas regular large rain events may have stimulated ER. Even though no interannual differences were detected in the sensitivity of ER to VWC, on annual basis the ratio of ER to NPP_B increased with annual rainfall. C losses from soil through R_h , which on interannual scale correlated positively with VWC, exceeded new C inputs by litter by 18%. The loss of soil C was greatest during the wettest year with lowest GEP and highest SR, outlining the vulnerability of large soil C stocks in similar ecosystems. Further studies of the effect of draining and other management practices on SR, and the exact sources of respired C in these ecosystems are warranted.

Acknowledgements

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