

Long-term carbon flux and balance in managed and natural coastal forested wetlands of the Southeastern USA

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ABSTRACT

Wetlands store large carbon (C) stocks and play important roles in biogeochemical C cycling. However, the effects of environmental and anthropogenic pressures on C dynamics in lower coastal plain forested wetlands in the southern U.S. are not well understood. We established four eddy flux stations in two post-harvest and newly-planted loblolly pine plantations (YP₂₋₆, 2–6 yrs old; YP₂₋₈, 2–8 yrs old), a rotation-aged loblolly pine plantations (MP, 15–27 yrs old), and a mixed bottomland hardwood forest (BHF, >100 yrs old) in the lower coastal plain of North Carolina, USA. We analyzed the gross primary productivity (GPP), ecosystem respiration (RE) and net ecosystem exchange (NEE) for age-related trends, interannual variability in response to climate forcing, and management-related disturbances from 2005 – 2017. For the first few years after being harvested, pine plantations were net C sources (NEE = 1133 and 897 g C m⁻² yr⁻¹ in YP₂₋₆ and YP₂₋₈, respectively). The MP was a strong C sink (–369 to –1131 g C m⁻² yr⁻¹) over the entire study period. In contrast, BHF was a C source (NEE = 87 g C m⁻² yr⁻¹ to 759 g C m⁻² yr⁻¹) in most years, although in the first year it did show a net C uptake (NEE = –368 g C m⁻² yr⁻¹). The source activity of BHF may have been related to increasing overstory tree mortality and diameter growth suppression. Decreases in relative extractable water in pine plantations enhanced GPP and RE. Pine plantations regained status as C sinks 5–8 years after harvest and recovered C equivalent to post-harvest losses at 8–14 years. Thus, coastal pine plantations have a net C uptake for only about half the 25-year rotation period, suggesting that they have decreased climate mitigation potential in comparison to protecting primary forests. However, primary forests in this area may be vulnerable to ecosystem transition, and subsequent C loss, due to the changing environmental conditions at the land-ocean interface.

1. Introduction

Wetlands are among the most productive and economically valuable ecosystems in the world (Moreno-Mateos et al., 2012). They perform unique biogeochemical functions and represent a large component of the terrestrial carbon (C) pool (Chmura et al., 2003). Large C stocks stored in wetland soils and vegetation highlights the important role they play in the global C cycle. However, wetland forests face environmental and anthropogenic pressures, including land-use change (White and Kaplan, 2017; Day et al., 2008). Land cover change and forest management in coastal wetlands, such as production and commercial harvesting of loblolly pine (*Pinus taeda* L.) plantations in the

southeastern USA, have the potential to impact CO₂ exchange between the forested land surface and the atmosphere. Therefore, forest management must be considered when quantifying long-term regional C balance in forested wetland landscapes. Although the effects of harvesting on forest C balance are relatively well-known for upland systems (Paul-Limoges et al., 2015), understanding the impacts of forest management, including drainage of wetlands for silvicultural purposes, on C cycling in lower coastal plain (LCP) forests is still in its infancy (Domec et al., 2015; Noormets et al., 2010, 2012; Sun et al., 2011). Drainage of C-rich wetland soils enhances organic matter decomposition, leading to increased C flux to the atmosphere (Hirano et al., 2007; Lloyd, 2006). The low topographic setting of coastal plain wetlands are

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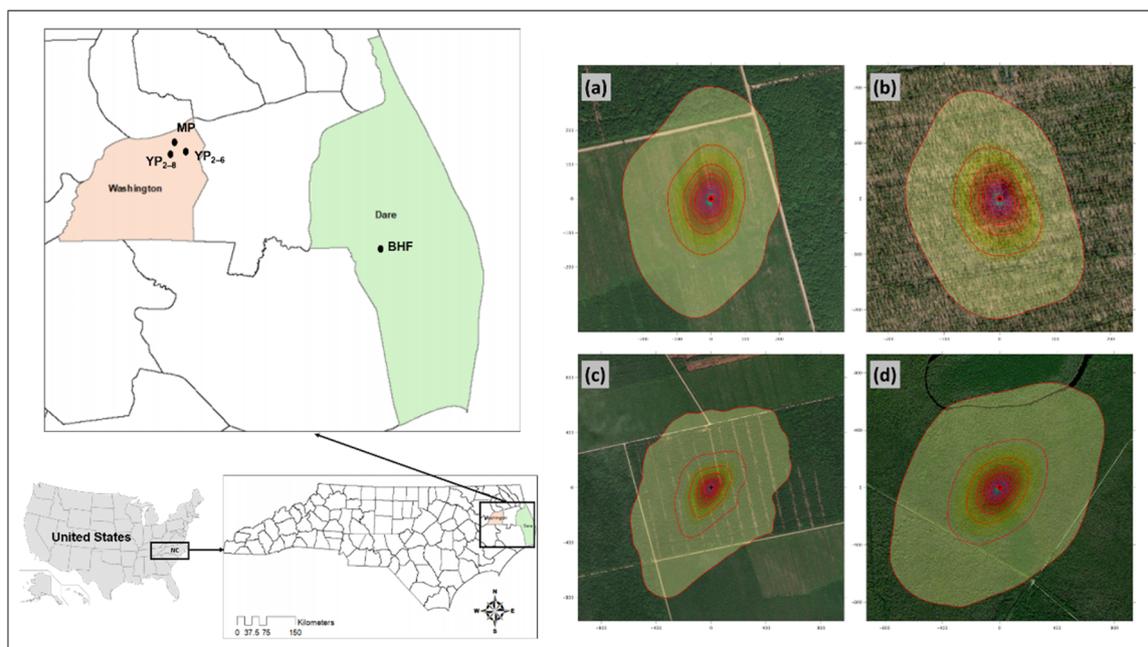


Fig. 1. Location of carbon flux monitoring sites in the lower coastal plain of North Carolina. Flux footprints for (a) YP₂₋₆, (b) YP₂₋₈, (c) MP and (d) BHF sites showing the land cover contribution to the measured flux. The red dot depicts the flux tower location.

also characterized by seasonally dynamic high water tables and deep organic soils comprising of regionally important C stores that are threatened by extreme weather events, sea level rise, and climate change (Miao et al., 2017, 2013). Therefore, understanding the impact of short-term disturbances on temporal patterns of LCP forest C cycling against the backdrop of longer-term environmental change is needed to develop accurate assessments of ecosystem trajectories and regional C budgets (Sun et al., 2011).

Stand age/development has been recognized as having a large influence on C dynamics (King et al., 1999; Magnani et al., 2007; Pregitzer and Euskirchen, 2004), including the distribution of C pools and fluxes in different forested ecosystems (Pregitzer and Euskirchen, 2004). Age-related forest variability may also be a predominant source of spatial variation in C storage (Desai et al., 2008). Gross primary productivity (GPP) and ecosystem respiration (RE) generally increase with age after stand establishment, and the magnitude of net ecosystem exchange (NEE) differences between forests is often proportional to differences in forest age (Mkhabela et al., 2009; Schwalm et al., 2007; Noormets et al., 2007). Like most metrics of stand development (e.g. biomass, LAI, forest structure etc.), the fastest change in GPP, RE and NEE occur in early stand development (Noormets et al., 2007).

Forest C fluxes are also influenced by climate (Amiro et al., 2010). Previous studies have shown that forest GPP is highly sensitive to changes in solar irradiance, atmospheric temperature and water availability (Aguilos et al., 2018; Barr et al., 2007; Reichstein et al., 2007), while RE is mainly controlled by air and soil temperature, and soil water availability (Baker et al., 2013). Determining the influence of climatic drivers on the forest C balance in natural forested wetlands and in managed forested wetlands after disturbance is important because the climate-C cycle feedbacks control landscape C balances in response to climate warming (Aguilos et al., 2013; Barford et al., 2001; Zeng et al., 2005). Moreover, the frequency and intensity of disturbances, such as drought, are predicted to increase in the mid and high latitudes in the coming decades (Trenberth et al., 2007), with significant implications for the terrestrial C cycle (Ciais et al., 2005). Although annual precipitation is not expected to change in the southern US in the near term (but confidence is low), the frequency, intensity and duration of growing season droughts and atmospheric water stress are expected to

become worse (IPCC, 2013; Novick et al., 2016), yet quantitative understanding of these effects remains limited (Barr et al., 2007).

To disentangle the effects of stand development, land use, and changing environmental conditions on forest C cycling along the LCP of the southeastern USA, we established four eddy covariance research towers in several age classes of commercially managed loblolly pine plantations and a mature, natural (undrained) bottomland hardwood forest in eastern North Carolina, USA (Domec et al., 2015; Noormets et al., 2010; Sun et al., 2011). These four sites comprise of a newly-established pine (2–6 years old), young pine (2–8 years old), and rotation-aged pine (15–27 years old) plantations, and a mature natural forested wetland (> 100 years old). We aimed to evaluate the long-term trends in ecosystem productivity, respiration and the resulting net C uptake following stand-replacing disturbances (harvest). We analyzed age-related trends and variabilities in C fluxes and balance in response to climate forcing to understand the ecosystem C response and recovery after harvest, and examined the impact of extreme events (e.g. drought) on C cycling between young and older managed forests. We hypothesized that harvesting would lead to net forest C loss (positive NEE) early on, eventually switching to a C sink due to rapid tree growth. We also expected that drought would decrease GPP and enhance RE. Further, C dynamics of the managed forests were compared to that of the nearby natural, undrained bottomland hardwood forest which represents one of the major (relatively undisturbed) ecosystem types within this LCP region of the US Atlantic seaboard.

2. Materials and methods

2.1. Study sites

Our study sites are registered in FLUXNET, which is a global network of micrometeorological tower sites that use eddy covariance methods to measure the exchanges C, water vapor, and energy between terrestrial ecosystems and the atmosphere. Under the FLUXNET database, our sites are coded as US-NC3, US-NC1, US-NC2 and US-NC4, herein referred to as newly-established loblolly pine (YP₂₋₆, 2–6 years old), young loblolly pine (YP₂₋₈, 2–8 years old), rotation-aged loblolly pine (MP, 15–27 years old), and a bottomland hardwood forest (BHF, more than 100 years old), respectively (Fig. 1).

YP₂₋₆, YP₂₋₈, and MP belong to commercially-managed plantation sites owned/operated by Weyerhaeuser NR Company located in the lower coastal plain near Plymouth, North Carolina, USA. During the 19th and early 20th centuries, this part of the region was logged intensively. These lands were bought by Weyerhaeuser NR Company in 1967 for agriculture and commercial logging purposes. The MP stand is now in the 5th pine rotation on this site and was established in 1992. The MP flux tower was established when the plantation was 15 years old in 2005. In that same year, another tower was set-up (YP₂₋₈) after a harvesting operation and replanting of 1-year old pine seedlings. This was to complement the MP site. Measurements at YP₂₋₈ ended in 2012 and it was replaced with YP₂₋₆ flux tower when another loblolly pine stand was harvested in winter of 2012. The BHF flux tower was established in 2009 to establish a frame of reference for the managed plantation sites. This is a 100+ year-old natural coastal bottomland hardwood forest at Alligator River National Wildlife Refuge in Dare County, NC, USA, that has had minimal disturbance since establishment. BHF is composed of mixed hardwood swamp forest where “hummocks” around tree bases are usually above the water table, and non-vegetated low-lying “hollows” are submerged for more than 70% of the year (Miao et al., 2013; Minick et al., 2019). This site is approximately 108 km away from the managed plantation sites (Fig. 1).

At YP₂₋₇, the sensor height in 2013 was 6.55 m when the aerodynamic canopy height was 0.29 m. This was moved up to 9.0 m in 2016 when trees grew to an average of 3.5 m. At YP₂₋₈, sensors were installed at a height of 6.0 m in 2005 when the canopy height was 0.2 m but were adjusted to 11.6 m in 2008 until 2012 when canopies reached 2.8 m to 8.0 m, respectively. In the case of MP site, sensors were at 22.5 m high from the start of measurement in 2005 until 2009 when the canopies were at 11.9 m to 16.5 m, respectively. Gradual readjustments were made in between 2010 and 2016. In 2017, the sensor height was adjusted to 28.7 m when the average canopy height was 21.0 m. Sensors at AR were readjusted twice in 2008 and 2012 at 30 m and 33.3 m, respectively. In 2018, the average vegetation height was 20.1 m.

All managed sites had elevations < 5 m while BHF was < 1 m above sea level. The average annual rainfall was 1318 mm ± 70 mm (1971–2017) at the managed plantations and 1163 mm ± 49 mm at BHF (1981–2017). Annual average temperature from 2005 – 2017 averaged 16.94°C ± 0.36°C at the plantation sites, while the natural forest had a long-term mean air temperature of 15.72°C ± 0.38°C from 2009 to 2017. The soils at managed sites and at BHF have thick (0.3–1.0 m) organic soil horizons (Oi, Oe, and Oa) belonging to the soil type haplosaprist. More description of the sites is found in Table 1. As is customary for the LCP region, the managed forest sites have been drained with parallel ditches 100 m apart to reduce the water table and facilitate forestry operations (Sun et al., 2011).

2.2. Biometric measurements

At each site, vegetation monitoring plots were established and were composed of 13 circular 7-m radius plots randomly located within the EC flux tower footprint. Within each plot, tree species were identified and individuals with diameter at breast height (i.e. DBH, 1.4 m above ground level) greater than 2.5 cm were identified and tagged each winter season. A thinning operation was conducted in August 2009 at MP, thereby reducing the subsequent biomass estimates. Standing biomass in aboveground and belowground woody tissues was estimated from species-specific allometric relationships compiled by Noormets et al. (2012), based on tree height and/or DBH. The biomass was separated into live and dead, herbaceous and woody components. Coarse woody debris (CWD) biomass was quantified at the plantation sites. The CWD CO₂ efflux rates were measured with eight permanently installed PVC collars using an LI-8100 soil respiration system and an 8100–102 survey chamber (Licor, Lincoln, NE). The level of decay of the substrate was evaluated periodically according to FIA protocols

(FIA, 2007). At BHF, three 30-m transects originating from the center of the plots towards 30°, 150° and 270° from due North were established on all the vegetation survey plots. CWD intersecting with the transects that were larger than 7.6 cm in diameter were counted and identified to hardwood and softwood. Leaf litter fall was measured with four to six 0.18 m² litter traps in each plot. The litter was collected every 90 days during spring and summer, and monthly during fall and early winter, and oven-dried to a constant mass at 65°C.

2.3. Soil respiration (Rs) measurement

Soil respiration (Rs) at the managed pine sites was measured in four vegetation survey plots centered around the tower at each site. Each plot included six 20 cm diameter soil respiration collars (10 cm diameter until 2008), which were measured with LI-8100 soil respiration system (Licor, Lincoln NE) and 8100–103 (8100–102 until 2008) survey chamber. Continuous automated measurements of Rs were conducted at the instrument tower starting 2009 at BHF and 2008 at MP. We used an LI-8100 soil respiration system with 8100–104 long-term chamber (8100–101 at MP until 2008). At the BHF site, soil CO₂ efflux was measured using an automated system consisting of a portable infrared gas analyzer (IRGA, LI-8100, Licor Inc.), multiplexer (LI-8150, Licor Inc.), and permanently installed 20 cm diameter PVC collars inserted ~5 cm into the soil with leaf litter intact in the collars, monitored at three microtopographic locations (i.e., “hummock”, “hollow”, intermediate) from summer 2009 to the end of 2010. The recorded data were used to develop/validate models of soil CO₂ efflux driven by soil temperature, soil water content, and groundwater table dynamics (Miao et al., 2013, 2017).

2.4. Ecosystem CO₂ flux measurement

Turbulent fluxes of CO₂ exchange were quantified by using EC systems at all sites. An open-path analyzer was used to measure the ecosystem exchange of CO₂ consisting of an LI-7500 infrared gas analyzer (LiCor, Lincoln, NE, USA), CSAT-3 sonic anemometer (Campbell Scientific (CSI), Logan, UT, USA) or in the case of BHF, a Gill Windmaster (R-350; Gill Instruments, Lymington, UK) and CR5000 dataloggers for the plantation sites and CR-1000 at BHF site. Only the MP and BHF sites had a CO₂ profile sampler based on a LI-820 infrared gas analyzer (Licor, Lincoln, NE) with air intakes at 0.05x, 0.2x, 0.6x, and 0.9x of canopy height at the MP site and 0.02x, 0.04x, 0.3x, 0.6x and 1x the height of canopies at the BHF site. These were used to estimate CO₂ storage in the canopy air space. These EC systems were all mounted at a height of 15.2 m (YP₂₋₆, fetch = 350 m – >450 m), 16.6 m (YP₂₋₈, fetch = 350 m – >450 m), 22.5 m (MP, fetch = 900 m – 1300 m), and 30.0 m (BHF, fetch = ~2500 m) throughout the study period.

Additional micrometeorological parameters measured above the canopy at all sites included air temperature (HMP45AC, Vaisala, Finland), photosynthetically active radiation (PAR, LI-190, LiCor Inc.), net radiation (CNR-1 and CNR-4, Kipp & Zonen, Delft, the Netherlands), and precipitation (TE-525, Campbell Scientific Inc., Logan, UT, USA). Soil temperature was measured at depths of 5 cm, and 10 or 20 cm with CS107 (CSI) temperature probes. Soil volumetric water content was averaged through the top 30 cm using a vertically inserted CS616 time domain reflectometry probe (Campbell Scientific Inc.). The depth of ground water table (GWT) was monitored using ultrasonic water level datalogger (Infinites, Port Orange, FL, USA). Relative extractable water (REW) was derived using the method of Vicca et al. (2012):

$$REW = (TEW / TEW_{max}), \quad (1)$$

where total extractable water (TEW) is equal to soil water content (SWC) less the SWC at wilting point (SWC_{wip}). The maximum extractable water over the entire rooting zone (TEW_{max}) is equal to SWC at field capacity (SWC_{fc}) less SWC_{wip}. Soil texture was identified at the

Table 1
Site locations, structural attributes and soil characteristics of lower coastal plain forested wetlands in eastern North Carolina.

Location/Parameters	YP ₂₋₆	YP ₂₋₈	MP	BHF
Location	Plymouth, NC	Plymouth, NC	Plymouth, NC	Manteo, NC
Latitude/Longitude	35.7990 to -76.6560	35.8118 to -76.7119	35.8030 to -76.6685	35.7879 to -75.9038
Structural attributes				
Stand type	Pine plantation	Pine plantation	Pine plantation	Natural hardwood
Age (years, as of 2017)	6 ^a	8 ^b	27 ^a	> 100
Measurement period	2013–2017	2005–2011	2005–2017	2009–2017
Year of most recent harvest	2012	2004	1992	Undisturbed
Major species	<i>Pinus taeda</i>	<i>Pinus taeda</i>	<i>Pinus taeda</i>	<i>Nyssa sylvatica</i> , <i>Nyssa biflora</i> , <i>Taxodium distichum</i> , <i>Acer rubrum</i> , <i>Liquidambar styraciflua</i> , <i>pond pine</i>
Mean stand height (m)	2 (in 2017)	6.9 (in 2011)	20.3 (in 2017)	32 (in 2017)
Mean stand density (trees ha ⁻¹)	1087 ^a	1087 ^a	675 [@]	2320
Soil characteristics				
Soil type	Belhaven series (loamy, mixed, with highly decomposed organic matter layer underlain by loamy marine sediments)	Cape fear series (slightly higher water holding capacity and a surface loam layer)	Belhaven series (loamy, with highly decomposed organic matter layer underlain by sediments)	Pungo series (poorly drained with highly decomposed muck and less decomposed peat layers; underlain by highly reduced mineral sediments)
Organic horizons (Oe + Oa)[%]				
<i>Soil Texture</i>	Muck, organic matter	Muck, organic matter	Muck, organic matter	Muck, organic matter
<i>Average depth (cm)</i>			22.9	48.1
<i>Bulk density (g C m⁻³)</i>			0.4 ± 0.04	0.2 ± 0.3
<i>Carbon content (g Kg⁻¹)</i>			367 ± 17	345 ± 22.8
<i>Organic matter (%)</i>			59.2 ± 3.57	62.8 ± 4.24
<i>C stock (Mg C ha⁻¹)</i>			83.4 ± 14.01	44.5 ± 6.34
Mineral Horizons (A + B)[%]				
<i>Soil Texture</i>	5–35% clay	5–35% clay	5–35% clay	35–60% clay
<i>Average depth (cm)</i>			26.3	30.3
<i>Bulk density (g C m⁻³)</i>			1.3 ± 0.06	0.5 ± 0.04
<i>Carbon content (g Kg⁻¹)</i>			28 ± 4.2	73 ± 9.2
<i>Organic matter (%)</i>			7 ± 0.85	15.1 ± 1.52
<i>C stock (Mg C ha⁻¹)</i>			29.5 ± 6.21	31.5 ± 3.89

^a Age at end of measurement period. ^bStandard planting density. [@]Post mid-rotation thinning. [%]YP soil properties were likely similar to MP.

four sites and SWC_{fc} and SWC_{wp} were obtained from soil water estimates by texture and organic matter based from Saxton and Rawls (2006).

Detecting anomalous drought years was determined using an ecological drought indicator called the soil water stress index (SWSI) (Granier et al., 1999). The SWSI is a dimensionless value computed as the difference between the daily REW and 0.4 (a threshold that induces stomatal closure in most trees), divided by 0.4. We also determined the water deficit duration as the number of days when REW is equal to or lower than 0.4. To test the direct effect of soil water limitation on C fluxes, we normalized GPP and NEE with Rn and RE with either $Tair$ or $Tsoil$. Linear models were fit to determine the residuals of these relationships. These residuals were used to analyze the relationship between Rn -normalized GPP or NEE with SWSI and Temperature-normalized RE with SWSI. Previous publications present comprehensive descriptions of CO_2 flux measurement (including biometrics and soil respiration) at these sites (Domec et al., 2015; Miao et al., 2013, 2017; Noormets et al., 2012).

2.5. Flux data processing and gap-filling

The net ecosystem CO_2 exchange for each 30-min period was calculated based on the mass exchange between the ecosystem and the atmosphere using Eddypro software (v. 6.1.0) (LICOR Inc, Lincoln, NE, USA). Standard quality checks and corrections were applied for spike detection (Vickers and Mahrt, 1997), planar fit coordinate rotation of wind vectors (Wilczak et al., 2001), correction of the time lags between scalar concentrations and wind speed (covariance maximization), air density fluctuation (Webb et al., 1980), and high (Ibrom et al., 2007) and low pass filtering (Moncrieff et al., 2004). We flagged as 0 (high quality), 1 (medium quality) and 2 (low quality) on flux outputs (Mauder and Foken, 2006). Fluxes with flags greater than 1 were discarded. Post-processing of the 30-min fluxes included filtering for low signal strength, integral turbulence characteristics, despiking filter, and low friction velocity (Papale et al., 2006). Exclusion of the data collected during the non-steady and the low turbulence conditions that were flagged 1 and 2 based on Mauder and Foken (2006) resulted in removal of 4–40% of data at the commercially-managed plantation sites. The exclusion based on this criterion for some of the years were as high as 60% for the wetland forested site (BHF site). This freshwater wetland site has microtopographical features i.e., elevated dry vegetated areas and the low-lying flooded non-vegetated areas (Miao et al., 2017). The presence of this relatively uneven terrain and its possible effect on turbulence and stationarity can probably explain the greater data exclusion at this site. Remaining data losses were due to low friction velocity, power losses and instrument malfunction. After all data quality checks had been performed, the final data coverage of quality-controlled NEE_{CO_2} was 33–49% for YP_{2-6} site, 35–78% for YP_{2-8} site, 32–95% for MP site and 12–44% for BHF site.

Missing NEE_{30min} were gap-filled following the protocol provided by the Max Planck Institute for Biogeochemistry (<https://www.bgc-jena.mpg.de/bgi/index.php/Services/REddyProcWeb>). This web tool also allowed us to partition 30-min NEE data into 30-min GPP and RE data. Gap-filling and flux partitioning using ReddyProc (Wutzler et al., 2018) left few remaining gaps of <2–6% for NEE, GPP and RE from each site. These were filled by means of linear interpolation from the corresponding daily NEE values of the previous and succeeding years. This gap-filling translates to an additional uncertainty of $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ at YP_{2-6} site, $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ at YP_{2-8} site, $56 \text{ g C m}^{-2} \text{ yr}^{-1}$ at MP site and $2 \text{ g C m}^{-2} \text{ yr}^{-1}$ at BHF. Daily NEE was computed as the sum of NEE_{30min} values over 24 h. We present the annual C balance in atmospheric sign convention where positive NEE values connote C loss by the ecosystem and negative values correspond to C gain (e.g. Baldocchi, 2008).

2.6. Data analyses

Cumulative gap-filling uncertainties for NEE were generated by adding the half-hourly random variance (when observed fluxes were used, random flux error was calculated in EddyPro) and half-hourly gap-filling variance (when gap filled values were used) across the entire year (Chamberlain et al., 2017).

In order to reveal the main climate gradients of our dataset while reducing multicollinearity problems, we processed the daily climate values for each site into a Principal Component Analysis (PCA) algorithm using the *res.pca* function from *FactoMineR* package in R. In order to predict the best climate drivers of variations in C fluxes and balance, we built generalized additive models with spline smoothers to predict NEE, GPP and RE as a function of the PCA selected climate variables (Shao et al., 2015). The gam function from the *mgcv* package allowed us to build the statistical models and the *MuMin* package allowed us to obtain the best smoothing dimension. We used the Tukey HSD Test for inter-site comparison. Smoothed-curve fitting and linear relationships were carried out with a locally weighted linear or polynomial regression in the *ggplot2* package and *smatr* package was used to test significant differences and multiple slope comparison. All analyses were processed in R version 3.4.4 (R Core Team, 2018).

3. Results

3.1. Climatic conditions among sites

There were small daily variations in net radiation (Rn) and air temperature ($Tair$) among sites, yet YP_{2-6} had the highest soil temperature ($Tsoil$) and relative humidity (RH), but with lowest vapor pressure deficit (VPD). However, the BHF had up to 36% higher relative extractable water (REW) and average windspeed was higher by 1.32 m s^{-1} compared to the YP_{2-6} , YP_{2-8} and MP sites ($P < 0.05$; Fig. 2). Interannual changes in $Tair$, $Tsoil$ and Rn at the plantation sites fluctuated by 3%–34%, whereas water-related meteorological variables (REW and $rainfall$) varied 2–3 fold among sites. However, the interannual range of difference in REW at the BHF site was only 4%.

3.2. Carbon fluxes and balance at managed plantation forests

A year after harvest in 2012, the annual GPP at the YP_{2-6} site was 56% of the annual RE, although the productivity trend was increasing ($P < 0.001$, Fig. 3(1a)). A greater respiratory flux was sustained until the end of the study period, when the trees were 6 years old. The overall annual average GPP at YP_{2-6} site was $1508 \text{ g C m}^{-2} \text{ yr}^{-1}$ and annual RE was $2077 \text{ g C m}^{-2} \text{ yr}^{-1}$ from 2013 to 2017 (Fig. 3, Panel 1a). The annual GPP following the harvest at the YP_{2-8} site was 60% of annual RE and this RE was larger than photosynthetic productivity for four years. However, as the stand reached 6 years of age annual GPP exceeded annual RE by 469 g C m^{-2} , followed by a switch back to RE being larger than GPP (by 16%) when saplings were 8 years old. For eight years (2005–2011), overall annual mean GPP and RE at the YP_{2-8} site was $1907 \text{ g C m}^{-2} \text{ yr}^{-1}$ and $2008 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively (Fig. 1, Panel 1b). At the MP site, annual GPP always exceeded annual RE throughout the duration of the study, from 2005 to 2017. Annual GPP was higher than RE by $369 \text{ g C m}^{-2} \text{ yr}^{-1}$ to $1131 \text{ g C m}^{-2} \text{ yr}^{-1}$. GPP ranged from 2390 [95% CI 2343–2461] to 2926 (95% CI 2880 to 2969) $\text{g C m}^{-2} \text{ yr}^{-1}$ (Fig. 3, Panel 1c). The interannual differences in GPP mainly reflected the differences in NEE, although larger variations were observed at the younger plantations (i.e., YP_{2-6} and YP_{2-8} sites) but not in the older MP site.

After harvest, the YP_{2-6} site became a large C source (i.e., annual $NEE = 1133 \text{ g C m}^{-2} \text{ yr}^{-1}$) with large variability (i.e., 95% CI [751 to $1519 \text{ g C m}^{-2} \text{ yr}^{-1}$]), but with a weakening source strength (NEE becoming less positive) as the stand aged (Fig. 3, Panel 1a). At the YP_{2-6} , annual NEE was never negative at any age. Similarly, the YP_{2-8} site was

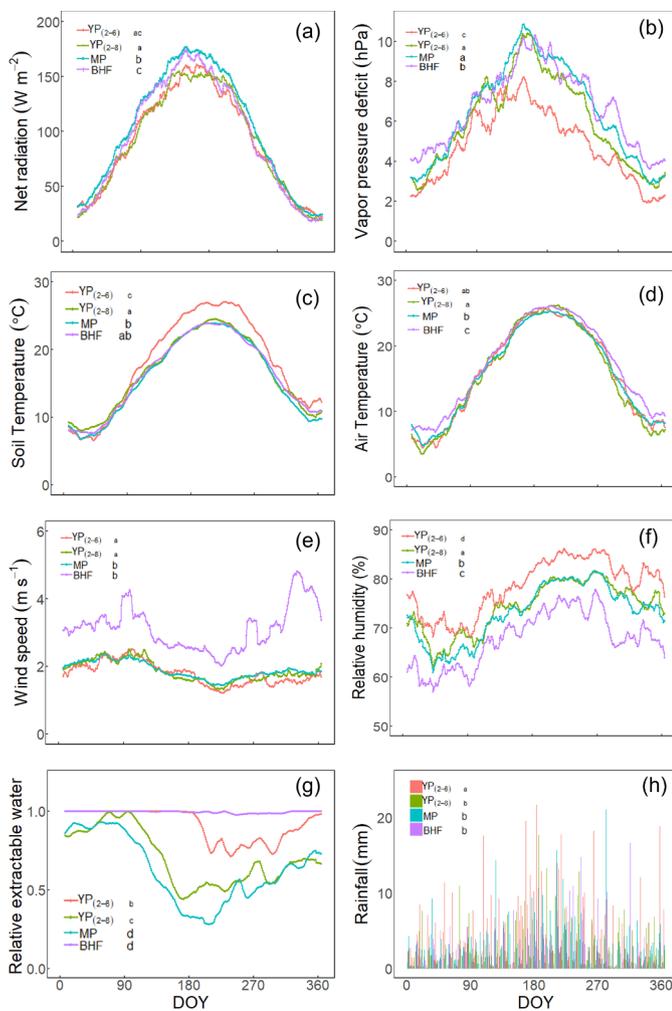


Fig. 2. Variation in climate variables among sites represented by different colored lines. Different letters after the site name in the legend denote significant differences among sites ($P < 0.05$) using the Tukey HSD Test. Daily data (averaged in a 15-day moving window) across the measurement period for each site was used.

also a strong C source (i.e. annual $NEE = 897 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [830 to $964 \text{ g C m}^{-2} \text{ yr}^{-1}$]) after harvest. It remained a weak C source until age 5, becoming a net C sink between 6 (annual $NEE = -469 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [-963 to $24 \text{ g C m}^{-2} \text{ yr}^{-1}$]) and 7 years old ($NEE = -603 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [-1115 to $-91 \text{ g C m}^{-2} \text{ yr}^{-1}$]). The site then shifted back to a net C source again in the 8th year (Fig. 3, Panel 1b). The MP site was a net C sink throughout the study period (15–27 years old), indicating a sustained sink strength at this rotation-aged forest (Fig. 3, Panel 1c). Annual NEE varied from $-369 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [-556 to $-11 \text{ g C m}^{-2} \text{ yr}^{-1}$] to $-1131 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [-1183 to $-256 \text{ g C m}^{-2} \text{ yr}^{-1}$].

At the start of measurements at BHF in 2009, annual GPP ($1922 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [1910 to $1952 \text{ g C m}^{-2} \text{ yr}^{-1}$]) was higher than annual RE ($1554 \text{ g C m}^{-2} \text{ yr}^{-1}$; 95% CI [1544 , $1566 \text{ g C m}^{-2} \text{ yr}^{-1}$]), thus leading to a net C sink ($NEE = -368 \text{ g C m}^{-2} \text{ yr}^{-1}$; Fig. 3, Panel 1d). However, from 2010 onwards, annual NEE was positive due to decreasing GPP. This weak C source was sustained until the end of the study in 2017, with large variability in annual NEE ranging from $87 \text{ g C m}^{-2} \text{ yr}^{-1}$ (95% CI -491 to 664) to $759 \text{ g C m}^{-2} \text{ yr}^{-1}$ (95% CI -353 to 1873).

3.3. Stand age effect on GPP, RE and NEE

We plotted the C fluxes and balance at the managed sites on a single graph according to their ages in Fig. 3, Panel 2 (a–c), and separated the

BHF site in Fig. 3, Panel 2 (d–f). We did not continue the regression curves up to the BHF site due to site differences between managed plantations and the natural forest. Stand age correlated well with GPP from the time of stand initiation (YP_{2-6} and YP_{2-8}), peaking at the rotation-aged stand (MP), and forming a plateau thereafter ($R^2 = 0.75$). The stand age – RE curve from harvest up to rotation-age was very weak ($R^2 = 0.01$). Given a weaker age – RE relationship but with a stronger GPP – age dependency ($R^2 = 0.75$), GPP clearly reflects the logarithmic trajectory of NEE along the initiation to rotation-age classes ($R^2 = 0.77$). Stand age–GPP curve for the BHF site showed less dependency ($R^2 = 0.19$) and the age-RE relationship was very weak ($R^2 = 0.01$).

3.4. Environmental controls on GPP, RE and NEE

The best model revealed the multiple effect of Rn , T_{soil} or T_{air} and REW to explain 55%, 70%, 67% and 65% of variation in GPP for Y_{2-6} , Y_{2-8} , MP and BHF sites, respectively ($P < 0.0001$; Supplemental Table 1, ranked according to F value). Rn best explained the variation in GPP, except at BHF where it was primarily driven by T_{air} . Mostly T_{air}/T_{soil} in combination with Rn and/or REW explained 69%, 79%, 69% and 66% of the variation in RE at Y_{2-6} , Y_{2-8} , MP and BHF sites, respectively ($P < 0.0001$). The major controlling climate factor of NEE among all plantation stands was Rn . However, the combined effect of Rn and other climatic variables only explained 21–37% of the changes in net C uptake, thus other biological components may play a greater role in NEE. This connotes that even though these variables were best predictors, uncertainty as to their effect remains, and correlative effects must be interpreted with caution.

3.5. Moisture sensitivity of GPP, RE and NEE at all sites

Due to large variability in REW (Fig. 2), we analyzed the inter-annual variations in soil water availability at managed pine sites and BHF and found they differed due to drainage construction at the managed sites (Supplemental Fig. 1). We also evaluated the water table depth (WTD) to understand clearly the difference in water level between MP (which represents the water table depth in managed sites as they are in close proximity) and BHF (Supplemental Fig. 2).

Indeed, there was large variability in water depth at managed sites and an all-time high water level at BHF site. In the managed sites, a decline in whole year daily REW showed a corresponding enhancement of GPP and RE in most years ($P < 0.05$, Supplemental Fig. 3). NEE was less responsive to changes in soil water availability. Overall, it was difficult to obtain precise REW values at BHF because the soil was always saturated, but we did observe $REW < 0.8$ on occasion.

Results after analyzing soil water anomalies during periods of soil water stress revealed that years with highly negative annual total soil water stress index (SWSI) and longer water deficit duration included 2008 in YP_{2-8} and 2007, 2008 and 2014 in MP, hereafter referred to as ‘drought’ years (Fig. 4). Drought year SWSI median values fell below $SWSI = 0$, a condition when the soil water was below the threshold level of $REW < 0.4$. These conditions only occurred at YP_{2-8} and MP, so we excluded YP_{2-6} and BHF in the subsequent drought analysis.

Results also revealed that the intensity and duration of severe soil water depletion periods, especially during dry months (July–October), are the key determinants for a given year to be considered as ‘drought’ year (Supplemental Fig. 4).

Reckoned from the annual average daily rate, the 176-day drought in 2008 at YP_{2-8} enhanced the daily rate of GPP and RE by 53% and 42%, respectively, and improved the daily rate in net C uptake by 35%. At MP, drought years in 2007, 2008 and 2014 enhanced daily rate of GPP by 5%–22%, and daily rate of RE by 8–29%, yet lessened the rate of net C uptake by 54% in 2007, 11% in 2008, and showed relatively no change in NEE in 2014 (Table 2). This was despite an 85%, 44% and 87% reduction in REW and a longer drought duration of 177, 304 and

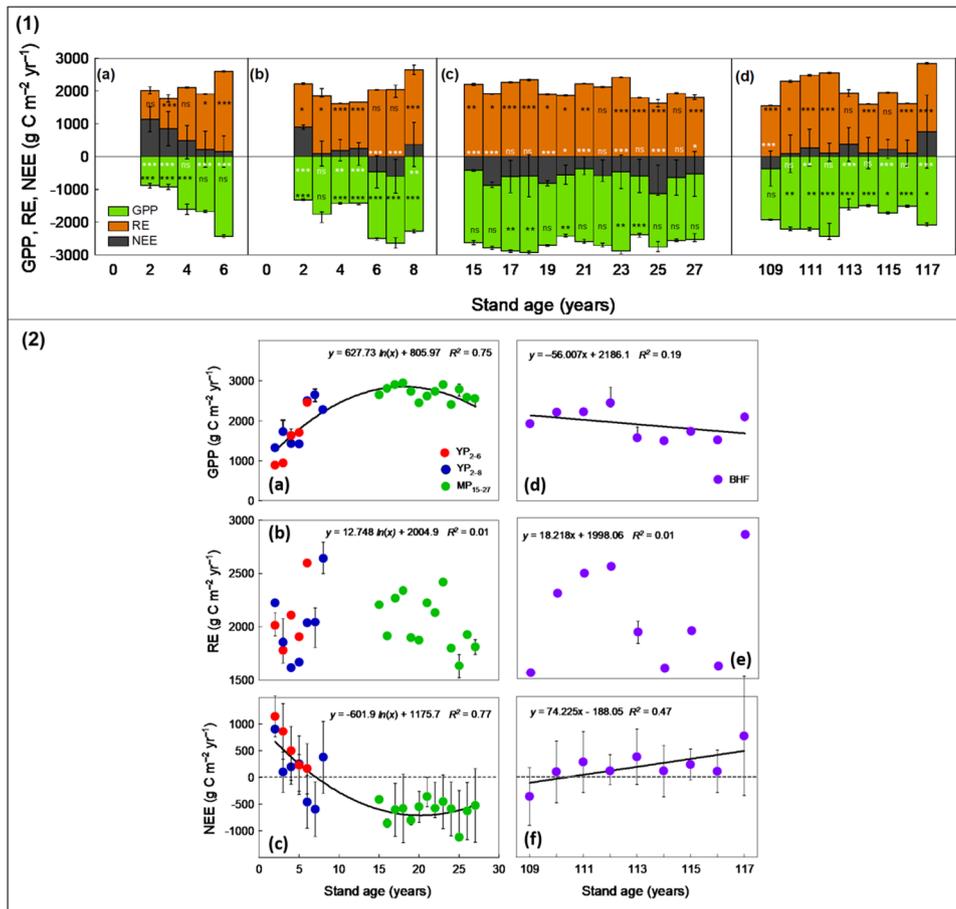


Fig. 3. Panel 1 are the net ecosystem exchange (i.e., NEE, dark gray bars), gross primary productivity (i.e., GPP, green bars but not stacked to NEE) and ecosystem respiration (i.e. RE, orange bars) for (a) YP₂₋₆, (b) YP₂₋₈, (c) MP and (d) BHF sites. Vertical bars indicate error estimates wherein cumulative gapfilling uncertainty ($\Sigma\mu$) across all gapfilled periods were used for NEE while bootstrapping ($n = 1000$ replications) was used for GPP and RE at 95% confidence interval using the daily values per year. Significant differences were denoted by asterisks using the Tukey HSD test. Note: Negative NEE values indicate carbon absorption; GPP values were converted into the negative to indicate carbon being absorbed by the ecosystem. Panel 2 are regressional relationships between GPP, RE and NEE with stand age (years) at plantation sites (YP₂₋₆, YP₂₋₈ and MP, (a–c) and BHF (d–f)). Each colored circle corresponds to one year and vertical lines are standard errors. Logarithmic curve was fitted in plantation sites Panel 2 (a–c) while linear fit was used in BHF site Panel 2 (d–f).

195 days with a severe water deficit in 2007, 2008 and 2014, respectively.

We examined further the drought impact on C fluxes and balance by removing the confounding effect of the major controlling climate variables at YP₂₋₈ and MP sites to analyze the soil water effect alone. We normalized GPP and NEE with R_n and removed the effect of T_{soil} or T_{air} for RE (Fig. 5). Worsening soil water stress slightly increased R_n -normalized GPP ($R^2 = 0.28, P < 0.01$; Fig. 5a) and T_{soil} -normalized RE

($RMSE = 0.31, P < 0.001$; Fig. 5b) during 2008 drought at YP₂₋₈ site. Whereas, severe water stress slightly decreased R_n -normalized GPP ($R^2 = 0.32, P < 0.01$; Fig. 5c) and T_{air} -normalized RE ($R^2 = 0.12, P < 0.01$; Fig. 5d) during the 2007 drought at MP, both normalized fluxes were less sensitive during the 2008 drought. No significant relationships were found for R_n -normalized NEE with SWSI at both sites.

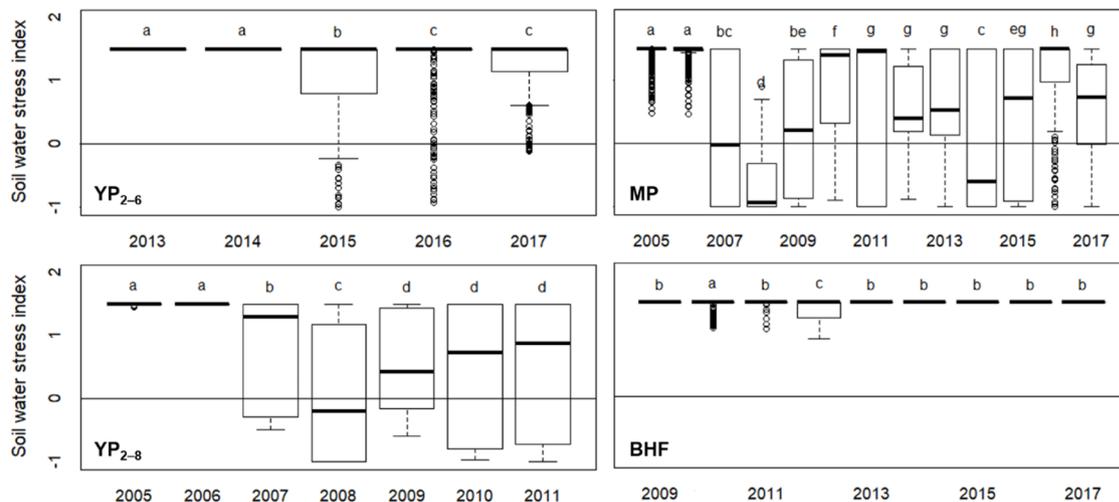


Fig. 4. Interannual variations in soil water stress index (SWSI). Daily SWSI values were used during the measurement period at YP₂₋₆, YP₂₋₈, MP and BHF. Tukey HSD tests were used for pairwise comparisons. Years which were significantly different at $P < 0.05$ were denoted by different letters. In the box plot, the thick horizontal line shows the median, the box extends to the upper and lower quartiles, vertical dashed lines indicate the nominal range, open circles indicate points which lie outside of the nominal range. SWSI at 0 indicates that $REW = 0.4$. The greater SWSI above 0, the lower is the stress level.

Table 2
Daily average fluxes in GPP, RE and NEE and their percentage rate of change during drought period relative to their annual values at YP₂₋₈ and MP managed sites.

Site	Year	GPP						NEE		
		Annual Period	Drought Period	Rate of change (%)	Annual Period	Drought Period	Rate of change (%)	Annual Period	Drought Period	Rate of change (%)
YP ₂₋₈	2008	3.91	5.99	53	4.57	6.49	42	0.66	0.49	35
MP	2007	7.90	8.37	6	6.21	7.26	17	-1.69	-1.10	54
	2008	8.03	8.41	5	6.41	6.94	8	-1.62	-1.46	11
	2014	6.57	8.00	22	4.92	6.37	29	-1.64	-1.63	1

4. Discussion

The scope of the current study to represent LCP C cycling responses to short- and long-term environmental drivers is broad in that it is based on 34 site-years of monitoring forest GPP, RE, and NEE fluxes in managed and natural coastal forested wetlands. The four individual sites bracket ranges of age, soils, management, hydrologic conditions, and exposure to climatic variation and extreme events representative of forests along the US Southeast and Gulf LCP. Although the current study is not a chronosequence in the strict sense, the long-term datasets from forests of similar climate allows us to draw meaningful inferences regarding broad patterns of C cycling in coastal forests as a function of age, management, hydrology, and climate.

4.1. Sources of uncertainties

NEE flux measurements entail different sources of uncertainty due to random (Hollinger and Richardson, 2005) and systematic errors (Gu et al., 2005). These are oftentimes difficult to assess. Several gap-filling methods have been developed for flux uncertainty estimation (Papale et al., 2006), however, various problems still exist. The choice of method to gap-fill missing data is crucial because many long-term sites experience a high percentage of data gaps resulting in annual NEE uncertainty from ± 25 to 50 g C m⁻² yr⁻¹ (Baldocchi, 2008;

Moffat et al., 2007), and some sites report much greater uncertainties (Soloway et al., 2017). Our annual NEE uncertainty of 2–56 g C m⁻² yr⁻¹ at all sites is within this range. We used the method developed by the MaxPlanck Institute of Biogeochemistry (Department of Biogeochemical Integration, 2018) wherein our missing data were gap-filled and NEE was partitioned into GPP and RE by the online “REddyProc: Eddy covariance data processing tool”. We used this approach because it is more generalized for the broader range of Fluxnet sites, but includes a strong temperate forest component (Soloway et al., 2017). With this approach, even though errors associated with the gap-filling procedure could clearly affect the absolute magnitude of the fluxes (Soloway et al., 2017), the different seasons and years should all be similarly affected, thus allowing us to make pertinent comparisons.

4.2. GPP and RE at the managed plantations and natural forest

Changes in C fluxes (GPP) were fastest during early stand development in the recently harvested sites (YP₂₋₆ and YP₂₋₈), in contrast to the MP and the natural bottomland hardwood forest. The increasing productivity is also shown by increasing total biomass at the plantation sites during the first few years after harvest (Table 3). We observed higher RE than GPP after harvest at the YP₂₋₆ and YP₂₋₈ sites for the duration of the study period, which is consistent with other studies (Kolari et al., 2004; Kowalski et al., 2004). Harvesting removed the

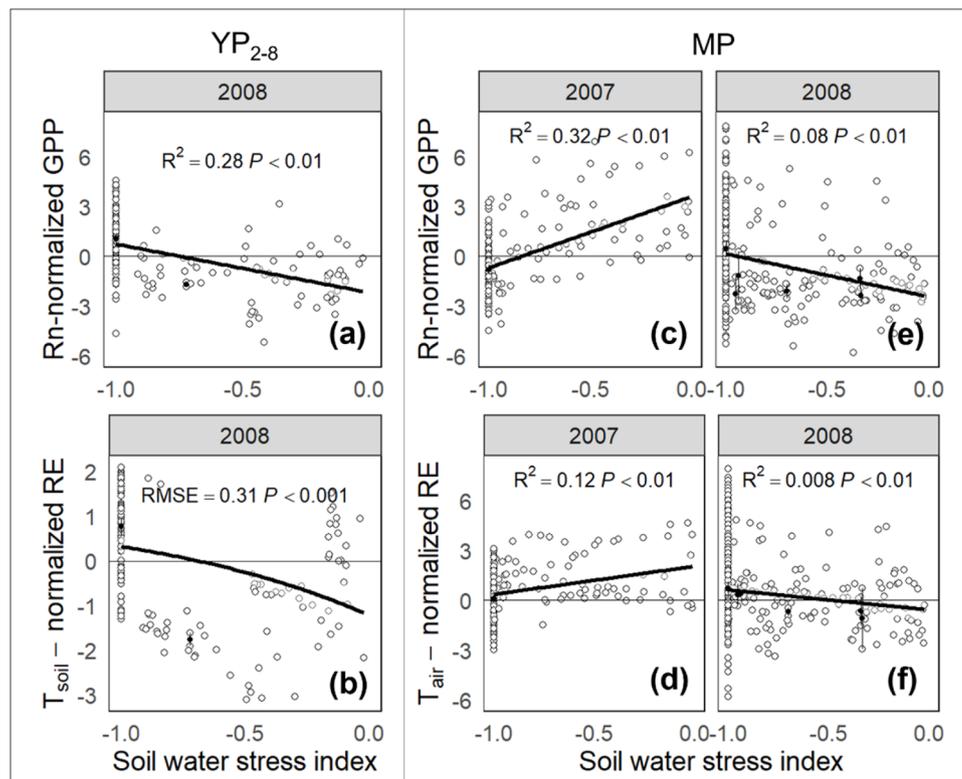


Fig. 5. Regression curves between gross primary productivity (GPP), ecosystem respiration (RE), Rn-normalized GPP and temperature-normalized RE with soil water stress index (SWSI) during the 2008 drought periods at the YP₂₋₈ site and the 2007 and 2008 drought at the MP site. Each symbol corresponds to one day. The greater the SWSI, the lower the soil water stress (SWSI = 0 means REW = 0.4 (threshold) and SWSI = -1.0 means REW = 0 (wilting point)).

Table 3

Annual soil respiration (Rs) and other biometric measurements at the four studied stands (Note: Rs values in (*) from 2005 to 2007 were from (Noormets et al., 2010). Rs at **BHF were estimated based on models developed by Miao et al., 2017, 2013).

Carbon pools and soil flux	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Soil respiration (g C m ⁻² yr ⁻²)													
YP ₂₋₆									1518	1404	1469	1683	1535
YP ₂₋₈	2030	1249	999	901	1024	1306	1449	1436					
MP	1331*	1114*	1141*	837	1349	1550	1377	1309	1334	1449	1442	1273	1956
**BHF					981	1413	1744	1183	1299	606	867	876	1236
Total aboveground biomass (g C m ⁻²)													
YP ₂₋₆										2	32	182	495
YP ₂₋₈	6	56	270	529	1205	1899	2640	3203					
MP	4228	4814	5642	6239	6742	3182	3376	3736	4252	4703	5199	5506	5982
BHF				13,149	13,281	13,341	13,446	13,639	13,728	13,806	13,898	13,917	
Total root biomass (g C m ⁻²)													
YP ₂₋₆										1	14	52	112
YP ₂₋₈	1	12	53	131	235	363	519	644					
MP	1050	1195	1402	1547	1671	794	846	946	1088	1218	1358	1428	1554
BHF				2659	2686	2700	2723	2761	2779	2793	2811	2817	
Coarse woody debris (g C m ⁻²)/													
YP ₂₋₆									240	258	231		
YP ₂₋₈		1172	652		428	282	74	30					
MP	278		267	413	415	288	254	240		221		336	322
BHF					131	126	139	131	272	245	657	755	
Litterfall (g C m ⁻²)													
YP ₂₋₆													
YP ₂₋₈					233	279	296	270					
MP	312	404	397	431	357	210	301	260	334	370	387	541	389
BHF					452	276			160	237	346	600	

forest canopies resulting in low post-harvest GPP. Although RE was higher in the young harvested stands than GPP, there was no distinct trend over time (Fig. 3), consistent with other studies (Amiro, 2001; Kowalski et al., 2004; Law et al., 2001; Litvak et al., 2003). The stimulation of ecosystem respiratory C losses following harvest was due in part to changes in the microclimate (Noormets et al., 2007), disturbance of soil (Diochon and Kellman, 2009; Minick et al., 2019, 2014), and the production of large amounts of harvest residues (Harmon et al., 1986; Noormets et al., 2014, 2012; Schwalm et al., 2007), all of which stimulate decomposition of soil C pools by microorganisms (Minick et al., 2019). We found annual soil respiration (Rs) to be 73% of annual RE in the YP₂₋₆ and 65% in YP₂₋₈ during early stand development (Table 3), consistent with a previous study at the MP site that found Rs to be 54–63% of RE (Noormets et al., 2010). Studies from other ecosystems have reported a 70–88% contribution of Rs to RE (Aguilos et al., 2014; Gaumont-Guay et al., 2006; Khomik et al., 2006; Lavigne et al., 1997). Therefore, changes in RE can largely be attributed to changes in Rs at the young, recently harvested sites.

At MP, GPP was always higher than RE and likely driven by high leaf area index having recovered 15 years after the harvest. RE also increased as the stand aged, but at a slower rate. Thus, before canopy closure GPP was much higher than RE at the MP site. This conforms to a literature synthesis reporting that total RE is highest when forests are young and declines during later stages of stand development (Pregitzer and Euskirchen, 2004).

Corroborating evidence of the increasing trend of RE at BHF is that we observed increasing tree mortality during the annual vegetation surveys, starting at only 4 dead trees ha⁻¹ in 2009, rising to 16 dead trees ha⁻¹ in 2017 (Fig. 6). Estimates of litterfall and CWD were also increasing with litterfall ranging from 160 g C m⁻² in 2013 to 600 g C m⁻² in 2017, whereas CWD ranged from 131 g C m⁻² to 755 g C m⁻² from 2010 – 2017 (Table 3; Fig. 6).

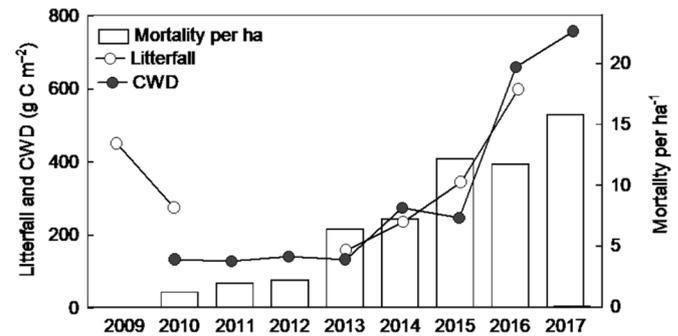


Fig. 6. Interannual change in tree mortality (dead trees per hectare), litterfall and coarse woody debris (CWD) at BHF site from 2009 to 2017.

Dead tree biomass has been reported to contribute up to 61% of all CWD in old growth forests in Pacific Northwest (Harmon et al., 1986). This large amount of decaying woody material on the forest floor contributed to high RE, similar to other mature forests in temperate regions (Mkhabela et al., 2009). This further supports our hypothesis that the natural forest is undergoing a major change in ecosystem function during the course of this study. Bacteria and fungi act together in the debris decomposition process in aquatic ecosystems (Romaní et al., 2006). Microbial communities produce extracellular enzymes that convert polymeric compounds (e.g. cellulose, hemicellulose, and lignin) into smaller molecules. The most relevant enzymes that break down plant fibers are cellulases, hemicellulases, pectinases and phenol oxidases (Romaní et al., 2006). A wood decomposition study in a freshwater ecosystem showed a slow degradation of lignin, which is highly recalcitrant (Zare-Maivan and Shearer, 1988). The slower rate of decomposition due to saturated wood and limited available oxygen would result in decreasing respiration rates from CWD (Rayner and

Boddy, 1988), but measurements at our site indicate CO₂ efflux from CWD is an important component of RE (Miao et al., 2017). It is also plausible that rising sea level may be slowing down site drainage thereby lengthening the inundation period (e.g. longer hydroperiod), potentially leading to tree mortality. In addition to increasing tree mortality, this hydrologic-stress hypothesis may be supported by the very small annual increment of tree diameter growth and top die-back of many trees, indicating the site is experiencing persistent stress. In 2009, bald cypress, red bay, water tupelo and red maple at BHF had an average diameter at breast height of 9.44 cm, 3.16 cm, 6.20 cm and 6.19 cm, respectively. By 2017, the DBH of these species only increased to 10.18 cm, 3.33 cm, 6.46 cm and 6.47 cm, respectively. Thus, in an 8-year period the average annual increment across all species was only 0.04 cm, indicating that overstorey growth is basically stagnant. Diameter growth suppression due to flooding was also observed in a wetland forest of Florida (Ernst and Brooks, 2003). This stress limited GPP and enhanced RE at BHF is consistent with a tidal wetland in Louisiana (Holm et al., 2016), although our site is non-tidal. Continued monitoring of tree mortality and C fluxes, along with other biological determinants and environmental factors influencing changes in NEE at this site are necessary to fully understand the increase in RE over time.

The RE:GPP ratio reflects the ecosystem C absorption potential. Average RE:GPP values varied from 1.54 (YP₂₋₆), 1.11 (YP₂₋₈), 0.76 MP and 1.10 BHF. The greater RE to GPP shows net C loss and thus younger sites (YP₂₋₆ and (YP₂₋₈) were losing more C than sequestering. This indicates stored C from soils, litters and coarse woody debris left after harvest were being emitted to the atmosphere. Higher GPP to RE at MP confers a net C sink. This suggests MP RE was more reliant on labile C from fresh inputs. The RE:GPP value of 1.10 at BHF site indicates that these two fluxes were slightly decoupled, with RE predominating.

4.3. Differences in NEE between the managed plantations and natural forest

We found that the newly established harvested sites differed from one another in C balance trends after clearcutting, even though they were in close proximity with similar climatic conditions. This suggests that even in a single geographical area there can be multiple trajectories in C fluxes after harvest (Amiro et al., 2010), and that local differences in soil conditions could create variability (Borders et al., 2004), particularly in drained coastal wetlands which have high water tables (Minick et al., 2019). Annual C losses of NEE of 569 g C m⁻² yr⁻¹ at the YP₂₋₆ and 101 g C m⁻² yr⁻¹ at the YP₂₋₈ sites following harvest is close to the range reported for a 4 year-old Scots pine stand (386 g C m⁻² yr⁻¹; Kolari et al., 2004), a 2 year-old jack pine stand (137 g C m⁻² yr⁻¹; Zha et al., 2009), a 3 year-old black spruce stand (124 g C m⁻² yr⁻¹; Bergeron et al., 2008) and an 8 year-old jack pine stand (130 g C m⁻² yr⁻¹; Mkhabela et al., 2009).

Annual NEE at MP remained strongly negative for the entire study period, demonstrating that this stand was a long-term C sink. Middle age stands are usually C sinks (Valentini et al., 2000), and the sink strength trajectory of the MP site would likely continue over time (Supplemental Fig. 5). However, as a commercially managed site, it was harvested in 2019. This resets the C balance back to the source side. Monitoring the C balance of this site over the transition from the end of commercial rotation, through the harvest disturbance, and several years after re-planting will provide valuable data on site preparation and tree establishment phases of southern pine silviculture. Although the sink strength of forests may continue to increase for 20 or even 30 years after stand-replacing disturbance (Litvak et al., 2003), as the stand matures the sink strength generally declines (Zha et al., 2009) and commercial operations may truncate long-term C trajectories. Long-term C cycle monitoring of these managed forested wetland after harvest is needed to determine the extent to which these patterns observed in upland forests are realized. It has been observed that wetland recovery is a slow process, arriving at only 77% of reference C conditions even 100 years after restoration (Moreno-Mateos et al., 2012),

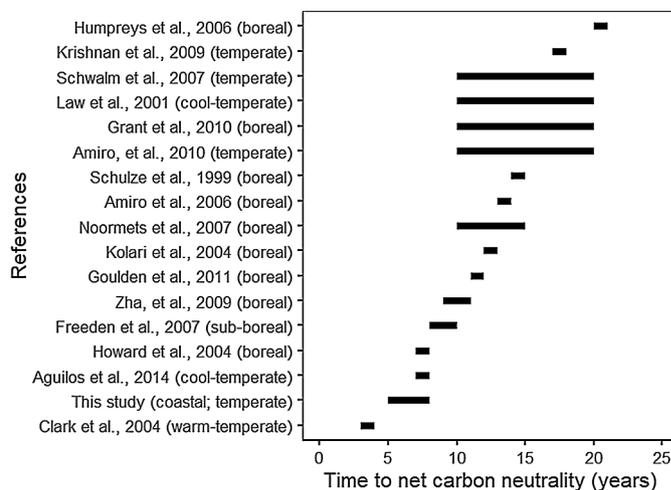


Fig. 7. Comparison studies conducted in temperate regions and the period where their ecosystem regain its status as a C sink again after a disturbance.

dependent on climate sensitivity and climate-C feedbacks (Matthews et al., 2009).

Using the cluster of intensively managed pine stands, we estimate that pine plantations in this region regain C sink status 5–8 years after harvest, which is earlier than has been reported in other studies (Fig. 7). Ecosystem C balance reached the break-even point (e.g. recovered C equivalent to post-harvest losses) at 8–14 years. Thus, these plantations contribute to net C uptake only during about half of the 25-year rotation period. These break-even points are slightly longer than our earlier estimates (Noormets et al., 2012) of 9.5 years, thus lending support to other analyses questioning the value of intensively managed plantation forests in climate mitigation efforts in comparison to protection of mature or old-growth forests (Luyssaert et al., 2007), and justifies the need for a longer monitoring to reduce uncertainties.

Old forest stands have been observed with a decadal average of NEE close to zero (Dunn et al., 2007) or to continue to sequester large amounts of C annually (Luyssaert et al., 2008). However, much of the stored C is vulnerable to loss to the atmosphere with disturbance. We hypothesize that some as yet unidentified environmental driver (change in hydrology, rising temperature, saltwater intrusion, etc.) is causing major changes in ecosystem function or transition at the BHF site, as expressed by the high tree mortality, very low NPP (data not shown), and consistent net positive NEE (e.g. weak C source) observed over 8 years now, which is a focus of ongoing investigation.

4.4. Stand age effect on GPP, RE and NEE between the managed plantations and natural forest

Evaluating the pattern of the stand age – C flux relationship yields a high coefficient of determination at recently harvested sites up to rotation age plantations, but less so in natural forests (Fig. 3). The initial increasing trend of GPP as a function of age was consistent with growth trajectories seen in other studies (Ryan et al., 2004; Schwalm et al., 2007). The enhancement in GPP with age was sustained up to rotation-age (MP). Productivity was expected to decrease with age in older forests, presumably as nutrients are immobilized in living plant material and dead organic matter (Zona et al., 2010). Accordingly, the productivity of temperate forests peaks at 50 – 70 years (Pregitzer and Euskirchen, 2004) and begins to decline afterwards because of various structural, physiological and environmental limitations (Ryan et al., 1997). This is similar to what we found in the GPP-stand age curve at BHF (Fig. 3). RE also increased with stand age after harvest of MP. This is consistent with data showing that all flux terms increase with age shortly after stand establishment (Schwalm et al., 2007). However, RE decreased more than GPP as MP approached rotation age. Other studies

also showed increasing RE after harvest, that declined after various thresholds were reached (Anthoni et al., 2002; Grant et al., 2010; Kolari et al., 2004). As forests age, total RE also declines during the later stages of forest development (Pregitzer and Euskirchen, 2004), and thus we would not expect the BHF site to exhibit high rates of ecosystem respiration. This may also reflect why no significant age – RE relationship was found at the BHF site, consistent with other studies (Law et al., 2003). Once the young forests became net C sinks at mid- to late-rotation age (MP), NEE reached a stable state that remained relatively constant throughout the measurement period. This pattern is consistent with that observed across a jack pine stand, where net C uptake increased linearly for approximately 15 years then peaked and leveled off until approximately 30 years following disturbance (Howard et al., 2004; Zha et al., 2009). The existence of multiple stands of varying age in close proximity in our study, and cumulative long-term monitoring (e.g. 34 site-years of observations), provides valuable insights into the importance of stand age as a determinant of C fluxes and balances in coastal plain regions.

4.5. Environmental controls in GPP, RE and NEE

Sustained favorable light availability resulting in increased photosynthesis is well-established (Aguilos et al., 2018; Wen et al., 2009), and is primarily a function of greater leaf area (Mkhabela et al., 2009). However, in our study the percentage of variance in R_n – NEE relationships across managed stands was low. This suggests that radiation alone is a less reliable predictor for modeling C balance in these coastal forests, and other biotic factors are likely to have contributed to the observed variability. RE was an exponential function of temperature at our sites, as has also commonly been observed in other studies (Krishnan et al., 2009; Mkhabela et al., 2009; Noormets et al., 2010), explaining up to 70% of the variation (Zha et al., 2009). T_{soil} together with REW (the second-ranked predictor of RE at harvested sites) can influence RE only when sufficient substrate is available (Noormets et al., 2007). The incorporation of harvest residues (e.g. CWD) and higher T_{soil} facilitated an initial burst in soil respiration at the harvested sites. This was very evident during harvest in 2013, when T_s was the main determinant of RE ($R^2 = 0.87$, $P < 0.0001$) compared to the entire duration at YP₂₋₆ ($R^2 = 0.69$, $P < 0.0001$) or in 2013 at the nearby MP site ($R^2 = 0.72$, $P < 0.0001$). We must therefore be cognizant of the potent positive feedbacks between disturbance, generation of massive amounts of CWD, and increasing T_{soil} that act in combination to enhance ecosystem C losses (Aguilos et al., 2013; Bronson et al., 2008; Schindlbacher et al., 2009). Air temperature was the key climate variable for GPP, RE and NEE at BHF site over the duration of the study. Even when we analyzed the environmental controls in 2009 alone, and during the net C source period in 2010 – 2017, T_{air} was always the main determinant of C fluxes and balance, and the functional relationship did not change much (GPP ranged from $R^2 = 0.65 \sim R^2 = 0.68$, RE from $R^2 = 0.65 \sim R^2 = 0.66$, and NEE from $R^2 = 0.21 \sim R^2 = 0.28$). The temperature sensitivity of RE in older forests may lead BHF to continue losing C due to hydrologic forcing coupled with increasing temperature in a future warmer climate.

4.6. Sensitivity of GPP, RE and NEE to soil water conditions

4.6.1. Sensitivity of managed plantations to severe water depletion

Inter-annual variation in the negative slope between REW and C fluxes in managed pine stands indicates that soil water availability moderately influences GPP and RE when radiation and temperature are not limiting (Supplemental Fig. 3). The absence of major inter-annual variation in NEE with change in REW suggests that even though the processes involved in GPP and RE may vary individually, collectively they converge towards a rather stable NEE regardless of soil water conditions.

Drought affected the YP₂₋₈ and MP sites, and the construction of

drainage ditches at these managed sites lowered the ground water table. Over time, this could increase soil C oxidation with implications for ecosystem C storage (Nahlik and Fennessy, 2016). It is difficult to compare our results with other studies because most drought-related literature to date has been focused on upland forests, and information for forested wetlands is scarce. Some upland studies report that both GPP and RE may be constrained by soil water deficit during drought periods (Bonal et al., 2008; Granier et al., 2007; Meir et al., 2008). However, this did not occur in our study as there was an enhancement of GPP and RE with soil water stress at both the YP₂₋₈ and the MP sites (Table 2). At YP₂₋₈, drought increased GPP slightly more than the respective increase in RE. This is an indication that during extreme soil water conditions, this site can better assimilate C despite being an overall net C source. If this persists, this site would be expected to become a net C sink similar to MP. Our hypothesis that drought leads to more C loss to the atmosphere was supported by the data, but not our hypothesis of a reduction in GPP during periods of soil water limitation. The rate of increase in GPP and RE with drought indicates that the impact of soil water stress on C fluxes was overridden by some other biotic/abiotic factors. This suggests that the effects of R_n on GPP and temperature on RE during drought years were greater than the possible effect of soil water limitation. At such LCP sites with high GWT, it is generally considered that rainfall-induced soil anoxia frequently limits decomposition and nutrient mineralization (Schoor and Matson, 2001; Silver et al., 1999), and thus drier conditions could enhance both soil C losses and C gains (Schoor, 2003). A previous study at the site reported that GPP drought sensitivity was masked by higher leaf area index (LAI) and incident radiation (Noormets et al., 2010). At the leaf level, stomatal closure during drought usually induces a stronger down-regulation of transpiration than of photosynthesis (Maréchaux et al., 2018). This is because photosynthesis may be limited by a variety of other factors and does not respond linearly to instantaneous changes in stomatal conductance (Chaves et al., 2003). A study also reported a delay in the onset of bud flushing with drought (Mijnsbrugge et al., 2016). Although we have not evaluated this in our study, any delays in leaf expansion may have helped preserve soil water availability during drought. Also, roots of understory vegetation may have exploited a greater soil volume that potentially increased ecosystem drought tolerance (Warren et al., 2015). In a previous study that included our site, it was reported that loblolly pines roots are less resistant to embolism than understory species, thus having roots less vulnerable to cavitation (Domec et al., 2015). Even when REW < 0.2 (less than the general threshold of REW = 0.4), cavitation-induced decrease in root conductivity had a small impact on whole tree resistance to soil drying at this site (Domec et al., 2015). An increase in RE during drought may have been mediated by carbohydrate availability for soil respiration (Noormets et al., 2010). Drought-induced increases in soil respiration may also be influenced by the concentration of dissolved organic matter, emphasizing that rates of microbial processes increase as a function of substrate concentration (Davidson et al., 2006) or due to decomposition of labile C and native soil C (Kuzakov et al., 2000). These results underline the complexity of understanding productivity and respiratory fluxes under drought condition.

Higher net C uptake in younger plantations during the 2008 drought may have been due to water supplied by efficient root systems that can tolerate water shortage, keeping fine roots hydrated for longer periods (Domec et al., 2004, 2010, 2012), which delayed the drying of top soil layers (Brooks et al., 2006). However, the prolonged drought in 2007–2008 caused a slight reduction in the rate of NEE at the MP site because a soil water deficit might have affected early leaf growth. The underdeveloped leaves and roots can have a legacy effect on seasonal photosynthesis and water uptake, and therefore decrease the rate of net C uptake (Shi et al., 2014). The prolonged 2007 – 2008 drought posed a greater challenge because of the increased C allocation required to replace lost leaf area (Domec et al., 2015), which in turn increased the proportion of water transport tissues relative to leaves that eventually

reduced net C assimilation (McNulty et al., 2014). Thus, in a future climate with longer drought duration, high net radiation and higher CO₂ concentration, younger (2–8 years old) pine plantations in coastal plain forests may become more efficient, absorbing greater net amounts of CO₂ than rotation-aged plantations. This has implications for forest management and provides insights for ecosystem modeling to consider drought impacts in forest stands of varying ages.

The contrasting effect of drought severity and duration on normalized GPP and RE at young and old plantations illustrates the complexity of the drivers of variation of these C fluxes and the challenges for process-based ecosystem modeling. Weak variation in *Rn*-normalized NEE observed during drought periods at young and old plantations indicates that the primary control of *Rn* and temperature were greater than that of soil water.

4.6.2. Sensitivity of the natural forest to periodic flooding and shallow groundwater table

Unlike in managed sites, the BHF site has distinct microtopography which strongly influences local hydrologic conditions. Hummocks around tree bases are usually above the water table and low-lying non-vegetated hollows are submerged for more than 70% of the year (Miao et al., 2013; 2017). Periodic floods and shallow groundwater table do not necessarily improve the net productivity of unmanaged forests in the Southeastern US (Megonigal et al., 1997). A flooding study using bald cypress and water tupelo, common species at our BHF site, reported a 33–68% reduction in total biomass with freshwater flooding (Conner et al., 1997). This may be because anaerobic respiration within the roots of plants leads to the production of toxic byproducts and limits the uptake of nutrients and water. Although bottomland hardwood trees have developed physical and/or metabolic adaptations to withstand inundation anoxia, periodic flooding may cause stress since anaerobic conditions can persist in the rooting zone for several weeks during the growing season (Faulkner and Patrick, 1992). Prolonged inundation may also affect the survival of tree regeneration. This limits population density of species and thus productivity. Even seedlings of wetland species still require an exposed soil surface to germinate and must attain a minimum size before they can survive prolonged hydroperiodicity (Jones et al., 1994). This may partly explain the rather low ecosystem productivity compared to ecosystem respiration from 2010 onwards, causing our BHF site to be a net C source over the years.

Interannual variation in GPP at the BHF site reached 27% and for RE was 36%. This suggests that change in hydrology is affecting respiratory processes more than photosynthesis. A previous study at BHF revealed a 57% contribution of soil respiration to RE during non-flooded periods and a 69% contribution of aboveground plant respiration to RE during flooded periods. Autotrophic respiration tended to be higher in hummocks near the base of the trees, and there was greater sensitivity of heterotrophic than autotrophic respiration to water table drawdown (Miao et al., 2017). Although only small variations in water table depth exist at BHF site (Supplemental Fig. 2), soil respiration may respond positively to any reduction in water level at this site. Plant litter decomposition generally responds quickly to changes in environmental conditions (Lee et al., 2004), and contributed most to RE when the water table was shallower. This hydrology-driven regulation of RE is thus partly associated with soil aeration and the composition and extracellular enzyme activity of soil microbial communities. Further investigation is needed to better understand the hydrologic and microbial controls over RE at this bottomland hardwood forest.

5. Conclusions

Thirty-four site years of monitoring C balance in managed and natural coastal forested wetlands along the southeastern US LCP revealed the C source-sink dynamics of these predominant land-use systems in a rapidly changing physiographic region. Carbon storage in

soils was high in both forest types, due to the historically high GWT impeding decomposition processes, and vegetation biomass accumulated proportional to time since disturbance. The young intensively managed (drained wetland) pine forests were strong C sources to the atmosphere (e.g. positive NEE) for at least 8 years post-disturbance (harvest), but in an adjacent mature pine forest there was a strong C sink during the mid- to late-rotation period of 15–27 years. The positive C gain in the mature managed forest was due to consistently greater GPP relative to RE. The managed forests were susceptible to periodic droughts. The mature natural bottomland hardwood forest was a C sink the first year of monitoring, but became a C source of increasing intensity over the monitoring period. This together with a spike in tree mortality suggests that environmental controls over NEE have transitioned during the course of this study and consequently, this ecosystem has begun to lose stored C. Both the managed pine and natural bottomland hardwood ecosystems appear to be functioning on the wet end of the soil water availability spectrum for forests, implying that increased hydrologic forcing and changing climate could shift the C balance trajectory of these important regional LCP C stocks.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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