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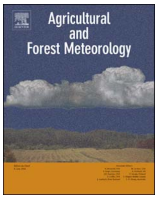

Hydrology and microtopography control carbon dynamics in wetlands: Implications in partitioning ecosystem respiration in a coastal plain forested wetland

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ABSTRACT

Wetlands store a disproportionately large fraction of organic carbon relative to their areal coverage, and thus play an important role in global climate mitigation. As destabilization of these stores through land use or environmental change represents a significant climate feedback, it is important to understand the functional regulation of respiratory processes that catabolize them. In this study, we established an eddy covariance flux tower project in a coastal plain forested wetland in North Carolina, USA, and measured total ecosystem respiration (R_e) over three years (2009–2011). We evaluated the magnitude and variability of three respiration components – belowground (R_s), coarse woody debris (R_{CWD}), and aboveground plant (R_{agp}) respiration at the ecosystem scale, by accounting microtopographic variation for upscaling and constraining the mass balance with R_e. Strong hydrologic control was detected for R_s and R_{CWD}, whereas R_{agp} and R_e were relatively insensitive to water table fluctuations. In a relatively dry year (2010), this forested wetland respired a total of about 2000 g CO_2-C m^{-2} y^{-1} annually, 51% as Rs, 37% as R_{agp}, and 12% as R_{CWD}. During non-flooded periods R_s contributed up to 57% of R_e and during flooded periods R_{agp} contributed up to 69%. The contribution of R_s to R_e increased by 2.4% for every cm of decrease in water level at intermediate water table level, and was nearly constant when flooded or when the water level more than 15 cm below ground. The contrasting sensitivity of different respiration components highlights the need for explicit consideration of this dynamic in ecosystem and Earth System Models.

1. Introduction

Natural wetland soils contain a large amount of carbon that has accumulated over millennia. Permanently or intermittently flooded conditions result in low decomposition rates of organic matter, by which the historic mean residence time of carbon in wetland soils has been estimated as exceeding 500 years (Chmura et al., 2003; Gorham, 1991; Raich and Schlesinger, 1992). Therefore, wetlands are viewed as important long-term carbon sinks (Bridgham et al., 2006; Mitsch et al., 2013). Recently, there has been a growing awareness that changes in climate and land use may alter wetland carbon source-sink relationships. Sea level rise, high-energy waves and flooding associated with extreme storm events accelerates coastal wetland soil erosion, threatening these globally important stores of carbon (Webb et al., 2013). Further, the conversion of wetlands to agriculture and other land uses can in short time undo millennia of carbon accumulation by promoting conditions favorable for aerobic decomposition (Armentano and Menges, 1986; Armentano, 1980; Laiho, 2006). Conversely, the current efforts at wetland restoration could help mitigate the rising atmospheric carbon dioxide (Craft et al., 1999). Unfortunately, the sensitivity of carbon dynamics to environmental change is much less well investigated in wetlands than in uplands, which limits our ability to

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quantify their future role in the global carbon cycle. Importantly, due to the scarcity of data, wetlands are still absent in most regional and global scale carbon assessments (Battin et al., 2009; Davidson, 2010; Luyssaert et al., 2007; Mahecha et al., 2010).

Compared to upland ecosystems, carbon cycling in wetlands is strongly affected by hydrology in addition to temperature and associated with microtopography (Ehrenfeld, 1995; Jones et al., 1996; Van der Ploeg et al., 2012; Waddington and Roulet, 1996). Together, they determine substrate availability to soil microbial communities, the growth status of plants and the potential upscaling bias of carbon pools and fluxes (Alm et al., 1997; Frei et al., 2012; Kreuzwieser and Rennenberg, 2014; Miao et al., 2013). Although microtopographic and hydrologic variations are common characteristics in wetlands (Barry et al., 1996; Burke et al., 1999; Nungesser, 2003; Riutta et al., 2007), linking these two key factors with carbon dynamics quantitatively has been a great challenge due to the difficulties in field data collection and not been well addressed. Studies in some restored wetlands have shown significant effects of microtopography and hydrology on soil and vegetation, providing insights of how carbon dynamics might be affected in natural systems (Barry et al., 1996; Bledsoe and Shear, 2000; Bruland and Richardson, 2005).

Ecosystem respiration (R_e) is a key process that regulates the role of an ecosystem as carbon source or sink (Grace and Rayment, 2000; Valentini et al., 2000). R_e integrates a variety of autotrophic and heterotrophic processes, every component of which may exhibit different sensitivities to changes in environmental conditions (Bahn et al., 2010; Davidson and Janssens, 2006; Hopkins et al., 2013; Teskey et al., 2008; Trumbore, 2006), making the investigations into respiration complex and challenging. This is particularly true in wetlands, where variable hydrology may have contrasting effects on different respiratory components (Lafleur et al., 2005). In the short term, belowground respiration (R_s) usually decreases immediately upon flooding due to the resistance of water on gas diffusion, of which the coefficient is 10,000 times smaller than in the air (Denny, 1993). Previously, we observed that during a rainfall event, when some microsites turned inundated, R_s decreased rapidly from more than 5 μmol CO_2-C $m^{-2}\,s^{-1}$ to less than 0.5 μmol CO_2-C $m^{-2}\,s^{-1}$ within two hours (Miao et al., 2013). Direct measurements on response of plant respiration to change in hydrologic regimes are rare, but many studies indicated that plant organs respond slowly to temporary or continuous flooding (from days to years), especially for flood-tolerant species (Anderson and Pezeshki, 2001; Keeland et al., 1997; Kreuzwieser and Rennenberg, 2014), because aboveground plant tissues are still exposed to adequate oxygen and respiration could use plant carbon storage or current photosynthates (Chapin et al., 1990).

The long-term effect of permanent or intermittent flooding, which favors peat accumulation but limits plant growth, may have been to store more carbon in soils than in wetland plants (Bridgham et al., 2006; Gorham, 1991). It appears that due to different carbon storage between pools and driver sensitivities of respiratory components, the ratios of these component fluxes to R_e differ by ecosystem type (Aerts, 1997; Davidson et al., 2006; Harmon et al., 2004). For example, boreal and temperate upland ecosystems generally store large amounts of carbon in both plants and soils, and R_s contributes to R_e comparable to plant respiration, with the R_s:R_e ratio reported at 0.4–0.8 (Janssens et al., 2001; Lavigne et al., 1997; Law et al., 1999). Tropical rainforests accumulate larger amounts of carbon in plants than in soils compared to higher latitude forests, resulting lower contribution of R_s to R_e with a ratio of 0.3–0.4 (Chambers et al., 2004; Saleska et al., 2003). Associated with the live plant components, plant debris also contribute differently between ecosystems. It was predicted that the decomposition of coarse woody debris (CWD, R_{CWD}) in a central Amazon forest could be 65–88% of total carbon loss (Chambers et al., 2001), whereas in some loblolly pine plantations in the Southeastern US it was reported to be only 20% (Noormets et al., 2012). Given the unique carbon storage in wetlands and the hydrologic effects on respiratory components, one would expect a different pattern of the ratios of respiratory components to R_e in wetlands. For example, in a forested wetland, soil might contribute similarly to or more than plants to R_e during non-flooded periods, while plant respiration might dominate during flooded periods.

To our knowledge, rigorous partitioning of R_e to its primary components has rarely been done in wetlands, and hydrology and microtopography are yet rarely taken into account in upscaling. The current study was designed to fill this gap. Specifically, we investigated a forested wetland in the coastal plain of the Southeastern US, where the majority of the forested wetlands in the US are located. These southern forested wetlands offer important values to the society, such as removing and transforming inorganic nutrients from the water column to improve the water quality, and providing a source of fixed carbon and organic nutrients to aquatic organisms that maintains productivity of aquatic ecosystems downstream (Walbridge 1993). These systems also face the threat of sea level rise as well as the conflict between conservation and development (Dugan 1993). A comprehensive understanding of the biogeochemical functions that these important functions are based upon is therefore urgently needed to better manage these ecosystems, especially under the changing climate and land use.

The objectives of the current study were to understand the ecosystem-scale CO_2 efflux from a forested wetland by (1) characterizing the seasonal variations of R_e and its three components – R_s, R_{CWD} and aboveground plant respiration (R_{agp}) and hydrologic effects on these seasonal variations; (2) partitioning R_e into R_s, R_{CWD}, and R_{agp} at monthly and annual scales, and (3) quantifying hydrologic effects on the contribution of component fluxes to R_e. In addition, we discussed the uncertainties of carbon budget closure related to different measuring techniques and resultant bias. Overall, based on a careful upscaling and budget estimate, this study attempts to provide a better understanding of the special characteristics of forested wetlands related to hydrologic variations and information for improving models of biogeochemical processes in wetlands.

2. Methods

2.1. Site description

The study area is located at the Alligator River National Wildlife Refuge (ARNWR), on the Albemarle-Pamlico peninsula of North Carolina, USA (35°47′N, 75°54′W, Fig. 1a). The site was established in the middle of the peninsula in November 2008, including a 35-m instrumented tower for eddy covariance (EC) flux measurements and micrometeorology above the canopy. A ground micrometeorological station was located about 30-m away from the flux tower, and 13 vegetation plots spread over a 4 km^2 area were distributed across the site (Fig. 1a).

The mean annual temperature and precipitation from climate records of an adjacent meteorological station (Manteo AP, NC, 35°55′N, 75°42′W, National Climatic Data Center) for the period 1981–2010 are 16.9 °C and 1270 mm, respectively. The forest type is mixed hardwood swamp forest; the overstory is predominantly composed of deciduous species – black gum (*Nyssa sylvatica*), swamp tupelo (*Nyssa biflora*) and bald cypress (*Taxodium distichum*), with occasional red maple (*Acer rubrum*), and evergreen species – Atlantic white cedar (*Chamaecyparis thyoides*) and loblolly pine (*Pinus taeda*); the understory is predominantly fetterbush (*Lyonia lucida*), bitter gallberry (*Ilex glabra*), and red bay (*Persea borbonia*).

The canopy height ranged 15–20 m, and the leaf area index generally peaked in July at 3.5 ± 0.3 (Smith et al., 2008). Aboveground live biomass was estimated allometrically at 37.5 ± 12.5 (mean ± SD) Mg C ha^{-1} (Jenkins et al., 2004). Coarse woody debris (CWD) stored 3.1 ± 2.0 (mean ± SD) Mg C ha^{-1} (Waddell 2002). The major soil series are poorly drained Pungo and Belhaven mucks, whose organic carbon content is approximately 40–100% and 20–100%, respectively (Web Soil Survey accessed on 14 December 2009). Dry soil

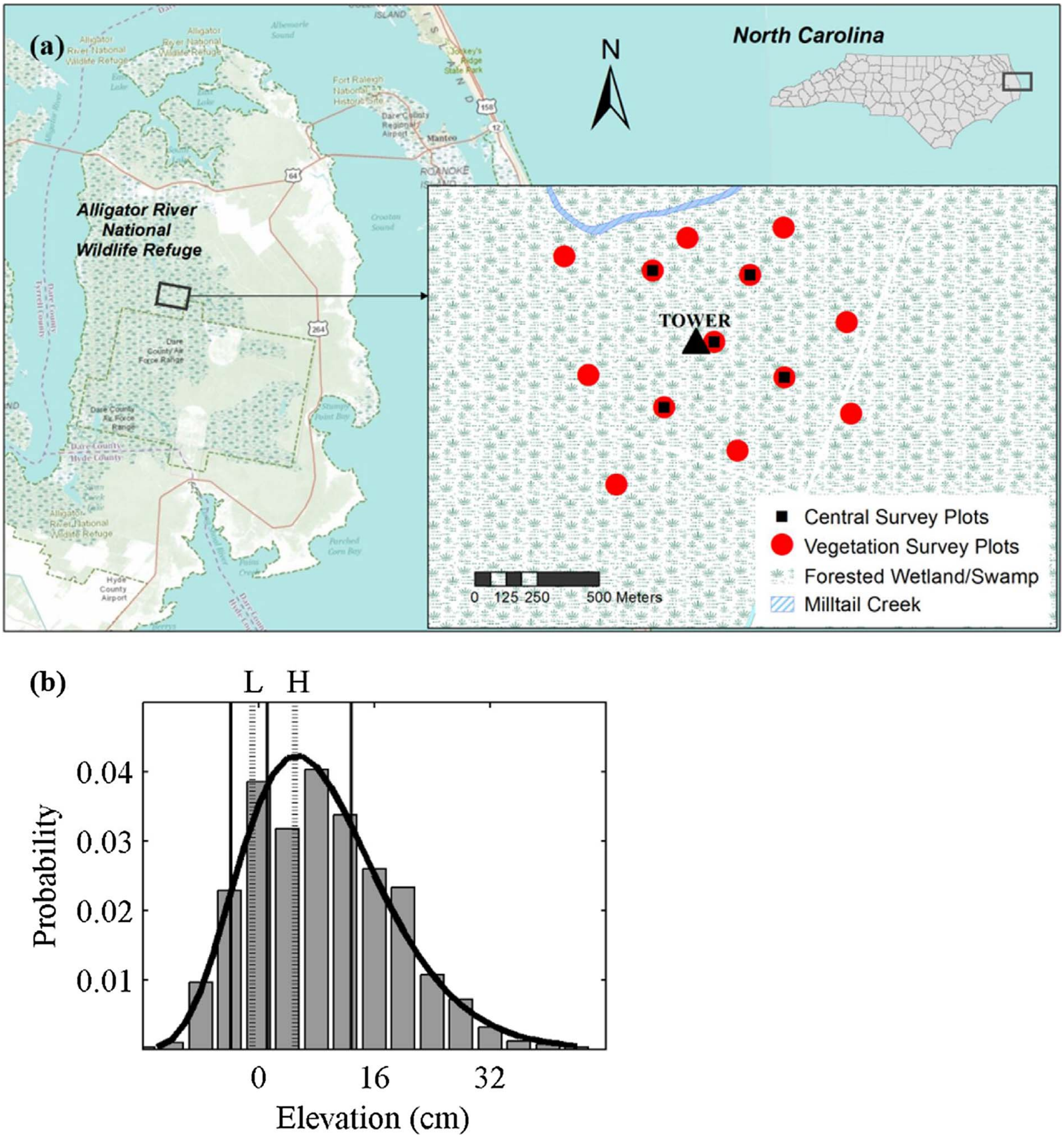

Fig. 1. (a) Location and field settings of study site at the Alligator River National Wildlife Refuge (35°47′N, 75°54′W) in eastern North Carolina, USA (refer to online materials for the original version of this figure in color). (b) Histogram and fitted gamma distribution of microtopography. Three solid straight lines represent the elevations of the three microsites (LOW, MID, and HIGH from left to right) where the automated belowground respiration (R_s) measurements were conducted (Section 2.5). Two dotted straight lines represent the cutoff points used to calculate the areal representativeness of each microsite. We assumed that belowground respiration (R_s) is linearly related to the microtopography. Therefore, the average R_s of all the microtopographic positions lower than 'L', where statistically half is lower than LOW microsite (the left solid line) and half is higher, equals to the R_s of the LOW microsite. A similar definition was applied to point 'H', i.e. the average R_s of positions higher than 'H' equals to the R_s of the HIGH microsite (the right solid line). The positions between 'L' and 'H' were assumed to respire equally to the MID microsite (the middle solid line).

bulk density was estimated at approximately 0.06–0.10 g cm^{-3} from soil samples collected during flooded periods.

2.2. Microtopography and hydrology

There are marked differences between microtopographic positions in local hydrologic conditions (Fig. S1) – mounds around tree bases are usually above water table, and non-vegetated low-lying sites are submerged for more than 70% of the year (Miao et al., 2013). These microhabitats have different vegetation distributions, and different soil CO_2 efflux rates (Miao et al., 2013). To weigh the contribution of these different microsites in the flux footprint, we quantified the frequency distribution of different microtopographic positions in the landscape. Three 30-m transects originating from the center of the plots towards 0°, 120° and 240° from due north were established in the 5 central vegetation survey plots (Fig. 1a). A tripod-mounted laser level (RoboLaser Green RT-7210-1G, RoboToolz Inc., CA, USA) provided a horizontal reference line from which the distance to ground was measured every 40 cm along each transect (Fig. S2). The elevation of different plots was normalized in relation to water level (WL) during a high water event when over 90% of the study area was submerged.

The frequency distribution of height-normalized elevation data across the 5 central plots approximated a gamma distribution (Fig. 1b). The mean value of this gamma distribution was calculated as the site average elevation (i.e. 8.7 cm relative to the water table probe location at the ground micrometeorological station, see Section 2.3). We then adjusted the WL to site average values and applied them to modeling R_e and site average R_s. The site average microtopography was also used to separate data into flooded and non-flooded bins (i.e. when the WL at the central water table probe exceeded 8.7 cm, the site was defined as flooded).

2.3. Micrometeorology

Micrometeorological parameters measured above the canopy (at 30 m) included air temperature (T_a) and relative humidity (HMP45, Vaisala, Finland), photosynthetically active radiation (PAR, PARLITE, Kipp & Zonen, Delft, Netherlands (KZ)), net radiation (R_n, NRLITE, KZ), and precipitation (TE525, Texas Instruments). The ground micrometeorological measurements included T_a and RH (HMP45AC, Vaisala), PAR (PARLITE), soil temperature (T_s) at 5 and 20 cm (CS 107, Campbell Scientific Inc., UT, USA (CSI)), volumetric soil water content (CS 616, CSI), soil surface heat flux (HFP01, KZ), and water level (WL, Infinities, FL). Water level changes were also monitored at the central 5 of the 13 vegetation survey plots (WL 16, Global Water Instrumentation, TX, USA). All the variables were continuously measured and recorded at 30 min interval.

The meteorological data from an adjacent meteorological station (Manteo AP, NC) were also analyzed through the observation period (2009–2011), and the monthly patterns of the three years were compared with the 30-year (1981–2010) means to provide a context of climate change for the observation period.

2.4. Eddy covariance flux

The EC flux measurements started in March 2009 and ran through the end of 2011. The instrumented tower was surrounded by uniform canopy in most directions. The fetch extended more than 2500 m around all the directions, and the turbulent flux did not show directional variability. The EC system consisted of LI-7500 open-path infrared gas analyzer (Licor Inc.), CSAT3 3-dimensional sonic anemometer (CSI), and CR1000 data logger (CSI). The instruments, mounted at 30 m, were about 16.7 m above the displacement height (two thirds of the canopy height). The turbulent fluxes were computed as the covariance of the vertical wind speed and the CO_2 concentration, and were corrected for density fluctuations (Webb et al., 1980). A CO_2 profile system consisted of a LI-820 infrared gas analyzer and a multiport system, recording 30-s averages of CO_2 concentration every 5 min at five levels (about 0.02, 0.04, 0.3, 0.6 and 1× of canopy height). CO_2 storage was calculated as the vertical integral of the mean rate change in CO_2 concentration at each level (Yang et al., 2007). The net ecosystem CO_2 exchange (NEE) between forest canopy and atmosphere was then computed as the sum of turbulent flux and change in CO_2 storage (Noormets et al., 2010).

Nighttime NEE was assumed to represent R_e, and used for developing R_e models. The data were screened based on atmospheric stability, flux stationarity, integral turbulence characteristics, sensor signal quality, and friction velocity. The site-specific friction velocity thresholds – 0.25 m/s when air temperature was lower than 20 °C and 0.27 m/s when air temperature was higher than 20 °C – were derived based on an analysis of the relationship between friction velocity and EC fluxes at seasonal scale (Noormets et al., 2010). After further reductions due to power problems and extreme weather, the nighttime data coverage was 20%, 17%, and 15% in 2009, 2010, and 2011, respectively. Despite the relatively low coverage, the accepted data had a reasonably uniform coverage over time and observed temperature and water table range (Fig. S3-e, f). This uniform coverage, on one hand, gave us confidence in developing R_e models. On the other hand, compared with the full driver data coverage during the study period (Fig. S3-a, b), these nighttime NEEs might not catch the records at the high temperature and low WL end, which likely corresponded to high NEE. Uncertainties were further discussed at Section 2.7.3.

2.5. Automated and manual survey soil CO_2 efflux

Soil CO_2 efflux was measured with both automated and manual survey systems. The automated system was deployed next to the micrometeorological station in the center of the study area and collected data at 30-min intervals. The handheld survey measurements were made in the 5 central plots at monthly intervals to supplement the automated measurements for characterizing spatial variation (Fig. 1a). Further details of the R_s measurements were described earlier (Miao et al., 2013).

The 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 three microtopographic locations with elevations relative to the water table probe of +12.9, +1.2 and −3.8 cm (named as HIGH, MID and LOW, the elevations shown as solid lines in Fig. 1b) from summer 2009 to the end of 2010.

The survey R_s system consisted of LI-8100 and a portable survey chamber (LI 8100-103, Licor Inc.). The survey measurements were conducted from early spring of 2010 to summer 2011. At each plot, six microsites were positioned in a 7 m diameter circle and also installed with 20 cm diameter PVC collars. The collars were re-randomized in early 2011 to minimize the potential artifact from disturbance of the surrounding soil. Thus 60 microsites in total were involved in survey measurements. Soil temperature at 5 and 10 cm depth and volumetric soil water content at top 12 cm were recorded at each measurement.

Elevation of each survey microsite was measured relative to the local water table well. The WL of each microsite at each measurement date was estimated based on their elevations and the WL readings from respective plot probes. All the survey microsites were also classified into three groups which corresponded to the HIGH, MID and LOW microsites in the automated measurements, and used as the replications of the three types of microsites. The cutoff points (the dashed lines ‘L’ = −1 cm and ‘H’ = 5 cm in Fig. 1b) were derived from the gamma microtopographic distribution and the simplified assumption that microsite R_s is linearly related to the microtopography.

2.6. Coarse woody debris CO_2 efflux and biomass survey

Coarse woody debris CO_2 efflux was measured on four downed trees (diameter > 10 cm) on each of the 5 central survey plots during the same periods as survey R_s measurements. 10 cm diameter PVC collars were mounted on the stems and sealed with silicone sealant. Some collars were replaced in early 2011 due to damage by severe flooding and wild life. In all, 22 CWD sections were sampled, with 3, 6, 10 and 3 pieces in decay classes 1, 2, 3 and 4, respectively. The decay classes were defined from freshly senesced plant litter (class 1) to highly decomposed debris (class 4) according to Harmon et al. (2004). Coarse woody debris CO_2 effluxes were measured with an EGM-4 environmental CO_2 monitor and SRC-1 closed system chambers (PP Systems International Inc., MA, USA) concurrently with the survey R_S measurements. The temperature of the woody substrate at 5 cm depth (T_{CWD}) was recorded at each measurement. Moisture content was assessed qualitatively by the appearance of the substrate as submerged, saturated, moist, dry or very dry. As CWD water content was inversely correlated with temperature and assessed only in qualitative terms, it was not considered as an explicit driver when modeling the CO_2 efflux.

Coarse woody debris biomass was measured at the end of 2010 and 2011 for scaling up R_{CWD}. Three 30-m transects originating from the center of the plots towards 30°, 150° and 270° from due north were established in all the vegetation survey plots (Fig. 1a). The pieces of CWD intersecting with the transects and larger than 7.6 cm in diameter were counted and identified to hardwood and softwood. The diameter and decay class were recorded for estimating biomass (FIA, 2007). The respective total CWD biomass was 1.6 ± 1.0 Mg C ha^{-1} in 2010 and 3.1 ± 2.0 Mg C ha^{-1} in 2011. In terms of the observation in the field, during summer when most areas were dry, there was no significant change in CWD during the study period and the difference in CWD biomass estimates between the two years was most likely the result of underestimating submerged debris in 2010. The site was wet at the survey day in 2010 (site average WL = −1 cm, but many LOW microtopographic locations were flooded), and dry in 2011 (site average WL = −12 cm). We then defined three biomass levels based on the WL at each survey day to upscale R_{CWD} under different WL for the whole study period: (1) if WL > −1 cm, the CWD survey results from 2010 were used; (2) if WL < −12 cm, the 2011 results were used; (3) if WL was between −1 and −12 cm, the mean value of the two survey results was used.

2.7. Partitioning assumption and derivation of respiratory fluxes at the ecosystem scale

Partitioning of R_e to its components was based on mass balance approach, assuming that R_e is functionally the integration of R_s, R_{CWD} and R_{agp}. R_{agp} was calculated as the residual from the three measured components − R_e, R_s and R_{CWD}. R_e was measured every 30 min at the ecosystem scale. Automated R_s was also measured every 30 min but at point scale. Survey R_s and R_{CWD} measurements were conducted monthly at point scale. To match both temporal and spatial scales between R_e, R_s, and R_{CWD}, different strategies were adopted to fill original data gaps and upscale to daily and ecosystem scales. These data were then used to calculate R_{agp} at the same scales. Every respiratory component was separately investigated for non-flooded ($R_{i\text{-}NFL}$) and flooded ($R_{i\text{-}FL}$) periods (Eq. (1)), by which hydrologic effects were quantified.

$$\begin{cases} R_e = R_s + R_{CWD} + R_{agp} \\ R_i = R_{i\text{-}NFL} + R_{i\text{-}FL} \\ (i = e,\ s,\ CWD,\ agp;\ NFL\text{: Non-flooded},\ FL\text{: Flooded}) \end{cases} \tag{1}$$

Models were developed for R_e, R_s (automated and survey) and R_{CWD} to fill the data gaps at original scales, using non-linear regression between measured fluxes and environmental driver(s). Our previous study demonstrated that adding WL into conventional temperature-based respiration model structure improved R_s model performance significantly (Miao et al., 2013). We therefore applied the modeling strategy into this current study. We first categorized measured R_e and R_s by flooded and non-flooded regimes, and R_{CWD} by three decay classes. We then used T_s and WL to develop R_e and non-flooded R_s models, T_s for flooded R_s model, T_{CWD} for R_{CWD} models of each decay class and WL was used for upscaling. Details about model development were presented in supplements (part 2 in Supplementary Material (SM)), and models adopted were listed in Table S2. Briefly, four model structures (Table S1): conventional Q_{10} (temperature sensitivity) model, dynamic basal respiration (R_b) model, dynamic Q_{10} model and nested (with dynamic R_b and Q_{10}) model, of which the latter three model structures are modified Q_{10} model with the basal temperature or/and Q_{10} varying with WL, were tested for each component, and appropriate models were selected based on the model performance and applied to fill the data gaps in each component.

2.7.1. Belowground respiration

The site average R_s was calculated separately from both automated and survey measurements to evaluate the effect of their different temporal and spatial coverage on the site-level estimates. Automated 30-min R_s from the three microtopographic locations was gap filled first with the nested Q_{10} models (Miao et al., 2013), and then integrated to derive site average R_s based on the areal representativeness (A_i) of each microsite given the frequency distribution of ground elevation:

$$R_s = \sum_{i=LOW,MID,HIGH} A_i R_{s,i} \tag{2}$$

where i is the index for individual microtopographic locations. Based on the area of the microtopography distribution (Fig. 1b), the A_i was 60%, 23% and 17% for the HIGH, MID and LOW microsites, respectively. Daily site-average R_s was then derived by summing the gap-filled and upscaled 30-min data.

To upscale survey measurements, a response model of R_s to T_s and WL was developed. The monthly measurements were assumed equivalent to daily mean R_s, and correspondingly the derived models were assumed valid for the daily scale as well. Daily mean T_s and WL were then used as drivers to fill the data gaps. The microtopography information was contained in the spatial variation of survey measurements and the T_s-R_s and WL-R_s relationship reflected in the survey data represented the response at the ecosystem scale. Therefore, the survey R_s was aggregated into one data set without microtopographic classification and only separated to flooded and non-flooded cases for deriving respective response models (see Miao et al., 2013 and SM). Results from survey measurements were only used as a reference to confirm the reliability of the quantification on site average R_s from automated measurements.

2.7.2. Coarse woody debris respiration

Annual site R_{CWD} was estimated as reported previously (Noormets et al., 2012). Site average R_{CWD} per unit ground area was estimated as the product of areal coverage of CWD ($A_{CWD,i}$, i represents decay class) and gap-filled R_{CWD} for each class ($R_{CWD,i}$, Eq. (3)). The $A_{CWD,i}$ was the ratio of CWD projected area to the transect area and assumed equivalent to the ratio of total CWD diameter to the transect length. The $A_{CWD,i}$ was positively related with the CWD biomass.

$$R_{CWD} = \sum_{i=2}^{4} A_{CWD,i} R_{CWD,i} \tag{3}$$

Similar to the survey R_s, the monthly-collected $R_{CWD,i}$ was assumed as the daily mean. The temperature response of daily $R_{CWD,i}$ was evaluated separately for each decay class based on chamber measurements, except for classes 1 and 2 which were combined because of similar efflux rates. The conventional Q_{10} models were then developed for each class to fill the data gaps in $R_{CWD,i}$ with daily T_{CWD} (model details in part 2 of SM). The daily T_{CWD} was estimated from the daily T_s at the micrometeorological station and based on the observed relationship between the T_{CWD} and T_s during CWD CO_2 efflux measurements.

2.7.3. Aboveground plant respiration and gapfilling uncertainties

The respiration of the aboveground biomass (R_{agp}) was calculated as residuals of the budget (Eq. (1)). However, for about 6% of the time such estimate resulted in a negative value ($R_e < R_s + R_{CWD}$), which indicates either underestimate of R_e or footprint representativeness bias between these components. R_e could be underestimated due to vertical flux divergence (Su et al., 2008), or the inclusion of stable nighttime periods with underestimated source strength (van Gorsel et al., 2009). More likely, however, the difference is attributable to the possible loss of R_e records with high values in mid-summer when the air temperature was high, WL was low and the turbulence condition was low, which did not pass the screening criteria. Alternative screening criteria did not increase annual cumulative fluxes, so the original screening criteria (Section 2.4) were kept. Consequently, these gaps resulted in the relatively low modeled R_e values (Table S2), whereas R_s values were measured. Thus, pairing the highest R_s data with modeled R_e values could easily result in scale mismatch.

We analyzed the distribution of the lack of budget closure with time, its relationship with T_s and WL, and found that all the negative results clustered at the periods when temperature was high and WL was low (daily average WL (WL_d) < −15 cm). We then applied corrections to R_{agp} and R_e at this cluster to close the respiration budget. We separated the non-flooded regime to two scenarios: (1) the daily average WL was between −15 cm and 0 cm (−15 cm < WL_d < 0 cm), the range that most available R_e data covered, and (2) the daily average WL was lower than −15 cm (WL_d < −15 cm) below ground, and then adjusted modeling, data gap-filling and partitioning strategy. Gap-filled R_e, R_s and R_{CWD} data at each scenario were converted to the same scales, i.e. daily and ecosystem scales. The derived daily data were used to calculate the fourth respiratory term – daily R_{agp}. A model for daily R_{agp} when −15 cm < WL_d < 0 cm was developed and used to predict R_{agp} when WL < −15 cm. With the predicted R_{agp} when WL_d < −15 cm, R_e under the same condition was corrected by integrating R_s, R_{CWD} and R_{agp}.

To check if low data coverage of nighttime R_e at high temperature and low WL end would affect the estimate of R_e under other environmental conditions due to the data gap uncertainty, we conducted a further modeling experiment as follows. We first derived a new model (Table S2) from the complete 2010 R_e dataset including the corrected R_e. This model was then used to predict R_e when −15 cm < WL < 0 cm. The difference in the predicted R_e between the new model and original model was derived as the uncertainty in R_e when −15 cm < WL < 0 cm that associated with the lack of data records when W < −15 cm.

2.8. Partitioning of ecosystem respiration

Monthly results of R_e and the three respiratory components were then derived from the daily data at the ecosystem scale. The trends were derived based on the data from 2010 when the records for all the measured components were relatively complete. Therefore the impacts of modeling and upscaling uncertainties were reduced. Ecosystem respiration was partitioned into R_s, R_{CWD} and R_{agp} at the annual and monthly scales, and also for flooded and non-flooded periods to estimate the hydrological effects on respiration partitioning. The carbon emissions estimated for 2009 and 2011 were compared at the annual scale for preliminary quantification of inter-annual variation. All the computations were done with MATLAB 7.14 R2012a (The MathWorks Inc., U.S.).

3. Results

3.1. Local climatic conditions and hydrology

The three study years had monthly mean temperatures similar to the 30-year mean at a nearby NOAA weather station. The average maximum-air-temperature was 20.8, 22.0 and 22.3 °C in 2009, 2010 and 2011, respectively, bracketing the 30-year normal of 21.2 °C. The average minimum-air-temperature was 12.2, 12.9 and 12.4 °C in 2009, 2010 and 2011, respectively, and also close to the 30-year normal. Annual precipitation, however, was nearly 30% lower (1002, 758 and 960 mm in 2009, 2010 and 2011, respectively) than the 30-year normal (1270 mm, Fig. S4).

The precipitation is distributed throughout the year at this coastal area, with greater events during the growing than dormant season. The biggest rainfall events are associated with the fall hurricane season (September to November), and typically trigger an increase in WL 30–50 cm or more (Fig. 2c). This also marks the end of the active season of vegetation, as by the time the water table subsides, the temperature would have dropped to near freezing, and leaves would have fallen. Of the three study years, 2009 was slightly wetter than 2010 and 2011, with the mean WL = −3 cm as opposed to −20 cm (Negative value means WL was below soil surface and positive means above). The area of flooded and non-flooded soil changed correspondingly (Fig. 2d). The amount of time with at least half of the area non-flooded was 42% in 2009 (starting from Mar. 19), 51% and 81% in 2010 and 2011, respectively.

The mean WL in 2010 was 8 ± 5 cm (mean ± SD,) in winter (Dec. 2009–Feb. 2010), −5 ± 7 cm in spring (Mar.–May), −20 ± 8 cm in summer (Jun.-Aug.), 5 ± 9 cm in autumn (Sep.–Nov.), and −4 ± 2 cm in the next winter (Dec. 2010–Feb. 2011), illustrating a typical hydroperiod pattern in this forested wetland (Fig. 2c) that WL began to drop from late winter or spring through summer due to water loss through lateral drainage and evapotranspiration and then rose quickly with the arrival of fall storms.

3.2. Seasonal and inter-annual variation in ecosystem respiration and components

The three measured respiratory components exhibited typical seasonal variation along with the change in temperature and hydroperiod (Fig. 3). In general, respiration varied primarily with temperature, but was significantly influenced by the WL fluctuation. Across all three years, summer (Jun.–Aug.) R_e averaged 10.9 ± 3.6 (mean ± SD) g CO_2-C m^{-2} d^{-1}, and winter (Dec.–Feb.) R_e averaged 1.5 ± 0.6 g CO_2-C m^{-2} d^{-1}, and spring (Mar.-May) fluxes were higher than those in autumn (Sep.-Nov.) with R_e of 4.3 ± 2.0 and 3.6 ± 1.3 g CO_2-C m^{-2} d^{-1}, respectively. The inter-annual differences correlated with dynamics of WL, with the wettest summer in 2009 having lower R_e (7.3 ± 2.0 g CO_2-C m^{-2} d^{-1}) compared to drier 2010 and 2011 (12.4 ± 2.7 g CO_2-C m^{-2} d^{-1}) (Fig. 3a).

Seasonality of R_s from survey and automated measurements was consistent between years in terms of the average magnitude at different microtopographic categories although the spatial variation resulted in marked deviation within each category (Fig. S5). Pronounced differences between microsites were present throughout the year in automated measurements, but decreased in magnitude during summer months in the survey measurements, when WL < 0 cm at all microsites. The 3-year average of summer R_s was 6.2 ± 2.8 g CO_2-C m^{-2} d^{-1} and winter R_s was 0.6 ± 0.4 g CO_2-C m^{-2} d^{-1}. Spring and autumn R_s were 2.3 ± 1.5 g CO_2-C m^{-2} d^{-1} and 1.0 ± 0.6 g CO_2-C m^{-2} d^{-1}, respectively. The coldest winter in the 3-year study was at the end of 2009, and resulted in the extremely low R_s of 0.3 ± 0.2 g CO_2-C m^{-2} d^{-1}. The summer of 2009 was the wettest of the three years, and corresponded to the lowest summer R_s of 3.2 ± 1.4 g CO_2-C m^{-2} d^{-1} (Fig. 3b).

Coarse woody debris also released the highest amount of CO_2 during summer, and R_{CWD} decreased with increasing CWD decay class (Fig. S6). The unit rates were similar between 2010 and 2011 (Fig. 3c). In 2010, the site R_{CWD} averaged at 0.5 ± 0.4 (mean ± SD) g CO_2-C m^{-2} d^{-1} in spring, 1.6 ± 0.3 CO_2-C m^{-2} d^{-1} in summer, 0.3 ± 0.2 CO_2-C m^{-2} d^{-1} in autumn, and 0.2 ± 0.1 CO_2-C m^{-2} d^{-1} in winter.

The 3-year derived R_{agp} averaged 3.4 ± 1.1 g C m^{-2} d^{-1} in summer and 0.8 ± 0.3 g C m^{-2} d^{-1} in winter. The 3-year spring and autumn R_{agp} were estimated at 1.4 ± 0.7 g C m^{-2} d^{-1} and 2.3 ± 1.0 g C m^{-2} d^{-1}, respectively (Fig. 3d). The inter-annual difference in R_{agp} was less significant than that of R_s. The R_{agp} in wet summer of 2009 was 3.2 ± 1.1 g C m^{-2} d^{-1}, 16% lower than in the dry summer of 2010, while the R_s decreased 58% in summer 2009 compared to summer 2010.

3.3. Annual totals of ecosystem respiration and components

With the data gap filled and upscaled for 2010, annual R_e was 1992 (95% CI: 1892–2093) g CO_2-C m^{-2} yr^{-1}, annual R_s was estimated at 1014 (961–1103) g CO_2-C m^{-2} yr^{-1} from automated measurements and 1077 (813–1499) g CO_2–C m^{-2} yr^{-1} from survey measurements, and R_{CWD} was 236 (182–291) g CO_2-C m^{-2} yr^{-1}, annual R_{agp} was therefore predicted at 741 (721–761) g CO_2-C m^{-2} yr^{-1} (Fig. 4a). Total CO_2 emissions of most respiratory components during the non-flooded

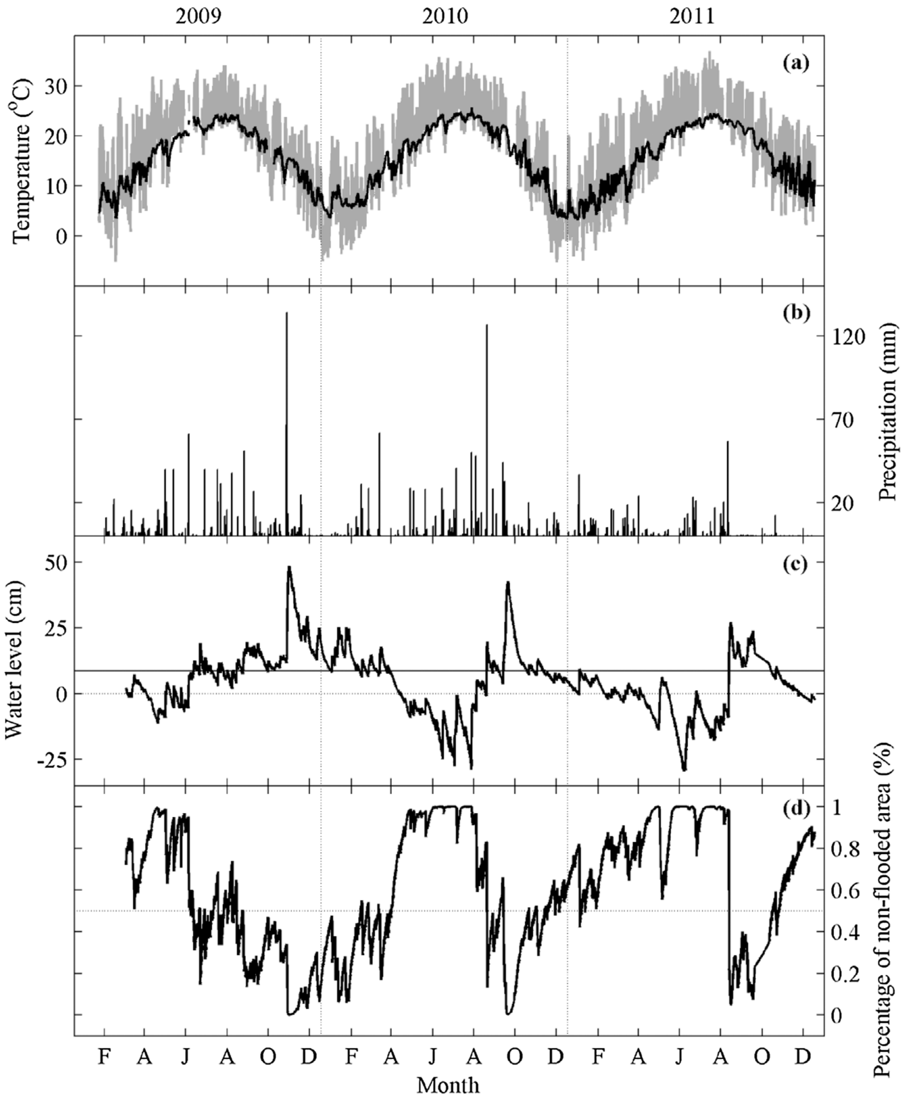

Fig. 2. Seasonal variations observed in a lower coastal plain forested wetland in North Carolina, USA, during the period 3/19/2009-12/31/2011 in (a) Air temperature (grey) and soil temperature at 5 cm depth (black), (b) Precipitation, (c) Water level (WL) with the site average elevation (solid line, WL = 8.7 cm) relative to ground water probe location at ground meteorological station (dotted line, WL = 0 cm), and (d) Percentage of non-flooded area calculated based on gamma distribution of microtopography across the study area.

period were much greater than during flooded period, except R_{agp}. The percentage of non-flooded days was 58% in the whole year of 2010, and the corresponding percentage of non-flooded CO_2 effluxes was 82% in R_e, 91% in R_s, 88% in R_{CWD}, and 66% in R_{agp}.

In the wet year of 2009 (3/19-12/31), R_e and all of the three components released less carbon into the atmosphere, with the estimates of 1376 (1303–1449) g CO_2-C m^{-2} from R_e, 586 (516–672) g CO_2-C m^{-2} from R_s, 152 (117–187) g CO_2-C m^{-2} from R_{CWD}, and 639 (636–641) g CO_2-C m^{-2} from R_{agp}. In the dry year of 2011 similar to 2010, CO_2 efflux estimates from all the components were also similar to those in 2010 although the mean R_e, R_s, and R_{CWD} were slightly higher while the R_{agp} was slightly lower in 2011.

3.4. Partitioning ecosystem respiration

Belowground respiration was estimated to contribute 51% to R_e in 2010; the R_s:R_e ratio was 0.57 for non-flooded period and 0.24 for flooded period. The monthly R_s:R_e ratio also exhibited clear seasonal variation (Fig. 4b), and averaged 0.22 ± 0.03 (mean ± SE) from January to March, increased significantly from 0.37 in April to 0.64 in May, and then stabilized in June (0.64) and July (0.60). A decrease in the R_s:R_e ratio occurred through August (0.53) and September (0.33), when the site was flooded from Hurricane Irene. During the post-hurricane period to the end of 2010, monthly R_s:R_e ratio was low at 0.30 ± 0.04 (Fig. 4b). R_s:R_e ratio was 0.43 in the 2009 wet year and 0.53 in 2011.

Coarse woody debris respiration contributed much less to R_e than R_s and the R_{CWD}:R_e ratio was estimated at 0.12 in 2010 (Fig. 4b). The pattern of monthly variation was similar to that in the R_s:R_e ratio, with the average of 0.08 ± 0.01 (mean ± SE) in early 2010 (Jan.–Mar.) and the peak value of 0.15 in May, and then stabilizing at 0.12 through summer and 0.09 through autumn. The inter-annual variation in R_{CWD}:R_e ratio was also small compared to R_s:R_e ratio, with the estimates of 0.11 in 2009 and 0.12 in 2011.

Aboveground plant respiration was estimated to contribute 37% to R_e in 2010, with the R_{agp}:R_e ratio of 0.30 for non-flooded period and 0.69 for flooded period. Opposite to R_s, R_{agp} was the major contributor during flooded periods, and therefore the pattern of monthly variation of R_{agp}:R_e ratio was also opposite to that of R_s:R_e ratio (Fig. 4b). The R_{agp}:R_e ratio decreased from the average of 0.70 ± 0.04 (mean ± SE) in early 2010 to the lowest value of 0.20 in May, and stabilized in June (0.24) and July (0.28). The ratio started increasing gradually to 0.35 in August, and then increased significantly to 0.60 ± 0.05 after the hurricane in September.

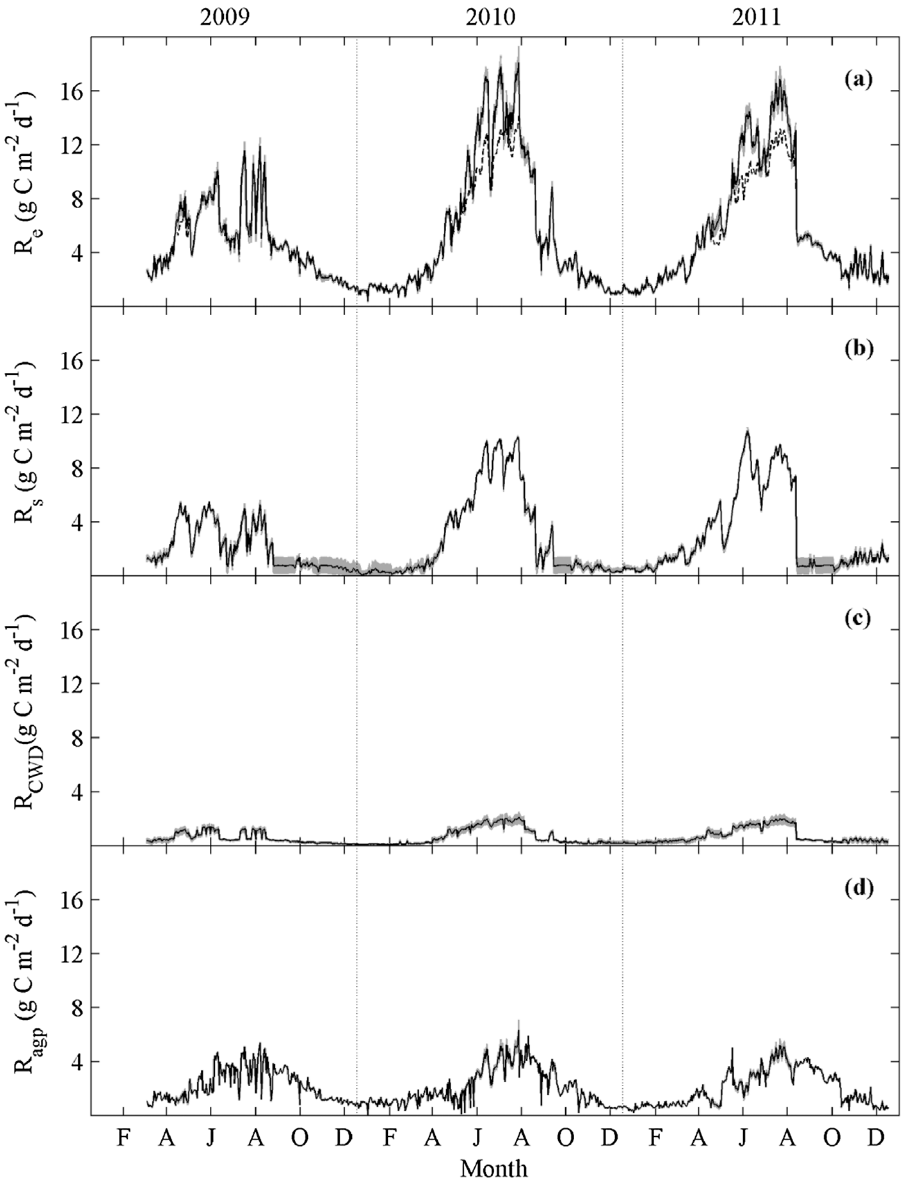

Fig. 3. Time series of daily ecosystem respiration and three respiratory components in a lower coastal plain forested wetland from 2009 to 2011 (unit: g CO_2-C m^{-2} d^{-1}). (a) Daily ecosystem respiration (R_e). The black solid line represented the data with gap filled and adjusted based on aboveground plant respiration when water level < −15 cm; and black dashed line represented the data with gap filled only by the model developed from available R_e measurements. (b) Daily belowground respiration (R_s), upscaled from long-term automated 30-min measurements at three microsites and the areal representativeness of each microsite based on the microtopography distribution. (c) Daily decomposition of coarse woody debris (CWD, R_{CWD}), upscaled from survey measurements of CWD in four decay classes. (d) Daily aboveground plant respiration (R_{agp}) estimated as the residuals of R_e, R_s and R_{CWD}. In all figures, the black solid line represents daily mean and shaded area is 95% confidence interval of daily value. See the Methods section and supplements for details.

4. Discussion

4.1. Hydrologic and microtopographic effects on seasonal variation of respiratory components

In contrast to uplands where temperature exerts the major control, hydroperiod exerted strong regulation on seasonal variation of carbon cycling in the forested wetland of the current study, consistent with other reports (Chimner and Cooper, 2003; Jimenez et al., 2012; Malone et al., 2013; Mitsch and Gosselink, 2007). However, the extent and mechanisms of the regulation might differ among different respiratory components. In the current study, we observed that both R_e and R_s exhibited a seasonal hysteresis in that the rates were higher early in the year then declined. The difference in the hysteresis pattern between R_e

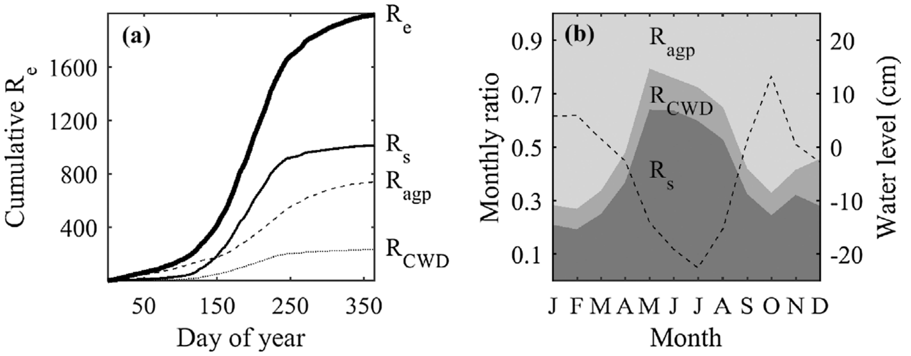

Fig. 4. Partitioning ecosystem respiration (R_e) into belowground respiration (R_s), decomposition of coarse woody debris (R_{CWD}) and aboveground plant respiration (R_{agp}) in a lower coastal plain forested wetland in 2010. (a) Cumulative daily values (g CO_2-C m^{-2} yr^{-1}); (b) Monthly ratios of component fluxes to R_e (left axis) and monthly average water level (dashed lines, right axis).

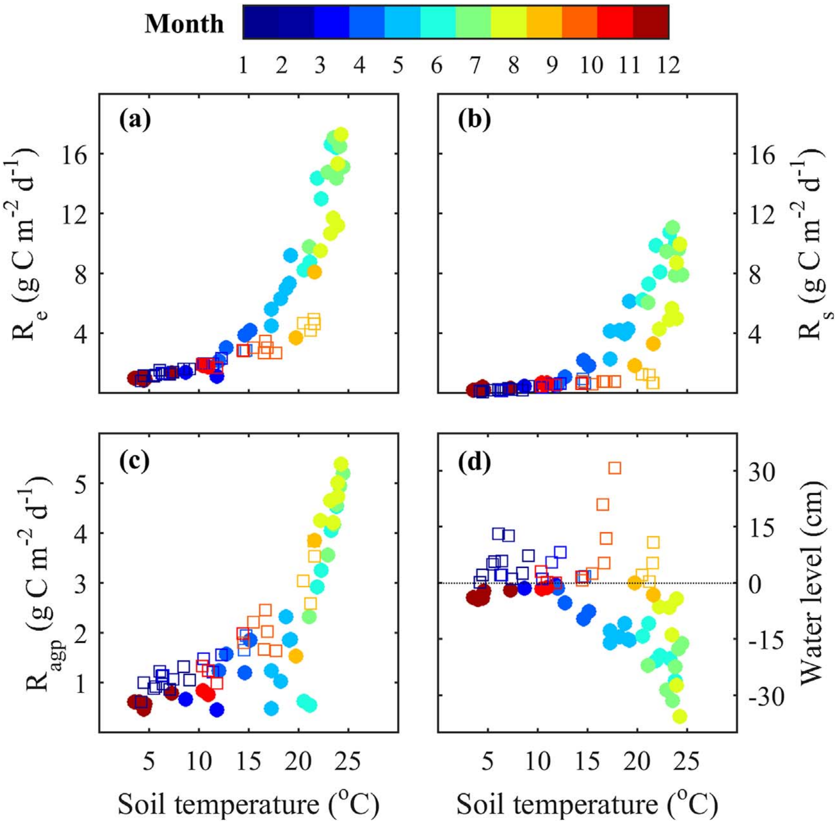

Fig. 5. The relationship between daily mean soil temperature and (a) ecosystem respiration (R_e), (b) site average belowground respiration (R_s), (c) aboveground plant respiration (R_{agp}), and (d) water level in 2010. Solid circles represent non-flooded scenarios and open squares represent flooded scenarios. Please refer to online materials for original figure in color.

and R_s was associated with R_{agp}, in which the seasonal hysteresis was insignificant (Fig. 5). All components exhibited similar patterns of seasonal hysteresis in 2009 and 2011, but the magnitude varied due to the difference in precipitation amount and slight shifts of hydroperiod between years (data not shown).

It is thought that seasonal or diel hysteresis reflects the different temperature sensitivity of an ecological process or its components at different time periods, and various explanations have been suggested from either biological or physical mechanisms (Gaumont-Guay et al., 2006; Goulden, 1998; Lee et al., 1999; Niu et al., 2011; Phillips et al., 2011; Vargas and Allen, 2008). The hysteresis pattern in R_s at this forested wetland was more likely associated with a pattern of seasonal hysteresis in which the WL was lower in spring than in autumn (Fig. 5b and d). In a previous study, we described a seasonal hysteresis of R_s at HIGH microsites but not at MID and LOW microsites, which was related to the effect of microtopography on surface soil immersion (Miao et al., 2013). In the current study, our survey of microtopography indicates there is a higher percentage of HIGH microsites in this wetland relative to MID and LOW microsites (Fig. 1b). As a result, the site average R_s exhibited a similar hysteresis to that at the HIGH microsites. Most of the area in this site was relatively dry during spring and summer and therefore R_s was higher, while heavy rains in the autumn raised the water table and submerged most of the area (Fig. 2d), decreasing the R_s. Even though the root systems of most flood-tolerant plants remain active when flooded (Angelov et al., 1996; Hook, 1984; Keeland et al., 1997; Mancuso and Shabala, 2010), standing surface water also impeded the diffusion of CO_2 from belowground resulting in low observed R_s. For example, in September 2010 when soil temperature was similar to June, R_s responded immediately to flooding and decreased to 1.8 ± 1.2 (mean ± SE) g CO_2-C m^{-2} d^{-1}, whereas the rate was 8.1 ± 1.8 g CO_2-C m^{-2} d^{-1} in June (Fig. 5b).

The weakly defined hysteresis in R_{agp} suggests that plant physiological activity was less affected by hydrologic regimes (Fig. 5c), arguably due to the adaptations of the dominant species to flooding. Although R_{agp} was indirectly calculated in this study, the high flooding tolerance of the dominant species, such as swamp tupelo, Atlantic white cedar and swamp cypress who have pneumatophores, root structures with large air-filled cells that protrude from ground and are hypothesized to facilitate gas exchange between the atmosphere and submerged roots, lends credibility to the adaptation hypothesis (Angelov et al., 1996; Hook, 1984). Gravatt and Kirby (1998) also reported that short-term (e.g. < 32 days) submersion events did not significantly decrease leaf and stem growth rates in flood-tolerant species. In our study, the difference in R_{agp} was small between early and late months in 2010, demonstrating consistent response to temperature and insignificant effect from WL (Fig. 5c). For example, there was no significant difference between June and September ($p = 0.58$) in 2010, when R_{agp} averaged 3.1 ± 0.9 (mean ± SE) g CO_2-C m^{-2} d^{-1}.

The combination of R_s and R_{agp} resulted in the pattern of seasonal hysteresis in R_e while the contribution from R_{CWD} was small. The magnitude of decrease in R_e between early and late months was primarily affected by R_s and the still-high rate of R_e after flooding was maintained by R_{agp}. Compared to R_s and R_{agp}, R_e was also significantly different between June and Septermber, with the average rate of 12.8 ± 2.8 (mean ± SE) g CO_2-C m^{-2} d^{-1} in June and 5.5 ± 1.8 g CO_2-C m^{-2} d^{-1} in September (Fig. 5a).

4.2. *Hydrologic effects on component contributions to ecosystem respiration*

We analyzed the effects of WL and temperature on the daily R_e partitioning. The R_{agp}:R_e ratio exhibited an opposite pattern to the R_s:R_e ratio in terms of the component integration method. When $-15\,\text{cm} \le WL_d < 0\,\text{cm}$ during non-flooded periods, R_s contributed increasingly to R_e as WL decreased and the volume of aerated soil increased. The ratio increased with T_s as its seasonal dynamics co-varied inversely with WL (Figs. 5d and 6a). The intercept of the linear regression ($p < 0.001$) between the R_s:R_e ratio and WL during non-flooded periods, 0.30 ± 0.01 (mean ± SE), indicated that at

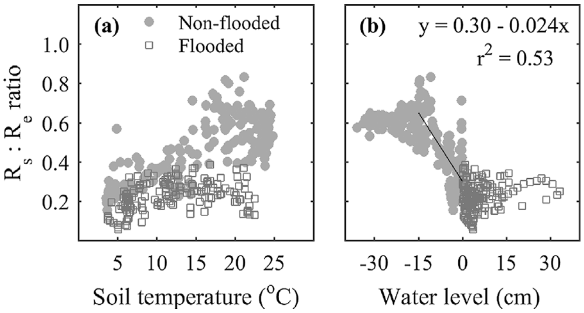

Fig. 6. Soil temperature and water level effects on the ratio between belowground respiration (R_s) and ecosystem respiration (R_e) in a lower coastal plain forested wetland. The solid line, equation and r^2 in (b) were the regression results of the relationship between R_s:R_e ratio and water level when -15 cm ≤ daily average WL $<$ 0 cm.

WL = 0 cm, 30% of R_e originated from belowground. The slope of the relationship implied that this contribution increased by 2.4% for every cm of decrease in WL, up until around WL = -15 cm, when the R_s:R_e ratio stabilized at 0.61 ± 0.05 (mean ± SE). During flooded periods, the ratio was stable at 0.23 ± 0.07 (Fig. 6b).

The positive relationship between the R_s:R_e ratio and T_s in this forested wetland contrasts with prior reports from upland forests where the relationship was found to be negative (Davidson et al., 2006; Jassal et al., 2007), indicating that the role of soil water content and WL is very different in these systems. The inverse relationship in upland forests was attributable to greater moisture sensitivity of heterotrophic than autotrophic respiration, with drought stress often accompanying higher temperatures (Davidson et al., 2006). In wetlands, however, declining WL does not mean decreasing water availability for biochemical processes, but rather an increased depth of aerated soil, and thus increased amount of available substrate and increased diffusion. Such strong hydrologic and microbial controls have been documented in northern wetlands, of which a key factor is the oxygen constraints on phenol oxidase (Freeman et al., 2004, 2001; Jaatinen et al., 2007). Higher photosynthesis during periods of low WL provided more substrate for both root growth as well as for root-associated microbial communities which could also result in the increase in R_s:R_e ratio (Ekblad and Högberg, 2001; Hartley et al., 2006).

However, the current analysis of aboveground-belowground partitioning did not separate autotrophic (R_a) from heterotrophic (R_h) respiration. During non-flooded periods, we might expect R_s to be partitioned into both root and heterotrophic components, and how the component contributions to R_s vary with WL will determine the relationship between R_h:R_e (or R_a:R_e) ratio and WL. Our previous study suggested that root respiration might increase more significantly with the WL drawdown than heterotrophic respiration (Miao et al., 2013). Thus, the variation of R_h:R_e ratio along with the WL fluctuation might be smaller than that of current R_s:R_e ratio (Fig. 6b). Delineating these possible patterns and mechanisms calls for models and data that we currently lack, but presents a new opportunity in wetland biogeochemistry research.

4.3. Comparison with other ecosystems

Forested wetlands are characterized by the two main elements of flooding and trees, and differ from upland forests and non-forested wetlands in carbon dynamics as well as the carbon budget (Arru and Fornaciari, 2010; Roehm, 2005). Transition between flooded and non-flooded conditions resulted in unique patterns of ecosystem respiration partitioning. Belowground respiration was the main contributor to R_e during non-flooded periods and the R_s:R_e ratio of 0.57 was similar to that reported for boreal and temperate upland forests (Janssens et al., 2001; Lavigne et al., 1997; Law et al., 1999). In contrast, aboveground plant respiration was the main contributor to R_e during flooded periods due to the flooding-tolerance of trees, and the low R_s:R_e ratio of 0.23 was close to the ratio of some tropical rainforests (Chambers et al., 2004; Saleska et al., 2003).

By adjusting respiration models to account for flooded and non-flooded conditions as influenced by variation in microtopography and WL, we estimated the annual ecosystem respiration (R_e) of nearly 2000 g C m^{-2} yr^{-1} in the relatively dry year of 2010. This amount of respired CO_2 was higher than many upland forests in the same climate zone (Luyssaert et al., 2007; Valentini et al., 2000), and speaks to the importance of quantifying the stronger than expected carbon source strength of such forested wetlands under drier future climate. The annual or periodic R_e in this forested wetland was much higher than the values reported for many herbaceous wetlands and wetlands with sparse trees irrespective of geographic locations (Barr et al., 2010; Chimner and Cooper, 2003; Chivers et al., 2009; Jimenez et al., 2012; Lafleur et al., 2001). In contrast, some studies have suggested that forested wetlands might not exhibit higher respiration than open wetlands due to the interaction between species composition, structural differences and environmental drivers (Jeglum and He, 1995; Strilesky and Humphreys, 2012). The annual R_e at our study site was much lower than that of a tropical peat swamp forest (3800–3900 g C m^{-2} yr^{-1}) (Hirano et al., 2007), while soil respiration (R_s) was similar between the two swamp forests (about 1000 g C m^{-2} yr^{-1}) (Jauhiainen et al., 2005). These differences were likely associated with the differences in the length of growing seasons and plant physiological activity.

4.4. Uncertainties in R_e partitioning

Even though all three study years were drier than the 30-year normal (Fig. S4), year 2009 had slightly higher mean WL and longer hydroperiod than the two subsequent years, and 2011 was slightly warmer than the two preceding ones. The T_s data had good coverage for both flooded and non-flooded periods, giving confidence in the representativeness of the gapfilling models developed (Fig. S3).

On the other hand, the presence of periods with R_e lower than the sum of components raises questions about the consistency of the dataset, and the robustness of the conclusions. Such lack of respiration budget closure has been reported repeatedly in the literature (Griffis et al., 2004; Hermle et al., 2010; Khomik et al., 2010; Lavigne et al., 1997; Schrier-Uijl et al., 2010), and the bias is always similar – turbulent fluxes tend to fall short of chamber fluxes, and the problem appears more prominent during warm season. Even though uncertainties in individual component measurements have been broadly discussed, such as nighttime weak turbulence and data gap filling in eddy covariance data (Aubinet, 2008; Goulden et al., 1996; Hollinger and Richardson, 2005; Moncrieff et al., 1996; Papale et al., 2006) and gap filling and upscaling of chamber flux measurements (Gomez-Casanovas et al., 2013), the reasons for the respiration budget closure at ecosystem scale have not been conclusively identified.

In the current study, we attribute the lack of respiration budget closure to different data coverage between R_e and R_s. With very low acceptance rate of nighttime eddy covariance data during low WL and high temperature periods, R_e was largely modeled. When pairing the modeled R_e values, which approximate the mean of available observations that did not capture the extremes, with the nearly continuous measured R_s values, it is plausible and even likely that there will be periods when R_s or $R_s + R_{CWD} > R_e$. When constraining R_e through R_{agp} and mass balance approach, R_e increased by about 20% when WL < -15 cm and total annual R_e increased about 10% compared to the gapfilled R_e based on turbulent flux measurements alone (dashed lines in Fig. 3a). This 10% underestimation of nighttime EC flux was lower than the 20–40% reported in other systems (Griffis et al., 2004; Lavigne et al., 1997; Schrier-Uijl et al., 2010).

Additionally and importantly, the poor coverage of nighttime NEE at the low WL and high temperature end did not significantly affect the estimate of R_e under other environmental conditions due to the data gap uncertainty. The difference in the predicted R_e when -15 cm $<$ WL $<$ 0 cm between original model and the new model derived from the complete R_e data set including the corrected R_e was less than 5%, with the new model predicting about 32 g C m^{-2} higher than the original one for 2010 (695 ± 7 vs 663 ± 5 g CO_2 m^{-2} d^{-1}, mean ± SE). This uncertainty is small, meaning flux budget during cooler periods is little affected, consistent with Richardson and Hollinger's (2007) conclusion that data during cool periods play a limited role in both the magnitude and the uncertainty of the annual flux budget.

Extrapolating from -15 cm ≤ WL $<$ 0 cm to WL $<$ –15 cm may be reasonable within the WL range observed during the current study period from the context of wetlands (Silvola et al., 1996; Sulman et al., 2009), but it is uncertain if this might lead to unrealistic R_{agp} estimates if WL decreased another 10–15 cm. This study shows the dynamic nature of respiration fluxes and partitioning during fluctuating WL, and the importance of accounting for the contribution from flooded and non-flooded areas. Therefore, characterizing microtopography and defining hydrologic regimes at the ecosystem scale are essential in upscaling fluxes in these systems (Alm et al., 1997; Dimitrov et al., 2010; Waddington and Roulet, 1996). While we improved the upscaling method by quantifying the microtopographic distribution, a linear relationship between the microtopography, R_s and R_{CWD} was over-simplified, and the relationship might also vary with the water table fluctuation. Currently, it is difficult to evaluate if we over- or underestimated the site-average R_s and R_{CWD}, and further studies are necessary to test the relationship.

4.5. Implications

Ecosystem respiration and all of its components were lower in the wet year of 2009 than in the dry years of 2010 and 2011 (Fig. 3). Given the increase in R_s:R_e ratio with the decreasing water level (Fig. 6), it is likely that the site acted as a greater carbon source than it has been in the past. This also suggests the sensitivity of respiratory emissions to any long-term changes in site hydrology, potentially leading to positive climate feedbacks (Jungkunst and Fiedler, 2007). If wetland conversion and drought-severity continue to increase over the next century, it will have serious implications for carbon storage in wetland ecosystems and the ecosystem service of carbon sink (King et al., 2013; Pendleton et al., 2012; Sun et al., 2013).

While we only demonstrated the CO_2-related respiration in this current study, it should be noted that methane (CH_4), another important greenhouse gas from wetlands is not estimated. The same hydrologic controls that we have shown to modulate CO_2 efflux are expected to have the inverse effect on CH_4 production, i.e. the flooded conditions might have a relatively high CH_4 release and the trend of water level decreasing might come with a trend of decreasing CH_4 release (Harriss et al., 1982). Thus, the combined effect of hydrologic change on wetland greenhouse gas balance remains to be elucidated.

The role of wetlands has drawn more attention recently in global carbon cycle and climate regulation (Davidson, 2010; McLeod et al., 2011; Murray and Vegh, 2012). Improving the modeling of carbon dynamics in wetlands is therefore important and necessary in the context of climate change. Our study demonstrates the importance of hydrologic and microtopographic variabilities in respiration fluxes of wetlands. Our dataset also provides a unique validation opportunity for the new wetland module being developed for the next generation Land Surface and Earth System Models (Lawrence and Fisher, 2013; Lawrence et al., 2011). More importantly, we argue that modules designed for upland forests cannot be modified for forested wetlands because of fundamental differences in their functional regulation, and their use may propagate systematic biases in global carbon budget estimates.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.08.022.

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