Component-specific dynamics of riverine mangrove CO₂ efflux in the Florida coastal
Everglades

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Abstract

Carbon cycling in mangrove forests represents a significant portion of the coastal wetland carbon (C) budget across the latitudes of the tropics and subtropics. Previous research suggests fluctuations in tidal inundation, temperature and salinity can influence forest metabolism and C cycling. Carbon dioxide (CO₂) from respiration that occurs from below the canopy is contributed from different components. In this study, we investigated variation in CO₂ flux among different below-canopy components (soil, leaf litter, coarse woody debris, soil including pneumatophores, prop roots, and surface water) in a riverine mangrove forest of Shark River Slough estuary, Everglades National Park (Florida, USA). The range in CO₂ flux from different components exceeded that measured among sites along the oligohaline-saline coastal gradient. Black mangrove (*Avicennia germinans*) pneumatophores contributed the largest average flux. Over a narrow range of estuarine salinity (25-35 practical salinity units (PSU)), increased salinity resulted in lower CO₂ flux to the atmosphere. Tidal inundation reduced soil CO₂ flux overall but increased the partial pressure of CO₂ ($p\text{CO}_2$) observed in the overlying surface water upon flooding. Higher $p\text{CO}_2$ in surface water is then subject to tidally-drive export, largely as HCO₃⁻. Integration and scaling of CO₂ flux rates to forest scale allowed for improved understanding of the relative contribution of different below-canopy components to mangrove forest ecosystem respiration (ER). Summing component CO₂ fluxes suggests a more significant contribution of below-canopy respiration to ER than previously considered. An understanding of below-canopy CO₂ component fluxes and their contributions to ER can help to elucidate how C cycling will change with discrete disturbance events (e.g., hurricanes) and long-term change, including sea-level rise, and potential impact upon the mangrove forest wetlands. As such, key controls on below-canopy ER must be taken into consideration when developing and modelling mangrove forest C budgets.

Introduction

Mangrove forests cover 0.1% of the continental surface but represent an important coastal ecosystem carbon (C) pool as a result of large biomass and soil C stocks (Twilley et al., 1992, Boullion et al., 2008). For example, in a Micronesian forest, the ecosystem C stock is 400-1400 Mg C ha⁻¹, largely held within biomass and soil (Donato et al., 2011). Net annual soil C sequestration and tidal export of C are key sources of uncertainty in coastal wetland C budgets (Bauer et al., 2013), yet recently published data syntheses are beginning to reduce these uncertainties (Breithaupt et al., 2012). Carbon dioxide (CO₂) flux can occur from different components below the forest canopy including soil, fine roots, aboveground root structures (i.e., pneumatophores, prop roots), coarse woody debris (CWD), and when inundated, to porewater or surface water, and contribute to mangrove ecosystem respiration (ER). Variability associated with these fluxes is reported to be a function of both physical and biological factors including temperature, duration and frequency of inundation, salinity, alkalinity, nutrient availability, root production, presence of pneumatophores, benthic microalgae, and invertebrates (Cai and Wang, 1998, Kitaya et al., 2002, Hope et al., 2004, Boullion et al., 2007, Jomura et al., 2008, Kristensen et al., 2008 Lovelock 2008, Sasaki et al., 2009). For instance, microbial and autotrophic respiration may be limited by tidal flooding and saturation of the soil surface, whereas roots may serve as a conduit for transport of both microbial- and autotrophic-derived CO₂, in addition to microbial respiration that occurs on the decomposing wood surface. However, few datasets are available for understanding CO₂ fluxes with respect to variability induced by physical and biological factors in riverine mangrove forests.

Chamber-based CO₂ flux is a frequently used technique for determining whole-ecosystem gross primary production (GPP) and ER at the plot-scale, especially in low-stature

vegetation communities (Olivas et al., 2010). In forest ecosystems, the chamber-based CO₂ flux method has been mostly used to determine CO₂ flux from the soil-atmosphere interface, whereas the eddy-flux technique is used to determine GPP and ER at the forest scale. Independently, chamber and eddy covariance techniques have limitations depending on the component and scale of interest (Thomas et al., 2008); however, coupled methods can allow for partitioning of ecosystem GPP and ER (Lavigne et al., 1997).

Our study was designed to estimate CO₂ flux rates (below-canopy respiration) as a function of both inter- and intra-site variability in a riverine mangrove system. We also sought to elucidate factors controlling below-canopy respiration fluxes that contribute to ER as a component of mangrove forest C cycling. We conducted chamber-based CO₂ flux measurements of different below-canopy components (soil, leaf litter, CWD, soil, including pneumatophores, prop roots, and surface water) over two years to quantify below-canopy CO₂ component fluxes and partition the contribution of these component fluxes to mangrove forest ER.

Key questions we sought to address were: (1) How do soil respiration rates vary along the oligohaline-saline margin? (2) What are the key components of below-canopy CO₂ flux in the near coast site? (3) How do respiration rates change seasonally and with changes in environmental controls, such as inundation, water and soil temperature? (4) How does *p*CO₂ vary with tidal influence in surface water and what proportion of dissolved CO₂ contributes to surface water dissolved inorganic C (DIC)? We hypothesized that: (1) soils exposed during low tide contribute to higher soil CO₂ flux than when soils were flooded with tidal water, (2) CWD contributes to the highest overall component CO₂ flux, and (3) surface water *p*CO₂ increases significantly when soils are inundated.

Methods

Site Description

The Shark River Slough (SRS) estuary discharges in the Gulf of Mexico and is located on the southwest coastal margin of the Florida Everglades within Everglades National Park (Figure 1). The extensive riverine mangrove forests are generally dominated by red (*Rhizophora mangle*), black (*Avicennia germinans*) or white (*Laguncularia racemosa*) mangroves (Chen and Twilley 1999). The climate of south Florida is subtropical moist (long-term annual precipitation = 155 cm yr⁻¹; average air temperature = 24° C) with distinctive wet (Jun-Oct) and dry (Nov-May) seasons (Duever et al., 1994). Mangrove peat soils range from 1.5 m to 5 m in depth and are supported by a limestone platform (Wanless et al., 1994). The hydrology of the mangrove forests is driven by seasonal freshwater inputs (rainfall and overland flow) and mixed semidiurnal tides with a salinity range of 10-40 PSU. Tropical storms, winter storm fronts and freezes are key drivers of mangrove community structure and long-term ecosystem dynamics (Davis et al., 2004, Castañeda-Moya et al., 2010).

Our study sites coincide with Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) program (Figure 1). LTER sites SRS-4, SRS-5 and SRS-6 were established along a transect from the more freshwater influenced, upstream site, SRS-4, to the more saline, downstream site, SRS-6. The three sites vary most notably in vegetation structure, frequency of inundation, salinity, soil total (T) P and soil organic matter content; soil organic matter concentrations are inversely related to soil TP concentrations, and increase inland along the SRS salinity gradient (Chen and Twilley 1999, Castañeda-Moya et al., 2013). Higher soil TP correlates with higher Ca-bound P in the lower estuary, illustrating the greater significance of mineral soil processes (Chen and Twilley 1999) where storm-derived mineral inputs can occur (Castañeda-Moya et al., 2010). SRS-6 has been reported with greatest frequency of inundation (# tides yr⁻¹), flooding duration (h yr⁻¹) and tidal range (Castañeda-Moya et al., 2013). It is representative of tall (>15 m height) forests adjacent to

the coast and Gulf of Mexico. SRS-5 is characterized by vegetation dominated by red mangrove with few black mangrove (and pneumatophores), and reported with moderate salinity, lowest frequency of inundation and moderate flood duration (Castañeda-Moya et al., 2013). SRS-4 experiences the lowest flooding duration and salinity, has the lowest TP content by volume and the highest tree density (<2.5 cm DBH; Chen and Twilley 1999, Castañeda-Moya et al., 2013).

Tidal inundation and temperature variability

Salinity and water level data were obtained from a nearby United States Geological Survey (USGS) instantaneous recording gage (SH3) located in the riverine mangrove forest, 20 m from Shark River, and ~120 m NW of the FCE LTER site, SRS-6. Water quality data (temperature, salinity, and water level) coinciding with CO₂ flux measurements were obtained for both groundwater and surface water (gage SH3 has both a surface well [peat above limestone platform] and a groundwater well bored into the limestone bedrock to a depth of 7.3 m below the ground surface). The groundwater well water levels were measured with a pressure transducer and the surface water well water levels with a shaft-encoder float/pulley (Anderson et al., 2014). We measured soil temperature in two sites within the SRS-6 study area (January –August 2011) using Onset Hobo (Bourne, MA, USA) outdoor temperature sensors deployed just below the soil surface (~2 cm).

Carbon dioxide below-canopy efflux

We conducted extensive measurements of soil CO₂ flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at sites SRS-4, SRS-5 and SRS-6 of the Shark River Slough transect of the FCE LTER study area (Figure 1). Site SRS-6 was the focus of our most intensive research. Soil CO₂ flux rates were determined with a LI-COR 8100 soil respiration system (LI-COR Biosciences, Lincoln, NE,

USA) using polyvinyl chloride (PVC) collars 20 cm in diameter, inserted 2 cm into the soil. Soil collars were installed at least 1 month prior to the first set of measurements in 2008. Intact leaves not adhered to the soil surface were removed from inside the collars prior to measurements. Soil flux measurements were typically conducted at low tide. Depending on the semidiurnal tidal cycle and time of season (dry or wet), soils were exposed (no standing water on soil surface), partly exposed (partial exposure of the soil surface) or inundated (soils completely covered by surface water). In 2010, extent of standing water and pneumatophore density were recorded to account for intra-site variability in soil CO₂ flux at SRS-6.

In 2011, we explicitly evaluated soil respiration fluxes as a function of black mangrove pneumatophore presence at SRS-6 by augmenting our experimental design. We installed soil collar pairs so that a pneumatophore-free soil collar had a paired collar with pneumatophores present (N=16). In 2010 and 2011, measurements at SRS-6 were conducted every 1-2 months at SRS-6. Extent of standing water and pneumatophore density in each collar were recorded. The CO₂ flux from CWD was determined following the general approach of Barker (2008). Briefly, for large CWD (>20 cm diam.), collars (20 cm diam.) were cut to size and a combination of Styrofoam and silicone adhesive were used to affix the collar into a gas-tight seal on the surface of the wood. CO₂ flux from small CWD (<20 cm diam.) and red mangrove (*Rhizophora mangle*) prop roots were determined using a 10 cm PVC collar affixed to a PVC “saddle T” (Figure 2). A gas-tight seal was created with gasket (silicone) foam and elastic nylon cords. Water-air CO₂ flux measurements were conducted by supporting the soil collar on a Styrofoam float directly over the surface of the water column, secured in place with PVC pipes to allow the height of the float to increase or decrease with change in water level. In a laboratory test, we evaluated the variation in CO₂ flux with wet leaf mass of *Rhizophora* (N=14). We measured CO₂ flux from wet leaf litter and converted wet weight to dry air weight.

Aqueous CO₂

In 2011, we also began measurements of *in-situ* dissolved aqueous *p*CO₂. We determined concentrations of dissolved CO₂ using a non-dispersive, infrared (NDIR) sensor (Vaisala Oyj; Vanta, Finland) sealed in a water-tight, gas-permeable membrane installed 2 cm above the soil surface to be inundated by the surface water column upon tidal flooding (Tang et al., 2003 and Johnson et al., 2009). We corrected sensor output for temperature and pressure using Onset Hobo water level data loggers deployed in parallel with the NDIR sensor. The NDIR sensor measurement error is 1.5% of the calibration range and 2% of the reading. We converted *p*CO₂ (parts per million, ppm) to concentration of dissolved CO₂ (mg L⁻¹) following calculations determined by Weiss (1974) for CO₂ solubility as a function of temperature, pressure and salinity applying Henry's Law. Salinity, temperature, water level and atmospheric pressure data were measured and recorded using Hobo loggers. For estimation of dissolved inorganic carbon (DIC) in surface water, pH, total alkalinity, salinity, and temperature were determined on discrete water samples collected from Shark Slough at SRS-6 in May, August and November of 2011. Filtered water samples were used for total alkalinity analysis so as to remove any particulate matter, such as calcium carbonate. For total alkalinity measurements, a Brinkman Titrino 751 (Metrohm USA, Riverview, FL, USA) was used to titrate 40 mL water samples with 0.1 M hydrochloric acid to a pH of 2. The total alkalinity was calculated based on the mL of acid added at the inflection point of the titration curve closest to a pH of 4 and reported as mg L⁻¹ HCO₃⁻. Change in volume of the sample due to the addition of the titrant was not taken into account, as it was only a small portion of the total volume (<10%). The dissolved inorganic carbon (DIC) of the water samples was estimated as:

$$\text{DIC} = \text{H}_2\text{CO}_3^0 + \text{HCO}_3^- + \text{CO}_3^{2-} \quad \text{Eq. 1}$$

The $p\text{CO}_2$ of those water samples was estimated from the total alkalinity, pH, temperature and salinity of the water samples using CO2Sys v2.1 and equilibrium constants from Millero (2010). The percent fraction of dissolved CO_2 as DIC was estimated from the average computed values of DIC in surface water.

Statistical analyses

We assessed the average difference in soil CO_2 flux rates among sites along the low-to-high salinity margin of SRS-4, SRS-5 and SRS-6. For SRS-6, we determined the variation in soil CO_2 flux with level of tidal inundation (exposed, partly exposed and inundated) using one-way ANOVA. We tested the difference in mean rates of CO_2 flux among below-canopy components of surface water, CWD, soil, prop roots, and as a function of pneumatophore presence using one-way ANOVA. We determined the controls on soil CO_2 flux using measurements when soils were exposed and no documented presence of pneumatophores at SRS-6 using stepwise regression modelling (Matlab, Mathworks, Inc., Natick, MA, USA). Candidates included the abiotic variables of water level, salinity, and water temperature data from both surface water and in a groundwater well (USGS site SH3). Predictor variables were retained in the final linear regression model for coefficients exceeding the 95% significance level ($p \leq 0.05$). Linear regression was used to develop relationships for significant factors with JMP (SAS, Cary, NC, USA).

Integration and scaling

At SRS-6, we scaled below-canopy CO_2 flux to partition ER into component fluxes and relative contribution of these fluxes to eddy-covariance based estimates of ER (Barr et al., 2010). We also generated a component-based estimate of ER based on the sum of measured components. Scaled CO_2 flux rates ($\text{kg C ha}^{-1} \text{ period}^{-1}$) were determined by

230 multiplying the fraction of surface area exposed to the atmosphere by flux rate for each
 231 component during three surface soil flooding states: when soils were exposed, partly exposed
 232 and inundated. Extent of inundation was determined from gage SH3 water level data and
 233 used to approximate the fraction of surface area of each component that was exposed to the
 234 atmosphere for each soil flooding state. Total surface area was determined from the sum of
 235 the area of all surfaces. The fraction of surface area of soil plus leaf litter was determined by
 236 the difference of the sum of coarse woody debris (CWD) and prop root surface area in a 1 ha
 237 area. The surface area of CWD was determined from wood volume (Krauss et al., 2005),
 238 average tree height (13 m) and diameter (10 cm). *Rhizophora* prop root surface area was
 239 determined from the relationship between average DBH (Castañeda-Moya et al., 2013), prop
 240 root biomass (Smith and Whelan, 2006), average wood density, prop root diameter of 8 cm
 241 and average prop root height of 0.5 m for *Rhizophora* (Global Wood Density database). Other
 242 methods for quantifying prop root biomass for the DBH range we estimated yielded similar
 243 values, and estimate of uncertainty at less than 2% (Feliciano et al., 2014). *Avicennia*
 244 pneumatophore surface area was derived from an estimate of pneumatophore density per tree
 245 (Dahdouh-Guebas et al., 2007) and *Avicenna* tree density (Castañeda-Moya et al., 2013). This
 246 estimate of pneumatophore density was within the range of that based on approximate soil
 247 oxidation-reduction potential (redox) at SRS-6 (Castañeda-Moya et al., 2013) using a
 248 relationship between soil redox and pneumatophore density developed by Thibodeau and
 249 Nickerson (1986). Leaf litter respiration was determined from an exponential relationship
 250 between leaf mass and CO₂ flux in a laboratory test ($r^2=0.92$, $y = -0.024x^2 + 0.531x - 0.231$,
 251 $F=63.8$, $p<0.0001$, $n=14$). Leaf litter respiration was scaled to ha yr⁻¹ using leaf litterfall g C
 252 m⁻² d⁻¹ (Castañeda-Moya et al., 2013). The leaf litter component accounted for floating leaves
 253 on the water surface and was added to soil respiration rates to estimate *in-situ* soil plus leaf
 254 litter CO₂ flux. Surface area of soil plus leaf litter was 100% when soils were exposed. As

such, we developed annual estimates for CO₂ (tonnes CO₂-C ha⁻¹ yr⁻¹) flux from six components: surface water, leaf litter, soil plus leaf litter, prop roots, CWD, and soil plus pneumatophores. We binned these components into heterotrophic only (surface water, leaf litter, CWD), autotrophic only (prop roots) and heterotrophic plus autotrophic (soil plus leaf litter, soil plus pneumatophores; sum of components that could not be discretely binned) compartments of below-canopy CO₂ flux. Based on these binned components, we generated two estimates of the contribution of below-canopy components to ER where ER was determined from: (1) the sum of below-canopy respiration components, including dark leaf respiration derived from Barr et al. (2010) and (J. Barr, unpublished data), and (2) eddy-covariance (Barr et al., 2010), with the proportion of dark leaf respiration determined from the difference in ER and sum of below-canopy components measured in this study.

Results

Inter-site variability in soil CO₂ flux

Of the three sites, SRS-4 had the highest soil CO₂ flux rates; the difference between SRS-5 and SRS-6 was not significant (Figure 3).

Hydrologic and temperature variability at SRS-6

Average maximum Shark River stage ranged from 0.9 m during the dry season months (December to May) to 1.01 m during the wet season months (June to November) with an average annual tidal amplitude of 1.89 m (National Park Service gage, Shark River), from years 1996-2012 (data provided by Everglades National Park). Variation in surface water inundation resulted from mixed semidiurnal tidal flooding, spring and neap tidal cycles and seasonal freshwater discharge. At SRS-6, soils were inundated, partially exposed and exposed

for 81, 187, 97 days, respectively, in 2010. There was greater frequency of inundation in summer months than winter months, with surface inundation most predominant during the summer of 2010 (June-October). The greater extent of drawdown in periods between January and March 2011 coincided with a significant drought (Boucek and Rehage, 2014), as compared with 2010 during the same period.

Surface water temperature collected for the same period showed an increase of 15 °C between January and June 2010. The following year, there was a similar pattern between winter and summer surface water temperatures, with diurnal variation evident. Soil temperature, collected with sensors deployed at 2 cm soil depth, showed more dramatic decreases in overnight temperature as well as seasonal temperature. In January and February 2011, soil temperature dipped to nearly 10 °C, increasing to nearly 25 °C within days to weeks. By April 2011, the lowest soil temperature consistently exceeded 20 °C, and reached highs around 30 °C by the end of April. Soil temperatures ranged between 25 °C and 30 °C through the summer of 2011. Comparing surface water and soil temperature for the period February – May 2011 illustrates these warmer and more variable soil conditions relative to the surface water.

Intra-site variability in below-canopy CO₂ flux at SRS-6

Average CO₂ flux rates were variable among below-canopy components within SRS-6. Intra-site variability was characterized by differences between surface water, soil, prop root, CWD, and pneumatophores CO₂ fluxes (Figure 4). For measurements conducted in 2010, CWD exhibited the highest average CO₂ flux as compared with soil and surface water. Average soil respiration, which included inundated, partially exposed, and exposed soils, was similar to CO₂ flux from surface water (Figure 4). However, partitioning variability in soil CO₂ flux by inundation, exposed sites had higher CO₂ flux ($1.85 \pm 0.10 \mu\text{mol m}^{-2} \text{s}^{-1}$) than

those that were partially exposed ($1.27 \pm 0.19 \mu\text{mol m}^{-2} \text{s}^{-1}$) or fully inundated ($1.29 \pm 0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$; $F=5.56$, $p=0.0057$). Soil respiration fluxes were consistently nearly twice as high from collars with pneumatophores present ($3.18 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$) as compared with soil collars without pneumatophores ($1.26 \pm 0.06 \mu\text{mol m}^{-2} \text{s}^{-1}$; $F=240.4$, $p<0.001$, $n=104$; Figure 4). When all components were considered together, CO_2 flux from soil with pneumatophores present was highest on average (Figure 4).

Stepwise regression modeling of all abiotic parameters determined that surface water salinity (a proxy for soil pore water) and groundwater level were the significant ($p<0.001$) independent drivers of CO_2 flux when soils were exposed. In negative, linear relationships, soil salinity and groundwater level accounted for 0.93 and 0.70 of the variance in soil CO_2 flux, respectively (soil salinity: $y=-0.092x+4.219$; groundwater stage: $y=-2.738x+0.941$; Figure 5). The decline in soil CO_2 flux occurred within the range of 26 to 37 PSU.

Aqueous CO_2

Surface water column concentrations of dissolved CO_2 ($\text{CO}_2\text{-C}$) were determined for two distinct, one-week periods of June 1-6, 2011 and August 4-9, 2011 (Figure 6). These short-term datasets indicate $\text{CO}_2\text{-C}$ concentrations were generally lower in June than August, but similarly increased nearly 5 - 10 times from baseline concentrations as the creek tide flooding inundated the soil surface. Average $p\text{CO}_2$ for these periods was 55 ± 2 and 194 ± 3 Pa, respectively. The range for June values was $0.38 - 3.19 \text{ mg CO}_2\text{-C L}^{-1}$, averaging $0.60 \pm 0.02 \text{ CO}_2\text{-C mg L}^{-1}$. The range of concentrations measured in August was $1.45 - 5.40 \text{ mg CO}_2\text{-C L}^{-1}$, averaging $2.14 \pm 0.04 \text{ CO}_2\text{-C mg L}^{-1}$. Average ($\pm$ standard error) surface water temperature, salinity, pH and alkalinity used to determine DIC concentration were 27.9 ± 3.6 °C, 23.0 ± 4.3 PSU, 7.72 ± 0.18 and $264.1 \pm 34.6 \text{ mg HCO}_3 \text{ L}^{-1}$. Averaged from three

measurement periods, the DIC concentration was $165 \pm 80.9 \text{ mg L}^{-1}$. Thus, the fraction of dissolved aqueous CO_2 was approximately 1.5%.

Integration among components

Given the strong relationship between tidal inundation and ER for this mangrove forest (Barr et al., 2010), we used the extent of tidal inundation to scale the contribution of measured below-canopy fluxes over the annual cycle. We developed estimates for inundated ($>0.12 \text{ m}$ above the soil surface), partially exposed ($0.03\text{-}0.12 \text{ m}$ above the soil surface), and exposed ($<0.03 \text{ m}$ above the soil surface) soil conditions. These water levels were relative to a soil surface level that corresponded to on-site conditions where soils were inundated, partially exposed, and exposed (soil surface $\sim 0.10\text{-}0.12\text{m}$). The extent of inundation determined the surface area of the various below-canopy components exposed to the atmosphere and, in the case of soil plus leaf litter flux, the rate of CO_2 flux applied. Overall, total below-canopy CO_2 flux was similar between periods of partially exposed soils and periods when soils were exposed ($294.0 \text{ g CO}_2\text{-C m}^{-2}$ and $304.4 \text{ g CO}_2\text{-C m}^{-2}$, respectively). Given the significant difference in component flux rates, this similarity in scaled annual rates was largely due to the greater duration of partially exposed soils (186 d; exposed: 97 d) in 2010. When soils were exposed, total below-canopy CO_2 flux was about 50% lower ($117 \text{ g CO}_2\text{-C m}^{-2}$). Soil plus leaf litter CO_2 flux had the greatest contribution among components during periods when soils were exposed ($152.8 \text{ g CO}_2\text{-C m}^{-2}$). Despite the largest CO_2 flux from soil plus pneumatophores, low pneumatophore density (e, *Avicennia* tree density ha^{-1}) contributed to a lower annual flux as compared with other components on a ha^{-1} scale ($70.5 \text{ g CO}_2\text{-C m}^{-2}$). We observed the contribution of CO_2 flux from surface water overlying the forest peat soil increased from $0 \text{ g CO}_2\text{-C m}^{-2}$ when the forest peat was exposed (i.e., no

surface water present) to $112.6 \text{ g CO}_2\text{-C m}^{-2}$ when soils were partly exposed and declined to $62.8 \text{ g CO}_2\text{-C m}^{-2}$ when soils were fully inundated.

We scaled these fluxes to $\text{CO}_2\text{-C tonnes ha}^{-1} \text{ yr}^{-1}$ and compared these values with measured leaf area index (J. Barr, unpublished data) and ER (Barr et al., 2010) to derive the contribution of below-canopy heterotrophic, autotrophic, heterotrophic plus autotrophic components and dark leaf respiration to mangrove forest ecosystem respiration. The sum of heterotrophic respiration over the three inundation periods (inundated, partially exposed and exposed) was $351.5 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$. The sum of autotrophic components was $140.6 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$. CO_2 flux of components that could not be discretely separated into heterotrophic and autotrophic respiration was $223.3 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$. Average dark leaf respiration at the site was $1.62 \pm 1.38 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Barr et al., 2010). Leaf area index ($\text{m}^2 \text{ m}^{-2}$) averaged 2.80 ± 1.38 (J. Barr, unpublished data). Thus, dark leaf respiration was approximately $859 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$. The contributions of these components (below-canopy and dark leaf respiration) were derived from two different estimates of total ecosystem respiration: (1) ecosystem respiration from eddy covariance (Barr et al., 2010), and (2) the sum of all measured respiration components, including dark respiration as reported by Barr et al. (2010). We found that the sum of respiration components, including dark leaf respiration from an estimate derived from Barr et al. (2010) and J. Barr (unpublished data) exceeded that determined by eddy covariance in 2004-2005 (Table 1). Below-canopy components measured in this study contributed between 45- 65% of total ecosystem respiration, depending on the estimation method for ER, i.e., sum of all components and eddy covariance with dark leaf respiration determined by difference, respectively (Table 1), suggesting below-canopy CO_2 flux contributes a greater fraction to forest ER than dark leaf respiration, regardless of estimation method used.

Discussion

Accumulation of soil C as peat and variability in C export associated with tidal inundation are large and highly variable components of the C budget in riverine mangrove forests (Barr et al., 2010; Adame and Lovelock, 2011; Troxler et al., 2013). Inorganic C export through CO₂ flux to the atmosphere and aqueous CO₂ loss from soil, water and pneumatophores have not been well studied. Soil CO₂ flux to the atmosphere has been shown to be comparable to terrestrial forests (Lovelock, 2008) while aqueous CO₂ export has been demonstrated to be a more significant mechanism of CO₂ loss in some mangrove forests (Maher et al., 2013). Our study documents the significant variation in direct CO₂ loss to the atmosphere associated with below-canopy soil and biogenic structures (i.e., coarse woody debris (CWD), prop roots, and pneumatophores) and low flux from surface water. Collectively, these fluxes comprised a significant component of the ER and suggest a larger role of below-canopy components in mangrove forest ecosystem respiration (ER) than previously recognized.

CO₂ flux along the coastal margin

CO₂ flux from peat soils in riverine mangroves of the Shark River Slough estuary was in the mid-upper range of soil flux rates for fringe mangroves ($\sim 0.5\text{--}2.75\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$; Lovelock 2008). CO₂ flux is subject to between-site variation along an oligohaline-saline coastal gradient (ecotone) with sites contrasted by vegetation structure, soil properties and frequency/duration of tidal inundation (Chen and Twilley 1999; Castañeda-Moya et al., 2013). Longer tidal duration may have the largest influence over site differences, but salinity may also have an influence on the low soil flux rates at sites SRS-5 and SRS-6. While tidal inundation has been illustrated to be a strong driver of soil CO₂ flux in SRS-6 soils (Chambers et al., 2013), the influence of salinity in estuarine peat soils is not as well understood. A recent study conducted along a tidal freshwater-estuarine gradient in coastal

marshes corresponds with our results, with higher CO₂ flux (with ecosystem respiration) from tidal freshwater marshes as compared with oligohaline and mesohaline marshes (Weston et al., 2014). Lovelock (2008) reported soil respiration from scrub and fringe forests with no significant difference between average CO₂ flux rates. Scrub forests were more consistently characterized as *Avicennia* scrub forests, which tend to occur in more saline conditions. Moreover, contributions of autotrophic and heterotrophic components need to be constrained in order to better understand the influence of salinity on microbial respiration and soil C cycling in mangrove forests.

Variation in atmospheric and aqueous CO₂ loss at SRS-6

Within the SRS-6 site, intra-site variability in CO₂ flux was complex. The range in variability among below-canopy components exceeded the variability in soil respiration among the mangrove sites sampled in this study and among fringe mangrove forests reported by Lovelock (2008). We determined several sources of variation that influenced CO₂ fluxes from below the forest canopy (i.e., soil, CWD and surface water). CO₂ fluxes varied with: 1) component measured within the below-canopy compartment, 2) pneumatophore presence, 3) level of inundation, and 4) soil salinity when soils were exposed.

Partitioning of soils with and without pneumatophores illustrated that soils with pneumatophores contributed to the highest CO₂ flux. In a mangrove forest of Okinawa, Japan, CO₂ flux from *Avicennia marina* pneumatophores (without soils) averaged 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Kitaya et al., 2002). In our study, the difference between average values for rates of soil and soil plus pneumatophores CO₂ flux was about 1.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In a temperate broadleaf secondary forest in Kyoto, Japan (Jomura et al., 2007), respiration from CWD was estimated as 0.50 tonnes C ha⁻¹ yr⁻¹, about a third of our estimate (1.6 tonnes C ha⁻¹ yr⁻¹). To our knowledge, there are no previously reported measurements of CO₂ flux from CWD in

mangrove forests. Yet, hurricane disturbance events could have a significant impact on the contribution of this component to mangrove forest ER.

Comparison of CO₂ flux associated with the soil compartment and ER measured within (J. Barr, unpublished data) and above (Barr et al., 2010) the canopy shows that tidal inundation corresponds to decline in not only soil CO₂, but also CO₂ flux over the vertical forest profile and as CO₂ flux to the atmosphere. Our CO₂ flux data corroborate this mangrove ecosystem trend in two ways: (1) significantly higher below-canopy flux when soils are exposed and (2) an increase in soil CO₂ flux with decrease in groundwater stage after soils are exposed.

We found that CO₂ flux decreased with salinity within a 10 PSU range. While there were few studies that illustrated a decline in plant productivity with salinity, none reported soil CO₂ flux with variation in salinity within a site. For example, Barr et al. (2010) reported decreased photosynthetic active radiation use efficiency within a salinity range of approximately 20-35 PSU. Weston et al. (2014) reported lower maximum aboveground biomass with increased salinity in oligohaline and mesohaline marshes. Thus, as soil respiration flux captures both heterotrophic and autotrophic respiration, decreased root productivity under more saline conditions over the year may contribute to the lower rates we observed.

Flux of CO₂ from surface water (i.e., evasion; Figure 4) was among the lowest of the below-canopy components we measured. Ho et al. (2014) measured CO₂ flux rates from open water in the Shark River in two SF₆ tracer experiments as 232 ± 24 and 171 ± 20 mmol m⁻² d⁻¹. CO₂ flux below the canopy was 50-60% lower than that measured by Ho et al., (2014), but was higher than averages reported in other studies of mangrove river CO₂ flux (40-60 mmol m⁻² d⁻¹; Borges et al., 2003, Bouillon et al., 2008, Kone and Borges, 2008), if under continuous inundation over a 24-hr period. As pCO₂ and turbulence are likely lower in

surface water under the relatively closed mangrove canopy compared to the river channel, CO₂ flux in the open river could be expected to exceed the rates observed under the mangrove canopy. However, Crawford et al. (2013) found that first-order streams had higher and more variable *p*CO₂ and surface water CO₂ flux than higher-order streams as a result of the greater influx of shallow, CO₂-rich soil water to first-order streams. In a mangrove forest in East Timor, Alongi et al. (2011) estimated surface water CO₂ flux for six of seven sites with values ranging from 60 to 118 mmol m⁻² d⁻¹, approximating the rates we observed.

Concentrations of dissolved CO₂ in surface water that inundated the forest soil were in the low end of the range of values determined for some peatland catchments (Billet and Moore, 2008; 2-8 mg C L⁻¹). However, few continuous measurements of dissolved CO₂ exist for tidal water overlying soil in mangrove forests. In Shark River, and in close proximity to our sites, Ho et al. (2014) reported *p*CO₂ in the range of 3000-4000 µatm. While tidal inundation under the mangrove canopy reduces soil CO₂ flux to the atmosphere, dissolved CO₂ concentrations in surface water were observed to increase. Although our measurement intervals were brief, trends of increased *p*CO₂ in surface water and low CO₂ flux from the air-water interface suggest that tidal flooding contributes to aquatic C export. This mechanism, by which carbon is respired to tidal flood waters rather than to air, has been previously identified (Romigh et al., 2006, Barr et al., 2010). In carbonate systems, these dynamics become more complex given the potential for conversion of respired CO₂ to other C forms and CaCO₃ precipitation or dissolution, in addition to assimilation by aquatic plants and other forms of inorganic C transformation (Liu et al., 2010, Jianhau et al., 2012).

Porewater flushing with tidal inundation and advective flux is suggested to be an important mechanism for C export from Shark River mangrove forests (Romigh et al., 2006). Estimates of different DIC and DOC constituents contributing to aquatic C export was estimated by Barr et al. (2010) for Shark River as 3-10 times the DOC flux, following

Bouillon et al. (2008). However, direct measurements of forest-river C exchange at the scale of the mangrove ecosystem (i.e., SRS-6) for all C constituents simultaneously are still lacking.

Integration and scaling

In eddy-covariance based studies, ER is often estimated from net ecosystem exchange (NEE) and GPP, and previous results suggest that this method may underestimate ER (Thomas et al., 2008). Summing component fluxes can help to identify sources of variability, so that those components can be targeted and their contribution to ecosystem respiration flux partitioned (Law et al., 1999, Makiranta et al., 2008). While soils contribute a relatively small fraction of CO₂ flux in this and other previous studies (Barr et al., 2010, Lovelock, 2008), they represent only one component of the below-canopy CO₂ flux that includes soil, pneumatophores, roots and coarse woody debris.

Our study provided well-constrained values of CO₂ flux from below-canopy components in a riverine mangrove forest over a range of environmental conditions. When scaling to the forest level, estimates of surface area of the respective components and the percent of surface area that was exposed to air under three soil flooding states (exposed, partially exposed, and inundated) likely introduced uncertainties in scaled estimates. The extent to which pneumatophore density, volume of CWD and other variables described could be used to determine surface area of each below-canopy component was critical in scaling CO₂ flux to annual rates at the forest scale. For example, in a Kenyan *Avicennia* forest, Dahdouh-Guebasetal et al. (2007) showed that pneumatophore density could increase from seaward to landward positions, and with approximately 10 cm decline in surface elevation, from 200 to 2500 stems m⁻² within a landward position. Other sources of uncertainty included components that were not included, i.e., the extent to which live mangrove branch or bole respiration contributed to ER (i.e. Clough et al., 1997) or how leaf area varies over the extent

of the forest. For example, vertical surface area of trunks in the forest stand at SRS-6 may contribute to a higher proportion of below-canopy respiration, assuming that CO₂ flux from boles (tree trunks) is similar to rates from prop roots. Acknowledging these uncertainties, this analysis provided: (1) the first account of partitioned CO₂ flux for a mangrove forest and (2) an improved understanding of the relative contribution of different below-canopy components to mangrove forest ER. Integrating chamber-based component estimates as presented and discussed in this study is an effective means of constraining ecosystem-level respiration rates derived from eddy covariance methods.

This study illustrates the importance of both spatial and temporal drivers in mangrove ecosystem C balance by identifying important sources of variability in C flux that contribute to ecosystem respiration. Factors that drive variation in tidal inundation, salinity and vegetation structure will influence both heterotrophic and autotrophic sources and sinks of C within this riverine mangrove forest system. Shifts in the biotic and abiotic factors that influence the relative contribution of components of below-canopy CO₂ flux can help to elucidate how discrete disturbance events (e.g., hurricanes) and long-term change including sea-level rise will in turn influence carbon cycling in riverine mangrove forests.

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	Below-canopy component CO ₂ efflux	% Contribution to ER	
	(tonnes C ha ⁻¹ yr ⁻¹)	Based on eddy covariance- derived ER ^a	Based on sum of respiration components
Heterotrophic only	3.51	32	22
Autotrophic (not including dark leaf respiration) only	1.41	13	9
Heterotrophic + Autotrophic	2.23	20	14
Dark leaf respiration	8.59 ^b	35 ^c	55
Total Ecosystem Respiration ^d (tonnes C ha ⁻¹ yr ⁻¹)	15.7		
^a Using Barr et al. (2010) value of 11 tonnes C ha ⁻¹ yr ⁻¹ ^b Barr et al., 2010; J. Barr, unpublished ^c Estimated from the difference in eddy covariance value of ER (Barr et al. (2010) and the sum of below-canopy components measured in this study ^d Sum of below-canopy components measured in this study and dark leaf respiration from J. Barr, unpublished			

Table 1. The contribution of below-canopy respiration components and dark leaf respiration based on estimates of mangrove forest ecosystem respiration (ER) derived from eddy covariance and sum of all respiration components.

Figure 1. Florida Coastal Everglades Long Term Ecological Research (FCE LTER) site map including location of the 3 study sites reported in the paper: Shark River Slough (SRS) 4, 5 and 6. Map created by M. Rugge

Figure 2. Measurement technique for CO₂ flux from coarse woody debris. LICOR 8cm chamber affixed to a downed tree using a PVC saddle T, silicone foam and elastic cords.

Figure 3. Inter-site variability in soil CO₂ flux, 2008-2011. Error bars are standard error

Figure 4. Below-canopy components of CO₂ flux partitioned by surface water (SW; $n=16$, $1.02 \pm 0.10 \mu\text{mol m}^{-2} \text{s}^{-1}$), soil ($n=86$, $1.27 \pm 0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$), prop roots ($n=8$, $1.94 \pm 0.45 \mu\text{mol m}^{-2} \text{s}^{-1}$), coarse woody debris (CWD; $n=29$, $2.34 \pm 0.23 \mu\text{mol m}^{-2} \text{s}^{-1}$), and soil with pneumatophores present (soil + pneut; $n=47$, $3.17 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$).

A.

B.

Figure 5. Soil CO₂ efflux and (A) groundwater stage and (B) soil porewater salinity in 2011 at SRS6. Error bars are standard error.

Figure 6. Dissolved CO₂ in tidal flood water overlying the soil surface for two periods: June 1-6, 2011 and August 5-10, 2011 at SRS-6