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Carbon exchange between the atmosphere and subtropical forested cypress and pine wetlands

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Abstract

Carbon dioxide exchange between the atmosphere and forested subtropical wetlands is largely unknown. Here we report a first step in characterizing this atmospheric–ecosystem carbon (C) exchange, for cypress strands and pine forests in the Greater Everglades of Florida as measured with eddy covariance methods at three locations (Cypress Swamp, Dwarf Cypress and Pine Upland) for one year. Links between water and C cycles are examined at these three sites, and methane emission measured only at the Dwarf Cypress site. Each forested wetland showed net C uptake (retained in the soil and biomass or transported laterally via overland flow) from the atmosphere monthly and annually. Net ecosystem exchange (NEE) of carbon dioxide (CO_2) (difference between photosynthesis and respiration, with negative values representing net ecosystem uptake) was greatest at the Cypress Swamp ($-1000\,g\,C\,m^{-2}\,year^{-1}$), moderate at the Pine Upland ($-900\,g\,C\,m^{-2}\,year^{-1}$), and least at the Dwarf Cypress ($-500\,g\,C\,m^{-2}\,year^{-1}$). Methane emission was a negligible part of the C ($12\,g\,C\,m^{-2}\,year^{-1}$) budget when compared to NEE. However, methane (CH_4) production was considerable in terms of global warming potential, as about 20 g CH_4 emitted per m^2 year was equivalent to about 500 g CO_2 emitted per m^2 year. Changes in NEE were clearly a function of seasonality in solar insolation, air temperature and water availability from rainfall. We also note that changes in the satellite-derived enhanced-vegetation index (EVI) served as a useful surrogate for changes in net and gross atmospheric–ecosystem C exchange at these forested wetland sites.

1 Introduction

Wetlands are generally considered large natural sources for methane emission (Whalen, 2005; Sjogersten et al., 2014) and sinks for atmospheric carbon dioxide (Troxler et al., 2013; Bridgham et al., 2006). Wetlands in southern Florida's greater Everglades (http://sofia.usgs.gov/) are expansive subtropical ecosystems that are

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generally believed to be carbon (C) accumulating over geologic time scales (Jones et al., 2014). Here we report a first step in characterizing this atmospheric–ecosystem carbon (C) exchange, for cypress strands and pine forests in the Greater Everglades of Florida.

The primary goal of this paper is to quantify the magnitude and controls of C exchange within cypress and pine forested wetlands; in this paper, these wetland communities are defined by McPherson (1973) and Duever et al. (1986, 2002). Quantities of interest include net atmospheric/ecosystem C exchange (NEE), ecosystem respiration (RE), gross ecosystem exchange (GEE), and methane emissions. Latent heat flux (LE) and evapotranspiration (ET) also are quantified so that links between water and C cycles can be quantitatively studied, such as photosynthesis and water-use efficiencies. We address several specific objectives on daily, monthly and annual time scales, including (1) the magnitude of cypress (tall and dwarf) and pine forested wetlands as net atmospheric C sources or sinks, (2) site differences in water and C exchange metrics (i.e., –NEE, GEE, RE, and surface energy fluxes), and (3) the magnitude of methane emission over a dwarf cypress wetland. Results from this study are expected to help define and predict subtropical forested wetland responses to regional (e.g., freshwater discharge) and global (e.g., air temperature) environmental change, and to provide some insights into the relationships between carbon, water, and methane fluxes.

In addition to the insight provided by this study on the role of subtropical forested wetlands in the global carbon cycle, this research also is expected to be useful for determining the consequences of land-use changes in the Everglades region. Canal building and drainage projects in south Florida have reduced the original extent of the Everglades (Parker et al., 1955) and diminished ecosystem services. In response, State and Federal governments are planning and executing complex projects to restore Everglade's wetlands (http://www.evergladesplan.org/) while concurrently avoiding flooding in urbanized areas and maintaining water supply.

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Restoring ecosystems will affect water, energy and C cycles, as plants and soil processes adjust to changing water levels, albedos, salinities, nutrient loads and forest fires. For example, Jimenez et al. (2012) and Schedlbauer et al. (2010) indicate that additional deliveries of water into peat and marl sawgrass wetlands may diminish C accumulation within these wetlands. Eddy-covariance derived estimates of net ecosystem productivity declined with increasing inundation during the wet season (Jimenez et al., 2012; Schedlbauer et al., 2010). These results were partially attributed to the amount of vegetation that, due to flooding, could not directly exchange carbon dioxide with the atmosphere. The opposite trend was observed in a tidally influenced mangrove forest in Everglades National Park. Lowered salinities, resulting from increased freshwater flow, resulted in increased daily PAR-use efficiency (i.e. ratio of gross ecosystem productivity to photosynthetically active irradiance (PAR), Barr et al., 2010, 2012). Also, ecosystem respiration losses were lower during periods of inundation (Barr et al., 2010, 2012), which increased net C uptake over the mangrove forest. These studies provide insights on water and C cycling over coastal sawgrass wetlands and mangrove forests. C cycling over other subtropical wetlands, such as cypress strands and pine forests, is largely unstudied (Sjogersten et al., 2014).

2 Methods

2.1 Site description

The study area is the Big Cypress National Preserve (BCNP) in southern Florida (Fig. 1). A variety of subtropical forested and non-forested wetland ecosystems are present in BCNP, including Pine Upland, Wet Prairie, Marsh, Hardwood Hammocks, Cypress Swamps, Dwarf Cypress and Mangrove Forests as formally characterized by McPherson (1973) and Duever et al. (1986, 2002). The distribution of ecosystems and plant communities in the BCNP is controlled by topography, hydrologic and fire regimes, and soil conditions (Duever et al., 1986). Marsh, Cypress Swamp, and

Mangrove Forests typically occupy low elevations (< 2.5 m National Geodetic Vertical Datum, NGVD-29), Wet Prairie occupies middle elevations (3–4 m NGVD-29), and Pine Uplands and Hardwood Hammocks occupy high elevations (> 4 m NGVD-29). These wetlands provide floodwater protection, hurricane buffering, substrate stabilization, sediment trapping, water filtration, and other ecosystem services for urban areas and coastal estuaries.

Water and C fluxes were determined over Pine Upland, Cypress Swamp and Dwarf Cypress ecosystems (Fig. 1, Table 1) from December 2012 to December 2013. The Pine Upland site (Fig. 1, Table 1), is classified as a mixed lowland pine site, and is located in an extensive open-canopy pine forest with numerous small- to medium-sized cypress domes. The canopy is dominated by slash pine (*Pinus elliottii*) with an understory of saw palmetto (*Serenoa repens*), small trees and shrubs including holly (*Ilex cassine*), swamp bay (*Persea palustris*), myrsine (*Myrsine cubana*), and wax myrtle (*Myrica cerifera*), and scattered sabal palms (*Sabal palmetto*) (Fig. 2). The ground cover is a diverse mix of short (less than 1 m) grasses, sedges, and forbs that are scattered in open-to-dense patches around the site. The open character of the site indicates regular burning with fire recurrence every 5 years, on average. Large cypress domes have a dense canopy of cypress, but open subcanopy and shrub strata, probably due to frequent fires. Substrates are primarily limestone bedrock, with sandy marl in the shallow depressions. Cypress domes in the area have a shallow organic substrate in the deeper areas.

The Cypress Swamp site (Fig. 1, Table 1) is classified as a swamp forest (Duever et al., 1986) and supports a tall dense cypress forest with a subcanopy of mixed hardwoods (Fig. 2). Plant varieties include bald cypress (*Taxodium distichum*), holly, swamp bay, maple (*Acer rubrum*), an open-to-dense shrub layer with coco plum (*Chrysobalanus icaco*), myrsine, wax myrtle, an open-to-dense ground cover of swamp fern (*Blechnum serrulatum*), and a variety of grasses, sedges, and forbs. The substrate is primarily topographically irregular limestone bedrock with organic accumulations in depressions in the rock.

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The Dwarf Cypress site is classified as scrub cypress and is dominated by cypress, *Taxodium distichum*, and scattered (5–10 % cover) sawgrass less than 1 m high (Fig. 2). Small to medium-sized cypress domes are present, and periphyton is seasonally abundant (Fig. 2) from about July to December. The substrate is shallow marl overlying topographically irregular limestone bedrock.

2.2 Carbon balance

A mass balance equation can be used to conceptualize C fluxes. Net ecosystem C balance (NECB) is the amount of C accumulating in the ecosystem, in units of mass per area time (Chapin et al., 2006; Troxler et al., 2013). NECB can be partly approximated using eddy-covariance methods by measuring (1) the net vertical (1-dimensional) exchange of carbon dioxide (−NEE) across the ecosystem–atmosphere interface, (2) the net lateral flux (F_{net}) of dissolved/particulate organic/inorganic C leaving the system, and (3) the C released from methane emission (F_{CH_4}):

$$\mathrm{NECB} = -\mathrm{NEE} - F_{net} - F_{CH_4} \quad (1)$$

A negative sign for NEE indicates a loss of carbon dioxide from the atmosphere. The net lateral flux of C (F_{net}) occurs primarily within surface water that flows down topographic gradients toward mangrove wetlands on the coast (Fig. 1). Technical difficulties inherent in measuring “sheet flow” and the dissolved/particulate organic/inorganic C concentrations within surface water did not allow quantification of this term. Therefore, we only report exchanges of gases between the atmosphere and the ecosystem. Methane emission (F_{CH_4}) at the Dwarf Cypress site was determined using a LICOR-7700 open-path methane analyzer. The cost of the methane analyzer and safety issues related to climbing tall towers limited measurements of F_{CH_4} to a single site (Dwarf Cypress, Fig. 2). Thus, our daily and annual NEE estimates are likely an upper bound for C accumulation at the Pine Upland and Cypress Swamp sites (and lower bound for atmospheric transfer to the ecosystem) due to uncertainty associated with methane emission and lateral C fluxes.

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2.3 Eddy covariance method and gap-filling

The eddy covariance method (Dyer, 1961; Tanner and Greene, 1989) is a one-dimensional (vertical) approach for measuring the exchange of gases within the atmospheric surface layer (Campbell and Norman, 1998). Key instrumentation (Table 2) includes sonic anemometers that rapidly (10 Hz) measure wind velocity and gas analyzers that rapidly measure gas concentrations (Table 2) in the atmosphere. The covariance between vertical wind velocities and gas concentrations determines the net exchange of gases between the ecosystem and atmosphere. Additional instrumentation (Table 2) was installed at each site to measure net radiation, soil-heat flux, soil temperatures, air temperature and relative humidity, and distance of water above or below land surface (using pressure transducers, Shoemaker et al., 2014a, b, c). Pressure transducers were placed in the bottom of groundwater wells to measure the distance of water above and below land surface. Pressure transducers were corrected monthly for instrumentation drift using manual depth-to-water measurements from the top of the well casings. The manual depth-to-water measurements allowed precise calibration of continuous water distance above or below land-surface (Shoemaker et al., 2014a, b, c). Monthly site visits were made to download data, perform sensor inspections and complete other site maintenance. All instrumentation was visually inspected, leveled, cleaned, or replaced as necessary.

Raw, 10 Hz, vertical wind speed, temperature, and gas concentration data were processed to half-hourly fluxes using EddyPro software (version 4.0.0) following Express protocols that included spiking filters, double coordinate rotations, blocked-average detrending, statistical filters, air density and oxygen corrections (Tanner and Thurtell, 1969; Baldocchi et al., 1988; Webb et al., 1980; Tanner et al., 1993), and high-pass filtering. Processed data yielded half-hourly mean values of NEE, methane, sensible and latent heat fluxes that were filtered to remove periods with (1) unrealistic fluxes (latent and sensible heat fluxes > 400 and $< -50\,\mathrm{W\,m^{-2}}$, NEE > 10 and $< -10\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ at the Dwarf Cypress site, NEE > 25 and $< -25\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ at the

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Cypress Swamp site, NEE > 20 and < −20 μmol m^{-2} s^{-1} at the Pine Upland site, and (2) friction velocity (u^*) < 0.05 m s^{-1} (Shoemaker et al., 2014a, b, c). Friction velocity is an indicator of time periods when turbulent wind conditions are well developed. Eddy covariance methods are theoretically appropriate for turbulent wind conditions. The u^* threshold was selected based on a sensitivity analysis of daily and monthly gap-filled NEE to u^* thresholds of 0.05, 0.15, and 0.25. NEE was essentially the same under each u^* threshold, while the u^* filter of < 0.05 m s^{-1} preserved more of the observed data and thus required less gap-filling. Roughly 4, 2, and 5 % of the water and C fluxes were removed by the u^* filter at the Cypress Swamp, Dwarf Cypress and Pine Upland sites, respectively. Relatively small u^* values were generally observed at night, as expected, due to low wind velocity at night.

A final mathematical filter removed all C fluxes at the Pine Upland site (Fig. 3) when contamination was possible due to fossil fuel combustion by generators and trucks supporting oil-drilling activities adjacent to the eddy-covariance tower. All carbon fluxes were removed at Pine Upland when the wind blew from the east of the tower (0–180°) (Shoemaker et al., 2014a, b, c). This filter removed 60 % of the carbon flux data, under the assumption the instruments were likely affected by drilling activities.

Missing 30 min latent heat fluxes were gap-filled with a regression-calibrated Priestly–Taylor (Priestley and Taylor, 1972) equation (Fig. 3), using the methods of Shoemaker and Sumner (2006). The Priestley–Taylor equation was formulated as:

$$\lambda E = \alpha \frac{\Delta}{\Delta + \gamma} (\mathrm{Ae}) \quad (2)$$

where Δ is the slope of the saturated vapor pressure with respect to air temperature, in kPa °C^{-1}; γ is the psychrometer constant equal to 0.07 kPa °C^{-1}, Ae is available energy (difference between net radiation and the soil heat flux), in W m^{-2}; and α is a regression-defined coefficient (Fig. 3) that minimized residuals between measured and computed (Eq. 2) latent-heat fluxes.

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Previous investigators describe a recurring problem with the eddy covariance method. The sum of measured latent- and sensible-heat fluxes is generally less than the measured available energy. Foken (2008) explained this discrepancy with low-frequency (large-scale) eddies unmeasured by the chosen averaging period (usually 30 min). Measured 30 min latent- and sensible-heat fluxes were corrected to account for low-frequency (large scale) eddies by assuming the ratio of turbulent fluxes (Bowen ratio; Bowen, 1926) was adequately measured and partitioning the residual available energy by the Bowen ratio (Twine et al., 2000).

Missing 30 min NEE values were gap-filled using a sequential approach (Fig. 3; Shoemaker et al., 2014a, b, c). Gaps with duration less than 4 h were filled using a 4 h centered moving mean, computed every half hour. Subsequent gap-filling was based upon the predominance of photosynthesis or respiration (RE) within the NEE time series. Photosynthesis generally dominated during the day-time, resulting in negative values for NEE. Respiration generally dominated during the night, resulting in positive values for NEE. Negative NEE was gap-filled using relations between 30 min NEE and latent heat fluxes (Fig. 4) as measured or modeled with the Priestly–Taylor equation (Eq. 2). Latent heat flux explained more −NEE variability ($R^2 = 0.22$ at Dwarf Cypress, for example) than non-linear light-response curves with solar radiation ($R^2 = 0.09$) and air temperature ($R^2 = 0.05$). Photosynthesis simultaneously released water while storing C, according to each ecosystem's water-use efficiency, which may explain improved performance of latent heat for gap-filling −NEE. Furthermore, NEE and latent heat fluxes are auto-correlated through vertical wind velocity.

Positive NEE during the night was assumed to represent RE. RE was weakly correlated with quantities such as air temperature ($R^2 = 0.01$ and 0.03 for linear and exponential regression at the Cypress Swamp site, for example); thus, a statistical model was used for gap-filling (Shoemaker et al., 2014a, b, c). RE was gap-filled with a 4 h moving mean, followed by the statistical model. The statistical model randomly estimated values for RE within one SD of the mean RE measured each day. For example, if 20 RE values were available within a 24 h period, a mean and SD was

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computed using the 20 available values. Subsequently, 28 missing RE values were randomly estimated from a range that was one SD from the mean. The statistical RE model also was applied to approximate RE during the day. Assuming day-time and night-time respiration statistics are equal could be a source of error in project results. Identification of an alternative to the statistical model was precluded by weak relations between respiration and ancillary variables such as air temperature.

Daily −NEE and RE were converted from molar to mass units. Gross daily transfer of C from the atmosphere to the ecosystem (GEE, $g\,C\,m^{-2}\,d^{-1}$) was calculated as the sum of NEE and RE. Daily −NEE, RE, and GEE values were summed to generate monthly and annual totals.

Methane emissions (F_{CH_4}) at the Dwarf Cypress site had the most missing 30 min data (Shoemaker et al., 2014a, b, c). About 80 % of the F_{CH_4} time series was missing, mostly due to poor signal strength of the methane CH_4 analyzer (signal strength filter < 10), and spikes in methane fluxes when the analyzer signal strength indicator (RSSI) changed by ±10 between half-hourly time periods. Gap-filling with empirical regression models was not attempted due to weak correlation with explanatory data, the greatest was $R^2 = 0.11$ with net radiation. Correlations were similarly weak when isolating methane emissions measured in the day-time between 10 a.m. and 2 p.m., specifically, the greatest $R^2 = 0.12$ was with vapor pressure deficit. Given these weak correlations, daily and monthly methane fluxes were computed by averaging the available data over days and months.

3 Results and discussion

3.1 Seasonality in rainfall, temperature, water levels and energy fluxes

The subtropics in south Florida are characterized by distinct wet and dry seasons driven by changes in solar insolation, air temperature, humidity, and rainfall. Rainfall and photosynthesis are greatest in the relatively hot and humid spring and summer months from about May to October. The end of October generally marks the end of the wet season (and hurricane season). Wetland water levels and surface energy fluxes are tightly coupled to seasonality in rainfall and solar insolation. Cold fronts are especially remarkable within surface energy budgets, as dry cold air interacts with relatively warm soil and surface water, creating large variations in both stored-heat energy and turbulent fluxes of heat and water vapor (Shoemaker et al., 2011).

During this study, air temperatures at all three sites (Fig. 5a–c) were seasonally lowest (ranging from 15 to 25 °C) during December through March, and as low as 12 °C for several days during the passage of cold fronts in the winter. Cold fronts typically lasted 5 days or less. During April and May, air temperatures rose above 25 °C and were less variable as hot and humid air masses dominated the subtropical region. By late May, air temperatures were consistently 25 to 30 °C and remained within this range until the onset of the dry season in mid-to-late October. Water and soil temperatures (measured 0.15 m below land surface) were nearly identical (absolute differences < 1 °C) but were 1 to 5 °C higher than air temperature during the passage of cold fronts (Fig. 5). Land surface served as a heat reservoir during cold fronts, and water and soil temperatures seldom fell below 15 °C. Cold fronts also increase vapor pressure deficits due to cool, dry air moving rapidly over the relatively wet and warm landscape.

Seasonality was observed in water levels at each site (Fig. 5a–c) in response to rainfall duration and intensity. Water levels were lower in the winter and early spring due to reduced rainfall in the dry season (i.e., November to May). Water levels rose in response to increased rainfall at the end of April 2013, reaching ~ 1 m above land surface during July through October at the Dwarf Cypress site. In contrast, water levels declined as much as 0.5 m below land surface at Pine Upland during the early spring dry season in February to April. Water levels remained approximately at land surface or slightly above land surface at the Cypress Swamp site for the entire study time period.

Surface energy fluxes reflected the seasonality in air temperature and rainfall (Fig. 5a–c). Mean daily net radiation ranged from about 50 to over 200 $\mathrm{W\,m^{-2}}$ and was greatest in the summer months of June, July and August 2013. Net radiation

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was least from November to February when incoming solar radiation was seasonally smallest. Net radiation was the primary driver of latent heat flux (Figs. 3 and 4; Eq. 2), the energy equivalent of evapotranspiration (ET). Mean daily latent heat fluxes ranged from about 0 to more than 150 $W m^{-2}$ and were greatest in the summer months of June, July and August 2013 at the Cypress Swamp site. Latent heat fluxes were lowest from November to February when incoming solar radiation was seasonally lowest, and less water was available for evaporation. During these cooler and drier periods, surface evaporation also was limited by lower physiological activity of trees, especially of the deciduous cypress trees during fall-winter leaf drop (Fig. 5b and c). Surface inundation combined with more incoming solar radiation resulted in more energy partitioned as latent vs. sensible heat during May to November. Also, cypress leaves were notably greener during this period suggesting increased physiological activity and seasonally higher transpiration rates.

3.2 Carbon exchange between the atmosphere and forested wetlands

All three sites were generally sinks of atmospheric carbon dioxide (CO_2) on daily (Fig. 6), monthly (Fig. 7) and annual time scales (Table 3). The sink strength of CO_2 at the Cypress Swamp and Dwarf Cypress sites, as evidenced in −NEE, was reduced during the fall and winter of 2012 and 2013 (Table 3, Figs. 6 and 7). Reductions in daily −NEE at the Pine Upland site were less dramatic during the same period with daily −NEE of 1.5–2.5 $g C m^{-2} day^{-1}$ compared to 0–1 $g C m^{-2}$ and 1–2 $g C m^{-2}$ at the Dwarf Cypress and Cypress Swamp sites, respectively. Pines trees grow and maintain leaves all year (evergreen trees), which may explain dampened seasonality in −NEE at the Pine Upland site.

The Moderate-resolution Imaging Spectroradiometer (MODIS) enhanced vegetation index (EVI) served as a useful qualitative surrogate for seasonal terrestrial photosynthetic activity and canopy structural variations (Fig. 7), as reported for some other studies (Huete et al., 2002). EVI over tall mangrove forest, for example, varied seasonally between 0.35 and 0.55, and decreased to ∼ 0.2 following defoliation

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after hurricane Wilma (Barr et al., 2013). Likewise, EVI over evergreen forest (Xiao et al., 2004) varied seasonally between 0.25 during the winter and 0.5 during the summer growing season. MODIS was launched by National Aeronautics and Space Administration (NASA) in 1999 on the Terra (EOS AM) Satellite, and in 2002 on the Aqua (EOS PM) satellite. EVI data were obtained from the MOD13A1 product (EOS; http://modis.gsfc.nasa.gov/). Sixteen-day composite EVI values for the pixel corresponding to each station, and the 8 adjacent pixels were extracted for comparison with monthly C fluxes (Fig. 7). This 9-pixel domain approximately corresponds with the measurement footprint of each flux station.

Seasonal patterns in −NEE and GEE were consistent with changes in EVI (Fig. 7). Increases in EVI from 0.25 to 0.35 (Fig. 7b) corresponded with the growth of cypress leaves on relatively tall (18 to 21 m) and densely-spaced cypress trees (Fig. 2) beginning in about March to April. Cypress leaves discontinued growing in August to September and turned brown in October, eventually falling into the sawgrass and hardwood understory. This lack of photosynthetic activity corresponded with changes in EVI from 0.4 in the summer to 0.2 in the winter (Fig. 7b), at the Cypress Swamp flux station.

Gross atmosphere–ecosystem C exchange (GEE) provides a first approximation of gross ecosystem productivity (GEP), or accumulation of C in the plant canopy. Growth and senescence of cypress leaves was most evident in monthly GEE (Fig. 7, Table 3) at the Cypress Swamp site, where rates increased from about 100 $\mathrm{g\,C\,m^{-2}}$ in February to 200 $\mathrm{g\,C\,m^{-2}}$ in April (a 116 % increase). At the Dwarf Cypress site, seasonal changes in GEE were more moderate; the February to April increase was from about 60 to 90 $\mathrm{g\,C\,m^{-2}}$ (a 41 % increase). Foliage change at the Cypress Swamp site likely contributed to a larger fraction of the site's change in photosynthetic CO_2 uptake compared to that of the Dwarf Cypress site, which consists of a sparse cypress canopy (Fig. 2) during the height of the growing season (i.e., April to September). Of the three sites, the Pine Upland site exhibited the least amount of seasonal variability

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in GEE (Fig. 7, Table 3). Pines trees grow and maintain leaves (needles) all year (evergreen), which may explain the lack of seasonality in GEE at this location.

Correlations between monthly RE and GEE at the Cypress Swamp, Dwarf Cypress, and Pine Upland sites were 0.82, 0.76, and 0.10, respectively, suggesting RE at Cypress Swamp and Dwarf Cypress was linked to photosynthesis within green plants (autotrophic respiration) rather than decomposition (heterotrophic respiration) of litter, periphyton and/or soil organic matter. Conversely, the lack of correlation between RE and GEE at the Pine Upland site indicates decomposition controls most of the variability in RE. Inundation at the Dwarf Cypress and Cypress Swamp sites may have suppressed heterotrophic respiration, as observed water levels were generally above land surface (Fig. 5a). Additional RE data during dry periods is needed to confirm suppressed heterotrophic respiration at the Dwarf Cypress and Cypress Swamp sites due to flooding. Likewise, additional data are required to rigorously assess the impact of flooding on RE at the Pine Upland sites (Fig. 5).

3.3 Links between C and water cycles

Relationships between net ecosystem C exchange (−NEE) and latent heat flux (LE) illustrate an important link between water and C cycles (Fig. 4), that is, plant stomata that release water (transpiration) while storing C (photosynthesis). R^2 between −NEE and LE provides an indication of the relative magnitudes of transpiration and evaporation at each site. Stronger correlations between NEE and LE indicate increased transpiration relative to evaporation, as water is transpired during photosynthesis while the plant fixes a unit mass of C. In contrast, weaker correlations indicate a site with more open water evaporation where the source for ET is less related to photosynthesis and more related to evaporation from a water or soil surface. Correlations between −NEE and LE were 0.37, 0.36 and 0.22 (Fig. 4) at the Cypress Swamp, Pine Upland and Dwarf Cypress sites, respectively. These correlations indicate transpiration is a larger portion of evapotranspiration at the forested wetlands with their larger and more densely spaced cypress and pine trees (Fig. 2). Closed or partially

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closed forested canopies reduced penetration of solar radiation to water surfaces, creating lowered lapse rates between the water surface and canopy crown (Barr et al., 2012), and added resistance to evaporation. Collectively, these results suggest a redistribution of plant communities toward more open-water ecosystems (such as sparse sawgrass) could result in less C uptake and greater evaporative losses. Prior studies of C accumulation further support this generalization; for example, NEE rates were greater over mangrove systems (Barr et al., 2010, 2012) than over sawgrass wetlands (Schedlbauer et al., 2010). Prior ET studies (German, 2000) indicate ET losses are greater over Everglade's wetlands with sparse sawgrass and open-water conditions.

Coupling between water and C cycles was examined via water-use efficiencies computed as the ratio of (1) daily GEE to ET (WUE's, Fig. 8) and (2) ratio of annual NEE to ET (Table 4). As such, WUE are the net (Table 4) or gross (Fig. 8) mass or moles of C transferred to the ecosystem per mm or mole of ET. Computing WUE with NEE accounts for the loss of C through Re. The Cypress Swamp and Pine Upland sites were most efficient at using water to store C, with WUE equal to about 1.7 and 1.6 g C per mm ET; respectively, on a GEE basis (Fig. 8). Accounting for the loss of C though respiration (Table 4), the Cypress Swamp and Pine Upland sites were still most efficient at using water to store C, with WUE equal to 1.0 g C (mm ET)$^{-1}$. About 0.5 g C uptake occurs per mm of ET (0.8 mol CO_2 (mol ET)$^{-1}$) at the Dwarf Cypress site (Table 4). Apparently, wetlands with more open-water surface (Fig. 2) are less efficient than forested wetlands at converting water use into net and gross C uptake. This conclusion is likely to be true both regionally and perhaps globally, and thus, may have implications for the global C cycle.

3.4 Methane emission

Methane is produced by anaerobic bacteria decomposing soil organic matter. Methane can be oxidized during transport from the soil to the atmosphere. Transport to the atmosphere can occur through (1) roots and stems of vascular plants (Wang and Han, 2005; Morrissey et al., 1993; Kim and Verma, 1998), (2) ebullition as gas bubbles from anaerobic soils (Comas and Wright, 2012), and (3) diffusion through the soil and surface water (Van Huissteden et al., 2006; Christensen et al., 2003a, b). Methane is oxidized during diffusion through soils and surface water (Alberto et al., 2014). Methane emission is enhanced by temperature because anaerobic bacteria become more active as the soil warms (Simpson et al., 1995). Increasing soil temperature also increases molecular diffusion and ebullition of methane (Alberto et al., 2014).

At the Dwarf Cypress site, methane emission increased in the summer months from June to September (Figs. 6c and 7c) as air temperature, solar radiation and water levels increased (Fig. 5a). Methane emission peaked at different times in the summer compared to GEE at the Dwarf Cypress site (Fig. 7). GEE peaked with photosynthesis in July 2013 whereas methane emission peaked in August 2013. This time lag indicates that processes governing C exchange and methane emissions are quite different, with GEE controlled by photosynthesis of cypress leaves and sawgrass which grow vigorously from March to April and discontinue growth in August to September. In contrast, methane emission is likely driven by decomposition of organic matter with subsequent oxidation through the soil and surface water. Anaerobic decomposition was enhanced in August 2013 by flooding and relatively warm air, soil and surface-water.

Methane emission is believed to be important in terms of global warming potential (GWP), but appears to be immaterial in C budgets that build and maintain subtropical wetland land-surface topography. C released from methane emission was relatively small (about 12 g C) compared to NEE (about 500 $g\,C\,m^{-2}\,year^{-1}$, Table 3). However, approximately 15 g CH_4 was released to the atmosphere which is roughly equivalent to about 330 g CO_2, assuming the GWP of CH_4 is 25 times greater than CO_2 (over a 100 year period, IPCC). These results suggest that methane monitoring is needed when assessing the GWP of wetlands. In contrast, C cycling studies that address changes in peat accumulation and land-surface topography may not benefit from monitoring methane fluxes.

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3.5 Comparison of C uptake with prior studies

Comparison of results from this study with −NEE from selected prior studies (Schedlbauer et al., 2010; Jimenez et al., 2012; Barr et al., 2010; Botkin et al., 1970; Jones et al., 2014) reveals substantial spatial and temporal heterogeneity in C uptake from the atmosphere over geologic time and among different ecosystems (Table 4). Subtropical forested wetlands exchange more C than temperate forests (Botkin et al., 1970; Sjogersten et al., 2014). A study assessing this exchange on a geologic time scale (Jones et al., 2014) also concluded that long-term rates of C uptake in the Everglades are higher than in northern latitudes, and in some cases rival C uptake in tropical peat-lands, such as Indonesia. Mangrove ecosystems may serve as an upper limit for subtropical C uptake, with NEE of about $-1170\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$ (Barr et al., 2010).

Sparse sawgrass wetlands in the Everglades, such as Taylor and Shark River Sloughs, are relatively minor atmospheric C sources or sinks, with −NEE ranging from −50 (Taylor Slough) to +45 (Shark River Slough) $\mathrm{g\,C\,m^{-2}\,year^{-1}}$ (Table 5). Jones et al. (2014) also concluded that sloughs sequester the least amount of C in their study of C accumulation over geologic time scales. Given the C released from methane emissions ($12\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$, Table 3), as measured at Dwarf Cypress (Figs. 6 and 7), sparse sawgrass wetlands may generally be atmospheric C sources at monthly and annual time scales, with questionable value as local, regional and global C sinks.

4 Conclusions

Atmospheric/ecosystem carbon dioxide exchange, methane emission, latent and sensible heat fluxes were estimated with eddy covariance methods for subtropical forested cypress and pine wetlands for one year. Seasonality in solar insolation, air temperature, plant physiological activity and rainfall created seasonality in C exchange rates and surface energy fluxes. Links between water and C fluxes also were revealed.

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Each forested wetland was an atmospheric C sink on monthly and annual time scales. NEE was greatest at the Cypress Swamp site ($-1000\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$), moderate at the Pine Upland site ($-900\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$), and least at the Dwarf Cypress site ($-500\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$). The size (about 20 m) and number of cypress trees enhanced C uptake at the Cypress Swamp site and seasonality in C uptake was enhanced by the growth of cypress leaves in early April and decay of cypress leaves in late October, as confirmed by changes in the satellite-derived EVI index. Changes in EVI (from 0.25 in the dry season to 0.4 in the wet season) served as a useful surrogate for monthly and seasonal changes in net (NEE) and gross (GEE) ecosystem C exchange.

Links between water and C cycles were examined via (1) WUE's expressed as the ratio of (a) daily GEE to ET and (b) annual NEE to ET, and (2) correlations between −NEE and LE. Computing WUE with NEE accounts for the loss of C through Re. The Cypress Swamp and Pine Upland sites were most efficient at using water to store C, with WUE's equal to 1.7 and 1.6 $\mathrm{g\,C\,(mm\,ET)^{-1}}$; respectively, on a GEE basis. About 1 g C was stored in the ecosystem per mm of ET at the Dwarf Cypress site. Accounting for the loss of C though respiration, the Cypress Swamp and Pine Upland sites were still most efficient at using water to store C. These results indicate that wetlands with more open-water surface are less efficient at using water to store C than forested wetlands. This pattern is likely to be true both regionally and perhaps globally, and thus, may have implications for the global C cycle.

Correlations between −NEE and LE reflected an important link between water and C cycles, specifically, photosynthesis which released water as transpiration while storing C. The strength of the −NEE and LE correlation provided an indication of the relative magnitudes of transpiration and evaporation at each site. Transpiration was a large proportion of evapotranspiration at the Cypress Swamp and Pine Upland sites, as indicated by correlations of 0.37, 0.36 and 0.22 for the Cypress Swamp, Pine Upland and Dwarf Cypress sites, respectively. These results indicate that a redistribution of plant communities toward more open-water ecosystems could create less C uptake and greater evaporative losses.

Methane emission at the Dwarf Cypress site was considerable in terms of global warming potential, but immaterial in C budgets that build and maintain land-surface topography. Approximately 15 g CH_4 was released into the atmosphere, roughly equivalent to 330 g CO_2, assuming the global warming potential of CH_4 is about 25 times greater than CO_2. Methane emission, however, did not reverse carbon accumulation for building and maintaining topography at the Dwarf Cypress site, because the C released from methane emission (12 $g\,C\,m^{-2}\,year^{-1}$) was relatively small compared to NEE (−500 $g\,C\,m^{-2}\,year^{-1}$). These results indicate that while methane monitoring is needed when assessing the global warming potential of wetlands; C cycling studies that address changes in topography and peat accumulation may not benefit from monitoring methane fluxes.

Acknowledgements. This study was funded, in part, by the U.S. Geological Survey (USGS) Greater Everglades Priority Ecosystems Science (GEEES). Nick Aumen is gratefully acknowledged for helpful conversations about the Everglades during project meetings and fieldwork in BCNP. Michael J. Duever provided detailed vegetation descriptions and guidance during site selection. Steve Krupa and Cynthia Gefvert from the South Florida Water Management District funded tower construction. Peer reviews by Lisamarie Windham-Myers, Frank Anderson, Dave Sumner and Kim Haag of the USGS improved the quality of the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 1. Site locations, tower heights and summary of vegetation.

Site	Latitude	Longitude	Height of tower (m)	Height of vegetation (m)	Vegetation
Dwarf Cypress	25.7624	−80.8934	16.8	0.5 to 10	Small cypress and sawgrass
Cypress Swamp	25.8265	−81.1020	38.1	0.5 to 21	Tall cypress
Pine Upland	26.0004	−80.9260	38.1	0.5 to 21	Pine, sawgrass and cypress

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Table 2. Instrumentation installed at the Dwarf Cypress, Cypress Swamp and Pine Upland flux stations.

Instrument	Model	Measurement	Distance above or below land surface, in m		
			Dwarf Cypress	Pine Upland	Cypress Swamp
Sonic anemometer	CSAT[1], Gill Windmaster Pro[2]	Wind velocity and direction	15.5	35.8	35.7
Gas analyzer	LI-7500A	Gas concentrations	15.5	35.8	35.7
Methane analyzer	LI-7700	Methane concentration	15.5	NA	NA
Pressure transducer	CS450	Water depth	−0.8	−0.5	−0.5
Air temperature	HMP-45C	Air temperature	15.5	35.8	35.8
Relative humidity	HMP-45C	Relative humidity	15.5	35.8	35.8
Net radiometer	NR-Lite	Net radiation	13.2	33.7	33.9
Soil heat flux	REB's	Soil heat flux	−0.2	−0.2	−0.2
Soil temperature	107L	Soil temperature	−0.2	−0.2	−0.2

[1] CSAT deployed at the Dwarf Cypress and Pine Upland sites.
[2] Gill Windmaster Pro deployed at the Cypress Swamp site.

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Table 3. Monthly and annual C and methane fluxes.

	Cypress Swamp			Dwarf Cypress				Pine Upland		
Month	–NEE*	Re*	GEE*	–NEE*	Re[1]	GEE*	CH_4*	–NEE*	Re*	GEE*
Dec 2012	–20	34	54	–18	27	45	0.7	–51	45	97
Jan 2013	–38	63	101	–24	36	59	0.6	–54	64	118
Feb 2013	–37	66	103	–27	43	70	0.5	–48	45	93
Mar 2013	–75	82	157	–27	40	66	0.5	–69	55	123
Apr 2013	–109	114	223	–51	44	94	0.7	–79	62	141
May 2013	–129	111	240	–60	45	105	0.6	–103	45	148
Jun 2013	–152	88	240	–60	43	103	1.3	–105	48	153
Jul 2013	–125	93	218	–60	46	106	1.5	–109	45	154
Aug 2013	–109	76	185	–47	37	84	2.2	–102	49	151
Sep 2013	–84	85	169	–35	35	70	1.8	–70	48	118
Oct 2013	–61	59	120	–27	29	55	1.2	–62	45	108
Nov 2013	–51	78	129	–25	31	56	0.8	–40	46	85
Annual total	–990	949	1939	–461	456	913	12	–892	597	1489

* Units are $g\,C\,m^{-2}\,month^{-1}$ or $g\,C\,m^{-2}\,year^{-1}$ for net ecosystem exchange (NEE), respiration (RE), gross exchange (GEE) and methane production (CH_4).

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Table 4. ET, NEE and WUE at the flux stations.

Site	ET[a]	−NEE[b]	WUE[c]
Pine Upland	955	−892	0.9/1.4
Dwarf Cypress	943	−461	0.5/0.8
Cypress Swamp	1150	−990	0.9/1.4

[a] Units are $mm\,year^{-1}$.
[b] Units are $g\,C\,year^{-1}$.
[c] Units are $g\,C\,(mm\,ET)^{-1}$ or (/) $mol\,CO_2\,(mol\,ET)^{-1}$.

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Table 5. Comparison of annual totals for NEE for different studies.

Ecosystem	NEE*	Climate	Reference
Taylor Slough (short sawgrass)	−50	Subtropics	Schedlbauer (2010)
Shark River Slough (short sawgrass)	45	Subtropics	Jimenez (2012)
Mangrove	−1170	Subtropics	Barr (2010)
Cypress Swamp	−990	Subtropics	This study
Dwarf Cypress	−461	Subtropics	This study
Pine Upland	−892	Subtropics	This study
White Oak	−296	Temperate	Botkin (1070)
Scarlet Oak	−274	Temperate	Botkin (1070)
Pitch Pine	−124	Temperate	Botkin (1070)
Everglades	−100 to > −200	Subtropics	Jones et al. (2014)

* Units are $g\,C\,m^{-2}\,year^{-1}$.

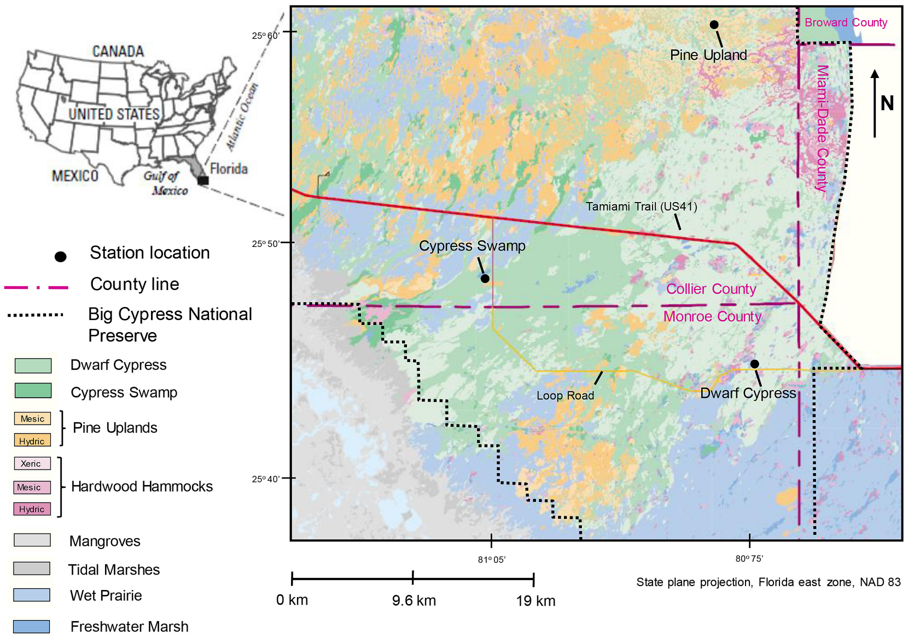

Figure 1. Location of the study area and vegetation communities, modified from Duever (2002).

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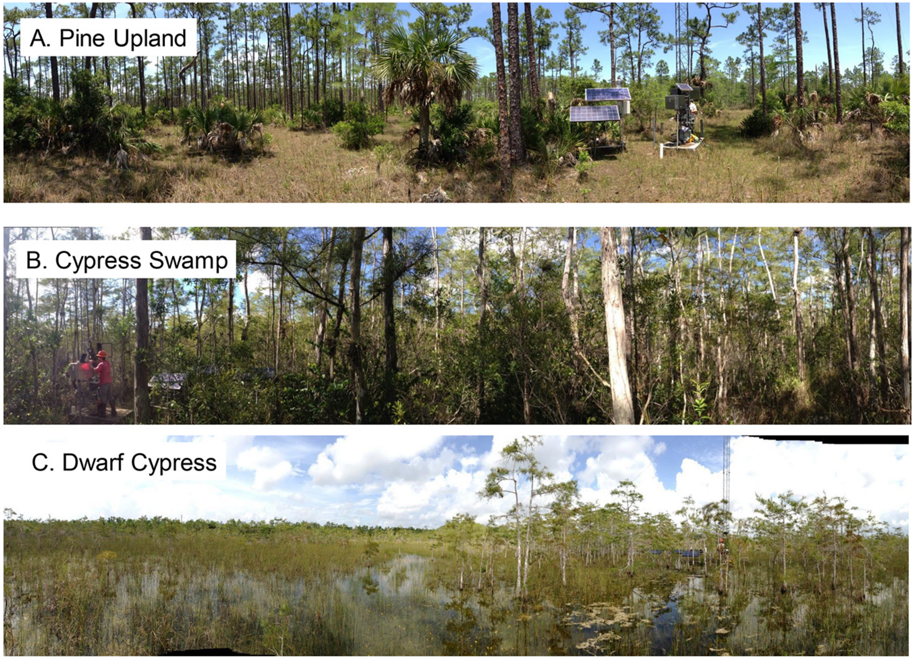

Figure 2. Panoramic photos of the **(a)** Pine Upland, **(b)** Cypress Swamp, and **(c)** Dwarf Cypress plant communities.

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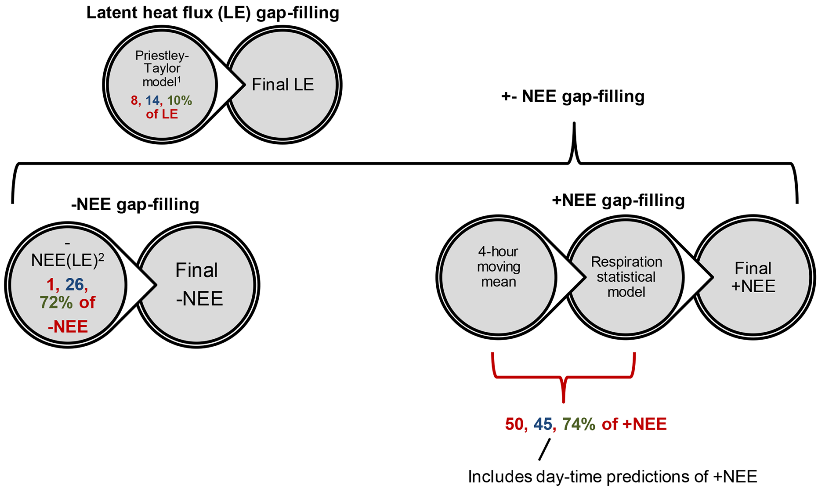

[1]Preistley-Taylor α = 0.45, 0.42, and 0.57 with R^2 = 0.57, 0.47, and 0.56 for Dwarf Cypress, Cypress Swamp and Pine Upland sites, respectively.

[2]Regression coefficients m= -0.0115, -0.0284, -0.0341 and b= -1.2297, -1.403, 0.00 with R^2 = 0.22, 0.37, and 0.36 for Dwarf Cypress, Cypress Swamp and Pine Upland sites, respectively.

Red, blue and **green** colors indicate the percentage of the time-series gap-filled with the model or function for the **Dwarf Cypress**, **Cypress Swamp** and **Pine Upland** sites, respectively.

Figure 3. Gap-filling equations for water and C fluxes.

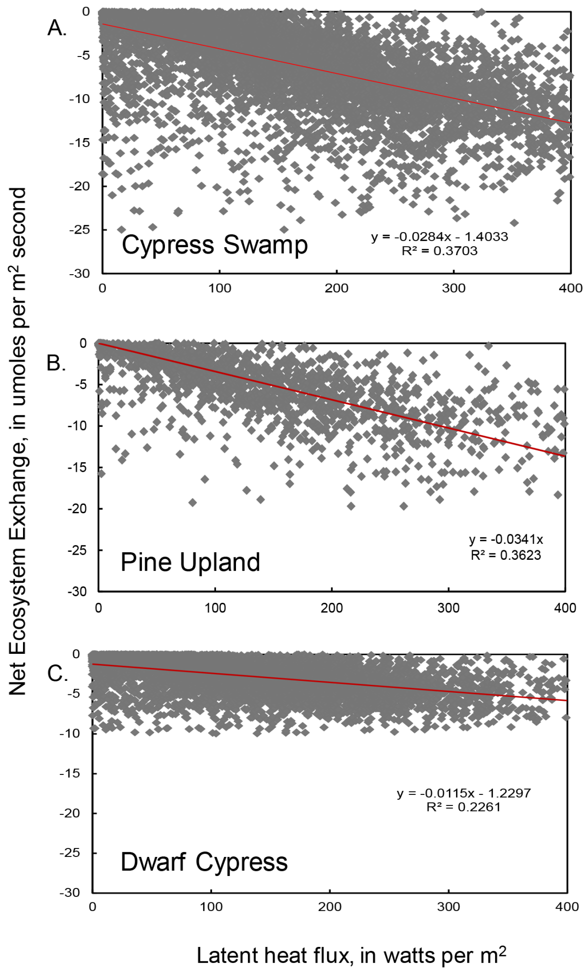

Figure 4. Relations between latent heat flux and net ecosystem exchange.

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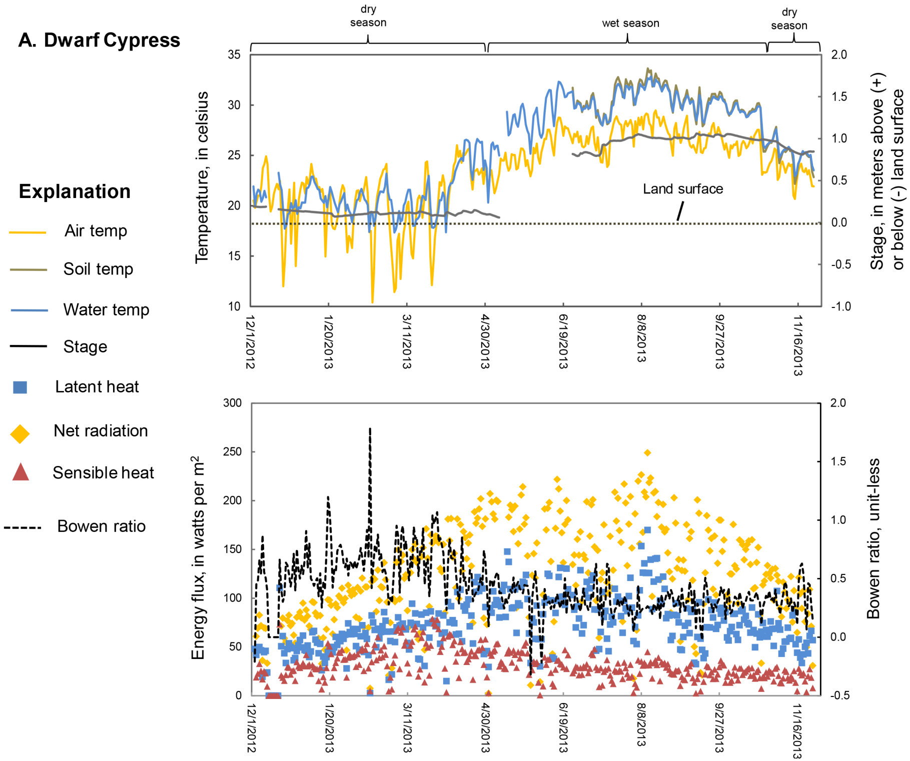

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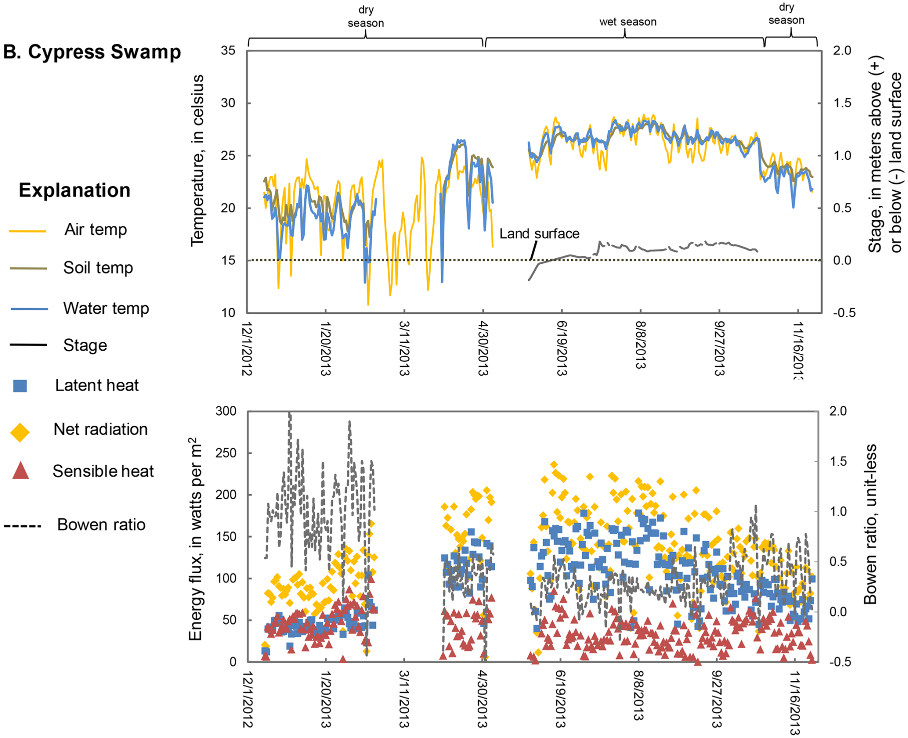

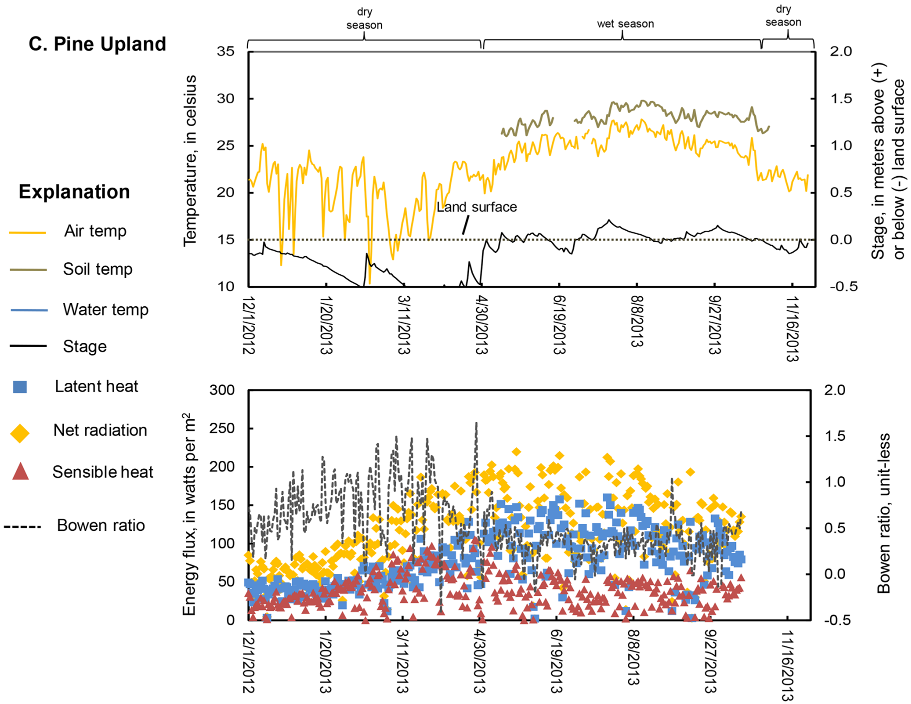

Figure 3. Mean daily temperature and surface energy fluxes at the **(a)** Dwarf Cypress, **(b)** Cypress Swamp and **(c)** Pine Upland sites.

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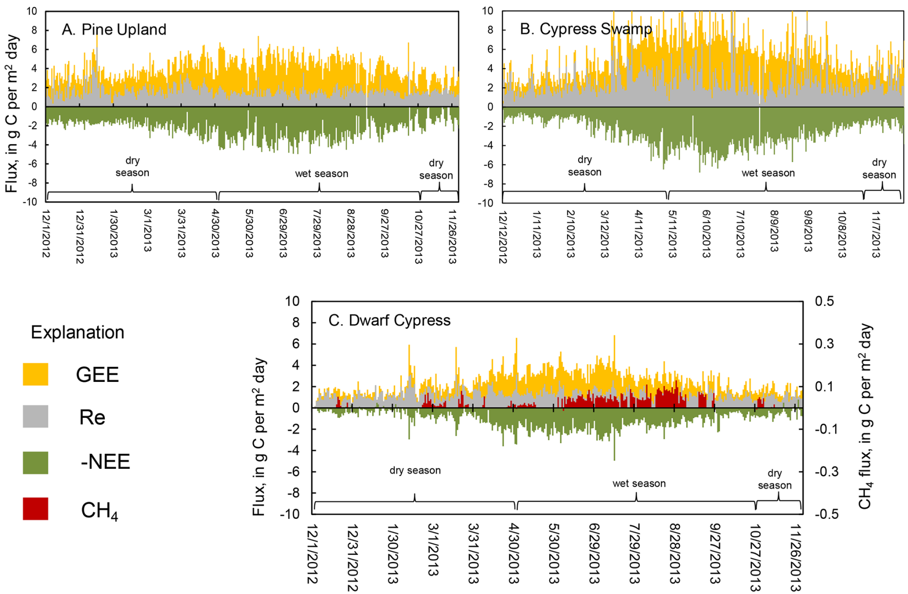

Figure 4. Daily C fluxes at the **(a)** Pine Upland, **(b)** Cypress Swamp and **(c)** Dwarf Cypress sites.

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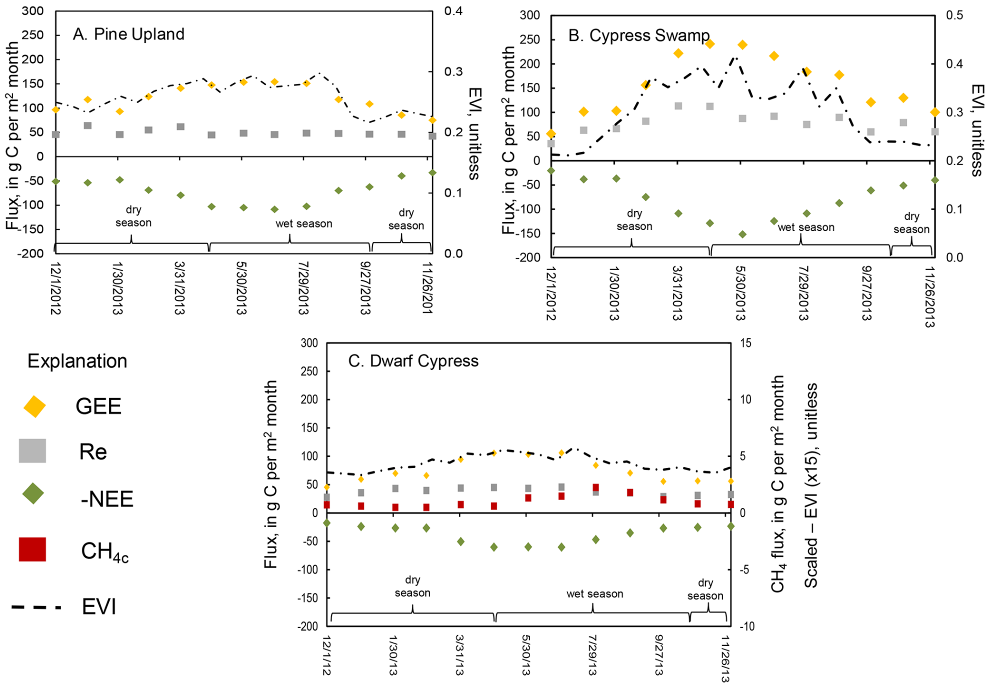

Figure 5. Monthly C fluxes and EVI at the **(a)** Pine Upland, **(b)** Cypress Swamp and **(c)** Dwarf Cypress sites.

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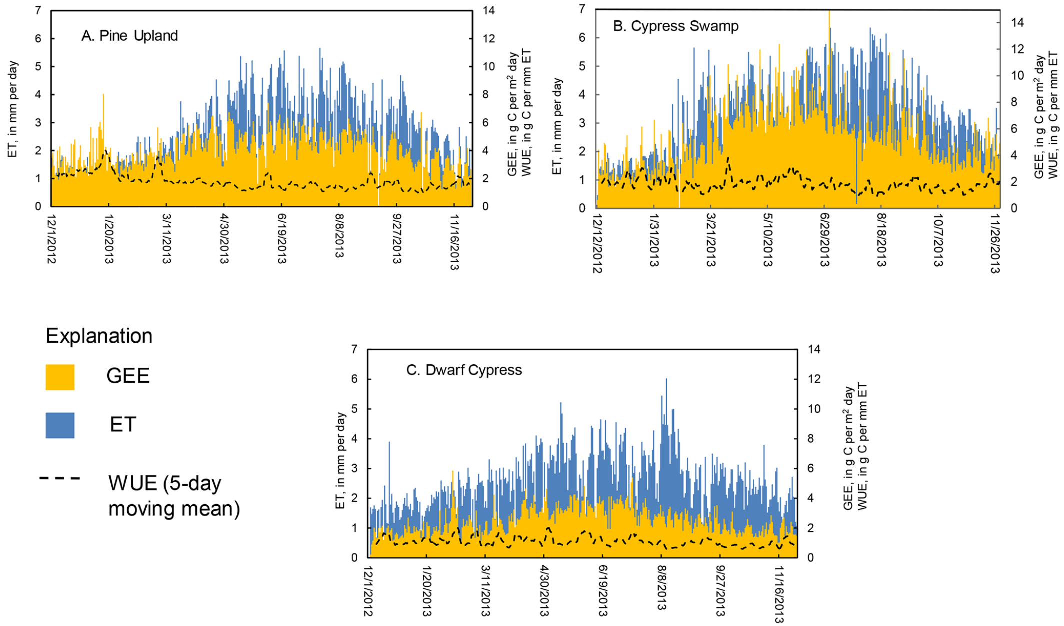

Figure 6. ET, GEE and WUE at the **(a)** Pine Upland, **(b)** Cypress Swamp and **(c)** Dwarf Cypress sites.

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C exchange between the atmosphere and subtropical forested wetlands

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