

Environmental controls over net ecosystem carbon exchange of scrub oak in central Florida

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Received 10 February 2006; accepted 8 September 2006

Abstract

Biological and physical controls regulating variation of seasonal and interannual ecosystem carbon exchange in a scrub oak ecosystem in central Florida were determined by measuring net ecosystem exchange of CO₂ (NEE) between the atmosphere and vegetation using the eddy covariance technique continuously for 6 years (April 2000–March 2006). Total net ecosystem production (NEP) was nearly 20 t C m⁻² during the 6-year study and annual NEP for each phenological year (April–March) increased annually from 107 to 467 g C m⁻² year⁻¹. Although this ecosystem was productive during all parts of each year, greatest absolute values of daytime NEE (NEE_{day max}) were –12.0 to –16.0 μmol CO₂ m⁻² s⁻¹ in the summertime when leaf area, air temperature and soil moisture peaked. NEE_{day max} decreased in magnitude to its lowest point in March when leaf area was lowest, and ranged between –7.6 and –9.8 μmol CO₂ m⁻² s⁻¹. Mean monthly nighttime NEE (NEE_{night}) was between 2.0 and 6.9 μmol CO₂ m⁻² s⁻¹ in the winter and summer, respectively, and was controlled primarily by temperature. Variation in seasonal NEP in this ecosystem occurred in three distinct phases. The first phase occurred in April through May with the emergence of new leaves and when soil respiration was low; daily carbon assimilation (1.0–2.4 g C m⁻² day⁻¹) was greatest during this 2-month period during which an average 38% of annual C assimilation occurred. During the second phase, June–September, the rate of carbon uptake (0.8–1.6 g C m⁻² day⁻¹) was dependent mainly on variation in temperature, precipitation and VPD; on average, only 12% of annual carbon assimilation occurred during these 4 months and in dry years (2000 and 2001), the ecosystem was a carbon source during this period. During the third phase, October–March, daily carbon assimilation (0.3–1.1 g C m⁻² day⁻¹) was intermediate between the first two phases, and accounted for nearly 50% of annual carbon accumulated during these 6 months. While mean daily NEP was highest in spring, NEE_{day} reached its greatest intensity in summer. In order of importance, PPFD, temperature, SWC, LAI, and VPD regulated NEE_{day}. Temperature and SWC were the main environmental variables controlling soil respiration, which was more than 85% of ecosystem respiration. Scrub oak represents a unique ecosystem in the southeastern US and within the Ameriflux network. These results are unique in establishing the role scrub oak plays in landscape and regional carbon budgets of this subtropical, evergreen, fire dependent and highly active ecosystem.

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Keywords: Eddy flux; Subtropical; Scrub oak; Net ecosystem exchange; Net ecosystem production; Ecosystem respiration; Soil respiration; Carbon balance

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Nomenclature

a	regression coefficient (Eq. (2))
b	regression coefficient (Eq. (2))
F_{CO_2}	CO_2 flux at measurement height ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
F_s	storage of CO_2 below measurement height ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
G	soil heat flux (W m^{-2})
H	sensible heat flux (W m^{-2})
LAI	leaf area index ($\text{m}^2 \text{ m}^{-2}$)
LE	latent heat flux (W m^{-2})
NEE	mean half-hour net ecosystem exchange ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
NEE_{day}	daytime, mean, half-hour, net ecosystem exchange ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
$\text{NEE}_{\text{day max}}$	monthly, mean-maximum, daytime net ecosystem exchange ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
$\text{NEE}_{\text{night}}$	nighttime, mean, half-hour, net ecosystem exchange ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
NEE_{opt}	optimum net ecosystem exchange at $\text{PPFD} = 2200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Eq. (1), $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
NEE_{res}	residuals of the relationship between NEE_{day} and PPFD
NEP	net ecosystem production (g C m^{-2})
PPFD	photosynthetically active photon flux density ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
Q_{10}	temperature coefficient
R_d	ecosystem dark respiration (Eq. (1), $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
R_{net}	net radiation (W m^{-2})
R_s	soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
SWC	volumetric soil water content (vol.%)
T_a	air temperature ($^{\circ}\text{C}$)
$T_{a \text{ avg}}$	monthly mean air temperature ($^{\circ}\text{C}$)
T_s	soil temperature ($^{\circ}\text{C}$)
u^*	friction velocity (m s^{-1})
VPD	vapor pressure deficit (kPa)
<i>Greek letter</i>	
α	apparent ecosystem quantum yield (Eq. (1))

1. Introduction

Understanding the carbon (C) balance of forests is central to predicting the role terrestrial ecosystems will

play in mitigating rising atmospheric CO_2 concentrations. Broadleaf forests comprise a considerable portion of global forests and range from deciduous in upper latitudes to evergreen in the tropics. Carbon budgets and the effects of environmental controls have been quantified with eddy covariance for many forests across this range producing variable results. Northern-hemisphere, temperate, broadleaf forests have been identified as an important sink for storing atmospheric CO_2 with annual uptake values ranging between 70 and 870 $\text{g C m}^{-2} \text{ year}^{-1}$ (Baldocchi et al., 2001; Law et al., 2002). The seasonality of C exchange in temperate broadleaf forests is marked by high productivity in the summer and low productivity in the winter (Falge et al., 2002) due to wide fluctuations in leaf area and temperature between seasons. Tropical broadleaf forests are moderate to strong C sinks, assimilating 100–792 $\text{g C m}^{-2} \text{ year}^{-1}$ (Grace et al., 1995; Malhi et al., 1998; Loescher et al., 2003), or small carbon sources (Miller et al., 2004). In contrast to temperate forests, tropical forests are productive throughout the year and the seasonality of C fluxes is small and controlled by precipitation (Malhi et al., 1998; Falge et al., 2002; Miller et al., 2004). Interannual variation in annual C uptake for both temperate and tropical forests has been attributed to macro-scale changes in climate, such as events regulated by El Niño Southern Oscillation, that affect precipitation, temperature and total insolation between years (Yamamoto et al., 1999; Baldocchi et al., 2001; Barr et al., 2002; Loescher et al., 2003).

In between these two regions are the subtropics where large-scale C isotopic measurements indicate that terrestrial regions are a small C source (Ciais et al., 1995). However, direct measurements of net ecosystem C exchange (NEE) of different ecosystems in the subtropical, humid climate of Florida have shown that forests in this region are moderate to strong C sinks (Clark et al., 1999, 2004; Dore et al., 2003; Hymus et al., 2003). We have made eddy covariance measurements over a scrub oak forest in central Florida since 2000 to evaluate its long term C budget. Central Florida's climate consists of seasonal precipitation and temperature patterns that are asynchronous: spring (April and May) is warm and dry, summer is warm and wet (June–October) and winter is cool and dry with temperatures that rarely fall below zero (Myers and Ewel, 1990). This general climatic pattern does not reflect the high variability of spring and summer precipitation nor weather events such as hurricanes, El Niño and La Niña, which greatly influence precipitation patterns (Myers and Ewel, 1990). La Niña is often associated with severe droughts in Florida. During this study, this scrub

oak ecosystem was subjected to a broad range of precipitation from severe drought to hurricanes. Moreover, scrub oak occurs on well drained sandy soils, suggesting that highly variable soil moisture may be an important factor regulating C exchange (Schmalzer and Hinkle, 1996).

Studying the C dynamics of the scrub oak ecosystem was important for two additional reasons. First, scrub oak has been identified as a distinctively unique ecosystem within the Ameriflux network (Hargrove et al., 2003; W. Hargrove, personal communication). Secondly, fire is an important process in regulating many of Florida's natural ecosystems including scrub oak, which has a fire return cycle of 10 or more years (Myers and Ewel, 1990). Aboveground C gains between burn cycles are temporary since substantial amounts of aboveground C are lost to the atmosphere during a fire. However, the amount of C accumulated belowground between burns may be the key to understanding the long-term C sequestration potential of fire maintained systems.

We had two research objectives. The first was to quantify scrub oak net ecosystem exchange over a range of temporal scales from half-hour to annual. This work will greatly aid the interpretation of our 10-year record of the effects of elevated atmospheric CO₂ on ecosystem gas exchange measured using open-top chambers. The second was to identify the magnitude and temporal scales that leaf area, air temperature, soil moisture, vapor pressure, and solar radiation influence scrub oak C fluxes.

2. Study site and methods

2.1. Study site

The study site was situated in a 10 ha scrub oak ecosystem within the Kennedy Space Center on the east coast of central Florida (28°36'N, 80°42'W). Scrub oak is an evergreen, xeromorphic, shrub community with a canopy height of 1–2 m. It is dominated by three oak species, *Quercus myrtifolia* Willd., *Q. geminata* Small, and *Q. chapmanii* Sargent, and saw palmetto, *Serenoa repens* Small (Myers and Ewel, 1990; Schmalzer and Hinkle, 1992; Dijkstra et al., 2002). Scrub oak sheds old leaves in February and March and new leaves emerge during April with a secondary smaller flush in July or August (Li et al., 2000). Soils are well-drained Pomello sands (Huckle et al., 1974; Schmalzer and Hinkle, 1996). The Kennedy Space Center has managed this ecosystem with periodic (5–7 years) controlled burns since 1969 (Duncan et al., 1999). A prescribed fire in

August 1995 burned the site. The ecosystem regenerated naturally from roots and rhizomes within a few weeks of the burn. The site was completely covered with new shoots after the spring flush in April 1996 and by the Spring of 2000 achieved LAI of 1.7, when measurements reported here began.

2.2. Eddy covariance

From April 2000 to March 2006, net ecosystem exchange of CO₂, H₂O and sensible heat were measured using the eddy covariance technique (Aubinet et al., 2000; Baldocchi, 2003; Lee et al., 2004). From April 2000 to July 2004 a closed-path IRGA (LI-6262, LI-COR Inc., Lincoln, NE) was used with a Gill R3 sonic anemometer (Gill Instruments, Lymington, UK). The anemometer was mounted on top of a mast with the sensor head 3.5 m above the forest floor. Scalar concentrations were sampled through a 13 m long, 4 mm internal diameter, Impolene tube. The tube inlet was protected with a Gelman filter and positioned 10 cm horizontally from the anemometer head. Air was drawn through the IRGA at 9 l min⁻¹ to generate turbulent flow and attenuate temperature fluctuations (Leuning and Judd, 1996). The last 2 m of the tube was covered with a heating element and insulation to help prevent condensation. The IRGA was calibrated weekly using a traceable ($\pm 1\%$) standard for CO₂ and a dew point generator (LI-COR 610, LI-COR, Inc.) for water vapor. Raw data were logged at 20 Hz and calculated fluxes were averaged over 30 min. Corrections for coordinate rotation, and dampening of gas concentrations due to the sampling tube, sensor separation and sampling frequency were applied (Aubinet et al., 2000; Dore et al., 2003). Between March 2004 and March 2006 an open-path IRGA (LI-7500, LI-COR, Inc.) was used with a CSAT3 sonic anemometer (Campbell Scientific, Logan, UT). The open-path flux measurements were made at 4.1 m above the forest floor. The LI-7500 head was situated 20 cm horizontally from the sonic anemometer head and tilted 45°N to prevent contamination from solar radiation. Raw data were logged at 10 Hz and the WPL correction (Webb et al., 1980), coordinate rotation, and frequency response correction were applied to mean half-hourly fluxes of NEE. A comparison of data collected simultaneously from both systems showed that there was only a 3% difference in CO₂ flux measurements. The fetch from the tower was greater than 200 m in all directions. A simulation of the flux footprint (Schmid, 1997) showed that a majority of the fluxes were generated within 15–30 m of the tower and that >70% of the fluxes

originated within 100 m during the day and 140 m at night (Dore et al., 2003).

Half-hour flux data were eliminated if they met the following criteria: (1) incomplete half-hour measurement, (2) precipitation occurred during that half-hour, (3) decoupling of the canopy from the atmosphere as determined by a friction velocity (u^*) below a critical value between 0.07 and 0.15 m s⁻¹ (seasonally determined, Dore et al., 2003), (4) spurious variance values for either of the three wind velocities or scalars. In total, ecosystem fluxes were measured 70% and >90% of the time with the closed-path and open-path systems, respectively, and approximately 30% of those values were eliminated by the screening criteria listed above. The system was not operational from October to December 2000 and parts of July and August 2003, due to instrument damage. The quality of our data were evaluated in two ways; first by the degree of energy closure ($R_{\text{net}} - G$ versus $LE + H$), which was >85% each year, and second, in a comparison with simultaneous measurements from the roving Ameriflux calibration system, where flux estimates from both systems were within 3%.

Measurements of half-hour NEE were calculated as $NEE = F_{\text{CO}_2} + F_S$, where F_{CO_2} was the mean flux of CO₂ at measurement height and F_S was the half-hour change in CO₂ stored below measurement height. Because of the short stature (~1.5 m) of this ecosystem, the change in CO₂ storage was calculated from the difference in successive CO₂ concentrations at the measurement height (Hollinger et al., 1994). The terrain of the site was flat and therefore we assumed that CO₂ drainage was insignificant. We used the meteorological convention that a positive sign indicated transfer of CO₂ from the ecosystem to the atmosphere.

Half-hourly measurements of NEE were divided into daytime (NEE_{day} , PPFD > 10 μmol m⁻² s⁻¹) and nighttime (NEE_{night}) periods to develop non-linear regressions for both evaluating environmental effects on NEE and gap filling missing half-hours. Light response curves were established by further dividing daytime data into monthly bins and then fitting the relationship between NEE_{day} and PPFD to a modified Michaelis–Menten (Michaelis and Menten, 1913) function in the form (Falge et al., 2001):

$$NEE_{\text{day}} = \frac{\alpha \text{PPFD}}{1 - (\text{PPFD}/2200) + (\alpha \text{PPFD}/NEE_{\text{opt}})} + R_d \quad (1)$$

NEE_{opt} (μmol CO₂ m⁻² s⁻¹) was the optimum rate of CO₂ exchange at maximum observed PPFD = 2200 μmol m⁻² s⁻¹, α (μmol CO₂ μmol⁻¹ of photon)

was the ecosystem apparent quantum yield when PPFD = 0, and R_d (μmol CO₂ m⁻² s⁻¹) was mean dark ecosystem respiration (NEE_{day} at PPFD = 0). Missing half-hours of daytime NEE were modeled using half-hourly measurements of PPFD and monthly parameters fitted to Eq. (1) (Falge et al., 2001).

The exponential function:

$$NEE = a \exp^{(bT)} \quad (2)$$

where a and b are regression coefficients, was used to describe the effects of temperature (T , °C) on NEE. Regressions between monthly mean measurements of NEE_{night} and mean air temperature were established for each phenological year, April–March. In the year April 2004 to March 2005, two regressions were used, each representing the period before and after the hurricane, respectively. This parameterization was subsequently used to gap fill missing half-hours of NEE_{night} (Falge et al., 2001). SigmaPlot 8.0 Regression Wizard software (SPSS Inc., Chicago, IL) was used to calculate regression parameters fitted to Eqs. (1) and (2) and their significance. Measured plus gap-filled NEE_{day} and NEE_{night} data were summed to estimate net ecosystem productivity, NEP ($NEE = -\text{NEP}$).

2.3. Soil respiration

Twenty-two PVC collars were permanently inserted 5 cm into the soil inside the fetch of the eddy covariance system. Carbon dioxide efflux from the soil (R_s) was measured periodically from June 2000 to December 2005 by placing a portable gas exchange system (LI-6400, LI-COR, Inc.) over the collars. Soil temperature (T_s) and soil water content (SWC) were recorded for each measurement.

2.4. Meteorological measurements

Photosynthetically active photon flux density (PPFD, LI-190, LI-COR, Inc.), air temperature (T_a , copper/constantan thermocouple, Omega, CT), relative humidity (RH, HMP45C, Campbell Scientific), net radiation (R_{net} , Q-7.1, Radiation and Energy Balance Systems, Inc., Bellevue, WA), and precipitation (TE525 tipping bucket, Campbell Scientific) were measured continuously at 3.5 m on a meteorological tower located 30 m from the eddy flux tower. Soil temperature (T_s , copper/constantan thermocouple) and soil water content (SWC, CS615, Campbell Scientific) were measured adjacent to the meteorological tower. T_s was measured at depths of 3 and 10 cm. The SWC probe was inserted diagonally

into the soil to integrate over the top 15 cm of soil. Ecosystem soil heat flux (G) was estimated by averaging soil heat flux measurements calculated from two soil heat flux plates (HFT-3, Radiation and Energy Balance Systems, Inc.) buried 10 cm below the soil surface in two separate locations, 10 m from the meteorological tower. The soil heat flux for each sensor was calculated as the sum of soil heat flux measured at sensor depth (10 cm) and the energy stored in the soil above the sensor, S ($G = G_{10\text{ cm}} + S$). Soil bulk density of 0.99 g cm^{-3} (Schmalzer et al., 2001) and a dry-soil heat capacity of $840\text{ J kg}^{-1}\text{ K}^{-1}$ were used with half-hourly measurements of T_s and SWC to calculate S (HFT-3 technical reference).

2.5. Measurement of biomass

Species inventories and above ground biomass were sampled in January of 2003 and 2004 using 12 census plots ($1.5\text{ m} \times 1.5\text{ m}$). The census plots were situated 15 m apart, along two transects that intersected at the eddy flux tower. Species biomass and growth increment were estimated from allometric relationships based on basal stem diameter at soil level for the oak species (Dijkstra et al., 2002) and minor woody species (S. Dore, unpublished data), and frond length for the saw palmetto (Gholz et al., 1999). Litterfall was collected monthly from sixteen 0.1 m^2 litterfall traps. Litterfall was dried for 3 days at $70\text{ }^\circ\text{C}$, and then weighed once separated into leaves, palm biomass, and woody and miscellaneous material. Monthly litterfall values were corrected for a decomposition rate of 40% (R. Gifford, unpublished data) prorated over the 12-month collection interval.

Leaf area index was estimated by applying the Beer–Lambert Law to the attenuation of PPFD through the canopy (Hymus et al., 2002). A 40 cm sunfleck ceptometer (Decagon Devices, Pullman, WA) was used to measure PPFD above and below the canopy at 32 points situated 5 m apart along N–S and E–W transects with the tower intersecting the midpoint of both transects.

3. Results

3.1. Environmental conditions

Long-term (1971–2000) mean annual precipitation recorded on the Kennedy Space Center was 1340 mm (NCDC, 2002). The ecosystem was subjected to a severe drought during the first 2 years of the study. Annual precipitation during each phenological year

(April–March) was 993 mm in 2000–2001, 828 mm in 2001–2002, 1177 mm in 2002–2003, and 1130 mm in 2003–2004, 1395 mm in 2004–2005, and 1340 mm in 2005–2006 (Fig. 1a). Summer months were wet and winter and spring months dry (Fig. 1a). Soil water content was highly variable from week to week owing to the well-drained sandy soil; however, mean monthly SWC followed precipitation patterns (Fig. 1b). SWC was persistently low during the first year of the study due to the drought. Hurricanes that impacted central Florida in September 2004 and October 2005 resulted in exceptionally high amounts of precipitation and SWC for those months reflect this.

Minimum mean air temperature occurred in January and maximum mean air temperature occurred in July–September of each year (Fig. 1c). The departure of mean monthly air temperature from the long-term mean is given in Fig. 1d. The annual maximum for integrated monthly PPFD occurred in May, 1 month prior to the summer solstice (Fig. 1e). Cloud cover from the rainy season starting in June caused integrated monthly PPFD to be lower in June and July compared to April and May.

3.2. Biomass and leaf area

Three oak species, *Q. myrtifolia*, *Q. geminata* and *Q. Chapmanii* accounted for 89% of the standing above-ground biomass. Saw palmetto, *Serenoa repens*, accounted for approximately 10% and all other species amounted to 1% of the remaining aboveground biomass. Biomass components for this ecosystem are given in Table 1. Total aboveground plant growth for 2003 was $220.0\text{ g C m}^{-2}\text{ year}^{-1}$ and litter production was $165.4\text{ g C m}^{-2}\text{ year}^{-1}$, yielding a total of $385.4\text{ g C m}^{-2}\text{ year}^{-1}$ (Table 1).

The seasonal trend of LAI was similar each year (Fig. 1f). Minimum LAI occurred in March when the oak species exchanged their leaves. Maximum LAI was generally sustained from July to October each year. Maximum summertime LAI during the first two summers (2000–2001) was approximately 1.9 (Fig. 1f). Maximum summertime LAI increased by approximately 25% in 2003–2005. LAI was not measured during 2002. High winds from the hurricane in September 2004 resulted in an abrupt 25% reduction in LAI, which was not recovered until the following spring leaf flush.

3.3. Net ecosystem exchange

The seasonal pattern of monthly, mean–maximum daytime NEE ($NEE_{\text{day max}}$) followed the same trend each year (Fig. 2) ($NEE_{\text{day max}}$, was calculated as

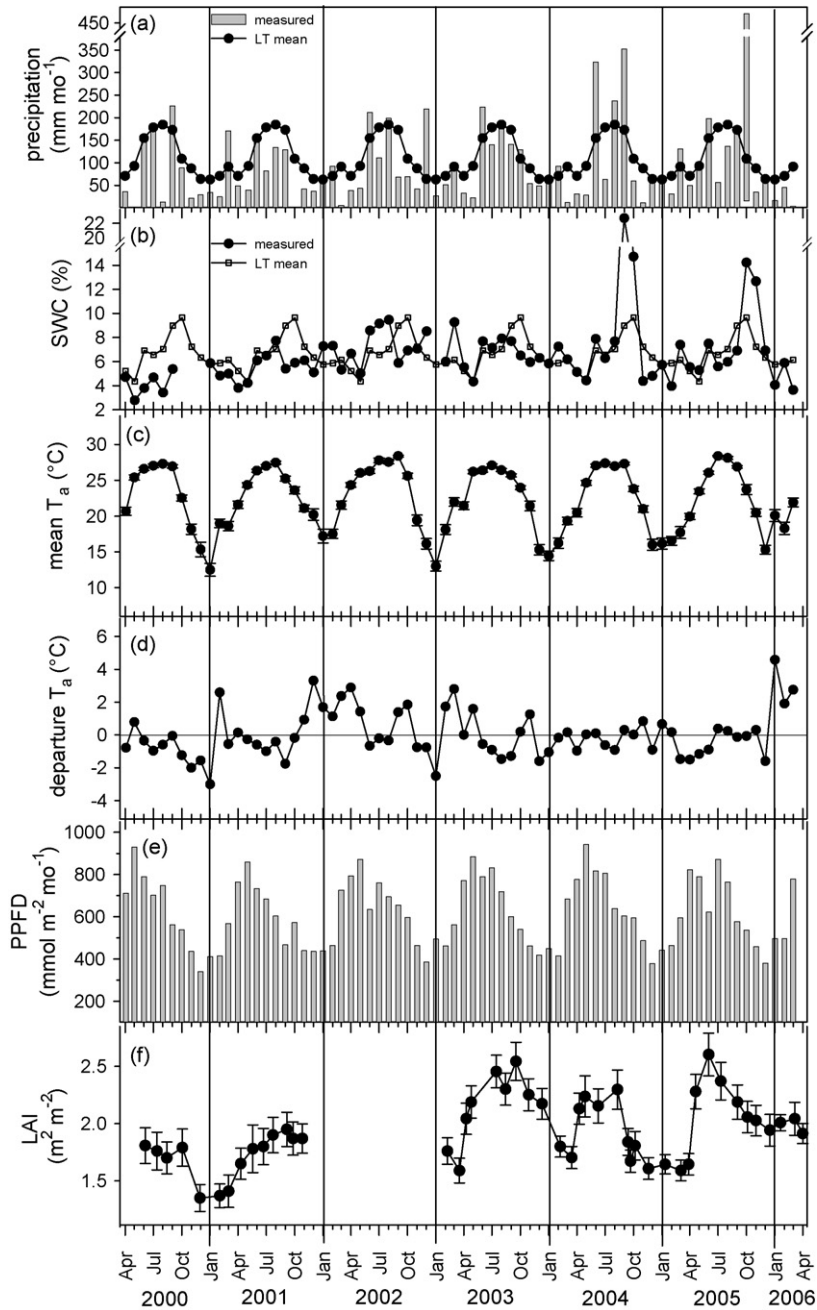


Fig. 1. (a) Monthly precipitation for the scrub oak site (bars) and long-term monthly mean precipitation from 1971 to 2000 (NCDC, circles). (b) Monthly surface (0–15 cm) soil water content, SWC (closed circles), and monthly mean SWC averaged over the study period (open squares). (c) Monthly mean air temperature, T_a (± 1 S.E.). (d) Departure of mean monthly T_a from long-term averages. (e) Monthly integrated photosynthetically active photon flux density (PPFD). (f) Monthly leaf area index (LAI, mean ± 1 S.E., $n = 20$).

NEE_{day} using light response curve parameters and the theoretical maximum PPFD for each month fitted to Eq. (1)). The absolute magnitude of $NEE_{day\ max}$ sharply increased each spring and reached -12.0 to $-16.0\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ during the summertime and peak rainy season (June–October) each year (Fig. 2a).

The magnitude of $NEE_{day\ max}$ began to decrease in November and reached -7.6 to $-9.8\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ in March when LAI was lowest. $NEE_{day\ max}$ for May and June 2000 contrasted sharply with successive years, reaching only $-7.5\ \mu\text{mol CO}_2\ \text{m}^{-2}\ \text{s}^{-1}$ —a value otherwise observed in March and was attributed to the severe

Table 1
Biomass estimates from the January 2003 census and estimates of annual carbon increment for 2003

Standing biomass (g C m ⁻²)	
Aboveground	
Oak species (<i>Quercus myrtifolia</i> , <i>geminata</i> , <i>chapmanii</i>)	
Woody tissue	653.8 ± 225.5
Foliage	300.3 ± 95.6
Saw palmetto (<i>Serenoa repens</i>)	121.5 ± 32.5
Other species	4.5 ± 4.2
All roots ^a	2323.0
Forest floor ^b	342.4
Total	3745.5
Biomass increment (g C m ⁻² year ⁻¹)	
Oak species	
Aboveground woody tissue	153.0 ± 36.6
Foliage	67.8 ± 16.9
Saw palmetto	-2.0 ± 3.1
Other species	1.2 ± 0.7
Litter production ^c	165.4 ± 17.7
Total above ground production	385.4

Mean ± S.E., n = 12.

^a Root biomass sampling May 2002, Frank Day (personal communication).

^b Age = 7 years, log₁₀ litter biomass (g) = 0.558 log₁₀ age + 2.364 (Schmalzer and Hinkle, 1996), assuming biomass = 50% C.

^c Corrected for an annual decomposition rate of 40%, unpublished data from Roger Gifford.

drought effect. In September 2004, NEE_{day max} abruptly decreased in magnitude by 22% due to defoliation from the hurricane. NEE_{day max} for July and August 2005 were out of phase with previous years and this was attributed to very dry conditions. (Although total precipitation in

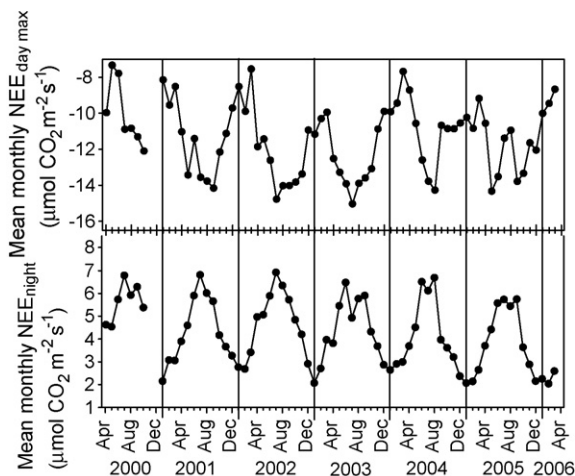


Fig. 2. Seasonal course of (a) monthly, mean-maximum, daytime net ecosystem exchange (NEE_{day max}) and (b) monthly, mean, nighttime net ecosystem exchange (NEE_{night}).

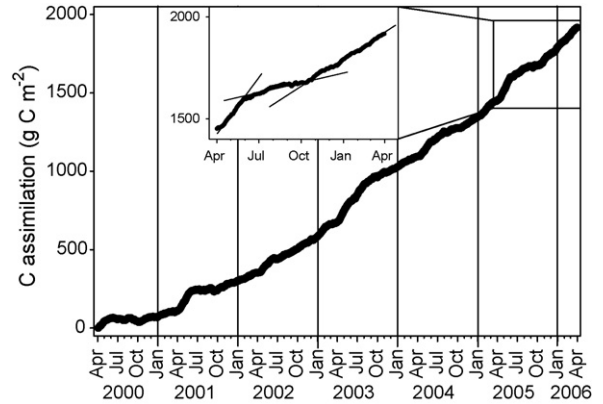


Fig. 3. Scrub oak net C assimilation over the study period. The inset is an enlargement of 2005 to highlight, with inserted lines, the three distinctive periods of C assimilation.

August 2005 was average, rain quality was poor, where events of 50+ mm were preceded and followed by long hot spells with little or no rain.)

The seasonal evolution of nighttime respiration was similar each year except 2004 when respiration fell sharply in September following the hurricane (Fig. 2b). Maximum NEE_{night} was 6.4–6.9 μmol CO₂ m⁻² s⁻¹ and occurred between June and July. Minimum NEE_{night} was 2.0–2.8 μmol CO₂ m⁻² s⁻¹ and occurred between January and February.

This ecosystem gained nearly 20 t C m⁻² during the 6-year study, April 2000–March 2006 (Fig. 3). Annual NEP increased each year of the study from 107 to 467 g C m⁻² year⁻¹ with the exception of 2004–2005, when hurricane Frances reduced LAI by 25% (Table 2). Carbon assimilation was seasonal with three distinctive phases during each phenological year (Fig. 3, inset). The highest rate of carbon assimilation occurred in the 2-month period, April and May, when new leaves appeared (Fig. 3). During this time, the rate of carbon assimilation was between 1.0 and 2.4 g C m⁻² day⁻¹ with the highest rates occurring during the relatively

Table 2

Daily rate of C assimilation for each season (g C m⁻² day⁻¹ = 24 h) and annual net ecosystem production (g C m⁻² year⁻¹) for each phenological year (April–March)

Year	April–May	June–September	October–March	Annual NEP
2000–2001	1.0	na	0.3	107
2001–2002	2.1	na	0.5	246
2002–2003	1.3	0.8	0.8	321
2003–2004	2.6	1.6	0.6	419
2004–2005	1.5	1.0	0.8	352
2005–2006	2.41	0.9	1.1	467

warm, wet spring of 2003 (Table 2). This contrasts with the summer period, June through September, when the daily rate of carbon assimilation was 0.8–1.6 g C m⁻² day⁻¹ (Table 2, Fig. 3). Carbon uptake per day was lowest during winter (October through March) at 0.3–1.3 g C m⁻² day⁻¹. Although the correlation between annual NEP and precipitation (Fig. 4a) was relatively low ($R^2 = 0.44$), SWC was an important factor controlling the interannual variation in mean daily NEP during the winter months (Figs. 4b and 9). Almost 40% (range: 23–61%) of total annual carbon assimilation occurred in the 2-month period between April and early June, an additional 50% (range: 32–65% of total) came in during the winter months, while an average of about 12% (range: -25 to 36% of total) came in during the 4-month summer (Table 2, Fig. 3). Although the magnitude for both NEE_{day} and NEE_{night} was greatest in June, July and August (Fig. 2), NEP was

greatest during spring (Fig. 3). Summer was also the most variable period for carbon assimilation when the system was a source of carbon during years when severe drought occurred.

3.4. Environmental controls over NEE

This ecosystem was photosynthetically active during all parts of the year and PPFD was the strongest control over half-hourly daytime C fluxes (Fig. 5). During any month, PPFD accounted for >75% of the variation in mean half-hour NEE_{day} . The parameters describing the response of NEE_{day} to light for each month are given in Fig. 6. Relatively high VPD also produced a secondary constraint on NEE_{day} (Fig. 5b). However, the magnitude of its effect was variable and seemed to depend on the availability of soil water. For example, high VPD suppressed NEE_{day} during drier summertime months,

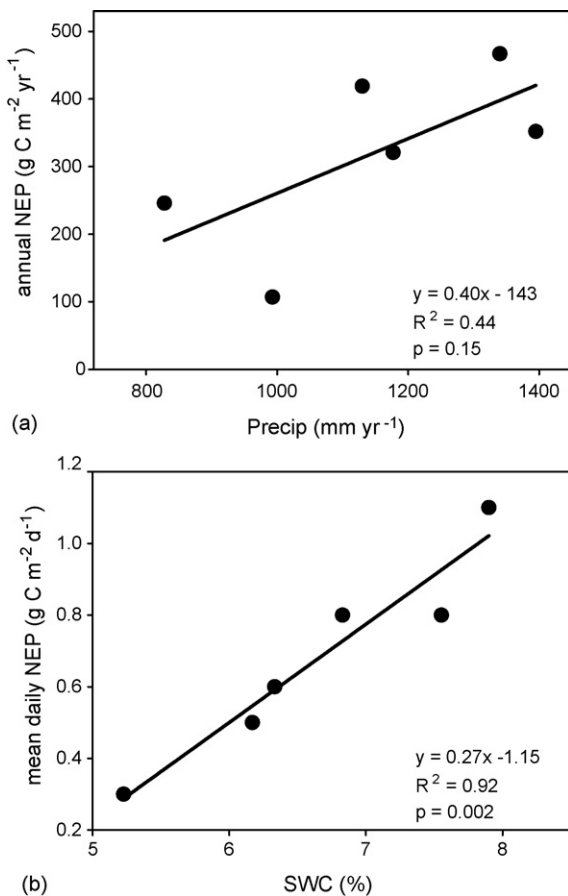


Fig. 4. (a) Annual net ecosystem production (NEP) as a function of annual precipitation. (b) Mean daily NEP as a function of mean surface soil moisture (SWC, 0–15 cm) during the period of October–March for each year.

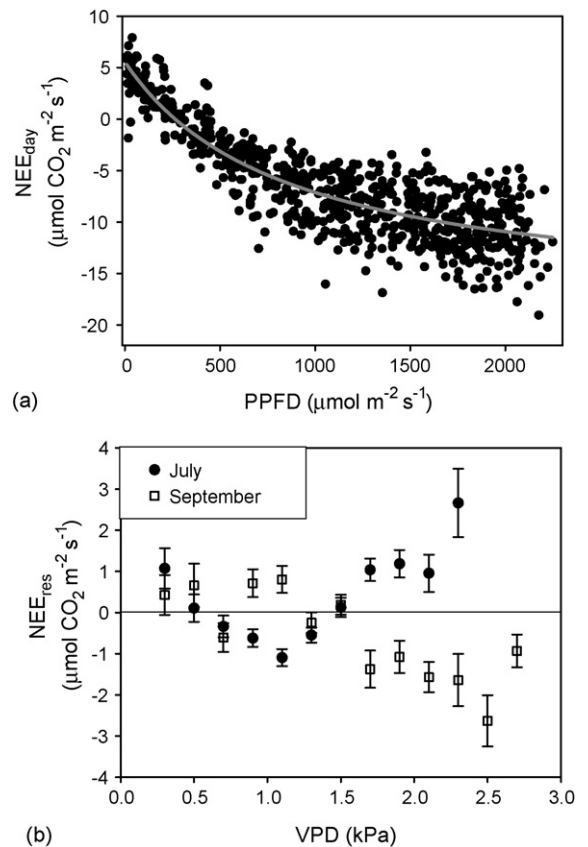


Fig. 5. (a) The relationship between daytime net CO₂ exchange (NEE_{day}) and photosynthetically active photon flux density (PPFD) for July 2005 ($R^2 = 0.79$, $p < 0.001$, $n = 722$). (b) Two contrasting monthly relationships between the residuals of the relationship between NEE_{day} and PPFD—closed circles: July 2005 (dry month), open squares: September 2005 (wet month).

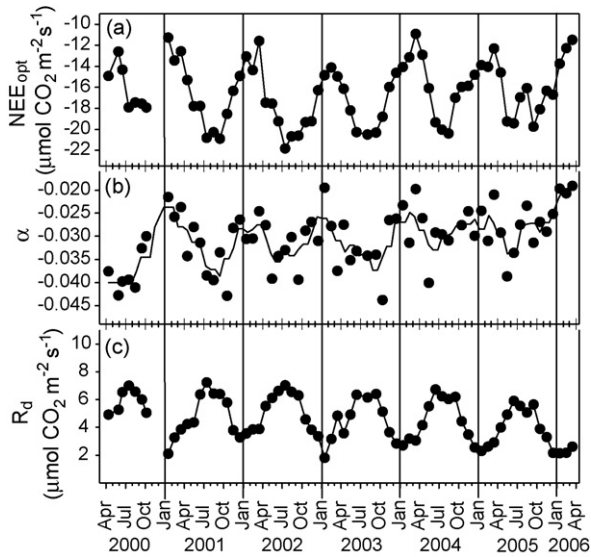


Fig. 6. Seasonal course of light response curve parameters derived from Eq. (1). (a) Monthly optimum net ecosystem exchange, NEE_{opt} . (b) Monthly apparent ecosystem quantum yield, α , with a 3-month, running mean fit through the data. (c) Dark respiration, R_d .

such as July 2005, and appeared to have little effect on NEE_{day} during warmer months with plenty of precipitation, such as September 2005 (Fig. 5b).

An analysis of monthly light response curve parameters NEE_{opt} , and α (Eq. (1)) was used to evaluate which environmental and biological variables imposed seasonal constraints on NEE_{day} . NEE_{opt} is the lower boundary of points on the light response curve (Fig. 5a) and represents the maximum capacity of this ecosystem to take up C during each month when light is not limiting. NEE_{opt} showed a strong seasonal pattern. Minimum NEE_{opt} ($-20 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) occurred between July and September and maximum NEE_{opt} (-12 to $-14 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) occurred between January and March (Fig. 6a).

The seasonal variation in NEE_{opt} was explained by variation in mean monthly air temperature ($T_{a \text{ avg}}$), SWC and LAI (Fig. 7). LAI and $T_{a \text{ avg}}$ were weakly correlated ($R^2 = 0.27$, $p = 0.002$) and therefore, it was difficult to determine the degree each contributed to regulating NEE_{opt} . Soil moisture was not significantly related to either LAI or $T_{a \text{ avg}}$. When pooled over the entire study period, $T_{a \text{ avg}}$ predicted 51% of the variation in NEE_{opt} (Fig. 7a). Soil moisture significantly

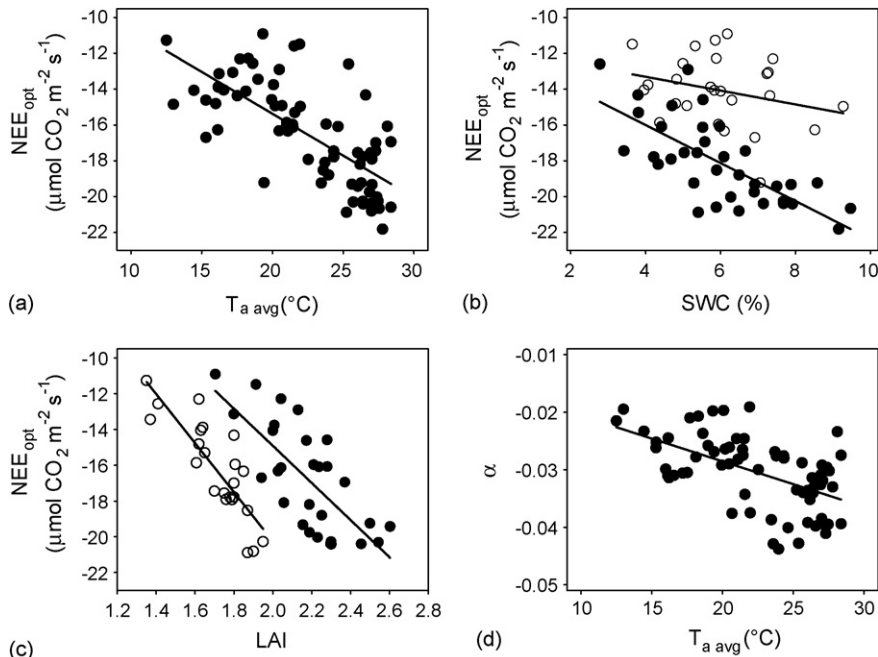


Fig. 7. Environmental and biological controls over light response curve parameters NEE_{opt} and α (Eq. (1)). The relationships between monthly NEE_{opt} and (a) monthly, mean air temperature, $T_{a \text{ avg}}$ ($R^2 = 0.51$, $p < 0.001$), (b) soil water content at 0–15 cm, SWC, for April–October (closed circles, $R^2 = 0.53$, $p < 0.001$) and November–March (open circles, $R^2 = 0.07$, $p = 0.18$), and LAI when the ecosystem was stressed by drought or hurricane damage, 2000–2001 and September 2004–March 2005, respectively (open circles, $R^2 = 0.71$, $p = 0.002$), or under average environmental conditions January 2003–July 2004 and April 2005–March 2006 (closed circles, $R^2 = 0.53$, $p < 0.001$). (d) The relationship between $T_{a \text{ avg}}$ and apparent ecosystem quantum yield, α ($R^2 = 0.38$, $p < 0.001$).

Table 3

Model parameters, statistics and Q_{10} values for the relationship between mean monthly nighttime net exchange of CO_2 and mean monthly air temperature (Eq. (2))

Period	Model parameters		Statistics			Q_{10}
	a	b	R^2	n	p -Value	
Pooled over all 6 years						
April 2000–March 2006	0.70 ± 0.08	0.079 ± 0.005	0.83	70	<0.001	2.2
Phenological years						
April 2000–March 2001	0.94 ± 0.28	0.069 ± 0.012	0.86	10	<0.001	2.0
April 2001–March 2002	0.52 ± 0.10	0.092 ± 0.008	0.95	12	<0.001	2.5
April 2002–March 2003	0.92 ± 0.20	0.069 ± 0.009	0.90	12	<0.001	2.0
April 2003–March 2004	0.91 ± 0.21	0.069 ± 0.010	0.87	12	<0.001	2.0
January 2004–August 2004 ^a	1.44 ± 0.04	0.052 ± 0.001	0.61	1930	<0.001	2.2
September 2004–March 2005 ^a	0.88 ± 0.04	0.074 ± 0.002	0.43	1949	<0.001	1.7
April 2005–March 2006	1.29 ± 0.04	0.054 ± 0.001	0.47	2491	<0.001	2.4

^a The respiration function in this phenological year was altered by a hurricane that affected the research site in September 2004. Therefore, pre-hurricane data that dates back to January 2004 and post-hurricane respirations functions were established.

influenced NEE_{opt} during April–October ($R^2 = 0.55$, $p < 0.001$), yet between November and March there was no effect ($R^2 = 0.07$, $p = 0.18$, Fig. 7b). (The SWC data points from the hurricane influenced months September and October 2004 and October 2005; these outliers are excluded from this analysis.) A general linear model (GLM procedure in Systat 11, Systat Software Inc., Richmond CA) showed that the interactive effect of $T_{\text{a avg}}$ and SWC pooled over the entire study accounted for 66% of the seasonal variation in NEE_{opt} ($\text{NEE}_{\text{opt}} = -0.73\text{SWC} (\%) - 0.48T_{\text{a avg}} (\text{°C}) - 1.45$, $R^2 = 0.66$, $p < 0.01$, $n = 64$, SWC: $p = 0.01$, $T_{\text{a avg}}$: $p < 0.01$). Not surprisingly, the role LAI played in C uptake was markedly different under two contrasting environmental conditions—one when the ecosystem was stressed by either drought (2000 and 2001) or hurricane damage (September 2004–March 2005), and the other when the ecosystem was not under any apparent long-term or extreme environmental stress (Fig. 7c). LAI seemed to be the strongest over all control over the seasonality of NEE_{opt} when the ecosystem was under environmental stress accounting for 71% of its variation. However, LAI accounted for 53% of the variation in NEE_{opt} when the ecosystem was not under environmental stress. Moreover, the parallel shift in the relationship in Fig. 7c suggests that self-shading was more predominant when the ecosystem flourished under non-stressed conditions.

Apparent quantum yield is a measure of the apparent maximum light-use efficiency for C assimilation (i.e. initial slope of the light response curve). Lower α values (-0.035 to -0.045) occurred between July and October and higher values (-0.025 to -0.030) occurred between January and March (Fig. 6b). Annual mean

α decreased in magnitude each year from -0.033 to -0.027 and the 6-year-mean was -0.031 . The seasonality of α was weakly correlated with mean monthly $T_{\text{a avg}}$ (Fig. 7d, $R^2 = 0.31$, $p < 0.001$). The α value for September 2004 (-0.059) was not included in this regression because it is an extreme outlier that may be an artifact of the sparse data collected during this month when the hurricane was affecting the site.

Mean monthly $\text{NEE}_{\text{night}}$ was exponentially related with $T_{\text{a avg}}$ (Table 3, Fig. 8). Following the hurricane, mean monthly $\text{NEE}_{\text{night}}$ was reduced by 30% at 25 °C , a typical nighttime temperature for September (Fig. 8). Q_{10} ranged from 1.7 (following the hurricane) to 2.5 and mean Q_{10} over the 6-year study was 2.2 (Table 3).

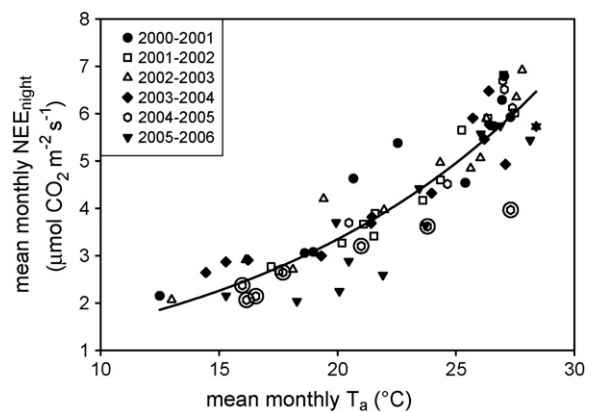


Fig. 8. Monthly, mean nighttime CO_2 exchange ($\text{NEE}_{\text{night}}$) as a function of monthly, mean air temperature ($T_{\text{a avg}}$) for each phenological year (April–March) during the study. The regression is fit through all months combined. Regression parameters and statistics are given in Table 3. Large open circles highlight the months following the September 2004 hurricane, September 2004–March 2005.

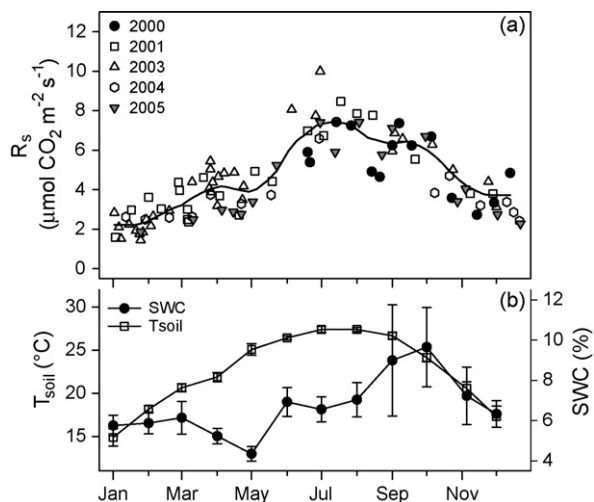


Fig. 9. (a) The seasonality of soil respiration (R_s) measured during the study (R_s not measured in 2002). A 4-week running mean is fit through the data. (b) Mean (\pm S.E.) monthly soil moisture (SWC) and soil temperature (T_s) for 2000–2005.

Soil respiration was measured during the morning hours (9:00–12:00) each year except 2002. Maximum R_s occurred in July and August and minimum R_s occurred in January (Fig. 9a). Seasonality of R_s was primarily dependent on T_s with the exception of April and May when low soil moisture produced an additional constraint (Fig. 9).

4. Discussion

This subtropical, evergreen broadleaf ecosystem assimilated approximately 20 t C ha^{-1} over a 6-year period. Carbon assimilation occurred during all parts of the year owing to relatively mild winter temperatures. The first year, 2000, was 4 years after the burn, so we cannot say how many, if any, of the years prior were sinks. Carbon assimilation was seasonal, with spring the most intensive period of assimilation and summer the least. Although C assimilation increased each year of the study, the seasonality of C assimilation was remarkably consistent between years (Fig. 3).

4.1. Environmental variables controlling NEE

4.1.1. Daytime fluxes

For the scrub oak ecosystem, PPFD, VPD, T_a , SWC, and LAI each affected NEE_{day} to differing degrees and temporal scales. On a half-hourly time step, PPFD was the dominant environmental variant controlling NEE_{day} (Fig. 5a), accounting for 72–91% of its variation within each month. Vapor pressure deficit also seemed to affect

half-hourly C uptake during months when there was an extended gap between “high-quality” rain events such as July 2005 (Fig. 5b) or during the severe drought affecting all of Florida between 1998 and 2001. During some months, such as September 2005, half-hourly daytime C uptake seemed to be insensitive to high VPD (Fig. 5b) even though the surface layer (0–15 cm) of these well-drained sandy soils dried (SWC < 5%) within a few days following rain events. The insensitivity of NEE_{day} to short term dry conditions may be because this xeromorphic ecosystem is adapted to dry sandy ridges (Schmalzer and Hinkle, 1996) and avoids water stress by relying on the water table (typically 1–2 m below ground), where *Q. myrtifolia* and *Q. geminata* obtain 79 and 95%, respectively, of their water (Hungate et al., 2002).

Although freezing temperatures were very rare at our research site, T_a dipped below 10°C on some nights in December and January during our study. Photosynthesis in some species becomes depressed for a few days following episodes of cold temperature even if exposed to environmental conditions conducive for high rates of photosynthesis. For example, photosynthesis of *Xanthium strumarium* decreased by approximately 30% after being exposed for 24 h to daytime temperatures of 10°C and nighttime temperatures of 5°C (Drake and Raschke, 1974). At the ecosystem level, NEE_{day} of a mixed coniferous and deciduous beech forest in the Belgian Ardennes became depressed when temperatures dropped below 15°C (Aubinet et al., 2001). To evaluate this effect on scrub oak ecosystem photosynthesis, January NEE_{day} was sorted into two groups that only included high light conditions (PPFD > $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$). The first group included data from the first or second day following a night when T_a dropped below 10°C for more than 5 h. The second group included data that were removed from cold night episodes by more than 4 days. There was a temperature effect present only in January 2002 (t -test, $p = 0.03$) where midday NEE_{day} was reduced by 10% following cold events. However, there was no temperature effect in January 2001, 2003 and 2004 (t -test, 2001: $p = 0.90$; 2003: $p = 0.17$; 2004: $p = 0.86$).

Air temperature and leaf area were important variables controlling daytime C exchange within and between seasons in this ecosystem (Fig. 7). Hymus et al. (2003) showed that the effects of elevated CO_2 on maximum NEE_{day} were tightly correlated with SWC. In the present study, SWC explained within season variation of daytime C fluxes during the spring and summer months, but not during the winter (Fig. 7b).

However, SWC did explain the interannual variation in wintertime daily C uptake (Table 2, Fig. 4b). The dynamic interaction of these environmental controls over daytime net CO₂ exchange in a scrub oak produces a sharp contrast in seasonal behavior with two other common Florida ecosystems, a mature pine plantation and deciduous wetland. Although LAI decreased by 50% in the pine plantation between summer and winter, there was almost no difference in NEE_{day max} (ca. $-15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for both seasons), which was attributed to a compensatory effect of respiration on net CO₂ exchange between the seasons (Clark et al., 1999). NEE_{day max} for the deciduous wetlands went from ca. $-9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the summer and near zero in the winter due to a complete loss of canopy foliage (Clark et al., 1999).

The seasonality of the daytime C uptake potential for this subtropical broadleaf forest was intermediate between low seasonality observed in tropical broadleaf forests (Malhi et al., 1998; Falge et al., 2002) and high seasonality observed in temperate broadleaf forests (Falge et al., 2002). This scrub oak ecosystem maintained a substantial capacity for C uptake during the winter (Figs. 2a, 3 and 6a) when nearly 50% of annual C assimilation occurred. It was at this time of the year that interannual differences in soil water content regulated the differences in mean daily C assimilation between years (Fig. 5).

The magnitude of summertime NEE_{day max} of this site (-12 to $-16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was less than the magnitude of annual values reported for tropical forests (ca. $-18 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, Malhi et al., 1998; Loescher et al., 2003), and considerably lower than summertime values (-20 to $-30 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) reported for temperate deciduous hardwood forests (Goulden et al., 1996b; Baldocchi, 1997; Schmid et al., 2000; Aubinet et al., 2001). Furthermore, in an analysis of when the greatest NEE_{day max} occurred for two temperate deciduous forests across a latitudinal gradient of eastern N. America – late May for the southern deciduous forest (Baldocchi, 1997) and mid-June for the northern deciduous forest (Goulden et al., 1996b) – Baldocchi (1997) attributed the difference to bud break, which was a full month later in the northern forest than the southern forest. Scrub oak occurs south along this North American gradient and, although bud break was late March, NEE_{day max} was greatest after June (Fig. 2a). We attributed this to coinciding with peak annual LAI and soil moisture (Fig. 1), which was consistent with results found for an Amazon tropical rain forest (Malhi et al., 1998).

The apparent quantum yield for this ecosystem was weakly correlated with air temperature (Fig. 7d). This correlation is consistent with previous leaf-level measurements of the oak species that showed a positive correlation between photosynthesis and T_a (J.H. Li, unpublished data). However, Wofsy et al. (1993) found that α for a temperate deciduous forest was also only slightly influenced by climatic conditions, and thus concluded it is a well-defined ecosystem property. The 6-year average of α , -0.031 , for this scrub oak ecosystem was less efficient than the global mean value of -0.037 reported for broadleaf forests (Ruimy et al., 1995). The scrub oak was similar in C uptake efficiency during the summertime ($\alpha = -0.039$ to -0.040) to two other Florida ecosystems, a mature pine plantation ($\alpha = -0.044$) and a deciduous cypress wetland ($\alpha = -0.038$, Clark et al., 1999). However, in the wintertime the scrub oak was less efficient ($\alpha = -0.026$) than the pine plantation ($\alpha = -0.038$) and considerably more efficient than the deciduous cypress wetlands ($\alpha = -0.002$, Clark et al., 1999).

4.1.2. Nighttime fluxes

Variation in T_a and T_s , were clearly the dominant controls over NEE_{night} and soil respiration, respectively (Figs. 8 and 9). Soil respiration also showed a clear dependency on SWC between April and June (Fig. 9). The dependency of respiration on SWC was also evident at the ecosystem level in the R_d parameter from the light response curves (Fig. 6d). It was not clearly evident in the half-hourly NEE_{night} data, and the reasons for this remain unclear since R_s accounts for $>85\%$ of ecosystem respiration (Hymus et al., 2003). Because of this, we were not able to build SWC into our respiration model for gap filling.

Nighttime fluxes gave Q_{10} values (Table 3) that were higher in those years that included winters with above average temperatures (Fig. 1d)—i.e. 2001 and 2005. We also constructed respiration models that covered only 6-month periods, January–June and July–December, and used half-hourly NEE_{night} and T_a to evaluate if data averaged over a shorter time step (i.e. half-hourly versus monthly) and covering a shorter period (i.e. 6 months versus 12 months) produced any difference in our respiration results. Using half-hourly data did result in model parameters values different from those given in Table 3 and Q_{10} values were lower. Yet, these differences only affected the annual sums of NEP $<6\%$ and made little difference in the response to environment or season. Other eddy covariance studies found similar results in their respiration sensitivity analyses (Barr et al., 2002; Clark et al., 2004).

4.2. Seasonal and annual NEP

Although the largest magnitude of daytime fluxes occurred in summer, this was not when the maximum amount of carbon was assimilated per day. Almost 50% of annual NEP occurred in the 6 months of winter from the end of September through March, nearly 40% assimilated in the 2 months of April and May, and on average, only 12% of annual carbon assimilation occurred in the 4 months of summer between the end of May and the end of September (Fig. 3). There was a weak correlation between annual NEP and annual precipitation (Fig. 4a), but a much stronger correlation between mean daily NEP and mean SWC during the winter (Fig. 4b). Although maximum NEE_{day} occurred in summer, the substantial effect of temperature on soil and plant respiration reduced NEP during this 4-month period. Thus, after solar radiation, temperature appears to play the next most important role in ecosystem carbon assimilation followed by effects of soil water content on both photosynthesis and soil respiration (Fig. 4).

The rapid increase in C assimilation in spring (Fig. 3) is the result of several interacting factors. New leaves produced in April have a much higher capacity for photosynthesis than old leaves (Li et al., 2000), so a comparison of the increased LAI with increased NEE_{day} (Figs. 1 and 6) is not sufficient to explain the rapid increase in NEP during this time of year. However, adding the effect of soil moisture on respiration (Figs. 6 and 9) suggests that the decline in respiration added to the increased activity of leaves accounts for most of the spring burst in NEP (Fig. 3).

This ecosystem assimilated almost 20 t C ha^{-1} during this 6-year study (Fig. 3). The amount of carbon added each year increased from 2000 to 2005 with one exception: during 2004, when hurricane Francis removed 25% of the leaves (Table 2), NEP was less than the previous year. The magnitudes for all major carbon fluxes, NEE_{day} , NEE_{night} , and soil respiration (R_s) (Figs. 2, 6 and 9) were reduced substantially in the fall of 2004 following the hurricane. Over the 6-year term of the study, summertime values for both NEE_{day} and NEE_{night} declined in magnitude (Fig. 6). We are unable to explain this result which is particularly puzzling since throughout this period, NEP increased every year but one and that was the year when Hurricane Francis struck the site. The effect of this hurricane may shed some light on how both day and night fluxes could decline with no effect on NEP.

The September 2004 hurricane resulted in an abrupt reduction in both daytime and nighttime CO_2 exchange

(Fig. 2). The magnitudes of NEE_{day} and NEE_{night} were reduced by 22% and 33%, respectively, in September 2004 and 20% for both fluxes in October 2004 relative to the previous 2 years. However, these reductions were compensatory and NEP for September and October 2004 was very similar to the previous 2 years (Fig. 3). The reduction in LAI likely accounted for the preponderance of the reduction in photosynthesis for September and October 2004 since other variables that control NEE_{day} – PFD, $T_{a \text{ avg}}$, and SWC – were either similar to past years or, in the case of SWC, not limiting (Fig. 1). The reduction in NEE_{night} also may have been related to the reduction in LAI, particularly since $T_{a \text{ avg}}$ and SWC were not limiting. Several studies have demonstrated that fresh photosynthate to roots was a key driver of soil respiration (Kuzyakov and Cheng, 2001; Hogberg et al., 2001; Tang et al., 2005). For example, autotrophic respiration accounted for approximately 85% of soil respiration under blue oak trees in an oak savannah, and was highly correlated to canopy photosynthesis when a time lag of 7–12 h was introduced (Tang et al., 2005). Similarly, soil respiration was reduced by 37% in a Scots pine forest in Sweden 5 days after the supply of fresh photosynthate was stopped by girdling the surrounding trees (Hogberg et al., 2001). Since R_s is such a large proportion of ecosystem respiration in this scrub oak ecosystem (e.g. >85%, Hymus et al., 2003), it follows that a reduction in LAI would also lead to reduced respiration. Thus, although the reduction of NEE_{day} and NEE_{night} seemed to be compensatory in the short term of days to weeks, less than 350 g C m^{-2} was assimilated during the phenological year of 2004.

Monthly measurements of biomass growth indicate that much of the aboveground C increment for 2003 ($385.4 \text{ g C m}^{-2} \text{ year}^{-1}$, Table 1) was added between April and July in the form of stem growth (data not shown) and leaf growth (Fig. 1f). The gas exchange data show that 240 g C m^{-2} or 57% of annual NEP (419 g C m^{-2} , Table 2) was accumulated during the same period. The imbalance of C between biomass data and gas exchange data suggest that C fixed during the remaining part of the year goes into labile C storage for growth during the spring or recovery after periods of stress, such as fire or hurricane. Cropper and Gholz (1993) reported that pine trees in Florida behave in a similar way mobilizing labile C in the spring and early summer to meet C deficit demands for stem growth and needle expansion. In 2003, woody tissue accounted for 37% of total annual aboveground C assimilation in this ecosystem (Table 1). Woody tissue accounted for a similar amount of the annual C budget (46%) in mature

pine plantation in north Florida (Clark et al., 1999), which suggests similarities in C allocation between these two distinctly different Florida forest ecosystems.

There was approximately $34 \text{ g C m}^{-2} \text{ year}^{-1}$ difference between NEP for April 2003 to March 2004 and the 2003 aboveground biomass increment (Tables 1 and 2). In two separate studies conducted at this site, root biomass within the top 20 cm was estimated to be 2578 g C m^{-2} in 1995, prior to the burn in 1995 (P. Dijkstra, unpublished data), and 2323 g C m^{-2} in 2002, 7 years after the burn (F. Day, personal communication). This relatively small difference between the pre-burn root sampling in 1995 and the sampling 7 years later, suggests either that belowground biomass aggrades C in relatively small increments each year or the error in estimating root biomass is large enough that increments of biomass across 7 years is unable to detect changes within the same range of estimate as aboveground growth increment. Recent data using radar to estimate carbon in roots of this ecosystem suggest that the data in Table 1 may underestimate total root biomass by as much as a factor of 5 (F. Day, personal communication). Moreover, our work with elevated CO_2 effects on ecosystem gas exchange (Dore et al., 2003; Hymus et al., 2003) suggests that the capacity of this ecosystem to assimilate carbon greatly exceeds estimates based on aboveground biomass. Furthermore, a recent study conducted right after a prescribed fire in a scrub oak forest near our site found that approximately 70% of aboveground C was burned and charcoal production was only 4–6% (Alexis et al., in press). Therefore, the conclusion from our results reported here, that between burn cycles the majority of C assimilation is in aboveground biomass, must be considered preliminary until we have a better grasp of the size and capacity of carbon in roots and soil. It is not yet possible to assert that most of the carbon assimilated between burns will reside in aboveground biomass and be released to the atmosphere during a fire. Our study is therefore inconclusive whether this subtropical ecosystem will become a long-term C sink.

4.3. Comparisons of NEP with other sites

The C sink strength of this short-stature, scrub oak ecosystem was comparatively weak relative to other much larger, temperate broadleaf forests. For example, here C uptake was greatest between April and May and averaged $1\text{--}2.4 \text{ g C m}^{-2} \text{ day}^{-1}$ (Table 2). In contrast, during the summer, southern temperate broadleaf forests gained as much as $10 \text{ g C m}^{-2} \text{ day}^{-1}$ (Greco and Baldocchi, 1996) and northern temperate broadleaf

forests gained $3\text{--}6 \text{ g C m}^{-2} \text{ day}^{-1}$ (Goulden et al., 1996a; Barr et al., 2002). However, annual C assimilation of this ecosystem ($107\text{--}467 \text{ g C m}^{-2} \text{ year}^{-1}$, Table 2) was within the range reported for temperate deciduous forests ($70\text{--}870 \text{ g C m}^{-2} \text{ year}^{-1}$, Baldocchi et al., 2001; Law et al., 2002) because it was productive throughout the year compared to very low wintertime productivity of deciduous forests. In comparison to tropical forests, annual estimates of NEP ranged from near neutral (Miller et al., 2004) to an important sink assimilating nearly $800 \text{ g C m}^{-2} \text{ year}^{-1}$ (Loescher et al., 2003) when a u^* filter was applied to the data. In comparison to a subtropical evergreen coniferous forest in Florida, mean daily C uptake also peaked in the spring but was approximately $3 \text{ g C m}^{-2} \text{ day}^{-1}$ with annual C uptake between 610 and $740 \text{ g C m}^{-2} \text{ year}^{-1}$ (Clark et al., 1999).

5. Conclusions

The 6-year record of ecosystem carbon exchange permits us to analyze the data to determine inter-annual and seasonal variations and to characterize the response of this ecosystem to light, temperature, soil water, and atmospheric humidity. This study makes a unique contribution to the literature on this subtropical, broadleaf, fire dependent ecosystem by characterizing the magnitude of the potential sink and the role of environmental factors in regulating carbon assimilation. Although we conclude that much of the added carbon is stored in aboveground biomass which periodically burns off, this conclusion has to be tempered by the realization that we may not yet have adequately determined either the belowground carbon pool size in roots and soil carbon or the rate of export from this ecosystem through ground water.

Four to ten years after a burn, the Florida scrub oak ecosystem has the potential to be a significant C sinks because, except during severe drought, scrub oak is productive during all seasons of the year. Carbon uptake is seasonal with the intensity in the order: spring (April–May) > winter (October–March) > summer (June–September). The dominant environmental factors controlling the seasonality of C assimilation change between the seasons. During all periods, temperature and PPFD are the main variants controlling half-hourly ecosystem C fluxes. When the temporal scale is increased to the season, precipitation, SWC, LAI and air temperature play more important roles. In the spring, low soil moisture causes soil respiration to be suppressed and consequently the net daily exchange of CO_2 is dominated by daytime C uptake. However, in

the summer, the hot, rainy season, NEE_{night} and R_s was not limited by precipitation, while NEE_{day} varied with LAI, soil moisture, temperature, and vapor pressure deficit. In the winter, LAI and temperature explained the within season variation in NEE_{day} , while soil moisture was highly important in determining interannual variation of daily C uptake. Interannual variation in extreme conditions, such as drought or hurricane, control NEP through reduction of leaf area.

Acknowledgements

This research was funded by a grant to the Smithsonian Institution from the US Department of Energy (ER619930000313). We wish to thank David Johnson and Hans Anderson for their assistance with field work. We are grateful to Frank Day and Roger Gifford for their unpublished data. We acknowledge the support of the Biomedical Office of NASA at the Kennedy Space Center, the US Fish and Wildlife Service, Dynamac Corporation, and Merritt Island National Wildlife Refuge. We gratefully acknowledge the very useful suggestions of two anonymous reviewers of an earlier version of the manuscript.

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