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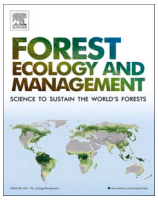

Two decades of carbon dynamics in an actively-managed, naturally-regenerated longleaf/slash pine forest

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ABSTRACT

Naturally regenerated pine ecosystems cover 11.7 Mha of the southeastern United States, comprising 13.8% of the forested land, and represent an important component in the carbon balance for the region. These forests are exposed to strong climatic variability from extreme multiyear droughts to above average precipitation years, many are actively managed with prescribed fire and some modification of tree density by cutting. This study is unique in assessing the effects of management and climatic variability for two decades on the carbon (C) dynamics and long-term net ecosystem C balance (NECB) for an actively-managed naturally regenerated pine ecosystem. We used 21 years of eddy covariance estimates of net ecosystem C production (NEP), combined with periodic tree inventories, understory biomass and forest floor assessments. Forest management included six prescribed fire cycles on a three-year rotation beginning in the third year of the study, and a preparatory cut which reduced basal area by 20% from 17.05 ± 0.66 m^2/ha during the spring of 2016. The mean annual NEP was 3.32 ± 1.37 Mg C/ha yr^{-1}, with a range of 5.35 Mg C/ha (1.30 to 6.65 Mg C ha/yr), was not significantly affected by fire and was mainly controlled by water availability. A combination of aboveground C assessments (tree and understory) and NEP indicates that C stored belowground accounted for 23% of NEP, with part of this used to support aboveground understory growth after fire. Net ecosystem carbon balance (NECB, integrated NEP and C losses from management) fluctuated in a range of 15.5 Mg Cha^{-1} (6.7 to −8.8 Mg C ha^{-1}) and was sensitive to management. However, a higher NECB during the second decade than in the first (15.3 Mg C/ha vs. 2.7 Mg C/ha) reflected increased NEP (40 Mg C/ha vs. 25.4 Mg C/ha) as it responded to a greater water availability, despite similar amounts of C lost from management activities during both decades. At the end of the 21 years study, the ecosystem had incorporated 22.6 Mg C ha^{-1}, indicating that actively managed naturally regenerated pine ecosystems in the region can mitigate C dioxide emissions under a broad range of climatic conditions, reduce wildfire risks, while providing numerous ecosystem services.

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1. Introduction

Forests in the southern USA cover 46% of the land surface (99.3 Mha) (Oswalt et al., 2012), providing many ecological and economic services including biodiversity, habitat for endangered species, timber and non-timber forest products, and clean water (Wear and Greis, 2012). Forests play an important function in the region's C cycle, as they mitigate anthropogenic C emissions via net C uptake and storage (Han et al., 2007; Lu et al., 2015; Oswalt et al., 2019) and provide about 60% of the nation's timber (Prestemon and Abt, 2002) in the form of lumber, paper, and cardboard products, all of which also serve as carbon storage pools (Gonzalez-Benecke et al., 2010).

Prior to European settlement, there were about 37 million ha of longleaf pine (*Pinus palustris*) forest in the southern USA (Oswalt et al., 2019). About 23 million ha of these forests had longleaf pine as their dominant tree species, while the rest had longleaf mixed with other pine and hardwood species (Frost, 2006). Typically, these forests were savannas, with a sparse overstory of pine, and a diverse understory of herbaceous or shrubby vegetation. Most of these forests experienced low-intensity fires ignited by humans or lightning, with a 2-to-5-year return interval. These frequent fires prevented the establishment, and eventual dominance, of hardwood tree species, fostered regeneration of *P. palustris*, and maintained high biodiversity (Frost, 2006; Oswalt et al., 2012). With frequent low-intensity fires, the shade-intolerant, fire-resistant pine overstories persisted and maintained a diverse understory species composition. Forest composition and structure changed dramatically during the centuries after European settlement, as longleaf pine savannas were harvested and converted to farmland or pasture, settlements, successional forests, or pine plantations (usually *Pinus taeda* or *P. elliottii* var. *elliottii*). Currently, there are about 1.4 million hectares of fire-maintained, naturally regenerated longleaf pine forests remaining (Oswalt et al., 2012). Increasingly, however, conservation-oriented landowners in the region including government agencies, non-governmental organizations, and many non-corporate forest landowners have been working to restore their forestland composition and structure to one more resembling pre-colonial forests (Oswalt, 2015).

Restoration goals for southeastern US forests can be ambitious. For example, the America's Longleaf Restoration Initiative coordinates collaboration among diverse forestland owners to eventually restore longleaf pine on millions of hectares in the region (Guldin, 2017). Restoration close to pre-colonial structure and composition on this scale will necessarily involve the modification of large swaths of forests ranging in character from even-aged, planted forests to relatively unmanaged naturally regenerated forests. Restoring these forests typically involves intensive management to achieve the transition, including frequent application of prescribed fire, and reduction in hardwood composition or pine overstory density (FNAI, 2010; Guldin, 2019; Oswalt et al., 2012), although restoration is based on the starting condition, is situational and not always required. Fire drives pine stands to become a temporary carbon source since large amounts of carbon are released from the understory vegetation and litter pools during ignition (Lavoie et al., 2011). In addition, understory photosynthetic capacity is also reduced after fire (Bracho et al., 2021). Cutting extract large amounts of C affecting ecosystem C budget (Gonzalez-Benecke et al., 2010), and reduces carbon uptake by reducing overstory foliage biomass (Campbell et al., 2009); however, preparatory cut or harvests in a shelterwood system promotes seedling establishment (Palik et al., 2003), and allows for higher radiation to reach the understory and increase its carbon assimilation (Gholz et al., 1991). All these intensive management practices takes place in a context of high climate variability with recent multiyear extreme droughts (NOAA, 2022). Droughts affect forest structure and recovery after disturbance (Bracho et al., 2012; Crosby et al., 2015; Henderson and Grissino-Mayer, 2009; Starr et al., 2016), with forecasted climatic changes for the region suggesting more frequent droughts in the coming decades, precipitation will be distributed in localized heavy events with a longer times between events, increasing evaporative demand, drier conditions and more intensive droughts (Christensen et al., 2007; Dai, 2011; Ranasinghe et al., 2021; Seager et al., 2009). While conversion at this scale will yield many benefits in terms of ecosystem services, the impacts of these conversions interacting with climate variability on regional carbon dynamics are difficult to predict.

The objective of this study was to quantify ecosystem C dynamics in a naturally regenerated longleaf pine ecosystem actively managed with prescribed low-intensity understory fire and a one-time basal area reduction by harvest during the study period. The study was conducted over 21 years, encompassing periods of strong climatic variability. The research site at the Austin Cary Forest, north central Florida, during the study period had the largest fluctuation in water availability recorded in the last 100 years (NOAA, 2022). In addition, site management included six low-intensity fires, one in 2003 at six years after the last fire and 3-year fire cycles after the third year of study, and a ~20% basal area reduction by preparatory cut in spring 2016. We expected a significant reduction in ecosystem C uptake during drought years; that the site would be a C source during fire years and recovery after fire to be affected by water availability; and that a reduction in basal area would produce a proportional reduction in NEP. Despite periodic C losses, we expected the ecosystem to be a net C sink on the decadal time scale and after 21 years.

2. Materials and methods

2.1. Site description

The study was conducted from July 2000 to February 2021 at the University of Florida's Austin Cary Forest (ACF, 29.738 N; 82.2188 W) located ~15 km northeast of Gainesville, Florida, USA. Prior to 1936, the area was cut for timber, the residual trees were worked for turpentine, and cattle grazed on the property (Powell et al., 2008). After state acquisition in 1936, the forest regenerated naturally from residual trees (mostly slash pine and longleaf pine). The School of Forest, Fisheries and Geomatics Sciences, University of Florida, manages ACF as a research, education, extension, and demonstration Forest. Management strategies include the application of prescribed fire that mimics the presumed natural occurrence frequency (3-years cycle), and periodic cuts to reduce basal area and overstory pine density and allow for natural regeneration. The study site had a basal area of 17.53 m^2/ha at the beginning of the study, dominated by longleaf pine (*Pinus palustris* Mill.) (64.5% of basal area) and slash pine (*Pinus elliotii* Engelm) (35.5% of basal area). It is difficult to determine site index for old, mixed-species forests such as the study stand. However, slash pine site index (base age 25 years) for nearby stands on similar spodosols was about 23 m (Jokela et al., 2010). The shrubby understory is dense, dominated by saw palmetto (*Serenoa repens* Bartr.), gallberry (*Ilex glabra* L.), wiregrass (*Aristida sp*), and wax myrtle (*Morella cerifera L.*). Cuts were performed in 1991 and again in 2016, removing 27% and 20% of the basal area, respectively. Prescribed fires were conducted in 1996, 2003, 2006 and 2009 during the dormant season (January-February), partially burnt in both the dormant and growing season of 2012, between March and May of 2015, and the growing season (May) of 2018. Fires were conducted when relative humidity ranged between 30 and 55%, air temperature below 37 °C, and wind speed in the stand between 0.4 m s^{-1} and 1.3 m s^{-1}. Fire is applied as back-fire off the downwind side, it slowly burns into the wind. Flames can reach between 2 and 10 m (Lavoie et al., 2010).

Soils are Ultic Alaquods (Pomona series), deep and poorly drained; texture is sandy, with a spodic horizon extending from 25 to 89 cm, and an argillic horizon with low permeability from 90 to 203 cm (https://casoilresource.lawr.ucdavis.edu/soilweb-apps/). Total soil organic C in the first 30 cm of mineral soil was ~45 Mg C/ha (Vogel et al., 2015). The long-term mean annual precipitation (1971 – 2000) was 1225 ± 203 mm, 51% of that falls from June to September, mean annual air

temperature (T_{AIR}) was 20.4 ± 0.6 °C, January is the month with lowest mean T_{AIR} (12.5 ± 2.6 °C) and July with the highest (27.2 ± 0.6 °C) of the year (https://www.ncdc.noaa.gov/cdo-web, Gainesville FL, Regional Airport).

2.2. Ecosystem carbon fluxes and ancillary measurements

2.2.1. Eddy covariance carbon fluxes

Net ecosystem production (NEP) is the net gain or loss of C for an ecosystem in a time interval. NEP is the balance between C uptake by plants (gross primary production, GPP) and ecosystem respiration losses (R_{ECO}; autotrophic, R_A + heterotrophic, R_H), where the difference between GPP and R_A represents the net primary production (NPP). NEP represents the potential for C accumulation by the ecosystem (Lovett et al., 2006), and is calculated by integrating measured and gap-filled half-hourly net ecosystem C exchange (NEE). Net ecosystem carbon exchange was calculated by integrating measured CO_2 flux and storage, this last term was calculated as changes in CO_2 concentration at 30 min intervals at measurement height. Cumulative NEE was assumed equal to NEP. Positive signs are assigned to GPP and $R_{ECO,}$ where NEP equals GPP minus R_{ECO}, where positive NEP values imply C uptake (sink) by the ecosystem. The eddy covariance approach (Aubinet et al., 2000; Baldocchi, 2003), was used to measure NEE from July 2000 until February 2021. A closed path system comprised of an infrared gas analyzer (LI-6262/LI-7000, Licor, Lincoln, NE), and a Gill sonic anemometer (R3A, Gill instruments, Lymington, UK) (Supplements table 1) were used from the beginning of the study until May 2011, and a WindMaster Pro and an open path system (LI-7500A, Licor, NE) used until the end of this study. Sensors were mounted at 32 m on top of a tower, extending 8 m above the canopy. Calibration was performed twice per week on the closed path and twice per year on the open path analyzers using a zero CO_2 air source and a ± 1% standard CO_2 concentration close to the atmospheric concentration, and a dew point generator (LiCOR 610) for water vapor. In the closed path system, air was drawn through a tube with the inlet next to the sonic anemometer and through the infrared gas analyzer at a rate of 8 L/m to attenuate temperature fluctuations. Fluctuations in the wind components u, v, & w (where u and v are the orthogonal horizontal wind speed components and w is the vertical wind speed), CO_2, water vapor and air temperature were sampled at 10 Hz and integrated to half-hourly values using EdiRe software (Clement, 2012). Quality control on high frequency was applied according to (Foken et al., 2004). Turbulent fluxes were calculated from the half hourly averaged covariance of CO_2, water and temperature and vertical wind speed, and then corrected for the frequency attenuation, sensors separation and coordinate rotation (Foken et al., 2012), and density fluctuations (Webb et al., 1980). Data screening eliminated half-hourly fluxes estimated from incomplete half hours, during rain, conditions when the canopy was decoupled from the atmospheric conditions as defined by the friction velocity (u* threshold of 0.2 m s^{-1}), and non-steady conditions (Foken et al., 2004). The flux processing methodology was validated by Ameriflux Q_A/Q_C team visits and by comparisons of flux estimations using the Ameriflux closed and open gold files.

2.2.2. Carbon flux partitioning

Gaps in the measured fluxes after the screening protocol were filled as follows. Daytime conditions were assumed when PAR was greater than 10 μmol·m^{-2}·s^{-1}, missing 30 min NEE values were filled using monthly parameters after fitting measured NEE to PAR using a non-rectangular hyperbola (Falge et al., 2001) (SAS 9.4).

$$NEE_{day} = \frac{\propto \hat{A} \cdot PAR}{1 - (PAR/PAR_{max}) + (\propto \hat{A} \cdot PAR/GPP_{opt})} + R_d \quad (1)$$

Where α is the ecosystem quantum yield (μmol CO_2·m^{-2}·s^{-1}/μmol quantum·m^{-2}·s^{-1}), GPP_{opt} (μmol CO_2·m^{-2}·s^{-1}) is the optimum rate of CO_2 exchange at maximum observed PAR (PAR_{max}), and R_d is the ecosystem dark respiration (e.g., NEE at $PAR = 0$).

Nighttime conditions were assumed when PAR was < 10 μmol·m^{-2}·s^{-1} and gaps in R_{ECO} were filled using annual parameters by fitting measured NEE to T_{AIR} using an exponential relationship (SAS 9.4):

$$NEE_{night} = A \bullet e^{bT_{AIR}} \quad (2)$$

Where A and b are empirical parameters and T_{AIR} (°C) is half hourly air temperature. Parameters were obtained using maximum likelihood. Daytime R_{ECO} was estimated by extrapolating nighttime parameters and T_{AIR}, GPP calculated as the sum of NEE and R_{ECO}. Measured and gap-filled C fluxes were integrated to obtain totals over monthly and yearly basis. Annual C fluxes were calculated as phenological years, assuming it starts with the beginning of the growing season on March 1st of the current year until the last day of February of the following year, and the highest increase in monthly GPP and NEP occurs from February to March of each year. Missing monthly C fluxes for years 2000 (4), 2002 (8) and 2014 (6) were gapfilled using a Random Forest technique (Kim et al., 2020), the model used meteorological and biological variables including T_{AIR}, PAR, PDSI, maximum vapor pressure deficit (VPD_{MAX}; average vapor pressure deficit, VPD, between 10 am and 4 pm) and LAI_M (Leaf area index extracted from MODIS). Model performance was evaluated by root mean square errors (RMSE) and explained 93% of the variance for NEP, and 95% for GPP and R_{ECO} (Supplements Table 2).

2.2.3. Meteorological measurements

Standard meteorological variables measured above the canopy included (Supplements Table 1) photosynthetically active radiation (PAR), air temperature (T_{AIR}), relative humidity (RH), net radiation (R_{NET}), precipitation, and soil heat flux. The mean annual T_{AIR} for Florida Climatic Zone 2 and the Palmer Drought Severity Index (PDSI) were downloaded from the National Center for Environmental Information (NOAA, 2022), PDSI was used as an indicator for water availability.

2.3. Biomass assessments, Fire, Harvest, and net ecosystem carbon balance.

Carbon stock dynamics were assessed by establishing four 50 m × 50 m inventory plots around the footprint of the eddy covariance tower at the beginning of the study (Powell et al., 2008). Tree density, stem diameter at breast height (dbh at 1.37 m height), and tree height were measured during the dormant season of each year. Tree biomass and coarse root biomass were calculated from allometric equations (Gonzalez-Benecke et al., 2010; Samuelson et al., 2017). An additional inventory was performed immediately after the preparatory cut during the spring of 2016 and cut trees were accounted for. The all-side leaf area index was estimated from monthly needlefall (LAI_N) (Gholz et al., 1991; Martin and Jokela, 2004) collected from 20 1-m^2 traps randomly located within the footprint of the eddy covariance measurements. A logistic model was applied to monthly needlefall, (Dougherty et al., 1995; Kinerson et al., 1974), it assumes that the needle accrual of the current year starts by March 1st and that the needle retention time is two years (Gholz and Boring, 1991; Gholz et al., 1991). Independent ecosystem-level LAI estimates were extracted from MODIS 500 m resolution images at sixteen day intervals (half-sided LAI, LAI_M) around the eddy covariance footprint using the online Application for Extracting and Exploring Analysis Ready Samples (AppEEARS), courtesy of the NASA EOSDIS Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, https://lpdaacsvc.cr.usgs.gov/appeears/.

The site had six prescribed fire applications, one in January of 2003 after six years without fire and very dry conditions; three year intervals from January 2006 until 2012, March – May of 2015 and May of 2018. Prescribed fires conducted in January were assigned to the end of the

Table 1
Annual carbon (C) fluxes (Mg C/ha yr^{-1}), net ecosystem production (NEP), gross primary production (GPP) and ecosystem respiration (R_{ECO}), C emissions by ignition, C balance (NEP minus C emissions), C tree biomass (Mg C/ha), tree aboveground biomass increment (Mg C/ha yr^{-1}), cumulative annual precipitation (Precip., mm yr^{-1}), and phenological year mean annual air temperature (T_{AIR} ℃) for a naturally-regenerated pine ecosystem, Florida, USA.

P_year	NEP	R_{ECO}	GPP	Carbon emission	Carbon balance	Carbon tree biomass	Trees AG Growth	Understory AG Growth	BG Growth	Precip. (mm)	T_{AIR}℃
2000	2.66	15.37	18.03	0	2.66	39.9	NA	NA	NA	818	20.4
2001	1.86	16.22	18.08	0	1.86	40.3	1.90	NA	NA	1157	20.7
2002	2.54	16.94	19.48	−11.38	−8.84	40.6	1.56	NA	NA	1421	20.5
2003	3.34	17.56	20.9	0	3.34	40.9	1.99	1.80	−0.45	1221	20.7
2004	3.21	11.72	14.92	0	3.21	41.3	1.72	0	1.49	1358	21.1
2005	2.18	15.51	17.69	−5.51	−3.33	41.6	1.65	0	0.53	1404	20.2
2006	1.65	17.15	18.8	0	1.65	41.9	1.71	2.26	−2.32	867	20.3
2007	1.3	14.26	15.54	0	1.30	42.2	1.33	0	−0.03	1165	18.1
2008	3.1	12.99	16.06	−5.74	−2.64	42.4	1.70	0	1.4	975	18.7
2009	3.51	15.87	19.37	0	3.51	42.7	1.74	2.00	−0.23	1263	19.8
2010	5.47	15.14	20.62	0	5.47	43	1.88	0	3.59	980	19.9
2011	1.99	14.19	16.16	−5.74	−3.75	43.2	1.21	0	0.78	712	21.1
2012	1.6	17.03	18.63	0	1.60	43.5	1.58	2.00	−1.98	1430	20.9
2013	4.43	17.79	22.2	0	4.43	43.7	1.42	0	3.01	1389	20.2
2014	4.98	15.41	20.39	0	4.98	44	1.81	0	3.17	1205	19.6
2015	3.79	19.01	22.8	−5.74	−1.95	44.3	1.41	2.00	0.38	1237	21.3
2016	3.49	16.64	20.13	−7.55*	−4.06	35.8	NA	NA	NA	941	21.7
2017	3.97	14.6	18.57	0	3.97	NA	NA	NA	NA	1915	20.6
2018	3.61	19.78	23.39	−5.63	−2.02	NA	NA	NA	NA	1547	21.5
2019	6.65	17.16	23.81	0	6.65	NA	NA	NA	NA	1181	21.6
2020	4.52	16.52	21.03	0	4.52	NA	NA	NA	NA	1297	21.7

*Extraction by harvest in 2016.
AG = Aboveground; BG = Belowground.
NA = data not available.

Table 2
Mean optimum rate of CO_2 exchange (GPP_{OPT}), integrated GPP, R_{ECO} and NEP (Mg C/ha) from May to September of two fire years contrasting in PDSI (2006 & 2009) and two after fire years also contrasting in PDSI (2007 & 2010) for a naturally-regenerated pine ecosystem, Florida, US.

Year	GPP_{OPT}	GPP	R_{ECO}	NEP	PDSI
2006	14.09 ± 2.31 (a)	9.57	8.22	1.35	−3.12 ± 0.96
2007	13.69 ± 1.45 (a)	7.51	7.54	0.37	−4.81 ± 0.20
2009	23.35 ± 3.83 (b)	10.86	8.46	2.40	0.11 ± 1.26
2010	22.18 ± 3.83 (b)	11.37	8.40	2.96	−1.23 ± 0.81

GPP_{OPT}: (μmol $CO_2 \cdot m^{-2}$ $2 \cdot s^{-1}$) is the optimum rate of CO_2 exchange at maximum observed PAR (PARmax), obtained from equation (1).

phenological year, e.g., estimated C emissions due to the prescribed burn in January of 2006 were used to estimate annual C balance of 2005.

Understory biomass was measured during prefire conditions in December 2002 using eight 1 m^2 clip plots (2 randomly located inside each inventory plot) (Lavoie et al., 2010; Powell et al., 2008), and 20 1 m^2 clip plots (5 subplots randomly located inside each inventory plot) in 2006, all biomass was clipped to ground and separated by species. The forest floor was collected from a 100 cm^2 quadrat inside each clip plot down to the mineral soil and included both L (litter) and O (organic matter) horizons. All clipped biomass and forest floor samples were dried at 60 ℃ to constant weight. Living biomass and forest floor remaining after fires were sampled inside the same plots at about one month after and then quarterly until a year after fire (January 2004), and yearly until the next fire cycle in 2006, and quarterly after fire until January 2007. Pre-fire understory biomass was measured again during the growing season of 2018 and post-fire recovery until three years after fire following the same approach as the previous two pre- and post-fire assessments (Shrestha et al., 2021). Carbon released to the atmosphere directly from living biomass due to ignition was assumed to be 58.4% of the dry weight (Alexis et al., 2007; Bracho et al., 2021), C released from the forest floor was estimated as the difference between measured pre- and post-fire C. Carbon in standing dead material after fire was calculated as follows: C in original vegetation minus C emissions (58.4%), minus C remaining in living vegetation after fire, which was similar after each fire independently of the season when prescribed fire was conducted. Post-fire C remaining in the ecosystem was estimated as the sum of C in standing biomass, living and charred material, and forest floor. Carbon released during the fire events was estimated as the difference between pre- and post-fire C stocks. The preparatory cut or harvest conducted during the spring of 2016 was used to eliminate unwanted competitors and poor form trees, increase crown vigor among remaining longleaf and slash pine, and encourage seedling establishment. Most of the harvested trees were pines of adequate size for products. Carbon extracted from the ecosystem by the harvest was assessed by first, estimating C contained in the logged trees as for the inventory in early 2016 and post-cut inventory, second, merchantable products (C extracted) and residues remaining on site (C content in tree crowns including stems < 7.5 cm diameter) were estimated using a growth and yield model for slash and longleaf pine (Gonzalez-Benecke and Martin, 2010; Gonzalez-Benecke et al., 2015).

Net ecosystem C balance (NECB) was estimated by integrating NEP and C losses, both by fire or logging (Chapin et al., 2006); herbivory or other potential C exports out of the ecosystem were not assessed. Integrated NECB was calculated per decade, assuming the first decade started at the beginning of the study in 2000, and over 21 years. NECB and net biome productivity (NBP) can be used independently and are assumed as production indicators for long-term studies or extended areas (Chapin et al., 2006; Schulze et al., 1999).

2.4. Statistical analysis

Differences in mean annual C fluxes for fire and non-fire years were tested using an unbalanced ANOVA (proc GLM, SAS 9.4). Differences in GPP_{OPT} between drought and non-drought years were tested using ANOVA (SAS 9.4). Analyses of environmental drivers of C fluxes were assessed monthly. We used generalized additive models (GAM) (Wood, 2017) to identify the effects of monthly averaged or aggregated measured environmental variables (T_{AIR}, PDSI, VPD_{MAX}, PAR) and time component (month) on monthly C fluxes (n = 231). GAM allows spline terms to characterize the non-linear dependency of a response (C Flux:

NEP, GPP & R_{ECO}) on driving factors. Regression parameters were calculated using smoothing functions with penalized likelihood estimation, and the total contribution of each spline function was tested. The penalized smoothing basis used for the month variable was a cyclic cubic regression spline and for all other variables was a thin plate spline. This model was executed using the *gam* function in the *mgcv* package of R (Wood, 2011). A full model with all environmental and month variables was considered as an initial model and then a reduced model with non-significant variables was compared using a likelihood ratio test to select best-fit model. All statistical tests used an alpha of 0.05 for significance.

3. Results

3.1. Environmental conditions and leaf area index (LAI)

Annual precipitation varied widely during the study period, ranging from 848 mm in 2011 to 1812 mm in 2017 (Table 1). The site experienced four multiyear droughts during the 21 years of study (Fig. 1a). By the time this study started in 2000, the site was undergoing a drought that extended from May 1998 until June 2002, when PDSI values ranged from moderate (-2) to extreme ($\langle -4$) for 39 consecutive months. Wet conditions prevailed from June 2002 through the beginning of 2006, when another deficit in precipitation led to an extended drought from May 2006 to April 2012, with a short period of average precipitation for few months from 2009 to 2010. Moderate to extreme drought conditions (PDSI < -2) prevailed through March 2009, and from September 2010 to April 2012. The calendar year 2017 had the highest precipitation during the study; however, moderate to extreme drought conditions extended from July 2016 until May 2017, after which tropical systems delivered 1390 mm from June to September, more than 800 mm above the long-term average for the period. In total, the area had a cumulative PDSI of −173.3 during the first decade of study (2000 – 2009) and −50.6 during the second (2010 – 2019). Monthly average water table depth (e.g., saturation zone) (Fig. 1b) measured over ten years ranged from below three meters to close to the soil surface. At PDSI of zero the saturated zone is found at one meter depth (Inset in Fig. 1b); recent data (not shown), indicate that at this distance to the water table, soil water content at 50 cm deep is still well above the soil field capacity.

The mean annual T_{AIR} for Florida Climatic Zone 2 (NOAA, 2022) has

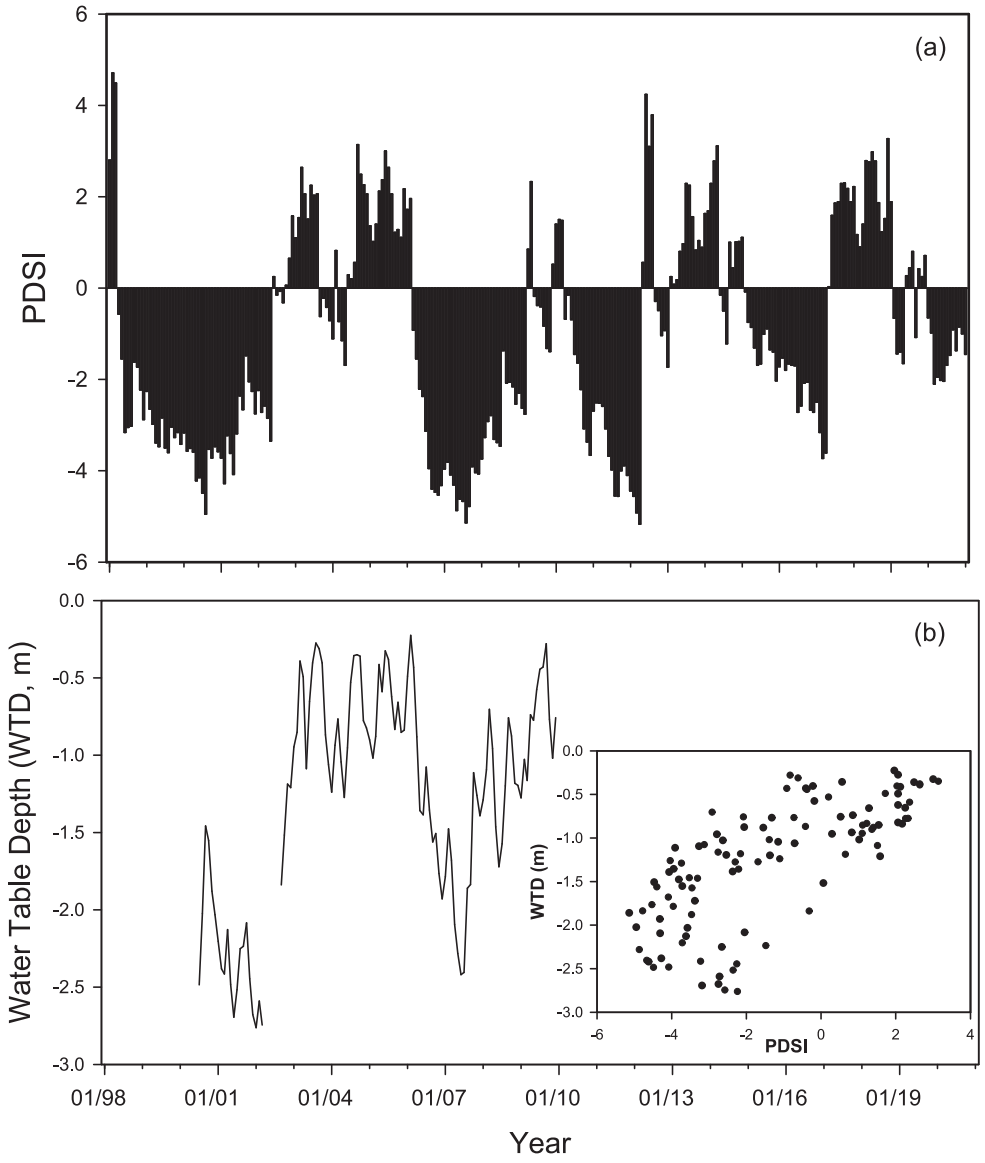

Fig. 1. Monthly Palmer drought severity index (PDSI) (a), and distance to the water table (WTD) (b), for a naturally-regenerated pine ecosystem, Florida, USA. The inset represents the relation of WTD to PDSI.

increased at 0.19 °C per decade since 1950, for a cumulative increase of 1.3 °C across a 70-year period ($p < 0.0001$) (Fig. 2). The site had a significant increase of 0.3 °C per decade during the last 30 years ($p = 0.008$), with the highest mean annual temperatures on record registered after 2011.

Monthly LAI values derived from MODIS (LAI_M) and derived from needlefall (LAI_N) (Supplements Fig. 1), had a similar seasonal pattern ($LAI_M = LAI_N$ *1.276 + 0.99, $r^2 = 0.50p < 0.0001$); however, LAI_M seemed to saturate reaching maximums between 5 and 6 m^2 m^{-2} between May and August; but minimum LAI_M had a wider fluctuation reaching between 2.8 m^2 m^{-2} in December 2012 and 4.2 m^2 m^{-2} in December 2016. Monthly LAI_N reached a maximum monthly greater than 3.5 m^2 m^{-2} between June and September of each year and minimum below 2.5 m^2 m^{-2} between January and February. LAI_N was lower in drought years (2006 – 2007 and 2011 & 2012), but not LAI_M.

3.2. Carbon stocks and biometric fluxes, fire, and harvest effects

The forest had 39.9 ± 8.7 Mg C/ha in woody biomass at the beginning of the study in 2000, accumulated up to 44.3 ± 9.1 Mg C/ha with a net gain of 4.4 Mg C/ha up to 2016 (Table 1). Tree aboveground biomass increment (tree growth + foliage production) averaged 1.64 ± 0.21 Mg C/ha yr^{-1}. Basal area was reduced by harvest from 17.05 ± 0.66 m^2/ha to 13.63 ± 3.13 m^2/ha (20%) in 2016. Average understory growth after fire was 0.77 ± 1.02 Mg C/ha yr^{-1}; however, understory biomass increment tended to be higher than tree growth during the fire years. Extraction by harvest in 2016 removed 7.55 ± 0.3 Mg C ha^{-1} as merchantable products.

Carbon content in the understory biomass was similar before fire during the three assessments events (Fig. 3a), the C content associated with aboveground understory biomass in non-fire years was 2.3 ± 0.3 Mg C ha^{-1}. Forest floor accumulated in non-fire years, reaching up to 14.5 ± 2.1 Mg C/ha after six years without fire (1.8 times higher in 2003 than in 2006), and averaged 8.1 ± 1.9 Mg C/ha after the implementation of the 3-year fire cycle (Fig. 4b), consequently, a larger amount of C was released from forest floor during the fire in January 2003, producing a higher total C release in the 2003 fire (-11.38 ± 1.64 Mg C ha^{-1}) than in the 2006 fire (-5.85 ± 1.64 Mg C ha^{-1}) (Fig. 4). Similar

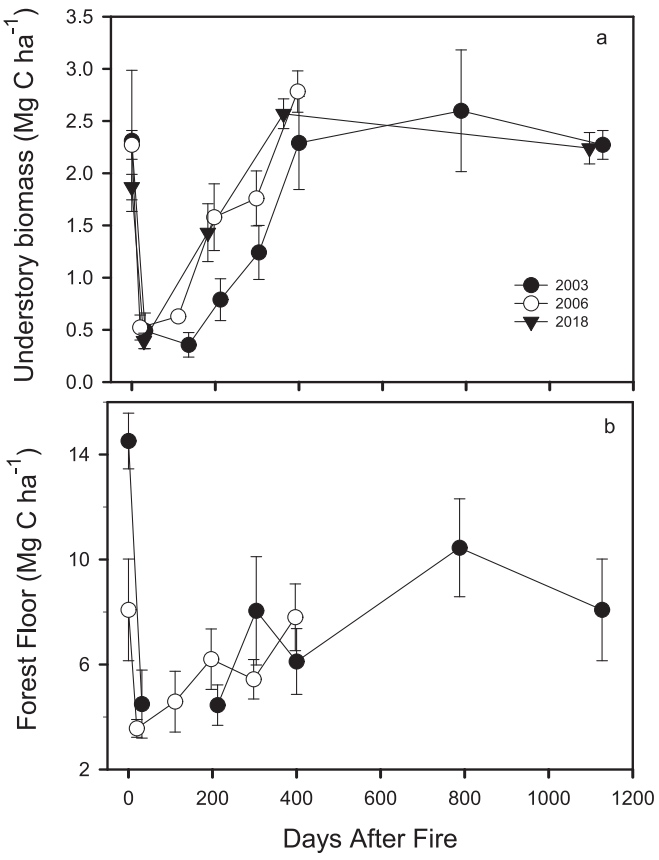

Fig. 3. Changes in carbon content in understory biomass (a) and forest floor (b) (Mg C ha^{-1}) during three fire cycles (2003, 2006 & 2018) for a naturally-regenerated pine ecosystem, Florida, US. Data for the 2018 fire from Shrestha 2020.

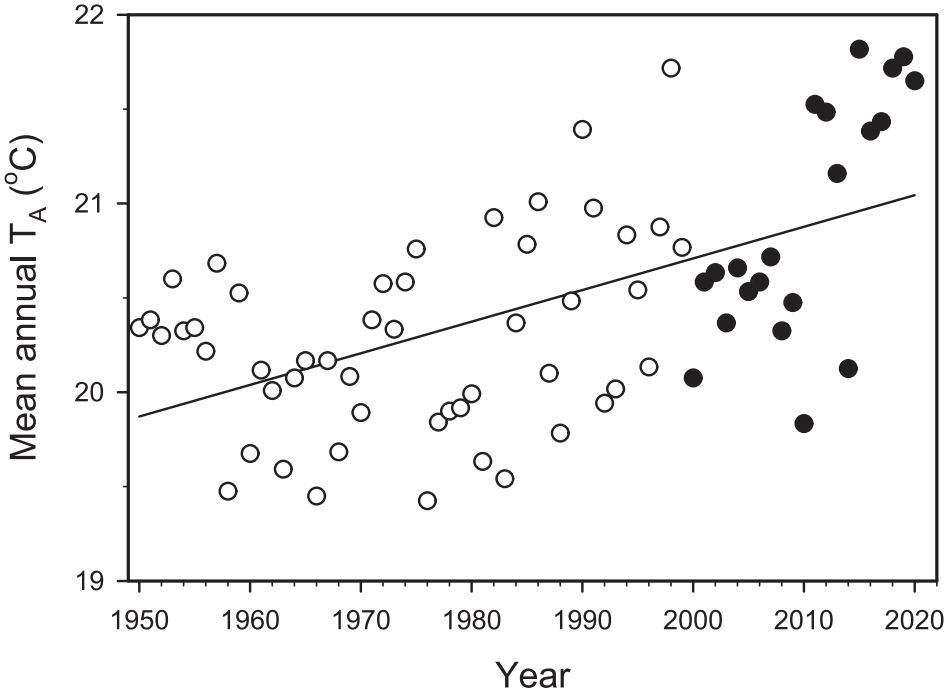

Fig. 2. Mean annual temperature (calendar year) since 1950 Florida Climatic Zone 2, NOAA 2022. Black dots correspond to the extent of the study period.

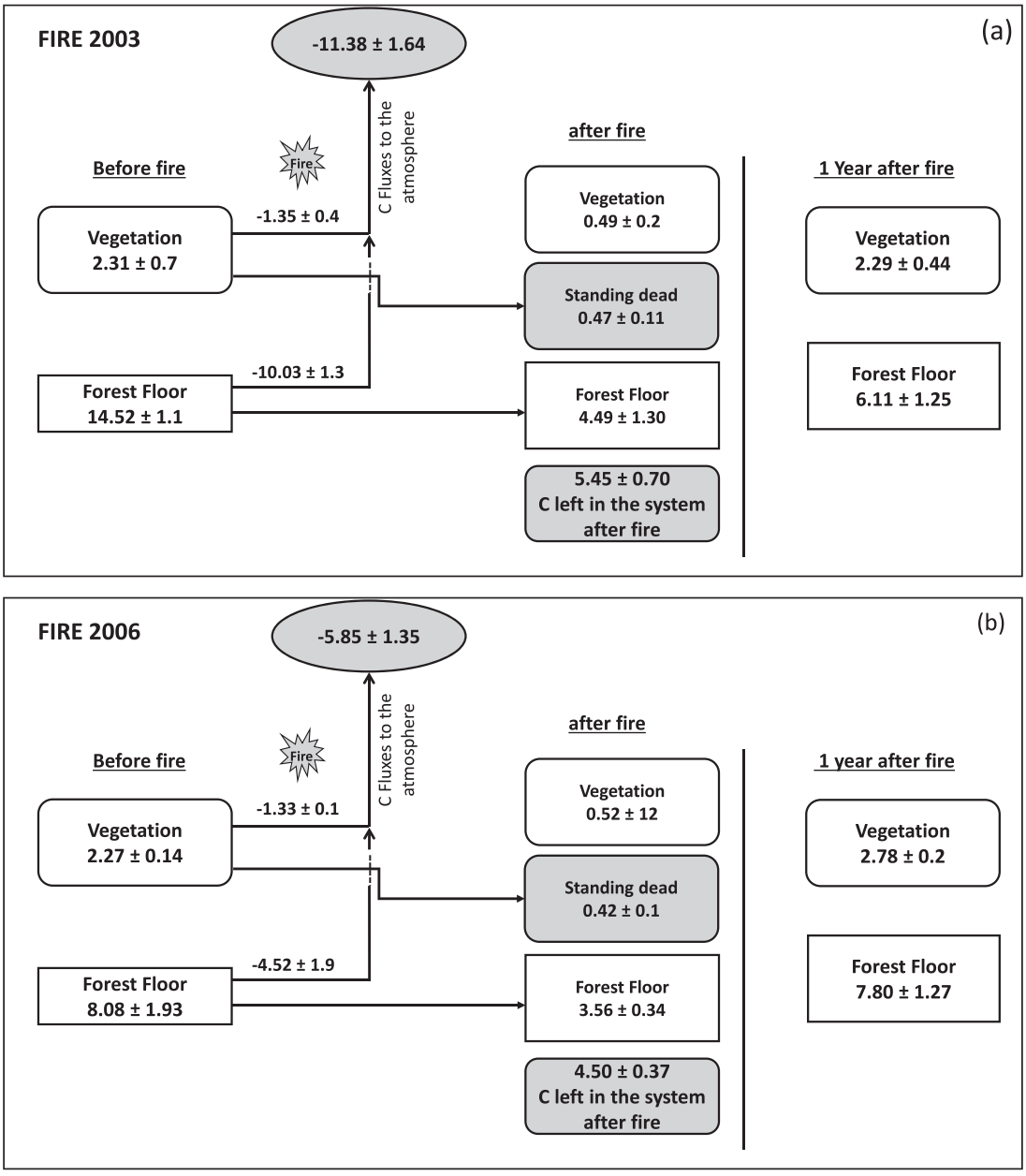

Fig. 4. Fire effects on carbon budgets in understory biomass in a naturally-regenerated pine ecosystem, Florida, USA. a) Fire in 2003, b) Fire in 2006. Values are in Mg C/ha (mean ± SE). Values in gray boxes and arrows were estimated, other values were measured.

amounts of unburnt forest floor remained after the fires in 2003 and 2006, notwithstanding the larger amount before the fire in 2003. Carbon content in living vegetation after fire was also similar among the three studied fire cycles (Fig. 3a & 4), and similar amounts of C were left in the ecosystem after the fires in 2003 and 2006 (Fig. 4a, b). Recovery after fire was also very similar during the three assessments, with understory biomass reaching pre-fire conditions one year after fire and plateauing thereafter (Fig. 3a, 4). Forest floor, tended to reach a plateau one year after fire during the 2003 and 2006 fire cycles (Fig. 3b). For the 2006 fire, the first 3-year fire cycle in this study, initial C content in above-ground understory biomass was 2.27 ± 0.14 Mg C/ha (Fig. 4b), it was dominated by saw palmetto (55%), and gallberry (22%). Understory biomass decreased to 0.52 ± 0.12 Mg C ha $^{-1}$ after fire, saw palmetto decreased to 0.39 ± 0.15 Mg C/ha and gallberry to 0.05 ± 0.02 Mg C/ha. By July of 2006, total understory vegetation increased by 1.06 Mg C/ha (Fig. 3a), saw palmetto increased by 0.49 Mg C/ha and gallberry increased by 0.21 Mg C/ha (66% of total understory growth). Understory vegetation showed full recovery one year after fire, including both dominant species. Considering that C content in understory biomass and forest floor plateau after a year, the average maximum values (plateaus) in biomass and forest floor were used to estimate C emissions from fires in 2009, 2012, and 2015.

3.3. Atmospheric carbon fluxes (GPP, R_{ECO} & NEP)

Mean annual NEP was 3.3 ± 1.4 Mg C/ha yr^{-1} (mean ± std), varying from 1.30 Mg C/ha yr^{-1} to 6.65 Mg C/ha yr^{-1} (Table 1). There were no significant differences in annual NEP between fire and non-fire years ($p = 0.42$), either between fire years and the years after fire ($p = 0.28$); however, years with lower NEP were associated to drought years (2001, 2007, 2011) or a combination of drought and fire (2006 & 2012).

Mean annual GPP was 19.36 ± 2.52 Mg C/ha yr^{-1}, varying from 14.92 Mg C/ha yr^{-1} to 23.81 Mg C/ha yr^{-1} (Table 1), there was not a significant difference in mean annual GPP between fire and non-fire

years (p = 0.17), either between fire year nor years after fire (p = 0.23), although annual GPP tended to be higher during fire years. However, R_{ECO} was significantly higher (p = 0.009) during fire years (17.73 ± 1.43 Mg C/ha yr^{-1}) than non-fire years (15.24 ± 1.80 Mg C/ha yr^{-1}). Annual R_{ECO} was higher during the fire year than one (p = 0.04) or two years (p = 0.016) after fire years, but differences between year one and two after the fire were not detected.

The ecosystem was a C sink throughout the two decades (NEP) (Fig. 5a), accumulating a total of 69.85 Mg C/ha after 21 years. However, cumulative NEP was 14.6 Mg C/ha lower during the first decade (2000 – 2009) compared to the second decade (2010 – 2019) (25.35 Mg C/ha vs. 39.98 Mg C/ha) (Fig. 5b). Cumulative GPP was 178.8 Mg C/ha for the first decade of study and 206.7 Mg C/ha for the second one, 27.9 Mg C/ha higher, while cumulative R_{ECO} was 153.6 Mg C/ha for the first decade and 166.8 Mg C/ha for the second one, 13.2 Mg C/ha higher.

Across all years, mean monthly NEP increased from January to May of each year (Fig. 6a), with the largest sink increase in mean monthly NEP happening from February to March when it changed by a factor of 3.6; highest mean monthly NEP were recorded between March and May, averaging 0.51 ± 0.26 Mg C/ha for the three months period, while mean NEP for the period June - August was 0.35 ± 0.20 Mg C/ha, lower mean NEP were reached from November to January. In general, NEP during the six months period - March to August- represented an average 80% of the annual C fluxes. However, for drought years mean NEP was negative (C source) in January (e.g., January 2007, Fig. 6a), reached an average 0.36 ± 0.24 Mg C/ha from March to May, and 0.17 ± 0.16 Mg C/ha from June to August, whereas in wet years, average NEP was 0.66 ± 0.24 Mg C/ha between March – May and 0.43 ± 0.18 Mg C/ha in the period June - August. Contrasting the two years with the lowest (2007) and highest (2019) annual NEP, (Fig. 6a), monthly NEP in March 2019 reached 1.00 Mg C/ha, almost twice the March NEP in 2007, and a difference ~0.56 MgC ha^{-1} between the two years was sustained until September; NEP in August 2007 was neutral (around zero) and negative September - October.

Across all years, mean monthly GPP (Fig. 6b) increased from January to August, reaching an average of 2.0 ± 0.32 Mg C/ha between June and August, decreasing after through the end of the year. For drought years, GPP had an average of 1.4 ± 0.23 Mg C/ha for the period March – May, and 1.8 ± 0.23 Mg C/ha for June – August, while for wet years the average GPP between March – May was 1.8 ± 0.33 Mg C/ha and 2.2 ± 0.28 Mg C/ha from June through August. Ecosystem photosynthetic capacity (GPP_{OPT}, Equation (1)) was affected by drought (Table 2). Mean monthly GPP_{OPT} from May to September (months with the highest GPP) were compared between two fires years contrasting in PDSI (2006 and 2009), and the immediate years after fire (2007 and2010), also contrasting in PDSI. GPP_{OPT} was significantly lower in 2006 (PDSI = -3.12 ± 0.96) than in 2009 (PDSI = 0.11 ± 1.26) (P = 0.001); and lower in 2007 (PDSI = -4.81 ± 0.20) than in 2010 (PDSI = -1.23 ± 0.81) (P = 0.002). No differences in GPP_{OPT} were detected between 2006 & 2007 or between 2009 & 2010.

Mean monthly R_{ECO} varied little from January to April (Fig. 6c), with an average of 1.03 ± 0.19 Mg C/ha for the four months; however, mean monthly temperature increased from 12.5 ℃ in January to 20.1 ℃ in April. R_{ECO} increased from April to August – September, reaching monthly greater than 2.0 Mg C/ha. A difference in monthly GPP of ~0.70 Mg C/ha was sustained form March to September between the two extreme years, while for R_{ECO} the difference was only 0.18 Mg C/ha (Fig. 7).

3.4. Belowground carbon fluxes

Considering that NEP reflects the net change in above (AG) and belowground (BG) carbon stocks for a given year (e.g., NEP – (ΔC_{AG} + ΔC_{BG}) = 0), belowground net carbon flux can be estimated by subtracting AG growth from NEP. Aboveground tree and understory growth was measured through fire cycles from 2003 to 2015 (Table 1). Results indicate that by the end of each fire year, aboveground growth exceeded NEP, except in 2015, in a range from −0.23 to −2.32 Mg C/ha yr^{-1}. However, NEP exceeded aboveground growth in years between fire cycles in a range from 0.53 to 3.59 Mg C/ha yr^{-1}. After 13 years of these measurements, NEP exceeded aboveground growth by 9.34 Mg C/ha.

3.5. Net ecosystem carbon balance (NECB)

The NECB had a strong interannual variability after C emissions from fire and extraction by harvest was added to NEP (Table 1, Fig. 5a). NECB varied by 15.5 Mg C/ha from the largest C sink of 6.65 Mg C/ha to the largest source of −8.84 Mg C/ha. The highest C emissions during a prescribed fire occurred at the end of the phenological year 2002 (e.g., January of 2003) (-11.38 ± 1.64 Mg C/ha), when the ecosystem had six

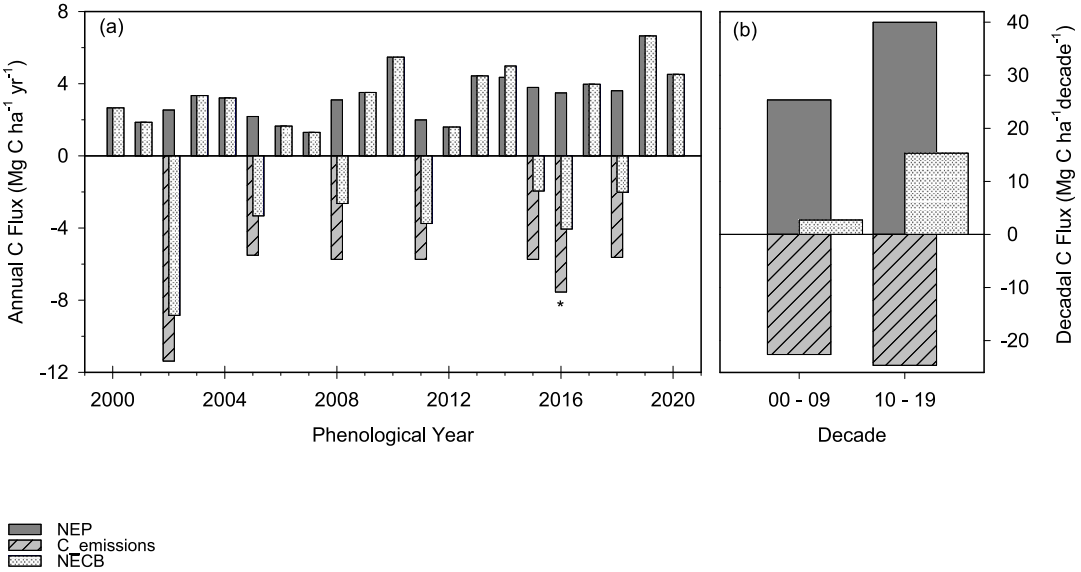

Fig. 5. A) annual ecosystem carbon exchanges, and b) decadal carbon balance for a naturally-regenerated pine ecosystem in florida, us. dark grey bar = NEP, dashed grey bars = C emissions by fire or C extraction by harvest operations (*), doted bars = Net Ecosystem Carbon balance, NECB (e.g., NEP minus carbon loses either by fire or extraction).

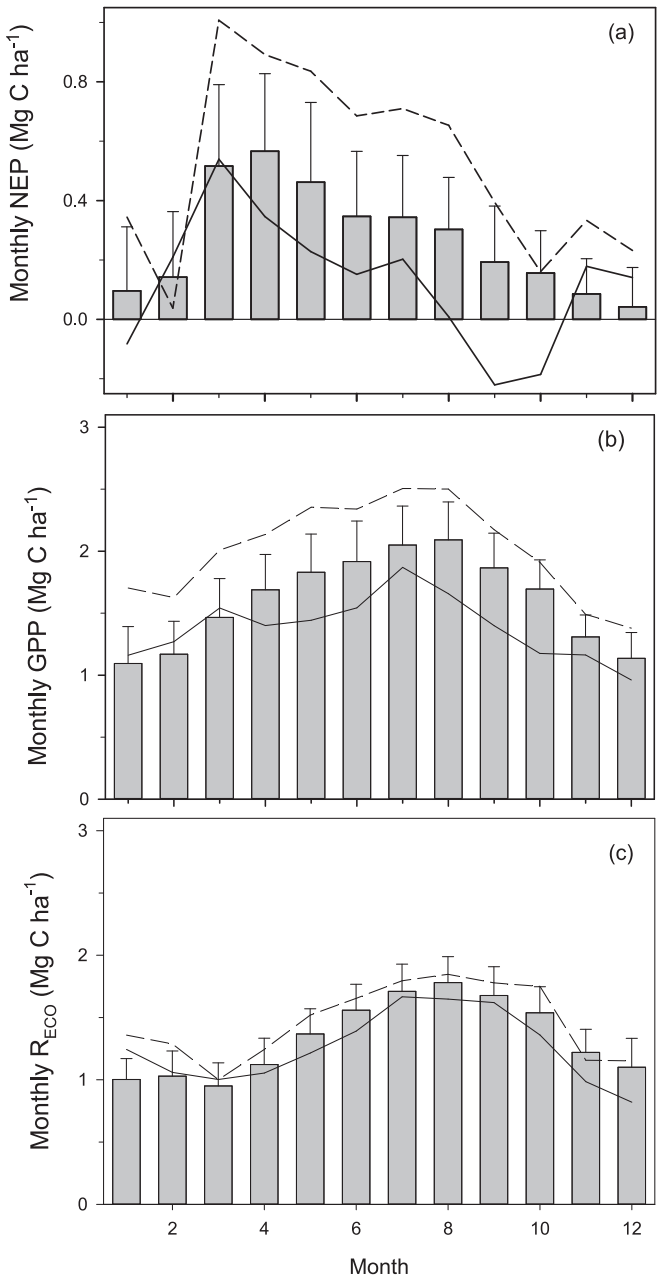

Fig. 6. Mean monthly Carbon fluxes (Mg C/ha month^{-1}), a) Net ecosystem productivity (NEP), b) Gross primary production (GPP), c) Ecosystem respiration (R_{ECO}), solid line = monthly C fluxes drought year (2007), dashed line = monthly C fluxes wet year (2019), for a naturally-regenerated pine ecosystem, Florida, US.

years since last fire, and half of it (-5.85 ± 1.35 Mg C/ha) three years after during the fire in January of 2006, and we estimated similar amounts during the consecutive fire cycles; overall, –22.63 Mg C/ha were released by fire during the three fire cycles of the first decade and −17.11 Mg C/ha during the three fire cycles of the second (Fig. 5b). The ecosystem was also a C source in 2016, when −7.55 ± 3.03 Mg C/ha were extracted by cutting operations, for a total of 24.7 Mg C/ha exported during the second decade. Considering the decadal NECB (Fig. 5b), the ecosystem was a low C sink of 2.72 Mg C/ha during the first decade of study (2000 – 2009); however, it was a higher C sink during the following decade (2010—2019), NECB accumulated up to 15.32 Mg C/ha. After integrating the 21 years of NEP as measured by eddy covariance, C emissions caused by fires, and C extracted by harvest (69.85–39.74–7.55 Mg C/ha, respectively), NECB for the study site was 22.56 Mg C/ha.

3.6. Main drivers of C fluxes

Interannual variability in C fluxes was not explained by any of annual environmental drivers (T_{AIR}, PAR, precipitation, or PDSI); however, controls on C fluxes over monthly scales were evident. Environmental monthly variables (T_{AIR}, PAR, PDSI, VPD_{MAX}) were included in GAM optimization models to assess their effects on integrated monthly C fluxes (NEP, GPP & R_{ECO}) (n = 231) (Table 3). Response to each variable is complex as indicated by the effective degree of freedom (edf) for each (e.g., 3.4 for PDSI). The model for NEP explained 51% of the variance, 73% for GPP and 76% for R_{ECO}. The analysis indicated that NEP and GPP are highly sensitive to low PDSI and PAR (Fig. 7a, b & d, e); both NEP and GPP increased to a maximum around PDSI of −0.4. A region of positive effect of PDSI on NEP and GPP (positive lower 95%) was reached between ~-1.8 and ~ +1.5; GPP tended to plateau after PDSI greater than 1; however, uncertainties increased at both ends of PDSI due to a low number of data points. Similarly, in response to PAR, NEP increased and reached maximum at PAR of 13 M mols photon ha^{-1} month^{-1}, while GPP reached maximum at PAR of 15 M mols photon ha^{-1} month^{-1}, a region of maximum (positive effect) is reached between 10 and 15 M mols photon ha^{-1} month^{-1} for both fluxes. NEP is also sensitive to the time effect (month) (Fig. 7c), maximum effect on NEP is reached in March and a region of positive effect was shown between the period February – April; while for GPP, the third significant factor was T_{AIR}, VPD_{MAX} and the time term did not have a significant effect on GPP; however, it slightly improved model performance. Response of R_{ECO} to PDSI is completely linear (edf = 1, Table 3) (Fig. 7g), and R_{ECO} also increased with monthly T_{AIR} (Fig. 7h); however, the month effect had a negative impact from January to April and increased from May to the rest of the year (Fig. 7i).

4. Discussion

This study presents 21 years of C dynamics in an actively-managed, naturally-regenerated pine forest in the southeastern United States, among the longest reported for forest ecosystems (Arain et al., 2022; Finzi et al., 2020; Hollinger et al., 2021; Launiainen et al., 2022). Most other long-term reports of forest C dynamics are for forests with no management activity, in contrast to the present study, which documents the effects of forest management activities such as frequent prescribed fire and periodic harvest. The site experienced a broad range of weather conditions, ranging from multiyear droughts to annual precipitation over the annual mean, six prescribed fire cycles and a 20% basal area reduction during the study period. Ecosystem capacity to accumulate C (NEP) was affected by the response of GPP and R_{ECO} to water availability, where GPP was more affected than R_{ECO}; however, C losses caused by management activities (fire emissions and extraction by harvest) had the greater impact on interannual variability in NECB. However, differences in NECB between the two decades was driven by changing GPP and ultimately NEP in response to water availability, since management (fire and cutting) produced a similar amount of C loss in each decade. A combination of biomass estimates for trees and understory, and NEP measurements indicated that a large proportion of the assimilated C is translocated below ground. For the full 21-year period the forest was a C sink with a NECB of 22.56 Mg C ha^{-1}.

4.1. Carbon fluxes

Annual NEP for this site averaged 3.32 ± 1.38 Mg C/ha over 21 years, with a broad range of 5.35 Mg C/ha between the lower (1.3 Mg C/ha, 2007) and the upper (6.65 Mg C/ha, 2019) annual NEP estimates. Overall, the site was a continuous C sink through the 21 years of study, accumulating 69.85 Mg C/ha as NEP. Tree growth dominated

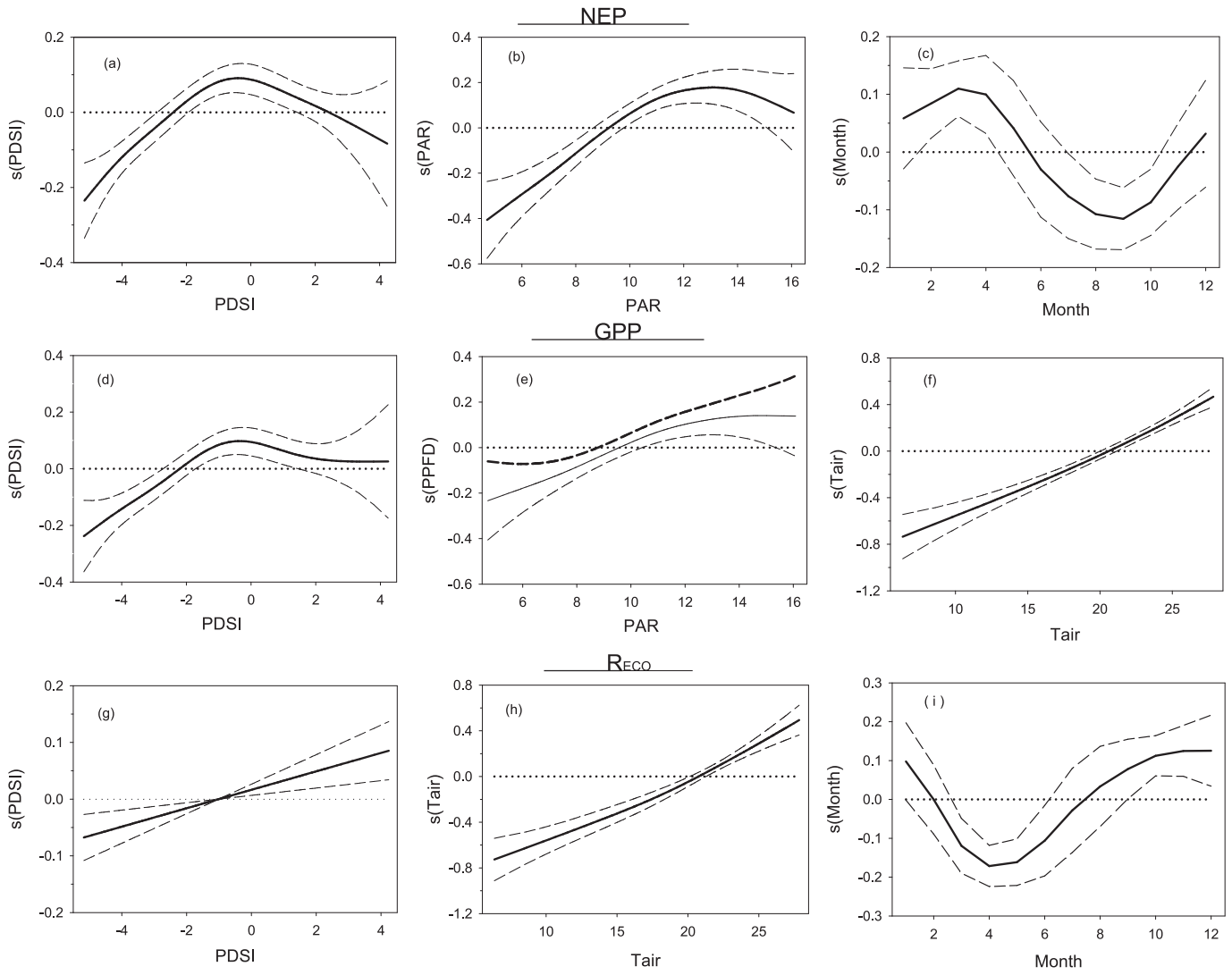

Fig. 7. Effects of physical drivers and time on integrated monthly carbon fluxes, net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (R_{ECO}) for a naturally-regenerated pine ecosystem, Florida, US. Black solid lines represent the response curves obtained using a generalized additive model (GAM), dashed lines represent the 95% confidence intervals and dotted lines represent the zero effect. PDSI = Palmer drought severity index, PPFD = monthly total photosynthetic photon flux (M mols photon phlox h-1), Tair = average air temperature (°C). (s) represent the model smooth terms.

aboveground growth accumulating 26.27 Mg C/ha for a period of 16 years of biomass measurements. NEP values for this naturally regenerated pine forest are within the same range for other terrestrial ecosystems in the southeastern United States, including natural and planted ecosystems (Bracho et al., 2021; Bracho et al., 2012; Bracho et al., 2018; Hinkle et al., 2019; Powell et al., 2006; Starr et al., 2016), and other temperate forests (Arain et al., 2022; Finzi et al., 2020; Launiainen et al., 2022), and place this managed naturally regenerated pine ecosystem within the most productive ecosystems around the world (Aguilos et al., 2020; Baldocchi et al., 2018; Bracho et al., 2012; Cho et al., 2021; Li et al., 2021; Yu et al., 2014).

The potential effects of fire on interannual variability in NEP and GPP are likely masked by the strong interannual variability in mean climatic conditions. Prescribed burns were conducted during both drought and wet years creating a large range in annual carbon fluxes; however, GPP tended to be higher during fire years, likely related to the fast recovery of understory vegetation. Higher R_{ECO} during fire years was probably related to increased mean soil temperature and increased decomposition caused by the large amount of semi-burned material deposited on the soil surface coupled with increased nutrient availability. Similarly, a native rangeland, a treeless flatwoods site in the region, had a higher GPP during a fire year due to a fast recovery in photosynthetic tissue and also exhibited a higher R_{ECO}, driven by increased soil respiration rates (Bracho et al., 2021). Prescribed fire in longleaf pine can produce moderate decline in annual tree growth after fire; however, tree growth can recover between fire years, leading to no significant differences in growth between fire intervals (Ames et al., 2015; Ford et al., 2010). However, these results contrast with the carbon uptake capacity recovery from other forests around the world. In general, most forests become a carbon source during the fire year, either a prescribed or wild fire, and recovery of the C sink capacity can take from months up to several decades after fire, depending on forest type and disturbance (Amiro et al., 2010; Dore et al., 2012; Oliveira et al., 2021; Starr et al., 2015; Sun et al., 2020).

The monthly NEP pattern under average or any climate condition indicated that the typical dry period (March – May) has the highest NEP of the year. The combination of sustained low R_{ECO} and increasing GPP explains the observed sharp shift and sustained high NEP during this period. Ecosystem respiration remains low and with very little variation regardless of an increase in mean T_{AIR} greater than 7 °C from January to April, as wilting point conditions that are reached in the topsoil limit heterotrophic respiration. Whereas, GPP continued to increase with

Table 3
Generalized additive model (GAM) summary for monthly carbon fluxes, net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (R_{ECO}). Model smooth terms (s), effective degree of freedom (edf), F statistics and model performance (adjusted r^2) for a naturally-regenerated pine ecosystem, Florida, USA.

Parametric coefficients (Intercept)		Estimate	Std. error	t-value	p-value
NEP		0.27	0.012	21.97	<0.0001
GPP		1.60	0.015	104.80	<0.0001
R_{ECO}		1.33	0.011	116.50	<0.0001
C Flux	**Smooth terms**	**edf**	**F-value**	**p-value**	**Adjusted r^2**
NEP	s(PDSI)	3.4	10.05	<0.0001	0.51
	s(PPFD)	3.5	9.14	<0.0001	
	s(month)	3.2	4.86	<0.0001	
GPP	s(PDSI)	3.3	7.44	<0.0001	0.73
	s(VPDmax)	2.2	1.861	0.1017	
	s(PPFD)	2.3	4.86	0.0029	
	s(Tair)	1.9	62.58	<0.0001	
	S(month)	0.00001	0.000	0.7594	
R_{ECO}	s(PDSI)	1.0	10.62	0.0013	0.76
	s(Tair)	2.2	30.77	<0.0001	
	s(Month)	4.0	10.35	<0.0001	

PDSI = Palmer Drought Severity Index; PPFD Photosynthetic Photon Flux Density; Tair = Air temperature.

T_{AIR}, indicating plants continued access to the water table due to a combination of deep rooting and soil water preservation owed to low evapotranspiration during the period December – February (Bracho et al., 2008), this phenomenon is also typical for terrestrial ecosystems in the region (Bracho et al., 2021; Bracho et al., 2018; Hinkle et al., 2019; Hungate et al., 2002).

The average monthly C fluxes response to climatic fluctuations indicated that C fluxes were affected by varying degrees to water availability (PDSI), T_{AIR}, PAR and by the month of the year. Both, GPP and R_{ECO} were sensitive to very low water availability (PDSI < -2) but GPP to a greater degree, and consequently NEP decreased under drought conditions. However, a clear region of positive response of GPP and NEP to PDSI between mild drought to incipient wet spells (PDSI > -1.9, PDSI < 1) indicated a soil moisture range for optimal plant function. At this range in PDSI, the saturation zone was in average above 1 m depth, indicating water was not a limiting factor for ecosystem functioning, supporting the use of PDSI to explain drought driven variability in ecosystem C fluxes. A combination of low soil water availability, high radiation and high T_{AIR} increased the air evaporative demand (high VPD) and induced stomatal closure (Bracho et al., 2008; Bracho et al., 2021; Bracho et al., 2012), leading to lower rates of carbon uptake. Ecosystem photosynthetic capacity (GPP_{OPT}) was reduced by 40% during a drought year (PDSI < -2) as compared with GPP_{OPT} for an average precipitation year, with a few months even becoming net C sources with the consequent effect on the low annual NEP. Both, longleaf and slash pine respond to low soil water availability by controlling stomata opening affecting C uptake (Samuelson et al., 2012; Samuelson et al., 2019). Reductions in C uptake capacity is also impacted by drought conditions in pine plantations, and other ecosystems in the region (Bracho et al., 2021; Bracho et al., 2012; Bracho et al., 2018; Powell et al., 2006; Powell et al., 2008; Starr et al., 2016), and in ecosystems elsewhere (Aguilos et al., 2018; Phillips et al., 2009).

The cumulative effects of environmental variables, water availability and T_{AIR}, at the monthly, scale had complex effects on annual NEP. An informative contrast is the year with the highest NEP (2019, 6.65 Mg C/ha yr^{-1}), where water availability was optimal (PDSI > -1.44, PDSI < 0.25), and the highest mean annual T_{AIR}, while 2007, the year with the lowest NEP (1.30 Mg C/ha yr^{-1}) had a year-round PDSI < -3.8, and the lowest mean annual T_{AIR} registered during the study. The additive effect of both variables resulted in the largest difference (5.35 Mg C/ha) in NEP between years. In general, years with the lowest NEP were associated to the lowest yearly average PDSI, and the relation between annual NEP and PDSI followed a similar trend as in the monthly relationship. Droughts reduced annual NEP in terrestrial ecosystems in China, ponderosa pine and in north American forests, affecting GPP more than R_{ECO} (Arain et al., 2022; Kolb et al., 2013; Liu et al., 2014; Xu et al., 2020). Moreover, the cumulative effects across decades illustrated environmental effects on carbon fluxes, mainly GPP and NEP. Here, for the first decade since the beginning of the study, PDSI had a cumulative of −170 and a mean T_{AIR} was 20.0 ℃, while during the second decade, PDSI had a cumulative of −50 and an average T_{AIR} of 20.8 ℃. Consequently, GPP was 27.9 Mg C/ha higher during the second decade, while R_{ECO} increased only by half leading to a second decade with a NEP 14.6 Mg C/ha higher.

4.2. Fire and harvest effects on C balance

Fire and reduction in basal area affected NECB. Although drought severity controlled interannual variability in GPP and consequently NEP, the strong interannual variability in NECB of 15.5 Mg C ha^{-1} (from 6.65 to −8.84 Mg C/ha yr^{-1}), was mainly controlled by the amounts of C emitted by fire or extracted by cutting each time one of those management activities were conducted. Carbon emissions by fire were also affected by fire frequency. The 2003 fire, which occurred six years after the previous fire, had twice the carbon emissions of subsequent prescribed fires occurring on a three-year interval. This was mainly due to increased forest floor material that had accumulated over six years. Forest floor in these systems tends to accumulate over time in the absence of disturbance, as pine needle fall averages 1.07 ± 0.20 Mg C/ha yr^{-1} and annual decomposition rate is typically <20% (Gholz et al., 1985; Gholz et al., 1986).

Understory aboveground vegetation did not exceed 3 Mg C/ha, and after each fire, 21% to 23% of it remains intact. It fully recovers during the first year after fire, reaching and maintaining maximum biomass until the next fire cycle; resembling a native rangeland in the area, e.g., a treeless flatwoods recovering the pre-fire biomass within the first year after fire and a scrub oak-palmetto ecosystem (Bracho et al., 2021; Schmalzer, 2003). Saw palmetto and gallberry, the dominant species in the pine flatwoods understory, typically recover their pre-fire biomass and remain stable until the next fire (Hughes and Knox, 1964; Saha et al., 2010). Further growth between fire cycles after plateau in biomass is reached is probably limited by growth form and light availability. The rapid understory aboveground growth after fire may be supported by a combination of nutrient availability after the fire, but mainly by a rapid mobilization of belowground carbon reserves to support aboveground growth. Understory growth of 1.06 Mg C/ha was observed since after fire to July of 2006, five months after fire, when understory plant photosynthesis was likely not sufficient to support such rapid growth. Saw palmetto and gallberry represented 66% (0.49 & 0.21 Mg C/ha) of the total understory growth period. These two species are known to be adapted to recurrent fire, they both develop belowground structures where non-structural carbohydrates are stored and then remobilized to facilitate rapid aboveground regrowth after fire (Kalmbacher et al., 1983; Schmalzer, 2003). Although new leaves developed and contributed to the growth, more than 1 Mg C/ha of belowground C was likely mobilized to support aboveground growth. It has been shown that immediately after a fire total carbohydrate content in saw palmetto and gallberry rhizomes drops to a minimum for four to five months, sugar content increases simultaneously indicating simple carbon compounds are mobilized out of the rhizomes, total carbohydrate stabilizes for the following three to four months and recover up to 50% by a year after fire, and may take between three to four years to fully recover (Hough, 1968; Hughes and Knox, 1964; Kalmbacher et al., 1983).

The timing of mobilization of belowground carbon pools toward aboveground growth of understory vegetation is affected by water availability. After the 2006 fire (during a very dry period) belowground carbon remobilization lasted two years. During periods of average precipitation, post-fire belowground carbon remobilization lasted only a

single year. Based on understory biomass recovery after fire combined with NEP measurements, belowground acted as a net carbon sink of 9.34 Mg C/ha for the period 2003–2015.

Over the 21 years of study, the actively managed naturally regenerated ecosystem at ACF accumulated a net of 22.56 Mg C/ha, at an average annual rate of 1.07 ± 3.97 Mg C/ha yr^{-1}. Differences in NECB between the two decades in study (2.72 vs. 15.32 Mg C/ha) were driven by differences in NEP since carbon releases by management were similar between the two decades (22.63 vs. 24.66 Mg C/ha). Carbon fire emissions were higher during the first decade; forest floor accumulated for six years without fire, causing a higher carbon emission during next fire, while during the second decade, in addition to carbon emissions caused by each of the three fire cycles, an extra amount of carbon similar to those released by each fire was extracted by the harvest. These results contrast with other studies, where climate variability controlled interannual variability in carbon balance while disturbance controlled the long-term (Barford et al., 2001; Hirata et al., 2014), and highlight the importance of integrating management and climatic variability at different timescales to understand and predict C accumulation in the landscape.

5. Conclusions

The 21 years of C dynamics assessment in an actively-managed naturally regenerated pine ecosystem in the southeastern United States allowed us to elucidate the interactions of climatic fluctuations and management on C balance at different time scales from days to decades, and how C balance may respond to climate change. The forest was a C sink during the study period with monthly variability in GPP and NEP responding primarily to water availability in a non-linear pattern that scaled across years and through the two decades of study to indicate a strong control of water availability on NECB. Yet the ecosystem's NEP tolerates mild seasonal and yearly droughts, possibly by tapping into deep water sources and adjusting water loss. Interannual variability in NECB was controlled by management (prescribed fire and cutting), and by water availability over decadal time scales. The understory represents an important component in the ecosystem carbon uptake and storage capacity. Losses of C after fire are rapidly recovered in part because understory recovery after fire is fast, likely due to the allocation of large amounts of C to belowground structures, and to a rapid mobilization of these belowground reserves to support aboveground growth, but the extent of this response is also affected by water availability. These characteristics make this ecosystem resilient to drought and fire disturbance and a viable option to mitigate carbon dioxide emissions in a changing climate. These benefits are on top of the many other ecosystem services provided by forests of this type, including biodiversity, fiber, economic revenue, and water regulation and filtration.

Declaration of Competing Interest

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

Data availability

AmeriFlux web site

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Appendix A. Supplementary data

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