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# Carbon dynamics of prescribed fire in pine- and oak-dominated forests on the mid-Atlantic coastal plain, USA

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ABSTRACT

The use of prescribed fire to reduce the risk of wildfires and maintain or enhance desired ecological conditions is increasing in forests of the Mid-Atlantic region. Accurate estimates of forest carbon (C) dynamics associated with prescribed burning, including net ecosystem productivity (NEP) and time to accumulate the C lost during burns, termed neutral net ecosystem C balance (NECB), as a function of fire intensity and burn intervals would assist fire managers optimize treatment timing while balancing other ecosystem services provided by forests. We quantified forest C dynamics and evapotranspiration in two pine- and oak-dominated forests in the Pinelands National Reserve of southern New Jersey that have been managed using prescribed fire over two decades. Using long-term C flux data, we found that NEP, ecosystem respiration (RE) and gross ecosystem production (GEP) were similar among stands during undisturbed years. Estimated C loss during three prescribed burns at the pine-dominated stand averaged 4.3 ± 0.9 Mg C $ha^{-1}$, which is equivalent to 2–3 years of NEP during undisturbed years, and consistent with fuel consumption during prescribed burns throughout the Pinelands. Only annual NEP was lower during years when burns were conducted compared to unburned years, while annual RE, GEP, evapotranspiration and ecosystem water use efficiency were similar. Over a two-decade period, NEP totaled 28.3 Mg C $ha^{-1}$ and NECB was 15.5 Mg C $ha^{-1}$, indicating that stands managed using repeated prescribed burns still sequester moderate amounts of C. At an oak-dominated stand, a prescribed burn released lower amounts of C (1.7 Mg C $ha^{-1}$), and annual NEP was greater over the following 3-year period compared to a decade of low annual NEP following severe spongy moth defoliation and associated tree mortality, suggesting that prescribed fires could play a role in the restoration of ecosystem functioning in insect-damaged stands. Patterns of forest C dynamics during and following prescribed burns in these mid-Atlantic forests are similar to intermediate age pine-dominated stands throughout the southeastern USA, which also sequester moderate amounts of C through repeated prescribed burning regimes.

## 1. Introduction

Intermediate age forests dominated by pines and oaks are extensive in the mid-Atlantic region, USA, and scattered throughout the southeast USA (Pan et al., 2013, Forest Inventory and Analysis; www.fia.fs.usda.gov). Combined flux tower-based and biometric approaches to measure forest carbon (C) dynamics indicate that net ecosystem productivity (NEP) decreases with increasing stand age, and when undisturbed, intermediate age forests on the Atlantic coastal plain are moderately productive, with NEP approximately a third to a half of rates characterizing younger, intensively managed short-rotation pine plantations (Bracho et al., 2012; Aguilos et al., 2020, Table A1). As the intermediate age stands have aged, the ratio of ecosystem respiration (RE) to gross ecosystem productivity (GEP) increased and now approaches 0.9 in both managed and unmanaged stands (Table A1).

The effects of disturbance on C dynamics of pine- and oak-dominated forests have been the focus of numerous research efforts (e.g., Amiro et al., 2010, Hicke et al., 2012, Goetz et al., 2012, Quirion et al., 2021). In an extensive synthesis, Amiro et al. (2010) used information from flux towers and chronosequence studies of forest harvesting, insect infestations, and wildfires to evaluate the impact of major disturbances on forest C dynamics. Disturbance intensity, duration and the fate of detritus and coarse woody debris, together with climatic factors, strongly influence the time forests take to return to pre-disturbance NEP

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levels and to achieve neutral net ecosystem C balance (NECB = 0), defined as the time to accumulate the amount of C lost as a result of disturbance. Clear-cut harvesting and wildfires typically have the longest recovery times until NEP and NECB reach pre-disturbance levels, with some of the most rapid recovery rates occurring in short rotation slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*P. taeda* L.) plantations in the southeastern USA (Clark et al., 2004; Bracho et al., 2012; Aguilos et al., 2020).

Initially lower reductions in NEP and shorter recovery times to pre-disturbance NEP and NECB values tend to occur following non-stand replacing disturbances such as forest thinning, insect infestations and low-intensity prescribed fires compared to stand replacing disturbances (Gough et al., 2013, 2021; Clark et al., 2018; Mathes et al., 2021). Successional changes during the recovery period can further reduce recovery times to pre-disturbance NEP and NECB (Curtis and Gough, 2018; Gough et al., 2021).

Prescribed burning currently accounts for up to 75% of statewide wildland fire emissions in the Eastern USA (Larkin et al., 2020; Li et al., 2023; National Interagency Fire Center (NIFC), 2023). As increasingly greater areas of forest are proposed to be treated using prescribed fire to reduce the risk of wildfires and/or maintain and enhance desired ecological conditions, it is important to understand how repeated prescribed burning affects forest ecosystem functioning. Numerous studies have quantified forest C dynamics associated with prescribed burning and other fuels management activities (Whelan et al., 2013; Clark et al., 2015; Starr et al., 2015; Coates et al., 2020; Wright et al., 2021), while fewer have integrated long-term C flux measurements with fine-scale biometric data to estimate processes such as consumption and crown scorching during burns, or how accumulating C is partitioned among fuel types following prescribed burns, contributing to future fire behavior. Such long-term measurements can improve our ability to "fine-tune" the timing of fuel reduction treatments to maximize rates of C sequestration while simultaneously reducing wildfire risk and generating or maintaining desired stand composition and structure (Clark et al., 2015; Coates et al., 2020; Wright et al., 2021).

Prescribed burns potentially have complex and, in some cases, compensatory effects on forest C dynamics. For example, consumption of recently fallen litter can reduce decomposition and limit RE, potentially offsetting reductions in GEP during the following growing season resulting from scorching or limited regeneration of needles and leaves. Further, although total C and nitrogen (N) in the forest floor are typically reduced during prescribed burns, "pyro-mineralization" during low-intensity fires results in the release of inorganic N, phosphorus, and cations (Nave et al., 2011; Li et al., 2021), and may stimulate photosynthetic rates, GEP, and ecosystem water use efficiency (WUE), as has been observed at the individual tree level (Renninger et al., 2013; Carlo et al., 2016). Repeated prescribed burns can also encourage the regeneration of fire-tolerant species and contribute to the persistence of mixed-composition stands, thus they may improve resistance and resilience to future disturbance events (i.e., insect infestations, diseases; Kern et al., 2021; Clark et al., 2022). Further, prescribed burning may play a role in the restoration of ecosystem functioning of insect damaged stands by both releasing nutrients in detritus and promoting regeneration.

To better understand how prescribed burning affects long-term C dynamics of forests on the mid-Atlantic coastal plain, we used near-continuous carbon dioxide ($CO_2$) and water vapor flux measurements along with associated biometric data collected over a two-decade period to estimate NEP, NECB, Et and WUE in two intermediate age pine- and oak-dominated stands in the Pinelands National Reserve of southern New Jersey. At the pine-dominated stand, three operational prescribed fires (2008, 2013, 2020) were conducted by the New Jersey Forest Fire Service (NJFFS) to reduce hazardous fuel accumulations, consistent with long-term management goal of maintaining landscape-scale fuel breaks along an adjacent highway corridor (Clark et al., 2014a). At the oak-dominated stand, a single prescribed fire was conducted in 2019 following a decade of reduced NEP following spongy moth (*Lymantria dispar* L.) infestations and extensive tree and sapling mortality.

In this research, we addressed the following questions: 1) How many years of accumulated C are released during prescribed burns conducted in pine and oak-dominated stands? 2) How long until NEP recovers to pre-disturbance levels following prescribed burns? 3) How long until neutral NECB is achieved, the time at which net C accumulation equals the amount of C released during burns? and 4) Do patterns of recovery of NEP differ between prescribed burning and insect infestations, another frequently occurring disturbance in Eastern USA forests?

## 2. Materials and methods

### 2.1. Study sites

Research sites are in Burlington and Ocean Counties in the Pinelands National Reserve of southern New Jersey, USA (referred to as the "Pinelands" below). Oak-dominated, mixed-pine and oak, and pitch pine-dominated stands comprise the majority of upland forests. Most stands have regenerated naturally following cessation of timber harvesting and charcoal production towards the end of the 19th century, and severe wildfires throughout the 20th century (Little, 1998; Clark et al., 2014a). The climate is cool temperate, with cool winters, cool dry springs, and warm humid summers. Mean monthly temperatures are 0.7 ± 2.4 and 24.6 ± 1.1°C in January and July, respectively (mean ± 1 SD;1988–2018; State Climatologist of New Jersey). Mean annual precipitation is 1183 ± 168 mm. Soils are derived from the Cohansey and Kirkwood formations, and upland soils are sandy, coarse-grained, and have low nutrient status, cation exchange capacity, and base saturation (Tedrow 1983). The Pinelands are characterized by a relatively high frequency of wildfires and prescribed burns compared to other forest ecosystems in the mid-Atlantic region; from 2006 to 2015, over 12,000 wildfires burned 34,013 ha and prescribed fires were conducted on 63, 721 ha (Gallagher, 2017; National Interagency Fire Center (NIFC), 2023).

The Cedar Bridge flux tower site (Ameriflux site US-Ced) is located in a 240-ha pitch pine-scrub oak stand in the Greenwood Wildlife Management Area (39.8398°N, 74.3787°W). The overstory is composed of pitch pine (*Pinus rigida* Mill.), with occasional post (*Quercus stellata* Wangenh.) and scrub oak (*Q. marlandica* Muench.) saplings in the lower canopy. Overstory tree ages averaged 82 years old at the beginning of the study in 2004. The understory consists of scrub and bear oaks [*Q. illicifolia* Wangenh.), huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch, and *G. frondosa* (L.) Torr. & A. Gray), blueberry (*Vaccinium* spp.), bracken fern (*Pteridium aquilinum* (L.) Kuhn), and sedges (*Carex pensylvanica* Lam.). Stand characteristics are shown in Table 1. The most recent large wildfires affecting the stand occurred in April 1963 and April 1995. All prescribed burns were conducted by the NJFFS, most

**Table 1**
Structural characteristics of the canopy and understory at the pine- and oak-dominated stands in the Pinelands. Data are for the beginning and end of measurements in 2005 and 2022. Values are means ± 1 SE. Further descriptions of each stand can be found in (Clark et al., 2018 and 2022).

| Variable | Pine stand at Cedar Bridge | | Oak stand at Silas Little EF | |
|---|---|---|---|---|
| | 2004 | 2022 | 2004 | 2022 |
| Canopy height (m) | 9.7 ± 0.5 | 11.1 ± 0.3 | 13.9 ± 1.5 | 13.2 ± 0.3 |
| Stem density (trees $ha^{-1}$) | 388 ± 51 | 508 ± 68 | 418 ± 90 | 338 ± 51 |
| Basal area ($m^2$ $ha^{-1}$) | 14.3 ± 1.5 | 25.1 ± 2.2 | 15.9 ± 2.5 | 17.5 ± 2.0 |
| Biomass (Mg C $ha^{-1}$) | | | | |
| Trees and saplings | 24.2 ± 5.1 | 43.7 ± 5.2 | 41.9 ± 5.7 | 44.4 ± 2.5 |
| Understory vegetation | 2.0 ± 0.2 | 1.9 ± 0.1 | 0.9 ± 0.2 | 0.9 ± 0.2 |
| Litter layer | 7.3 ± 0.5 | 8.1 ± 0.8 | 5.1 ± 0.2 | 6.8 ± 0.6 |
| Snags and coarse wood | 0.4 ± 0.2 | 1.3 ± 0.1 | 1.2 ± 0.4 | 8.2 ± 2.5 |
| Total | 33.9 ± 5.1 | 55.0 ± 5.3 | 49.1 ± 5.7 | 60.3 ± 3.5 |

recently in March 2008, March 2013, and late February 2020, and spongy moth (*Lymantria dispar* L.) partially defoliated understory oaks and shrubs in 2007.

The Silas Little Experimental Forest flux tower site (Ameriflux site US-Slt; 39.9156N, −74.5955E) is located in a 239-ha stand of oaks and pines in Brendan Byrne State Forest. The stand is dominated by mixed oak species, primarily chestnut oak (*Quercus prinus* L.), black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh.), and post oak, with scattered pitch and shortleaf pines (*Pinus echinata* Mill.). Overstory trees averaged 90 years old at the beginning of the study in 2004. The understory is composed of huckleberry and blueberry, with scattered scrub and bear oaks. Sedges, bracken fern, mosses and lichens are also present (Table 1). The stand had been prescribed burned repeatedly from the early 1940's through the mid 1980's, and then not burned by the NJFFS until March 2019. The stand was heavily infested by spongy moth in 2007 and 2008, which caused approximately 30% mortality of oak trees > 12.5 cm DBH.

### 2.2. Meteorological and flux measurements

Above-canopy meteorological and flux measurements were made from 15.5-m and 2-m antenna towers at the pine stand at Cedar Bridge, and 19.5-m and 2-m antenna towers at the oak stand at Silas Little EF. Both stands are relatively flat and minimum fetch is approximately 690 and 1260 m at the pine and oak stands, respectively. Detailed flux footprint analyses for each stand appear in Chu et al. (2021). Meteorological measurements included incident solar radiation, photosynthetically active radiation (PAR), net radiation, air temperature, relative humidity, windspeed and direction, soil temperature, and soil heat flux, and were made using identical sensors at each site (summarized in Table B1). Meteorological sensors were measured at 10-sec intervals and 30-min averages or sums were calculated using dataloggers (Campbell Scientific CR-23x or CR-1000; Table B1). Any missing meteorological data were gap filled using the values from the closest meteorological tower in the New Jersey Weather Network (Berkeley township, NJ; https://www.njweather.org/station/1032) for the pine stand or from a second overstory meteorological tower located at Silas Little EF for the oak stand.

Net ecosystem exchange of $CO_2$ (NEE, mmol $CO_2$ $m^{-2}$ $s^{-1}$), sensible heat flux (H, W $m^{-2}$), and latent heat flux (λE, W $m^{-2}$) were measured with closed-path eddy covariance systems consisting of a three-dimensional sonic anemometer (R. M. Young 81000 v or 81000RE, Traverse City, MI, USA) mounted at 15 m height at the pine stand and 19.5 m height at the oak stand (≈4–5 m above mean canopy height at each site), a closed-path infrared gas analyzer (IRGA, LI-7000, LI-COR Inc. Lincoln, NE, USA), a laptop computer, and air flow controllers in a large meteorological box mounted on each overstory tower (Clark et al., 2010, 2018). In summary, raw data from the sonic anemometers and IRGAs were logged at 10 Hz, and we used EdiRE for all flux data processing. Daytime half-hourly net $CO_2$ exchange was best modeled as a nonrectangular hyperbola during the growing season and a linear function during winter months, and nighttime exchange was best expressed as an exponential function of air or soil temperature. Bi-monthly to seasonal parameter values for each function were used to gap fill any missing half-hourly data to calculate daily to annual NEE values. Details of system design, calibration and data processing are in Supplement C.

### 2.3. Forest biometric measurements

Tree and sapling inventories were conducted annually in five circular plots (201 $m^2$) located within 100 m of each eddy covariance tower starting in 2004 (). In addition, 1-$km^2$ grids consisting of 16 FIA-type plots in a 4 by 4 arrangement centered on each eddy covariance tower were sampled periodically (based on FIA protocols; https://www.fs.usda.gov/research/inventory/FIA; Cole et al., 2013), with plots that occurred in non-forested areas such as sand roads or fire breaks omitted from analyses. During each annual inventory of the 201 $m^2$ plots, species, diameter at breast height (DBH; 1.37 m), height, and crown condition were recorded for all live and dead trees (> 12.5 cm DBH) and saplings (> 2.5–12.5 cm DBH). The 201 $m^2$ plots at each site were also used to monitor seedling and sapling recruitment and mortality. Allometric equations were used to calculate aboveground and coarse root biomass of trees and saplings (Whittaker and Woodwell, 1968; Clark et al., 2013). Net annual C accumulation by aboveground stems and coarse roots was calculated by subtracting previous year stem, coarse root, and woody litterfall mass from the current year values (e.g., Clark et al., 2018). To estimate stem and foliage biomass of scrub oaks, shrubs, herbs and sedges in the understory, two to four 1.0 $m^2$ destructively harvested subplots adjacent to each 201 $m^2$ inventory plot were harvested at peak leaf area during the growing season. Samples were dried at 70 °C, sorted into understory oak and shrub leaves and stems, sedges, and herbs, and then weighed. Fine litter and woody fuels in the Oi horizon of the forest floor were sampled periodically in two to five 0.5 or 1.0 $m^2$ subplots randomly located adjacent to each tree inventory plot, and before and after prescribed burns at both sites. Samples were dried at 70 °C, sorted into fine litter consisting of needles and leaves, wood by time lag class wood by size class, and reproductive material, and then weighed (Clark et al., 2015, 2020b). Time lag classes for woody fuels were defined by diameter and consisted of 1-hour (< 0.64 cm diameter), 10-hour (0.64–2.54 cm diameter), and occasionally 100-hour (2.54–7.62 cm diameter) woody fuels. Coarse woody debris > 7.62 cm diameter was sampled periodically in each FIA-type subplot by measuring any coarse woody debris > 7.62 cm diameter and > 0.9 m length that crossed any of three 7.3 m long radial transects located at 30°, 150°, and 270° in the plot (Renninger et al., 2014). For each log, the small-end diameter, large-end diameter, transect diameter, length, species (if discernible) or genus, and decay class were recorded. Decay classes for coarse woody debris were defined following FIA protocols (https://www.fia.fs.usda.gov/library/field-guides-methods-proc/). Litterfall was collected monthly when present from 10 0.4-$m^2$ litterfall traps located nearby each inventory plot at each site. Litter samples were dried, separated into needles, leaves, wood, and reproductive material, and then weighed. Forest floor dynamics of the Oi horizon at pine and oak stands were then estimated using two methods; sequential biometric sampling and using a model based on litterfall and litterbag decomposition rates for each component (see Clark et al., 2018 for details).

### 2.4. Carbon loss during prescribed burns

Three methods were compared to estimate C loss and $CO_2$ emissions during prescribed burns; 1) sums of half-hourly NEE measured using flux systems during prescribed burns, 2) using pre- and post-burn biometric measurements of understory and forest floor biomass to estimate consumption during each burn, and 3) using pre-burn biometric measurements only and combustion coefficients (*sensu* Prichard et al., 2020) developed from pre- and post-burn measurements made at 48 prescribed burns in the Pinelands to estimate consumption (Clark et al., 2015, 2020b, Gallagher, 2017; Table D1). For NEE measurements during prescribed burns, IRGA outputs were set to a maximum $CO_2$ concentration range (300–3000 μmol $CO_2$ mol $air^{-1}$) the morning of each prescribed burn, and $CO_2$ concentrations measured above the canopy at 10 Hz during burns rarely spiked above this range. IRGA outputs were then reset to a standard range (300–600 μmol $CO_2$ mol $air^{-1}$) and recalibrated during the next day following burns. For the methods based on biometric measurements, we assumed equal proportions of flaming and smoldering combustion during each fire, and $CO_2$ emissions were estimated as 1576.0 ± 248.0 kg $CO_2$ Mg fuel $consumed^{-1}$ (mean ± 1 SD; "combined" value in Prichard et al., 2020; Andreae, 2019; Smoke Emissions Repository Application (SERA) (2022)). Energy release and convective and latent (LE) heat fluxes during prescribed burns were calculated from pre- and post-burn biometric measurements and moisture contents of major fuel types measured during each burn (see Clark et al., 2020b for details).

### 2.5. Statistical analyses

Datasets used for statistical analyses were tested for normality using Kolmogorov-Smirnov tests, and homogeneity of variances among groups was tested using Levene's test. Half-hourly values of NEE for daytime and nighttime periods, and daily values of NEP, Et and WUE were compared among pre- and post-burn periods using paired-sample T-tests. Because half-hourly and daily values were not independent, we randomly selected 25 subsets consisting of 25 values for each variable, and then tested for differences among stands or time periods (e.g., Clark et al., 2014b). Annual values of NEP, RE, GEP, Et and WUE for pre- and post-burn periods at the pine stand were tested using unpaired T-tests. Paired sample T-tests were used to compare pre- and post-burn values within stands for basal area and aboveground biomass of trees and saplings, and for understory foliage and stem biomass. Trends in annual net ecosystem carbon balance and biometric C accumulation were evaluated with Pierson's product moment correlation coefficients. All statistical analyses were conducted using SYSTAT 12 or SigmaPlot software (Systat Software, Inc., San Jose, CA, USA).

## 3. Results

### 3.1. Carbon dynamics during undisturbed years

Annual NEP, RE and GEP during years in the absence of fire or insect infestations were similar at the pine and oak stands (Fig. 1, Tables E1 and E2). Annual precipitation averaged 1206 ± 134 mm yr$^{-1}$ and 1098 ± 158 mm yr$^{-1}$ (mean ± 1 SD) at the pine and oak stands, respectively. Years with below-average precipitation, defined here as deviations ≤ −1 SD of the 2004–2022 means for each site, were 2007, 2010, 2016 and 2022 at the pine stand, and 2007, 2008 (both of which were omitted because of spongy moth infestations), 2016 and 2022 at the oak stand. However, prolonged dry periods during the summer months which strongly depressed half-hourly NEE during the afternoon hours were infrequent, thus we used data from all undisturbed years for these analyses. Daily evapotranspiration and ecosystem water use efficiency during the summer months (June 1 to August 31) during years in the absence of disturbance were also similar at the pine and oak stands (Fig. 1d,e).

### 3.2. Forest biometric measurements during undisturbed years

Annual aboveground net C accumulation at the pine and oak stands was dominated by trees and saplings during years in the absence of prescribed burns or spongy moth infestations (Table 2). Net C accumulation by the litter layer derived from litterfall and litterbag estimates of decomposition for undisturbed years, represented 33% and 35% of the total, while understory stems accounted for 13% and 5% of net C accumulation at pine and oak stands, respectively (Table 2).

### 3.3. Biomass consumption during prescribed fires

Biomass consumption during the relatively low intensity, dormant season prescribed burns at the pine stand averaged 4.8, 4.7, and 3.3 Mg C ha$^{-1}$, and fine litter consumption was 86%, 76% and 82% of total consumption for the prescribed burns conducted in 2008, 2013, and 2020, respectively (Fig. 2). At the oak stand, estimated consumption was 1.7 Mg C ha$^{-1}$, and fine litter consumption was 94% of the total (Fig. 2).

### 3.4. Net $CO_2$ and energy exchange during and following prescribed burns

Prescribed burns greatly enhanced half-hourly net $CO_2$ exchange rates, with maximum values occurring during fire front passage when peak half-hourly NEE averaged 1937 ± 672 μmol $CO_2$ m$^{-2}$ s$^{-1}$ (Appendix Fig. F1). Enhanced NEE values during burns corresponded with increased sensible heat fluxes (H; Fig. F1), and linear relationships between half-hourly H and NEE were significant for each burn at the pine stand, indicating a strong linkage between convective heat flux in buoyant plumes and net $CO_2$ emissions during fire front passage

**Table 2**
Average annual carbon accumulation by aboveground biomass and coarse roots of trees and saplings, understory vegetation, and the forest floor at the pine and oak stands. Data are means ± 1 SE of biometric plots sampled during years in the absence of prescribed burns or insect infestations and associated tree mortality.

| Variable | Pine stand | Oak stand |
|---|---|---|
| | Biomass accumulation (Mg C ha$^{-1}$ yr$^{-1}$ ± 1 SE) | |
| Trees and saplings | 1.16 ± 0.27 | 1.05 ± 0.11 |
| Understory vegetation | 0.25 ± 0.07 | 0.10 ± 0.17 |
| Snags and coarse wood | -0.13 ± 0.04 | 0.04 ± 0.15 |
| Forest floor | 0.63 ± 0.20 | 0.65 ± 0.15 |
| Total | 1.91 ± 0.25 | 1.84 ± 0.15 |

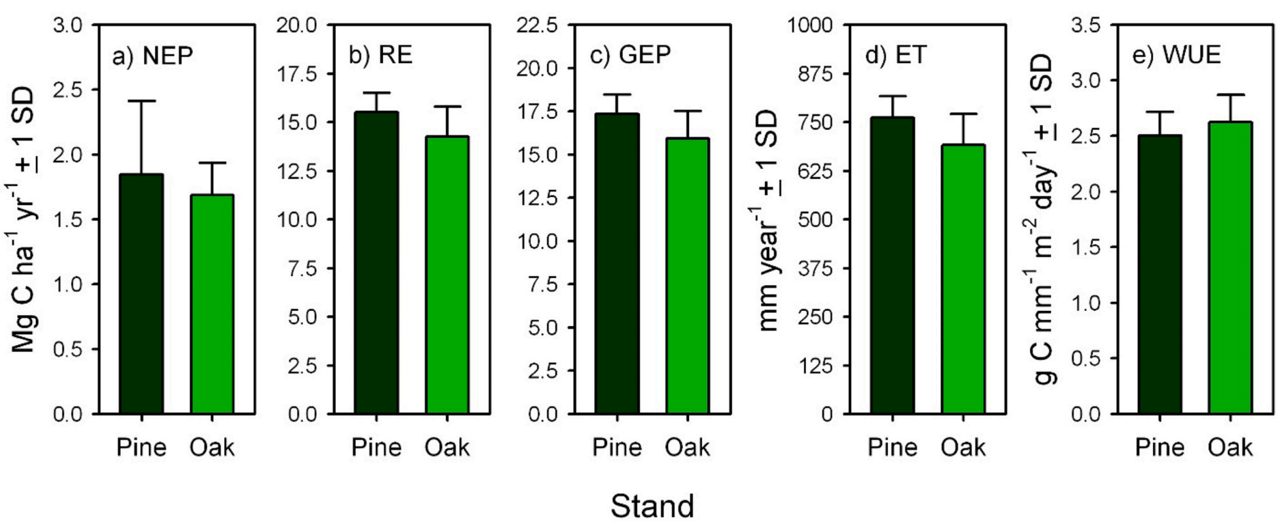


**Fig. 1.** a) Annual net ecosystem production (NEP, Mg C ha$^{-1}$ yr$^{-1}$), b) ecosystem respiration (RE, Mg C ha$^{-1}$ yr$^{-1}$), c) gross ecosystem production (GEP; Mg C ha$^{-1}$ yr$^{-1}$), d) evapotranspiration (Et, mm year$^{-1}$), and ecosystem water use efficiency during the summer months (WUE, g C mm $H_20^{-1}$ m$^{-2}$ day$^{-1}$, June 1 to August 31) at the pine and oak stands during years in the absence of prescribed burns or spongy moth infestations.

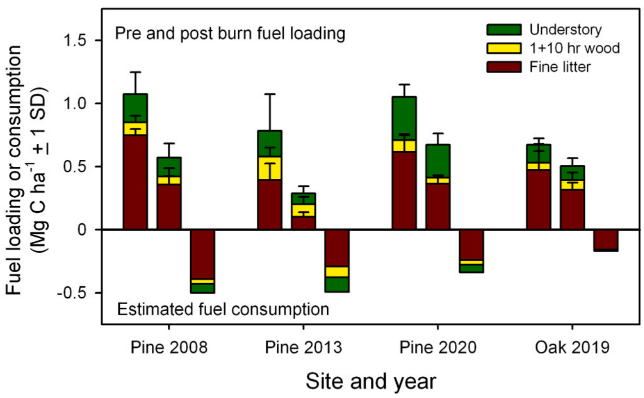


**Fig. 2.** Pre- and post-prescribed burn mass of understory vegetation, 1-hr and 10-hr wood on the forest floor, and fine litter (Mg C $ha^{-1}$) measured in 0.5 $m^2$ or 1.0 $m^2$ plots at the pine and oak stands. Estimated consumption is indicated by the third bar for each prescribed burn.

(Appendix Fig. G1, Table G1). However, net $CO_2$ emissions during fires estimated using summed half-hourly NEE measured during each burn were only 49.9 ± 21.0% of emission estimates derived from pre- and post-burn biometric measurements (Fig. 3), in part because deposition of particulates on filters (1.0 μm pore size) in front of the LI-7000's interfered with flow rates, requiring replacement immediately following fire front passage.

Following prescribed burns at the pine stand, daytime half-hourly NEE was reduced to a greater extent than nighttime NEE, with the reduction in daytime NEE during the growing season coinciding with fire intensity and the degree of pine needle scorching and consumption (as estimated from litterfall data) (Appendix Figs. H1 and I1). The slope of the relationship between NEE at full sunlight conditions and 30-day time periods following burns differed for burned and unburned years; half-hourly daytime NEE during years when prescribe burns were conducted were better modeled as a two-parameter exponential function ($r^2 = 0.882$, $F = 83.0$, $P < 0.01$), while unburned years were best modeled as a linear function of time period ($r^2 = 0.899$, $F = 53.6$, $P < 0.01$) (Appendix Fig. H1). By the summer months following burns (June 1 to August 31), daytime NEE at PAR ≥ 1500 μmol $m^{-2}$ $s^{-1}$ averaged − 12.6 ± 3.4 μmol $CO_2$ $m^{-2}$ $s^{-1}$, compared to − 15.2 ± 3.4 μmol $CO_2$ $m^{-2}$ $s^{-1}$ measured during the years before each burn. When expressed as a function of ambient air temperature, reduced nighttime NEE only occurred at the pine stand following the prescribed burn conducted in 2008 (Appendix Fig. I1 and Table I1).

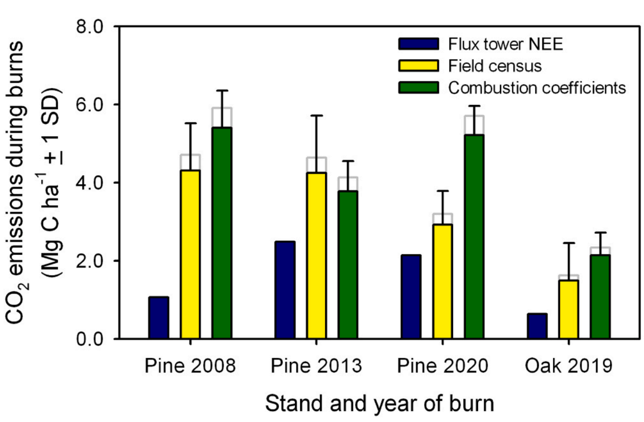


**Fig. 3.** Estimates of carbon loss and net $CO_2$ emissions during prescribed burns derived from 1) the sum of half-hourly NEE during the day of prescribed fires ("Flux tower NEE"; data collected from 8:00–20:00; shown in Appendix Fig. F1), 2) biometric estimates from 0.5 $m^2$ or 1.0 $m^2$ plots harvested pre- and post-burn ("Field census"; shown in Fig. 2; yellow portion of the bars indicate net $CO_2$ emissions ± 1 SD), and 3) calculations from pre-burn destructively harvested plots and combustion coefficients in Table D1 ("Combustion coefficients"; green portion of the bars indicate net $CO_2$ emissions ± 1 SD).

### *3.5. Annual post-fire carbon dynamics and time to Net ecosystem carbon balance*

At the pine stand, annual NEP during the years when prescribed fires were conducted was 38 ± 12% of annual NEP during unburned years (Fig. 4a; Table 3 and E1). Differences in annual RE, GEP, ET and summertime daily values of ecosystem WUE for burned and unburned years were not significant (Fig. 4). Time series of annual NEP and cumulative NECB for the pine stand indicated that positive values of annual NEP occurred in all years that prescribed burns were conducted, partially offsetting combustion losses of C from the forest floor and understory (Fig. 5). Annual NEP values during the year following prescribed burn years were similar to annual values measured during all other unburned years. Cumulative annual NECB was similar in the years following each burn, resulting in nearly parallel slopes averaging 1.91 Mg C $ha^{-1}$ $yr^{-1}$ (Fig. 5b, Table 5). The time it took the forest to accumulate the amount of C equivalent to that released during prescribed burns, or the time to achieve NECB = 0 calculated from the sum of annual NEP and combustion losses of C, was approximately 3.5 years following prescribed burns conducted in late February or March (Fig. 5). Cumulative NEP over the 18 years of study at the pine stand totaled 28.34 Mg C $ha^{-1}$, carbon loss during the three prescribed burns totaled 12.82 Mg C $ha^{-1}$, and net ecosystem carbon balance was 15.52 Mg C $ha^{-1}$, approximately 55% of cumulative NEP.

At the oak stand, annual NEP during 2019 when the prescribed burn was conducted was only 34% of pre-disturbance values, while RE and GEP following the prescribed burn represented 84% and 79% of pre-disturbance values (Fig. 6, Table E2). The time series of annual NEP at the oak stand indicates that average annual NEP following spongy moth infestations was only 0.43 Mg C $ha^{-1}$ $yr^{-1}$ from 2009 to 2018, approximately 25% of pre-infestation values, and that following the prescribed burn in 2019, average annual NEP had increased to 1.26 Mg C $ha^{-1}$ $yr^{-1}$, approximately 74% of pre-defoliation values (Fig. 7a). Cumulative NECB at the oak stand was strongly reduced by spongy moth infestations and subsequent oak tree and sapling mortality (Fig. 7b), and slopes for cumulative annual NECB were different for pre-disturbance, post-infestation, and post-prescribed burn periods (Table 4). The time it took the oak stand to achieve neutral NECB was approximately two growing seasons following prescribed burn conducted in mid-March (Fig. 7b). Cumulative NEP during the 19 years of study at the oak stand totaled 10.71 Mg C $ha^{-1}$, and NECB during the study was 9.04 Mg C $ha^{-1}$, approximately 84% of cumulative NEP.

### *3.6. Carbon accumulation in biomass and the litter layer following prescribed burns*

Carbon accumulation in aboveground biomass following prescribed burns at the pine and oak stands was dominated by tree and sapling stems (65% and 60%), while litter layer accumulation represented 23% and 31% and the understory accumulated 12% and 10% of the total net C accumulation, respectively. Over the course of the study at the pine stand, basal area of trees and saplings increased 76% (Fig. 8a and b). There was minimal effect of prescribed burning on annual basal area increment by trees and saplings; values averaged 0.63 ± 0.33 and 0.63 ± 0.14 $m^{-2}$ $ha^{-1}$ during years when prescribed burns were conducted and unburned years, respectively (Fig. H1). Net C accumulation by stems and coarse roots of trees and saplings was also unaffected by prescribed burning, and averaged 1.30 ± 0.26 Mg C $ha^{-1}$ $yr^{-1}$ on the years that prescribed fires were conducted and 1.32 ± 0.27 Mg C $ha^{-1}$ $yr^{-1}$ on all other years. Over the course of the study, biomass of trees and saplings increased by 19.5 Mg C $ha^{-1}$. In the understory, aboveground biomass C was linearly related to time since last fire, and net C accumulation

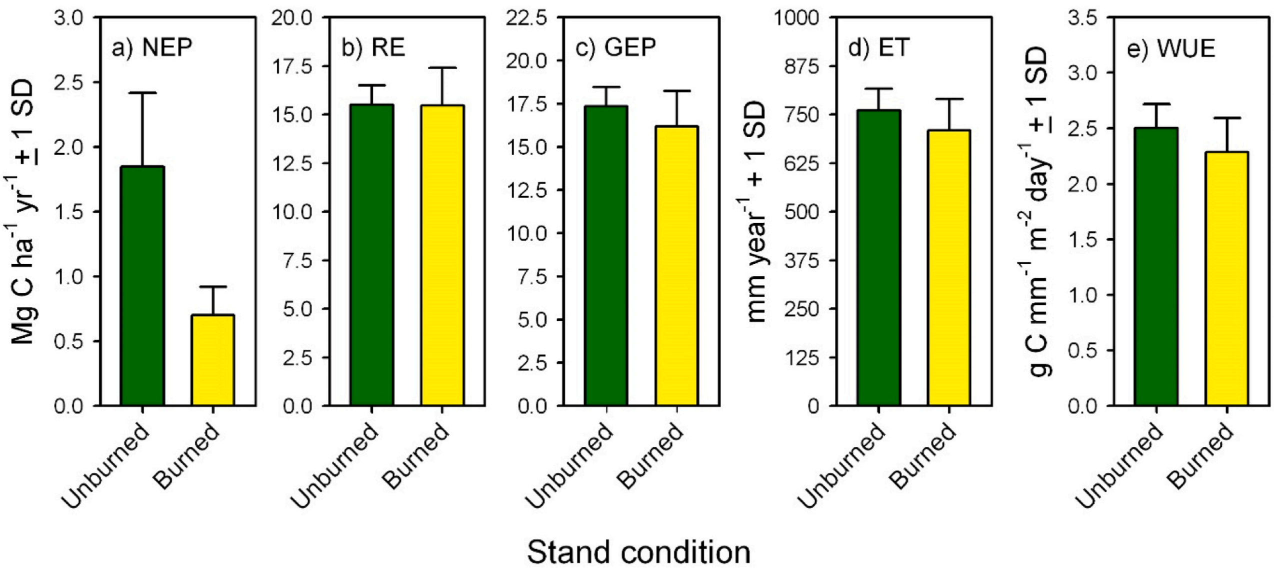


**Fig. 4.** a) Annual net ecosystem production (NEP, Mg C ha$^{-1}$ yr$^{-1}$), b) ecosystem respiration (RE, Mg C ha$^{-1}$ yr$^{-1}$) c) gross ecosystem production (GEP; Mg C ha$^{-1}$ yr$^{-1}$), d) evapotranspiration (ET, mm year$^{-1}$), and e) ecosystem water use efficiency during the summer months (WUE, g C mm $H_20^{-1}$ m$^{-2}$ day$^{-1}$) at the pine stand during unburned years and years when prescribed burns were conducted. Data from 2007 when a spongy moth infestation occurred were omitted.

**Table 3**
Values and statistics for net ecosystem production (NEP), respiration (RE), gross ecosystem production (GEP), evapotranspiration (ET), and ecosystem water use efficiency (WUE) during unburned and burned years at the pine stand shown in Fig. 4.

| Process | Unburned | Burned | $T_{1,15}$ | P |
|---|---|---|---|---|
| NEP (Mg C ha$^{-1}$ yr$^{-1}$) | 1.85 ± 0.57 | 0.70 ± 0.22 | 11.288 | < 0.01 |
| RE (Mg C ha$^{-1}$ yr$^{-1}$) | 15.51 ± 1.00 | 15.47 ± 1.93 | 0.002 | NS |
| GEP (Mg ha$^{-1}$ yr$^{-1}$) | 17.35 ± 1.11 | 16.17 ± 1.78 | 2.112 | NS |
| ET (mm yr$^{-1}$) | 760.5 ± 56.0 | 709.3 ± 80.2 | 1.808 | NS |
| WUE (g C mm$^{-1}$ day$^{-1}$) | 2.504 ± 0.213 | 2.287 ± 0.307 | 2.070 | NS |

averaged 0.40 ± 0.14 Mg C ha$^{-1}$ yr$^{-1}$ during years that prescribed burns were conducted and 0.25 ± 0.07 Mg C ha$^{-1}$ yr$^{-1}$ during all other years (Fig. 8c). Following prescribed burns, foliage production by understory oaks and shrubs was either reduced only during the first growing season or no different than undisturbed years (Fig. 8c). Average annual litterfall from trees, saplings and understory vegetation at the pine stand was only reduced following the relatively intense prescribed burn conducted at the pine stand in 2008, which resulted in crown scorching and some needle consumption in the lower canopy (Fig. 8d). Needle and leaf litterfall recovered by the following year, while the prescribed burns conducted in 2013 and 2020 had little effect on foliar litterfall. Net C accumulation in the litter layer estimated from chronosequences of time since last fire at the pine stand averaged 0.46 ± 0.20 Mg C ha$^{-1}$ yr$^{-1}$ (Appendix Fig. J1). Using litterfall amounts and coarse woody debris minus decomposition of each component per year to estimate net C accumulation on the forest floor (litter and organic matter layers) resulted in an estimate of 0.63 ± 13 Mg C ha$^{-1}$ yr$^{-1}$ at the pine stand (Table 2; see Clark et al., 2018 for details). Over the course of the study at the pine stand, tree, sapling and understory biomass and the forest floor had increased by 21.1 Mg C ha$^{-1}$, an increase of approximately 62%.

At the oak stand, basal area and biomass of trees and saplings was reduced because of extensive mortality following spongy moth infestations (Fig. 9a and b). Oak tree and sapling basal area had increased to 13.2 m$^2$ ha$^{-1}$ in 2008 before significant mortality occurred, and then recovered to only 10.7 m$^2$ ha$^{-1}$ by 2022, 81% of pre-infestation values. Continued pine tree growth and increased regeneration and growth of pine seedlings and saplings increased pine basal area from 4.2 to 6.6 m$^2$

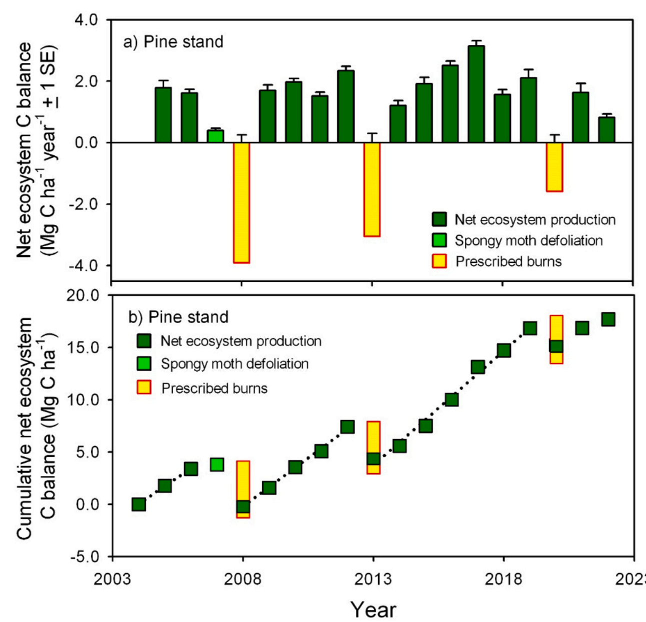


**Fig. 5.** a) Annual net ecosystem C balance (NECB; Mg C ha$^{-1}$ yr$^{-1}$), and b) cumulative NECB (Mg C ha$^{-1}$) at the pine stand from 2005 to 2022. Values for each burn are annual NEP derived from flux tower measurements and C loss during prescribed burns estimated from pre- and post-burn field measurements in Fig. 2. Statistics for the relationships between time since last fire and net C accumulation following each prescribed burn are in Table 4.

ha$^{-1}$, approximately 155% of values at the beginning of the study (Fig. 9b). Net C accumulation by stems and coarse roots of trees and saplings at the oak stand averaged 1.15 ± 0.30 Mg C ha$^{-1}$ yr$^{-1}$ in 2019 when the prescribed burn was conducted and 1.05 ± 0.11 Mg C ha$^{-1}$ yr$^{-1}$ during undisturbed years. Over the course of the study, total biomass of trees and saplings at the oak stand had increased by only 2.53 Mg C ha$^{-1}$, an increase of 6%. Understory vegetation at the oak stand responded to both spongy moth infestations and the prescribed burns. Following the prescribed burn in March 2019, net C accumulation by understory vegetation at the oak stand averaged 0.17 ± 0.01 Mg C ha$^{-1}$ yr$^{-1}$

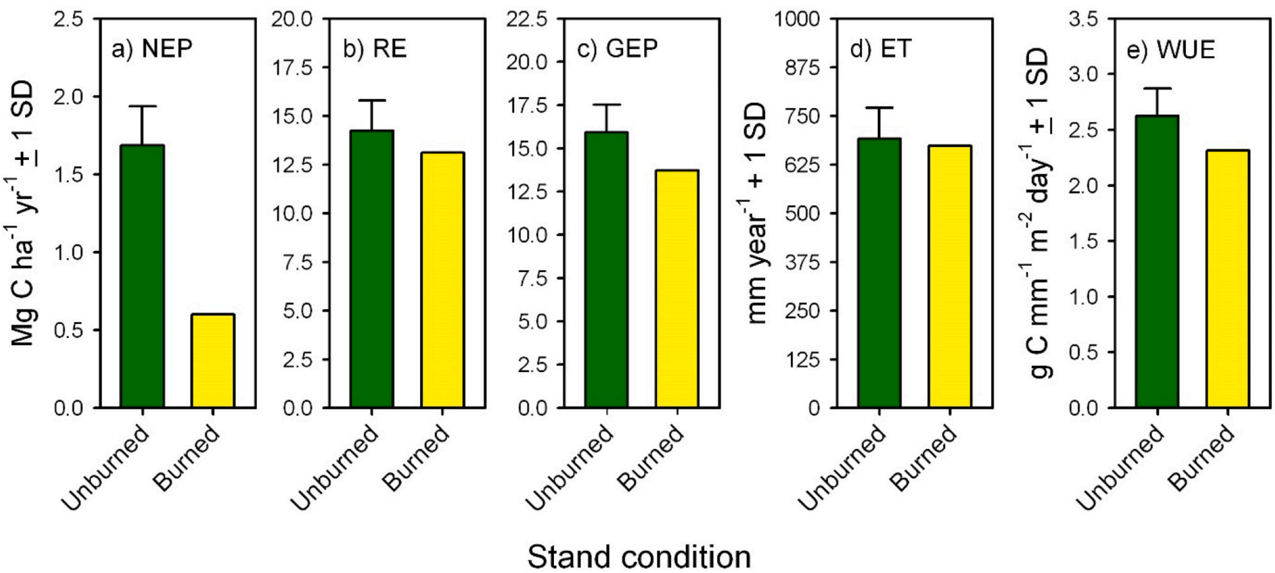


**Fig. 6.** a) Annual net ecosystem production (NEP, Mg C ha$^{-1}$ yr$^{-1}$), b) ecosystem respiration (RE, Mg C ha$^{-1}$ yr$^{-1}$) c) gross ecosystem production (GEP; Mg C ha$^{-1}$ yr$^{-1}$), d) evapotranspiration (ET, mm year$^{-1}$), and ecosystem water use efficiency during the summer months (WUE, g C mm $H_20^{-1}$ m$^{-2}$ day$^{-1}$) at the oak stand during unburned years and in 2019 when a prescribed burn was conducted.

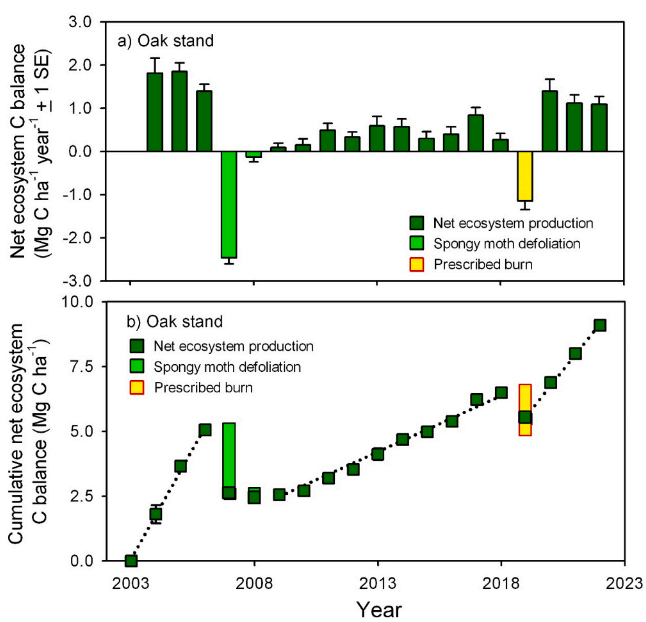


**Fig. 7.** a) Annual net ecosystem carbon balance (NECB; Mg C ha$^{-1}$ yr$^{-1}$), and b) cumulative net ecosystem carbon balance (Mg C ha$^{-1}$) at the oak stand from 2004 to 2022. Values for the year of the burn are annual NEP derived from flux tower measurements and C loss during combustion estimated from pre- and post-burn biometric measurements shown in Fig. 3. Statistics for the relationship between time since last fire and net C accumulation are shown in Table 4.

(Fig. 9c.). Following infestations, oak tree and sapling mortality further reduced oak litterfall compared to pre-defoliation values (Fig. 9d). In contrast, pine regeneration increased pine litterfall by approximately 0.02 Mg C ha$^{-1}$ yr$^{-1}$ and was 9.7 times greater in 2022 than in 2004. The prescribed fire conducted at the oak stand in 2019 had a negligible effect on canopy litterfall (Fig. 9d), and net C accumulation by the forest floor estimated from litterfall amounts and coarse woody debris minus decomposition of each component was 0.65 ± 0.08 Mg C ha$^{-1}$ yr$^{-1}$ (Table 2.).

**Table 4**
Slopes and initial values for the relationship between time since last fire in years and cumulative NEP following each fire indicated by the dotted lines in Fig. 5b for the pine stand and Fig. 7b for the oak stand. "SM" = spongy moth infestation.

| Date | Years | Slope | Initial value | $r^2$ | F | P |
|---|---|---|---|---|---|---|
| Pine stand net ecosystem production (Mg C ha$^{-1}$ yr$^{-1}$;Fig. 5). | | | | | | |
| Pre-burn | 3 | 1.70 ± 0.05 | 0.0 ± 0.10 | 0.998 | 1354.7 | < 0.05 |
| 2008 Burn | 5 | 1.85 ± 0.03 | -0.20 ± 0.15 | 0.995 | 758.9 | < 0.001 |
| 2013 Burn | 7 | 2.19 ± 0.03 | 3.80 ± 0.27 | 0.987 | 472.8 | < 0.001 |
| Oak stand net ecosystem production (Mg C ha$^{-1}$ yr$^{-1}$; Fig. 7). | | | | | | |
| Pre-SM | 3 | 1.70 ± 0.07 | 0.0 ± 0.20 | 0.994 | 536.7 | < 0.01 |
| Post-SM | 10 | 0.43 ± 0.01 | 2.48 ± 0.12 | 0.977 | 422.1 | < 0.01 |
| 2019 Burn | 4 | 1.26 ± 0.05 | 5.49 ± 0.05 | 0.992 | 243.0 | < 0.05 |

**Table 5**
Annual trends in net carbon accumulation in understory vegetation and overstory litterfall amounts following prescribed burns at the pine stand, and spongy moth infestations and a prescribed burn at the oak stand. Understory vegetation ≤ 2 m height was estimated from clip plots harvested during peak leaf area during the growing season (0.5 and 1.0 m$^2$; n = 10–20 per stand), and litterfall was estimated from litter traps (0.4 m$^2$; n = 10 per stand). Values are slopes and intercepts for the dotted lines for each prescribed burn in Figs. 8 and 9.

| Date | Years | Slope | Initial value | $r^2$ | F | P |
|---|---|---|---|---|---|---|
| Pine stand; understory productivity (Mg C ha$^{-1}$ yr$^{-1}$;Fig. 8c). | | | | | | |
| After 2008 | 5 | 0.29 ± 0.04 | 0.70 ± 0.21 | 0.691 | 9.9 | = 0.05 |
| After 2013 | 7 | 0.25 ± 0.01 | 1.34 ± 0.12 | 0.849 | 34.7 | < 0.01 |
| After 2020 | 3 | 0.45 ± 0.01 | 1.02 ± 0.12 | 0.999 | 3090 | = 0.01 |
| Oak stand; understory productivity (Mg C ha$^{-1}$ yr$^{-1}$;Fig. 9c). | | | | | | |
| After 2007 | 12 | 0.09 ± 0.01 | 0.79 ± 0.11 | 0.706 | 27.3 | < 0.01 |
| After 2019 | 4 | 0.17 ± 0.01 | 0.41 ± 0.06 | 0.992 | 354.7 | < 0.01 |
| Pine stand; annual litterfall (Mg C ha$^{-1}$ yr$^{-1}$;Fig. 8d). | | | | | | |
| After 2008 | 5 | 0.43 ± 0.05 | 1.61 ± 0.30 | 0.707 | 10.6 | < 0.05 |
| After 2013 | 7 | 0.19 ± 0.02 | 1.89 ± 0.17 | 0.605 | 10.2 | < 0.05 |

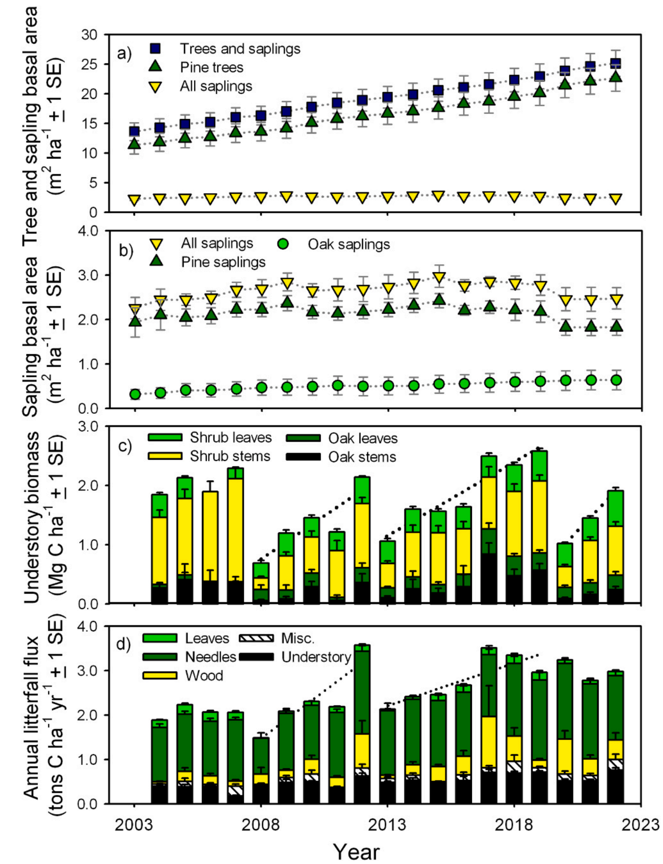


**Fig. 8.** Forest biometric data for the pine stand from 2003 to 2023. a) Basal area of trees and saplings (m$^2$ ha$^{-1}$), b) basal area of pine and oak saplings, c) live understory biomass (Mg C ha$^{-1}$) of shrub leaves, shrub stems, oak leaves, and oak stems at the peak of the growing season, and d) annual litterfall (Mg C ha$^{-1}$ yr$^{-1}$) of canopy leaves, canopy needles, wood, miscellaneous material, and understory leaves. Statistics for all dotted lines are in Table 5, and basal area increments for trees and saplings are shown in Appendix Fig. H1.

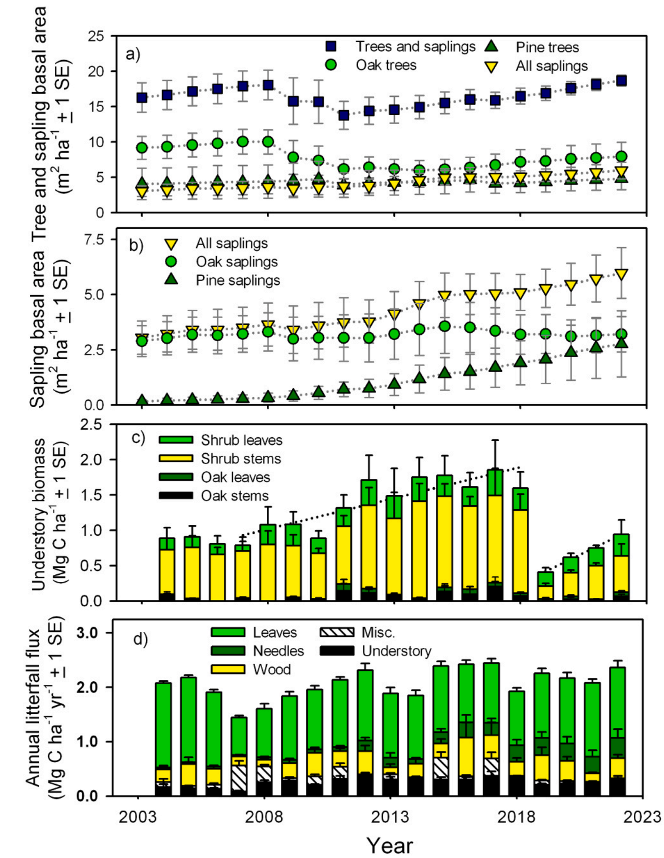


**Fig. 9.** Forest biometric data for the oak stand from 2003 to 2023. a) Basal area of trees and saplings (m$^2$ ha$^{-1}$), b) basal area of pine and oak saplings, c) live understory biomass (Mg C ha$^{-1}$) of shrub leaves, shrub stems, oak leaves, and oak stems during the peak of the growing season, and d) annual litterfall (Mg C ha$^{-1}$ yr$^{-1}$) of canopy leaves, canopy needles, wood, miscellaneous material, and understory leaves. Statistics for dotted lines are in Table 5, and basal area increments for trees and saplings are shown in Appendix Fig. H1.

## 4. Discussion

We used near-continuous $CO_2$ and hydrologic flux data combined with biometric measurements made over a two-decade period to quantify the effects of prescribed burning in two intermediate age forests on the mid-Atlantic coastal plain. Dormant season prescribed burns released from one (oak stand) to three (pine stand) years of accumulated C, primarily from the consumption of fine litter on the forest floor. Peak daytime NEE during the growing season following each burn was reduced only after the most intense prescribed burn, and annual NEP was positive during the year of every burn, partially offsetting combustion losses of C. At the pine stand, only annual NEP was reduced during the year prescribed burns were conducted compared to unburned years, while annual RE, GEP and ET were nearly unaffected. Annual NEP during the following year was similar to values measured during other undisturbed years, thus neutral net ecosystem C balance (NECB = 0) was achieved within three to four years. At the oak stand, annual NEP during the year of the prescribed burn was lower than during undisturbed periods, but then was greater over the following years than during the previous decade following severe spongy moth infestations and tree and sapling mortality. With typical prescribed burn rotation times of 5–8 years for many stands under current management in the Pinelands, they will likely continue to accumulate C at moderate rates at decadal time scales.

Intermediate age stands that have been managed using repeated prescribed fires are less likely to be impacted by wildfires because of reduced surface fuel loading and ladder fuel continuity (Skowronski et al., 2011; Warner et al., 2020). Excluding prescribed burning or other fuels management treatments would result in greater amounts of stored C on the forest floor, in understory and sub-canopy vegetation, and ultimately as soil organic matter, but not necessarily in trees and saplings, which were nearly unaffected by prescribed burning. In a pitch pine-dominated stand adjacent to the pine stand we studied, fire exclusion for almost five decades (1962–2009) resulted in litter layer and understory biomass of over 11.0 ± 2.8 and 5.5 ± 1.9 Mg C ha$^{-1}$, approximately 51% and 175% greater than average values measured at the pine stand, respectively (Clark et al., 2015). Conversely, long-term fire exclusion can also facilitate the regeneration of oaks in pitch pine dominated stands, as has been observed following wildfire suppression and/or exclusion in forests throughout the Pinelands (Little, 1998; La Puma et al., 2013). Similar results for increasing oak dominance have been projected using LANDIS-II for the Pinelands (Scheller et al., 2011), and enhanced hardwood regeneration associated with reduced wildland fire activity has occurred throughout the mid-Atlantic region (Nowacki and Abrams 2008; Varner et al., 2021). However, such a "no management" scenario is undesirable in dense pitch pine-scrub oak stands because of the enhanced risk of crown fires in unburned stands. Carbon emissions from wildfires in pitch pine forests are greater than from most prescribed burns in the Pinelands, with consumption estimates ranging from 8.7 ± 2.6–25.7 ± 3.5 Mg C ha$^{-1}$ (Clark et al., 2010b; 2013; Gallagher, 2017; Mueller et al., 2017), and time to achieve NECB following severe wildfires is likely to be considerably longer than times following prescribed burns.

When intermediate age pine and oak stands in the Pinelands are undisturbed and relatively drought-free, they accumulate C at comparable rates to intermediate age pine dominated stands throughout the eastern USA (Table A1). Drought reduced seasonal and annual GEP and NEP at all intermediate age sites in Table A1, and during severe drought, annual NEP was as low or lower than during years prescribed burns were conducted (e.g., 2022 at the pine stand; Powell et al., 2008; Whelan et al., 2013; Bracho et al., 2023). During wetter years, maximum annual NEP at the pine stand reached 3.1 Mg C $ha^{-1}$ $yr^{-1}$, similar to maximum rates measured at a mesic intermediate age longleaf pine stand in Georgia USA, but only half of the maximum annual NEP measured at a longleaf and slash pine stand in N. Florida USA (6.6 Mg C $ha^{-1}$ $yr^{-1}$). Measurements of long-term forest C dynamics associated with fire management in these longleaf and slash pine-dominated stands also indicate a similar, relatively rapid recovery of NEP following prescribed burns, with annual pre-burn values typically occurring within one or two years following each burn (Powell et al., 2008; Whelan et al., 2013; Starr et al., 2015; Bracho et al., 2023). Starr et al. (2015) reported that NEP was positive during a year when a prescribed fire was conducted at a mesic longleaf pine stand (1.6 ± 0.3 Mg C $ha^{-1}$ $yr^{-1}$) but not a xeric longleaf pine stand (−0.06 ± 0.3 Mg C $ha^{-1}$ $yr^{-1}$). Overall consumption at their sites was 4.1 and 1.5 Mg C $ha^{-1}$, and NECB during the year of each burn was − 2.5 and − 1.6 Mg C $ha^{-1}$ $yr^{-1}$. During the next year, NEP had recovered to near pre-disturbance levels, indicating that approximately two to three years are required to achieve neutral NECB, similar to estimates for the pitch pine dominated stand reported here (Whelan et al., 2013; Starr et al., 2015). In an intermediate age longleaf and slash pine stand in N. Florida, Bracho et al. (2023) reported that NEP averaged 2.97 ± 0.8 Mg C $ha^{-1}$ $yr^{-1}$ during years that prescribed fires were conducted and 3.5 ± 1.6 Mg C $ha^{-1}$ $yr^{-1}$ during all other years over a two-decade period, 82% of values measured during unburned years. Consumption during fires averaged 6.6 ± 2.3 Mg C $ha^{-1}$, and NECB averaged − 3.8 ± 2.6 Mg C $ha^{-1}$ $yr^{-1}$ during years prescribed burns were conducted. Overall, the stand in their study accumulated 26.6 Mg C $ha^{-1}$ over two decades and six prescribed burns conducted, compared to 15.5 Mg C $ha^{-1}$ over an 18-year period by the pine-dominated stand in the Pinelands in our study.

Although a number of sources of error can result in uncertainties in net C accumulation estimates derived from flux measurements or biometric data, we were consistent in our field sampling and data processing throughout the duration of the study. Both random and systematic errors occur in C flux data, and gap-filling can result in additional uncertainties in C and hydrologic flux estimates. We used a relatively simple gap-filling strategy, employing key meteorological variables (PAR, air and soil temperature for C fluxes, available energy for Et and WUE estimates) and standard equations that explained the greatest variation in C or hydrologic fluxes to gap-fill missing half-hourly data.

In our analyses, we chose to use pre- and post-burn field measurements to estimate fuel consumption and $CO_2$ emissions during prescribed burns. Above-canopy NEE measurements made during prescribed burns accounted for only approximately half of the estimated $CO_2$ emissions calculated from fuel consumption measurements. Integrated sensible heat flux measurements at the top of the canopy were also lower compared to convective heat fluxes calculated from consumed fuels during these low-intensity fires, averaging 66 ± 30% (see Clark et al., 2020b for details). However, convective and latent heat fluxes generated near the forest floor during prescribed burns would be expected to be greater than above-canopy measurements because of heat storage and dissipation in organic matter on the forest floor and soil, and in the canopy air space below the sonic anemometers. Smoke particulates did accumulate on 1.0 μm pore size filters on air sampling lines and reduced flow rates through the IRGA's during some of the burns, and had to be replaced immediately following fire front passage. In addition, although footprint characteristics of the pine and oak stands are well-known (Chu et al., 2021), turbulence, expressed as turbulent kinetic energy (TKE), is greatly enhanced above fire fronts through the canopy, and especially at the top of the canopy (Heilman et al., 2015; 2021).

The use of pre- and post-burn biometric sampling to estimate consumption and $CO_2$ emissions during prescribe burns can also introduce errors into estimates of consumption and $CO_2$ emissions. Fine litter was the predominant fuel consumed during prescribed burns, and although it had the lowest spatial variation of the three major surface fuel types in 0.5 or 1.0 $m^2$ plots both pre- and post-fire, different locations were sampled to estimate consumption (Clark et al., 2015; 2020b). The flux of $CO_2$ estimated from C loss in consumed fuels is also dependent on fire behavior, but there is typically lower variation in $CO_2$ emissions during flaming versus smoldering combustion compared to CO or particulate emissions from wildland fires (1692 vs. 1462 g $CO_2$ $kg^{-1}$; Prichard et al., 2020; Andreae, 2019). Overall, methodological limitations, complex flux footprints during fire front passage, and variability in biometric sampling all likely contributed to differences between estimates derived from flux data and biometric fuel consumption reported here.

Measurements of litter layer and understory fuel loading and consumption during prescribed burns at the pine and oak stands are consistent with management-scale prescribed burns conducted throughout the Pinelands (Wright et al., 2007; Clark et al., 2015; 2020b; Gallagher, 2017), and with other pine-dominated forests further south on the Atlantic coastal plain (e.g., Prichard et al., 2017; Appendix Table L1). Following prescribed burns, tree and sapling growth accounted for the largest amount of C accumulated aboveground, while the litter layer accumulation was intermediate and understory stems accumulated relatively small amounts of C. Although the Pinelands are not extensively managed for timber or other wood products, relatively high growth rates of trees and saplings are maintained under current fire management practices. At the pine stand, tree and sapling basal area and aboveground biomass had increased by 76% and 81% over the course of the study, to 25.1 $m^{-2}$ $ha^{-1}$ and 43.7 Mg C $ha^{-1}$, respectively. Thus, although the primary objective of prescribed burning in the Pinelands is hazardous fuel reduction, other management objectives, including long-term C sequestration and timber production, can be sustained (Little and Moore, 1949; Isaacson et al., 2023). Unfortunately, pitch pine-dominated stands with > 20–25 $m^{-2}$ $ha^{-1}$ basal area in the Pinelands are at risk for southern pine beetle infestations and extensive tree mortality (Weed et al., 2013; Dodds et al., 2018; Heuss et al., 2017; Clark et al., 2022). The litter layer was a highly dynamic pool of C in our study, with large reductions occurring during prescribed burns, and large additions during tree and sapling mortality driven by insect infestations (Renninger et al., 2014; Clark et al., 2020a; 2022) Although woody stems of understory vegetation accumulate relatively little C each year, shrub and understory oak foliage recovers rapidly following fires and contributes significantly to GEP and NEP during the growing season (Clark et al., 2010a). Following prescribed burns, increases in height and structure of understory vegetation occur, contributing to ladder fuels over time (Warner et al., 2020; Skowronski et al., 2020). We also found that standing dead and fallen stems from the previous fire contributed to fuel loads, thus when rotation times occur more frequently than time it takes stems fall and decompose, they are available woody fuels for the next fire.

Upland forest stands in the Pinelands maintain relatively high rates of NEP during the growing season following dormant season prescribed burns compared to other forest management practices (e.g., clearcutting for pulpwood, extensive thinning for timber) or insect infestations (Amiro et al., 2010; Bracho et al., 2012; Clark et al., 2020a; Aguilos et al., 2020). Although timber management is limited in the Pinelands, insect damage has been widespread, and between 2005 and 2016, spongy moth infested 328,700 ha, causing heavy (50–75%) to severe (>75%) canopy defoliation. Peak defoliation occurred in 2007 when 68, 650 ha in the four major Pinelands counties (Atlantic, Burlington, Cumberland, and Ocean Cos.) were heavily to severely defoliated. We estimated that mean annual NEP at the landscape scale in 2007 was reduced from 1.69 to 0.93 Mg C ha$^{-1}$ yr$^{-1}$, a reduction of 45% (Clark et al., 2010a). Model simulations provide similar estimates of reduced NEP during infestations in the Pinelands (Schaefer et al., 2010; Medvigy et al., 2012; Kretchun et al., 2014), as have simulations of spongy moth defoliation in other mid-Atlantic forests (Xu et al., 2017). Repeated defoliation of oak-dominated stands then resulted in mortality of larger oak trees, while mortality was lower in mixed-composition and pine-dominated stands. In subsequent years, RE has been enhanced because of increased wood decomposition, and NEP lower than during pre-infestation periods (Renninger et al., 2014). At the oak stand, recovery of NECB following spongy moth infestations required approximately 10 years, much longer than that for prescribed burns. In pine-dominated forests of the Pinelands, infestations of southern pine beetle have occurred since 2000, and by 2016 approximately 19,500 ha of pine stands had experienced extensive pine tree and sapling mortality (Dodds et al., 2018; Clark et al., 2022). Although much less extensive than spongy moth infestations, mortality of large pine trees can be > 90% of pine basal area and aboveground biomass. Oak trees and saplings are mostly undamaged following infestations, and GEP was estimated to be 65–73% of values in undisturbed stands in the years following infestations. However, pine mortality in unmanaged infested stands or "cut and leave" suppression treatments results in large amounts of CWD, and annual NEP was estimated to be − 2.8 to − 7.6 Mg C ha$^{-1}$ yr$^{-1}$ following infestations (Heuss et al., 2019; Clark et al., 2020a). Because numerous lowland pitch pine stands had relatively high basal area (25 – 32 m$^2$ ha$^{-1}$) and aboveground tree and sapling biomass (74 ± 4 Mg C ha$^{-1}$) pre-infestation, time to reach neutral NECB is likely much longer than following prescribed burns.

Simulated long-term C dynamics of pine and oak-dominated stands in the mid-Atlantic region that include prescribed burning indicate that they would continue to be moderate sinks for atmospheric $CO_2$ in the absence of severe drought or other disturbances (Scheller et al., 2011; Zhao et al., 2021). Integrated studies of fire management and forest C dynamics in longleaf pine stands in the southeastern USA indicate similar trends (Flanagan et al., 2019; Bracho et al., 2023). However, both climatic (drought, storms) and biotic (insect infestations, herbivory) events can strongly alter the C dynamics of these stands, and some do on decadal time scales. In addition, older forests are potentially more sensitive to other factors such as climate driven increases in VPD, and thus the water relations of these forests on sandy, rapidly draining soils throughout the Atlantic coastal plain could become more dynamic in the future (McDowell et al., 2020, Aguilos et al., 2021, Isaacson et al., 2023). When coupled with weather conditions that are conducive to wildfire activity, the potential will always exist for crowning wildfires in pine-dominated stands in the Pinelands.

## 5. Conclusions

We quantified the responses of two intermediate age pine- and oak-dominated stands on the mid-Atlantic coastal plain to operational prescribed burns. The equivalent of one to three years of C accumulated during undisturbed years was consumed during each dormant season burn. At the pitch pine stand, NEP was reduced only during the year of each burn, and then recovery times to reach neutral net ecosystem C balance (NECB = 0), were approximately two to four growing seasons following each burn. GEP and RE were unchanged or slightly reduced during the year of each burn, but were also sensitive to drought conditions. Prescribed burn rotations consistent with forest management objectives in the Pinelands are resulting in moderate amounts of sequestered carbon, much of which has accumulated in tree and sapling stems. During the 18-year study, net ecosystem carbon balance was 15.5 Mg C ha$^{-1}$. At an oak-dominated stand that had been previously infested by spongy moth, the prescribed burn released lower amounts of C, and then NEP increased over the following 3-year period compared to rates following defoliation and associated tree mortality, suggesting that prescribed fires could play a role in the restoration of ecosystem functioning in insect-damaged stands. Fuel consumption and forest C dynamics following prescribed burns in pine- and oak-dominated forests of the Pinelands are similar to those characterizing intermediate age stands throughout the Atlantic coastal plain, USA.

## CRediT authorship contribution statement

**Kenneth Clark**: Conceptualization, Investigation, Formal analyses, Data curation, Writing – original draft. **Nicholas Skowronski**: Investigation, Supervision, Writing – review & editing. **Michael Gallagher**: Investigation, Writing – review & editing.

## 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

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121589.

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