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Invasive insects impact forest carbon dynamics

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Abstract

Invasive insects can impact ecosystem functioning by altering carbon, nutrient, and hydrologic cycles. In this study, we used eddy covariance to measure net CO_2 exchange with the atmosphere (NEE), and biometric measurements to characterize net ecosystem productivity (NEP) in oak- and pine-dominated forests that were defoliated by Gypsy moth (*Lymantria dispar* L.) in the New Jersey Pine Barrens. Three years of data were used to compare C dynamics; 2005 with minimal defoliation, 2006 with partial defoliation of the canopy and understory in a mixed stand, and 2007 with complete defoliation of an oak-dominated stand, and partial defoliation of the mixed and pine-dominated stands. Previous to defoliation in 2005, annual net CO_2 exchange (NEE_{yr}) was estimated at -187, -137 and $-204\,g\,C\,m^{-2}\,yr^{-1}$ at the oak-, mixed-, and pine-dominated stands, respectively. Annual NEP estimated from biometric measurements was 108%, 100%, and 98% of NEE_{yr} in 2005 for the oak-, mixed-, and pine-dominated stands, respectively. Gypsy moth defoliation strongly reduced fluxes in 2006 and 2007 compared with 2005; NEE_{yr} was -122, $+103$, and $-161\,g\,C\,m^{-2}\,yr^{-1}$ in 2006, and $+293$, $+129$, and $-17\,g\,C\,m^{-2}\,yr^{-1}$ in 2007 at the oak-, mixed-, and pine-dominated stands, respectively. At the landscape scale, Gypsy moths defoliated 20.2% of upland forests in 2007. We calculated that defoliation in these upland forests reduced NEE_{yr} by 41%, with a 55% reduction in the heavily impacted oak-dominated stands. 'Transient' disturbances such as insect defoliation, nonstand replacing wildfires, and prescribed burns are major factors controlling NEE across this landscape, and when integrated over time, may explain much of the patterning of aboveground biomass and forest floor mass in these upland forests.

Keywords: carbon cycle, ecosystem function, eddy covariance, invasive species, net carbon exchange, New Jersey Pine Barrens, Pitch Pine

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Introduction

Quantifying and predicting the effects of disturbance are central to our understanding of forest carbon dynamics. Recent measurements and modeling studies have shown that catastrophic disturbances such as wildfire or clearcutting result in substantial carbon (C) loss from forest ecosystems (Thornton *et al*., 2002; Clark *et al*., 2004; Amiro *et al*., 2006; Humphreys *et al*., 2006). Catastrophic disturbance typically involves severe perturbations to hydrologic and nutrient cycles, in addition to loss of C from long-term storage pools in tree boles, forest floor, and soil. Recovery of positive C gain may require 5 or more years (Thornton *et al*., 2002; Binford *et al*., 2006; Humphreys *et al*., 2006). Recovery of long-term storage pools of C in stem biomass, forest floor, and soil following catastrophic disturbance may take millennia in some forests.

In contrast to catastrophic disturbances, transient, low intensity disturbances such as defoliation by insects, wind or frost may result in little change in overall woody biomass and C storage on the forest floor and in soil, but can affect ecosystem functioning by altering the amount and timing of leaf area display. In temperate regions, these events can strongly reduce net CO_2 exchange with the atmosphere (NEE) if they occur during the summer months when the majority of C accumulation typically occurs. Hydrologic and nutrient cycles can also be affected, occasionally over large spatial scales. When integrated over longer time scales, repeated transient disturbances can impact long-term C storage in woody stems, forest floor, and soil, due in part to reduced litterfall production and stem increment, and increased tree mortality.

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Although invasive insects are now ubiquitous in forest ecosystems of North America (Lovett *et al.*, 2006; Krist *et al.*, 2007), their effects on ecosystem functioning have been only partially quantified, limiting the development and accuracy of predictive models (e.g., Miao *et al.*, unpublished data, Cook *et al.*, 2008). Research efforts have occasionally revealed counter-intuitive results. For example, while severe defoliation of an Oak forest canopy in Pennsylvania, USA during the summer months altered the composition and seasonal distribution of litterfall, total annual amounts were unchanged compared with undisturbed stands, due to a second flush of foliage and subsequent litterfall (Grace, 1986). Gypsy moth defoliation did accelerate nitrogen (N) cycling in litterfall, and increased N flux from $3.1\,\mathrm{g\,N\,m^{-2}}$ in undefoliated stands to $5.2\,\mathrm{g\,N\,m^{-2}}$ in the defoliated stands studied by Grace (1986). Green foliage and frass composed of labile C and N can enhance microbial activity and accelerate soil N cycling in defoliated stands, potentially leading to increased NO_3^- leaching into stream water (Webb *et al.*, 1995; Eshleman *et al.*, 1998). However, labile C in frass also can stimulate microbial immobilization of N; thus much of the N deposited to the forest floor may be retained in soil organic matter (Lovett & Ruesink, 1995). Lovett *et al.* (2002) concluded that defoliation by Gypsy moth represents a major perturbation to the internal N cycle of the forest, but primarily causes a redistribution of N within the ecosystem rather than large losses of N via leaching.

When Red oak (*Quercus rubra*) saplings in pots were defoliated by Gypsy moth, net CO_2 release from soil increased over controls, but soil respiration was independent from the addition of frass (Frost & Hunter, 2004). Frost & Hunter (2004) hypothesized that increased CO_2 release from soil resulted from greater exudation of labile C from roots, and concluded that defoliation events had the potential to affect C dynamics at the ecosystem level. Using a modeling approach, Cook *et al.* (2008) reported that partial defoliation (34%) of the canopy of a northern hardwood forest in WI, USA by tent caterpillar (*Malacosoma disstria*) reduced gross primary production (GPP) and annual NEE, and increased ecosystem respiration, consistent with the results of Frost & Hunter (2004).

Despite past research, we have little quantitative information on the effects of insect defoliation on rates of NEE in forest ecosystems. Rates of recovery of NEE following defoliation events are also largely unknown. However, since 1980, Gypsy moth have defoliated ca. $500\,000\,\mathrm{ha\,yr^{-1}}$ in the Eastern US, and they are a primary agent of tree mortality in Eastern forests (Lovett *et al.*, 2006; Krist *et al.*, 2007). Because Gypsy moth presently occupy only ca. 23% of their potential range in North America, they will likely continue to represent a major impact to forest C dynamics in the future (Morin *et al.*, 2005; Krist *et al.*, 2007).

We investigated the impacts of transient disturbance due to Gypsy moth (*Lymantria dispar* L.) defoliation in the Pine Barrens of New Jersey. We used eddy covariance (EC) and biometric measurements at three stands of contrasting dominance of overstory species (deciduous-, mixed-, and conifer-dominated) to quantify forest C dynamics in the Pine Barrens of New Jersey. We obtained at least 1 year of measurements before defoliation, and then measured fluxes for 2 more years with varying levels of defoliation at each site. We then used maps of Gypsy moth defoliation produced by the New Jersey Department of Environmental Protection and the US Forest Service to approximate their impact across upland forest types in the Pinelands National Reserve, encompassing ca. 400 000 ha in southern New Jersey. We integrated eddy flux and meteorological data from an extensive network of weather towers across the Pinelands National Reserve with a forest classification map (Lathrop & Kaplan, 2004; Skowronski *et al.*, 2007), and compared potential and actual rates of C sequestration for 2007. We asked:

(1) How do patterns of net CO_2 exchange differ among forest types at different temporal scales (half-hourly, seasonally, annually)?
(2) Do differences in annual productivity in deciduous vs. conifer dominated stands account for the observed patterns of aboveground biomass distribution in these nutrient limited forests?
(3) To what extent does Gypsy moth defoliation alter patterns of net CO_2 exchange at stand and landscape scales?

Materials and methods

Site description

Research sites were located in Burlington and Ocean Co. in the Pine Barrens of New Jersey. The Pine Barrens is the largest continuous forested landscape on the Northeastern coastal plain. The climate is cool temperate, with mean monthly temperatures of 0.3 and 23.8 °C in January and June, respectively (1930–2004; State Climatologist of NJ, USA). Mean annual precipitation is 1123 ± 182 mm. Soils are derived from the Cohansey and Kirkwood Formations (Lakewood and Sassafras soils), and are sandy, coarse-grained, and have extremely low nutrient status (Ehrenfeld *et al.*, 1995, 1997), cation exchange capacity, and base saturation (Tedrow, 1986). This landscape is also characterized by a high frequency and intensity of wildfires relative to other forest ecosystems in the Northeastern US, further exacerbating nutrient limitation (Little & Moore, 1949; Little, 1998).

Upland forests occupy 62% of the forested areas in the Pine Barrens, and are dominated by three major forest communities; (1) Oak/Pine, consisting of black oak (*Quercus velutina*), chestnut oak (*Quercus prinus*), white oak (*Quercus alba*), and pitch (*Pinus rigida*) and shortleaf pine (*Pinus echinata*), (2) Pine/Oak, consisting of pitch pine with mixed oaks in the overstory, and (3) Pine/Scrub oak, dominated by pitch pine with scrub oaks (*Quercus ilicifolia*, *Quercus marlandica*) in the understory (McCormick & Jones, 1973; Lathrop & Kaplan, 2004; Skowronski *et al.*, 2007). All stands have ericaceous shrubs in the understory, primarily huckleberry (*Gaylussacia bacata, Gaylussacia frondosa*) and blueberry (*Vaccinium* spp.). Sedges, mosses and lichens also are present.

Most upland forest stands in the Pine Barrens have regenerated naturally following cessation of logging and charcoaling activities in the late 1800s. Among mature upland stands of approximately the same age, tree stature and aboveground biomass are typically greatest in oak-dominated stands and least in Pine/Scrub oak stands (Skowronski *et al.*, 2007, Forest Inventory and Analysis data at http://www.fia.fed.us/), implying that oak-dominated stands are more productive than pine-dominated stands. We selected three representative stands of approximately the same intermediate age for intensive study, an Oak/Pine stand at the Silas Little Experimental Forest, a Pine/Oak stand at Fort Dix Army Base, and a Pine/Scrub oak stand near the Cedar Bridge fire tower (Skowronski *et al.*, 2007).

EC measurements

Turbulent flux of CO_2 (F_{CO_2}; $\mu mol\,CO_2\,m^{-1}\,s^{-1}$) was estimated using a closed-path EC system at each site. Near-continuous measurements were initiated in April 2004 at the Oak/Pine stand, November 2004 at the Pine/Oak stand, and June 2005 at the Pine/Scrub oak stand. EC systems were composed of a 3-dimensional sonic anemometer (Windmaster Pro, Gill Instruments Ltd., Lymington, UK, or RM 80001V, R. M. Young Inc., Traverse City, MI, USA), a closed-path infrared gas analyzer (LI-7000, Li-Cor Inc., Lincoln, NE, USA), a 5 m long, 0.4 cm ID teflon-coated tube and an air pump, and a lap-top PC that collected raw time series data at 10 hz (Moncrieff *et al.*, 1997; Clark *et al.*, 2004). The sonic anemometer was mounted ca. 4 m above the canopy on a tower at each site. The inlet of the air sampling tube was placed between the upper and lower sensors of the sonic anemometer, and air drawn through the sample channel of the LI-7000s at a rate of $8.0\,L\,min^{-1}$. The LI-7000s were operated in absolute mode with the pressure transducer on the sample channel set to 101.35 kPa. N_2 scrubbed with soda lime and magnesium perchlorate was used as a blank in the reference channel at a rate of $0.2\,L\,min^{-1}$, and to zero the LI-7000s. The LI-7000's were calibrated for CO_2 every 2–7 days using CO_2 tanks that were traceable to World Meteorological Organization CMDL primary standards, and for water vapor using a sling psychrometer or a dew point generator (LI-610, Li-Cor Inc.). Our CO_2 calibrations at the Oak/Pine site were within 1–2% of the Ameriflux roving system in 2004 and 2008. Two-dimensional coordinate rotation of the raw sonic anemometer signals was used to obtain turbulence statistics perpendicular to the local streamline. Deviations from half-hourly block averages were used to calculate fluxes. Fluxes were corrected for frequency attenuation of scalar concentrations down the sampling tube and nonideal frequency response of the LI-7000 using transfer functions (Moncrieff *et al.*, 1997; Loescher *et al.*, 2006, http://public.ornl.gov/ameriflux/). Barometric pressure data were then used to calculate half-hourly fluxes at ambient atmospheric pressure.

Flux data were rejected when the friction velocity (u^*) $< 0.2\,m\,s^{-1}$, when measurable precipitation occurred, or when instrument malfunction occurred. Energy balance measurements indicated that sensible and latent heat fluxes accounted for 79–101% of the sum of net radiation and soil heat fluxes (Table 1; data available at http://ornl.public.gov/ameriflux). Half-hourly F_{CO_2} values were within 4–9% of those measured by the Ameriflux roving system at the Oak/Pine site in 2004 and 2008. The flux associated with the change in storage of CO_2 in the air column beneath the inlet was estimated using top of tower and 2-m height measurements (LI-870, Li-Cor Inc.) or a profile system with inlets at 0.2, 2, 5, 10, 15, and 20 m height (Oak/Pine stand only). The LI-870's were calibrated at the same time as the LI-7000's, using the same calibration standard. Half-hourly NEE ($\mu mol\,CO_2\,m^{-1}\,s^{-1}$) was then calculated as the sum of F_{CO_2} and the storage flux for each half hour period. We used the convention that negative values of NEE represented CO_2 uptake.

Annual estimates of NEE require continuous values of half-hourly CO_2 exchange (Falge *et al.*, 2001). To estimate daytime net CO_2 exchange (NEE_{day}) for periods when we did not have measurements (due to precipitation, insufficient turbulence, instrument failure, etc.), we fit a rectangular hyperbola to the relationship between PPFD and NEE_{day} at bi-weekly (May) to seasonal (wintertime) intervals (Ruimy *et al.*, 1995):

$$NEE_{day} = \frac{\alpha\,PPFD\,F_{max}}{\alpha\,PPFD + F_{max}} - R, \tag{1}$$

where α is the apparent quantum yield ($\alpha F_{CO_2}/\Delta PPFD$ at $PPFD = 0$), F_{max} is the net CO_2 exchange at light saturation, and R is the mean net CO_2 exchange at

PPFD = 0. To estimate nighttime net CO_2 exchange (NEE_{night}), half-hourly net exchange rates were regressed on air or soil temperature using an exponential function with the form:

$$NEE_{night} = \alpha e^{\beta T}, \qquad (2)$$

where α and β are regression coefficients, and T is the mean half-hourly air or soil temperature. We then used modeled values calculated from continuous meteorological data for periods when we did not have measured fluxes to fill gaps to estimate daily and annual NEE for each site. We used ± 1 SE of the value of each parameter in Eqns (1) and (2) to evaluate the sensitivity of annual estimates to modeled values for all nighttime data, and for daytime data during the summer months, which corresponded with peak rates of net CO_2 exchange. Annual ecosystem respiration (R_{eco}; $g\,C\,m^{-2}\,yr^{-1}$) was calculated for each site using continuous half-hourly air or soil temperature and Eqn (2). We summed annual NEE and R_{eco} to estimate gross ecosystem production (GEP; $g\,C\,m^{-2}\,yr^{-1}$). 'Summer' was defined as June 1–August 31, and 'winter' as December 1–February 28. In addition, we focused on eddy flux data collected from June 1 to July 15 because this period was the peak of defoliation by Gypsy moth in each stand in 2006 and 2007.

Meteorological measurements

Continuous meteorological measurements were made at each flux tower. Incoming shortwave radiation (LI-200, Li-Cor Inc.), photosynthetically active radiation (PPFD; LI-190, Li-Cor Inc.), net radiation (NRLite, Kipp and Zonen Inc., Delft, the Netherlands), aspirated air temperature and relative humidity (HMP45, Vaisala Inc., Woburn, MA, USA), windspeed and direction (05013-5, R. M. Young Co.), and precipitation (TE525, Texas Electronics Inc., Dallas, TX, USA) were measured above each canopy at 15–19 m height. Soil heat flux was measured using three heat flux transducers (HFT-3.1, Radiation and Energy Balance Systems Inc., Seattle, WA, USA) buried at 10 cm depth within 10 m of the tower at each site, and soil temperature was measured at 5 cm depth (CS-107, Campbell Scientific Inc., Logan, UT, USA) at all sites. Volumetric soil moisture content at 0–30 cm depth was measured with water content reflectometers (CS-616, Campbell Scientific Inc.) which were calibrated gravimetrically. Maximum values at saturation in these sandy soils corresponded to 21% soil moisture content. Barometric pressure (PTB 100A, Vaisala Inc.) was measured from the tower at the Oak/Pine stand. Meteorological data were recorded with automated data loggers (CR23x, Campbell Scientific Inc.). Additional meteorological data for scaling the impacts of defoliation to the landscape were obtained from USFS fire weather towers and weather towers operated by the New Jersey State Climatologist (NJWxnet; http://www.rutgers.climate.edu).

Table 1 Total number of half-hourly data values of NEE_{CO_2}, number of values following u^* and precipitation filtering, percent of year sampled by filtered data, and energy balance coefficients for the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands by year

	Total	Filtered	%	*a*	*b*	r^2
Oak/Pine						
2005	11948	8880	51	0.87	18.42	0.870
2006	12367	9344	53	0.92	15.99	0.869
2007	13395	9466	54	0.79	18.80	0.843
Pine/Oak						
2005	10479	8938	51	1.00	16.69	0.920
2006	10209	7760	44	0.91	14.41	0.892
2007	11106	7995	46	0.88	13.20	0.920
Pine/Scrub Oak						
2005	5212	3990	23	1.02	19.66	0.919
2006	11211	8343	48	1.01	13.52	0.922
2007	13932	10179	58	0.91	11.27	0.907

Energy balance coefficients were calculated as $R_{net} - G = a \times (\lambda E + H) + b$ for all filtered values.

R_{net}, net radiation; G, soil heat flux; λE, latent heat flux; and H, sensible heat flux. λE and H were calculated from the 10 hz raw data using EdiR_e.

Biometric measurements

Five 201 m^2 forest census plots located randomly within 100 m of each tower were established at each flux site (Table 2). Measurements of tree diameter at 1.3 m (dbh, cm) and height (m) were conducted annually (Skowronski *et al*., 2007). Tree biomass and growth increments were estimated from published allometric relationships (Whittaker & Woodwell, 1968). Fine litterfall was collected monthly (bi-weekly for frass) from two 0.42 m^2 wire mesh traps adjacent to each tree census plot at each site ($n = 10$ traps per site). Samples were separated into leaves, needles, stems, and reproductive material of trees and shrubs, sedges, herbs, and frass, then dried at 60 °C, and weighed when dry. Leaf area was measured using a portable leaf area meter (LI-3000a, Li-Cor Inc.) and a conveyer belt (LI-3050c, Licor Inc.) using leaf and fresh litter samples which were then dried and weighed. Annual aboveground biomass accumulation of understory vegetation was estimated by harvesting 10–20 clip plots (1.0 m^2) in the vicinity of each tower every year during the time of peak biomass in the late summer. Forest floor mass (five 1.0 m^2 samples in the vicinity of each tree census plot) and coarse woody debris were sampled at the beginning and after the end of the study.

Table 2 Forest structural characteristics of Oak/Pine, Pine/Oak, and Pine/Scrub oak stands in the New Jersey Pine Barrens in 2005

Attribute	Oak/Pine Silas Little	Pine/Oak Fort Dix	Pine/Scrub oak Cedar Bridge
Stand age (years)*	91	73	82
Stem density (stems ha^{-1}*)*			
Pine	90 ± 19	269 ± 162	1035 ± 87
Oak	1233 ± 293	676 ± 114	418 ± 145
Total	1323 ± 300	945 ± 123	1452 ± 158
Basal area ($m^2\,ha^{-1}$*)*			
Pine	4.4 ± 2.4	5.6 ± 1.8	14.3 ± 2.1
Oak	11.5 ± 1.4	6.3 ± 4.2	0.3 ± 0.1
Total	15.9 ± 2.5	11.8 ± 3.0	14.7 ± 2.1
Height (m)			
Pine	11.2 ± 2.9	9.9 ± 1.0	6.4 ± 0.4
Oak	9.3 ± 1.0	6.6 ± 1.5	2.8 ± 0.7
Total	9.5 ± 1.0	7.3 ± 1.3	5.7 ± 0.4
Overstory biomass ($g\,m^{-2}$*)*			
Pine	2134 ± 1179	1957 ± 612	4956 ± 1018
Oak	6360 ± 736	3227 ± 2294	54 ± 21
Total	8494 ± 1220	5184 ± 1859	5010 ± 1023
Understory biomass ($g\,m^{-2}$*)*			
Shrub	168 ± 38	112 ± 32	322 ± 27
Oak	20 ± 15	217 ± 71	70 ± 23
Total	189 ± 35	329 ± 68	397 ± 44
Forest floor mass ($g\,m^{-2}$*)*			
Fine litter	845 ± 45	842 ± 71	1131 ± 35
Wood	223 ± 47	319 ± 63	447 ± 110
Total	1068 ± 75	1160 ± 115	1578 ± 119

Overstory data are from five 201 m^2 plots, and understory biomass and forest floor mass (Oi layer) was sampled in 10–20 1.0 m^2 plots in the vicinity of the tower at each site. Values are means ± 1 SE.

*Maximum age (in 2005) of two dominant trees in 16 201 m^2 plots in a 1 km^2 grid centered on the flux tower at each site. Cores were sampled with an increment borer.

Litterbags (10 cm × 20 cm, 1 mm mesh size) containing 5 g of pine needles, overstory oak foliage, understory oak foliage, or shrub foliage were used to estimate mass loss from fine litter. Litterbags ($n = 40$ for each component) were placed at random locations within the vicinity of each census plot at the Oak/Pine site, and harvested at 6, 12, 24, and 36 months. Annual woody biomass accumulation was calculated from plot data, published allometric equations, and clip plots. Forest floor mass balance was calculated by accounting for the decomposition of litterfall from the overstory and foliage from clip plots for shrubs and herbs in the understory, as estimated from decay constants derived from mass loss in litterbags. Values obtained from a C/N analyzer (Leco C/N Determinator 200–288, Leco Inc., St. Joseph, MI, USA) and mass loss on ignition at 550 °C were used to convert biomass to C mass. Collectively, these data were used to estimate net ecosystem productivity (NEP; $g\,C\,m^{-2}\,yr^{-1}$) for each site in 2005.

Gypsy moth defoliation

New Jersey Department of Environmental Protection and USFS have tracked Gypsy moth outbreaks since 1976, and define defoliation as $\geq 75\%$ reduction of canopy foliage in Oak/Pine stands, and $\geq 75\%$ reduction of the foliage of deciduous species in Pine/Oak and Pine/Scrub oak stands. We used maps derived from aerial censuses for 2005–2007 to estimate the spatial extent of defoliation by forest type using a forest classification map for the Pinelands National Reserve (Lathrop & Kaplan, 2004; Skowronski *et al.*, 2007). To calculate their effect on C dynamics at the landscape scale, we first used daytime and nighttime parameters for nondefoliated periods in Eqns (1) and (2) and continuous meteorological data for 2007 to estimate $\mathrm{NEE_{yr}}$ for each site in the absence of Gypsy moth. We then multiplied the resultant NEE values by the area of each forest type in the Pinelands National Reserve, and calculated a potential C sequestration for upland forests in 2007. NEE data for 2007 measured at each stand was multiplied by the area defoliated in each forest type to calculate C sequestration for defoliated areas, and estimates were combined to calculate actual C sequestration for upland forests in 2007.

Results

EC measurements

Daytime net CO_2 exchange ($\mathrm{NEE_{day}}$) at the Oak/Pine site was initially low in winter and spring of all years measured, and then increased rapidly with bud break and leaf expansion starting in early May. $\mathrm{NEE_{day}}$ reached near maximum rates at the Oak/Pine site over a 1-week period, (May 7–14), and then exceeded those measured at the Pine/Oak and Pine/Scrub oak stands through the summers of 2005 and 2006. In 2005, $\mathrm{NEE_{day}}$ averaged −17.2, −13.8, and −14.1 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at 1500 μmol PPFD $m^{-2}\,s^{-1}$ at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands in summer, respectively (Fig. 1, Table 3). $\mathrm{NEE_{day}}$ during the summer was sensitive to soil moisture levels at all sites. For example, daytime NEE at the Oak/Pine stand in early July 2004 averaged −11.9 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at 1500 μmol PPFD $m^{-2}\,s^{-1}$ when volumetric soil moisture content was $<7\%$ (0–30 cm depth), and increased to an average of −19.7 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at 1500 μmol PPFD $m^{-2}\,s^{-1}$ following the onset of summer convective precipitation and the occurrence of higher soil moisture contents (data not shown). Vapor pressure deficit (VPD) of the atmosphere >2 kPa had little effect on stomatal conductance and daytime net CO_2 exchange during the summer until soil moisture content averaged <7%. NEE_{day} at the Pine/Oak site was similarly affected by drought in August and September 2005; NEE_{day} averaged only $-6.5\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at $1500\,\mu mol\,PPFD\,m^{-2}\,s^{-1}$ during this period. Following precipitation events, daytime NEE in the summer typically recovered rapidly to near maximum rates at each stand.

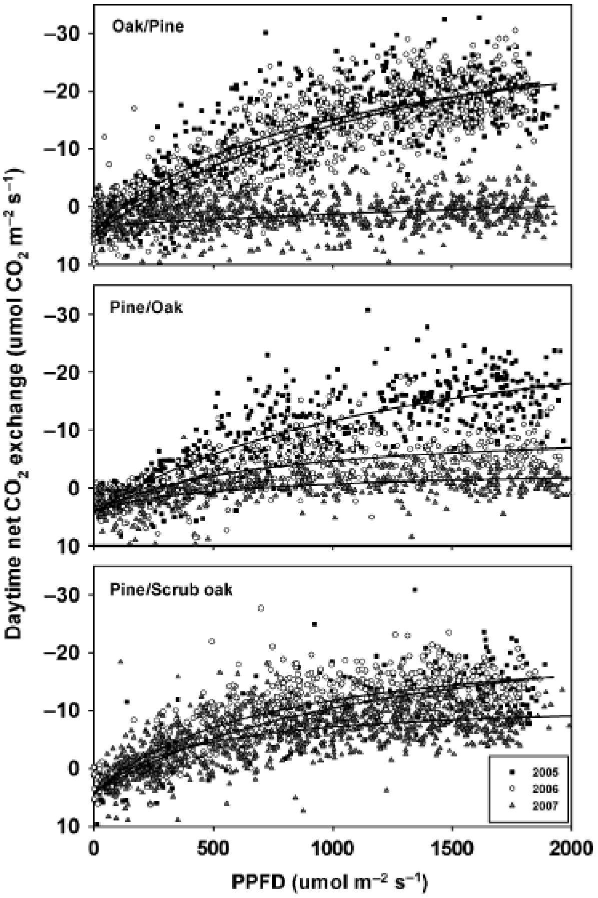

Fig. 1 Daytime net CO_2 exchange ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$) as a function of incident radiation ($\mu mol\,PPFD\,m^{-2}\,s^{-1}$) during June 1–July 15 at Oak/Pine, Pine/Oak, and Pine/Scrub oak stands in 2005, 2006, and 2007. Statistics for each light response curve are in Table 3.

Canopy oaks and understory oaks and shrubs at the Pine/Oak stand were defoliated by Gypsy moth in 2006 and 2007, reducing NEE_{day} between June 1 and July 15 compared with the same period in 2005 (Fig. 1, Table 3). NEE_{day} at $1500\,\mu mol\,PPFD\,m^{-2}\,s^{-1}$ averaged $-15.3\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ during this period in 2005, but only -6.0 and $-1.3\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ in 2006 and 2007, respectively. Following the cessation of herbivory with maturation of Gypsy moth, leaf area increased in both years to ca. 70% of the summer maxima that had occurred in 2005. By August and September in 2006 and 2007, net CO_2 exchange rates had recovered to $-11.0\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at $1500\,\mu mol\,PPFD\,m^{-2}\,s^{-1}$ at the Pine/Oak site.

In 2007, the Oak/Pine stand was completely defoliated from the end of May until mid-July. Complete defoliation reduced NEE_{day} dramatically through the June 1–July 15 period, with mean values reaching only $0.3\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at $1500\,\mu mol\,PPFD\,m^{-2}\,s^{-1}$ (Fig. 1, Table 3). Following the cessation of herbivory, leaf area recovered to ca. 50% of the summer maxima that had occurred in 2005 and 2006. NEE_{day} reached only $-7.5\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ at $1500\,\mu mol\,PPFD\,m^{-2}\,s^{-1}$ during August and September 2007, ca. half of the values that had occurred in 2005 and 2006. Understory oaks and shrubs were moderately defoliated at the Pine/Scrub oak site in 2007, but canopy pines were largely unaffected. However, even moderate defoliation of deciduous species apparently reduced NEE_{day} during the June 1 to July 15 period in 2007. NEE_{day} at the Pine/

Table 3 Coefficients for the relationship between incident light and net CO_2 exchange from June 1 to July 15 at the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stand shown in Fig. 1

Site/year	α	F_{max}	R	n	r^2	F
Oak/Pine						
2005	0.040 ± 0.002	38.27 ± 1.30	4.38 ± 0.16	716	0.690	796.8
2006	0.032 ± 0.001	47.65 ± 2.18	4.96 ± 0.14	842	0.819	1900.2
2007	0.003 ± 0.001	10.47 ± 6.62	3.42 ± 0.11	882	0.069	33.8
Pine/Oak						
2005	0.027 ± 0.001	37.64 ± 1.64	4.23 ± 0.13	537	0.707	647.7
2006	0.021 ± 0.002	14.84 ± 0.75	4.06 ± 0.12	478	0.400	158.6
2007	0.013 ± 0.001	7.35 ± 0.39	3.99 ± 0.09	503	0.283	100.2
Pine/Scrub Oak						
2005	0.027 ± 0.001	33.42 ± 1.58	4.25 ± 0.13	256	0.699	296.6
2006	0.038 ± 0.002	27.58 ± 0.74	4.12 ± 0.11	675	0.671	688.5
2007	0.043 ± 0.003	16.40 ± 0.40	4.65 ± 0.12	956	0.488	455.2

Data were fit to Eqn (1). All models are significant at $P < 0.0001$.

Scrub oak site averaged $-14.3\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$ at 1500 μmol PPFD $m^{-2}\,s^{-1}$ during this period in 2005 and 2006, while in 2007 it averaged only $-8.4\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$ at 1500 μmol PPFD $m^{-2}\,s^{-1}$ (Fig. 1, Table 3).

Half-hourly daytime NEE decreased through the fall at all sites, corresponding with leaf senescence of deciduous species by the end of October. During the winter, NEE_{day} averaged 2.0, 1.6 and 0.7 μmol $CO_2\,m^{-2}\,s^{-1}$ at 1000 μmol PPFD $m^{-2}\,s^{-1}$ at the Oak/Pine, Pine/Oak and Pine/Scrub oak stands, respectively (Table 4). While PPFD and air temperature had little effect on NEE_{day} at the Oak/Pine and Pine/Oak sites during the winter, values at the Pine/Scrub oak site were negative at higher PPFD levels following nights when air temperature was $>0\,^{\circ}C$. On these days, NEE_{day} at the Pine/Scrub Oak stand averaged $-2.4\,\mu$mol $CO_2\,m^{-2}\,s^{-1}$ at 1000 μmol PPFD $m^{-2}\,s^{-1}$ (Table 4). Overall, seasonality in daytime net CO_2 exchange rates was most pronounced at the Oak/Pine site in 2005 and 2006, corresponding to the largest changes in leaf area (ca. 4.1–$<0.5\,m^2\,m^{-2}$).

Half-hourly nighttime net CO_2 exchange (NEE_{night}) during well mixed conditions ($u^* > 0.2\,m\,s^{-1}$) was an exponential function of air or soil temperature at all sites (Table 5). NEE_{night} averaged 4.2, 3.1, and 4.5 μmol $CO_2\,m^{-2}\,s^{-1}$ in the summer in 2005, and 1.1, 0.9, and 1.4 μmol $CO_2\,m^{-2}\,s^{-1}$ during the winter of all years measured at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively.

Only severe Gypsy moth defoliation apparently affected NEE_{night}. For example, during June 1–July 15 in 2007 at the Oak/Pine site, complete defoliation resulted in a near doubling of soil heat flux (6.4 vs. 12.4 $W\,m^{-2}$) and a 2.7 °C increase in soil temperature compared with 2005 and 2006. However, NEE_{night} averaged only 2.5 μmol $CO_2\,m^{-2}\,s^{-1}$ in 2007, while rates had averaged 4.6 μmol $CO_2\,m^{-2}\,s^{-1}$ during the same period in 2005 and 2006. Mean air temperature during June 1–July 15 was similar during all 3 years, averaging 22.6, 22.0, and 22.2 °C in 2005, 2006, and 2007, respectively. When data were analyzed for the entire year at the Oak/Pine site, nighttime net CO_2 exchange was a much weaker function of air temperature, and Q_{10} values were lower in 2007 compared with 2005 and 2006 (Table 5). In contrast, NEE_{night} was a stronger function of air temperature at the Pine/Scrub oak stand, and was characterized by a more typical Q_{10} value of 1.8 for 15–25 °C over the 3 years measured (Table 5).

During 2005, daily net CO_2 exchange in the summer averaged -4.4 ± 0.2, -3.1 ± 0.2, and $-2.4 \pm 0.2\,g\,C\,m^{-2}\,day^{-1}$ (mean ± 1 SE) at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively (Fig. 2). Daily C flux decreased by November, corresponding to near total leaf senescence of deciduous species. Daily C flux

Table 4 Coefficients for the relationship between incident light and net CO_2 exchange in the daytime during the winter months (December 1–February 28) at the Oak/Pine, Pine/Oak, and Pine Scrub Oak stands

Site	α	ß	n	r^2	F	P
Oak/Pine	0.0003 ± 0.0001	0.810 ± 0.060	2897	0.003	10.13	0.002
Pine/Oak	0.0007 ± 0.0001	1.216 ± 0.063	3504	0.012	42.69	<0.0001
Pine/Scrub Oak	0.0000 ± 0.0001	0.714 ± 0.076	2734	0.000	0.26	0.611
Pine/Scrub Oak*	-0.0034 ± 0.0002	1.006 ± 0.127	827	0.210	218.33	<0.0001

Data from 2005 to 2007 are pooled within site. Data are fit to the equation $NEE_{day} = \alpha\,(PPFD) + \beta$

*Winter months when the previous night air temperature $>0^{o}C$.

Table 5 Coefficients for the relationship between air temperature and nighttime net CO_2 exchange (NEE_{night}) at the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands in Eqn (2)

Site/year	α	β	n	r^2	F	Q_{10}
Oak/Pine						
2005–2006	1.010 ± 0.018	0.062 ± 0.001	6301	0.199	1566.9	1.9
2007	1.178 ± 0.027	0.037 ± 0.001	3461	0.098	377.7	1.5
Pine/Oak						
2005	1.013 ± 0.025	0.045 ± 0.001	2562	0.132	390.3	1.6
2006–2007	0.962 ± 0.016	0.057 ± 0.001	5980	0.232	1805.2	1.8
Pine/Scrub Oak						
2005–2006	1.284 ± 0.020	0.061 ± 0.001	4673	0.315	2151.2	1.8
2007	1.342 ± 0.026	0.056 ± 0.001	4019	0.317	1863.7	1.8

Data from 2-year periods are pooled. All models are significant at $P < 0.0001$. Q_{10} values are calculated for 15–25 °C.

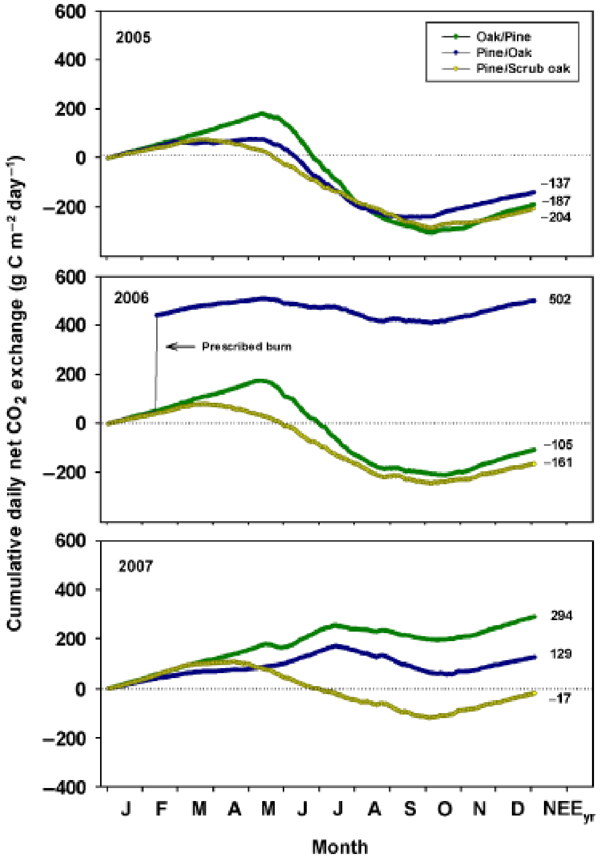

Fig. 2 Cumulative daily carbon flux (g C m^{-2} day^{-1}) for the Oak/Pine, Pine/Oak and Pine/Scrub oak stands in 2005, 2006 and 2007. A prescribed fire was conducted at the Pine/Oak stand on February 12, 2006. Canopy and understory oaks were defoliated by Gypsy moth at the Pine/Oak stand in 2006 and 2007, and the Oak/Pine stand was completely defoliated in 2007. Annual carbon flux (g C m^{-2} yr^{-1}) for each site is shown to the right of each curve.

during the winter averaged 1.4 ± 0.0, 1.1 ± 0.0, and 1.2 ± 0.1 g C m^{-2} day^{-1} at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, consistent with cold temperatures and relatively low leaf areas at that time.

Similar patterns of daily net CO_2 exchange occurred at the Oak/Pine and Pine/Scrub Oak stands during the summer in 2006. However, defoliation of canopy and understory oaks and shrubs by Gypsy moths reduced daily NEE substantially at the Pine/Oak stand in 2006, and a similar reduction in daily C flux occurred in 2007 (Fig. 2). Consistent with the complete removal of leaf area and very low values of NEE_{day} at the Oak/Pine stand in 2007, daily C flux was strongly reduced in 2007. Daily net CO_2 exchange during the summer averaged −3.8 ± 0.2 g C day^{-1} at the Oak/Pine stand in 2005 and 2006, but only −0.7 ± 0.2 g C day^{-1} during 2007 (Fig. 2).

Table 6 Annual net ecosystem exchange of CO_2 (NEE_{yr}), ecosystem respiration (R_{eco}), gross ecosystem production (GEP), and the proportion GEP released by ecosystem respiration (%) for the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands

Site	Year	NEE_{yr}	R_{eco}	GEP	R_{eco}/ GEP (%)
Oak/Pine	2005	−187	962	1150	83.7
	2006	−105	1051	1156	90.9
	2007	294	785	491	159.9
Pine/Mixed Oak	2005	−137	740	877	84.4
	2006	103*	907	804	112.8
	2007	129	831	702	118.4
Pine/Scrub Oak	2005	−204	1132	1336	84.7
	2006	−161	1242	1404	88.5
	2007	−17	1153	1170	98.5

Units are g C m^{-2} yr^{-1}
*Inclusion of combustion losses from understory vegetation and the forest floor during a prescribed fire conducted on February 12, 2006, resulted in an NEE_{yr} value of 502 g C m^{-2} yr^{-1}.

In 2005, all stands were moderate sinks for CO_2, with annual NEE (NEE_{yr}) estimated at −187, −137, and −204 g C m^{-2} yr^{-1} at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively (Table 6). In 2006, NEE_{yr} values were 82 and 43 g C m^{-2} lower at the Oak/Pine and Pine/Scrub oak stands than in 2005, and the Pine/Oak stand was a moderate source of CO_2 to the atmosphere. When net CO_2 exchange and fuel combustion measurements associated with a prescribed fire conducted on February 12, 2006, were included, the Pine/Oak stand became a large source of CO_2 to the atmosphere in 2006 (502 g C m^{-2} yr^{-1}; Clark *et al*., 2009). In 2007, Gypsy moth defoliation strongly reduced NEE_{yr} at all three stands (Table 6). When summed over the 3 years measured, NEE values totaled 2, 505, and −382 g C m^{-2} at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively (Fig. 2, Table 6).

A large number of modeled values were used to calculate nighttime fluxes in the estimation of NEE_{yr}, because relatively low windspeed conditions prevailed throughout the night during the study. Using ± 1 SE of the mean parameter values for nighttime net CO_2 exchange in Table 4 individually in Eqn (2), maximum deviations of 5.3%, 7.2%, and 4.4% were calculated for NEE_{yr} values for 2005 at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively (Table 7). During daytime in the summer, annual NEE estimates were most sensitive to variation in values of α, the apparent quantum yield, in Eqn (1). Using ± 1 SE of the mean α values, maximum deviations of 12.3%, 15.3%, and 14.7% from NEE_{yr} estimates were calculated for the

Table 7 Number of filtered half-hourly data values for nighttime net CO_2 exchange (NEE_{night}), percent of total nighttime half hours, and NEEyr estimates calculated using ± 1 SE of mean values in Table 4 in Eqn (2) for the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands by year

				α		β	
Site/Year	n	%	NEE_{yr}	+ SE	−SE	+ SE	−SE
Oak/Pine							
2005	3022	35	−187	−197	−177	−195	−179
2006	3276	37	−105	−113	−97	−111	−99
2007	3462	40	294	287	301	289	299
Pine/Oak							
2005	2563	29	−137	−147	−127	−144	−129
2006	2881	33	103	93	113	95	111
2007	3263	37	129	121	137	123	135
Pine/Scrub Oak							
2005	1468	17	−204	−213	−195	−210	−198
2006	3196	37	−161	−171	−151	−169	−153
2007	4020	46	−17	−24	−10	−22	−12

Table 8 Number of filtered half-hourly data values for daytime net CO_2 exchange (NEE_{day}) during the summer months, percent of total daytime half hours in the summer measured, and NEE_{yr} calculated using ± 1 S.E. of mean values in Eqn (1) for the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands by year

				α		F_{max}		R	
	n	%	NEE	−SE	+ SE	−SE	+ SE	−SE	+ SE
Oak/Pine									
2005	1114	42	−187	−164	−208	−179	−195	−208	−166
2006	1098	43	−105	−79	−128	−97	−113	−128	−82
2007	1549	59	294	306	285	297	291	283	305
Pine/Oak									
2005	1049	40	−137	−116	−156	−130	−145	−154	−120
2006	1168	45	103	119	89	109	98	89	117
2007	1173	45	129	150	112	135	123	109	149
Pine/Scrub Oak									
2005	654	25	−204	−176	−234	−194	−215	−228	−180
2006	1050	40	−161	−134	−168	−153	−168	−170	−137
2007	1831	70	−17	−11	−23	−15	−19	−24	−10

Summer months are defined as June 1–August 31.

Oak/Pine, Pine/Oak, and Pine/Scrub oak stands in 2005 (Table 8).

Estimated R_{eco} averaged within each site for all 3 years was greatest at the Pine/Scrub oak site and least at the Pine/Oak site (Table 6). Maximum differences between annual R_{eco} estimates among sites occurred between the Pine/Oak and Pine/Scrub oak stands in 2005 ($391\,g\,C\,m^{-2}$), and between the Oak/Pine and Pine/Scrub oak stands in 2007 ($368\,g\,C\,m^{-2}$). Largest differences between sites could be attributed to local drought effects (2005), and to defoliation (2007). The maximum difference from the 3-year average within a site was $148\,g\,C\,m^{-2}$ for the Oak/Pine site in 2007, representing a 16% difference. Overall, these relatively stable annual R_{eco} values contrasted with the large variation in annual NEE associated with various disturbances.

Annual R_{eco} estimates for all years were equally sensitive to the two parameters in Eqn (2), with a maximum deviation of $38\,g\,C\,m^{-2}\,yr^{-1}$ calculated for the Pine/Scrub Oak site in 2006. Annual R_{eco} averaged 83.7% of estimated GEP among sites in 2005 (Table 6). When Gypsy moth defoliation impacted each stand, R_{eco} approached or exceeded GEP, with a maximum of 160% at the Oak/Pine site in 2007.

Biometric measurements

Aboveground NPP was dominated by foliage production from the overstory at all sites in 2005, and by a combination of foliage and frass in 2006 and 2007. Despite large differences in overstory species dominance and canopy cover, total foliage production (litterfall + foliage from clip plots) was similar among sites in 2005 (Tables 1 and 9). Wood increment represented only 22–34% of aboveground productivity in 2005. Decomposition of foliage estimated using litterbags was 22.5 ± 11.2% to 31.0 ± 5.1% of initial mass after the first year, and was most rapid for shrub foliage, and least for foliage of overstory oaks. Annual forest floor accumulation calculated from current-year litterfall and corrected for decomposition was $159–170\,g\,C\,m^{-2}\,yr^{-1}$ for all sites in 2005. When forest floor increment was calculated using a 5-year running mean of litterfall and litter decomposition estimated from litter bags for each site, forest floor accumulation was estimated at 82, 79, and $91\,g\,C\,m^{-2}\,yr^{-1}$ at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands in 2005. Forest floor accumulation for 2005 represented 41%, 58%, and 46% of annual NEP at the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands, respectively. Overall, annual NEP estimates accounted for 108%, 100%, and 98% of NEE_{yr} at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands in 2005, respectively (Tables 6 and 10).

During the summer of 2006, defoliation of canopy oaks and understory oaks and shrubs at the Pine/Oak site resulted in $27.3 \pm 41.8\,g\,m^{-2}$ of frass deposition to the forest floor in June and July, representing ca. 19% of litterfall from deciduous species in fall 2005 (Table 9). In 2007, frass deposition totaled $83.6 \pm 86.3\,g\,m^{-2}$ at the Pine/Oak stand, representing 59% of litterfall from deciduous species in 2005. Defoliation of the Oak/Pine

Table 9 Fine litterfall (g mass $m^{-2} yr^{-1}$) at the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands in the Pine Barrens of New Jersey

Site	Needles	Foliage	Stems	Frass	Misc.	Total
Oak/Pine						
2005	6 ± 6	333 ± 39	86 ± 94	<2	16 ± 6	441 ± 105
2006	8 ± 4	290 ± 27	63 ± 43	<5	23 ± 15	389 ± 61
2007	6 ± 3	216 ± 26	36 ± 19	97 ± 45	4 ± 6	357 ± 72
Pine/Oak						
2005	146 ± 90	141 ± 60	42 ± 52	<2	31 ± 23	364 ± 171
2006	112 ± 56	88 ± 60	96 ± 155	27 ± 41	3 ± 6	327 ± 195
2007	73 ± 41	86 ± 33	35 ± 33	84 ± 86	18 ± 30	299 ± 168
Pine/Scrub Oak						
2005	274 ± 82	45 ± 17	47 ± 41	<2	30 ± 38	411 ± 125
2006	262 ± 78	43 ± 20	41 ± 44	<2	13 ± 24	372 ± 136
2007	294 ± 82	35 ± 27	24 ± 23	32 ± 20	14 ± 33	408 ± 99

Litterfall traps ($n = 10$ per site) are $0.42 m^2$.

Table 10 Biomass increment and forest floor accumulation at the Oak/Pine, Pine/Oak, and Pine/Scrub Oak stands in 2005

	Oak/Pine	Pine/Oak	Pine/Scrub Oak
Overstory Biomass			
Foliage*	3.9 ± 0.4	0.0 ± 2.6	3.2 ± 2.0
Stems and branches*	87.1 ± 13.3	34.4 ± 23.8	60.3 ± 44.7
Coarse roots*	26.5 ± 5.5	7.5 ± 4.5	11.1 ± 8.3
Understory Biomass			
Foliage†	−1.8 ± 22.0	−3.1 ± 22.0	−1.2 ± 7.3
Stems†	3.9 ± 16.4	19.1 ± 33.3	35.2 ± 57.7
Biomass total	119.6	57.9	108.6
Forest Floor†,‡			
Overstory	75.8	61.1	74.4
Understory	6.0	17.5	16.7
Total	201.4	136.4	199.2

Units are g C $m^{-2} yr^{-1}$ ± 1 SD.

*Calculated from annual plot censuses and allometric equations.

†Calculated from annual clip plots.

‡Forest floor accumulation was calculated from total litterfall flux and weighted mass loss for each litter components (range of estimates is 21–31% yr^{-1}) until mass reached 20% of original total.

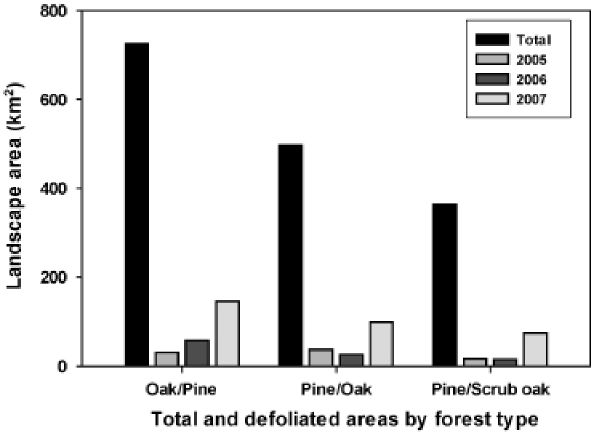

Fig. 3 Extent of major upland forest types in the Pinelands National Reserve in the Pine Barrens of New Jersey and area defoliated in 2005, 2006, and 2007 (adapted from Lathrop & Kaplan, 2004; Skowronski *et al.*, 2007). Defoliation was defined as ≥ 75% canopy defoliation in Oak/Pine stands, and ≥ 75% deciduous species defoliated in Pine/Oak and Pine/Scrub oak stands. Data are from aerial censuses conducted by the New Jersey Department of Environmental Protection. All units are km^2.

stand in 2007 resulted in $96.4 \pm 45.0 g m^{-2}$ of frass, which fell in late May to the end of June. Frass deposition at the Oak/Pine site represented only 29% of litterfall from deciduous species in 2005, but because herbivory was concurrent with leaf expansion, defoliation was complete through mid-July. When integrated over the entire year, total litterfall (frass + litterfall) values for years when defoliation occurred were never <79% of total litterfall during 2005, in part because of the second leaf flush and subsequent litterfall (Table 9).

Gypsy moth defoliation

Gypsy moth defoliation, defined as ≥ 75% reduction of canopy foliage in Oak/Pine stands, and ≥ 75% reduction of the foliage of deciduous species in Pine/Oak and Pine/Scrub oak stands, totaled 85.8 km^2 in upland forests in the Pine Barrens in 2005 (New Jersey Department of Environmental Protection 2007, Fig. 3). Greater amounts of the landscape were defoliated in 2006 and 2007, with a maximum defoliation of 320.3 km^2 in 2007, representing an average of 20.2% of the area of the three major upland forests (Fig. 3). Using daytime and nighttime parameters for nondefoliated periods in Eqns (1) and (2), and continuous meteorological data for 2007 to estimate $\mathrm{NEE}_{\mathrm{yr}}$ for each site in the absence of Gypsy moth, we calculated values of −168.9, −149.8, and $-152.5\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively. We then multiplied $\mathrm{NEE}_{\mathrm{yr}}$ values by the area of each forest type in the Pinelands National Reserve (Fig. 3), and calculated that upland forests in the Pine Barrens potentially sequestered 252 647 tons C over a total of $1588\,\mathrm{km}^2$. When actual NEE data for 2007 measured at each site were multiplied by the area defoliated in each forest type (Table 6, Fig. 3), estimated C sequestration in upland forests was only 147 332 tons C, representing 58.7% of the potential amount calculated for 2007. The reduction in oak-dominated stands was most dramatic; potential C sequestration was estimated at 122 515 tons C across $725\,\mathrm{km}^2$, while actual C sequestration was estimated at only 55 047 tons C, representing 44.9% of the potential amount. Although our calculations assume that daytime and nighttime net CO_2 exchange measured at our sites characterize all sites in upland Oak- and Pine-dominated stands in the Pine Barrens, and that defoliation levels recorded by the NJDEP were similar to our sites, they illustrate the magnitude of the impact that Gypsy moth defoliation can have on forest C dynamics at the landscape level.

Discussion

EC measurements

Before Gypsy moth defoliation, seasonal patterns of net CO_2 exchange were related to species dominance in the canopy, where basal area ranged from 72% Oak to >95% Pitch Pine, and overstory biomass ranged from 75% Oak to >95% Pitch Pine at the three sites. Both daytime half-hourly and daily NEE were greatest at the stand dominated by Oaks and least at the Pine-dominated stand in summer 2005. This pattern is similar to leaf-level measurements of A_{max} using canopy oaks and pines in the Pine Barrens (K. Schaffer & N. Skowronski, unpublished data). However, both the Pine/Oak and the Pine/Scrub oak stands had higher rates of net CO_2 exchange in the daytime during spring and fall months compared with the Oak/Pine stand, consistent with patterns of leaf area display. The conifer-dominated stand had the greatest half-hourly and daily NEE values in the winter, especially during days when air temperature during the previous night was $>0\,^{\circ}\mathrm{C}$. Cumulative C flux in 2005 indicated that the Oak/Pine site experienced the greatest amplitude in flux rates; net losses during the winter and spring totaled ca. 200 g C, while they totaled ca. 100 g C at the Pine/Oak and Pine/Scrub oak sites (see Fig. 2). These large seasonal differences in daytime half-hourly and daily NEE values among stands in 2005 resulted in annual NEE values that were similar at the Oak/Pine and Pine/Scrub oak sites. This period was characterized by near-average annual precipitation and the near absence of herbivory. $\mathrm{NEE}_{\mathrm{yr}}$ at the Pine/Oak stand in 2005 was 70% of the average of these two sites, and was apparently constrained by localized drought due to lack of convective precipitation during late August and September. Thus, in the absence of drought, herbivory, or other disturbance, $\mathrm{NEE}_{\mathrm{yr}}$ and annual NEP were similar at the Oak/Pine, Pine Oak, and Pine/Scrub Oak stands. Our results suggest that differences in aboveground biomass among stands are not necessarily due to differences in annual productivity among upland forest types in the Pine Barrens (Skowronski *et al*., 2007).

Lower $\mathrm{NEE}_{\mathrm{yr}}$ values are typically observed for older stands compared with younger forests (Thornton *et al*., 2002; Black *et al*., 2005). Consistent with this pattern, $\mathrm{NEE}_{\mathrm{yr}}$ of the three stands in the Pine Barrens in 2005 were within the range of those measured at other temperate forest sites of intermediate age (see data in Black *et al*., 2005), and to a number of intermediate age sites on the Atlantic Coastal Plain (Clark *et al*., 1999; Powell *et al*., 2008). For example, reported $\mathrm{NEE}_{\mathrm{yr}}$ values ranged from 158 to $192\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ over 4 years of measurement at a 60-year-old Slash (*Pinus elliottii*) and Longleaf pine (*Pinus palustris*) stand (Powell *et al*., 2008). $\mathrm{NEE}_{\mathrm{yr}}$ values at our intermediate age stands are much lower than those characterizing younger, rapidly growing pine plantations on the Atlantic coastal plain (Clark *et al*., 1999, 2004; Oren *et al*., 2006).

Water and soil nutrient availability are major constraints to forest productivity (Oren *et al*., 2006; Pan *et al*., 2006). NEE in both the Oak/Pine and Pine/Oak stands was reduced during dry periods in the summer when soil moisture was below 7% volumetric soil water content. The reduction of stomatal conductance at $\mathrm{VPD} > 2.0\,\mathrm{kPa}$ was also apparent when soil water content was low. Sensitivity of NEE to drought at half-hourly to annual time scales has been shown in numerous forests on the Atlantic coastal plain (e.g., Clark *et al*., 2004; Powell *et al*., 2008), and in the Pine Barrens using modeling approaches (e.g., Pan *et al*., 2006). Although soil nutrient status was very low at all three sites in the Pine Barrens, moderate rates of productivity were maintained in the absence of drought or herbivory. Many species in the Pine Barrens are mycorrhizal (Dighton *et al*., 2004), as they are in many forested stands throughout the Atlantic Coastal Plain, facilitating efficient nutrient retention and turnover. The abundance of mycorrhizae likely contribute to the maintenance of moderate rates of productivity in upland forest stands in the Pine Barrens.

In 2006, C losses from defoliation and prescribed fire totaled $502\,\mathrm{g\,C\,m^{-2}}$ at the Pine/Oak site, and in 2007 $\mathrm{NEE_{yr}}$ at the defoliated Oak/Pine site was $293\,\mathrm{g\,C\,m^{-2}}$. C losses of this magnitude are less than those associated with catastrophic disturbance (clearcutting) in other pine dominated stands on the Atlantic Coastal Plain. For example, $\mathrm{NEE_{yr}}$ was 1200 and $800\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ 1 and 2 years following harvest in a Slash Pine stand that had been clearcut in North Florida (Clark *et al.*, 2004). Values were also less than those calculated for wildfire losses that occurred in a 8200 ha wildfire in the Pine Barrens in 2007 (ca. $996 \pm 354\,\mathrm{g\,C\,m^{-2}}$ in the Warren Grove wildfire, May 15–19, 2007; Skowronski *et al.*, 2007). However, Gypsy moth defoliation resulted in a wide range of $\mathrm{NEE_{yr}}$ responses; over the 3 years measured, $\mathrm{NEE_{yr}}$ values differed by $480\,\mathrm{g\,C\,m^{-2}}$ at the Oak/Pine stand, and by $266\,\mathrm{g\,C\,m^{-2}}$ at the Pine/Oak stand. When combustion losses of C associated with the prescribed burn in February 2006 were included, $\mathrm{NEE_{yr}}$ values at the Pine/Oak stand differed by $639\,\mathrm{g\,C\,m^{-2}}$ over the 3 years measured. The maximum difference among years at the Pine/Scrub oak stand was $187\,\mathrm{g\,C\,m^{-2}}$. These results demonstrate the large impact that transient disturbances can have on net CO_2 exchange at instantaneous to annual time scales.

Initially, the large variations in annual NEE occurred despite only minor changes to overall C storage pools. However, wood increment was reduced, and totaled only $-4 \pm 45\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ at the Oak/Pine stand and $-28 \pm 34\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ at the Pine/Oak stand in 2007. Further tree mortality occurred at both sites in 2008, resulting in a transfer of C from live to dead wood pools. In the years following severe defoliation, NEE may increase substantially due to enhanced regeneration following mortality, and because dead stems and coarse wood on the forest floor decompose relatively slowly. However, these intermediate age stands are characterized by relatively low biomass (Skowronski *et al.*, 2007), thus the long-term average NEE values are unlikely to be large.

While defoliation by Gypsy moth had a major impact on GPP and thus $\mathrm{NEE_{day}}$ during the summertime, it apparently had much less effect on rates of ecosystem respiration and nighttime net CO_2 exchange. At the Pine/Oak stand, Gypsy moth defoliation apparently had little effect on R_{eco}, because annual values varied by $<11\%$ from the average R_{eco} value calculated for all 3 years. Values obtained at the Pine/Oak stand are consistent with those of Cook *et al.* (2008), who predicted a decrease in GPP and a slight increase in R_{eco} of $45\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ during defoliation by Tent caterpillars which reduced LAI by ca. 34% in a northern hardwood forest. These results are also consistent with Frost & Hunter (2004), who reported enhanced soil respiration following defoliation of red oak seedlings by Gypsy moth.

Only when the Oak/Pine site was completely defoliated at the end of June 2007 was R_{eco} reduced substantially, despite the fact that mean soil temperature from June 1 to July 15 was 2.7 °C warmer in 2007 compared with 2005 and 2006. Nighttime net CO_2 exchange was essentially decoupled from air or soil temperature during this period, resulting in the poorest relationship between $\mathrm{NEE_{night}}$ and air temperature for all years and sites measured ($r^2 = 0.098$ vs. an average $r^2 = 0.245$ for all other years and sites), and the lowest annual Q_{10} value for all years and sites measured ($Q_{10} = 1.5$ vs. an average $Q_{10} = 1.8$ for all other years and sites). Foliar respiration was nonexistent at this time, and the observed progressive decoupling over a 3-week-period suggests that after labile C supply was exhausted, root and rhizosphere respiration was also reduced. Heterotrophic respiration, however, may have increased due to higher soil temperature and moisture conditions (due to reduced transpiration rates), and increased inputs of frass and green leaf fragments to the forest floor during late May and June 2007.

Biometric measurements

Although there were large differences in basal area, canopy cover, and biomass of deciduous vs. coniferous species among stands, NEP values were similar at the Oak/Pine and Pine/Scrub oak stands in 2005. Foliage production was the largest component of aboveground productivity at all stands during all years. First-year mass loss from Pitch pine needles in litterbags (26.7 ± 2.8%) was slightly greater than mass loss rates for Red pine (*Pinus resinosa*) averaged across temperate sites (21 ± 7%) during the LIDET litter decomposition experiment (calculated from Gholz *et al.*, 2000), and similar to that of Longleaf pine (*Pinus palustris*) in North Florida (24 ± 4%; Clark *et al.* in preparation). First-year mass loss from both canopy and understory oaks in the Pine Barrens (mean of 24.8%) was similar to mass loss rates from Turkey oak (*Quercus laevis*) in North Florida (26 ± 4%). Longer-term decomposition, however, was nearly linear are our site, and when these estimates were used to calculate a 5-year running balance for the litter layer, total C accumulation on the forest floor in 2005 represented 90%, 147%, and 95% of C accumulation in wood at the Oak/Pine, Pine/Oak, and Pine/Scrub oak stands, respectively.

Annual NEE estimated from EC measurements were similar to NEP values estimated from biometric measurements at all three stands in 2005. The largest deviation was observed at the Oak/Pine site (8%). However, during 2006 and 2007 when stands were defoliated by Gypsy moth, NEE values differed from NEP estimates substantially. The largest difference was observed at the Oak/Pine site in 2007 (ca. $346\,\mathrm{g\,C\,m^{-2}}$). Although many individuals were severely defoliated, they had the ability to produce a second flush of foliage later in the summer. For example, leaf area of oaks and shrubs had recovered to 70% of values during the previous year by early August at the Pine/Oak site in 2006, and total litterfall in 2006 was 84% of litterfall amounts in previous years at this site. Only slight reductions in total annual litterfall with defoliation are consistent with results in hardwood stands in Pennsylvania, USA, where litterfall totals were nearly unaffected by defoliation (Grace, 1986). The large disparity between NEE and NEP estimates and the second leaf out in consecutive years indicates the capacity of these species to mobilize C from storage pools to support the second leaf flush, presumably in stems and root tissues. The large disparity between NEE and NEP values also illustrates the difficulty in estimating effects of herbivory on C dynamics at the landscape scale using only forest census measurements. However, the relationship between annual NEE and 'biometric' measurements – in this case the amount of frass in litterfall, was strong. For all sites and years, the amount of frass in litterfall was strongly related to $\mathrm{NEE_{yr}}$ [$\mathrm{NEE_{yr}} = -4.36$ (litterfall frass) + 158.02, $n = 9$, $r^2 = 0.859$]. Thus, a relatively simple measurement (litterfall) may help quantify C dynamics in defoliated stands.

Gypsy moth defoliation

Gypsy moth first appeared in forests in New Jersey in 1966. Since then, three major defoliation events have occurred, with peak defoliation in 1972 (103 600 ha), 1981 (323 000 ha), and 1990 (174 400 ha). Spatially extensive defoliation events, such as those experienced in 2006 and 2007 in the Pine Barrens, have the capacity to strongly reduce NEE at the landscape scale.

Although our calculations assume that daytime and nighttime net CO_2 exchange measured at our sites characterize those in upland Oak- and Pine-dominated stands across the landscape, and that defoliation levels recorded by the NJDEP were similar to our sites, they indicate the magnitude of the impact that Gypsy moth defoliation can have on forests in the Pine Barrens. It is notable that remote sensing applications (MODIS) and large-scale simulation models (BiomBGC and PnET CN) may not accurately detect or predict large variations in $\mathrm{NEE_{yr}}$ at the landscape scale, because of the difficulty in quantifying within-season changes in leaf area.

In upland forests in the Pine Barrens, stand composition modulates the type and intensity of disturbance. For example, wildfires rarely crown in Oak-dominated stands, while herbivory of leaf mass can be near-complete, resulting in large losses of C as was observed at the Oak/Pine site in 2007. In contrast, wildfires crown readily in stands dominated by Pitch pine, due in part to 'ladder fuels' produced by epicormic budding (Skowronski *et al.*, 2007). In recent history, the Pine/Scrub Oak stand was affected by a nonstand replacing wildfire in 1995 (ca. 9000 ha). Pine-dominated stands are only partially defoliated by Gypsy moth, but can be defoliated by other herbivores, most notably Pine Looper (*Lambdina pellucidaria*; USDA 1998). Defoliation of the Pine/Scrub oak stand in 1998 strongly reduced woody increment of mature pines (NJFFS 1995, USDA 1998, Skowronski *et al.*, 2007). Extensive Gypsy moth defoliation events have occurred at least two other times at the Oak/Pine stand, and numerous prescribed fires have been conducted at this and the Pine/Oak stand. Thus, transient disturbances such as insect defoliation, prescribed burns, nonstand replacing wildfires, and wind and ice storms are likely major factors controlling NEE at the landscape scale, and when integrated over time, these disturbances may explain much of the patterning of aboveground biomass in upland forests.

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