Contrasting Effects of Invasive Insects and Fire on Ecosystem Water Use Efficiency

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Abstract

We used eddy covariance and meteorological measurements to estimate net ecosystem exchange of CO_2 (NEE), gross ecosystem production (GEP), evapotranspiration (Et), and ecosystem water use efficiency (WUE_e; calculated as GEP/Et during dry canopy conditions) in three upland forests in the New Jersey Pinelands, USA, that were defoliated by gypsy moth (*Lymantria dispar* L.) or burned using prescribed fire. Before disturbance, half-hourly daytime NEE during full sunlight conditions, daily GEP, and daily WUE_e during the summer months were greater at the oak-dominated stand compared to the mixed or pine-dominated stands. Both defoliation by gypsy moth and prescribed burning reduced stand leaf area and nitrogen mass in foliage. During complete defolation in 2007 at the oak stand, NEE during full sunlight conditions and daily GEP during the summer averaged only 14% and 35% of pre-disturbance values. Midday NEE and daily GEP then averaged 58% and 85%, and 71% and 78 % of pre-defoliation values one and two years following complete defoliation, respectively. Prescribed fires conducted in the dormant season at the mixed and pine-dominated stands reduced NEE during full sunlight conditions and daily GEP during the following summer to 57% and 68%, and 79% and 82% of pre-disturbance values, respectively. Daily GEP during the summer was a strong function of N mass in foliage at the oak and mixed stands, but a weaker function N in foliage at the pine-dominated stand. Ecosystem WUE_e during the summer at the oak and mixed stands during defoliation by gypsy moth averaged 1.6 and 1.1 g C kg H_2O^{-1}, representing 60% and 46% of pre-disturbance values. In contrast, prescribed fires at the mixed and pine-dominated stands had little effect on WUE_e. Two years following complete defoliation by gypsy moth, WUE_e during the summer averaged 2.1 g C kg H_2O^{-1}, 80% of pre-disturbance values. WUE_e was correlated with canopy N content only at the oak-dominated stand. Overall, our results indicate that WUE_e during and following non-stand replacing disturbance is dependent on both the type and time since disturbance.

1 Introduction

Understanding the effects of disturbance and recovery on stand productivity and evapotranspiration (Et) is essential for accurate estimates of carbon storage and water yield in forest ecosystems. Successful forest management decisions in the future will need to consider the impacts of invasive insects, fire, windstorms and other perturbations when evaluating trade-offs between maximizing carbon sequestration to mitigate the effects of climate change, while simultaneously providing water for agriculture and municipal needs. A useful metric for characterizing the interactions between CO_2 assimilation and water use by plants is water use efficiency (WUE), defined as the amount of C assimilated per unit of water transpired (Farquhar and Sharkey 1982). At the ecosystem scale, a related metric is ecosystem water use efficiency (WUE_e), which can be calculated from eddy covariance data as gross ecosystem productivity (GEP) per unit Et during dry canopy conditions (Law et al. 2002, Kuglitsch et al. 2008, Jassal et al. 2009).

GEP and Et are reduced immediately following major disturbances in forests, and remain below pre-disturbance levels for some period of time during recovery (Thornton et al. 2002, Clark et al. 2004, Mkhabela et al. 2009, Amiro et al. 2010, Dore et al. 2010, Hicke et al. 2012). Recovery of GEP following disturbance is strongly linked to increases in leaf area and foliar nutrient capital, as well as climatic variation (Amiro et al. 2010, Thornton et al. 2002). In comparison, Et rates typically recover more rapidly following disturbance, in part because of the increased importance of evaporation from litter and soil in disturbed stands (Gholz and Clark 2002, Mkabela et al. 2009, Bierderman et al. 2014). As a consequence, WUE_e may require a number of years to recover to pre-disturbance values following severe disturbances such as clearcut harvesting or severe wildfires (Clark et al. 2004, Makhebela et al. 2009, Dore et al. 2010). Ecosystem respiration (R_{eco}) has been shown to be relatively invariant through time following a wide range of disturbances and intensities (Amiro et al. 2010, Moore et al. 2013, Reed et al. 2014). Thus, large variations in net CO_2 exchange (NEE) can occur during and immediately following disturbance during the recovery process (Amiro et al. 2010). Overall, an important result of these research efforts is that GEP and NEE are typically more sensitive to severe disturbances than Et during the recovery phase in forest ecosystems.

Fewer studies have estimated changes in GEP and Et following non-stand replacing disturbances such as insect defoliation or low intensity fires, limiting our understanding of patterns of forest productivity and water use during recovery. These events can reduce leaf area, alter forest floor mass, and affect the distribution of nutrients, but typically do not significantly reduce overall stand biomass (Lovett et al. 2006, Clark et al., 2010, 2012, 2014). An important question becomes how closely are the recovery of GEP and WUE_e related to leaf area and canopy nutrient status following non-stand replacing disturbances?

In this study, we quantified the effects of insect defoliation and prescribed fire on NEE, R_{eco}, GEP and Et in three upland forests in the Pinelands National Reserve in southern New Jersey, USA, from 2005 to 2009. We used biometric measurements to quantify leaf area index (LAI), biomass accumulation, and canopy and understory N pools in foliage. Eddy covariance and meteorological measurements were used to estimate NEE, R_{eco}, GEP and Et at half-hourly, daily and annual time steps. We then used flux data collected during dry canopy conditions in the summer to calculate WUE_e for pre- and post-disturbance periods. Finally, we evaluated factors contributing to temporal variability in GEP, Et and WUE_e in each stand as they recovered from disturbance. We asked; 1) how do GEP and WUE_e vary among oak and pine-dominated stands growing in the same climate and soil type before disturbance, and 2) how are LAI and canopy N content linked to GEP and WUE_e during recovery from non-stand replacing disturbances (gypsy moth defoliation and prescribed fire) in these stands?

2 Methods

2.1 Research sites

Research sites were located in Burlington and Ocean Counties in the Pinelands National Reserve (PNR) in southern New Jersey, USA. The PNR comprises 445,000 ha of upland and wetland forest, and is the largest continuous forested landscape on the Northeastern Coastal Plain. The climate is cool temperate, with mean monthly temperatures averaging 0.3 and 24.3 ºC in January and July, respectively (1980-2009; State Climatologist of New Jersey). Average annual precipitation is 1159 ± 156 mm (mean ± 1 standard deviation; SD), approximately half of which is estimated to return to the atmosphere as evapotranspiration (Et; Rhodehamel 1979, Dow 2007, Clark et al. 2012). Soils of the Kirkwood and Cohansey formations are sandy, coarse-grained, and have extremely low nutrient status and cation exchange capacity (Tedrow 1986). Although commercial forestry is limited in the PNR, upland forests are characterized by frequent disturbances such as wildfires and prescribed burns (Little and Moore 1949, Forman and Boerner 1981), wind events (Matlack et al. 1993), and insect defoliation events (Clark et al. 2010) , all of which can significantly reduce LAI and affect the distribution of nutrients within stands.

Upland forests comprise 62 % of the forested area in the PNR, and are composed of three major communities; 1) oak-dominated stands, consisting of chestnut oak (*Q. prinus* L.), black oak (*Quercus velutina* Lam.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh.), and scattered pitch pine (*Pinus rigida* Mill.) and shortleaf pine (*P. echinata* Mill.), 2) mixed pine-oak stands, with pitch pine and mixed oaks in the overstory, and 3) pitch pine-dominated stands, with few overstory oaks but abundant scrub oaks (*Q. marlandica* Münchh., *Q. ilicifolia* Wangenh.) in the understory (McCormick and Jones 1973, Lathrop and Kaplan 2004, Skowronski et al. 2007). Ericaceous shrubs occur in the understory in all stands, primarily huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch) and blueberry (*Vaccinium* spp.). Sedges, mosses and lichens also occur in the understory.

2.2 Biometric measurements

Three intermediate age stands were selected for intensive study; an oak-dominated stand at the Silas Little Experimental Forest in Brendan Byrne State Forest, a mixed pine-oak stand on the

Department of Defense McGuire-Dix-Lakehurst Base, and a pine-dominated stand in the New Jersey Division of Fish and Wildlife's Greenwood Wildlife Management Area (Table 1; Skowronski et al. 2007, Clark et al. 2010, 2012), referred to below as the oak, mixed, and pine stands, respectively. Stands were located 17.2 ± 2.8 km apart (mean ±1 SD) in an approximate triangle formation. Stands were selected to represent the dominant age class (75 – 95 years) of the three major upland forest types in the PNR, based on USFS Forest Inventory and Analysis data (www.FIA.gov). We randomly located five circular 201 m^2 forest census plots within 100 m of the eddy covariance tower in each stand (Table 1). Annual measurements of tree diameter at breast height (1.37 m) and tree height were conducted for all stems ≥ 5.0 cm dbh in each plot, and tree biomass was estimated from published allometric relationships (Whittaker & Woodwell 1968, Skowronski et al. 2007). Fine litterfall was collected approx. monthly when present from two 0.42 m^2 wire mesh traps adjacent to each tree census plot, for a total of n = 10 traps in each stand. Litterfall was separated into needles, leaves, stems, reproductive material and frass from trees and shrubs, dried at 70 ºC and then weighed. Ten to 20 clip plots (1.0 m^2) located randomly within 200 m of each tower were harvested during the time of peak biomass in mid-summer every year to estimate the aboveground biomass of understory shrubs and oaks < 2 m tall. Understory vegetation samples were separated into leaves, needles, stems and reproductive material, dried at 70 ºC and then weighed. Specific leaf area (SLA; m^2 g dry $weight^{-1}$) for each major species was measured with a leaf area meter (LI-3000a, LI-COR Inc., Lincoln, Nebraska, USA) and a conveyer belt (LI-3050c, LI-COR Inc.) using fresh leaf, needle or litterfall samples, which were then dried at 70 ºC and weighed. Maximum annual canopy leaf area index (LAI; m^2 m^{-2} ground area) was estimated for each species by multiplying litterfall mass by the appropriate SLA value and then summing results for all species. Projected leaf area of pine needle fascicles was multiplied by π to calculate an all-sided LAI (e.g., Gholz et al. 1994). Understory LAI was estimated by multiplying foliage mass obtained from each clip plot by the corresponding SLA values.

Canopy and understory foliage were sampled for N content at the time of peak leaf area during the summer at each stand throughout the study. The oak stand was completely defoliated by gypsy moth prior to maximum leaf area during the growing season in 2007, therefore foliage was sampled in mid-July following the second leaf flush. Oven-dry samples of live foliage were ground using a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) and digested along with appropriate standards using a modified Kjeldahl method (Allen 1989). An Astoria 2 Analyzer (Astoria-Pacific

International, Clackamas, OR, USA) was used to measure the ammonium concentration of each sample, and results were converted to N concentration in foliage. Nitrogen mass (g N m^{-2} ground area) in canopy and understory foliage was calculated for dominant species by multiplying species-specific N concentrations by corresponding estimates of foliar biomass (e.g., Hoover 2008).

2.3 NEE, GEP, Et, and water use efficiency

Net ecosystem exchange of CO_2 (NEE) and latent heat flux (λE) were measured using eddy covariance systems mounted on towers above the canopy at each stand, and then gap-filled to estimate daily to annual NEE and Et (Falge et al. 2001, Clark et al. 2010, 2012). Ecosystem respiration (R_{eco}) was calculated for each site using continuous half-hourly air (growing season) or soil (dormant season) temperature data and an exponential equation to predict the temperature dependence of respiration developed from nighttime NEE measurements. We summed NEE and R_{eco} at daily and annual time scales to estimate gross ecosystem production, GEP.

$$GEP = NEE + R_{eco} \qquad (1)$$

Ecosystem water use efficiency (WUE_e; g C kg H_2O^{-1}) was defined as the ratio of daily gross ecosystem productivity (GEP) to evapotranspiration (Et) during dry canopy conditions.

$$WUE_e = GEP/Et \qquad (2)$$

Meteorological and eddy flux measurements were made from pairs of overstory (16 or 18.5 m) and understory (3 m) towers in each stand. Shortwave radiation (R_g; LI-200, LI-COR, Inc.), photosynthetically active radiation (PAR; LI-190, LI-COR, Inc.), net radiation (R_{net}; NRLite, Kipp and Zonen, Inc., Delft, the Netherlands), air temperature and relative humidity (HMP45, Vaisala, Inc., Woburn, MA, USA), windspeed and direction (05013-5, R. M. Young Co., Traverse City, MI, USA), and precipitation (TE525, Texas Electronics, Inc., Dallas, TX, USA) were measured at the top of each overstory tower and at 2 m height on each understory tower. 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 towers. Soil temperature (CS-107 or CS-109, Campbell Scientific, Inc., Logan, UT, USA) was measured at 5 cm depth in at least three locations at each stand. Meteorological data were recorded at half-hourly intervals with automated data loggers (CR10x, CR23x and CR1000, Campbell Scientific, Inc.). A complete description of sensor type and location appears in Clark et al. (2012).

Eddy covariance systems were composed of a 3-dimensional sonic anemometer (Windmaster Pro, Gill Instruments Ltd., Lymington, UK, or RM 80001V, R. M. Young, Inc.), a closed-path infrared gas analyzer (LI-7000, LI-COR Inc.), a 5 m long, 0.4 cm ID teflon coated tube and an air pump (UN726-FTP, KNF-Neuberger, Trenton, NJ, USA). 10-hz data were recorded on lap-top computers at each stand. The sonic anemometer was mounted 4 m above the canopy at each stand. The inlet of the air sampling tube was located between the upper and lower sensors of the sonic anemometer, and air was drawn through the LI-7000 at a rate of approx. 8.0 L min^{-1} so that the mean lag time was $\leq$ 2.5 sec. The LI-7000's were calibrated every 2-10 days using CO_2 traceable to primary standards and a sling psychrometer or a LI-610 dew point generator. Net CO_2, H, and λE fluxes were calculated at half-hour intervals using the EdiRe program (Edinburgh, UK). Barometric pressure data (PTB 110, Vaisala, Inc.) was then used to calculate fluxes at ambient atmospheric pressure. The flux associated with the change in storage of CO_2 in the air column beneath the sonic anemometer was estimated using top of tower and 2-m height measurements (LI-840, LI-COR Inc.) or a profile system with inlets at 0.2, 2, 5, 10, 15, and 18.5 m height (oak stand only). Half-hourly NEE was then calculated as the sum of net CO_2 flux (f_{CO2}) and the storage flux for each half hour period. Data were filtered for low turbulence conditions when friction velocity (u*; m s^{-1}) was $<$ 0.2 m s^{-1} (Falge et al. 2001), when precipitation occurred, and for instrument malfunction. All meteorological and eddy flux data are available from the AmeriFlux web site (http://public.ornl.gov/ameriflux; US-slt, US-dix, US-ced).

The three extensive, relatively flat stands had near ideal fetch for above-canopy eddy covariance measurements (Skowronski et al. 2007). Minimum fetch was approximately 1260, 530, and 690 m at the oak, mixed, and pine stands, respectively. We evaluated energy balance closure using the relationship between the sum of H + λE and available energy ($R_{net} - G - \Delta S_{air} - \Delta S_{bio}$) for all half-hourly data collected at each stand using linear regression in SigmaPlot 10 (SYSTAT Software, Inc.) (Clark et al. 2012, Table 2). To estimate NEE for daytime periods when we did not have measurements (due to low windspeed conditions, precipitation, instrument failure, etc.), we fit a parabolic function (growing season) or a linear function (dormant season) to the relationship between PAR and NEE at bi-weekly to monthly intervals (Clark et al. 2004, 2010).

For nighttime periods, we fit an exponential function to the relationship between air temperature (growing season) or soil temperature (dormant season) and NEE. Coefficients for gap filling were calculated from data collected during the appropriate time periods using SigmaPlot regression software. We used ± 1 standard error (SE) of the value of each parameter in the parabolic function for daytime data during the summer, and in the exponential function for all nighttime data to evaluate the sensitivity of annual NEE estimates to modeled values. To estimate λE for periods when we did not have measurements, we fit a linear function to the relationship between available energy and λE at bi-weekly (e.g., May 1- May 14) to bi-monthly (e.g., July 1– August 31) intervals (Clark et al. 2012). We then used modeled half-hourly data to fill in periods when we did not have measured fluxes to calculate daily to annual NEE and Et for each stand.

2.4 Statistical analyses

We focused our analyses of NEE, Et and GEP on the summer months (June 1 to August 31), corresponding to the period when deciduous species were at their peak photosynthetic activity (Renninger et al., 2013). We evaluated patterns of WUE_e during the summers before, during and after each disturbance event. In order to maximize the contribution of transpiration to Et in these calculations, we used data collected when we assumed the canopy was dry, and days with recorded precipitation and the day following each rain event when precipitation ≥ 10 mm were excluded from further analyses. We used ANOVA analyses to test significance levels of the differences in daytime and nighttime NEE among stands before disturbance, and within stands pre- and post-disturbance. Half-hourly NEE values were not independent or normally distributed, thus we randomly sampled $n = 50$ NEE values and then calculated a mean value 100 times for each period (day or night), stand (oak, mixed, pine), and year for ANOVA analyses (SYSTAT 12, SYSTAT Software, Inc.). Daily values of GEP, Et and WUE_e among stands and within stands among years during the summer were compared using repeated-measures ANOVA analyses that permit correlated error structure to account for the lack of independence among variables. Comparisons among stands or years within each stand were made with Tukey´s Honestly Significant Difference (HSD) tests that adjusted significance levels for multiple comparisons. We used non-linear regression analyses to determine the relationship between daily Et and GEP.

Differences in the values of regressions between daily Et and GEP were detected using T-tests and ANCOVA analyses.

3. Results

3.1 Leaf area and nitrogen content of foliage

Maximum LAI during the summer averaged 4.8 to 6.0 at the three stands before disturbance, with overstory species accounting for 89 %, 73 %, and 77 % of total LAI during the summer at the oak, mixed and pine stands, respectively (Fig. 1a). LAI during the winter averaged 0.5 ± 0.5, 0.7 ± 0.4 and 1.4 ± 0.4 at the oak, mixed and pine stands, respectively (data not shown). Nitrogen mass in foliage during the summer before disturbance was greatest at the oak stand and least at the pine stand (Fig. 1b).

At the oak stand, herbivory by gypsy moth during the early summer of 2007 reduced LAI to < 0.5 (see Schäfer et al. 2010). Following the peak of herbivory in June, a second partial leaf-out resulted in a total LAI of only 2.3 (Fig. 1a). Nitrogen mass of canopy and understory foliage following the second leaf out was only ca. 42 % of pre-disturbance levels (Fig. 1b). In 2008, partial defoliation reduced LAI again, although a second leaf out did not occur. Nitrogen mass in foliage was lower in 2008 compared to pre-defoliation periods, because species-weighted foliar N concentration of the canopy was slightly lower (1.7 % N vs. 1.9 % N pre-defoliation), and understory foliage, which composed 1.6 times greater LAI post-defoliation, had an average N concentration of only 1.3 % N (Fig. 1b). By summer 2009, total LAI had nearly recovered to pre-defoliation levels, but the understory comprised 23 % of total LAI, compared to 11 % pre-defoliation. Nitrogen mass of canopy and understory foliage in 2009 was 77 % and 192 % of pre-disturbance values, respectively.

At the mixed stand, the prescribed fire conducted in February 2006 and herbivory by gypsy moth during the summers of 2006 and 2007 reduced LAI of deciduous species during the growing season, but had relatively little effect on pine foliage in the canopy (Fig. 1a). Nitrogen mass in canopy and understory foliage was reduced in 2006, but by 2007 understory N mass had nearly recovered to pre-disturbance levels, while canopy N mass remained relatively low (Fig. 1b).

At the pine stand, partial defoliation of ericaceous shrubs and understory oaks by gypsy moth in 2007 reduced understory LAI and N mass compared to pre-disturbance periods (Fig. 1a,b). The prescribed fire conducted in March 2008 was hot enough to scorch some pine foliage, which reduced overstory LAI during the summer to 74% of pre-disturbance values, and reduced canopy N. The prescribed fire had little effect on understory LAI later in growing season of 2008, because of rapid resprouting of scrub oaks and shrubs. By 2009, leaf area and N mass in foliage at the pine stand had recovered to pre-disturbance levels.

3.2 NEE, GEP, Et and water use efficiency

Daytime NEE during midday, clear sky conditions (≥1500 µmol PAR m^{-2} s^{-1}) and nighttime NEE in the summer were greater at the oak stand than at the mixed and pine stands before disturbance (Fig. 2, Table 3). Mean daily GEP during the summer also was greater at the oak stand than at the mixed and pine stands, while mean daily Et rates during the summer were greater at the oak and pine stands than at the mixed stand (Fig. 3, Table 3). Daily GEP and Et were highly correlated during the summer months at each stand before disturbance, and when data from the mixed and pine stands were pooled, the slope of the relationship between Et and GEP was greater at the oak stand than at the mixed and pine stands (Fig. 4, Table 4; ANCOVA, $F_{1,393} = 157$, $P < 0.001$). Pre-disturbance WUE_e in the summer also was greater at the oak stand than at the mixed and pine stands (Fig. 3c, Table 3).

During complete defoliation by gypsy moth and second leaf-out of the oak stand during the summer in 2007, half-hourly NEE, averaged -2.5 µmol CO_2 m^{-2} s^{-1}, which was only 14% of pre-defoliation rates during midday, and 57 % of pre-defoliation NEE at night (Fig. 2). Mean daily GEP and Et during the summer at the oak stand averaged 3.7 ± 1.7 g C m^{-2} day^{-1} and 2.4 ± 0.9 mm day^{-1} (mean ± 1 SD)which represented 35% and 57% of pre-defoliation values, respectively. The slope of the relationship between Et and GEP was lower during summer 2007 compared to pre-defoliation periods (Fig. 5a, Table 4). Similarly, WUE_e was significantly lower in 2007 compared to pre-defoliation periods, averaging only 1.6 g C kg H_2O day^{-1} (Fig. 3c, Table 3). Partial defoliation of the oak stand occurred in the summer of 2008, and NEE during mid-day periods averaged 58% of pre-defoliation rates. By the next growing season in 2009, mid-day NEE had reached 85% of pre-defoliation rates (Fig. 2). Nighttime NEE during the second year following complete defoliation was greater than pre-defoliation periods, and corresponded with mortality of mature oaks and wet conditions in 2009. It is notable that many of the oaks that died had basdiocarps of honey fungus (*Armillaria* sp.) around their bases in fall 2009. Daily GEP during the summer was 71% and 78% of pre-defoliation levels, and Et had increased to 79% and 92% of pre-defoliation levels in 2008 and 2009, respectively (Fig. 3, Table 3). WUE_e averaged 2.3 g C kg H_2O day^{-1} during the summers of 2008 and 2009, which was 86% of pre-defoliation values.

Following the prescribed burn in early spring of 2006 at the mixed stand, mid-day NEE during the summer during near clear sky conditions was 59 % of pre-disturbance values, and during complete defoliation of deciduous species by gypsy moth in 2007, midday NEE average 6.7 μmol CO_2 m^{-2} s^{-1}, which was only 43% of pre-disturbance values (Fig. 2, Table 3). Nighttime NEE during the summer was nearly unaffected by either disturbance. Daily GEP was 79% of pre-disturbance values during the summer following the prescribed fire in 2006, and only 28% of pre-disturbance values during and following defoliation of deciduous species by gypsy moth in 2007. Summer daily Et was 73% and 69% of pre-disturbance values in 2006 and 2007, respectively (Fig. 3b, Table 3). Slopes for the relationship between GEP and Et were similar pre- and post-prescribed burn, but the intercept for this relationship was lower during defoliation by gypsy moth in 2007 compared to pre-defoliation periods (Fig. 5). Similarly, WUE_e at the mixed stand was similar pre- and post-prescribed burn, but significantly lower during defoliation in 2007, averaging only 1.1 g C kg H_2O day^{-1} (Fig. 3c, Table 3).

At the pine stand, midday NEE during clear sky conditions in the summer was 79% of pre-disturbance values during defoliation of the understory by gypsy moth in 2007. During the first growing season following the prescribed burn conducted in March 2008, midday NEE averaged -9.5μmol CO_2 m^{-2} s^{-1}, which was 69 % of pre-disturbance values (Fig. 2). By the next growing season following the prescribed burn, mid-day NEE had recovered to pre-disturbance values (Fig. 2, Table 3). Nighttime NEE at the pine stand was apparently unaffected by either disturbance. Summer daily GEP averaged 84% of pre-disturbance values during defoliation of deciduous species by gypsy moth in 2007, and 82% following the prescribed burn in 2008 (Fig. 3a, Table 3). Post-disturbance, daily GEP in 2009 averaged 9.6 ± 2.6 g C m^{-2} day^{-1}, representing 109% of pre-disturbance values. Summer daily Et averaged 85%, 83% and 99% of pre-disturbance levels in 2007, 2008 and 2009, respectively (Fig. 3b, Table 3). The relationship between daily Et and GEP was similar pre- and post-disturbance (Fig. 5c, Table 4), and WUE_e

was unaffected by defoliation of deciduous species in the understory or the prescribed burn when compared to pre-disturbance values (Fig. 3, Table 3).

The relationship between annual maximum N mass in foliage and mean daily GEP during the summer months was significant at the oak stand, accounting for 84% of the variability in GEP during the summer (Table 5). When data for the oak and mixed stands were pooled, maximum N mass in foliage accounted for 79% of the variability in mean daily GEP during the summer. In contrast, only 46% of the variability in mean daily GEP during the summer was accounted for by annual maximum N in foliage at the pine stand (Table 5). Daily Et during the summer was significantly correlated with maximum annual LAI at the oak stand, and at the mixed and pine stands when data were pooled (see also Clark et al. 2012). The relationship between maximum N mass in foliage and mean daily WUE_e was nearly significant at the oak stand, and at the oak and mixed stand when data were pooled (Table 5).

Annual estimates of NEE, R_{eco}, GEP and Et for the three upland forest stands are shown in Table 6. Over all years measured, the oak and mixed stands were only weak sinks for CO_2. Variation in NEE was greatest at the oak stand, ranging from a sink averaging approx. -170 g C m^{-2} yr^{-1} before defoliation to a source of 248 g C m^{-2} yr^{-1} during the year of complete defoliation by gypsy moth in 2007. The pine-dominated stand was a moderate sink for CO_2, but when consumption estimated from pre- and post-burn samples of the understory and forest floor (approx. 441 g C m^{-2}) was incorporated into the longer term C balance, the estimated average C sink strength was only -30 g C m^{-2} yr^{-1}. Variation in annual R_{eco} was relatively low at the mixed and pine stands, but the range in annual values was 550 g m^{-2} yr^{-1} at the oak dominated stand, representing a coefficient of variation of 44% of mean annual R_{eco}. The greatest reduction in GEP occurred during the year of complete defoliation at the oak stand, and both defoliation and prescribed burns reduced annual GEP and Et at the mixed and pine stands (Table 6). The greatest reduction in annual Et occurred at the mixed stand, where both disturbances had occurred sequentially.

4 DISCUSSION

Gypsy moth are now ubiquitous in forests of the Mid-Atlantic region. Approximately 24% of forests in the region are classified as highly susceptible to gypsy moth, and 7% are classified as extremely susceptible (Leibhold et al. 2003, www.fia.gov). In New Jersey, 36% and 15% of forests are classified as highly and extremely susceptible to gypsy moth defoliation, respectively. Although recent surveys indicate that gypsy moth populations have largely crashed since 2009 in the Mid-Atlantic region, populations can exhibit cyclical dynamics, with 4-5 year and 8-10 year cycles co-occurring (Allstadt et al. 2013). During the peak of the last outbreak, approximately 20% of upland forests were defoliated in the PNR in 2007 (http://www.state.nj.us/agriculture /divisions/pi /pdf/07defoliationtable.pdf). In many oak-dominated stands, LAI and N in foliage during the early summer were reduced to levels characterizing the dormant season. In pine-dominated stands, defoliation of pines by gypsy moth was typically minor, but foliage of sub-canopy oaks and shrubs in the understory was susceptible to defoliation. When defoliation is severe and occurs over multiple years, such as in oak-dominated and mixed stands in the PNR from 2006-2008, invasive insects can have major, and likely long term, impacts on canopy N pools. In addition to the immediate reduction in leaf area and canopy N in defoliated stands, a second mechanism leading to the reduction of N in foliage in oak stands was selective herbivory and subsequent mortality of black oak, which initially had the highest mean foliar N content (approximately 2.1 % N) in our study. By 2009, many of the mature black oaks had either died or had moderate to severe crown damage, which reduced their leaf area. In contrast, chestnut oak, which had a lower N content in foliage (approximately 1.8 % N), had relatively low mortality and less canopy damage, and accounted for a greater amount of canopy leaf area following defoliation. A third factor contributing to the overall reduction of the foliar N pool is the response of the understory to gap formation caused by overstory defoliation and subsequent mortality. Understory LAI had increased two-fold over pre-defoliation periods by 2008, and this pattern has persisted through 2013, six years following complete defoliation of the oak stand. This has led to a much larger contribution of understory foliage to stand LAI, however, shrub foliage had consistently lower N content than canopy oaks and therefore did not completely replace the N lost from the canopy. Overall, changes in canopy composition and increased LAI in the understory resulted in lower N content in foliage in severely defoliated stands.

Lovett et al. (2002, 2006) have shown that defoliation by invasive insects can cause large N transfers within the forest, but indicated that overall leaching losses are relatively minor. Our results suggest that recovery from internal transfers of N attributed to defoliation by gypsy moth may require a number of years, because of the time required to restore canopy foliar nutrient pools. As the defoliation in our oak study area has caused mortality somewhat selectively by species, we expect long-term shifts in species composition, and resultant changes to N mass in canopy foliage. This finding is consistent with results published by Medvigy et al. (2012), who used the ED2 model to explore the interactive effects of herbivory and drought on long term carbon dynamics and found reduced GEP and forest productivity over time following intensive, repeated defoliation events (Medvigy et al. 2012). Lack of recovery of foliar N pools in the canopy may also predispose stands to be more sensitive to other stresses. For example, daytime NEE at the oak stand was apparently more sensitive to summer drought that occurred in 2010 compared to pre-disturbance periods, and further mortality of overstory oaks occurred (Renninger et al. 2014b).

The effects of prescribed burning on LAI and canopy N content at the mixed and pine stands were relatively less intense than defoliation at the oak and mixed stands. Pitch and shortleaf pines have epicormic meristems that can sprout rapidly following disturbance, thus overstory needle recovery can occur rapidly. Although many aboveground stems of shrubs and understory oaks were killed during the burns, they can readily resprout from belowground stems following fire and their leaf area recovered quickly (Clark et al. 2014). Prescribed burning also apparently had little effect on WUE_e. A potential explanation for this observation is also related to stand nutrient dynamics, because it is likely that the burn pyro-mineralized stored nutrients such as phosphorus and calcium in the forest floor, and these became available to canopy and understory vegetation following the prescribed fire (Gray and Dighton 2006, 2009).

Variation in foliar N mass and LAI were major biotic factors affecting GEP and Et during our study. N mass in foliage was significantly correlated with summer daily GEP at the oak and mixed stands, both of which had a significant component of deciduous species (Skowronski et al. 2007, Clark et al. 2010). On an annual basis, however, GEP was greatest at the pine stand, which had the longest leaf area display when integrated throughout the year and the highest GEP during spring and summer; the relationship between canopy N content and daily GEP during the summer was weaker at this stand. Clark et al. (2012) reported that LAI was strongly related to daily Et during the summer at all three stands. Interestingly, mean daily WUE_e during the summer was only weakly correlated with foliar N content or LAI at the oak or mixed stands, although this relationship may become significant using a longer term data set.

Before each disturbance, daily NEE, GEP and WUE_e during the summer were greater at the oak stand than at the mixed or pine-dominated stands. Previously reported summer NEE light response curves support this result (Clark et al. 2010), as do leaf-level measurements of oak vs. pine foliage (Schäfer 2011, Renninger et al. 2013, 2014a). Pre-disturbance daily GEP rates during the summer at the three stands in the PNR were intermediate between published rates of undisturbed forest in more southerly sites on the Atlantic coastal plain (ca. 8 – 13 g C m^{-2} day^{-1}; Clark et al. 1999, 2004, Stoy et al. 2006, Normets et al. 2010) and stands further to the north (ca. 4 - 10 g C-2 day^{-1}; Mkhebela et al. 2009, Brümmer et al. 2012). Pre-disturbance mean daily Et at the oak and pine-dominated stands stand during the summer (4.2 ± 1.5 mm and 3.9 ± 1.3 day^{-1}) were within the range of values reported from other temperate broad-leaved and conifer-dominated forests (reviewed in Clark et al. 2012).

Highly significant relationships between GEP and Et have been noted at a wide range of time scales (e.g., daily to annual) in many forests. For example, Law et al. (2002) reported a significant relationship between monthly Et (expressed as Et/precipitation) and GEP for a wide range of Ameriflux sites, and Brümmer et al. (2012) reported significant relationships between Et and GEP across a range of forests in Canada. Pre-disturbance WUE_e values for stands in the Pinelands were at the low end of values reported from temperate hardwood forests, rather they were more similar to closed-canopy conifer dominated and boreal forests (Law et al. 2002, Kuglitsch et al. 2008, Brümmer et al. 2012). For example, Law et al. (2002) reported values of up to 6 g C kg^{-1} H_2O for monthly WUE_e in temperate hardwood forests, while closed canopy stands in Boreal forest and conifer-dominated stands had WUE_e values ranging from 2.0 to 3.6 g C kg^{-1} H_2O (Mkhebela et al. 2009, Brümmer et al. 2012, Vickers et al. 2012). On the Atlantic coastal plain, WUE_e of a rotation age slash pine (*Pinus elliottii* Engelm.) plantation on sandy soils in N. Florida averaged 2.7 g C kg^{-1} H_2O (reanalyzed data from Clark et al. 2004).

Defoliation by Gypsy moth reduced both daytime and nighttime NEE at the oak and mixed stands compared to pre-disturbance periods. Clark et al. (2010) showed that the relationship between air or soil temperature and half-hourly nighttime NEE during defoliation in the summer during 2007 was significantly different and that mean nighttime NEE was lower when compared to undisturbed periods, despite the fact that soil temperatures were ca. 2 °C higher, while air temperature was similar to pre-disturbance periods. As a result, annual R_{eco} was lower in 2007 and 2008 compared to pre-disturbance years. Following this period of reduced nighttime NEE, higher rates at nighttime half-hourly and annual time scales corresponded with tree mortality and wet conditions in 2009 (Renninger et al. 2014b). Annual GEP at the oak stand had approached pre-disturbance values by 2009, but relatively high R_{eco} lagged complete defoliation by two years, and resulted in very low annual NEE in 2009. When integrated over 2007-2013, however, annual R_{eco} averaged 1394 ± 274 (mean ± 1 SD) g C m^{-2} yr^{-1} at the oak stand, thus the long-term average following defoliation was more similar to pre-disturbance values, which averaged 1340 g C m^{-2} yr^{-1}. The relatively high variability in nighttime NEE and annual R_{eco} contrasts somewhat with results reported from other disturbed forests on the Atlantic coastal plain (e.g., Amiro et al 2010). For example, following clearcutting of a slash pine plantation in N. Florida, variation in R_{eco} was only 304 g C m^{-2} yr^{-1} pre- and post-harvest, representing a coefficient of variation of 14 % of mean annual values, despite major changes in biomass and detrital pools on the forest floor and soil disturbance associated with site preparation (Clark et al. 2004, Binford et al. 2006).

Defoliation by Gypsy moth reduced GEP and WUE_e at the oak and mixed stands, but WUE_e values were not as low as those reported following clearcutting or severe wildfires in other forest ecosystems (Clark et al. 2004, Mkhebela et al. 2009, Dore et al. 2010). For example, following clearcutting of the slash pine plantation noted above, GEP was initially minimal and recovered relatively slowly, while Et was similar to pre-harvest rates because of partial flooding of the stand (Gholz and Clark 2002, Clark et al. 2004). WUE_e averaged 0.7 g C kg H_2O^{-1} during the first year following harvest, and had increased to 1.7 g C kg H_2O^{-1} during the second year, compared to a pre-harvest value of 2.7 g C kg H_2O^{-1}. In a ponderosa pine (*P. ponderosa* P. & C. Lawson) stand that had burned 10 years previously in a severe wildfire, GEP was only 43% of values at an undisturbed ponderosa pine stand, while Et had recovered to a greater extent, averaging 2.0 mm day^{-1} compared to 2.4 mm day^{-1} at the undisturbed stand during the summer (Dore et al. 2010). Monthly WUE_e during the summer averaged ca. 1.2 g C kg H_2O^{-1} at the stand that had been burned severely, and 1.7 g C kg H_2O^{-1} at the undisturbed stand over the two years measured. Mkhabela et al. (2009) summarized the effects of harvesting and wildfires in boreal forest in Canada using a chronosequence approach, and reported that recovery of GEP was slower than Et. Two to three years following harvest of a jack pine (*Pinus banksiana* Lamb.) stand, WUE_e averaged only 0.6 g C kg H_2O^{-1}, and they estimated that recovery to pre-disturbance values would not occur until ca. 15 years following harvest. Similarly, WUE_e averaged 1.4 g C kg H_2O^{-}

^{1} six to seven years following a severe wildfire, compared to 2.2 g C kg H_2O^{-1} in an undisturbed stand. Overall, our results suggest that WUE_e in forests following non-stand replacing disturbance is dependent on the type of disturbance and the impact on N status of canopy and understory foliage, in addition to time since disturbance. Defoliation by gypsy moth had a stronger effect on WUE_e, with consistently lower daily values occurring during the summer of the year when defoliation occurred at the oak and mixed stands, while WUE_e was largely unaffected by prescribed burning at the mixed and pine stands.

Using the relationships between λE and available energy (R_{net} – G – storage terms) for non-defoliated periods in Clark et al. (2012) and continuous meteorological data for 2005-2009, we estimated that annual Et in the absence of gypsy moth or fire would have averaged 661 ± 32 and 757 ± 6 mm yr^{-1} at the oak and pine stands, respectively. When compared to Et measured at each site, 5-year averages differed by only 47 and 59 mm at the oak and pine stands, respectively, representing a 9% decrease in Et. Assuming an average precipitation depth of 1159 mm yr^{-1} across all upland forests, we estimated that ground water recharge was approximately 9% and 15% higher during and following disturbance at each stand (Schäfer et al. 2013). Similarly, using relationships between PAR and daytime NEE, and between air or soil temperature and nighttime NEE of undisturbed years, we estimated that annual NEE at the oak stand in the absence of gypsy moth defoliation potentially averaged -191 ± 40 g C m^{-2} yr^{-1} from 2005-2009, and that potential R_{eco} and GEP averaged 1276 ± 76 and 1467 ± 67 g C m^{-2} yr^{-1} over the same period, respectively. In contrast, our measured average annual NEE was only 17% of the potential value that would have occurred in the absence of gypsy moth at the oak stand for 2005-2009. Annual NEE measured at the oak stand in 2010, 2011, 2012, and 2013 was -15, -49, -84, and -59 g C m^{-2} yr^{-1}, indicating that recovery from complete defoliation takes at least six years. Potential and estimated annual GEP differed by an average of 186 g C m^{-2} yr^{-1} at the oak stand. R_{eco} estimated for the oak stand over 2005-2009 was only 28 g C m^{-2} yr^{-1} less than potential values, supporting the observation that R_{eco} is largely invariant with disturbance over longer time scales (e.g., Amiro et al. 2010). At the pine stand, we estimated that annual NEE in the absence of Gypsy moth defoliation and prescribed burning potentially averaged -142 ± 40 g C m^{-2} yr^{-1} from 2005-2009, and that potential R_{eco} and GEP were 1437 ± 39 and 1579 ± 65 g C m^{-2} yr^{-1}, respectively. Measured average annual NEEwas 76 % of the potential value that would have occurred in the absence of disturbance, but when consumption losses due to the prescribed burn are included, annual NEE was only 14 % of the potential value at the pine stand for 2005-2009. Similarly, potential and estimated annual GEP differed by an average of only 19 g C m^{-2} yr^{-1} at the pine stand. Although these calculations assume that λE, NEE and GEP measured at our sites during pre-disturbance periods characterize potential rates during later years in the absence of disturbance, they illustrate the magnitude of the impact that gypsy moth defoliation and prescribed burning can have on stand carbon dynamics, while having relatively little effect on Et and ground water recharge (Schäfer et al. 2013).

Our results illustrate two important points; forest C dynamics and especially NEE are apparently much more sensitive to non-stand replacing disturbances than Et, and disturbances that result in large N transfers within stands may have long-term impacts on rates of GEP and NEE at half-hourly to annual time scales. When evaluating tradeoffs between hydrologic resources and forest carbon dynamics, forest managers may incorrectly assume that disturbance that results in minimal impact on hydrological cycling (such as estimated from USGS weir data) would also result in minimal impact on carbon sequestration rates, when in fact the size of the carbon sink may actually be quite small. It is also clear that if climate change results in a greater likelihood of insect invasions, fire or other perturbations, and we consider temporal variation in canopy N status and WUE_e with disturbance, our ability to predict interactions between carbon and hydrologic cycles in the future will improve.

5 CONCLUSIONS

Eddy covariance and biometric measurements made in three stands in the Pinelands National Reserve in southern New Jersey, USA, were used to estimate the effects of defoliation by gypsy moth and prescribed burning on net ecosystem exchange of CO_2 (NEE), gross ecosystem production (GEP), evapotranspiration (Et) and ecosystem water use efficiency (WUE_e). Pre-disturbance half-hourly NEE at full sunlight conditions (> 1500 μmol PPFD m^{-2} s^{-1}) and during the nighttime in the summer months, and GEP and WUE_e during the summer were greater at the oak-dominated stand compared to the mixed and pine-dominated stands. Defoliation by gypsy moth reduced leaf area (LAI) and nitrogen content in foliage, resulting in decreased NEE, GEP and Et at the oak-dominated and mixed stands during the summer months. WUE_e was reduced to 60% and 46% of pre-disturbance values at the oak-dominated and mixed stands during defoliation, Two years following complete defoliation at the oak stand, WUE$_e$ during the summer was 80% of pre-defoliation values. LAI and foliar N mass were also reduced by dormant season prescribed burning at the mixed and pine-dominated stands during the next growing season. Midday NEE and daily GEP during the summer months following prescribed burning at the mixed and pine stands averaged 57% and 68%, and 79% and 82% of pre-disturbance values, respectively. In contrast to gypsy moth defoliation at the oak and mixed stands, prescribed burning at the mixed and pine-dominated stands had no significant effect on WUE$_e$. Long-term NEE was reduced at the oak-dominated stand, likely due to reduced N mass in canopy foliage, as well as slightly increased R$_{eco}$ following mortality of approximately 20 % of mature oak trees. LAI, N in foliage, NEE, GEP and Et had all recovered to pre-disturbance levels during the next growing season following the prescribed burn at the pine-dominated stand. Overall, our results suggest that WUE$_e$ in forests during and following non-stand replacing disturbance is dependent on the type of disturbance and the impact on N status of canopy and understory foliage, in addition to time since disturbance.

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Table 1. Forest structure at the oak, mixed, and pine stands at the beginning of the study in 2005. Overstory data are from five 201 m^2 plots measured in 2005, understory biomass is from 10 to 20 1.0 m^2 clip plots, and forest floor mass (Oi layer) is from ten 1.0 m^2 plots in the vicinity of the tower at each site. Values are means ± 1 standard error.

Variable	Oak	Mixed	Pine
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
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})			
Oaks	20 ± 15	217 ± 71	70 ± 23
Ericaceae	168 ± 38	112 ± 32	322 ± 27
Total	189 ± 35	529 ± 150	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

Table 2. Energy balance closure for the oak, mixed and pine stands for all half-hourly data collected from 2005 to 2009. Half-hourly flux data were fit to the equation R_{net} – G – storage terms = α (H + λE) + β. Data were filtered for u* values < 0.2 m^{-2}, precipitation, and instrument malfunction. Values are means ± 1 Standard error, and all correlations are significant at $P < 0.001$. Energy balance closure for each stand by year is in Clark et al. (2012).

Stand	α	β	r^2	n
Oak	0.96 ± 0.01	14.53 ± 0.27	0.86	44,941
Mixed	0.99 ± 0.01	8.88 ± 0.26	0.92	21,682
Pine	0.96 ± 0.01	8.39 ± 0.26	0.90	44,912

Table 3. Statistics for ANOVA and contrasts for half-hourly daytime and nighttime net CO_2 exchange during the summer (June 1- August 31; Fig. 2), and daily evapotranspiration, gross ecosystem production, and ecosystem water use efficiency during the summer among stands before disturbance, and within stands among years (Fig. 3). df = degrees of freedom, F = the value of the F statistic, and P is the significance level for ANOVA analyses. Contrasts for all stands before disturbance are; a. oak vs. mixed and pine, b. mixed vs. pine, c. oak and pine vs. mixed, d. oak vs. pine. Oak stand contrasts are; e. complete defoliation vs. pre- and post-defoliation, f. pre-defoliation vs. post-defoliation. Mixed stand contrasts are; g. pre-disturbance vs. disturbance, h. prescribed burn vs. defoliation. Pine stand contrasts are; i. pre- and post-disturbance vs. disturbance, j. defoliation vs. prescribed burn. Tukey's Honestly Significant Difference (HSD) tests were used to determine significance levels of each contrast, and P is the significance level for each contrast.

Variable/stand	df	F	P	Contrast	HSD	P
Daytime NEE_c (μmol CO_2 m^{-2} s^{-1} at $\geq$ 1500 μmol PAR m^{-2} s^{-1}); Fig. 2.						
All stands	2; 297	977	< 0.001	a, b	0.25	< 0.01, < 0.01
Oak	3; 396	10,957	< 0.001	e, f	0.28	< 0.01, < 0.01
Mixed	2; 297	6,520	< 0.001	g, h	0.24	< 0.01, < 0.01
Pine	3; 396	4,793	< 0.001	i, j	0.19	< 0.01, < 0.01
Nighttime NEE_c (μmol CO_2 m^{-2} s^{-1}); Fig. 2.						
All stands	2; 297	324	< 0.001	a, b	0.15	< 0.01, <0.01
Oak	3; 396	1,330	< 0.001	e, f	0.22	< 0.01, < 0.01
Mixed	2; 297	128	< 0.001	g, h	0.10	< 0.01, < 0.01
Pine	3; 396	519	< 0.001	i, j	0.15	< 0.01, < 0.01
Gross ecosystem production (g C m^{-2} day^{-1}); Fig. 3a						
All stands	2; 427	53	< 0.001	a, b	0.86	< 0.01, < 0.01
Oak	3; 456	212	< 0.001	e, f	0.94	< 0.01, < 0.01
Mixed	2; 273	233	< 0.001	g, h	0.79	< 0.01, < 0.01
Pine	3; 426	29	< 0.001	i, j	0.91, 0.75	< 0.01, < 0.05
Evapotranspiration (mm day^{-1}); Fig. 3b.						
All stands	2; 427	14	< 0.001	c, d	0.43	< 0.05, ns

Oak	3; 456	43	< 0.001	e, f	0.56	< 0.01, ns
Mixed	2; 273	30	< 0.001	g, h	0.42	< 0.01, < 0.01
Pine	3; 367	6	< 0.01	i, j	0.56	< 0.01, < 0.01
Ecosystem water use efficiency (g C kg H_2O^{-1} day^{-1}); Fig. 3c.						
All stands	2; 285	14	< 0.001	a, b	0.23	< 0.01, ns
Oak	3; 291	52	< 0.001	e, f	0.31	< 0.01, < 0.01
Mixed	2;156	103	< 0.001	g, h	0.31	ns, < 0.01
Pine	3; 281	3	< 0.05	i, j	0.24	ns, < 0.05

Table 4. Parameter values and statistics for the relationship between daily evapotranspiration and gross ecosystem productivity from June 1 to August 31 for the oak vs. mixed and pine stands in 2005 before disturbance (Figure 4), the oak stand from 2005-2009 (Figure 5a), the mixed stand from 2005-2007 (Figure 5b), and the pine stand from 2005-2009 (Figure 5c). Data were fit to GEP = α (1 – exp (– β (Et))). Parameter values are means ± 1 standard error, r^2 is the value of the Pearson's product moment coefficient, F is the value of the F statistic, and P is the significance level of the ANOVA analyses for each model.

Stand/period	α	β	r^2	F	P
Oak vs. mixed and pine stands (shown in Fig. 4)					
Oak	15.54 ± 0.70	0.34 ± 0.03	0.79	335	<0.0001
Mixed, pine	14.29 ± 0.74	0.25 ± 0.02	0.83	722	<0.0001
Oak (shown in Fig. 5a)					
Pre-defoliation	15.97 ± 0.69	0.29 ± 0.03	0.72	476	<0.0001
Defoliation 2007	12.93 ± 6.30	0.15 ± 0.09	0.51	96	<0.0001
Defoliation 2008	10.33 ± 0.56	0.43 ± 0.05	0.47	81	<0.0001
Post-defoliation	11.44 ± 0.53	0.37 ± 0.04	0.74	264	<0.0001
Mixed (shown in Fig. 5b)					
Pre-disturbance	11.75 ± 0.60	0.36 ± 0.04	0.81	378	<0.0001
Prescribed fire	9.64 ± 0.12	2.40 ± 0.31	0.63	158	<0.0001
Defoliation	-0.32 ± 0.46	1.07 ± 0.19	0.25	32	<0.001
Pine (shown in Fig. 5c)					
Pre-disturbance	13.42 ± 0.53	0.28 ± 0.02	0.81	671	<0.0001
Partial defoliation	9.70 ± 0.53	0.50 ± 0.05	0.83	436	<0.0001
Prescribed fire	9.59 ± 0.36	0.49 ± 0.05	0.70	208	<0.0001
Post-disturbance	13.57 ± 0.50	0.37 ± 0.06	0.85	530	<0.0001

Table 5. Parameters and statistics for the relationship between maximum canopy and understory N content and mean daily gross ecosystem productivity, and between maximum LAI and mean daily Et during the summer from June 1 to August 31. Data were fit to GEP = α (canopy N) + β. Parameter values are means ± 1 standard error, r^2 is the value of the Pearson's product moment coefficient, F is the value of the F statistic, and P is the significance level of the ANOVA analyses for each model. Values are for the oak stand from 2005-2009, the mixed stand from 2005-2007, and the pine stand from 2005-2009.

Stand	α	β	r^2	F	P
Nitrogen in foliage (g N m^{-2}) and daily gross ecosystem production (g C m^{-2} day^{-1})					
Oak	1.50 ± 0.32	0.58 ± 1.71	0.84	22.6	< 0.05
Oak, mixed	1.64 ± 0.32	-0.49 ± 1.58	0.79	27.0	< 0.01
Pine	1.22 ± 0.58	3.49 ± 2.38	0.46	4.4	ns
Leaf area index (m^2 m^{-2}) and evapotranspiration (mm day^{-1})					
Oak	0.72 ± 0.15	0.84 ± 0.62	0.81	18.6	< 0.05
Mixed, pine	0.62 ± 0.12	0.20 ± 0.58	0.80	29.8	< 0.01
Pine	0.43 ± 0.20	1.31 ± 1.06	0.46	4.4	ns
Nitrogen in foliage (g N m^{-2}) and ecosystem water use efficiency (g C m^{-2} kg H_2O day^{-1})					
Oak	0.26 ± 0.09	0.93 ± 0.50	0.63	7.8	< 0.07
Oak, mixed	0.26 ± 0.11	0.92 ± 0.58	0.33	4.5	< 0.08

Table 6. Annual net CO_2 exchange (NEE), ecosystem respiration (R_{eco}), gross ecosystem production (GEP, g C m^{-2} yr^{-1}), evapotranspiration (Et, mm $year^{-1}$), and the ratio of GEP to ET for the oak, mixed, and pine stands. Percent filtered half hourly NEE data for each year used to calculate annual NEE, R_{eco} and GEP are shown in the first column. Values in parentheses for NEE are maximum deviations from annual values as a result of gap filling using ± 1 standard error of daytime or nighttime parameters.

Stand, Period	Percent NEE data	NEE	R_{eco} (g C m^{-2} yr^{-1})	GEP	Et (mm yr^{-1})	GEP/Et
Oak						
2005	49	-185 (21)	1285	1470	616	2.39
2006	52	-140 (23)	1395	1535	677	2.27
2007, defoliated	54	246 (11)	972	726	442	1.64
2008, defoliated	56	-77 (18)	1066	1143	637	1.79
2009	55	-9 (25)	1523	1532	699	2.19
Mean ± 1 SD		-33±169	1248±228	1281±350	614±102	
Mixed						
2005	35	-99 (17)	1068	1167	607	1.92
2006, burned	42	37 (14)	1111	1073	452	2.37
2007, defoliated	45	20 (20)	1012	992	419	2.37
Mean ± 1 SD		-14±74	1064± 50	1077± 88	493±100	
Pine						
2005	38	-178 (24)	1445	1623	761	2.13
2006	47	-165 (17)	1477	1642	757	2.17
2007, defoliated	58	-40 (7)	1362	1402	593	2.36
2008, burned	60	-48 (26)	1329	1377	617	2.23
2009	55	-158 (18)	1597	1755	764	2.30
Mean ± 1 SD		-118±68	1442±105	1560±164	699±86	

NEE_c for 2005 to 2007 have been previously reported in Clark et al. 2010, and Et values have been previously reported in Clark et al. 2012.

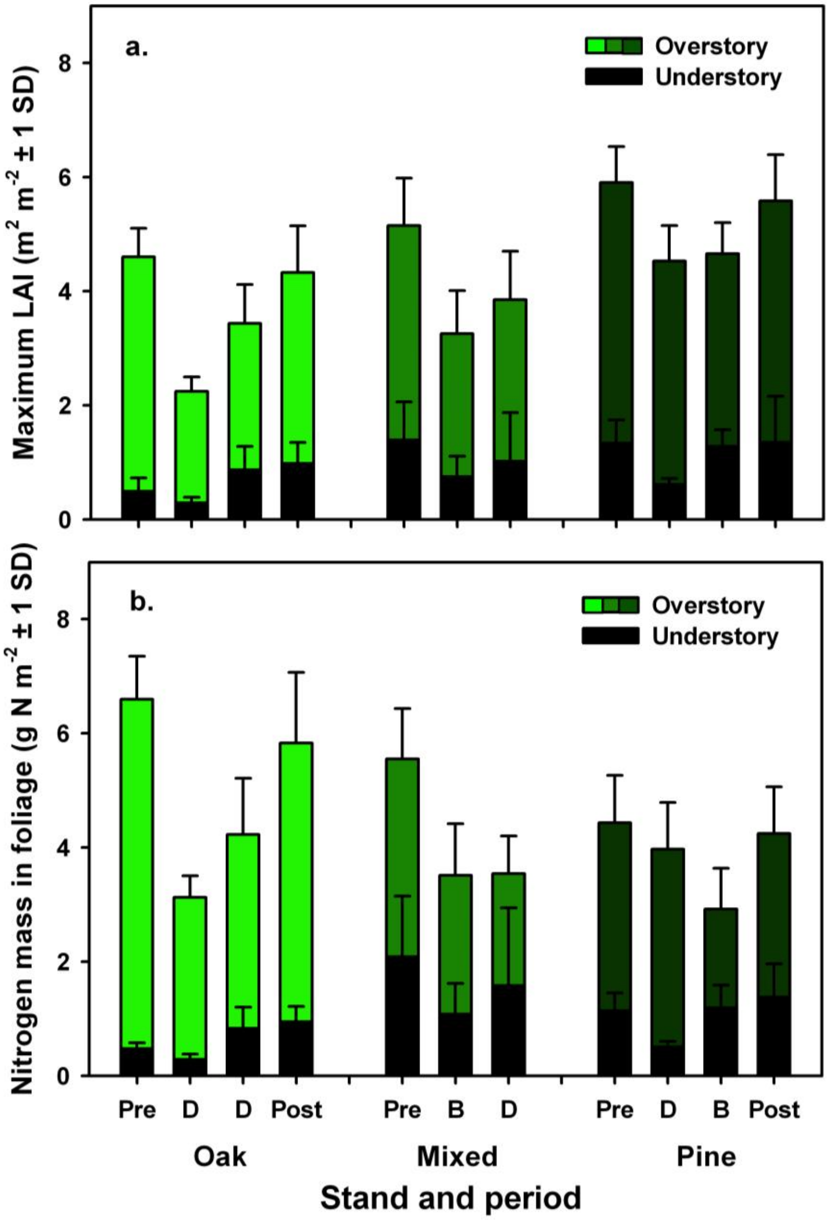

Figure 1. a) Maximum leaf area index (LAI; m^2 m^{-2} ground area ± 1 standard deviation) and b) maximum nitrogen content in foliage (g N m^{-2} ground area ± 1 standard deviation) during the summer at the oak, mixed, and pine stands from 2004 to 2009. Data are shown for understory, overstory and total LAI and N content. Pre = pre-disturbance, D = defoliation by Gypsy moth, B = burned in prescribed fire, Post = post-disturbance. Pre-disturbance at the oak stand was 2004-2006, complete defoliation by gypsy moth occurred in 2007, partial defoliation by gypsy moth

occurred in 2008, and post-disturbance was 2009. Pre-disturbance at the mixed stand was 2005, a prescribed fire was conducted on Feb 9, 2006, and defoliation of deciduous species by gypsy moth occurred in 2007. Pre-disturbance at the pine stand was 2005-2006, defoliation of primarily understory vegetation by gypsy moth occurred in 2007, a prescribed fire was conducted on March 23, 2008, and post-disturbance was 2009.

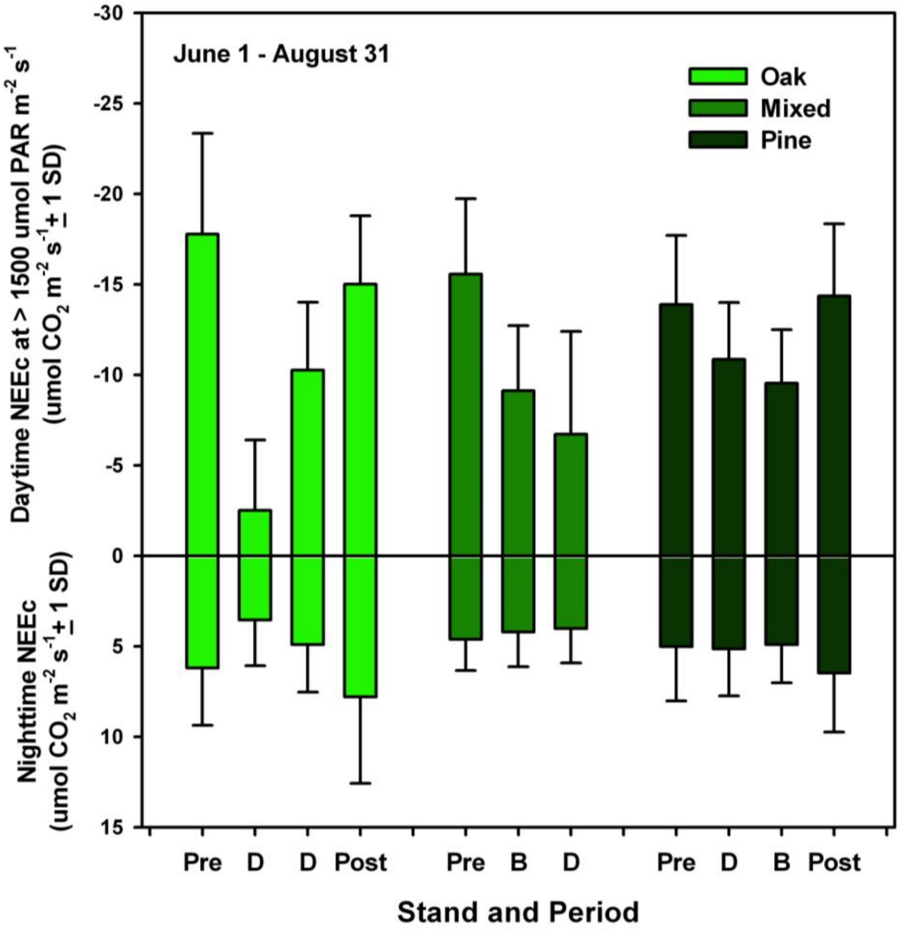

Figure 2. Daytime net CO$_2$ exchange (µmol CO$_2$ m^{-2} s^{-1}) at ≥ 1500 µmol PAR m^{-2} s^{-1} and mean nighttime net CO$_2$ exchange during the summer (June 1 – August 31) from 2005 to 2009 at the oak, mixed and pine stands. Pre = pre-disturbance, D = defoliation by gypsy moth, B = burned in prescribed fire, Post = post-disturbance. Statistics are in Table 3.

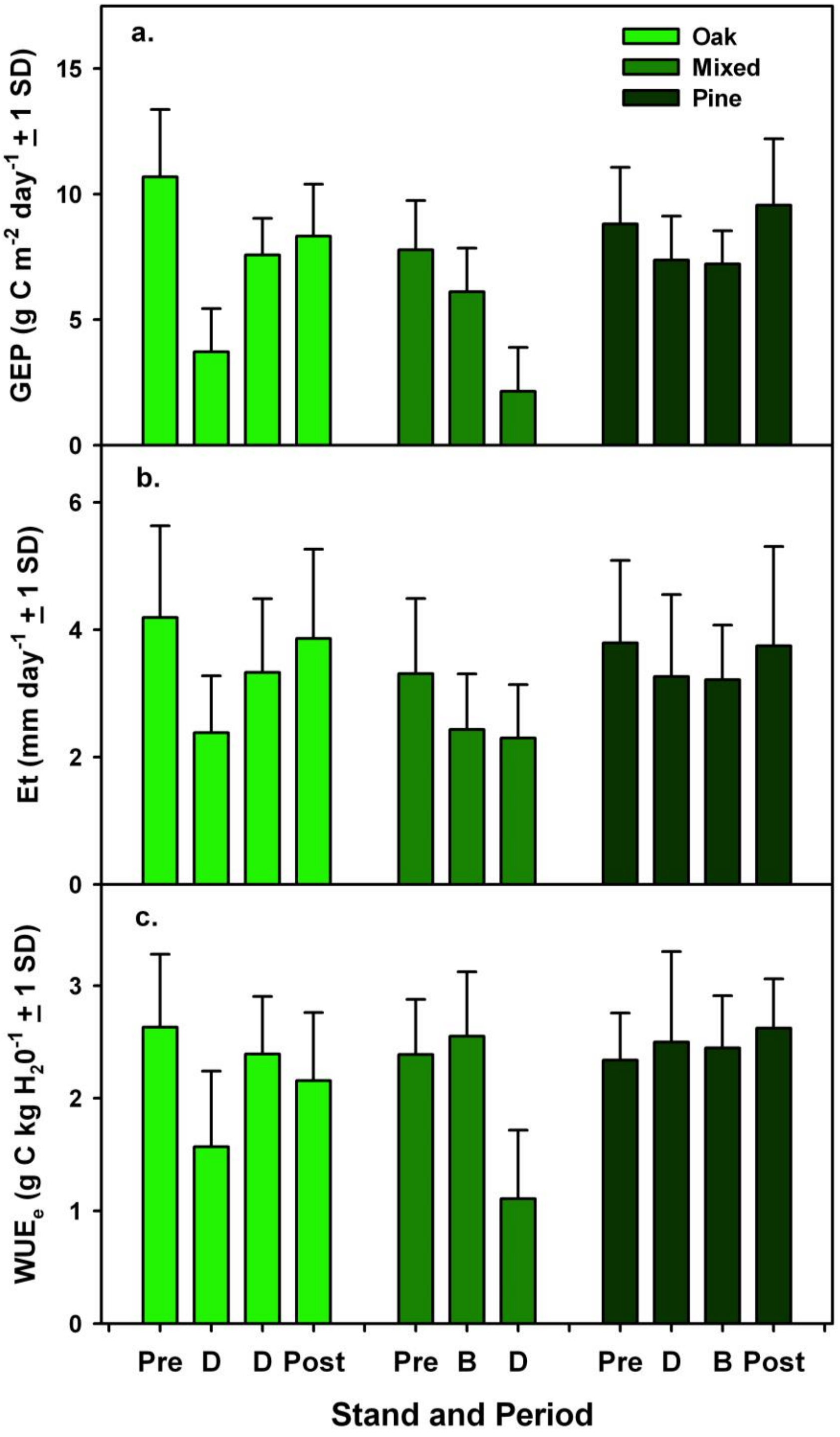

Figure 3. (a) Gross ecosystem productivity (GEP, g C m^{-2} day^{-1}), (b) daily evapotranspiration (Et, mm day^{-1}), and (c) ecosystem water use efficiency (WUE$_e$, g C mm Et day^{-1}) calculated for the oak stand from 2005-2009, the mixed stand from 2005-2007, and the pine stand from 2005-

2009 during the summer. WUE_e was calculated from the ratio of GEP to Et for dry canopy conditions. Pre = pre-disturbance, D = defoliation by Gypsy moth, B = burned in prescribed fire, Post = post-disturbance. Statistics are in Table 3.

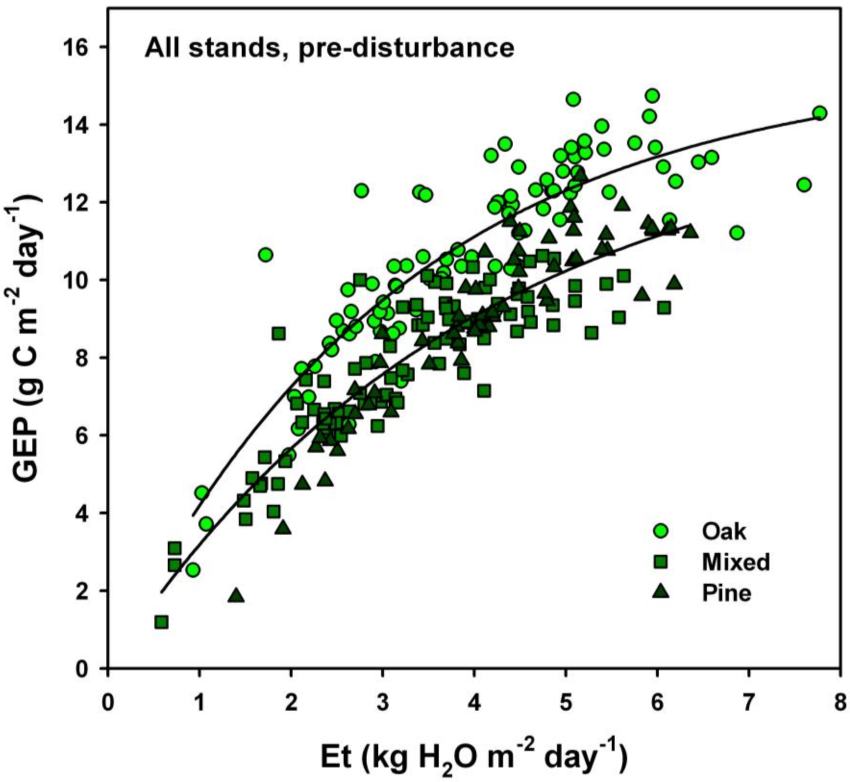

Figure 4. The relationship between daily evapotranspiration (Et, mm day^{-1}) and daily gross ecosystem production (GEP, g C m^{-2} day^{-1}) for the oak, mixed and pine stands from June 1 to August 31, 2005, before disturbance. Statistics are in Table 4.

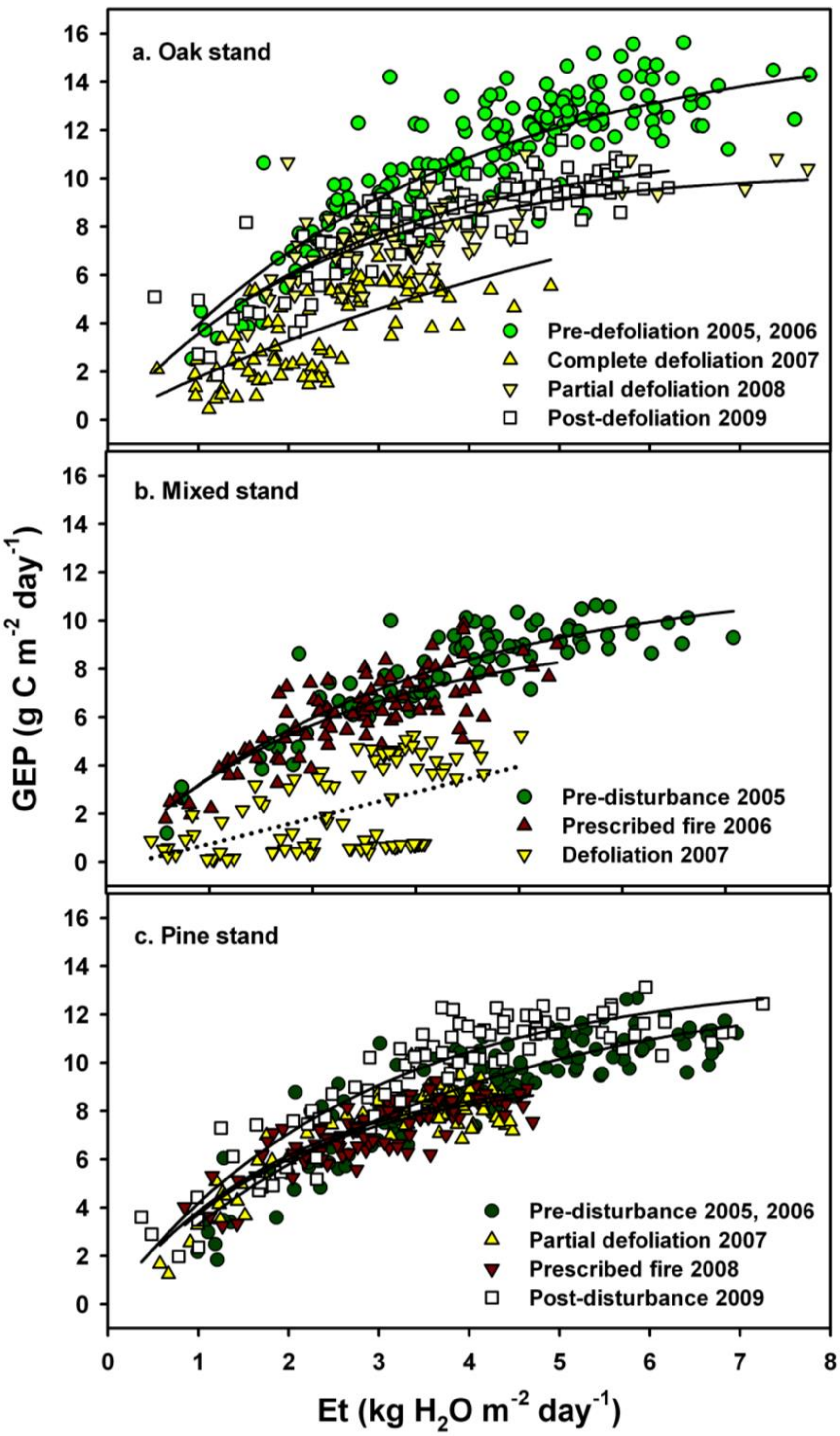

Figure 5. The relationship between daily evapotranspiration (Et, mm day^{-1}) and daily gross ecosystem production (GEP, g C m^{-2} day^{-1}) for the (a) oak stand from June 1 to August 31 for

005-2009, the (b) mixed stand from June 1 to August 31 for 2005-2007, and the (c) pine stand from June 1 to August 31 for 2005-2009. Statistics are in Table 4.