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Effects of invasive insects and fire on forest energy exchange and evapotranspiration in the New Jersey pinelands

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ABSTRACT

We used eddy covariance and meteorological measurements to quantify energy exchange and evapotranspiration (Et) in three representative upland forest stands in the New Jersey Pinelands that were either defoliated by gypsy moth (*Lymantria dispar* L.) or burned in prescribed fires during the study period. Latent (λE) and sensible heat (H) fluxes were linear functions of available energy, and seasonality had a major effect on the partitioning of available energy into λE and H at each stand. Both defoliation and prescribed fire reduced leaf area, altered the partitioning of available energy, and reduced λE flux compared to undisturbed periods. Summer daily Et averaged 4.2 ± 1.5, 3.3 ± 1.2 and 3.9 ± 1.3 mm day^{-1} at the oak-, mixed, and pine-dominated stands during undisturbed periods, but only 2.4 ± 0.9 mm day^{-1} during defoliation at the oak stand in 2007, and 2.4 ± 0.9 and 3.2 ± 0.9 mm day^{-1} following spring fires at the mixed and pine-dominated stands, respectively. For all years measured, seasonal maximum leaf area index (LAI) explained 82% of the variability in daily Et during the summer at the oak stand, and 80% of the variability at the mixed and pine-dominated stands. Annual Et averaged 614, 493, and 683 mm yr^{-1} at the oak, mixed, and pine stands, respectively. When averaged across all stands and years, annual Et was 606 mm yr^{-1}, ca. 53.6% of incident precipitation, and similar to long-term averages reported in other studies in the Pinelands. Gypsy moth defoliation potentially reduced Et by ca. 31 mm yr^{-1} across all upland forests in 2007, resulting in a 7.3% increase in groundwater recharge. Our research indicates that non-stand replacing disturbances can have significant effects on energy partitioning, and can reduce Et at the stand and landscape scales.

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1. Introduction

The canopy is the primary interface for land–atmosphere exchanges of energy and water vapor in forest ecosystems. Disturbance can have significant impacts on energy partitioning and evapotranspiration (Et), because it typically alters canopy structure, leaf area, and the forest floor. Studies of clearcutting and forest removal on paired watersheds have demonstrated that removal of >20% of stand basal area results in higher streamflow from the disturbed watershed, because of lower transpiration and interception loss (Hornbeck et al., 1993; Jones and Post, 2004; Swank et al., 2001; Vose et al., 2011). Streamflow from the disturbed watershed then becomes a curvilinear function of further reductions in stand basal area, and is influenced by both forest composition and climate (Jones and Post, 2004). Reduction in streamflow in the disturbed watershed typically tracks the recovery of leaf area, and in general pre-disturbance levels are achieved when canopy closure occurs.

Results from a number of studies using eddy covariance to estimate energy exchange and Et are generally consistent with paired watershed studies, and have demonstrated that disturbances that significantly affect canopy structure and leaf area index (LAI) alter energy partitioning and reduce Et. For example, Amiro et al. (2006b) summarized the effects of intense wildfires on energy exchanges across a wide range of Boreal forests, and reported that Et was reduced during the first several years following disturbance. In their synthesis, latent heat flux averaged 20% of available energy in the youngest stands, and then increased to levels characterizing pre-disturbance levels (40–60% of available energy) in older stands following disturbance. However, a number of research efforts also have indicated that major disturbances have only moderate impacts on Et at hourly to annual time scales, while others studies have reported non-intuitive results following disturbance. When data from Amiro et al. (2006a) are compared within a single forest type, younger, recovering jack pine (*Pinus banksiana* Lamb.)

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stands that had been recently burned or harvested had nearly equal or greater daily Et compared to an older jack pine stand (Amiro et al., 2006a). Even when a stand-replacing wildfire resulted in a different cover type, Et rates were little changed from pre-disturbance levels. Dore et al. (2010) reported that ten years following an intense wildfire which converted a Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stand to a grass- and shrub-dominated ecosystem, LAI and overall energy exchanges were reduced significantly, while maximum daily Et was 2.0 mm day^{-1} compared to 2.4 mm day^{-1} in an undisturbed pine stand. In their study, annual Et was only 18% less at the grass and shrub-dominated site compared to the undisturbed pine stand. In an extreme example, eddy covariance and biometric measurements along a harvest chronosequence of slash pine (*Pinus elliottii* var. *elliottii* Engelm.) stands in N. Florida indicated that although clearcutting reduced LAI to near zero, flooding of the stand resulted in Et rates that averaged 3.6 mm day^{-1}, similar to rates characterizing pre-harvest periods (Gholz and Clark, 2002). Annual Et at their clearcut site during the first and second years following harvest was similar to that measured at a mid-rotation age stand, and averaged only 12% less than that measured at the rotation age stand before harvest, suggesting an overall decoupling of Et from forest structure and LAI during recovery. Contrary to their initial hypothesis regarding the effects of harvesting on energy partitioning and reduced Et, they concluded that Et does not change much over the landscape dominated by managed pine forests in relation to clearcutting and regeneration, but rather is likely to be altered only by severe drought (Gholz and Clark, 2002).

Taken together, the results of the eddy covariance studies suggest that major disturbances may have only a moderate, and in some cases, minimal effects on Et at hourly to annual time scales, and that recovery of Et to pre-disturbance levels occurs rapidly following disturbance. These results support the hypothesis that Et rates are highly conservative, much like the effects of drought on Et rates observed in some forests (e.g. Oishi et al., 2010). A potential confounding factor in some of the eddy covariance studies is that a "space for time" substitution employing different stands was used to infer changes in energy exchanges and Et because of major disturbances (e.g. Amiro et al., 2006a, b; Dore et al., 2010). The sometimes contrasting results among studies make it difficult to accurately predict the effects of non stand-replacing disturbances on energy exchange and Et in forest ecosystems.

In this study, we measured forest energy exchange and Et at half-hourly to annual time scales using meteorological and eddy covariance systems in three representative upland forests of similar intermediate age but contrasting species composition in the Pinelands National Reserve of southern New Jersey from 2005 to 2009. While development and commercial forestry are limited in the Pinelands, these forests are characterized by frequent non stand-replacing disturbances such as wildfires and prescribed burns (Clark et al., 2009; Little and Moore, 1949), insect defoliation events (Clark et al., 2010) and wind events (Matlack et al., 1993), all of which can impact LAI without significantly altering overall stand biomass. Following 1–2 years of energy exchange and Et measurements during undisturbed periods, all three stands were defoliated by gypsy moth (*Lymantria dispar* L.) during the summer to varying degrees, and prescribed fires were conducted during the spring in two of the stands. Measurements were then continued at two of the stands until LAI had nearly recovered to pre-disturbance levels. We asked (1) how does energy exchange and Et in oak- vs. pine-dominated stands growing in the same climate and soil type differ, and (2) how do non-stand replacing disturbances (gypsy moth defoliation and prescribed fire) affect energy exchange and Et at half-hourly to annual time scales?

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 SE.

Attribute	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
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})			
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

2. Methods

2.1. Study sites

Study sites were located in the Pinelands National Reserve in Burlington and Ocean Counties in southern New Jersey. The Pinelands is the largest continuous forested landscape on the Northeastern coastal plain, and covers ca. 23% of New Jersey. The climate is cool temperate, with mean monthly temperatures of 0.3 and 24.3 °C in January and July, respectively (1980–2009; NJ State Climatologist). Mean annual precipitation is 1159 ± 156 mm (mean ± 1 SD). The terrain consists of plains, low-angle slopes and wetlands, with a maximum elevation of 62.5 m. Soils are derived from the Cohansey and Kirkwood Formations, and are coarse-textured, sandy, acidic, and have extremely low cation exchange capacity and nutrient status (Tedrow, 1986).

Upland forests comprise 62% of forested lands in the Pinelands, and are dominated by three major communities; 1) oak-dominated stands, consisting of black oak (*Quercus velutina* Lam.), chestnut oak (*Q. prinus* L.), white oak (*Q. alba* L.), pitch pine (*Pinus rigida* Mill.) and shortleaf pine (*P. echinata* Mill.), (2) mixed stands, with pitch pine and mixed oaks in the overstory, and (3) pitch pine-dominated stands, consisting of pitch pine with few overstory oaks and abundant scrub oaks (*Q. marilandica* Muenchh., *Q. ilicifolia* Wangenh.) in the understory (Lathrop and Kaplan, 2004; McCormick and Jones, 1973; Skowronski et al., 2007). All upland forests have moderate to dense shrub cover in the understory, primarily *Vaccinium* spp., *Galussacia* spp., *Kalmia* spp. and *Quercus* spp., with sedges, mosses and lichens also present. Despite the widespread occurrence of sandy, well-drained, nutrient-poor soils, upland forests in the Pinelands are moderately productive (Clark et al., 2010; Pan et al., 2006). We selected three intermediate-aged upland forest stands for intensive study; an oak-dominated stand at the Silas Little Experimental Forest, a mixed stand at Fort Dix Army Base, and a pine-dominated stand in the Greenwood Wildlife Management Area (Table 1; Clark et al., 2010; Skowronski et al., 2007), hereafter oak, mixed, and pine stands, respectively. Stands were selected to represent the major upland forest types, and the dominant age class

(75–95 years) across this landscape, based on USFS Forest Inventory and Analysis data (http://www.FIA.gov).

2.2. Biometric measurements

Five 201 m^2 forest census plots were located randomly within 100 m of the eddy covariance tower in each stand (Table 1). Measurements of tree species, diameter at breast height (1.37 m) and height in each plot were conducted annually. Tree biomass was estimated from published allometric relationships (Whittaker and Woodwell, 1968). Fine litterfall was collected ca. monthly (bi-weekly for frass) from two 0.42 m^2 wire mesh traps adjacent to each tree census plot at each stand (n = 10 traps per stand). Samples were separated into leaves, needles, stems and reproductive material of trees, and shrubs, sedges, herbs and frass, dried at 60 °C, and weighed. Annual aboveground biomass 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 (Table 1). Specific leaf area was measured for each species with a portable leaf area meter (LI-3000a, Li-Cor Inc., Lincoln, NE, USA) and a conveyer belt (LI-3050c, Li-Cor Inc.) using fresh leaf or litter samples which were then dried and weighed. We multiplied foliar biomass values (understory oaks and shrubs) or litterfall mass values (overstory oaks and pines) by the appropriate specific leaf area to estimate LAI. Projected leaf area of pine needle fascicles was multiplied by π to calculate all-sided LAI (e.g. Gholz et al., 1994).

2.3. Meteorological and eddy covariance measurements

The energy balance of a forest can be expressed as:

$$R_{net} = \lambda E + H + G + \Delta S_{air} + \Delta S_{bio} + Q \quad (1)$$

where R_{net} is net radiation flux density, λE is latent heat flux density, H is sensible heat flux density, G is heat flux density into the soil surface, ΔS_{air} is change in heat storage in the air space between the net radiometer and the soil surface, ΔS_{bio} is the change in heat storage in the above-ground biomass, and Q represents other sources and sinks for energy, all expressed in units of W m^{-2} (Leuning et al., 2012; Wilson et al., 2002). In our study, R_{net}, λE, and H were measured, G was estimated from measurements of soil temperature and heat flux density, ΔS_{air} and ΔS_{bio} were estimated from measurements of air temperature, humidity and aboveground biomass, and the Q term was assumed to be negligible. Eq. (1) was rearranged to calculate available energy (A; W m^{-2}) as:

$$A = R_{net} - G - \Delta S_{air} - \Delta S_{bio} \quad (2)$$

Meteorological measurements were made from overstory (17 or 20 m) and understory (3 m) towers in each stand (Table 2). Incoming shortwave radiation (R_g; LI-200, 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 the understory towers (Table 2). We used a second radiometer (CNR1, Kipp and Zonen, Inc.) at the top of the tower at the oak and mixed stands to measure upward and downward, short- and longwave radiation, and to estimate albedo values. Soil temperature was measured at 5 cm depth using three temperature probes buried within 10 m of the towers at each site (CS-107, Campbell Scientific, Inc., Logan, UT, USA). Soil heat flux was measured using three heat flux transducers (G; HFT-3.1, Radiation and Energy Balance Systems, Inc., Seattle, WA, USA) buried at 10 cm depth within 10 m of each overstory tower. Meteorological data were recorded with automated data loggers (CR10x, CR23x and CR1000, Campbell Scientific, Inc.).

Soil heat storage was calculated as:

$$G = G_{10\ cm} + C_{soil}\Delta T_{soil} \quad (3)$$

where $G_{10\,cm}$ is soil heat flux measured at 10 cm depth, C_{soil} is the heat capacity of the soil at 0–10 cm depth, and ΔT_{soil} is the half-hourly change in soil temperature measured half-way between the surface and the soil heat flux plates (5 cm). Soil heat capacity was calculated as:

$$C_{soil} = \rho_{soil}C_{dry} + \theta_{vol}C_{soil\ water} \quad (4)$$

where ρ_{soil} is the measured density of soil (1.3 kg m^{-2} to a depth of 10 cm), C_{dry} is the specific heat of dry, sandy soil (830 J kg^{-1} K^{-1}), θ_{vol} is the volumetric soil water content, and $C_{soil\ water}$ is the specific heat of soil water (4190 J kg^{-1} K^{-1}). We had only continuous measurements of θ_{vol} using water content reflectometers (CS-615, Campbell Scientific, Inc.) at the oak stand, but did have continuous litter layer moisture estimates (CS-505, Campbell Scientific, Inc.) at all three stands, and used the relationship between these two sets of sensors to estimate continuous soil moisture at each stand. Heat storage in the air column between the net radiometer and the soil surface was calculated as:

$$\Delta S_{air} = \rho_{air}C_{air}z_{R_{net}}\Delta T_{air} \quad (5)$$

where ρ_{air} is the density of air estimated from air pressure and temperature measurements, C_{air} is the specific heat of dry air (1010 J kg K^{-1}), $z_{R_{net}}$ is the height of the air column between the net radiometer and the soil surface (Table 2), and ΔT_{air} is the half-hourly change in air temperature, estimated using a weighted average of half-hourly air temperature measurements made near the top of the tower and at 2 m height (Table 2). We assumed that air temperature measurements at 2 m height characterized the first 4 m of the reference air column, and measurements made at near the top of the tower characterized the remaining space in the air column below the net radiometer, although these were nearly identical during most midday periods. Heat storage in biomass was calculated from measured biomass values in Table 1, a specific heat of biomass of 3340 J kg^{-1} K^{-1}. We lacked continuous data on bole temperature, thus we assumed that biomass temperature was coupled to weighed mean half-hourly air temperature in the air column between the net radiometer and the soil surface. We recognize that this simplification led to a slight overestimation of heat storage in biomass during the morning hours.

Eddy covariance systems were located on each overstory tower, and 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, and a lap-top PC (Clark et al., 2010; Gholz and Clark, 2002; Table 2). The sonic anemometer was mounted 4 m above the maximum canopy height of trees near the tower at each site. The inlet of the air sampling tube was located mid-way between the upper and lower sensor arrays of the sonic anemometer. Air was drawn through the tube connected to the LI-7000 at a rate of ca. 8.0 L min^{-1}. The mean lag time from the tube inlet on the tower to the LI-7000 was $\leq$ 2 sec. at each site, minimizing the loss of high-frequency fluctuations in water vapor concentrations. The LI-7000s were calibrated every 2–7 days using a sling psychrometer or a LI-610 dew point generator. Net sensible and latent heat exchanges were calculated at half-hourly intervals using the EdiRe program (Edinburgh, UK). Barometric pressure data (PTB 100A Pressure transmitter, Vaisala, Inc.) was then used to calculate fluxes at ambient atmospheric pressure. Data were filtered for low turbulence conditions when friction velocity (u^*; m s^{-1}) was <0.2 m s^{-1}, for half-hourly periods when

Table 2
Details of sensor descriptions and measurement heights for the oak, mixed and pine stands.

Tower/variable	Instrument	Measurement height (m)		
		Oak	Mixed	Pine
Overstory towers				
Solar radiation (R_g; W m^{-2})	LI-190	18.0	15.0	14.5
Net radiation (R_{net}; W m^{-2})	NR Lite	18.5	15.5	15.0
Albedo	CNR-1	18.5	15.5	–
PAR (PAR; μmol m^{-2} s^{-1})	LI-200	18.0	15.0	14.5
Air temperature/RH (°C, %)	HMP-53c	17.5	15.0	14.5
Windspeed/direction (m s^{-1}, deg)	RM 05013	18.0	15.0	14.5
U, v, w, sonic temperature (cm s^{-1}, °C)	RM 81000,	18.5	–	15.0
	WindMaster Pro	–	15.5	–
Water vapor (mmol mol^{-1})	LI-7000	18.5	15.5	15.0
Understory towers				
Solar radiation ($R_{g\,und}$; W m^{-2})	LI-190	2.0	2.0	2.0
Net radiation ($R_{net\,und}$; W m^{-2})	NR Lite	2.0	2.0	2.0
PAR (PAR_{und}; μmol m^{-2} s^{-1})	LI-200	2.0, 1.0	2.0	2.0
Air temperature/RH (° C, %)	HMP-53c	2.0	2.0	2.0
Soil				
Soil temperature (T_{soil}; °C)	CS-107	0.05	0.05	0.05
Soil heat flux ($G_{10\,cm}$; W m^{-2})	HFT-3.1	0.10	0.10	0.10

Barometric pressure was logged at 2 m height on the understory tower at the oak stand only.

precipitation occurred, and for instrument malfunction (Falge et al., 2001).

Energy balance closure for each stand and year was evaluated for all u^* filtered values using linear regression coefficients (slope and intercept) from least squares regression between the half-hourly estimates of $\lambda E + H$ against A (Leuning et al., 2012; Wilson et al., 2002). Ideal energy balance closure is defined as a slope of 1 and an intercept of zero. Computations were conducted using SigmaPlot Version 10.0 (SYSTAT Software, Inc., San Jose, CA, USA), and slopes and intercepts were reported as means ± 1 SE. To estimate λE and H for periods when we did not have measurements (because of low windspeed conditions, precipitation, instrument failure, etc.), linear regressions were calculated for the relationship between A and λE or H at two-week to three-month intervals using SigmaPlot. We then used modeled half-hourly data to fill in periods when we did not have measured fluxes to calculate daily to annual Et for each site. Gap-filling was evaluated by calculating how ±1 SE of the slope and intercept values for each stand and year affected Et during the summer months.

For the analyses presented here, "growing season" was defined as May 15 to October 31, corresponding approximately with leaf expansion and senescence of deciduous oaks and shrubs, and "dormant season" as November 1 to May 14. "Summer months" were defined as June, July and August, and "winter months" as November, December and January. We compared data collected during the summer of pre-disturbance periods among stands, and within stands pre-, during, and post-disturbance. To further illustrate the effects of non-stand replacing disturbance on energy partitioning and Et, we focused on data collected at the oak stand between June 1 and July 14 from all years, because this period represented the peak of Gypsy moth defoliation in 2007, and on data collected at the pine stand during the mid-summer (July 1 to August 31) for all years, because this period corresponds to the display of two annual cohorts of pitch pine foliage. To test significance levels of the contrasts of daily Et rates among stands and within stands among years during the summer, we used repeated measures ANOVA analyses that permit correlated error structure to account for the lack of independence among variables (SYSTAT 12, SYSTAT Software, Inc.). Comparisons among stands or years were made with Tukey's Honestly Significant difference tests that adjusted P values for multiple comparisons.

3. Results

3.1. Leaf area

Maximum LAI averaged 4.8–6.0 at the three stands before disturbance (Fig. 1). Overstory species accounted for 89%, 73%, and 77% of total LAI during the growing season at the oak, mixed, and pine stands, respectively. LAI during the dormant season averaged 0.5 ± 0.6, 0.7 ± 0.4 and 1.4 ± 0.4 (mean ± 1 SE) at the oak, mixed and pine stands. At the oak stand, herbivory by gypsy moth reduced total LAI to a minimum of <0.5 during the early summer of 2007. Following the peak of herbivory in mid-June, a second, partial leaf-out occurred and resulted in a total LAI of only 2.3 (Fig. 1). In 2008, partial defoliation reduced canopy LAI again, although a second leaf out did not occur. By the summer of 2009, total LAI had nearly recovered to pre-defoliation levels, however, the understory comprised ca. twice (23% vs. 11%) as much of total LAI compared to pre-defoliation periods. At the mixed stand, the prescribed fire conducted in February 2006 and herbivory by gypsy moth in 2006 and 2007 reduced LAI of deciduous species during the early growing season, but had little effect on pine LAI (Fig. 1). At the pine stand, partial defoliation of ericaceous shrubs and oaks reduced total LAI in 2007 (Fig. 1). The prescribed fire conducted at the pine stand in March 2008 had little effect on understory LAI during the following growing season, because of rapid resprouting of shrubs and oaks. However, the prescribed fire was hot enough to scorch and kill some pine foliage, which reduced overstory LAI during the summer months to 74% of pre-disturbance values. By 2009, leaf area at the pine stand had recovered to pre-disturbance levels.

3.2. Available energy, albedo and intercepted photosynthetically active radiation

Complete defoliation by Gypsy moth at the oak stand in 2007 resulted in slightly decreased R_{net} and A relative to R_g during midday (10:00–14:00) in the summer (Table 3). By summer 2009, the relationships between R_g and R_{net}, and between R_g and A during midday were similar to pre-defoliation years. Defoliation of the oak stand reduced albedo when data from pre- and post-defoliation periods during the summer were compared (df = 358, t = 14.79, P < 0.001). Pre-defoliation, interception of photosynthetically active

Table 3
Midday solar radiation (R_g; W m^{-2}), net radiation (R_{net}; W m^{-2}), albedo, available energy (A; $R_{net}-\Delta S_{air}-\Delta S_{bio}-G$; W m^{-2}), photosynthetically active radiation above the canopy (PAR; μmol PAR m^{-2} s^{-1}), photosynthetically active radiation under the canopy at 2 m height (PAR_{und}; μmol PAR m^{-2} s^{-1}), and the ratio of percent absorption of PAR by the canopy during the summer at the oak, mixed, and pine stands. Values are means ± 1 SD of half-hourly values measured between 10:00 and 14:00 from June 1 to August 31, 2005 to 2009.

Stand/year	R_g	R_{net}	Albedo	A	PAR	PAR_{und}	PAR_{und}/PAR
Oak							
2005–2006	617 ± 224	474 ± 189	0.15 ± 0.01	440 ± 176	1253 ± 442	265 ± 110	0.21
2007, defoliated	592 ± 245	436 ± 194	0.13 ± 0.01	391 ± 180	1224 ± 496	431 ± 279	0.35
2008, defoliated	649 ± 194	505 ± 163	0.13 ± 0.01	460 ± 149	1365 ± 404	210 ± 87	0.15
2009	579 ± 251	446 ± 205	0.12 ± 0.01	412 ± 188	1214 ± 512	124 ± 71	0.10
Mixed							
2005	630 ± 227	484 ± 186	0.10 ± 0.01	456 ± 176	1247 ± 476	786 ± 411	0.63
2006, burn, defol.	585 ± 240	436 ± 202	0.10 ± 0.01	395 ± 190	1227 ± 497	936 ± 516	0.76
2007, defoliated	623 ± 255	460 ± 206	0.10 ± 0.01	428 ± 189	1323 ± 528	976 ± 526	0.74
Pine							
2005–2006	576 ± 219	469 ± 196	–	449 ± 191	1198 ± 469	–	–
2007, defoliated	564 ± 239	463 ± 213	–	437 ± 209	1200 ± 508	659 ± 483	0.55
2008, burned	602 ± 188	513 ± 174	–	469 ± 170	1255 ± 391	688 ± 446	0.55
2009	568 ± 254	459 ± 220	–	425 ± 204	1183 ± 529	544 ± 411	0.46

radiation (PAR) by the canopy at the oak stand during midday periods in the summer averaged ca. 79% of incident PAR (Table 3). In comparison, canopy interception of midday PAR averaged 65% in the summer of 2007, and only 22% during the peak of defoliation in mid-June 2007 (data not shown). Interception of PAR midday at the oak stands then increased to 85% and 89% of incident PAR in 2008 and 2009, respectively, as foliage density increased in the subcanopy following mortality of some stems in the upper canopy. At the mixed stand, the prescribed burn conducted in February 2006 and then defoliation in 2006 and 2007 resulted in a slight decrease in R_{net} and A relative to R_g in the summer, but had only a minor effect on albedo (Table 3). Defoliation in 2006 and 2007 reduced the interception of PAR by the canopy at the mixed stand. At the pine stand, defoliation of the understory by Gypsy moth in 2007 and the prescribed burn in 2008 had little effect on the relationship between R_g and R_{net} or between R_g and A. Following the prescribed fire in March 2008, canopy interception of PAR was 45% of incident PAR, and then increased to 54% with recovery of canopy LAI in 2009 (Table 3).

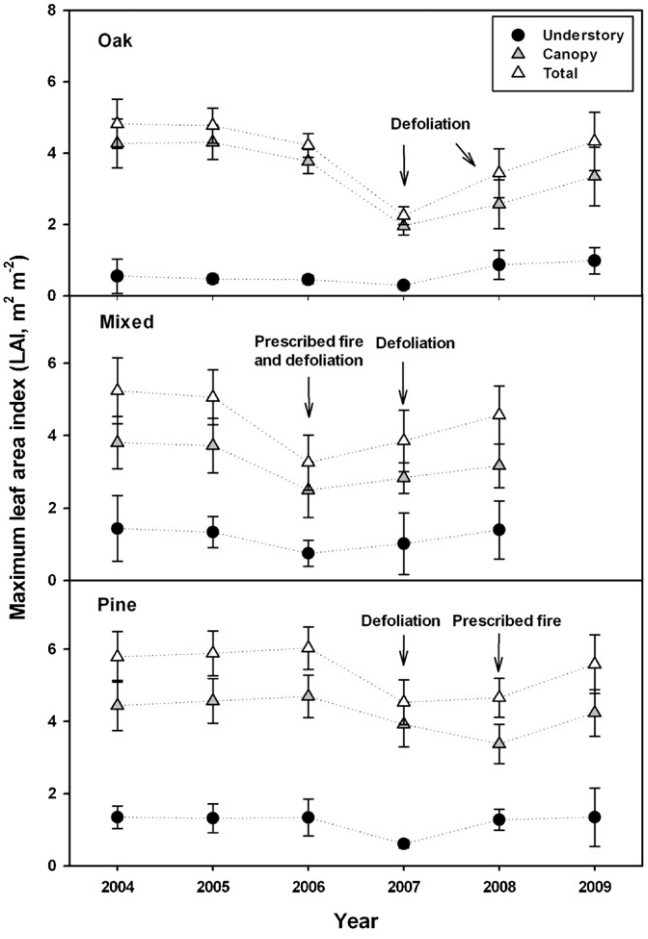

Fig. 1. Maximum leaf area index (LAI; m^2 m^{-2} ground area ± 1 SD) in the summer at the oak, mixed, and pine stands from 2004 to 2009. Data are shown for understory, overstory and total leaf area.

3.3. Latent, sensible and soil heat fluxes

A high degree of energy balance closure characterized measurements at each stand, with slopes and intercepts for the relationship between A and $\lambda E + H$ averaging 0.96, 0.99 and 0.99, and 14.5, 9.2 and 7.5 W m^{-2} for all years at the oak, mixed and pine stands, respectively (Table 4). Latent and sensible heat fluxes were linear functions of available energy at each stand during all time intervals analyzed (e.g. daily to seasonally). Seasonal differences in the partitioning of available energy into λE and H were most pronounced at the oak stand, with wintertime λE at midday values of A of 400 W m^{-2} averaging 15%, 19% and 22% of λE values during the summer at the oak, mixed and pine stands, respectively (data not shown).

The effects of defoliation and prescribed fire were observed in the partitioning of A between λE and H. During complete defoliation of the oak stand by Gypsy moth from June 1–July 14 in 2007, λE during midday periods averaged only 33% of those measured pre-defoliation in 2005 and 2006, while H more than doubled (Fig. 2a). Partitioning of A into λE and H was also affected by partial defoliation of the oak stand in 2008, and had nearly returned to pre-disturbance levels in 2009. Mean midday soil heat flux increased from 26.9 ± 1.4 W m^{-2} (mean ± 1 SE) to 37.2 ± 2.4 W m^{-2} as a result of defoliation, and mean soil temperature increased by 2.7 °C in 2007 compared to previous years, even though air temperature was similar among years. At the pine stand, defoliation in 2007 and the prescribed fire in March 2008 affected the partitioning of A during the summer (Fig. 2b). For example, midday λE at the pine stand from July 1 to August 31 following the prescribed burn in March 2008 averaged 62% of that measured at the same available energy during previous, undisturbed years (Fig. 2b). Overall, gypsy moth defoliation and prescribed fires altered the partitioning of A between λE and H, resulting in the lower λE and greater H fluxes at the same available energy flux, relative to undisturbed periods.

Table 4
Energy balance closure as evaluated using regression parameters of $H + \lambda E$ vs. available energy (A; $R_{net} - G - \Delta S_{air} - \Delta S_{bio}$) for each stand and year. Total number of half-hourly flux data values, number of values following u^* and precipitation filtering, percent of year sampled by filtered data, percent of summer months sampled by filtered data, and energy balance coefficients for the oak, mixed and pine stands are shown by year. All models are significant at $P < 0.001$.

	Stand/year	Total	Filtered	%	a	b	r^2
Oak							
	2005	11,948	8520	49, 37	0.947 ± 0.003	13.92 ± 0.59	0.867
	2006	12,367	8941	51, 41	1.007 ± 0.003	9.63 ± 0.56	0.891
	2007	13,395	9408	54, 48	0.881 ± 0.003	15.39 ± 0.62	0.835
	2008	13,960	9556	54, 56	0.984 ± 0.003	18.23 ± 0.62	0.864
	2009	13,460	8462	48, 49	0.998 ± 0.004	15.40 ± 0.62	0.859
Mixed							
	2005	10,479	5434	31, 32	1.041 ± 0.002	10.44 ± 0.49	0.931
	2006	10,209	7747	44, 36	0.998 ± 0.002	8.46 ± 0.44	0.933
	2007	11,106	8499	49, 39	0.945 ± 0.002	8.75 ± 0.44	0.910
Pine							
	2005	5212	3454	20, 22	1.027 ± 0.004	2.99 ± 0.73	0.923
	2006	11,211	8060	46, 40	1.058 ± 0.002	8.66 ± 0.48	0.932
	2007	13,932	10128	58, 58	0.945 ± 0.003	8.68 ± 0.53	0.906
	2008	15,084	10918	62, 50	0.927 ± 0.003	9.86 ± 0.52	0.893
	2009	13,557	10283	59, 55	1.011 ± 0.003	7.46 ± 0.57	0.882

3.4. Evapotranspiration

Prior to disturbance, mean hourly Et rates at 600 W m^{-2} available energy (near-full sunlight, clear sky conditions) and 25 °C during the summer months were 0.65, 0.51, and 0.54 mm h^{-1} at the oak, mixed, and pine stands, respectively. Winter Et rates averaged 0.07, 0.08, and 0.10 mm h^{-1} at value of 400 W m^{-2} for A and 5 °C at the oak, mixed, and pine stands, respectively. Using ± 1 SE values for the slopes and intercepts to gap fill missing half-hourly Et data for the summer months resulted in a maximum error of ±1.7% from the total estimated summer Et at the oak stand in 2005 (Table 5).

Daily midday VPD averaged by week during each summer is shown in Fig. 3a, and rarely exceeded 2.5 kPa at the three stands throughout the study. Only three weeks were characterized by the absence of precipitation during the summer, one at the end of summer in 2007, and two at the end of the summer in 2008, indicating that severe drought was minimal at the three stands during summer months throughout the study (Fig. 3b). At the oak stand, mean daily Et averaged by week tracked defoliation by Gypsy moth in 2007 and 2008 (Fig. 3c). Complete defoliation from early June to early July resulted in relatively low daily Et rates, which recovered somewhat during the second leaf-out later in the summer 2007. In 2008, mean daily Et at the oak stand was initially high, but as

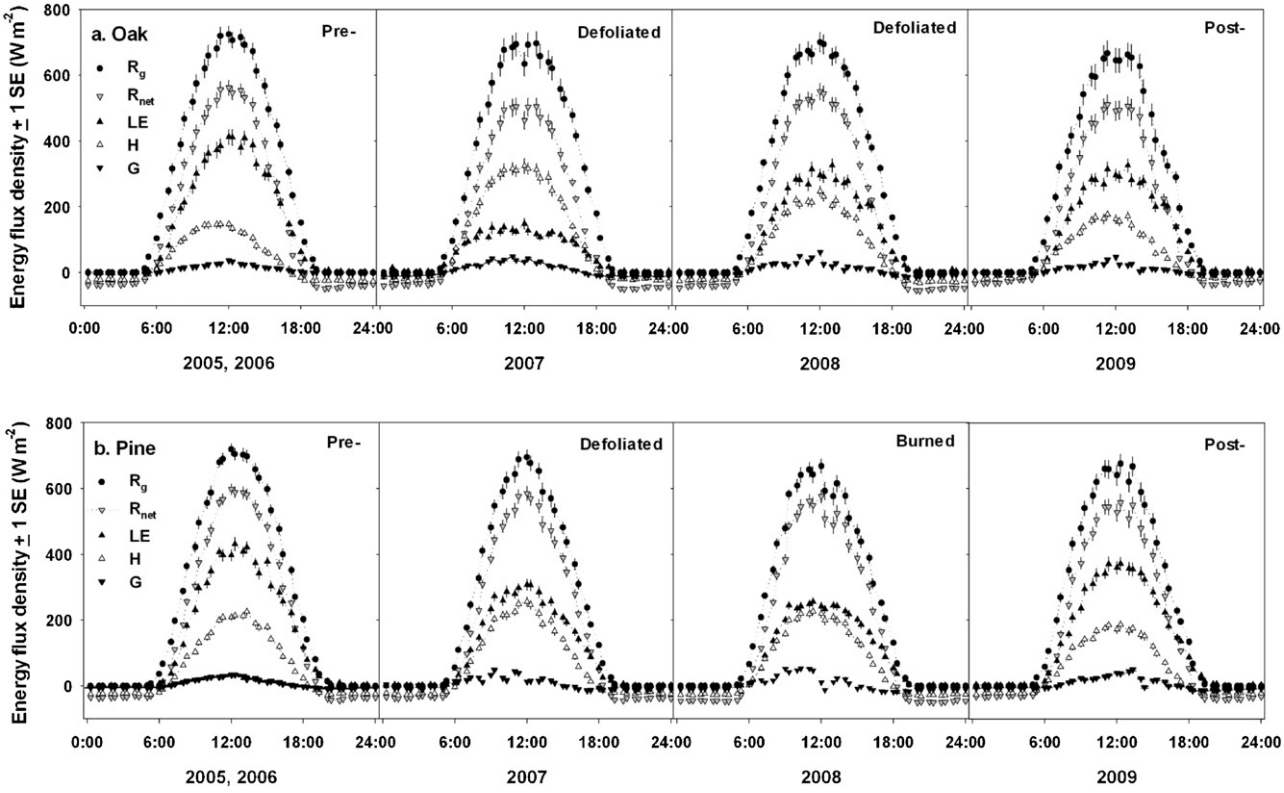

Fig. 2. (a) Ensemble diurnal energy flux density (W m^{-2}) at the oak stand from June 1 to July 15 before defoliation by gypsy moth in 2005 and 2006, during complete defoliation in 2007 and partial defoliate in 2008, and following defoliation in 2009. Error bars are ±1 SE. (b) Ensemble diurnal energy flux density (W m^{-2}) at the pine stand from July 1 to August 31 before defoliation and the prescribed burn in 2005 and 2006, during defoliation in 2007, following the prescribed fire in 2008, and following both disturbances in 2009. Error bars are ±1 SE.

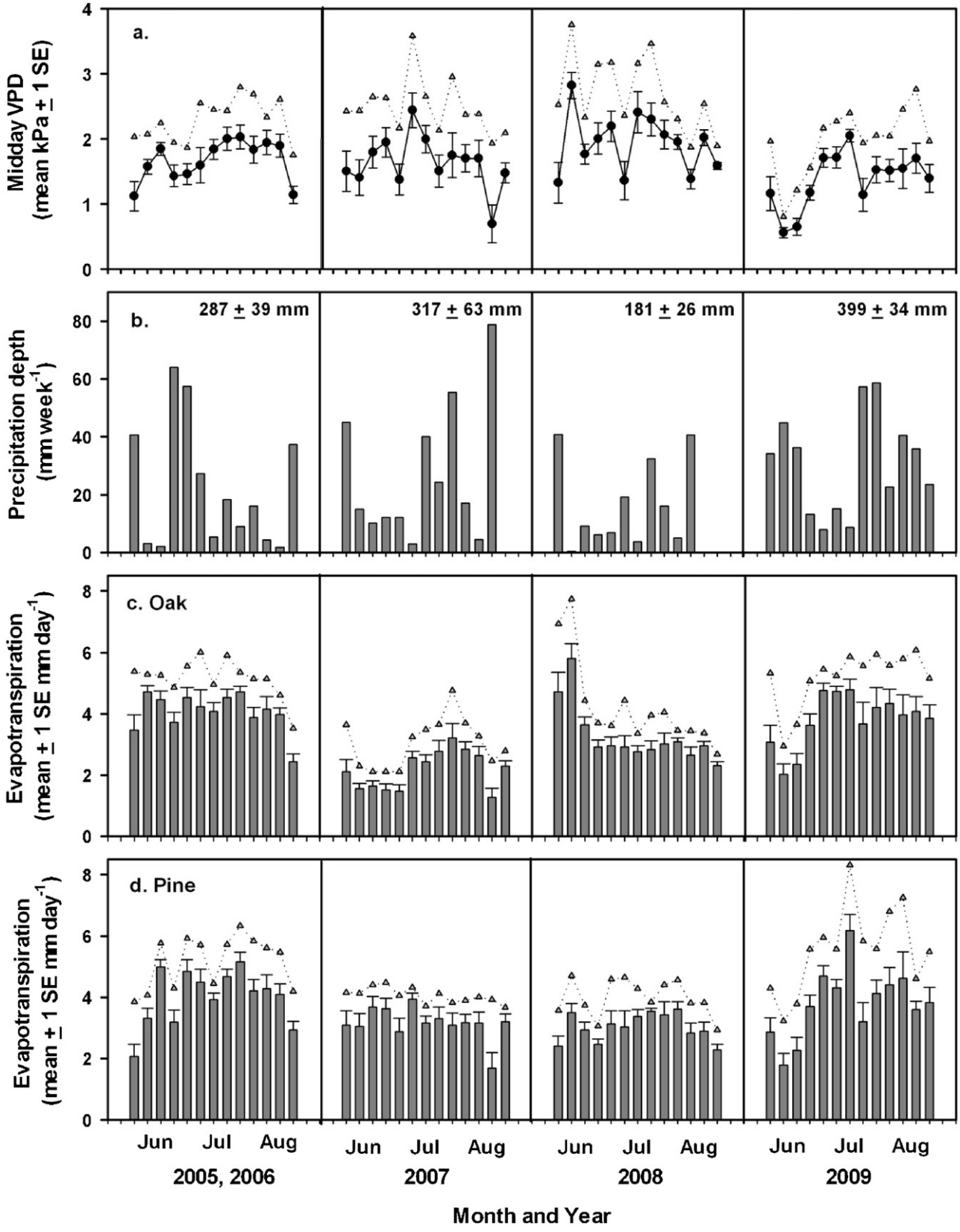

Fig. 3. (a) Mean and maximum daily vapor pressure deficit (VPD, kPa) by week from 10:00 to 16:00 for all three stands, (b) weekly precipitation (mm week^{-1}) for all three stands, and mean and maximum daily Et (mm day^{-1}) for the oak (c) and pine (d) stands before disturbance in 2005 and 2006, during defoliation in 2007, during defoliation at the oak stand and following the prescribed burn at the pine stand in 2008, and following disturbance in 2009. Δ symbols indicate maximum daily values of VPD or Et during the week.

Table 5
Relationship between available energy (A; $R_{net}-G-\Delta S_{air}-\Delta S_{bio}$; W m^{-2}) and latent heat flux (λE; W m^{-2}) at the oak, mixed and pine stands during the summer months. Total Et for summer months resulting from gap filling with mean parameters, and the largest deviation resulting from gap filling with ± 1 SE of each parameter is also shown. Data for the oak stand in 2007 are shown for periods of active defoliation (June 1 to July 14) and the 2nd leaf out (July 15 to August 31) for comparison. All correlations are significant at $P < 0.001$.

Stand/year	a	b	r^2	n	Et (mm)
Oak					
2005	0.659 ± 0.010	26.11 ± 3.17	0.735	1630	368.7 ± 6.4
2006	0.712 ± 0.008	35.63 ± 2.61	0.772	1796	402.3 ± 4.9
2007[a]	0.242 ± 0.007	25.79 ± 1.59	0.410	1121	
2007[b]	0.436 ± 0.007	23.52 ± 1.55	0.689	1020	212.2 ± 2.2
2008	0.471 ± 0.007	29.34 ± 1.63	0.679	2496	306.3 ± 2.9
2009	0.648 ± 0.007	30.55 ± 1.83	0.782	2196	355.5 ± 2.9
Mixed					
2005	0.551 ± 0.005	15.28 ± 1.19	0.812	1402	304.5 ± 1.6
2006	0.394 ± 0.004	16.26 ± 0.92	0.755	1589	223.7 ± 1.9
2007	0.362 ± 0.004	16.14 ± 0.98	0.685	1704	210.0 ± 1.6
Pine					
2005	0.568 ± 0.007	27.13 ± 1.84	0.703	739	381.8 ± 4.8
2006	0.572 ± 0.004	22.61 ± 1.09	0.827	1732	325.8 ± 2.1
2007	0.486 ± 0.004	22.18 ± 1.08	0.803	2555	300.6 ± 1.5
2008	0.434 ± 0.004	24.34 ± 1.07	0.768	2183	282.3 ± 1.7
2009	0.628 ± 0.005	22.60 ± 1.37	0.773	2409	349.2 ± 2.0

[a] June 1 to July 14.
[b] July 15 to August 31.

defoliation progressed, rates were again reduced relative to undefoliated periods (Fig. 3c). At the pine stand, defoliation of understory shrubs and oaks apparently reduced Et slightly relative to pre-disturbance periods, as did the prescribed fire conducted in 2008 (Fig. 3d).

Averaged for all summer days, mean daily Et previous to disturbance was 4.2 ± 1.5, 3.3 ± 1.2 and 3.9 ± 1.3 mm day^{-1} (mean ± 1 SD) at the oak, mixed and pine stands, respectively (Fig. 4). For the entire growing season, Et rates were lower at 3.1 ± 1.7, 2.6 ± 1.6, and 3.3 ± 1.5 mm day^{-1} at the oak, mixed and pine stands, respectively. During the winter months, mean daily Et rates were only 0.2 ± 0.1 mm day^{-1} at the oak and mixed stands, and 0.5 ± 0.3 mm day^{-1} at the pine stand (data not shown). Disturbance reduced daily Et during the summer months at all stands. At the oak stand, summer daily Et during complete defoliation and the second leaf out at the oak stand in 2007 was only 2.3 ± 0.9 mm day^{-1}, representing 55% of pre-defoliation Et (Fig. 4 and Table 6). Summer daily Et was also lower in 2008 when the canopy was partially defoliated, and had nearly recovered to pre-disturbance levels by 2009. At the mixed stand, Et following the prescribed fire in early spring 2006 and during partial defoliation by gypsy moth was significantly lower than pre-disturbance periods, representing 73% of pre-disturbance values (Fig. 4 and Table 6). The mixed stand was again defoliated by gypsy moth in 2007, and summer daily Et averaged only 2.3 ± 0.9 mm day^{-1}, representing 69% of pre-disturbance values. At the pine stand, summer daily Et averaged 3.2 ± 1.3 mm day^{-1} when defoliation of the understory occurred in 2007, and 3.1 ± 0.9 mm day^{-1} following the prescribed fire conducted in the spring of 2008. By 2009, summer Et at the pine stand had recovered to pre-disturbance Et values (Fig. 4 and Table 6).

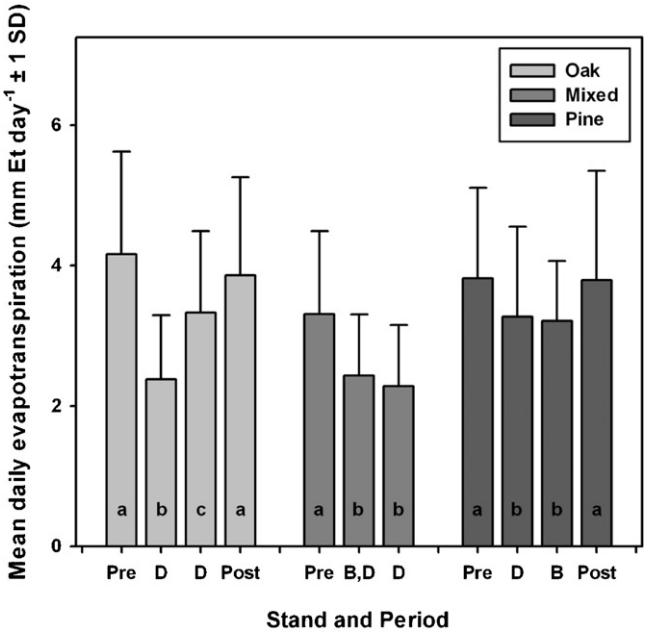

Fig. 4. Mean daily evapotranspiration (mm day^{-1} ± 1 SD) during the summer at the oak, mixed, and pine stands during pre-disturbance, disturbed and post-disturbance periods. Bars indicated with different lower case letters are significantly different, and statistics for each comparison are shown in Table 8. Pre, pre-disturbance; D, defoliation by gypsy moth; B, prescribed burn; Post, post-disturbance.

Mean daily Et during the summer was highly correlated with seasonal maximum leaf area index, which explained 82% of the variability in daily Et at the oak stand (daily Et = 0.75 LAI + 0.72, $r^2 = 0.82$, df = 5, $F = 19.2$, $P < 0.05$), and 80% of the variability at the pine-dominated stands (daily Et = 0.58 LAI + 0.39, $r^2 = 0.80$, df = 8, $F = 29.48$, $P < 0.01$) (Fig. 5). Annual estimates of Et for the three upland forest stands are shown in Table 7. Both defoliation and prescribed burns reduced annual Et amounts, with the greatest reduction occurring at the mixed stand where both disturbances had occurred sequentially.

4. Discussion

Defoliation by Gypsy moth (Clark et al., 2010) and prescribed fire (Clark et al., 2009) reduced leaf area of the canopy and understory during the growing season of some years during our study. Defoliation had the largest effect on LAI at the oak and mixed stands, reducing LAI of deciduous species during the peak of defoliation in 2006 and 2007 to levels that characterized winter months. Disturbance had relatively little effect on the overall relationship between R_g and A, but reduced albedo at the oak stand, and reduced the interception of radiation by the canopy in all stands. The partitioning of available energy into λE and H was

Table 6
Statistics for ANOVA and contrasts for daily evapotranspiration (Et, mm day^{-1}) during the summer among sites before disturbances, and within sites among years pre- and post-disturbance shown in Fig. 5. Tukey's HSD tests were used to determine significance levels of each contrast, and significantly different contrasts are indicated with different letters in Fig. 5.

Variable/site	df	*F*	*P*	Contrast	HSD	*P*
All stands, pre-disturbance						
Summer	2, 429	5.36	<0.01	[a]	0.43	<0.05
Winter	2, 435	75.76	<0.001	[b]	0.06	<0.01
Oak, 2005–2009	4, 459	52.80	<0.001	[c,d]	0.63, 0.50	<0.01, 0.05
Mixed, 2005–2007	2, 275	21.44	<0.01	[e]	0.44	<0.01
Pine, 2006–2009	3, 367	5.51	<0.01	[f]	0.56	<0.01

[a] Oak and pine stand vs. mixed stand.
[b] Pine stand vs. oak and mixed stands.
[c] Pre-defoliation (2005, 2006) and post-defoliation (2009) vs. complete defoliation and second leaf-out (2007).
[d] Pre-defoliation (2005, 2006) and post-defoliation (2009) vs. partial defoliation (2008).
[e] Pre-disturbance (2005) vs. prescribed burn and defoliation (2006, 2007).
[f] Pre-disturbance (2005 and 2006) and post disturbance (2009) vs. understory defoliation in 2007 and prescribed burn in 2008.

Table 7
Annual evapotranspiration estimates for the oak, mixed, and pine stands in the Pine Barrens of New Jersey.

Site/disturbance	Precipitation (mm year^{-1})	ET (mm year^{-1})	% ET
Oak			
2005	1092	616	56.4
2006	1108	677	61.1
2007, complete defoliation	934	442	47.3
2008, partial defoliation	936	637	68.1
2009	1173	699	59.6
Mixed			
2005	1184	607	51.3
2006, burn and defoliation	1163	452	38.9
2007, partial defoliation	1135	419	36.9
Pine			
2006	1230	757	61.5
2007, partial defoliation	1052	593	56.3
2008, prescribed burn	1163	611	53.5
2009	1382	759	54.9

altered significantly by disturbance. Mean daily Et rates during the summer months were reduced to as low as 52% of those characterizing pre-disturbance periods at the oak and mixed stands.

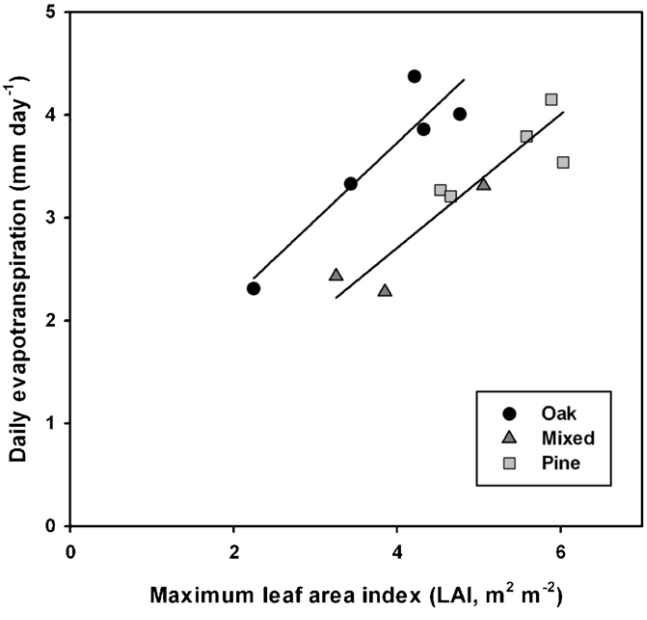

Fig. 5. Mean daily summer evapotranspiration (mm day^{-1}) vs. maximum summer leaf area expressed as LAI (m^2 m^{-2} ground area) for the oak, mixed, and pine stands.

Annual Et values were also lower during years when disturbances occurred, compared to undisturbed years. Changes in Et at hourly to annual time scales because of these non-stand replacing disturbances contrasts with results from some other studies on the Atlantic Coastal plain, which have reported less dynamic changes in Et in forest ecosystems that were disturbed (e.g. Gholz and Clark, 2002; Sun et al., 2010) or affected by severe drought (Oishi et al., 2010).

The display of leaf area was a major biotic factor contributing to the variation in energy partitioning and Et in these upland forests during our study. Leaf area was highly dynamic in time across the landscape. In oak-dominated stands, LAI reaches ca. 5 during the growing season of non-defoliated years, but <10% of that during the dormant season. Defoliation by gypsy moth in 2007 initially reduced LAI to values similar to wintertime, but then a second leaf out of canopy oaks, pines and understory shrubs later in the growing season lead to a partial recovery. Both pitch and shortleaf pines hold two annual cohorts of needles through the summer and fall, but typically only one cohort through the winter, thus seasonal variation in LAI in pine-dominated stands also is large. Pine LAI was not significantly reduced by gypsy moth defoliation, but crown scorch did reduce LAI at the pine stand (Skowronski et al., 2011). All stands have a nearly continuous understory of deciduous scrub oaks and shrubs, which contribute up to 35% of total LAI during the summer. Understory LAI was reduced by defoliation during the summer months, but typically recovers rapidly following prescribed burns (Clark et al., 2009; Skowronski et al., 2007).

4.1. Available energy, albedo and intercepted photosynthetically active radiation

Disturbance had only minor effects on the relationship between R_g and R_{net} or between R_g and A at each stand. Defoliation did reduce albedo at the oak stand, consistent with a recent synthesis of albedo data from Ameriflux sites, which found a significant positive relationship between albedo and canopy nitrogen (N) content (Hollinger et al., 2010). Defoliation resulted in a reduction of canopy N content to as low as 38% of pre-defoliation values during the second leaf out in 2007, and canopy N content had still not completely recovered to pre-disturbance levels by 2009. Changes in the absorption of PAR by the canopy at all three stands were driven by the reduction in LAI with disturbance. Slightly higher values at the oak site following defoliation resulted from a greater density of leaf mass in the lower canopy as the stand recovered. Similarly, increased absorption of PAR by the canopy at the pine stand in 2009 was consistent with the recovery of canopy LAI following the prescribed fire conducted in spring 2008.

Table 8
Leaf area index ($m^2\ m^{-2}$), daily Et (mm day^{-1}) and annual Et (mm $year^{-1}$) for selected stands. Daily and annual Et estimates are based on eddy covariance and meteorological measurements.

Site	Latitude, longitude	LAI ($m^2\ m^{-2}$)	Daily Et (mm day^{-1})	Annual Et (mm $year^{-1}$)	Citation
Hardwood-dominated stands					
Scrub Oak, FL	28.61, −80.67	1.9	3.1	713–737	Bracho et al. (2008)
Duke Forest, NC	35.97, −79.10	6.0–7.0	2.7	580–640	Stoy et al. (2006)
Oak Ridge, TN	35.99, −84.29	5.5–6.0	3.7	537–611	Wilson and Baldocchi (2000)
Oak stand, NJ	39.91, −74.60	5.0	3.1 ± 1.7	442–699	This study
Old Hardwood, WI	46.63, −91.10	4.0	2.6 ± 1.2	–	Sun et al. (2008)
Old Aspen, Canada	53.63, −106.19	4.0–5.2	3.0	405 ± 84	Zha et al. (2010)
Conifer-dominated stands					
Slash/longleaf pine, FL	29.74, −82.22	5.0	2.7	676–832	Powell et al. (2005)
Slash pine, FL	29.75, −82.16	5.1	3.1 ± 0.8	994–1122	Gholz and Clark (2002)
Slash pine, FL	29.76, −82.24	6.5	3.6 ± 0.4	1102–1284	Gholz and Clark (2002)
Loblolly pine, NC	35.97, −79.10	3.5[a]	2.7–3.6	560–740	Stoy et al. (2006)
Loblolly pine, NC	35.80, −76.67	4.0	4.6 ± 0.7	1011–1226	Sun et al. (2010)
Pitch pine, NJ	39.84, −74.38	5.5–6.0	3.3 ± 1.5	593–759	This study
Red pine, WI	46.74, −91.17	2.8	2.4 ± 0.8	–	Sun et al. (2008)
Black spruce, Canada	53.99, −105.12	4.2	2.0–2.5	374 ± 34	Amiro et al. (2006a)
Jack pine, Canada	53.92, −104.69	2.0–2.5	2.0–2.5	300 ± 20	Zha et al. (2010)

4.2. Latent, sensible and soil heat fluxes

The three extensive, relatively flat upland forest stands had near ideal fetch for above-canopy eddy covariance measurements (Skowronski et al., 2007). Relationships between A and the sum of λE and H indicate a high degree of energy balance closure at each stand. Highly significant relationships were observed between A and λE during the summer months in the absence of disturbance at each stand, and explained 70–83% of the variability in λE. Severe drought did not occur during the summer months during our study, and other variables which can have major effects on λE such as VPD of the atmosphere, were apparently less important in reducing stomatal conductance during periods of abundant precipitation. During the peak of defoliation at the oak stand in 2007, available energy explained only 42% of the variability in λE, but the overall regression model was still highly significant. Sensible heat, and to a lesser extent soil heat fluxes, accounted for a much larger proportion of available energy during defoliation and during the first growing season following the prescribed fires, although it is notable that energy balance closure was poorer during these periods. During defoliation and following the prescribed burn at the pine stand, available energy also explained a lower proportion of the variability in λE. Overall, highly significant relationships existed between available energy and λE during all time periods, and we used these relationships to gap fill missing data to calculate daily to annual Et values, rather than using the Penman Montieth equation or a canopy conductance model (e.g. Powell et al., 2005; Stoy et al., 2006). Highly significant, linear relationships between λE and available energy when soil water is available have been observed in many stands (e.g. Baldocchi et al., 1997; Barr et al., 2007; Bracho et al., 2008; Gholz and Clark, 2002; Powell et al., 2005; Stoy et al., 2006; Sun et al., 2010). For example, Gholz and Clark (2002) reported that R_{net}–G accounted for 82–89% of the variability in λE in slash pine plantations in northern Florida, and Powell et al. (2005) reported that R_{net}–G accounted for 65% of λE during wet periods in a mature longleaf (*P. palustris* Mill.) and slash pine forest in northern Florida. Our results support the observation that available energy is often the best predictor of λE during non-drought conditions during the growing season in many forests on the Atlantic coastal plain.

Slopes and intercepts for the relationship between λE and available energy reported for the summer months in Table 5 are similar to those reported from other forests in the southeast US. For example, in a southern hardwood stand at Oak Ridge, TN, the average slope and intercept for the relationship between λE and A was 0.66 and 21.7, respectively (Baldocchi and Vogel, 1996). Somewhat lower values of 0.46 and 12.1 were reported for the slope and intercept at a scrub oak stand in central Florida (Bracho et al., 2008). In a lowland loblolly pine (*P. taeda* L.) plantation in North Carolina, the slope and intercept for this relationship averaged 0.57 and 8.3 (Sun et al., 2010). In the younger slash pine plantations in northern Florida, slopes and intercepts for the relationship between λE and R_{net}–G ranged from 0.52 to 0.62, and 20.6 to 23.2, respectively (Gholz and Clark, 2002). In contrast to the similarities in slopes of the relationship between λE and A for stands in the pinelands and those in more southerly forests in the summer, the values for the slopes of this relationship during the winter months for stands in the Pinelands were much lower than those reported for winter months in pine and evergreen oak-dominated stands further south on the Atlantic coastal plain, which averaged 0.32 for all stands and years measured (Bracho et al., 2008; Gholz and Clark, 2002; Powell et al., 2005; Sun et al., 2010). Rather, slopes of the relationship between λE and A for the three stands in the Pinelands during the winter were more similar to N. temperate (Restrepo and Arain, 2005) and Boreal forests (Amiro et al., 2006b). Overall reduction in λE at half-hourly to seasonal time scales during the winter in the three stands in the Pinelands resulted from the integration of shorter days, and lower levels of incident solar radiation, and much lower LAI values, despite the fact that relatively high midday VPD levels can occur.

4.3. Evapotranspiration

Pre-disturbance mean daily Et at the oak-dominated stand during the growing season (3.1 ± 1.7 mm day^{-1}) was similar to values reported from other temperate and boreal broad-leaved forests, which range from 2.6–3.7 mm day^{-1} (Amiro et al., 2006b; Baldocchi and Vogel, 1996; Black et al., 1996; Sun et al., 2008; Wilson and Baldocchi, 2000; Table 8). Mean daily Et rates measured during the growing season at the mixed and pine stands (2.6 ± 1.6 and 3.3 ± 1.5 mm day^{-1}, respectively) were similar to estimates from other conifer-dominated forests, which range from 2 to 4.6 mm day^{-1} (Bracho et al., 2008; Gholz and Clark, 2002; Powell et al., 2005; Stoy et al., 2006; Sun et al., 2008, 2010; Table 8). Summer Et values at the mixed and pine stands (3.3 ± 1.2 and 3.8 ± 1.3 mm day^{-1}, respectively) were relatively high for values reported for other pine-dominated stands, and likely reflect the large amount of leaf area of deciduous species in the sub-canopy and understory during the summer, as well as very infrequent drought stress that occurred during our measurements through the summers of 2005–2009 in the Pinelands. In contrast to the closed-canopy ecosystems in the Eastern US reported in Table 8,

an open-canopied ponderosa pine (*P. ponderosa* P. & C. Lawson) forest with an LAI of 1.6 in Oregon had average daily Et rates of 1.6–1.7 mm day^{-1} during the growing season, and a maximum value of 4 mm day^{-1} following precipitation events (Anthoni et al., 1999; Thomas et al., 2009).

Our data indicate little difference in summer or growing season Et rates between oak- and pine-dominated stands during pre-disturbance periods. Similarly, Sun et al. (2008) reported no differences in Et rates among a number of hardwood and coniferous forests during the growing season in northern Wisconsin. Mean daily Et rates from broad-leaved and conifer-dominated forests in reported in Table 8 are also the same (3.0 ± 0.4 mm day^{-1} for hardwood stands, and 3.0 ± 0.8 mm day^{-1} for conifer dominated stands), despite the facts that coniferous species in a number of temperate forests typically have relatively lower stomatal and canopy conductances when compared to hardwood species (e.g. Amiro et al., 2006b; Stoy et al., 2006). However, when Et rates were compared as a function of LAI, such as in Fig. 5, the difference in intercept values among the oak and pine-dominated stands indicate that Et at the oak stand is greater per unit LAI than at the pine-dominated stands during the growing season. When integrated over the entire year, Et rates were greater during the fall through spring at the pine stand compared to the other stands, because LAI was greater at the pine stand during the dormant season. Measurements and model simulations by Sun et al. (2008) indicate that Et of a red pine stand was 6% higher than that of the hardwood stands, because the pine-dominated stand had greater canopy interception loss and greater transpiration during the dormant season, consistent with our results from the oak and pine stands during the winter months.

Annual Et at the oak stand during undisturbed periods was similar to other hardwood dominated stands in the southeast US. For example, annual Et was 580–640 mm yr^{-1} at a mixed hardwood stand in Duke Forest, North Carolina (Stoy et al., 2006), and 537–611 mm yr^{-1} at a mixed hardwood stand at Oak Ridge, TN (Wilson and Baldocchi, 2000). Annual Et at our mixed and pine-dominated stands in the absence of disturbance was lower than in pine plantations in Florida and on the Atlantic Coastal Plain in North Carolina, but similar to values reported for a loblolly pine stand at Duke Forest in North Carolina (Gholz and Clark, 2002; Powell et al., 2005; Stoy et al., 2006; Sun et al., 2010). During these studies, the range in annual precipitation depths was similar among sites, totaling between 811–1390 mm yr^{-1} in the Florida studies, 930–1350 mm yr^{-1} in the North Carolina studies, and 932-1382 mm yr^{-1} in the Pinelands. More northerly stands all had lower annual Et than stands in the Pinelands. For example, long-term annual Et from Aspen, black spruce and jack pine stands that were similar in age to the stands in the Pinelands averaged 405 ± 84, 374 ± 34 and 300 ± 20 mm yr^{-1}, respectively (Amiro et al., 2006a; Zha et al., 2010).

4.4. Landscape effects of disturbance on evapotranspiration

Our average annual Et estimate for all stands and years (606 ± 115 mm yr^{-1}, mean $\pm$ 1 SD) is similar to long-term, landscape-scale estimates of Et of ca. 50% of incident precipitation reported by Rhodehamel (1979), which results in an average Et value of 572 ± 91 mm yr^{-1}, and to Et estimates derived from long-term USGS weir data of ca. 603 mm yr^{-1} (http://www.nj.usgs.gov). Our results are also consistent with modeled Et values reported by Wang (1984) of 612–705 mm yr^{-1} for mixed stands in the Pinelands. When years in the absence of disturbance are used to calculate annual Et, the mean value for all three stands is 683 ± 73 mm yr^{-1}, which is at the high end of the range of estimates for the Pinelands reported by other investigators. Because our measurements incorporated multiple years of disturbance, the mean value for all stands and years more closely reflects the long term, landscape-scale average Et in the Pinelands.

Abandonment of commercial charcoal and logging activities in the late 1800s has allowed increasingly complex forest structure to develop in both upland and lowland forests (Skowronski et al., 2007, 2011). Similarly, highly effective management of wildfires through prescribed burns and suppression activities since the 1940s has maintained LAI and stand basal area at relatively high levels (Forman and Boerner, 1981). Designation of the Pinelands National Reserve in the late 1970s largely eliminated commercial timber harvest across this landscape. More recently, insect defoliation has become the major, non-stand replacing disturbance in the Pinelands. Gypsy moth first appeared in forests in New Jersey in 1966, and since then, four major defoliation events have occurred. Pine-dominated stands are typically only partially defoliated by gypsy moth, but can be defoliated by other herbivores, most notably pine looper (*Lambdina pellucidaria* Grote and Robinson) (USDA 1998) and Southern pine beetle (*Dendroctonus frontalis* Zimmerman). Spatially extensive defoliation events, similar to those experienced in 2006–2008 in the Pinelands, have the capacity to reduce Et at the landscape scale. Gypsy moth defoliation detected from aerial survey data (defined as $\geq$75% reduction of canopy foliage in oak stands, and $\geq$75% reduction of the foliage of deciduous species in mixed and pine stands) totaled 320.3 km^2 in 2007, and represented an average of 20.2% of the area of the three major upland forests (New Jersey Department of Environmental Protection 2007; Clark et al., 2010; Lathrop and Kaplan, 2004). As a first approximation, we used the relationships between λE and A for non-defoliated periods during the growing season and continuous meteorological data for 2007, and calculated an average Et, weighted by forest type, of 621 mm yr^{-1} for all upland forests in the absence of Gypsy moth defoliation. When actual ET measured at each site in 2007 was multiplied by the area defoliated in the appropriate forest type and calculated values were used to estimate annual Et across the remaining undefoliated stands, resultant average annual Et for all upland forests was 590 mm yr^{-1}. Assuming an average precipitation depth of 1040 mm yr^{-1} in 2007, we estimated that ground water recharge increased by 31 mm to 450 mm yr^{-1}, ca. 7.3% higher than would have occurred in the absence of Gypsy moth defoliation. If only oak-dominated stands are considered, which cover 48% (726 km^2) of upland forests, ground water recharge in this forest type increased ca 8.8% in 2007. Although our calculations assume that Et measured at our sites characterizes upland forests in the Pinelands, 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 hydrologic cycling at the landscape scale.

5. Conclusions

Our study indicates that non-stand replacing disturbances result in significant but transient effects on energy partitioning, and reduced Et at daily to annual time scales. Changes in the absorption of incident radiation and albedo as a result of disturbance were relatively small and short-lived. In contrast, radiation absorption by the canopy was lower, partitioning of available energy to λE and H was altered, and Et at daily to annual time scales was reduced during and following disturbance compared to pre-disturbance periods. Pre- and post- disturbance, Et at our sites in the Pinelands during the summer months was similar to results from many sites in the Southeast US. During the winter months, low LAI and climatic constraints limited Et, resulting in rates that are more characteristic of northern forests. Long-term measurements of Et which included non-stand replacing disturbances reflected other estimates of annual Et and groundwater recharge in the Pinelands.

Our results suggest that non-stand replacing disturbance may play an important role in regulating energy partitioning, Et and groundwater recharge in other forest ecosystems.

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