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Hydrological responses to defoliation and drought of an upland oak/pine forest

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Abstract:

Hydrologic variability during 2005–2011 was observed and analyzed at an upland oak/pine forest in the New Jersey Pinelands. The forest experienced defoliation by Gypsy moth (*Lymantria dispar* L.) in 2007, drought conditions in 2006 and a more severe drought in 2010. By using sap flux and eddy covariance measurements, stream discharge data from USGS, soil water changes, precipitation (P) and precipitation throughfall, a local water balance was derived.

Average annual canopy transpiration (E_C) during 2005–2011 was 201 mm a^{-1} ± 47 mm a^{-1}. A defoliation event reduced E_C by 20% in 2007 compared with the 2005–2011 mean. During drought years in 2006 and 2010, stand transpiration was reduced by 8% in July 2006 and by 18% in 2010, respectively, compared with the overall July average. During July 2007, after the defoliation and subsequent reflushing of half of the leaves, E_C was reduced by 25%. This stand may experience higher sensitivity to drought when recovering from a defoliation event as evidenced by the higher reduction of E_C in 2010 (post-defoliation) compared with 2006 (pre-defoliation).

Stream water discharge was normalized to the watershed area by dividing outflow with the watershed area. It showed the greatest correlation with transpiration for time lags of 24 days and 219 days, suggesting hydrological connectivity on the watershed scale; stream water discharge increases when transpiration decreases, coinciding with leaf-on and leaf-off conditions. Thus, any changes in transpiration or precipitation will also alter stream water discharge and therefore water availability. Under future climate change, frequency and intensity of precipitation and episodic defoliation events may alter local water balance components in this upland oak/pine forest. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS defoliation; drought; sap-flux; upland oak/pine forest; Atlantic Coastal Plain

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INTRODUCTION

Vegetation and particularly forests in the temperate zone typically transfer the majority of precipitation (P) back to the atmosphere *via* transpiration. Forest plantations that display higher leaf area than native forests have been shown to significantly reduce stream flow, counteracting the potential benefits of carbon sequestration (Jackson *et al*., 2005). Even smaller scale changes in transpiration such as seasonal drought in a forest catchment can change groundwater recharge (Oishi *et al*., 2010). In addition, forest pest infestations have been shown to increase run-off (Schwarze and Beudert, 2009). In the overall forest water budget, canopy transpiration (E_C) can account for 50–80% of evapotranspiration (ET) as measured by eddy covariance (Wullschleger *et al*., 2000; Wilson *et al*., 2001; Schäfer *et al*., 2002) thus greatly influencing groundwater recharge patterns. However, the influence of transpiration on groundwater recharge and how they are coupled is still an ongoing debate (Maréchal *et al*., 2009; Oishi *et al*., 2010).

The interaction between transpiration and groundwater recharge is particularly important because groundwater is a valuable natural resource. In 2005, the US Geologic Survey (USGS) estimated that the withdrawal of groundwater in the USA was approximately 236 Gl per day, of which 2.2 Gl were withdrawn in New Jersey alone (Vyas *et al*., 2004; Kenny *et al*., 2009). Water is a critical component for almost all aspects of the economy including manufacturing, energy production and agriculture as well as private residential uses. Thus, the reliability of groundwater resources is paramount to a functioning society. Any disturbance events, such as deforestation, wildfires, mortality due to pest infestations and so on, may change the amount of recharge or storage in an aquifer and thus represent a potential impact to water resource availability (Oishi *et al*., 2010).

Forested areas can be frequently subject to catastrophic events that lead to defoliation with subsequent mortality

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(Little, 1998; Kurz *et al*., 2008; Scheller *et al*., 2008; Schäfer, 2011; Clark *et al*., 2012). Defoliation events, including insect infestations and burning due to wildfires or managed fires, can alter the water cycle and lead to a reallocation of water in the environment. Water can be distributed in the saturated subsurface zone, the unsaturated subsurface zone, the surface, the biota and the atmosphere. Disturbances including defoliation and meteorological drought have the potential to alter transpiration and drainage, causing a redistribution of water within the ecosystem that may significantly impact the availability of water resources (Schwarze and Beudert, 2009). Mortality induced by either disturbance events or drought conditions will also affect forest community composition, and carbon, water and heat fluxes that could feed back to regional climate regimes (Marland *et al*., 2003; Medvigy *et al*., 2012).

The objective of this study was to investigate the effects of forest defoliation and drought on stand water components including E_C, *ET* and stream flow discharge (*Sf*). We then evaluated overall stand water balance, noting how well coupled components such as streamflow and transpiration are responding individually during disturbance and recovery periods. Particularly, as climate change may increase the severity and frequency of insect outbreaks (Jönsson *et al*., 2009) and lead to changes in rainfall patterns in the USA (Karl *et al*., 2009), a greater understanding of these effects on the hydrologic cycle is necessary for water management purposes.

MATERIALS AND METHODS

Study site

The study site is an upland oak/pine forest in the New Jersey Pineland National Reserve (USDA Forest Service Silas Little Experimental Forest; N 39º 55' 0", W 74º 36' 0") in the Brendan T. Byrne State Forest (formerly Lebanon State Forest). Annual *P* averages 1123 (±182) mm with a mean annual temperature of 11.5 ºC. The geology is late Miocene fluvial sediment of the Kirkwood formation with Cohansey sandy soil and the aboveground topography is relatively flat. These sandy soils have a low water holding capacity, low nutrient content and low cation exchange capacity (Schäfer, 2011). The dominant tree species are *Quercus prinus* Willd. (chestnut oak), *Q. velutina* Lam. (black oak), and *Q. coccinea* Münchh. (scarlet oak), with scattered *Pinus rigida* Mill. (pitch pine), and *P. echinata* Mill. (shortleaf pine). Less abundant oaks at the site include *Q. stellata* Wangenh. (post oak) and *Q. alba* L. (white oak) (Skowronski *et al*., 2007; Clark *et al*., 2010; Schäfer *et al*., 2010). The understory is composed of *Gaylussaccia baccata* (Wangenh.) K. Koch (black huckleberry) and *Vaccinium* spp. (blueberry). The forest contains a wide range of age and diameter classes indicating it is self-recruiting. As a reference, tree cores taken in 2009 indicated that trees between 25- to 30-cm diameter at breast height (DBH, 1.3 m aboveground) in this forest are, on average, 80–120 years old.

Meteorological data

Environmental measurements included air temperature (T_{air}) and relative humidity (*RH*, HMP45C Vaisala, Helsinki, Finland), net radiation (R_n, NRLite, Kipp and Zonen, Delft, Netherlands), photosynthetic photon flux density (*PPFD*, Li-190, LiCor Inc, Lincoln, NE, USA), precipitation (*P*, TE525, Texas Electronics Inc, TX, USA), precipitation throughfall (P_T, TE525, Texas Electronics Inc, TX, USA), soil moisture from 0–30 cm (Θ m^3 m^{-3}, CS616, Campbell Scientific, Inc, Logan, UT, USA), soil temperature at 5 cm depth (T_{soil}, 107-L, Campbell Scientific, Inc.) and wind speed and direction (05013-5, RM Young Co., Traverse City, MI, USA). Meteorological variables were collected at 10-s intervals and recorded every half-hour using data loggers (CR23X and CR1000, Campbell Scientific Inc, Logan, UT, USA). Water vapour and turbulence data for eddy covariance flux calculations of ET (Licor 7000, LiCor Inc, Lincoln, NE, USA and R M Young 81000, Traverse City, MI, USA) were recorded at 10 Hz using a laptop computer. Atmospheric and eddy covariance data were measured from a 19 m weather tower (Clark *et al*., 2012). Vapour pressure deficit of forest air was calculated using *RH* and T_{air} from tower measurements. All meteorological and eddy flux data are available on the Ameriflux website at http://public.ornl.gov/ameriflux/. The change in soil water storage was computed for the upper 30-cm layer as the difference of soil moisture (Θ) content from the last measurement of the year minus the first measurement of the year. Thus, negative values represent a loss to the system and positive values represent a gain in soil water.

Stream gauge and groundwater table data

At a nearby gauging station (USGS http://waterdata.usgs.gov/nwis/), about 10 km due southeast from the research site, the groundwater table at USGS 395150074284201 050689, Lebanon State Forest (23-D Obs) and streamflow discharge at USGS 01466500 McDonalds Branch in Brendan T. Byrne State Forest NJ (39°53'06" N, 74°30'19" W referenced to North American Datum of 1983, Woodland Township, Burlington County, NJ, Hydrologic Unit 02040202) were included in this analysis. The drainage area of McDonalds Branch in Brendan T. Byrne State Forest is 6.1 km^2. On the basis of a time lag analysis of the high time resolution data of streamflow discharge and *P* at the research site, the time of peak of the streamflow is about 14 h after the

rainstorm event. Thus, on daily to annual timescales *Sf* can be scaled to the watershed area in millimetre per annum by dividing the discharge by the watershed area (Palmroth *et al*., 2010; Gangodagamage *et al*., 2011). High temporal resolution data (hourly for groundwater table and every 15 min for stream gauge data) were available from October 2007 onwards, and daily mean groundwater table and stream flow from January 2005 to October 2007.

Biometric measurements

In order to scale sap flux measurements to canopy transpiration, a measurement plot was delineated within the forest stand, which consisted of a 'pie slice' with an 80-m radius and 54º angle that included the measured trees (Schäfer *et al*., 2010). In winter, DBH of all trees >2.5 cm within the plot was measured. Sapwood area and bark thickness were determined using increment cores of 12 trees from the three major oak species. A relationship of sapwood depth (cm) with DBH (cm) was used to calculate sapwood area of all the oak trees in the plot. The following equation was derived:

$$S_D = 0.0832(\text{std err of estimate } 0.0042)^*\text{DBH} \quad (1)$$

where S_D is sapwood depth ($r^2 = 0.60$, $p < 0.0001$, regression with Sigmaplot version 9.0, Systat Software, San Jose, CA). The regression was generated across all oak species. Bark thickness was only weakly related to DBH ($r^2 = 0.08$), thus the average bark thickness of 0.6 cm was used to calculate sapwood area from DBH measurements.

Sap flux measurements and scaling to canopy transpiration

Sap flux was first measured with the tissue heat balance method (THB) (Čermák *et al*., 1973), where sensors were inserted into the north side of the tree (Model P4.2, EMS Brno, CZ) in six mature individuals of *Q. prinus*, five *Q. velutina* and seven *Q. coccinea*. Starting in August 2006, an individual *P. rigida* was also monitored. Details about the experimental design can be found in Schäfer *et al*. (2010). Number of individuals per species was determined by proximity to the datalogger and sufficient size of the tree (DBH > 10 cm). Power input data were recorded every 30 s and 30 min averages were stored in the system datalogger, then converted to sap flux (g_{H2O} $m^{-2}_{sapwood}$ s^{-1}) using system software (Mini32 version 4.1.5.0, EMS, Brno, CZ) and sapwood area of the respective tree. In 2009, thermal dissipation probes (THP) according to Granier (1987) were inserted into previously monitored trees, and new trees were added to increase sample size and compensate for tree mortality due to gypsy moth defoliation (Schäfer, 2011). Thus, stand transpiration (E_C) from 2009 onward was estimated using the THP method. Details about scaling both THB and THP type sensor to stand level transpiration are found elsewhere (Renninger and Schäfer, 2012).

Sap flux was scaled to E_C by multiplying the mean sap flux for each species ($n = 5$–7) by sapwood area per unit ground area (A_S:A_G) of each tree species for the measurement plot (Table I). Daily mean sap flux (measured with the THB system for days when all sensors were working from 2005 to 2008) was not significantly related ($p > 0.1$) to DBH (Figure 1), a result that is consistent with previous studies (Granier *et al*., 2000; Oishi *et al*., 2008). Because there is no relationship between size of the tree and sap flux, sap flux can be scaled using A_S:A_G without having to account for size or canopy position (Köstner *et al*., 1992). The average sap flux of all oak trees was used to calculate E_C for *Q. stellata* and *Q. alba* trees by multiplying with respective A_S:A_G. The within-tree-species variation was computed from the variance of the sap flux densities measured ($n = 5$–7, depending on species), assuming no errors associated with A_S:A_G.

On a monthly basis, the maximum coefficient of variation of sensor variability was 5%. However, on a half-hourly basis, E_C of the different species varied 59% for *Q. prinus*, 65% for *Q. velutina* and 72% for *Q. coccinea* among different trees of the same species

Table I. Sapwood area per unit ground area (A_S:A_G in m^2 ha^{-1}) for each species and year

A_S:A_G (m^2 ha^{-1})	*Q. prinus*	*Q. velutina*	*Q. coccinea*	*P. rigida*
2005	1.94	1.26	0.65	0.83
2006	1.98	1.30	0.66	0.84
2007	2.03	1.32	0.68	0.84
2008	2.04	1.31	0.67	0.85
2009	2.16	1.33	0.69	0.87
2010	2.21	1.26	0.66	0.92
2011	2.27	0.36	0.21	0.96

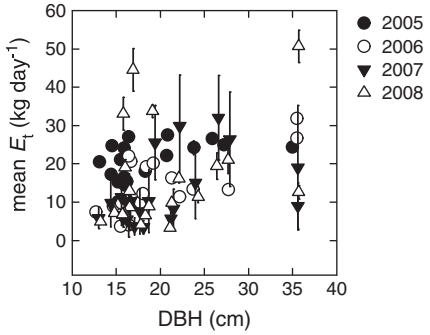

Figure 1. Mean tree transpiration (E_t in kg day^{-1}) versus diameter at breast height in cm (DBH) for 2005 (dark circles), 2006 (open circles), 2007 (dark triangles) and 2008 (open triangles) for the tissue heat balance method

when all sensors were working (Figure 2). Total variation in *Ec* within the entire forest stand on a half-hourly basis was 32%, reflecting the spatial variation within the stand.

Gap-filling of sap flux data and statistical analysis

Missing sap flux data at the individual tree level were gap-filled on a half-hourly basis using the Ecosystem Demography model version 2 (ED2) (Medvigy *et al*., 2009; Medvigy *et al*., 2012). ED2 is a mechanistic terrestrial biosphere model that is capable of simulating tree-level transpiration. As input, the model requires the observed stand composition and the meteorological observations. The model then solves the nonlinear, coupled photosynthesis-stomatal conductance equations developed by Farquhar, Ball, Berry and others to compute leaf-level fluxes of H_2O and CO_2 (see Appendix B of Medvigy *et al*., 2009). Transpiration is scaled from leaves to whole trees by using allometric relationships between tree diameter and leaf biomass. With this formulation, the nonlinear responses of environmental parameters are thus accounted for. ED2 has recently been evaluated and used successfully to simulate CO_2 fluxes at this site (Medvigy *et al*., 2012).

In order to scale to stand-level transpiration, the individual tree transpiration was first scaled to transpiration per unit sapwood area. Then, all trees for each species were averaged and scaled with A_S:A_G to the stand. For *Q. prinus*, 12% of the data were gap-filled during the 7-year record, and 11% of the *Q. velutina* data and 14% of the *Q. coccinea* data were gap-filled. For *P. rigida*, 57% of the sap flux data were gap-filled as this sensor was installed in the summer of 2006, and data from 2005 were modelled.

Generally, the E_C modelled with ED2 was comparable with measured values (Figure 3). However, for soil moisture conditions below 0.05 $m^3\,m^{-3}$, the E_C modelled with ED2 was 58% greater than measured values for *Q. prinus*, 78% greater for *Q. velutina* and 78% greater for *Q. coccinea*. Therefore, for soil moisture conditions below 0.05 $m^3\,m^{-3}$, a reduction factor was employed. Particularly, during the drought in 2010 and beyond, the model was not able to capture the decline in transpiration (see Figure 3 bottom panel for 2010). The variation explained by the model (r^2) ranged from 0.05 for

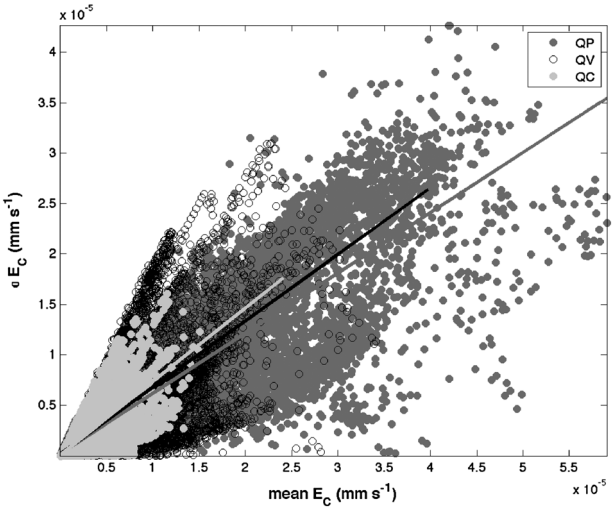

Figure 2. Mean canopy transpiration of the three oak species (E_C in mm s^{-1}) versus the standard error σ E_C (mm s^{-1})

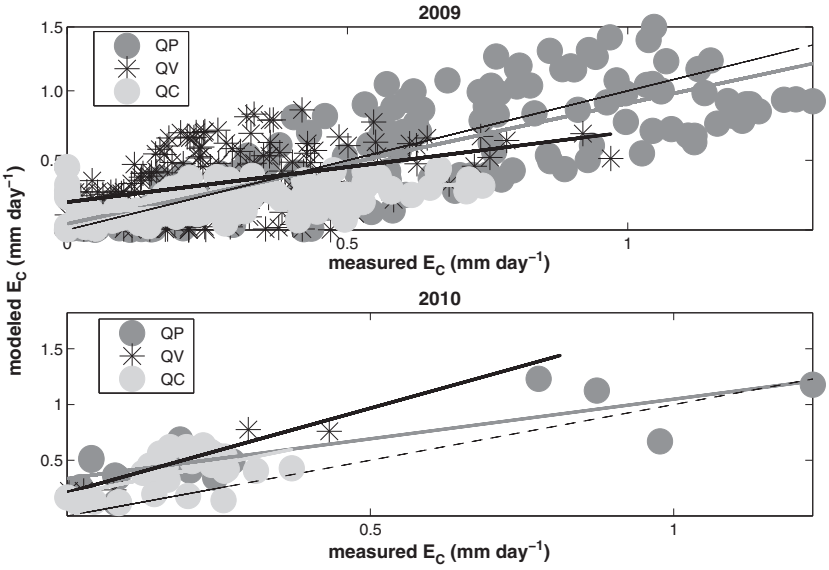

Figure 3. Measured canopy transpiration versus canopy transpiration modelled with ED2 (E_C in mm day^{-1}) for 2009 (top panel) and 2010 (bottom panel). QP – *Quercus prinus*, QV – *Quercus velutina* and QC – *Quercus coccinea*. Black dashed line is the 1 to 1 line

Q.velutina in 2007 to 0.88 for *Q. velutina* in 2010, albeit always highly significant with $p < 0.005$. The largest divergence between modelled E_C with ED2 and measured E_C occurred at the beginning and at the end of the season (data not shown), suggesting biases in the ED2 phenology parameterization. It is well known that model phenology schemes have large biases; however, novel datasets are beginning to lead to improved models (Jeong *et al*., 2013). The modelled E_C with ED2 displayed lower coefficient of variation than measured E_C with 15% for *Q. prinus*, 8% for *Q. velutina* and 13% for *Q. coccinea*.

Stand hydrologic balance

Assuming a fully hydrologically connected watershed, all the incoming and outgoing water can be accounted for as follows (Rodríguez-Iturbe and Rinaldo, 2001; Schäfer *et al*., 2002; Ford *et al*., 2007; Oishi *et al*., 2010; Palmroth *et al*., 2010):

$$P–I–Sf–E_C–E_U–E_S–R = 0 \quad (2)$$

where P is precipitation, I is interception water loss through the canopy, Sf is streamflow discharge, E_C is canopy transpiration, all in mm a^{-1}, E_U is the understory transpiration, E_S is soil and litter layer evaporation from the soil and forest floor, also in mm a^{-1} and R is the unaccounted fluxes and error in the parameter estimates, all in mm a^{-1}, (Schäfer *et al*., 2002). As E_U and E_S were not estimated in this study, it was calculated as the difference between ET and $E_C + I$ (Oishi *et al*., 2010; Clark *et al*., 2012). Any further imbalance (R) may be attributed to unaccounted losses such as changes in soil water storage in deeper soil layers, overland runoff and uncertainties associated with assessing any of the components (Ford *et al*., 2007).

RESULTS

Environmental conditions

In this 7-year record from 2005–2011, an extreme drought year (2010) and two unusually wet years (2009, 2011) were observed, as well as a gypsy moth defoliation event in 2007 and a partial defoliation in 2008 (Figure 4). The overall coefficient of variation in annual P was 12.8% during the study period. In August 2011, hurricane Irene affected the east coast of the USA. Thus, the overall P in 2011 was high, but precipitation frequency was low throughout the summer (see also soil moisture Figure 4, bottom panel). Fluctuations in P were reflected in fluctuations in stream flow and the groundwater table (Figure 4, bottom panel). Particularly, during snowmelt and a large precipitation event in March 2011, the groundwater table increased to 2 m above the average across the 7-year period.

Interception water losses differed between summer and winter for the years measured (2009–2011) whereby about 10% of P was lost to interception in the winter

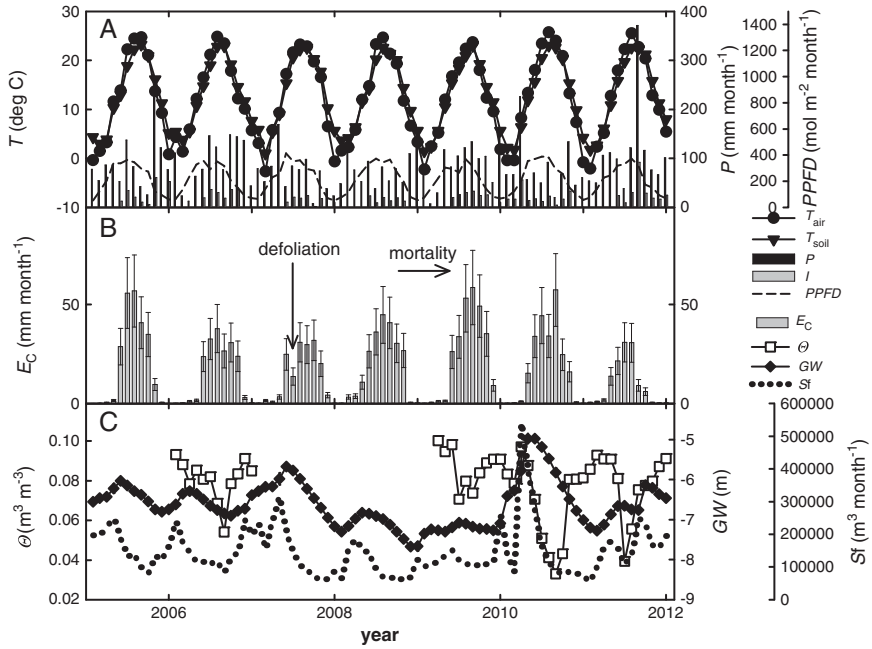

Figure 4. Top panel – soil (T_{soil}, black triangles) and air temperature (T_{air}, black circles, in °C), photon flux density (*PPFD* in μmol m^{-2} $month^{-1}$, dashed lines), precipitation (P, black bars) and interception (I, grey bars) middle panel – canopy transpiration (grey bars, E_C in mm $month^{-1}$) with standard error of the mean (Figure 2) bottom panel – soil moisture content (Θ in m^3 m^{-3}, open squares), streamflow (Sf in m^3 $month^{-1}$, dashed-dotted line) and groundwater table (GW in m below surface, black squares)

compared with 12% in the summer (Figure 4, top panel). Equations for modelling precipitation throughfall and thus interception water losses are as follows:

$$\text{Winter (November–April)} \quad P_T = 0.888{*}P + 0.941 \quad p < 0.0001, R^2 = 0.80 \tag{3}$$

$$\text{Summer (May–October)} \quad P_T = 0.869{*}P - 0.275 \quad p < 0.0001, R^2 = 0.85 \tag{4}$$

The water table dropped dramatically in 2010 during drought, as did stream flow (Figure 4, bottom panel). Before the drought in 2010, the water table was at its highest point of the 7-year study period, but during 2010 it eventually receded by over 2 m. In addition, the covariance between streamflow and E_C displayed a bimodal function throughout the year, indicating a half annual cycle (Figure 5). The biannual cycle coincides with time lagged leaf-on and leaf-off cycles, whereby streamflow is highest in winter, when minimal transpiration occurs and lowest in summer during periods of high-transpiration rates. Overall, these results suggest a very limited capacitance in the system and high hydrologic connectivity.

The maximum observed temperature on a half hourly basis within a given year ranged from 39.6 °C in 2010 to 34.8 °C in 2009. For the remaining years, the observed maximum temperature varied between 36.1–37.8 °C.

Transpiration and water balance

Growth and thus sapwood area per unit ground area (A_S:A_G) remained relatively stable in 2007 and 2008 for most species or decreased relative to 2006 (Table I). In 2008, a third of the canopy did not display leaves, but in 2009 several trees resprouted with epicormic branches along the stem without displaying a crown (Picture 1). After a severe drought in 2010, additional trees died that had been stressed by the complete defoliation event in 2007. Therefore, in 2011, the basal area of live trees was reduced by 25% compared with the previous year. Sapwood area per unit ground area (A_S:A_G) dropped in the 7-year study period by 19% (Table I). Stem increment growth increased in the wet year of 2009, but then remained relatively constant or decreased due to additional mortality over the following years. In 2011, the overall leaf area was reduced by 25% (Renninger *et al.*, in review) as compared with the leaf area of fully developed crowns calculated based on allometric relationships (Whittaker and Woodwell, 1968), (Picture 1).

The hydrologic components of this forest during the 7-year period are summarized in Table II. E_C and *Sf* accounted for approximately 61% of P_T, on average, throughout the study period. Likewise, *ET* accounted for about 60% of *P* (Table II). Transpiration combined with interception water losses displayed similar trends as *ET* accounting for, on average, two-thirds of *ET* with an upper limit of 94% and a lower limit of 44% accounting for spatial variation of sap flux measurements. Over the study period, transpiration varied by 25%, compared with *P*, which varied by about 13% (see in the previous text)

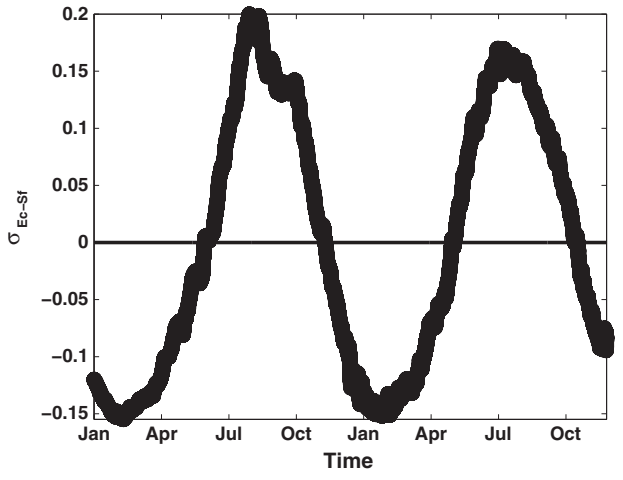

Figure 5. Normalized covariance of streamflow scaled to the watershed (in mm d^{-1}) to canopy transpiration E_C at the study site E_C (in mm day^{-1}), $\sigma_{EC\text{-}SF}$. All 7 years are used and the lag was applied ±1 year, thus 2 years are displayed

Picture 1. Epicormic sprouting along a stem of a *Q. velutina* tree. Please note the missing crown (red circle)

Table II. Hydrologic forest budget components at the New Jersey Pinelands from 2005–2011

(mm a^{-1})	2005	2006	2007	2008	2009	2010	2011
P	1092	1108	934	936	1098	984	1358
P_T[a]	907	922	628	713	854	740	1090
I[a]	184	186	205	223	244	220	225
Sf	315	298	291	204	252	346	311
E_C	230 ± 74	182 ± 58	162 ± 52	224 ± 72	269 ± 86	229 ± 73	117 ± 37
ET	616	677	442	637	699	625	690
$E_U + E_S$	202	309	75	190	186	176	348
ΔS[b]		−2.5			[c] −7.0	−4.9	2.0
$E_C + Sf + I + \Delta S + E_U + E_S$	931	972	733	841	944	966	1003
R (P-above)	161	135	201	95	154	−7	312

Abbreviations: P – precipitation, P_T – precipitation throughfall, I – interception water losses, Sf – streamflow discharge scaled to the watershed, E_C – canopy transpiration, ET – evapotranspiration measured *via* the eddy covariance method, E_U – estimated understory transpiration, E_S – estimated soil evaporation, ΔS – change in soil water storage in the upper 0.3 m and R – unaccounted remainder of the water balance

[a] interception water losses are calculated as the difference between precipitation and precipitation throughfall, and predicted for years when precipitation throughfall was not measured

[b] change in soil water storage in the upper 30 cm of the soil layer as measured with the CS616, hence only calculated for years when measurements are available

[c] only part of the year (April–December) was measured; therefore, the soil water storage change was calculated for this time

and *ET*, which also varied by about 13%. However, relatively little change in soil water storage on an annual basis was observed for the three and a half years of soil moisture measurements, suggesting fairly limited water storage capacity in the upper layer of the soil (Table II).

Effects of defoliation and drought

After a short drought period in 2006, transpiration rates recovered relatively quickly to pre-drought rates; however, the defoliation event in 2007 strongly reduced transpiration and *ET* (Table II). After about 50% of canopy leaf area re-emerged later in the growing season in 2007, transpiration resumed to the same or higher level, suggesting remaining foliage used more water per unit leaf area and compensated for the water not used by the lost foliage. By 2008, a portion of the trees had died or had their leaf area significantly reduced. Epicormic sprouting along the stem, particularly in *Q. velutina*, compensated for missing crowns representing 75% of the previous foliage displayed (Picture 1). In 2010, a severe summer drought occurred (Figure 4), and soil moisture levels dropped to a low of 0.02 $m^3 m^{-3}$ for a prolonged period. This drought reduced transpiration by 9% compared with the previous month and 18% compared with the 7-year mean in transpiration for the month of July (Figure 4, middle panel). On an annual basis, total transpiration was comparable among years, but declined in 2010 and 2011 due to mortality and severe drought (Table II, Figure 4). Seasonally, transpiration varied from year to year, whereby a large reduction in transpiration on a monthly basis was observed during the gypsy moth defoliation in 2007 and during the prolonged, more severe drought in 2010. Transpiration was reduced to a greater extent during defoliation and subsequent recovery of foliage and thus transpiration, than during the periods of droughts (Figure 4, middle panel). In 2007, maximum sap flux occurred following defoliation (Schäfer *et al.*, 2010), compensating for lost foliage and likely capitalizing on higher water availability due to reduced competition. Although there was also a drought period in early summer 2011, transpiration did not decline as drastically as in July 2010. This is likely because the 2011 drought occurred earlier in the season, and transpiration rates were already lower compared with the previous years (Figure 4, middle panel).

DISCUSSION

Transpiration and water balance

Throughout the study period, a range of conditions including defoliation and drought were observed which allowed their effects on tree transpiration to be assessed in an upland oak/pine forest on the Atlantic Coastal Plain. Long-term forest transpiration and hydrologic balance studies incorporating drought and disturbance are scarce, thus comparison with other studies is difficult. Phillips and Oren (2001) observed a relative conservation of forest transpiration throughout their 4-year study in pine-dominated forests in the North Carolina Atlantic Coastal Plain. However, the relative contribution to the overall transpiration of the measured species changed, whereby understory species were outcompeted by overstory ones. Similarly, in this forest stand, *Q. prinus* seems to capitalize on more water availability due to removal of competition through mortality as evidenced by its increase in growth (Table I). In a nearby pine forest stand, a reduction in understory competition due to fire

increased water use by overstory pines, maintaining overall stand water use (Renninger *et al*., 2013). Yet, the overall transpiration in the oak/pine stand declined over the 7-year period (Table II). Therefore, mortality and thus loss of sapwood area has consequences for stand transpiration and thus the overall water budget partitioning in this oak/pine forest. As these trees are growing on sandy soil, water savings due to reduced transpiration should translate to increased drainage and greater groundwater replenishment or, alternatively, increase water use by the surviving trees and understory, yielding no overall savings on the stand level (Stephens *et al*., 1972). At the beginning of the study, compensation had occurred in 2008 and 2009. However, at the end of the study a reduction in transpiration was observed, as remaining trees did not capitalize on additional water available due to the mortality in the stand. This is also partly due to a significant portion of P occurring during leaf-off times when most water drains out of the watershed instead being taken up (Figure 4 and Figure 5, Table II). This biannual cycle is also reflected in streamwater discharge and its covariance with E_C (Figure 5). The highest positive correlation occurs in summer and the highest negative correlation in winter, when there are less leaves and more P likely to drain, resulting in more streamwater discharge. The positive correlation signifies lower discharge with higher transpiration (Figure 5).

Transpiration as a fraction of ET is within the range previously found in forests where E_C and ET were measured (Wullschleger *et al*., 2000; Wilson *et al*., 2001; Schäfer *et al*., 2002) giving confidence to both forest water component estimates. However, it should be noted that the eddy covariance technique measures varying footprints depending on wind direction and thus a mismatch can exist between the sap flux measurement plot and the eddy covariance footprint (Stoy *et al*., 2006; Oishi *et al*., 2008). In addition, the understory, which can contribute considerably to overall ET, is not considered in the E_C estimates (Starr *et al*., 2005). Understory transpiration could be significant in this system especially because hydraulic lift is occurring in this forest (Robinson *et al*., 2012), potentially contributing to understory water availability (Domec *et al*., 2010). Considering that a larger fraction of the basal area or A_S:A_G in this forest consists of older trees, the lower E_C is not surprising as has been found previously in older-growth forests (Schäfer *et al*., 2000; Moore *et al*., 2004). In addition, sandy soil is not conducive to high-transpiration rates as it has very low soil water holding capacity and nutrient retention and would require additional irrigation and/or fertilization to have an appreciable impact on transpiration (Ewers *et al*., 2000; Ewers *et al*., 2001) and accordingly plant carbon uptake (Schulze, 2006).

Effects of defoliation and drought

As was previously shown in this forest, the different oak species responded differently to drought and defoliation with *Q. prinus* capitalizing on the increased water availability and showing less susceptibility to mortality after gypsy moth defoliation than *Q. velutina* or *Q. coccinea* (Schäfer, 2011). Also, after a short recovery period (2008/2009), the drought that occurred (2010) most severely affected *Q. velutina* and *Q. coccinea*, but had little effect on *Q. prinus*. Abrams (1990) and Hanson and Weltzin (2000) already showed that plant–plant interactions are of crucial importance to understand forest community dynamics in the face of climate change that could potentially increase the severity and frequency of drought events in North America (Seager *et al*., 2013). Furthermore, a temperature increase may hasten mortality of trees under drought stress (Dale *et al*., 2000; Adams *et al*., 2009; Allen *et al*., 2010). Decreased foliage, due to defoliation compounded by subsequent mortality and reduced foliage thereafter, increases the radiation load in lower parts of the canopy and lowers the cooling ability through transpiration, thus increasing local temperature, particularly in the soil, as has been demonstrated in this forest (Clark *et al*., 2012). Thus, the partitioning of latent to sensible heat fluxes was altered (Maness *et al*., 2013). Consequently, heightened heat stress may have contributed to increased mortality later in the study period. In addition, trees that resprout after defoliation are at a disadvantage considering they have smaller carbon reserves available for allocation to fine root production and may have leaves in a position that have more hydraulic resistance than 'normally' distributed leaves.

Compensatory mechanisms after defoliation have been previously shown (Stephens *et al*., 1972; Vanderklein and Reich, 1999), which help plants to accrue carbon reserves in order to survive. However, considering similar photosynthetic capacity and leaf area (Schäfer *et al*., 2010), but different stomatal conductance of these species (Schäfer, 2011), it is conceivable that *Q. prinus* has a growth advantage over *Q. velutina* and *Q. coccinea* under prolonged drought conditions, potentially outcompeting both over longer time scales. The soil in the upland forests of the New Jersey Pinelands is characterized as sandy; therefore, the resistance to soil evaporation increases dramatically as the upper soil layers dry. If oaks have access to deeper, moister soil layers or access to the water table at about 7 m, they can survive occasional drought periods (Figure 4). In fact, *Quercus* species have been shown to grow roots up to 18-m deep (Jackson *et al*., 1999), and at this stand, we have shown evidence for hydraulic lift (Robinson *et al*., 2012) increasing the possibility for access to water in deeper soil layers. However, as Hacke *et al*. (2001) also

demonstrated, recurring cavitation and refilling will cause 'cavitation fatigue' and may, therefore, result in carryover effects from the previous drought episodes. Consequently, drought may become increasingly severe for these trees leading to more mortality (Anderegg *et al*., 2013). Whether the xylem and thus water transport are viewed as a bundle of pipes (Tyree and Ewers, 1991) or as a porous media (Bohrer *et al*., 2005) and modelled accordingly, the question still remains as to the degree to which the water transport system is irreparably damaged leading to the death of the tree (Sperry *et al*., 1993; Sperry, 2000; Plaut *et al*., 2012; Anderegg *et al*., 2013). The mechanism of drought-induced mortality and whether it is due to hydraulic failure *per se* or due to carbon starvation because of stomatal closure is still subject to debate (McDowell *et al*., 2008). Future study using the finite element tree crown hydrodynamics model (Bohrer *et al*., 2005) could elucidate the potential mechanism underlying drought-induced mortality.

The reduction in transpiration in 2011 was primarily due to reduced A_S:A_G at the site and not reduced sap flux density (Table I). Whether these trees had died in summer of 2010, and thus whether transpiration may have been overestimated for part of the season is not clear. Also, problematic in scaling sap flux densities to stand transpiration is the estimation of sapwood area and not hydroactive xylem *per se* as functional xylem area can change diurnally and seasonally with cavitation and refilling cycles. Thus, seasonal and interannual differences may also partly be due to overestimation or underestimation of A_S:A_G as this is the crucial factor in scaling. Nevertheless, the trends are clear that drought and defoliation cause a reduction in transpiration and may be responsible for the mortality in this forest as previously noted (Schäfer *et al*., 2010; Schäfer, 2011). Also, there may be a synergy between defoliation and drought, because trees already weakened by gypsy moth defoliation may be at an increased risk of mortality when drought occurs and are potentially exacerbated through heat stress as well. Indeed, in modelling growth and mortality in this forest, drought caused, on average, a 6% mortality (Medvigy *et al*., 2012) consistent with global datasets on drought-induced mortality in temperate broadleaf forests (Allen *et al*., 2010). Historically, 4–10% mortality was recorded in the New England area due to gypsy moth defoliation (Baker, 1941). Therefore, an overall reduction of one third lower basal area found here (Schäfer, 2011) provides further evidence for a synergistic effect between both events (Rouault *et al*., 2006; Bréda and Badeau, 2008). It has been shown that reduced carbon reserves due to drought may also make trees more susceptible to insect attack due to reduced secondary metabolite defenses providing further evidence for a synergistic effect (Bréda and Badeau, 2008).

Global climate change predictions indicate that (1) precipitation patterns will change (Karl *et al*., 2009; Seager *et al*., 2013), (2) trees may be exposed to more insect pests (Jönsson *et al*., 2009) and (3) heat or higher temperature combined with drought will exacerbate mortality in trees (Adams *et al*., 2009). This could result in greater mortality in oak/pine forests on the Atlantic Coastal Plain in the future, leading to potential shifts in species composition. Oaks, as well as the pines, in these forest stands are drought-adapted; therefore, resilience of these ecosystems may be possible. However, changes in energy partitioning in this ecosystem could have an impact on regional climate as well (Li and Avissar, 1994; Marland *et al*., 2003) and potentially create a positive feedback between drought-heat-gypsy moth disturbance (Hanson and Weltzin, 2000). Overall, forest catchment water recharge and thus water availability will likely change with changing climate concomitant with increasing populations and their water usage. Thus, land management will need to adapt accordingly. The overall stream discharge throughout this study period was, on average, 18% less than previously reported values (Table II) (Cauller and Carleton, 2005; Walker *et al*., 2011), potentially because of increased ET due to recovery from historic disturbances in the watershed (Sumner *et al*., 2012) or a decrease in recharge.

CONCLUSIONS

Our original hypothesis that defoliation and drought with subsequent mortality of trees would significantly alter the hydrologic balance in this forest ecosystem was not confirmed. The overall recharge rates do not seem to be dramatically altered due to mortality in this forest, probably because of compensation from surviving trees and increased understory water consumption. However, severe drought reduced transpiration more dramatically the second time during the study period after a defoliation event had occurred. Therefore, the groundwater levels dropped more significantly due to lack of P and not forest water uptake. Thus, weather variations apparently exert an overriding effect to biological changes, thus it is likely that climate change will cause more changes to the groundwater table and thus water supply to humans in this region (Stoy *et al*., 2006). The forest composition will likely be altered by future droughts and gypsy moth defoliation and the changes in energy partitioning could potentially have impacts for regional climate in this forest ecosystem (Clark *et al*., 2012; Medvigy *et al*., 2012). It is predicted that, in the future, ET may exceed P in this part of the USA, potentially impacting forest ecosystem functioning and the underlying aquifer (Seager *et al*., 2013).

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