Water use by eastern hemlock (*Tsuga canadensis*) and black birch (*Betula lenta*): implications of effects of the hemlock woolly adelgid

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Abstract: Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a coniferous evergreen species found across the northeastern United States that is currently threatened by the exotic pest hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). As HWA kills eastern hemlock trees, black birch (*Betula lenta* L.) has been found to be a dominant replacement species in the region. Seasonal changes in water use by eastern hemlock and black birch were investigated utilizing whole-tree transpiration measurement techniques. Annual evapotranspiration in an eastern hemlock and deciduous stand was also estimated. During the peak growing season, daily rates of transpiration were 1.6 times greater in black birch. Cumulative transpiration in black birch exceeded hemlock transpiration by 77 mm from June until October. During the dormant season, evapotranspiration rates were higher in the hemlock stand; however, estimated annual evapotranspiration was 327 mm in eastern hemlock compared with 417 mm in the deciduous stand. Our results suggest that a transition from a hemlock-dominated to a black birch-dominated stand will alter the annual water balance with the greatest impact occurring during the peak growing season. Late in the growing season, flow may be unsustainable in streams that normally have light or moderate flow because ofincreased water use by black birch.

Résumé : La pruche du Canada (*Tsuga canadensis* (L.) Carr.) qui est une espèce de conifère à feuilles persistantes présente partout dans le nord-est des États-Unis est présentement menacée par un ravageur exotique, le puceron lanigère de la pruche (*Adelges tsugae* Annand). À mesure que le puceron tue les pruches du Canada, le bouleau flexible (*Betula lenta* L.) est l'espèce qui remplace le plus souvent la pruche dans la région. Les variations saisonnières dans l'utilisation de l'eau par la pruche du Canada et le bouleau flexible ont été étudiées à l'aide de techniques de mesure globale de la transpiration des arbres. L'évapotranspiration annuelle dans un peuplement de pruche du Canada et d'essences feuillues a aussi été estimée. Au plus fort de la saison de croissance, le taux journalier de transpiration était 1,6 fois plus élevé chez le bouleau flexible. La transpiration cumulative du bouleau flexible a excédé la transpiration de la pruche de 77 mm de juin à octobre. Pendant la saison dormante, l'évapotranspiration était plus élevée dans le peuplement de pruche. Cependant, l'évapotranspiration annuelle a été estimée à 327 mm chez la pruche du Canada comparativement à 417 mm dans le peuplement feuillu. Nos résultats indiquent que la transition d'un peuplement dominé par la pruche à un peuplement dominé par le bouleau flexible modifiera le bilan hydrique annuel et que l'impact le plus important surviendra au plus fort de la saison de croissance. Tard dans la saison de croissance, le débit dans les cours d'eau qui ont normalement un débit faible à modéré pourrait ne pas se maintenir à cause d'une plus forte utilisation d'eau par le bouleau flexible.

[Traduit par la Rédaction]

Introduction

Biological disturbances such as those due to the introduction of exotic pests and pathogens can result in the selective loss and replacement of a tree species at a regional scale, resulting in significant changes to ecosystem composition and processes (Castello et al. 1995; Liebhold et al. 1995). As the physiological ecology of each species is unique, changes in ecosystem composition may impact ecosystem processes such as the cycling of carbon and water (Catovsky et al. 2002; Wedin and Tilman 1996). Across the northeastern United States (US), the exotic pest hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) is rapidly altering the composition of eastern hemlock stands (*Tsuga canadensis* (L). Carr.). There is much interest in understanding the ecosystem impacts of the loss and replacement of eastern hemlock due to this exotic pest (e.g., Jenkins et al. 1999; Eschtruth et al. 2006). Evapotranspiration (ET) and its key component transpiration have large potential to be impacted by replacement of hemlock and are the focus of this study.

The ecological community and ecosystem associated with eastern hemlock trees is unique. This coniferous evergreen species is one of the most long-lived and shade-tolerant species found in its range. Trees may take 250 to 300 years to reach reproductive maturity and may live to be over 800 years old (Burns and Honkala 1990). The dense stands that develop typically only allow small amounts of incoming sunlight to reach the understory (Hadley 2000*b*), creating a

Received 31 August 2006. Accepted 23 February 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 27 October 2007.

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doi:10.1139/X07-045

unique microclimate. In addition, the soils under hemlock trees have characteristically low pH, high carbon to nitrogen ratios, and low rates of nitrogen mineralization and nitrification (Mladenoff 1987). Development of other species in the understory is severely constrained, often resulting in nearly pure hemlock stands. Because of these factors, eastern hemlock creates stable local conditions, modulates ecosystem processes, and is considered a foundation species (Ellison et al. 2005).

Eastern hemlock stands are currently threatened by the exotic pest hemlock woolly adelgid (HWA), an aphid-like insect native to Asia that feeds on needles of eastern hemlock. Trees can die within 4–15 years of infestation (Orwig et al. 2002; McClure 1991). In New England, eastern hemlock is largely being replaced by black birch (*Betula lenta* L.), a deciduous seral species (Orwig and Foster 1998; Orwig et al. 2002; Catovsky and Bazzaz 2000). In Connecticut forests where heavy HWA infestation has occurred, up to 75% of trees found in replacement forests are black birch trees, although other deciduous species such as red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.) have also been found in the gaps left by hemlock mortality (Orwig 2002; Kittredge and Ashton 1990; Smith and Ashton 1993; Ward and Stephens 1996). The replacement of eastern hemlock, a late successional species, by black birch represents an extreme change in the morphological, phenological, and physiological characteristics of the ecosystem (Bazzaz 1979).

As forest infestations from exotic pests and pathogens are expected to increase over the next century (Enserink 1999), the decline of eastern hemlock provides a unique opportunity to increase our understanding of the impacts that exotic pests and pathogens can have on ecosystem processes. The objective of this study was to assess the impact of the loss and replacement of eastern hemlock on key components of ecosystem water use. First, as more than two-thirds of precipitation in the US is returned to the atmosphere via transpiration from plants (Dunne and Leopold 1978), this research utilized whole-tree measurement techniques to estimate transpiration at the species level. Second, as the loss and replacement of eastern hemlock represents a shift from an evergreen coniferous forest to a broad-leaved deciduous forest, seasonal and annual evapotranspiration were estimated in an eastern hemlock and deciduous stand. Based on known attributes of early and late successional species (Bazzaz 1979), we hypothesized that transpiration during the growing season is greater in early successional, black birch compared with late successional, eastern hemlock. Further, during the nongrowing season, evapotranspiration will be greater in hemlock stands than in deciduous stands because of hemlock's maintenance of foliage.

Materials and methods

Study sites

All research was conducted in two stands in the Prospect Hill tract of Harvard Forest, Petersham, Massachusetts (42°32′N, 72°10′W, elevation 340 m). Harvard Forest has an average annual precipitation of 1050 mm and a mean annual temperature of 8.5 °C. Study sites were established in a hemlock stand and in a plot dominated by black birch in the mixed deciduous stand on Little Prospect Hill. The hemlock stand is a climax forest dominated by eastern hemlock and is about 7 ha in area (Hadley and Schedlbauer 2002). As shown in Table 1, 84% of the basal area within 100 m of the eddy covariance tower is eastern hemlock, with the remainder of the stand consisting of scattered hardwoods and white pine (*Pinus strobus* L.). The area referred to as Little Prospect Hill is a mixed deciduous stand dominated by red oak (Table 1). Other species found in the stand include black birch, red maple, paper birch (*Betula papyrifera* Marsh.), red pine (*Pinus resinosa* Ait.), white pine, and eastern hemlock. Because of the key role played by black birch in replacement of hemlock, within the Little Prospect Hill stand, we selected for measurement a plot dominated by black birch. In both the hemlock stand and the Little Prospect Hill stand, eddy covariance systems monitored ecosystem gas exchange including carbon and water fluxes. Both sites are located under 1.0 km from the Fisher Meteorological Station, which is equipped with CS500 temperature and relative humidity probes (Campbell Scientific, Logan, Utah), a LI-COR 190 SA quantum sensor (LI-COR Inc., Lincoln, Nebraska) to measure photosynthetically active radiation (PAR), and a Met One 385 heated rain gage (Met One, Grant Pass, Oregon) to measure precipitation.

Table 1. The percent of basal area 0–100 m from the hemlock and deciduous eddy covariance towers.

Species	Basal area (%) Hemlock stand	Basal area (%) Deciduous stand
Tsuga canadensis	84	6
Betula lenta	3	4
Quercus rubra	2	54
Acer rubrum	4	7
Pinus strobus	6	11
Pinus resinosa	—	11
Betula papyrifera	—	3

Transpiration measurements

We estimated whole-tree and crown transpiration with sap flux measurements. Constant-heat sap flux sensors (Granier 1985) were installed in eight eastern hemlock trees within the hemlock stand, within 20 m of the eddy covariance tower (Table 2). Similarly, sap flux sensors were installed in eight black birch trees located in the Little Prospect Hill stand 300–400 m from the deciduous stand eddy covariance tower. The trees selected for measurement were located within 20 m of the available power source. All trees were canopy dominants and chosen to be representative of dominant trees in the stand. The sensors were 20 mm long and contained a copper–constantan thermocouple junction. In each tree, at least two sets of sensors were installed on opposite sides of the tree to account for circumferential variability. All sensors were protected from precipitation and moisture by shielding with plastic containers. Additionally, the sensors were surrounded by reflective insulation to prevent direct solar heating and to minimize the effects of environmental temperature variations.

Measurements of sap flux are widely used to estimate whole-tree and canopy transpiration (Wullschleger et al.

Table 2. Diameter at breast height (DBH), sapwood depth, sapwood area, and projected crown area of the trees selected for study at Harvard Forest, Mass.

Tree no.	Species	DBH (cm)	Sapwood depth (cm)	Sapwood area (cm^2)	Projected crown area (m^2)
1	Hemlock	39.3	4.9	458	10.0
2	Hemlock	77.7	9.7	1941	65.0
3	Hemlock	67.8	8.5	1377	33.6
4	Hemlock	44.6	5.6	667	21.5
5	Hemlock	52.9	6.6	901	31.2
6	Hemlock	52.9	6.6	897	32.1
7	Hemlock	45.7	5.7	652	28.9
8	Hemlock	52.2	6.5	884	43.0
1	Black birch	12.2	6.0	113	23.4
2	Black birch	30.5	7.1	506	21.7
3	Black birch	18.9	6.3	237	24.2
4	Black birch	42.5	11.1	1050	31.6
5	Black birch	22.8	9.1	384	10.7
6	Black birch	24.2	7.3	365	15.2
7	Black birch	33.0	11.3	739	23.4
8	Black birch	27.4	7.3	409	14.9

1998). Many studies assume that sap flux is constant across the sapwood-conducting area when scaling to the whole tree (e.g., Catovsky et al. 2002; Phillips et al. 2003). However, this simplifying assumption does not hold for many species (Hatton et al. 1990; Phillips et al. 1996; Wullschleger and King 2000). Using this scaling assumption may significantly overestimate the magnitude of transpiration as sap flux velocities are often greatest in the outer sapwood (Wullschleger and King 2000). To account for radial flow, inner sap flux sensors were installed in three trees of each species. Deep sap flux sensors were built based on the designs of Ford et al. (2004), James et al. (2002), and Spicer and Holbrook (2005). To capture the difference in the radial profile in sap flux, 10 mm long sensors were positioned 3–4 and 4–5 cm from the cambium in black birch and 3–4, 4–5, and 5–6 cm in eastern hemlock.

Sap flux (g $H_2O\cdot(m^2$ sapwood area$)^{-1}\cdot s^{-1}$) was calculated using an empirical calibration equation (Granier 1985). Granier found that

$$[1] \qquad u = 119 \times 10^{-6} K^{1.23}$$

where u is sap flux density ($m^3\cdot m^{-2}\cdot s^{-1}$) and K is related to the temperature difference between the two probes:

$$[2] \qquad K = \frac{(\Delta T_{\mathrm{m}} - \Delta T)}{\Delta T}$$

where K is sap flux index, ΔT is the temperature difference between heated and reference probe, and ΔT_{m} is the temperature when there is no sap flux density ($u = 0$). The zero sap flux condition was assumed to occur during extended periods of zero vapor pressure deficit at night.

Data-logging in both stands started in August 2004. Data was collected every 30 s averaged into 1-min intervals using a CR10X or CR23X datalogger (Campbell Scientific). Measurements collected from 24 August to 19 September (days of year 237 to 263) were referred to as late season throughout the analysis. Data collected from 20 September to 13 October (days of year 264 to 287) were labeled leaf-fall season based on observations of leaf abscission in black birch during 2004 (J. O'Keefe, unpublished data). Damaged sensors were replaced in the spring of 2005 and operated until late July of the same season. The time period of 18 June to 26 July (days of year 169 to 207) was collectively referred to as the peak growing season. The peak growing season was defined based on the availability of data. Because of damage to multiplexors and solar power issues, data were not collected in the black birch stand from 13 October to 18 June. On 27 July 2005, lightning damage ended data collection at the eastern hemlock site.

Data analysis

An analysis was conducted to calculate total sap flow based on the methods described by Lu et al. (2000). The total flow at breast height ($g\cdot s^{-1}$) was found using

$$[3] \qquad F_{\mathrm{total}} = F_{\mathrm{in}} + F_{\mathrm{out}}$$

where F_{total} is the total flow for a cross section of a tree, F_{in} is flow rate from a depth of 2 cm to the heartwood–sapwood boundary, and F_{out} is the flow rate at 0–2 cm depth as measured from the cambium. The outer flow rate F_{out} was calculated using the following:

$$[4] \qquad F_{\mathrm{out}} = \text{flux density} \times \text{sapwood area}$$

$$[5] \qquad F_{\mathrm{out}} = J_{s_{0-2\ \mathrm{cm}}}[\pi R^2 - \pi(R - 0.02)^2]$$

where J_s is the sap flux rate ($g\cdot m^{-2}\cdot s^{-1}$) and R is the radius of the tree stem (m) minus the bark thickness. The flow rate at the inner depths (F_{in}) was calculated using

$$[6] \qquad F_{\mathrm{in}} = \int_{0.02}^{R} (\text{flux density} \times \text{circumference})\mathrm{d}x$$

where R is the sapwood depth (m). Sap flux sensors positioned deep in the sapwood indicated that sap flux decreased with depth in both species. However, sufficient depth measurements were not obtained to generate a sap flux profile. In both species, a linear decrease in sap flux with depth was applied using

$$[7]\qquad F_{\mathrm{in}} = \int_{0.02}^{R} J_s(1.125 - 12.0x)2\pi(R - x)\mathrm{d}x$$

The total quantity of water flow (in grams per day) was found using total flow (F_{total}) and time (in seconds). Many approaches to scaling whole-tree transpiration measurements to the stand level have been taken, including using sapwood area (e.g., Phillips and Oren 2001), basal area (e.g., Teskey and Sheriff 1996), canopy position (e.g., Granier 1987), and leaf area (e.g., Hatton et al. 1995). Scaling transpiration based on projected crown area is frequently used in ecosystem water use studies to maintain a ground area basis, particularly when measurements in pure plots are unattainable (e.g., Hatton et al. 1995; Oren et al. 1996; Catovsky et al. 2002). This scaling approach was selected for this study as our research question considered the replacement of an eastern hemlock stand by an equal area of black birch. The total flow (in grams), as measured by our sap flux sensors, was divided by the projected crown area (in square metres) of the tree and converted to hydrologic units (in millimetres). The projected crown area was found using the distance to the edge of the crown in eight directions from the stem. For gaps in transpiration data from June until August 2004, we created a multiple regression model using transpiration, daytime vapor pressure deficit (VPD), and daytime PAR data from June and July of 2005. The black birch model (R^2 = 0.91, p <0.0001) and hemlock model (R^2 = 0.84, p <0.0001) was run using VPD and PAR data from 2004 to fill in gaps.

The Student's paired t test was used to compare daily transpiration rates in eastern hemlock and black birch. Regression analysis was done using curve fit functions in Sigma Plot (Systat Software, Inc., San Jose, Calif.).

Evapotranspiration measurements

The eddy covariance or eddy flux technique (Baldocchi et al. 1988) was used to measure ET from both the hemlock and deciduous stands on Little Prospect Hill. Sonic anemometers to measure three-dimensional wind (CSAT-3; Campbell Scientific Inc., Logan, Utah) and intake ports for air samples were located approximately 5 m above the average canopy surface level at each site. An eddy flux footprint model (FSAM; Schmid 1994) was modified to estimate flux source areas for sampling points relatively close to the canopy surface. Footprint lengths for 80% of the measured gas fluxes during daytime typically ranged from 200 to 800 m for the eddy flux system in the hemlock stand (Hadley and Schedlbauer 2002). However, the presence of scattered white pines at least 30 m tall, higher than the level of the eddy covariance system, probably limited footprint lengths to near the lower end of the 200–800 m range. The FSAM model indicated similar footprint lengths for gas fluxes measured during daytime at the Little Prospect Hill site, but without the limiting influence of emergent tall trees. As nearly all ET was observed to occur during daylight hours, these footprint lengths include the relevant source areas for ET estimates.

Air was drawn to closed-path CO_2–H_2O analyzers (model LI-6262 or LI-7000; LI-COR Inc., Lincoln, Nebraska) in instrument shelters near the ground, and data were logged at 5 Hz. Covariances between vertical wind and CO_2 and H_2O concentrations were calculated every 30 min using deviations from 10-min running means. The proper time interval between measurement of wind vectors and gas concentrations that allowed for air sample transport from the intake point to the analyzer (the "lag time") was recalculated periodically by determining the lag times resulting in maximum covariance of H_2O concentration with vertical wind. To separate turbulent vertical transport from advection by mean flow along the streamlines, the coordinate plane of wind direction at both sites was rotated each half hour so that mean vertical wind was zero.

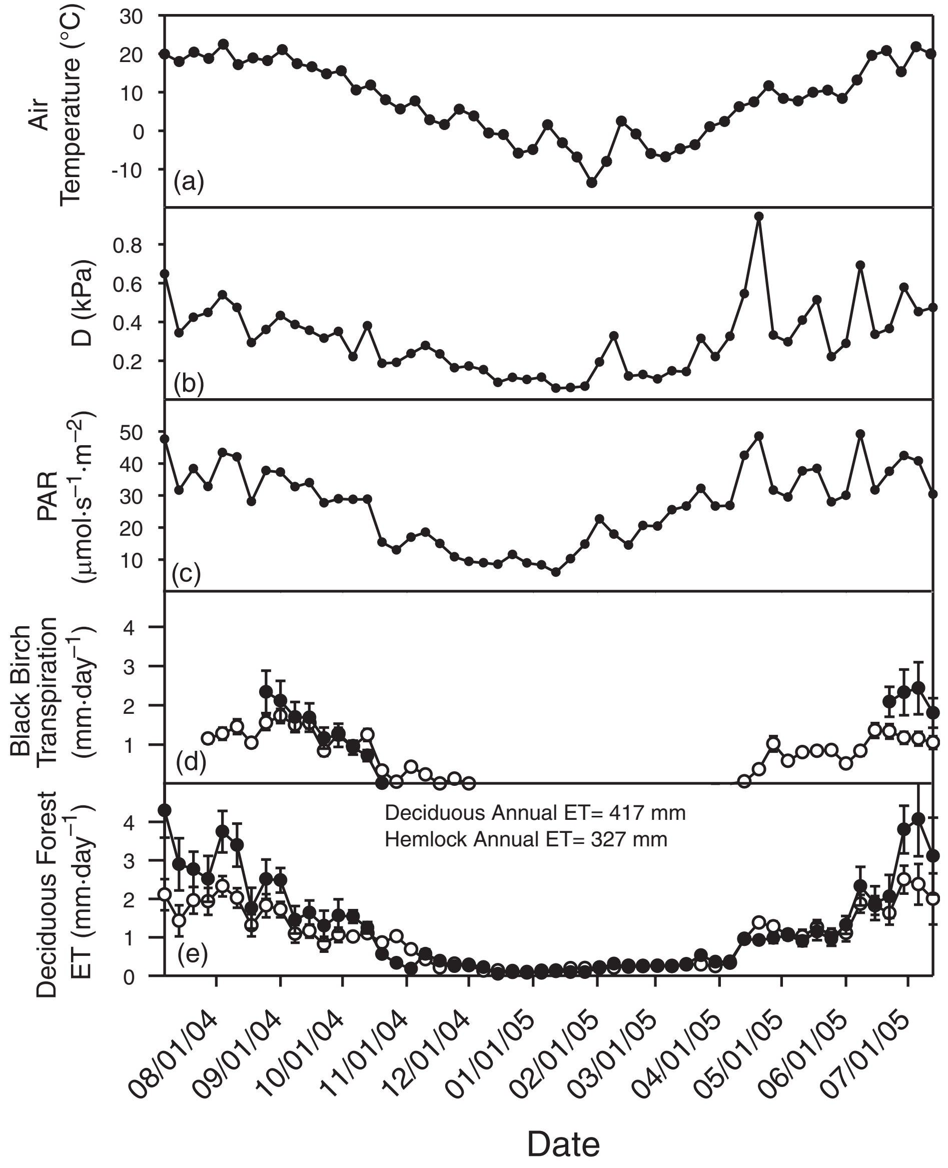
Eddy flux measurements using closed-path analyzers can underestimate ET, because small, high-frequency variations in water concentration are blurred during transport of air samples from the intake point above the forest to a gas analyzer at ground level. The extent to which this occurred was checked by a spectral correction procedure (Goulden et al. 1996) in which power spectra of sonic air temperature and CO_2 and H_2O concentrations are compared to determine a mathematical filtering for the temperature signal that matches the smoothing of CO_2 and H_2O signals resulting from gas mixing and adsorption or desorption of water vapor in the gas inlet line, plus electrical smoothing by the CO_2–H_2O analyzer. The ratio of original and smoothed temperature covariance with vertical wind is taken as an estimate of the CO_2 or H_2O covariance lost by attenuation of higher frequency variations. Corrections for loss of high-frequency flux using this procedure typically increased short-term and cumulative ET estimates by about 15%.

At both hemlock and LPH sites, we also measured PAR, air temperature, and relative humidity above the canopy every 60 s, with averages calculated every 30 min. Soil temperature at 10 cm depth at five locations near the base of each flux tower was measured and averaged at the same time intervals.

Valid ET data from eddy flux measurements were often unavailable at both study sites because of the locations of the eddy flux towers. In the hemlock stand, the measurement tower is in the northeast corner of the stand, so that southwest wind was necessary for ET measurements, whereas on Little Prospect Hill, only upslope winds, with directions ranging from west–southwest to north, produce valid data. For the time periods when wind direction did not allow valid ET measurements, we estimated ET from statistical models created in S-PLUS® (Insightful Inc., Seattle, Wash.). These models were derived from data collected in periods of appropriate wind direction and turbulence level, along with other environmental data collected at the flux towers. Data used in each model spanned fairly short intervals (1–2 months) to reduce the chance that the important driving variables changed over the period of model derivation.

In most periods of the year, PAR explained 60% to 70% of the variation in ET at each site, and VPD explained about an additional 20%. The coefficients for PAR and VPD changed over the course of the year, most dramatically during leaf development and leaf abscission in the deciduous

Fig. 1. Seasonal patterns of (*a*) air temperature, (*b*) vapor pressure deficit (D), (*c*) photosynthetically active radiation (PAR), (*d*) transpiration per projected crown area, and (*e*) evapotransiration (ET). Points represent mean daily values averaged for 1-week intervals. Black birch daily transpiration and ET are represented by solid circles and eastern hemlock are represented by open circles. Error bars represent ±1 standard error for transpiration and ±1 standard deviation for ET. Plotted points represent weekly means. Dates given as month/day/year.



forest (during May and June and in October, respectively), but also more slowly during aging of deciduous foliage in late summer to early fall. In spring and fall, water flux for the hemlock forest was affected by the nighttime minimum temperature, which has been shown to affect leaf conductance in many conifers including hemlock (Smith et al. 1984; Hadley 2000*a*).

Results

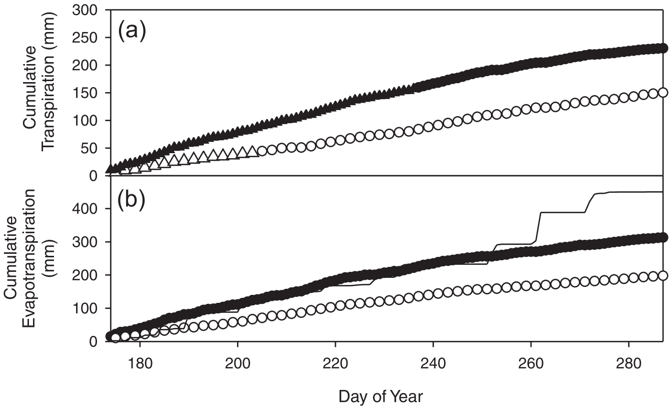
Annual evapotranspiration

The magnitude of transpiration and ET varied depending on the time of year, as well as on environmental conditions, including vapor pressure deficit, air temperature, and photosynthetically active radiation (Fig. 1). In June and July 2004, average ET by the deciduous forest on Little Prospect Hill was nearly twice that by the hemlock forest (Fig. 1). The difference in ET rates between the forests declined in late summer. For most of the period from leaf abscission in mid-October until deciduous leaves were fully developed again the following June, deciduous and hemlock forests used similar quantities of water, despite the presence of foliage on the hemlock trees and none on the deciduous trees (Fig. 1*e*). For the year from July 2004 through June 2005, the deciduous forest used about 90 mm more water than the hemlock forest (Fig. 1*e*). From late June 2004 until heavy rains in the second half of September (after day 260), water use in the deciduous forest was approximately equal to incoming precipitation, whereas hemlock forest water use was about 100 mm less (Fig. 2*b*).

Transpiration

During the peak growing season months of June and July, the mean transpiration rate was significantly greater

Fig. 2. (*a*) Cumulative transpiration per projected crown area in black birch (solid symbols) and eastern hemlock (open symbols) from June to October. Triangles represent data filled using multiple regression models, and circles represent measurements using sap flux sensors. (*b*) Cumulative evapotranspiration in the deciduous (solid circles) and eastern hemlock (open circles) stands based on estimates using the eddy covariance technique. Cumulative precipitation is also shown as a solid line.

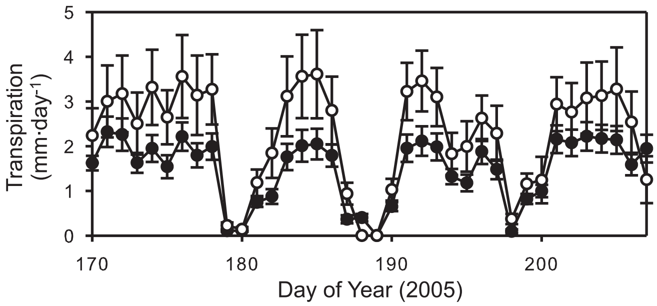


($p < 0.05$) in black birch than in eastern hemlock based on group mean comparison *t* test over the period shown in Fig. 3. Mean transpiration in black birch was 2.23 mm compared with 1.25 mm in hemlock. Cumulative transpiration per projected crown area was 77 mm greater in black birch than in eastern hemlock during June through October (Fig. 2*a*). As mean daytime temperature and mean daytime PAR gradually declined over the growing season (Fig. 1) and leaf abscission started in black birch, shifts in the relative magnitude of daily transpiration between black birch and eastern hemlock were observed (Fig. 4). On 21 June, peak rates (expressed per projected crown area) were 100 × 10^{-6} mm·s^{-1} (SE = 2.8 × 10^{-5}) in black birch compared with 58 × 10^{-6} mm·s^{-1} (SE = 1.3 × 10^{-5}) in eastern hemlock. In late August, just before leaf abscission, peak transpiration rates were nearly equal in the two species: the peak black birch rate was 81 × 10^{-6} mm·s^{-1} (SE = 1.7 × 10^{-5}), whereas eastern hemlock had a peak rate of 71 × 10^{-6} mm·s^{-1} (SE = 8.2 × 10^{-6}). Later in this period, after about 40% leaf fall in black birch (J. O'Keefe, unpublished data), there was a reversal in the relative magnitude of transpiration in black birch and eastern hemlock. On 9 October, peak transpiration rates were greater in eastern hemlock (69 × 10^{-6} mm·s^{-1}, SE = 9.0 × 10^{-6}) than in black birch (37 × 10^{-6} mm·s^{-1}, SE = 6.9 × 10^{-6}).

Total daily transpiration rates paralleled the patterns in peak transpiration. During the peak growing season, rates were 1.60 times greater in black birch than in eastern hemlock (Fig. 5). Daily transpiration was nearly equal during the late growing season in the two species. There was no significant difference in average daily transpiration in the late season between black birch and eastern hemlock. Daily transpiration rates during the fall were greater in eastern hemlock. During this overall period, there was a significant difference in transpiration between black birch and eastern hemlock: average daily transpiration was significantly greater ($p < 0.05$) in eastern hemlock.

Total transpiration per unit PAR was 19% greater in eastern hemlock than in black birch during the leaf-fall season (Fig. 6). This was a reversal of relative differences during the peak growing season, when transpiration per unit of PAR was greater in black birch. Fitting a sigmoidal curve shows a nearly linear decline in black birch transpiration per unit PAR near day 237, which we defined as the start of the late growing season. This decline was not seen in eastern hemlock until much later in the season near day 270.

Fig. 3. Daily patterns in transpiration per projected crown area in black birch (solid circles) and eastern hemlock (open circles) during a period of the peak growing season. Error bars represent ±1 standard error.



Discussion

Black birch is expected to be the dominant replacement species in declining hemlock stands across New England (Orwig 2002; Catovsky and Bazzaz 2000). In this study, we estimated the impact of species replacement on key components of ecosystem water use through measurements of transpiration and ET. Our hypothesis that transpiration during the growing season is greater in early successional, black birch trees compared with late successional, eastern hemlock trees was supported. During late fall, winter, and early spring, ET was similar in the two forests. This is likely because of very low evaporation in the heavily shaded understory of the hemlock forest (Hadley 2000*b*) compared with the sun-exposed understory of the leafless deciduous forest. As a result, we predict that loss and replacement of eastern hemlock by black birch has potential to alter the annual ecosystem water balance (Fig. 1).

Our results indicate that a transition from a hemlock to a black birch dominated stand will have the greatest impact on water balance during the peak growing season (Fig. 1) when transpiration is enhanced as a result of species replacement (Figs. 2, 3, and 4). The difference in transpiration between species is a function of the physiological controls exerted by vegetation and environmental forces. Generally, late successional species have high leaf resistances and low transpiration rates (Bazzaz 1979). Maximum leaf resistance to water vapor was found to be twice as high in eastern hemlock than in black birch during June and July in Harvard Forest (B. Hardiman and J. Hadley, unpublished data). Leaf resistance exerts large controls over whole-tree water flow (Jarvis and McNaughton 1986) and is likely a major factor in the greater transpiration rates measured in black birch during the peak growing season (Figs. 1, 3, 4, and 5). Differences in the hydraulic conductivity of sapwood may also affect transpiration rates (Lhomme 2001). The xylem anatomy in black birch is diffuse porous, whereas eastern hem-

Fig. 4. Diurnal pattern of transpiration rates expressed per projected crown area in black birch and eastern hemlock during (*a*) the peak growing season (21 June), (*b*) late growing season (29 August), and (*c*) fall (9 October). Transpiration is represented by solid circles for black birch and by open circles for eastern hemlock. Error bars represent ±1 standard error.

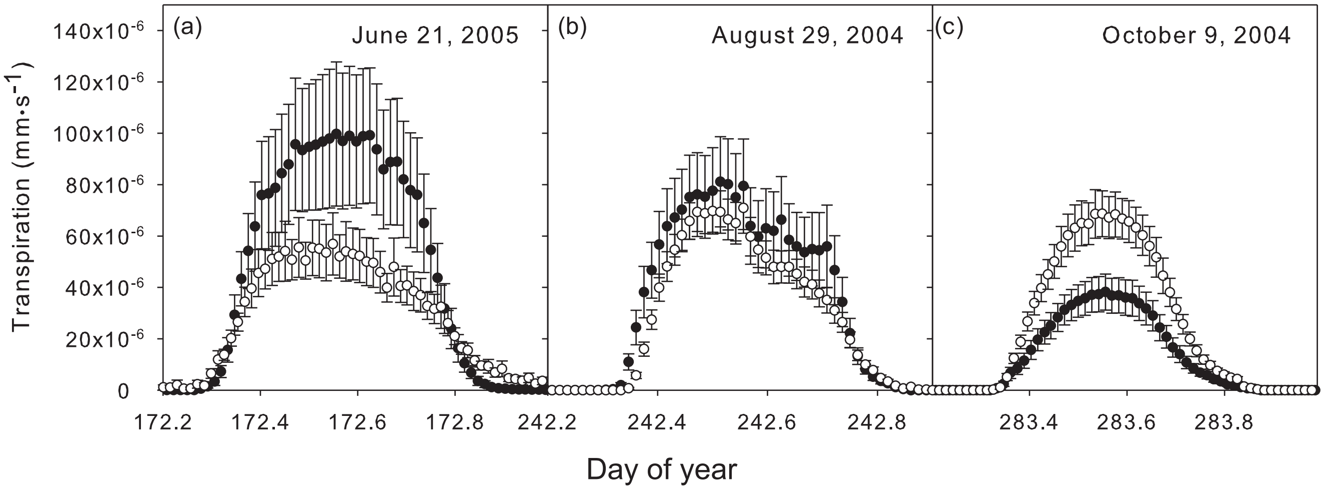
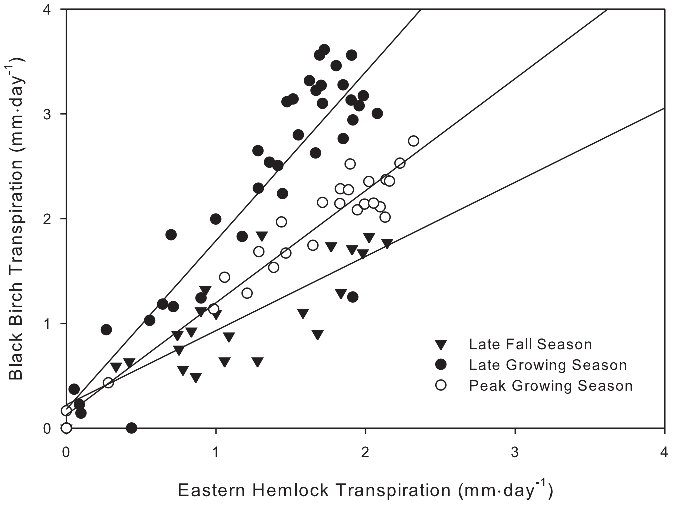
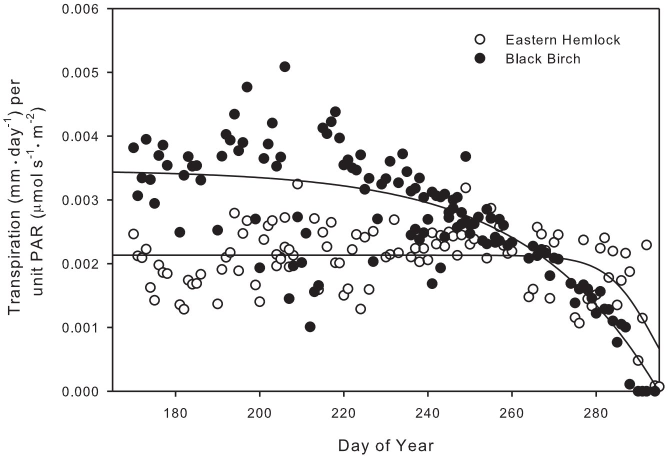


Fig. 5. The relationship between black birch and eastern hemlock daily transpiration during three periods of the growing season. During the peak growing season, the slope of the relationship is 1.60 ($r^2 = 0.81$), whereas during the late growing season and late fall season, slopes are 1.07 ($r^2 = 0.95$) and 0.70 ($r^2 = 0.67$), respectively. Fitted lines represent best-fit linear regressions.



lock has a tracheid anatomy. Deciduous diffuse porous species are capable of having a 10-fold greater hydraulic conductivity than evergreen conifers (Zimmermann and Brown 1971).

Fig. 6. Changes in transpiration per unit of photosynthetically active radiation (PAR) during the growing season. A sigmoidal curve is shown for each species.



Annual water flux rates have been found to be greater in some evergreen tree species compared with deciduous species because of the evergreens' ability to transpire during the dormant season (Jarvis and Leverenz 1983; Schulze et al. 1977). However, measurements from our eddy covariance system indicate that in Harvard Forest, ET from eastern hemlock ecosystems during the dormant season does not compensate for its lower flux rates during the growing season (Fig. 1). These results are consistent with conclusions by Catovsky et al. (2002) based on periodic transpiration measurements in hemlock, red oak, and red maple at Harvard Forest. Temperature, PAR, and VPD may regulate this pattern (Fig. 1). Although transpiration rates are greater in eastern hemlock late in the growing season (Figs. 1 and 5), transpiration in both species is observed to decrease with air temperature, VPD, and PAR during this time (Fig. 1). The decline in transpiration per unit of PAR around day 240 (Fig. 6) is surprising in black birch. This date is in late August and is still an opportune time for photosynthesis. Transpiration per unit vapor pressure deficit (*D*; data not shown) also decreased during this time, suggesting that leaf functioning was affected and the decline in transpiration was not simply due to changes in the environmental conditions.

Although transpiration is the dominant component of ecosystem ET, differences in interception evaporation between black birch and eastern hemlock may also influence ecosystem water balance. Interception was not measured in this study, and drawing conclusions based on forest type are difficult as rates are regulated by the type and intensity of rainfall and other meteorological conditions (Crockford and Richardson 2000). During the dormant season, precipitation falls to the surface in the leafless deciduous stand, whereas interception occurs in the canopy of the hemlock stand. However, from January through March when no transpiration was measured (Fig. 1), little difference in ET is observed between stands, suggesting evaporation rates are similar.

Eddy covariance systems were used in this study to quantify the differences in ET between hemlock and deciduous forests at Harvard. Our conclusions are limited as the vegetation in the deciduous stand measured by the eddy covariance system is dominated by red oak, not black birch (Table 1). Eddy covariance data from a black birch dominated ecosystem are currently not available. Our measurements from the deciduous stand provide a good indication of the impact of species replacement on ET during the nongrowing season as the interception and evaporation dynamics in a leafless red oak and black birch stand will be similar. During the growing season, water use in a red oak and black birch stand may also be similar as leaf conductance has been measured and found to be similar in red oak and black birch during the peak growing season (M. Daley, unpublished data).

Abrupt disturbances are not new to northeastern US ecosystems. A massive decline of eastern hemlock, hypothesized to be driven not only by climatic changes (Foster et al. 2006), but also by hemlock looper (*Lambdina fiscellaria* Gn.; Bhiry and Filion 1996; Davis 1981), occurred around 5000 years BP. Recovery from the disturbance took over 1000 years (Foster and Zebryk 1993). More recently, the exotic pathogen chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) eliminated American chestnut (*Castanea dentate* Marsh.) from northeastern forests during the early 1900s. Unlike the replacement of chestnut by oaks and other functionally similar hardwoods (Liebhold et al. 1995), the loss and replacement of eastern hemlock represents a substantial change in the transpiration processes of the ecosystem (Figs. 1 and 3). Based on water balance equations, an increase in transpiration must be compensated for by a combined reduction in stream outflow, groundwater outflow, and catchment water storage while holding precipitation and groundwater inflow constant.

The impacts of hemlock woolly adelgid on water cycling will be substantial at the local level. Although only 4% of the timberland area is eastern hemlock forest type in New England as a whole, in several counties of western Massachusetts, hemlock comprises over 12% of the timberland area (USDA Forest Service 2007). Although this may represent a limited fraction of the forest area in major watersheds, small headwater watersheds are often dominated by eastern hemlock as the species tends to occur in homogenous patches across the landscape. In the Connecticut River Valley of Massachusetts, hemlock stands mapped from aerial images range in area from 10 to 242 ha, averaging 51 ha (Orwig et al. 2002). Stands this size can encompass the entire area of small watersheds, particularly in hilly terrain.

Management plans must consider the potential shift in the timing and magnitude of water use as a result of eastern hemlock replacement. Our results indicate that a transition from a hemlock to a black birch dominated stand will result in a 30% increase in stand water transpiration from June through October (Fig. 2). Small streams draining from hemlock-dominated watersheds that would normally have a light or moderate flow during the late growing season will experience reduced flow and may cease flowing altogether as a result of increased water use by black birch trees. From June through early September, cumulative evapotranspiration in eastern hemlock was about 100 mm less than cumulative precipitation (Fig. 2*b*). However, cumulative evapotranspiration from the deciduous stand was nearly equal to cumulative precipitation. Stream flow in small catchments may be unsustainable as ET and precipitation are balanced. Evans (2004) found that small streams draining from hardwood forests are much more likely to dry up in summer than streams from hemlock forests. A shift in stream flow processes will affect stream macroinvertebrates (Snyder et al. 2002) and fish populations such as brook trout (*Salvelinus fontinalis* Mitchell) (Ross et al. 2003). Recreational opportunities and ecosystem services may be lost if water use by vegetation is not considered in management plans for stands affected by hemlock woolly adelgid.

Acknowledgements

This research was supported by a National Science Foundation Grant (Water Cycle Research EAR-0233643), a National Science Foundation Graduate Research Fellowship to MD, and the Harvard Forest Long-Term Ecological Research Program. We thank members of the Harvard Forest staff, including Paul Kuzeja, Lucas Griffith, Edythe Ellin, and Michael Scott, for their support and assistance. We also thank Rachel Spicer and Chelcy Ford for sharing advice on sap flux sensor construction.

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