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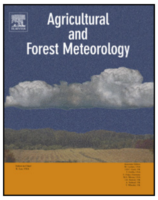

Sap flow of black ash in wetland forests of northern Minnesota, USA: Hydrologic implications of tree mortality due to emerald ash borer

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ABSTRACT

Black ash (*Fraxinus nigra*) mortality caused by the invasive emerald ash borer (EAB) is of concern to land managers in the upper Great Lakes region, given the large areas of ash-dominated forest and potential alteration of wetland hydrology following loss of this foundation tree species. The importance of changes in evapotranspiration (ET) following black ash mortality is currently unknown and is the focus of this study. Sap flux density rates were evaluated at three black ash stands with differing moisture regimes within the Chippewa National Forest, Minnesota, USA using the Granier thermal dissipation method. Sapwood area and sap flux density were combined to determine sap flow. Tree level sap flux density estimates were comparable to other reported values and averaged 4.59, 2.31, and 1.62 $m^3 m^{-2} day^{-1}$, respectively, for the very wet, wet, and moderately wet field sites. However, black ash exhibited small sapwood area in general, resulting in lower overall sap flow values. Scaled stand-level transpiration followed a similar trend as the tree-level estimates; mean daily transpiration over 10 weeks was 1.62 (80% of PET), 1.15 (53% of PET), and 0.90 (42% of PET) mm for the very wet, wet, and moderately wet site, respectively. Sap flux density was positively related to vapor pressure deficit when soil moisture was at or near saturation and negatively related when soil moisture content was lower. There was also a significant positive relationship between sap flux density and relative soil moisture saturation at the stand scale. Our results indicate that hydrologic regime has substantial influence on sap flow with highest transpiration when soil moisture is at saturation, underscoring the unique ecological role that black ash plays in these wetland forest types. The effects of EAB-induced black ash mortality on overall ET and related hydrologic processes will likely be greatest in the wettest hydrologic regimes.

1. Introduction

Black ash (*Fraxinus nigra*) is a common ring porous tree species found in forested wetlands in the northern Lake States (Michigan, Minnesota, and Wisconsin). This species is under threat of extirpation following the introduction of the invasive emerald ash borer (EAB; *Agrilus planipennis*), which girdles ash trees and causes stand mortality within 3–5 years of infestation (Gandhi et al., 2008). Since its discovery in 2002, EAB has spread rapidly and caused extensive economic and ecological damage throughout North America (Kovacs et al., 2010; Gandhi and Herms, 2010). In Minnesota, there is particular concern that EAB will have large impacts on black ash wetlands because the species occurs in almost pure stands on poorly drained sites across more than 400,000 ha (MN DNR, 2003). In particular, changes in hydrology following ash mortality are likely, potentially leading to changes in species composition and a shift to a non-forested ecosystem state (Toner and Keddy, 1997). Despite the widespread occurrence of black ash wetlands and the impending EAB threat, the likelihood and magnitude of changes in wetland hydrology following black ash loss is currently unknown.

One likely mechanism where loss of the black ash overstory would alter hydrological processes is through a reduction in overall stand transpiration. Transpiration is an important component of the water budget for plant-dominated environments as it is a

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primary component of evapotranspiration (ET) (Tang et al., 2006; Ford et al., 2010; Oishi et al., 2010). In forested wetlands with minimal groundwater or surface flow inputs, transpiration may be a particularly important controller of site hydrology, but the relative contribution of trees compared to other vegetation likely varies depending on species and site characteristics. Understanding the contribution of overstory trees to overall ET is critical for anticipating the impacts of human-induced and natural disturbances on the hydrology of forested watersheds (Ice and Stednick, 2004). Almost no information is available regarding black ash transpiration and the factors influencing it, constraining our ability to evaluate the potential impacts of EAB as they relate to wetland hydrology.

Sap flux density measurement is a common method used to assess tree water movement and estimate transpiration. We use the term sap flux density to denote the rate at which sap is moving through the xylem and sap flow to denote the volume of sap that moves through the xylem during a given time period. In particular, the thermal heat dissipation system pioneered by Granier (1985, 1987), has been widely used to measure sap flux density of many different forest types and assess radial variability of sap flux density, change in sap flux density with stand age, and estimate transpiration (Ford et al., 2004b, 2010; Delzon and Loustau, 2005; Tang et al., 2006). The method involves measurement of the voltage differential between thermal dissipation probes, which is then converted to an estimate of sap flux density with an empirically-derived equation. The validity of the original equation developed by Granier (1985) to estimate sap flux density in ring porous species has been questioned because the original equation was developed using a diffuse porous tree species that likely contained lower gradients of sap velocity through the sapwood and greater sapwood depth compared to ring porous trees (Gebauer et al., 2008; Bush et al., 2010; Wullschleger et al., 2011). Differences in pore structure between ring and diffuse porous tree species may warrant the use of other empirically-derived equations to estimate sap flux density in ring porous species (Herbst et al., 2007; Taneda and Sperry, 2008; Bush et al., 2010), but the utility of these equations in estimating black ash sap flux density is unclear.

In addition to physiological controls associated with wood structure, sap flux density is influenced by environmental factors, including soil water availability and atmospheric characteristics that influence evaporation from the leaf surface (i.e., wind speed and vapor pressure deficit). Soil water availability has fundamental control on transpiration, but studies which have examined relationships between soil moisture and sap flux density have reported mixed results (Stoy et al., 2006; Tang et al., 2006; Oishi et al., 2008, 2010; Ford et al., 2010). For example, soil moisture has been found to have limited effect on tree water use in a number of studies (Wullschleger et al., 1998; Granier et al., 2000; O'Brien et al., 2004), but others have found decreasing soil moisture to result in linearly decreasing sap flux density for many species, but not for European ash (Holscher et al., 2005). The variability of soil moisture control on transpiration is likely because of differences in site variables and climate that interact to cause soil moisture limitation in some instances, but not others (Oren et al., 1996; Ford et al., 2010). When soil moisture is not limiting, vapor pressure deficit has been found to be a dominant control over transpiration (Oren and Pataki, 2001); however, ring porous tree species have been found to be less responsive to vapor pressure deficit than diffuse porous tree species under similar conditions (Holscher et al., 2005). The relative degree to which black ash transpiration is controlled by soil moisture and vapor pressure deficit is currently unknown.

To address the above knowledge gaps, we measured sap flux density and estimated sap flow in three black ash dominated wetland sites with contrasting hydrologic regimes in north central Minnesota. Our primary objectives were to (1) estimate sap flux density and sap flow rates of black ash and compare them to previously reported rates for other species and estimates of PET, and (2) examine the role of soil water content and vapor pressure deficit on our estimates. The overall underlying objective of this study was to assess how site hydrology might be altered following EAB infestation and the corresponding loss of black ash, and increase our understanding of the ecohydrology of black ash wetland ecosystems.

2. Materials and methods

2.1. Site selection and description

The study was conducted on the Chippewa National Forest in Itasca County, Minnesota, USA and is part of an ongoing project examining the influence of forest harvesting and simulated EAB mortality on hydrology and plant community dynamics (Slesak et al., 2014). For this study, a subset of three field sites were selected to cover a range of soil moisture regimes and were designated as the very wet site (VWS), the wet site (WS), or the moderate site (MS) (Table 1). All of the sites were classified using the state's native plant community classification system (MN DNR, 2003). MS was classified as Northern Wet Ash Swamp (WFn55). WS and VWS were classified as Northern Very Wet Ash Swamp (WFn64). The overstory of all sites was dominated by black ash with minor components of American elm (*Ulmus americana*), American basswood (*Tilia americana*), bur oak (*Quercus macrocarpa*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), quaking aspen (*Populus tremuloides*), and yellow birch (*Betula alleghaniensis*) contributing no more than 7% of the total basal area. At each site, eight trees of varying size were selected for monitoring of sap flux density that encompassed the range of tree diameters present. Field measurements began for VWS and WS on June 12th, 2012 and for MS on June 27th, 2012. Data for VWS and WS were available through August 31st, 2012 and through September 4th, 2012 for MS.

2.2. Probe installation and heat dissipation measurement

The Granier (1987) heat dissipation method was used to determine sap flux density for black ash trees at each study site. Thermal dissipation probes were constructed in accordance with the method set forth by Lu et al. (2004). Two sensor probes, 20 mm in length, were inserted into the conducting sapwood of the tree at approximately 1.3 m above the ground. Probes were consis-

Table 1
Soil and stand characteristics at three black ash wetlands in Minnesota.

Parameter	Very wet site (VWS)	Wet site (WS)	Moderate site (MS)
Tree density (stems ha^{-1})	680	580	830
Mean DBH (cm)[a]	26.7 (3.1)	26.6 (3.4)	27.0 (3.9)
Range DBH (cm)[a]	14.4–40.5	15.6–41.8	13.9–41.9
Basal area (m^2 ha^{-1})	30.8	27.8	30.7
Sapwood area (m^2 ha^{-1})[b]	3.2	5.1	5.5
Leaf area index[c]	2.30 (0.05)	2.12 (0.13)	2.52 (0.04)
Soil texture[d]	Sandy clay loam	Loamy sand	Sandy loam
Bulk density[e]	1.46 (0.06)	1.39 (0.13)	1.38 (0.09)
Mean SWC[f]	0.43	0.31	0.22
SWC at field capacity[g]	0.28	0.13	0.22

[a] Mean DBH and range is for trees where sap flux was measured; standard error in parenthesis, $n = 8$.

[b] Estimated from empirically derived linear relationships between DBH and sapwood area developed for each site.

[c] Determined with hemispherical photography in 2013, stand error in parenthesis, $n = 12$.

[d] Determined with the hydrometer method from sample at 15–30 cm depth.

[e] Determined with the core method; standard error in parenthesis, $n = 8$.

[f] Soil water content at 15 cm depth from July 19 to August 31, 2012.

[g] Estimated from equations presented in Saxton and Rawls (2006).

tently installed 10 cm apart to avoid inaccuracies arising from probes being located too close together. Aluminum sleeves were used to apply consistent voltage to the conducting sapwood along the length of the heated probe (Wullschleger et al., 2011; Bush et al., 2010). Probe pairs were placed on the north and south facing sides of each tree to account for potential variability in sapwood depth and conductance based on aspect. Placing probes on multiple aspects has been shown to substantially reduce error compared to measuring sap flux density on one aspect of the tree (Lu, 1997). Probes were connected to multiplexers (Campbell AM 16/32 and Campbell AM 16/32B, Campbell Scientific Inc.) that relayed information to dataloggers (Campbell CR-10x and Campbell CR10WP, Campbell Scientific Inc.). Voltage difference between the two probes was measured every thirty seconds, and averages were calculated and recorded for every fifteen minute period.

2.3. Sapwood determination and corrections

Tree cores were collected from the north and south aspects of each of the monitored trees for calculating heartwood and conducting sapwood area. The average of the north and south radii was used to calculate the mean heartwood and conducting sapwood area for each tree. The boundary between sapwood and heartwood was estimated visually in the field (Ewers et al., 2002; Ford et al., 2004b; Tang et al., 2006; Peters et al., 2010; McCarthy et al., 2011; Pataki et al., 2011) and then confirmed in the lab by applying linseed oil to tree cores to make the active sapwood boundary easily visible. Exact sapwood and heartwood depth were measured to the nearest 0.01 mm using a Velmex micrometer.

2.4. Sap flow and scaled transpiration calculation

We initially used two different empirical relationships to calculate sap flux density from voltage differentials to assess the relative utility of the relationship developed by Herbst et al. (2007) for ring porous species compared to the more general and widely-used relationship for diffuse and ring porous species developed by Granier (1987). The Granier (1987) equation is defined as:

$$F_\mathrm{d} = 118.99 \times 10^{-6}\left[\frac{\Delta V_\mathrm{max} - \Delta V}{\Delta V}\right]^{1.231} \tag{1}$$

where ΔV_max is the maximum daily difference in voltage between the probes, ΔV is the voltage difference between probes for each of the 96 daily voltage differential values, and F_d is sap flux ($\mathrm{m_{sap}}^3\ \mathrm{m^{-2}}_\mathrm{sapwood}\ \mathrm{s}^{-1}$). The second equation was taken from Herbst et al. (2007). Similar to the Granier (1987) relationship, Herbst et al. (2007) incorporates voltage differential into an empirical relationship to yield sap flux (F_d):

$$\mathrm{Fd} = 2.023K^2 + 0.428(K) \tag{2}$$

where Fd is sap flux ($\mathrm{mm\,s^{-1}}$), and K is the difference between ΔV_max and ΔV divided by ΔV. K is a dimensionless value necessary for sap flux empirical relationships:

$$K = \frac{\Delta V_\mathrm{max} - \Delta V}{\Delta V} \tag{3}$$

Corrections for sap flux density were used from Clearwater et al. (1999) to account for problems associated with probe contact with the heartwood in the Granier calculations. Sap flux density estimates from the above equations were then converted to sap flow, extrapolated to the stand scale, and compared to potential evapotranspiration (PET) estimates to assess their relative utility in estimating black ash transpiration. PET was calculated with the Penman equation as modified by Shuttleworth (1993).

Stand-level estimates of transpiration were calculated using mean daily sap flux density values coupled with plot-level stem diameter data at each site. Measurements of stem diameters greater than 10 cm were conducted in the fall of 2011 on plots 400 m^2 in size at six locations in each stand. Linear equations relating DBH to sapwood area were developed for each stand using the detailed measures from the eight trees equipped with the thermal dissipation probes. These equations were then applied to the plot-level stem diameter data to estimate total sapwood area per plot. Mean daily sap flux density values for each stand were multiplied by plot-level sapwood area estimates to estimate plot-level sap flow, and the mean per hectare value among plots within a stand was used as the estimate for scaled transpiration.

2.5. Vapor pressure and soil moisture determination

Vapor pressure deficit (VPD) was calculated from relative humidity in conjunction with saturation vapor pressure (Brooks et al., 2003). Atmospheric variables used in VPD calculation were measured at 10 min intervals with a portable weather station (HOBO U30 NRC, Onset Computer Corp., Bourne, MA) located near the field sites during the study period. Daylight length was used to normalize VPD over the course of the measurement period as described in Oren et al. (1996).

Soil moisture sensors (model EC-5, Decagon Devices, Pullman, WA) were deployed at each of the field sites to measure soil moisture content. Sensors were installed within one meter of the bole of each of the monitored trees at 15 and 30 cm depth. Sensor readings were recorded at 15 min intervals from July 20th through September 4th and converted to soil water content estimates using factory equations. Soil water content values for a given tree and depth were first averaged by day, and then converted to relative soil water saturation estimates using equations from Saxton and Rawls (2006) to determine soil water content at saturation for each of the sites. Measurements of soil texture and organic matter from soil samples collected at 15–30 cm from each of the sites were used in calculating these equations. Our purpose in presenting the soil water data in this manner was to standardize measures of soil water status across sites of differing texture to aid in interpretation of the findings. Relationships between relative soil water saturation and sap flux density and sap flow were examined with linear regression at both the individual tree and stand scale. Statistical analyses were performed in SAS Version 9.3 (SAS Institute, Cary, NC).

3. Results

3.1. Comparison of sap flux density equations

The two different empirical sap flux density relationships used in this study yielded different estimates for sap flux density and sap flow. Sap flux density calculated with the equation developed by Herbst et al. (2007) yielded values that were 2–5 times higher than values determined using the Granier (1987) equation (data not shown). When scaled to the stand level, estimates from the Herbst et al. (2007) relationship far exceeded PET compared to estimates calculated with Granier's (1987) equation, which were lower than PET and more reasonable (Table 2). Because of this, we used Granier's (1985, 1987) equation in all additional calculations and assessments reported here.

3.2. Sapwood, sap flux density, and sap flow

Differences in sapwood depth and sapwood area were evident among the three field sites. Mean sapwood area was inversely related to sap flux density and sap flow, which varied considerably within and among sites. For example, MS exhibited the lowest mean daily sap flux density and sap flow despite having the greatest sapwood area, while VWS demonstrated the greatest mean daily

Table 2
Stand scale comparison of average scaled transpiration estimates (mm day^{-1}) shown using Granier (1987) and the Herbst et al. (2007) equations. Average PET is the mean value over the field season. Reported errors are one standard deviation of the mean.

Field site	Average scale transpiration Granier (mm day^{-1})	Average scale transpiration Herbst (mm day^{-1})	Average PET (mm day^{-1})[a]
VWS	1.80 ± 1.17	2.83 ± 0.88	2.21 ± 0.37
WS	1.17 ± 0.14	3.71 ± 0.44	2.21 ± 0.37
MS	0.90 ± 0.11	4.05 ± 0.55	2.21 ± 0.37

[a] PET estimated using modified Penman equation as described in Telander (2013).

sap flow due to high daily sap flux density despite exhibiting the smallest sapwood depth and area (Table 3). Although the variation within sites was substantial, the general patterns among sites were also reflected in significant relationships between sapwood depth and both sap flux density and sapwood area at the individual tree scale (Fig. 1).

3.3. *Sap flux density and sap flow through time*

Sap flux density and sap flow varied in a similar pattern over the course of the field season (Fig. 2). All sites showed a rise in sap flux density and sap flow at the beginning of the field season followed by a decline in the middle of the field season, but there was no consistent pattern at the end of the field season. VWS showed the greatest sap flux density over the entire field season, while WS and MS had much lower sap flux density. In contrast, sap flow was more similar between VWS and WS throughout much of the growing season because of the much larger sapwood area in WS trees compared to those at VWS (Table 3).

3.4. *Relationships with vapor pressure deficit and soil moisture*

We compared vapor pressure deficit (VPD) to sap flow for all three field sites with the beginning and the end of the field season excluded to remove time periods when tree physiological control could override the influence of VPD on sap flow (i.e., flow dynamics during leaf-out and fall translocation; Sakai et al., 1997). For this time period, there was a positive relationship between sap flow and VPD at VWS and WS, but a negative relationship at MS (Fig. 3).

There was no relationship between SWC and sap flux density on a daily time step (data not shown), but when averaged by week, mean sap flux density and SWC were positively related at both the tree and stand scale (Fig. 4). The relationship between sap flux density and SWC was similar for 15 cm and 30 cm depths (data not shown). The relationship was much stronger at the stand scale than the tree scale, because of a reduction in variability when averaging across all of the monitored trees in each stand. In contrast, there was no relationship between sap flow and SWC at any time period for either the tree or stand scale (data not shown).

4. Discussion

Black ash faces possible extirpation from North America due to the continued spread of emerald ash borer, and loss of this species

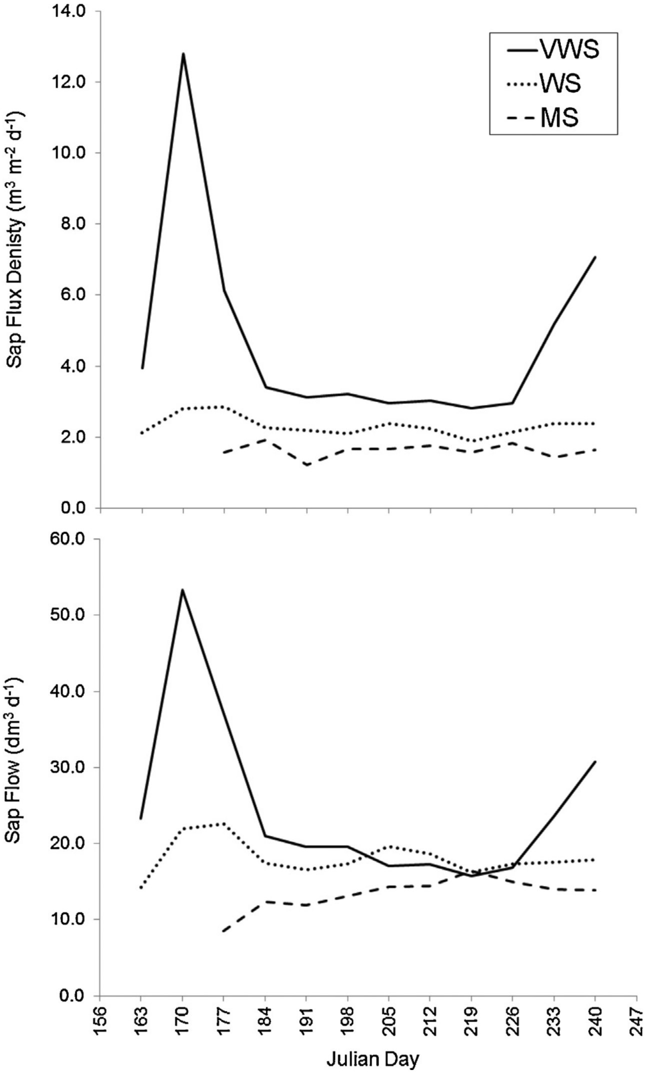

Fig. 2. Mean weekly sap flux density (m^3 m^{-2} day^{-1}, top panel) and sap flow (dm^3 day^{-1}, bottom panel) of monitored trees through the field season differentiated by site for the very wet site (VWS), the wet site (WS), and the moderate site (MS). The field season began in mid June and extended through early September.

Table 3
Tree scale estimates of sapwood depth (cm), sapwood area (cm^2), mean and maximum sap flux density (m^3 m^{-2} day^{-1}), and sap flow (dm^3 day^{-1}) values by site for the eight monitored trees at the very wet site (VWS), the wet site (WS), and the moderate site (MS). Sapwood depth refers to the depth from inside the cambium to the end of the hydroactive xylem. Mean sapwood area is the average area of the hydroactive xylem across the monitored trees at each field site. Reported errors are one standard deviation from the mean.

Parameter	Very wet site	Wet site	Moderate site
Mean sapwood depth (cm)	0.82 ± 0.19	1.41 ± 0.56	1.37 ± 0.46
Mean sapwood area (cm^2)	70.0 ± 28.5	96.2 ± 49.9	106.7 ± 67.2
Mean daily sap flux density (m^3 m^{-2} day^{-1})	4.59 ± 3.83	2.31 ± 0.68	1.62 ± 0.33
Mean Daily sap flow (dm^3 day^{-1})	24.3 ± 14.5	18.1 ± 4.7	13.5 ± 2.7
Maximum daily sap flux density (m^3 m^{-2} day^{-1})	13.89 ± 25.62	6.57 ± 2.52	3.65 ± 1.49
Maximum daily sap flow (dm^3 day^{-1})	63.2 ± 82.3	50.7 ± 17.7	24.7 ± 5.2

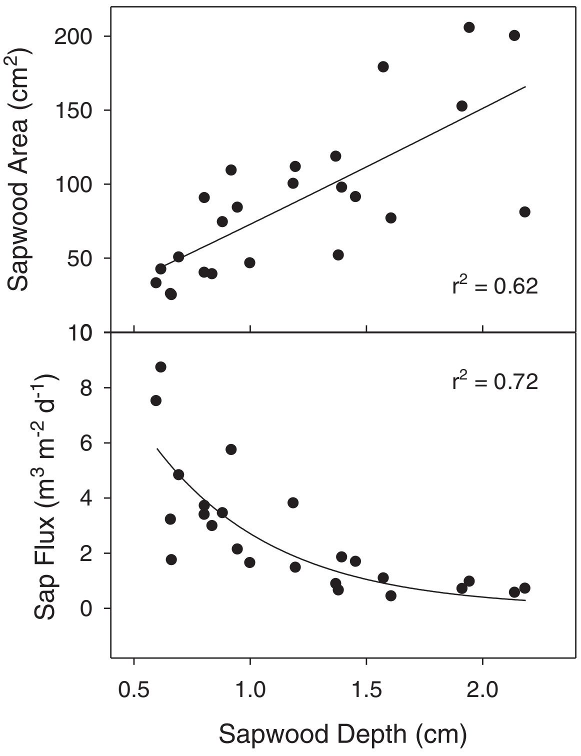

Fig. 1. Example relationships between sap flux density and tree physiological characteristics for field sites in aggregate including a comparison of sapwood depth (cm) and sapwood area (cm^2) of monitored trees (top panel) and a comparison of sapwood depth (cm) and sap flux density ($m^3\ m^{-2}\ day^{-1}$) for monitored trees during week three of the field season (bottom panel). Week three was selected for display as it was the first week of the field season with all field sites operational.

from ecosystems where it is a dominant component is likely to cause cascading effects on ecosystem functions. Here, we measured sap flow and estimated stand-level transpiration in black ash wetlands in an attempt to quantify the contribution of ash to ET and assess the magnitude of hydrologic alteration that might occur following black ash loss. Although there is some uncertainty in our estimates (see below), the data indicates that the contribution of black ash transpiration to ET is variable as inferred with comparisons to PET (Table 2). Given this, the magnitude of hydrologic alteration following EAB-induced mortality will likely be variable as well, but ecologically significant given the lack of other tree species that can grow on these sites.

Recent studies have found that the original Granier (1985, 1987),) empirical relationship is problematic for sap flux density determination in ring porous species, asserting that the original relationship could be underestimating sap flux density for these species by many orders of magnitude (Herbst et al., 2007; Taneda and Sperry, 2008; Bush et al., 2010). We applied each of the relationships put forth in Herbst et al. (2007), Taneda and Sperry (2008), and Bush et al. (2010) to a small subset of data to test each of the empirical relationships and see if the relationships yielded reasonable results. The equation developed by Herbst et al. (2007) was chosen for further exploration because it was the most conservative estimator of sap flux density compared with the other ring porous equations and because it was developed from European ash, a species anatomically similar to black ash. Despite this, sap flow values determined using the Herbst et al. (2007) equation were much higher than values determined using the Granier (1987) equation, and scaled estimates were also consistently much higher than PET over the entire field season compared to more reasonable estimates from Granier (Table 2).

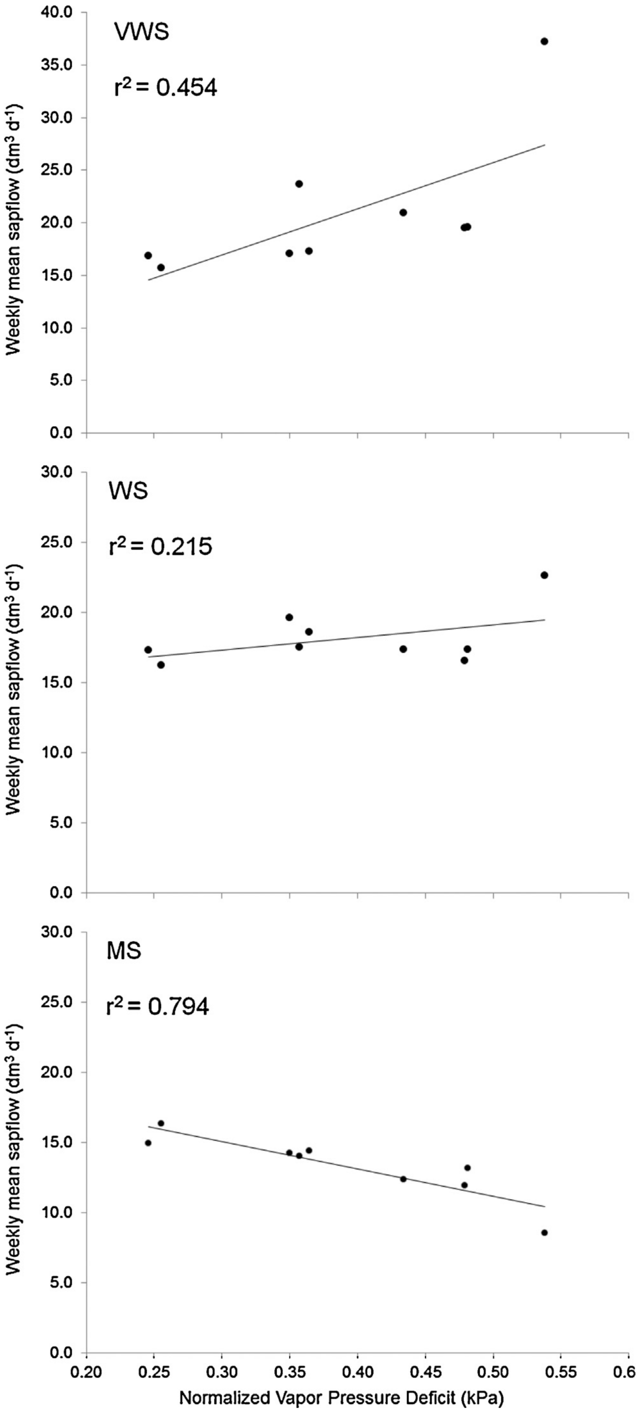

Fig. 3. Mean weekly sap flow as related to normalized vapor pressure deficit for VWS (top panel), WS (middle panel), and MS (bottom panel) for weeks 3 through 11 of the field season. Daylight hours expressed as a percentage of maximum daytime length was used to normalize VPD over the field season.

One potential reason that the Herbst et al. (2007) equation appeared to overestimate sap flux density in this study is the saturated growing conditions of the black ash site compared to their more mesic site conditions. Herbst et al. (2007) observed that much of the flux was restricted to the wide-luminous, early wood of the last two annual growth rings, which may not occur to the same extent in black ash. Extremes in soil water availability that occur during drought and flooding are known to influence vessel anatomy in ring-porous species (Corcuera et al., 2004; Tardiff and Conciatori 2006; St. George and Nielsen, 2000) and it is possible that the soil

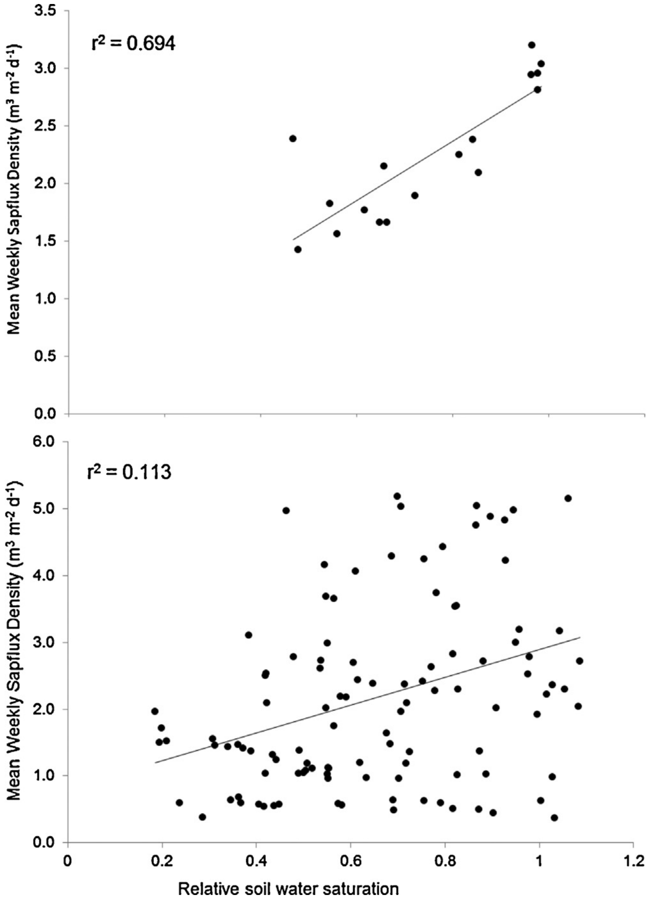

Fig. 4. Relationship between mean weekly sap flux density and relative soil water saturation at 15 cm depth at the stand (top panel) and tree (bottom panel) scale.

moisture conditions at our sites changed vessel anatomy, limiting the utility of the Herbst et al. (2007) equation. For these reasons, we determined that the Granier relationship was the best equation available to estimate sap flux density; however, it is likely that the Granier (1987) equation underestimates sap flux density of black ash to some extent (Clearwater et al., 1999; Gebauer et al., 2008; Bush et al., 2010) so our estimates should be considered conservative.

Daily sap flux density rates determined in this study were similar to those determined in other sap flux density studies (Ewers et al., 2002; Tang et al., 2006; Peters et al., 2010), including studies that examined ring porous tree species (Holscher et al., 2005; Oishi et al., 2010). However, black ash trees evaluated in this study had very shallow hydroactive sapwood and relatively small sapwood area compared to other species, resulting in lower sap flow estimates. Other studies examining sap flux density of ring porous oak tree species found average sapwood area of uneven-aged stands to be between 15 cm^2 and 395 cm^2 (Wullschleger et al., 2001; Gebauer et al., 2008; Ford et al., 2010). Sapwood area of black ash trees in this study varied between 25 cm^2 and 205 cm^2 with an average of 88 cm^2. The low sapwood area we observed could be the result of subjectivity in the visual field estimate, but corroboration of those estimates with more precise lab-based measures makes this unlikely. Leaf area could also play a role in the low amount of sapwood area in black ash given the functional linkage between these variables (Waring et al., 1982; Whitehead et al., 1984). Leaf area estimates of the overstory at our sites were low (Table 1) (Jonckheere et al., 2004), similar to observations in a larger survey of black ash forested wetlands (Palik et al., 2011).

Based on our findings, soil moisture appears to have large control on black ash transpiration, as relationships between sap flux density and VPD were dependent on the hydrologic regime of each stand. Previous work has established variability in transpiration response to soil moisture depending on precipitation and the moisture regime of the forest stand (Oren et al., 1996; Bovard et al., 2005; Ford et al., 2010), with generally greater control when water availability limits biological activity (i.e., either very high or low soil moisture). This study indicates that in these black ash wetland ecosystems, atmospheric control of transpiration is only apparent when soil moisture conditions are at or near soil saturation despite the relatively moist conditions present at all the field sites for much of the field season. Here, the wettest site demonstrated the highest sap flux density and sap flow values while the driest site exhibited the smallest sap flux density and sap flow values.

The combination of significant relationships between sap flux density and both VPD (Fig. 3) and relative soil water saturation (Fig. 4), indicates that low sap flux density rates are due to lower soil water availability even though soil water content was at levels typically believed available to plants (i.e., between field capacity and wilting point). Such a limitation may arise when rooting depths are shallow and the water table draws down during the summer, which commonly occurs at these sites (Slesak et al., 2014). Surprisingly, there was also no evidence that saturated conditions limited sap flux density, possibly due to many trees occurring at the most favorable microsite conditions in these systems (R. Slesak, pers. obs.). Taken together, these observations demonstrate the unique role that black ash plays in regulating hydrologic processes in these wetland ecosystems.

5. Additional implications

Overall temperature and moisture conditions experienced in north-central Minnesota in 2012 were normal when compared to the preceding decade. However, the precipitation distribution for the 2012 growing season was abnormal with much of the precipitation falling in the early portion of the growing season. Drier than usual conditions in the late growing season could be partially responsible for the relationship between relative soil water saturation and transpiration demonstrated at these sites. It is possible that under wetter, more normal conditions, sap flux density may increase and be more responsive to atmospheric drivers. If climate conditions continue to shift and late season droughts become more common, the late season hydrologic impacts of black ash mortality could be less than anticipated due to black ash's propensity to transpire more freely in saturated soil conditions.

Given the variability in sap flow results among the three field sites, black ash water use was at least partially dependent upon hydrologic regime. This indicates that if black ash were to be removed from the overstory, impacts to the landscape would be variable depending on the moisture regime of different areas, with the greatest impacts on the wettest sites. Past work examining harvesting impacts in black ash forests supports this, as the potential for conversion to marsh-like conditions following harvesting was much greater on the wettest sites (Erdmann et al., 1987). In our study, the gap between estimated black ash canopy transpiration and PET ranged from approximately 20–60% of PET, indicating that the understory could contribute more to overall total ET than was expected (Telander, 2013). Studies have found that understory vegetation can account for between 9% and 54% of stand transpiration depending on study site location and forest type (Loustau and Cochard, 1991; Wullschleger et al., 2001; Wedker et al., 1996; Blanken et al., 1997; Kelliher et al., 1998; Herbst et al., 2008). While sap flow of black ash was variable and lower than anticipated at some sites, impacts to the hydrology of these wetland systems will likely be significant following EAB-induced ash mortality as shown using other techniques (Slesak et al., 2014).

6. Conclusions

This study elucidates the potential hydrologic implications of black ash removal from wetland forests, which is of increasing concern in light of continued spread of EAB into the primary range of black ash dominated wetlands. Black ash sap flux density rates are similar to other species, but sap flow values were lower than expected due to small sapwood area. When extrapolated to the stand scale, our estimates comprised 40–80% of PET, suggesting that factors other than black ash transpiration are also important to site water balance in some instances. However, the relationships among sap flux density, VPD, and relative soil water saturation demonstrate the unique role that black ash plays in regulating these wetlands ecosystems. Given the influence of soil moisture on sap flow, the hydrologic impact of black ash removal is likely to be variable as well and dependent on the hydrologic regime of an individual site.

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