Wetlands Ecol Manage (2019) 27:157–170
https://doi.org/10.1007/s11273-018-9649-0

ORIGINAL PAPER

Temperature responses of carbon dioxide fluxes from coarse dead wood in a black ash wetland

Nam Jin Noh · Joseph P. Shannon · Nicholas W. Bolton · Joshua C. Davis · Matthew J. Van Grinsven · Thomas G. Pypker · Randall K. Kolka · Joseph W. Wagenbrenner

Received: 14 June 2018 / Accepted: 4 December 2018 / Published online: 11 December 2018

Abstract The invasive emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) causes widespread ash tree mortality in North America, and the CO_2 efflux (respiration, F) from coarse dead wood (CDW) following the EAB infestation is unknown. We examined seasonal variations in CO_2 fluxes from various types of CDW (cut ash stumps, downed logs, and standing girdled dead stems) and the surfaces of soil and live stem in a black ash wetland in which EAB infestation was simulated. Responses of F_{CDW} to seasonal changes in temperature were less sensitive than that of live stems. However, F_{CDW} from the stump and log cross-section were significantly greater than the other component fluxes. The mean CO_2 flux from girdled stems was similar to those from soil and live stems. The log and stump cross-sections may function as an unaccounted pathway of CO_2 flux following pre-emptive or salvage harvests associated with EAB mitigation. The increases in the amount of CDW and temperature caused by canopy openness and subsequent increased insolation, and potential long-term increase in water level and CDW moisture might accelerate the respirational carbon loss from soil and

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11273-018-9649-0) contains supplementary material, which is available to authorized users.

N. J. Noh (✉) · J. P. Shannon · N. W. Bolton ·
J. C. Davis · M. J. Van Grinsven
School of Forest Resources and Environmental Science,
Michigan Technological University, Houghton,
MI 49931, USA
e-mail: n.noh@westernsydney.edu.au

J. P. Shannon
e-mail: jpshanno@mtu.edu

N. W. Bolton
e-mail: nicholas.w.bolton@gmail.com

J. C. Davis
e-mail: joshuad@mtu.edu

M. J. Van Grinsven
e-mail: mvangrin@nmu.edu

N. J. Noh
Hawkesbury Institute for the Environment, Western
Sydney University, Penrith, NSW 2751, Australia

N. W. Bolton
Daniel B. Warnell School of Forestry and Natural
Resources, University of Georgia, Athens, GA 30602,
USA

J. C. Davis
Smithsonian-Mason School of Conservation, George
Mason University, Front Royal, VA 22630, USA

M. J. Van Grinsven
Department of Earth, Environmental, and Geographical
Sciences, Northern Michigan University, Marquette,
MI 49855, USA

T. G. Pypker
Department of Natural Resource Sciences, Thompson
Rivers University, Kamloops, BC V2C 0C8, Canada
e-mail: tpypker@tru.ca

CDW after black ash wetlands are infested by EAB. These results identify and quantify CO_2 pathways in EAB affected wetlands, which can be used to improve respiration modeling and carbon accounting in black ash wetlands.

Keywords Emerald ash borer · *Fraxinus nigra* · Heterotrophic respiration · Wood moisture content · Soil respiration · Stem respiration · Temperature sensitivity · Tree mortality

Introduction

Across North America, native ash species (*Fraxinus* spp.) are severely threatened by the invasive emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) (MacFarlane and Meyer 2005; Herms and McCullough 2014; Kolka et al. 2018). Since the confirmed introduction in 2002, tree mortality has been severe and is now apparent in large-scale forest inventory data (Pugh et al. 2011; Herms and McCullough 2014). EAB has been found in 35 American states and five Canadian provinces as of October 2018 (Emerald Ash Borer Information Network). In southeastern Michigan, USA near the epicenter of the EAB invasion, the percentage of fallen dead ash trees including white ash (*F. Americana* L.), green ash (*F. pennsylvanica* Marsh.), and black ash (*F. nigra* Marsh.) on the forest floor increased by 76% from 2008 to 2012 (Perry et al. 2018). Among host ash species, black ash, which is a native North American hardwood tree species generally found in wetlands or on poorly drained soil, is especially vulnerable (Herms and McCullough 2014; Iverson et al. 2016). In black ash ecosystems, tree mortality following severe EAB infestation affects ecological and hydrological processes (Nisbet et al. 2015; Klooster et al. 2018; Kolka et al. 2018) by altering vegetation (Kashian and Witter 2011; Davis et al. 2017; Looney et al. 2017a, b) and wetland hydrology (Slesak et al. 2014; Van Grinsven et al. 2017). Canopy manipulation research on black ash wetlands in the upper Midwest have investigated group selection harvests, clearcuts and girdling treatments, and alternative species plantings to understand vegetation and other ecosystem responses that are anticipated following EAB invasion (Looney et al. 2015, 2017a, b; Bolton et al. 2018). More specifically, the loss of dominant ash trees reduces ecosystem carbon (C) uptake (Flower et al. 2013), may increase the contribution of ash branches and boles to dead wood pools, and may accelerate release of CO_2 through decomposition processes (Edburg et al. 2012; Anderegg et al. 2016). However, there has not been any attempt to quantify the CO_2 release to the atmosphere from the sizable input of dead wood after EAB infestation.

Coarse dead wood (CDW) including standing dead stems, downed logs, and stumps plays an important role as a long-term C sink in forest ecosystems (Russell et al. 2015; Magnússon et al. 2016). During its slow decomposition, CDW contributes mainly to soil C sequestration through leaching and fragmentation and additionally to CO_2 emissions to the atmosphere by microbial respiration and biological transformations (Yoon et al. 2014a, b; Magnússon et al. 2016). The role of CDW as a net C sink alongside soil and living trees is well known, however the CO_2 emissions from CDW have been less studied than emissions from soils and forest canopies and is often overlooked in estimating ecosystem CO_2 budgets (Ohtsuka et al. 2014; Yoon et al. 2015). In upland forests, the CO_2 flux (respiration, F) from CDW (F_{CDW}) generally represents a small flux when compared to soil or leaf respiration, and is generally found to account for less than ten percent of total ecosystem respiration (Gough et al. 2007; Ohtsuka et al. 2014; Warner et al. 2017). However, cumulative F_{CDW} can be a substantial flux over several decades (Bond-Lamberty et al. 2003; Gough et al. 2007) and the C cycle in wetland ecosystems largely depends on water levels that affect organic matter decomposition (Yoon et al. 2014a; Nisbet et al. 2015).

The F_{CDW} during decomposition is directly or indirectly influenced by various biotic and abiotic factors, including temperature, moisture, microbial biomass and activity, and CDW physio-chemical properties (Anderegg et al. 2016; Forrester et al. 2012; Herrmann and Bauhus 2013; Jomura et al.

R. K. Kolka
USDA Forest Service, Northern Research Station,
Grand Rapids, MN 55744, USA
e-mail: rkolka@fs.fed.us

J. W. Wagenbrenner
USDA Forest Service, Pacific Southwest Research
Station, Arcata, CA 95521, USA
e-mail: jwagenbrenner@fs.fed.us

2015; Noh et al. 2017). Among these controlling factors, temperature is one of the most significant variables to regulate F_{CDW} (Yoon et al. 2014a; Forrester et al. 2015). A better understanding of the temperature sensitivity of F_{CDW} will allow improved modeling of component fluxes, leading to stand or ecosystem level flux estimates (Ohtsuka et al. 2014; Gough et al. 2007; Warner et al. 2017; Bond-Lamberty et al. 2003). Two related studies in black ash wetlands demonstrated that soil CO_2 flux was regulated by changes in water table, and that a simulated EAB disturbance significantly increased soil CO_2 flux (Van Grinsven et al. 2017, 2018). However, CO_2 fluxes from CDW in black ash forests and factors controlling those fluxes are still unknown, and this causes uncertainties in the estimation of stand-level CO_2 flux and limits the accuracy of forest C budgets in EAB infested black ash wetlands. In addition, as water tables in black ash wetlands are expected to increase following EAB infestation (Slesak et al. 2014; Van Grinsven et al. 2017), wood decomposition processes related to moisture need to be better understood (Meyer and Brischke 2015).

We examined CO_2 fluxes from various types of CDW (standing girdled dead stems, downed logs and cut ash stumps) from black ash stands that were manipulated to simulate EAB infestation and the subsequent complete loss of ash trees from the canopy. We compared CO_2 fluxes from reference soils and live stems over one growing season. We hypothesized that removal of the ash canopy component would increase soil and CDW surface temperatures, and higher temperatures and higher moisture in CDW would increase F_{CDW}. Specifically, we aim to answer the following questions: (1) How do CO_2 fluxes vary among C cycle components in black ash forests? (2) How do the fluxes from the various components respond to temperature and moisture levels? This study provides the first field evidence that will lead to a better understanding of how previously unaccounted for F_{CDW} may contribute to future C cycling in black ash ecosystems threatened by EAB.

Materials and methods

Study site

This study was conducted in black ash wetlands located on the Ottawa National Forest in the western Upper Peninsula of Michigan, USA (46°28′N, 89°58′W, 500–520 m a.s.l.) (Fig. S1). Black ash is the dominant overstory species, and yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), white cedar (*Thuja occidentalis* (L.) Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and balsam fir (*Abies balsamea* (L.) Mill) exist as lesser overstory components within the wetlands (Davis et al. 2017). Mean diameter at 1.37 m height and basal areas were 17.9 cm and 12.1 $m^2\ ha^{-1}$ for black ash and 19.5 cm and 16.1 $m^2\ ha^{-1}$ for other species, respectively (Davis et al. 2017). The average monthly temperatures range from − 11.3 °C in January to 18.2 °C in July (1981–2010) and mean annual precipitation is 1010 mm $year^{-1}$ (Arguez et al. 2012), with the majority occurring as rain from June through November and a persistent snow pack through the winter months (December–April). Surface soils consisted of woody peat histosols, typically underlain by a layer of clay or clay loam (Davis et al. 2017; Van Grinsven et al. 2017).

Three study sites within the Ottawa National Forest were established in 2011 to investigate the ecological and hydrological impacts of EAB on black ash wetlands (Fig. S1) (Van Grinsven et al. 2017). The three sites, ranging in size from 0.29 to 0.61 ha, were previously unimpacted by EAB and consisted of "Control" (unmanipulated), "Girdle" (simulated EAB infestation), and "Ash-Cut" (complete ash tree loss) treatments (Fig. 1). In the winter of 2012–2013, all black ash stems $\geq$ 2.5 cm in diameter at a height of 1.37 m in the manipulated sites were either hand-girdled with a drawknife in a 15–30 cm circumferential band (Girdle) or felled by a chainsaw and left on site (Ash-Cut). Following treatment application, abundant epicormic branching was observed in both the "Girdle" and "Ash-Cut" treatments (Davis et al. 2017). However, in the study year of 2017, examination of crown conditions in the "Girdle" treatment indicated 100% canopy loss with no foliage observed in the upper canopy, while epicormic branching from some stumps was observed in "Ash-Cut" treatment. Canopy openness obtained using hemispherical photographs taken at the center of each site in July 2017 and processed with the WinSCANOPY software (ProVersion 2013a, Regent Instruments, Inc., Quebec, Canada) was 9.7, 14.2 and 20.9% for Control, Girdle, and Ash-Cut sites, respectively (Fig. 1).

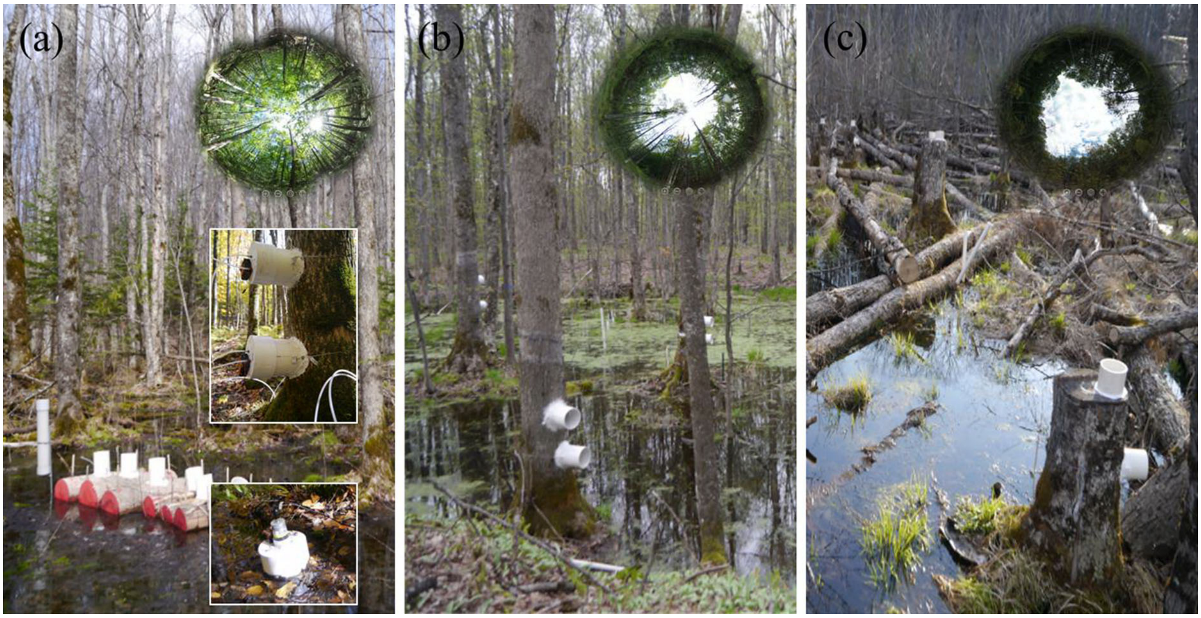

Fig. 1 Photographs of the simulated EAB infestation study sites. **a** Control, **b** Girdle, and **c** Ash-Cut. Inset hemispherical photos taken in summer show the canopy condition for each site. The other two inset photos show the chambers for living stem and soil measurements

CO_2 flux measurements and environmental parameters

To measure CO_2 fluxes from various C cycle components, PVC collars of 10.2 cm or 15.2 cm nominal inner diameter were inserted into soils or attached to live stems and CDW in April 2017, 4 years after girdling and ash-cut treatments. Three stem collars were attached to living stems at 0.5 m height as a reference for stem CO_2 fluxes and three soil collars were inserted into the wetland soils in the Control site. To examine the response of downed logs to moisture levels, low and high water levels for the downed logs were manipulated by placing three fresh and three decayed logs of 1 m length in one non-flooded location and one seasonally flooded location, respectively, under a closed canopy within the Control site in September 2016. The seasonally flooded condition immersed only the lower part of the CDW during the measurement period (Fig. 1a). The fresh logs were selected from freshly felled stems and the decayed logs were from stems that had been felled four years previously and from which the bark had been lost. A total of 37 collars were attached to the surfaces of the different types of CDW: four girdled standing dead stems at 0.5 m and 1.0 m above the ground in the Girdle site; nine cross-sections (cut ends) and three sides of stumps at 0.5 m above the ground in the Ash-Cut site; five cross-sections of logs in the Ash-Cut site; and three sides and three cross-sections of the fresh and decayed logs in the non-flooded and flooded conditions (Table 1, Fig. 1). Collars were attached to live or dead wood using inert silicone caulk.

A PVC end cap was attached to each collar to create a closed chamber, and a battery-powered fan was installed in the end cap to ensure thorough mixing of the gas inside the chamber. The area-based CO_2 fluxes (μmol CO_2 m^{-2} s^{-1}) were measured inside each chamber using a diffusion-type non-dispersive infrared gas analyzer (GMP343, Vaisala, Helsinki, Finland). The CO_2 concentrations in the chamber were recorded every 5 s over a period of 300 s by a data logger (MI-70, Vaisala). CO_2 fluxes from soil, live and dead (girdled) stems, logs and stumps were calculated from a linear regression as the CO_2 concentration

Table 1 Number of PVC collars, diameter of stem or CDW, gravimetric water content, soil or wood dry bulk density, C and N concentrations of the collar locations across all sites

Components	Number of Collars[1]	Diameter (cm)	Water content (g g^{-1})	Density (g cm^{-3})	C conc. (%)	N conc. (%)
Peat soil (0–50 cm depth)[2]	3	–	–	0.08 ± 0.01	51.1 ± 0.9	2.11 ± 0.16
Live stem	3	34.7 ± 1.7^a	–	–	47.9 ± 0.1^b	0.15 ± 0.01^a
CDW						
Girdled stem (0.5 m)	4	34.5 ± 1.4^a	0.54 ± 0.04^a	0.31 ± 0.02^a	46.4 ± 0.3^a	0.11 ± 0.01^b
Girdled stem (1.0 m)	4	–	–	–	–	–
Side of stump (0.5 m)	3	–	–	–	–	–
Stump cross-section	9 (7)	27.1 ± 2.1^b	0.53 ± 0.03^a	0.34 ± 0.02^a	46.4 ± 0.2^a	0.10 ± 0.00^b
Log cross-section	5 (4)	21.5 ± 3.6^b	0.53 ± 0.02^a	0.32 ± 0.03^a	46.1 ± 0.3^a	0.11 ± 0.01^b
Fresh log in non-flooded location	3	32.6 ± 2.1^A	0.52 ± 0.02^{AB}	0.37 ± 0.03^A	45.5 ± 0.4^A	0.09 ± 0.00^B
Decayed log without bark in non-flooded location	3	26.6 ± 0.8^B	0.44 ± 0.02^B	0.36 ± 0.03^A	46.0 ± 0.4^A	0.07 ± 0.00^B
Fresh log in flooded location	3	34.7 ± 1.9^A	0.59 ± 0.03^A	0.32 ± 0.04^A	45.5 ± 0.1^A	0.12 ± 0.01^A
Decayed log without bark in flooded location	3	26.1 ± 0.8^B	0.58 ± 0.03^A	0.35 ± 0.03^A	45.6 ± 0.3^A	0.09 ± 0.01^B

The numbers are the mean ± one standard error. Significant differences in mean values among the four wood components within the EAB infestation treatments and among the four groups of water level treatments in the control site are represented by different lower case and upper case letters, respectively ($p < 0.05$). – indicates no data

[1] Number of core samples for woody tissues is shown in parenthesis if different than the number of collars

[2] Kolka, USDA Forest Service (unpublished data)

versus time after the first 60 s by the following equation:

$$CO_2\,Flux = \frac{dCO_2}{dt} \times \frac{PV}{ART} \quad (1)$$

where dCO_2/dt is the slope of the regression, P is the atmospheric pressure, V is the chamber volume (1.42 L or 4.54 L), A is the surface area of the soil, live stem, or CDW encircled by the collar (0.0082 or 0.0181 m^2), R is the ideal gas constant, and T is the air temperature in the chamber (K). During the measurements, soil temperature at 5 cm depth and internal wood temperature at a depth of 5 cm in live and dead stems, logs and stumps were measured near all collars by a portable thermometer (CT-500WP, CUSTOM Co., Tokyo, Japan). At each site, air temperature at 1 m above the ground, soil temperature, and internal wood temperature of CDW was measured using temperature sensors (Thermo107; Campbell Scientific Inc., Logan, UT, USA) and recorded at 15 min intervals by data-loggers (CR800; Campbell Scientific Inc., Logan, UT, USA or Hobo Micro Station Data logger; Onset Computer Corporation, Bourne, MA, USA). To investigate the seasonal variation of the CO_2 fluxes from the components, the fluxes were measured during daytime hours (11:00 to 17:00) at biweekly intervals during the snow-free period (early May to late October) in 2017.

We measured C and nitrogen (N) concentrations in samples of soil, living stems, and fresh and decayed logs at the Control site, girdled stems at the Girdle site, and logs and stumps at the Ash-Cut site (Table 1). The wood samples were taken with an 8 mm diameter core to a depth of 5 cm using an electric drill in September 2017. All samples were dried, ground by a mill, and processed with an elemental analyzer (Elemental Combustion System 4010; Costech Inc.,Valencia, CA, USA). Additional core samples from the dead wood sources were used to measure wood water content and bulk density. The diameters of live and dead stems were measured at the point where the collars were attached.

Data analysis

We examined the seasonal changes in the CO_2 fluxes from soil, live stem, and CDW as a response to soil, air or stem temperature. To describe the temperature dependency of the CO_2 flux, we used the following exponential function (Davidson et al. 2006):

$$F = \beta_0 e^{\beta_1 T} \quad (2)$$

where F is the CO_2 flux (μmol CO_2 m^{-2} s^{-1}) from the components, β_0 is the respiration rate at a reference temperature of 0 °C, β_1 is a regression coefficient related to temperature sensitivity (Q_{10}) from the relationship:

$$Q_{10} = e^{10\beta_1} \quad (3)$$

T is the soil temperature (°C) at 5 cm depth for F_{Soil}, air temperature (°C) for F_{Stem}, or the CDW internal temperature (°C) at 5 cm depth for F_{CDW}. The Q_{10} value is the factor by which respiration increases by a 10 °C increase in temperature (Davidson et al. 2006). The apparent Q_{10} for a growing season was used to analyze the annual temperature sensitivities of CO_2 fluxes from soil, live and dead stems, logs and stumps. Spearman correlation was used to assess the strength of the relationships among CDW properties and F_{CDW}. Tukey HSD t-tests were used to detect significant differences in mean values of temperature among soil and wood sources. Linear mixed effects models were developed in SAS version 9.4 (SAS Institute Inc. 2012), with wood type as a fixed factor, the repeated measures on the replicated wood pieces in each type as a random factor, and temperature as a covariate (Littell et al. 2006):

$$F^{0.25} = mT + b \quad (4)$$

where F is the CO_2 flux from the components, m is the slope, T is the temperature, and b is the intercept. F was fourth-root transformed to normalize the model residuals. Moisture, wood density, and diameter were also tested as covariates but were removed from the model because they were not significant. An autoregressive covariance structure was used to account for the repeated measures throughout the growing season, and differences in estimated marginal means of the transformed fluxes among wood types were compared using a Tukey–Kramer adjustment. Equation 4 was used to calculate normalized F rates at 15 °C (F_{15}) and 20 °C (F_{20}), which were close to the average temperatures for soil and CDW, respectively. Two-way analysis of variance (ANOVA) was used to assess the effects of decay and water levels on F_{LOG}. The differences were considered to be significant if $p < 0.05$. The T-tests and ANOVA were performed using version 12.2 of the JMP Pro software (SAS Institute Inc. 2012) (Hinrichs and Boiler 2014).

Results

Temperature variations and CDW properties

In the Control site, the mean temperature was significantly higher in the logs (14.8 °C) than in the air (13.9 °C), soil (10.5 °C), and live stems (10.7 °C) during the 2017 growing season ($p < 0.05$, Fig. S2). The simulated EAB infestation resulted in slight increases in the daily mean air temperature of 1.0 °C and 1.3 °C during the growing season at the Girdle and Ash-Cut sites, respectively ($p < 0.05$). The simulation also significantly increased the daily mean temperatures of CDW by 4.7 °C and 5.4 °C at the Girdle and Ash-Cut sites, respectively ($p < 0.05$, Fig. 2a). Mean surface temperature during flux measurements generally followed the site trends with significantly different temperatures among the components ($p < 0.05$, Fig. 2b). Specifically, the mean temperature was highest in stumps (19.9 ± 0.7 °C) and lowest in the soil (14.4 ± 0.7 °C).

There were no significant differences in wood water content, wood density, or C or N concentrations among the girdled stems, logs, or stumps (Table 1). The mean diameter of the girdled stems was larger than those of the logs and stump cross sections ($p < 0.05$). There was no significant relationship among the CDW properties except for a negative correlation between wood density and nitrogen concentration ($n = 19$, $r = -0.63$, $p = 0.012$). Decayed logs placed in the flooded condition had increased water content compared to those placed in the non-flooded condition ($p < 0.05$), but there was no significant difference in wood density or C concentration between the non-flooded condition and flooded condition (Table 1). N concentration in fresh logs placed in the flooded condition was significantly higher than that of decayed logs in this condition ($p < 0.05$). A similar pattern was observed in the non-flooded condition, though the

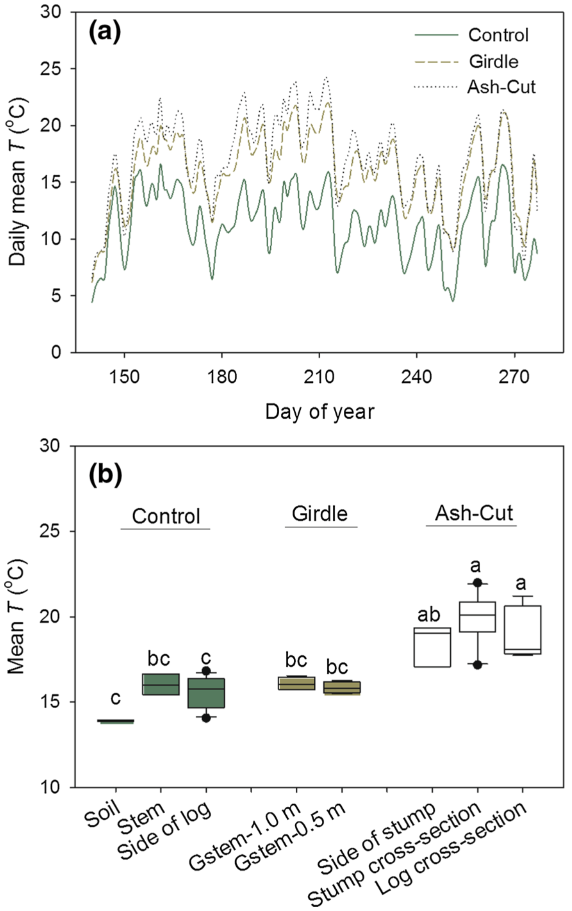

Fig. 2 **a** Daily mean temperature of live stem and coarse dead wood (CDW) (girdled stem and side of stump) in the Control, Girdle, and Ash-Cut sites from 20 May to 25 October 2017, **b** mean temperature of the soil, stems, logs, girdled stems (G_{Stem}), and stumps during CO_2 flux measurement through the study period. Box plot lines present the median, 25th and 75th percentiles, with whiskers at the 5th and 95th percentiles, and outliers shown as points. Significant differences in (**b**) are presented by different letters ($p < 0.05$)

observed differences were not significant. Additionally, N concentrations in live stems were greater when compared to those in CDW ($p < 0.05$, Table 1).

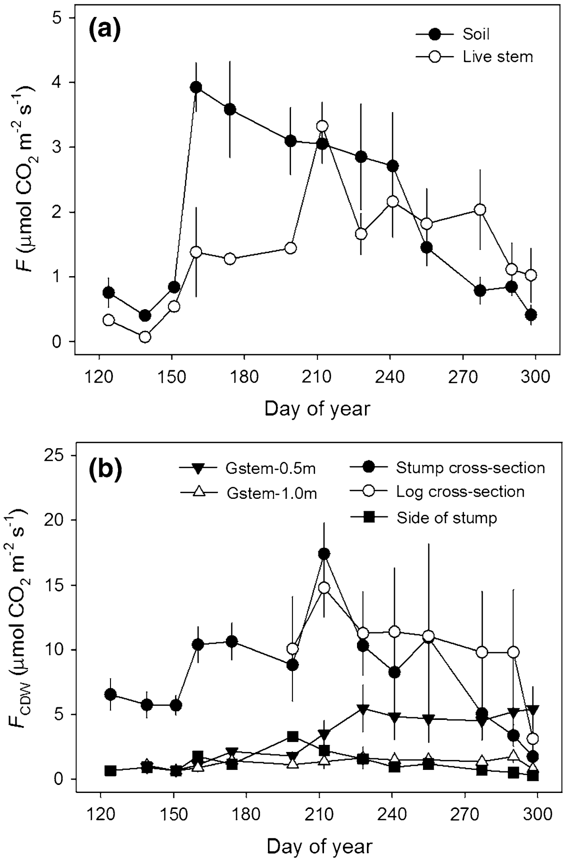

Fig. 3 Measured CO_2 fluxes (F) from **a** soil and live stems at the Control site, and **b** girdled (dead) stems (Gstem) at 0.5 m and 1.0 m height above the ground at the Girdle site, and stumps and logs at the Ash-Cut site. Vertical bars indicate the standard errors of means (n = 3–9; Table 1). Note the distinct y-axis scales for the purpose of comparing seasonal patterns

Temporal variations in CO_2 fluxes

The CO_2 fluxes from soil, stems, and CDW changed seasonally (Fig. 3). The F_{Soil} was highest in mid-growing season [late July, day of year (DOY) 212], then decreased until late October, while the F_{Stem} was highest in early growing season (early June, DOY160), soon after leaf emergence, after which it decreased gradually until leaf fall (late October) (Fig. 3a). In contrast, the CO_2 fluxes from girdled stem (F_{Gstem}) at 0.5 m increased gradually until mid-growing season and decreased slowly until later in the growing season, and then decreased rapidly with decreased temperature in late October (DOY298) (Fig. 3b). In contrast, F_{Gstem} at 1.0 m showed much less variation through the growing season and there was a significant difference in the mean F_{Gstem} between heights ($p < 0.05$, Fig. 4). During mid and late growing season, the mean values at the 0.5 m height were five times greater than the value at the 1.0 m height (Fig. 3b). The seasonal patterns were similar in all CDW at the Ash-Cut site. However, the fluxes from the log and stump cross-sections were significantly greater than the fluxes from soils, live and

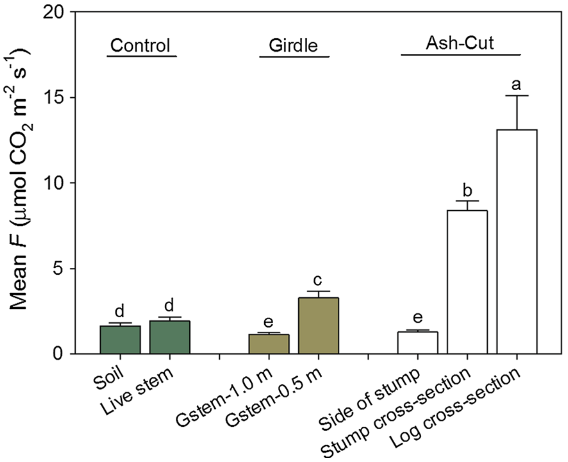

Fig. 4 Mean measured CO_2 fluxes (*F*) from soil, live stems, girdled (dead) stems (Gstem), stumps and logs. Values indicate mean ± standard errors ($n = 3$–9). Different letters indicate significant differences among components at $p < 0.05$

dead stems, and from the sides of the stumps ($p < 0.05$, Fig. 3). The highest mean flux from the stump cross-sections was 17.4 µmol CO_2 m^{-2} s^{-1} in late July (DOY212) as compared to the maximum mean of 3.3 µmol CO_2 m^{-2} s^{-1} from the sides of the stumps (DOY199). The peak F_{CDW} from the sides of the stumps was similar to the peaks in F_{Soil} (Fig. 3).

The mean CO_2 flux from log cross-sections (13.1 ± 1.98 µmol m^{-2} s^{-1}) was significantly greater than the means from the soil (1.65 µmol m^{-2} s^{-1}), live stems (1.95 µmol m^{-2} s^{-1}), and other CDW (1.14 to 8.38 µmol m^{-2} s^{-1}) ($p < 0.05$, Fig. 4). There were no significant differences in the mean fluxes between soil and live stems within the Control site.

Temperature sensitivities of CO_2 fluxes

F_{Soil} was strongly correlated with soil temperature ($r^2 = 0.43$, $p < 0.001$, Fig. 5a) and F_{Stem} was strongly correlated with air temperature ($r^2 = 0.39$, $p < 0.001$, Fig. 5a). The F_{Gstem} at 0.5 m height was not correlated with wood temperature ($p = 0.189$, Fig. 5b), whereas the lower values of F_{Gstem} at 1.0 m height were correlated to wood temperature ($r^2 = 0.14$, $p = 0.004$). The F_{CDW} for stump and log cross-sections, and sides of stumps were also positively related with their respective temperatures ($p < 0.001$, Fig. 5c). The Q_{10} values were 3.25 and 3.74 for the soil and live stems, respectively. Q_{10} values were highly variable among dead wood components (1.35 to 2.47) (Fig. 5).

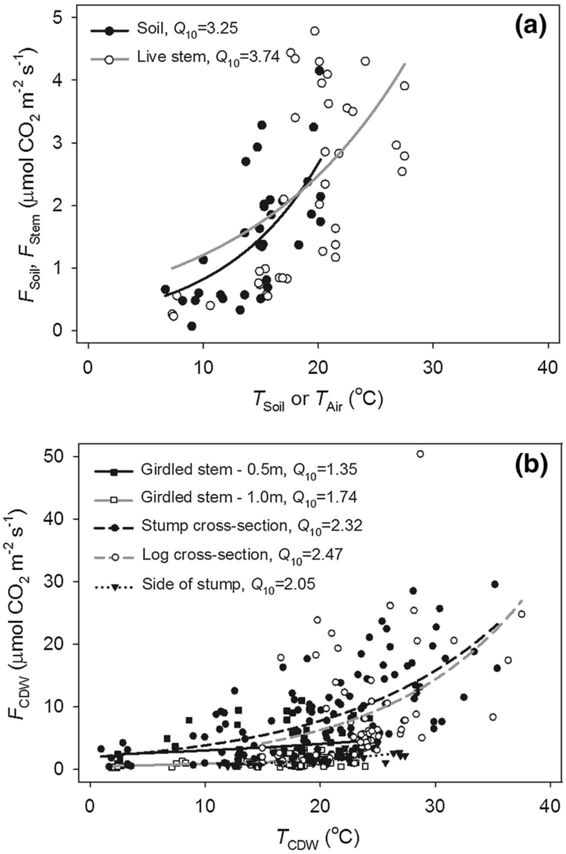

Fig. 5 Exponential relationships between CO_2 fluxes (*F*) and temperatures from **a** soil ($R^2 = 0.43$, $p < 0.001$, $n = 30$) and live stems ($R^2 = 0.39$, $p < 0.001$, $n = 30$) in the Control site, **b** girdled stems at 0.5 m ($R^2 = 0.04$, $p = 0.189$, $n = 52$) and 1.0 m ($R^2 = 0.14$, $p = 0.004$, $n = 52$) above the ground surface in the Girdle site, and stump cross-sections ($R^2 = 0.43$, $p < 0.001$, $n = 117$), log cross-sections ($R^2 = 0.19$, $p < 0.001$, $n = 69$) and side of stump ($R^2 = 0.50$, $p < 0.001$, $n = 33$) in the Ash-Cut site. Q_{10} values ($= e^{10\beta 1}$) were calculated from Eq. 3

The seasonal pattern in F_{LOG} of fresh logs at the flooded condition was similar to that at the non-flooded condition. While the decayed logs had lower fluxes when compared with the fresh logs, neither showed any clear seasonal variation (Fig. 6). There was a significant difference between the overall means of the flood conditions ($p < 0.05$), and the difference appears to be related to three days of high F_{LOG} from the flooded sites (Fig. 6). In addition, the mean F_{LOG} was significantly different in fresh versus decayed logs ($p < 0.05$), but was not affected by the flooding condition ($p > 0.05$) (Fig. 6). There was no difference in surface temperatures among the logs in flooded and non-flooded locations ($p > 0.05$). The mean CO_2 flux

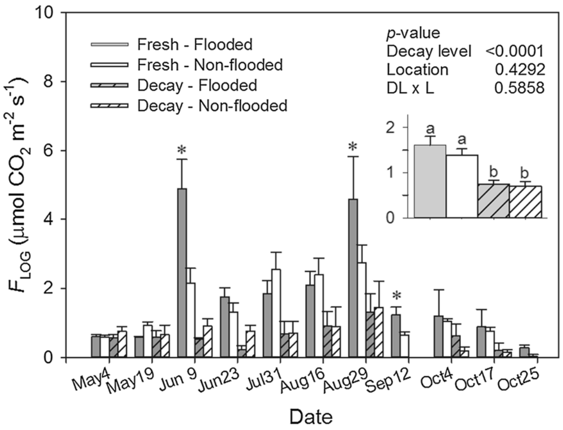

Fig. 6 Temporal variations of mean CO_2 fluxes from fresh and decayed logs (F_{LOG}) placed at flooded and non-flooded conditions. The inlet figure shows mean CO_2 fluxes for all measurements. Vertical bars are standard errors ($n = 3$). Asterisks indicate significant differences in F_{LOG} of fresh logs between the flooded and non-flooded conditions and different letters in inlet figure indicate significant differences among treatments ($p < 0.05$)

was higher in fresh logs (1.50 μmol CO_2 m^{-2} s^{-1}) than in decayed logs (0.71 μmol CO_2 m^{-2} s^{-1}) (p <0.05).

Slopes between the fourth-root transformed F and the corresponding temperature did not differ significantly but the intercepts were different among the CDW types in the mixed effects model. The intercept was highest in the log cross-section compared to the other CDW types ($p < 0.05$). Therefore, at a reference temperature of 15 °C, the CO_2 flux (F_{15}) was highest in the log cross-sections (7.76 μmol CO_2 m^{-2} s^{-1}), and this was greater than other CO_2 flux components including soil, live stems, girdled stems at 1.0 m height, and sides of stumps ($p < 0.05$, Table 2). By comparison, the F_{15} and F_{20} for all CDW was 3.35 μmol CO_2 m^{-2} $s^{-1}$and 4.72 μmol CO_2 m^{-2} s^{-1}, respectively.

Discussion

Effects of CDW type on CO_2 flux

At our black ash study sites, the mean CO_2 flux of 4.19 μmol m^{-2} s^{-1} for all types of black ash CDW across all sites (Fig. 4) was similar to the estimate of 4.23±3.42 μmol m^{-2} s^{-1} for CDW in an upland temperate forest in Maryland, USA (Warner et al. 2017). However, we observed significant differences in CO_2 fluxes among the different types of CDW. The most pronounced difference was observed between the sides of stumps and stump cross-sections within the Ash-Cut site. The CO_2 flux from stump cross-sections reached rates up to six times higher than that of the sides of stumps. Greater flux from stumps, when compared to logs, has also been reported in a northern hardwood forest in the Flambeau River State Forest, northern Wisconsin, USA (Forrester et al. 2015). Three possible explanations include (1) additional CO_2 released from surviving roots of stumps and root intrusions from other plants into the stump, and (2) different decomposer communities (Forrester et al.

Table 2 Model denominator degrees of freedom (DF), intercepts (b), and calculated CO_2 fluxes (μmol CO_2 m^{-2} s^{-1}) at reference temperatures of 15 °C (F_{15}) and 20 °C (F_{20}) from linear mixed effects model ($F^{0.25} = m\ T + b$) for soil, live stems, and CDW (girdled stems, logs and stumps)

Components	DF	Slope (m)	Intercept (b)	F_{15} (μmol CO_2 m^{-2} s^{-1})	F_{20} (μmol CO_2 m^{-2} s^{-1})
Soil	45.2	0.0300	0.640^{cd}	1.41	2.36
Live stem	46.0	0.0386	0.534^{cd}	1.54	2.91
CDW					
Girdled stem (0.5 m)	44.5	0.0110	1.133^{c}	2.84	3.35
Girdled stem (1.0 m)	44.2	0.0147	0.775^{d}	0.98	1.30
Side of stump (0.5 m)	44.6	0.0227	0.616^{d}	0.84	1.31
Stump cross-section	44.6	0.0324	0.960^{b}	4.37	6.68
Log cross-section	53.2	0.0356	1.109^{a}	7.28	10.98

Significant differences among the estimated marginal means of fourth-root transformed fluxes for the different components are represented by different letters ($p < 0.05$ level)

2015), and (3) differences in woody anatomical structure among the CDW components (Sorz and Hietz 2006). The first possibility may not be applicable to our Ash-Cut site because the CO_2 flux from the log cross-sections without any roots was similar to or higher than that from the stump cross-sections for the late growing season (Fig. 3b). However, the explanation of decomposer community composition is plausible because the CO_2 flux from the logs was higher in the flooded (wetter) condition, which could imply more wood-decay fungi colonization on fresh downed logs (Boddy and Watkinson 1995; Mosier et al. 2017), as compared to the non-flooded (drier) condition. In addition, the anatomical structure of tracheids, ring-pores, and extracellular pore spaces on the cross-section could increase conductivity in the axial direction and thereby increase transport of CO_2 (Sorz and Hietz 2006).

At the 0.5 m height, significantly higher CO_2 fluxes were observed on the sides of girdled standing stems than on the sides of stumps (Table 2, Fig. 4). On these girdled stems we often observed white-rot wood-decomposing fungi which are capable of decomposing cellulose, hemicellulose, lignin and other complex C components (Mosier et al. 2017), whereas white-rot fungi was not observed on any of the other logs or stump surfaces. Some previous studies reported that CO_2 flux was higher in decayed CDW than in fresh CDW (Bond-Lamberty et al. 2003; Gough et al. 2007; Herrmann and Bauhus 2013) because relatively high moisture and low density in high decay class CDW can enhance the macrofauna and microbial activity within optimal moisture levels (Noh et al. 2017). Our study showed that fresh logs released CO_2 at double the rate of the 4 year-old decayed log within a narrow range of the early decay stage. The observed differences in N concentrations of fresh versus decayed logs may provide an explanation for these relative CO_2 flux rates. Though the N concentration of whole logs generally increases with increased stage of decay, this pattern might be confounded by the presence of bark, which tends to be high in N (Laiho and Prescott 2004), and has been lost from the decayed logs in this study. However, because N contents of the fresh logs were not significantly higher than the decayed logs at the non-flooded location, increased moisture retention in the bark of the fresh logs may play a role in the observed differences in flux rates (Ulyshen et al. 2016). In the Girdle sites, the F_{Gstem} was significantly greater at the 0.5 m height. We did not examine difference in moisture between different heights of girdled stem, but the difference in F_{Gstem} between the heights could be a function of wood moisture (Schmid et al. 2016). To better isolate possible controls on CO_2 fluxes from CDW, longer-term studies on water availability and fungal and microbial communities are needed (Forrester et al. 2015; Van der Wal et al. 2015).

Observed mean F_{Soil} was much lower than that reported in a *F. americana* dominated upland forest in central New Hampshire, USA (Matthes et al. 2018) though it was greater than the wide range of F_{Soil} related to water levels reported by an earlier study at the same site (Van Grinsven et al. 2018). Since our sampling points were on saturated wetland soils, the anaerobic conditions and water-filled soil pores could reduce soil microbial activity and soil gas diffusion (Fissore et al. 2009; Yoon et al. 2014a). However, mean F_{Stem} was greater than the estimates for upland temperate forests (Warner et al. 2017). The normalized F_{20} of 2.19 μmol m^{-2} s^{-1} for live stems was within the range of 1.40 and 3.63 μmol m^{-2} s^{-1} for tree species in mixed deciduous forests in northern Wisconsin (Bolstad et al. 2004). F_{Stem} of black ash may be expected to be higher than upland species due to physiological structures such as stem lenticels and aerenchyma, which aid the passage of oxygen to reduce hypoxia during flooded conditions, and of xylem-transported CO_2 originating from the rhizosphere (Teskey et al. 2007; Trumbore et al. 2013; Salomón et al. 2016; Bolton 2017). Interestingly, at our undisturbed black ash site the ash stems had almost the same flux rate as the wetland soil, which is inconsistent with results in upland forests (Bolstad et al. 2004; Warner et al. 2017). However, a related study showed that black ash stem fluxes of methane were comparable or greater than soil methane flux, suggesting relatively high conductance of gases (Bolton 2017; Van Grinsven et al. 2018). Although the size of the fluxes may depend on stem size and stand age (Gough et al. 2007; Ryan et al. 2009), F_{Stem} for mature black ash trees at this study site was similar to those for other northern deciduous species with diameters between 19 and 58 cm (Bolstad et al. 2004).

Temperature responses of F_{CDW}

The CDW surface temperature was one of the most important predictors in regulating F_{CDW}, which is consistent with many previous studies on various factors controlling respiration (Bolstad et al. 2004; Gough et al. 2007; Forrester et al. 2012; Yoon et al. 2014a). The temperature sensitivity—as indicated by the Q_{10} value—ranged from 1.35 to 2.47 for F_{CDW}, which is wider than the range in Q_{10} values for CDW with five different decay classes in a mixed deciduous temperate forest in the upper Great Lakes region (Gough et al. 2007). In terms of F_{Stem}, the Q_{10} of 3.74 for black ash was much greater than the range of 2.11–2.26 for four northern deciduous upland species including blue ash (*F. pennsylvanica*) (Ryan et al. 2009). The high Q_{10} of black ash stems may reflect dramatic seasonal changes in the growth respiration as an adaptive response to the relatively short growing season when compared to southern upland species (Warner et al. 2017). Higher sap fluxes in black ash as compared to other species in our study sites suggests black ash is adapted to maximize certain physiological processes to reduce potential negative effects of a short growing season (Shannon et al. 2018). The wide range of Q_{10} values observed and the mismatching temperature responses of soil, live and dead stems should be taken into consideration when modeling ecosystem respiration and seasonal partitioning of CO_2 (Miao et al. 2017). The significant differences in the intercepts of the mixed effects model among substrate types indicate that substrate-specific CO_2 fluxes should be considered when quantifying stand level CO_2 fluxes in EAB infested black ash wetlands and possibly other forest types. In addition, future studies should address the diurnal variations in CO_2 from soil, stems, and CDW to quantify the annual CO_2 fluxes at stand level and better understand their contribution to C budgets after an actual EAB invasion.

EAB-induced tree mortality and C cycle

As we hypothesized, the removal of ash in the Ash-Cut treatment significantly increased the wood surface temperature. The increase in canopy openness, and subsequent increased insolation, increased respirational C loss from CDW because the F_{CDW} strongly responds to increasing temperature, which is consistent with the result of a gap opening experiment (Forrester et al. 2012). However, changes in wood moisture, density and N concentration were not observed in the girdling simulation. In the event of a complete loss of ash from the canopy, the change in moisture would be expected to increase the decomposition rate of residual CDW (Fig. 6) within an unsaturated moisture range (Bond-Lamberty et al. 2003). This change could result from pre-emptive or salvage harvest, an inability of the site to regenerate a full canopy because of higher water tables (Slesak et al. 2014; Van Grinsven et al. 2017), or excessive herbaceous competition (Davis et al. 2017; Bolton et al. 2018). Increases in the water tables following black ash tree mortality are likely to contribute to increased moisture content of downed woody debris in these wetlands when compared to upland forests or unimpacted black ash stands. The increased wood moisture might provide better environmental conditions for microbial community colonization (Van der Wal et al. 2015; Kahl et al. 2017), and this increased microbial activity would accelerate decomposition rates, and hence, CO_2 fluxes.

An earlier study at the same site reported that the girdled treatment increased F_{Soil} which was responsive to water table position and temperature (Van Grinsven et al. 2018). In concert with this increase in F_{Soil}, the corresponding decline of black ash photosynthesis will lead to declines in gross primary productivity over time (Flower et al. 2013; Anderegg et al. 2016) and decomposition of CDW is expected to drive lagged increases in heterotrophic respiration. In particular F_{CDW} is generally unaccounted for in C models and will contribute substantially to C losses until the disturbed wetland canopy has recovered completely. The recovery of EAB infested wetlands might take several decades (Edburg et al. 2012; Flower and Conzalez-Meler 2015) because of high competition from the release of the herbaceous understory by canopy opening (Davis et al. 2017) and the potential of poor recruitment from tree seedlings to saplings (Bolton et al. 2018). Therefore, future studies should build upon the short-term results from our study to investigate long-term rates of CDW decomposition to ascertain how soil C and N pools will be accumulated (Bantle et al. 2014; Meyer and Brischke 2015).

Conclusions

We measured growing season CO_2 fluxes from soil, stems, and different types of CDW in black ash wetlands where we simulated short-term response to EAB invasion and complete ash canopy loss. We observed different seasonal patterns of CO_2 flux among the wood components and found significantly greater CO_2 fluxes from the cross-sections of logs and stumps than from other components. Our field evidence indicates that different substrate types have different basal respiration rates, and this resulted in highly variable F_{15} values (0.84 to 7.28 μmol m^{-2} s^{-1}) among different flux components. We demonstrated that removal of the ash canopy component increased soil and CDW surface temperatures, and higher temperatures in CDW increased F_{CDW}. Furthermore, we showed that seasonal flooding, increased F_{CDW} of fresh logs, and this implies there will be greater CO_2 fluxes from fresh down wood in black ash wetlands after EAB infestation. Our results suggest that the increases in soil and CDW temperatures would enhance CO_2 fluxes from black ash wetland ecosystems. The log and stump cross-sections may function as an unaccounted-for pathway of CO_2 flux following pre-emptive or salvage harvests after EAB infestation. After infestation, the standing dead stems would gradually elevate coarse wood inputs to the forest floor and the increased biomass of CDW would cause additional CO_2 emissions. One implication is that earlier management actions such as removal of dead wood via salvage harvest could lead to wood in structures or other longer-term storage pools, maintaining the C in storage for a longer time period than if allowed to decay on-site.

Acknowledgements We thank the journal's subject-matter editor and the two anonymous reviewers for their comments. This study was funded by USDA Forest Service, US-EPA Great Lakes Restoration Initiative (Grant/Award No. DW-12-92429101-0). We appreciate the experimental support of Michigan Tech's Ecosystem Science Center.

References

Anderegg WRL, Martinez-Vilalta J, Cailleret M, Camarero JJ, Ewers BE, Galbraith D, Gessler A, Grote R, Huang C, Levick SR, Powell TL, Rowland L, Sánchez-Salguero R, Trotsiuk V (2016) When a tree dies in the forests: scaling climate-driven tree mortality to ecosystem water and carbon fluxes. Ecosystems 19:1133–1147

Arguez A, Durre I, Applequist S, Vose RS, Squires MF, Yin X, Heim RR, Owen TW (2012) NOAA's 1981–010 U.S. climate normals: an overview. Bull Am Meteorol Soc 93:1687–1697

Bantle A, Borken W, Matzner E (2014) Dissolved nitrogen release from coarse woody debris of different tree species in the early phase of decomposition. For Ecol Manag 334:277–283

Boddy L, Watkinson SC (1995) Wood decomposition, higher fungi, and their role in nutrient redistribution. Can J Bot 73:1377–1383

Bolstad PV, Davis KJ, Martin J, Cook BD, Wang W (2004) Component and whole-system respiration fluxes in northern deciduous forests. Tree Physiol 24:493–504

Bolton NW (2017) Methane flux of tree stems and mitigating the impacts of insect outbreak through planting alternative tree species within the Upper Great Lakes Region, USA. Dissertation, School of Forest Resources and Environmental Science, Michigan Technological University

Bolton N, Shannon J, Davis J, Van Grinsven M, Noh NJ, Schooler S, Kolka R, Pypker T, Wagenbrenner J (2018) Methods to improve alternative species seedlings survival and growth in black ash ecosystems threatened by emerald ash borer. Forests 9:146. https://doi.org/10.3390/f9030146

Bond-Lamberty B, Wang C, Gower ST (2003) Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. J Geophys Res 108(D3):8220. https://doi.org/10.1029/2001JD000839

Davidson EA, Janssens IA, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. Glob Change Biol 12:154–164

Davis JC, Shannon JP, Bolton NW, Kolka RK, Pypker TG (2017) Vegetation responses to simulated emerald ash borer infestation in *Fraxinus nigra* dominated wetlands of Upper Michigan, USA. Can J For Res 47:319–330

Edburg SL, Hicke JA, Brooks PD, Pendall EG, Ewers BE, Norton U, Gochis D, Gutmann ED, Meddens AJH (2012) Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Front Ecol Environ 10:416–424

Emerald Ash Borer Information Network. http://www.emeraldshborer.info. Accessed 7 Dec 2018

Fissore C, Giardina CP, Kolka RK, Trettin CC (2009) Soil organic carbon quality in forested mineral wetlands at different mean annual temperature. Soil Biol Biochem 41:458–466

Flower CE, Conzalez-Meler MA (2015) Responses of temperate forest productivity to insect and pathogen disturbances. Annu Plant Biol 66:547–569

Flower CE, Knight KS, Conzalez-Meler MA (2013) Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biol Invasion 15:931–944

Forrester JA, Mladenoff DJ, Gower ST, Stoffel JL (2012) Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. For Ecol Manag 265:124–132

Forrester JA, Mladenoff DJ, D'Amato AW, Fraver S, Linder DL, Brazee NJ, Clayton MK, Gower ST (2015) Temporal trends and sources of variation in carbon flux from coarse woody debris in experimental forest canopy openings. Oecologica 170:889–900

Gough CM, Vogel CS, Kazanski C, Nagel L, Flower CE, Curtis PS (2007) Coarse woody debris and the carbon balance of a north temperate forest. For Ecol Manag 244:60–67

Herms D, McCullough D (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts and management. Annu Rev Entomol 59:13–30

Herrmann S, Bauhus J (2013) Effects of moisture, temperature and decomposition stage on respirational carbon loss from coarse woody debris (CWD) of important European tree species. Scand J Forest Res 28:346–357

Hinrichs C, Boiler C (2014) JMP essentials: an illustrated step-by-step guide for new users, 2nd edn. SAS Institute Inc., Cary, NC, USA

Iverson L, Knight KS, Prasad A, Herms DA, Mattews S, Peters M, Smith A, Hartzler DM, Long R, Almendinger J (2016) Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: emerald ash borer and a changing climate. Ecosystems 19:248–270

Jomura M, Akashi Y, Itoh H, Yuki R, Sakai Y, Maruyama Y (2015) Biotic and abiotic factors controlling respiration rates of above- and belowground woody debris of *Fagus crenata* and *Quercus crispula* in Japan. PLoS ONE 10:e0145113. https://doi.org/10.1371/journal.pone.014113

Kahl T, Arnstadt T, Baber K, Bässler C, Bauhus J, Borken W, Buscot F, Floren A, Heibl C, Hessenmöller D, Hofrichter M, Hoppe B, Kellner H, Krüger D, Linsenmair KE, Matzner E, Otto P, Purahong W, Seilwinder C, Schulze ED, Wende B, Weisser WW, Gossner MM (2017) Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. For Ecol Manag 391:86–95

Kashian DM, Witter JA (2011) Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. For Ecol Manag 261:480–488

Klooster WS, Gandhi KJK, Long LC, Perry KI, Rice KB, Herms DA (2018) Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. Forests 9:250. https://doi.org/10.3390/f9050250

Kolka RK, D'Amato AW, Wagenbrenner JW, Slesak RA, Pypker TG, Youngquist MB, Grinde AR, Palik BJ (2018) Review of ecosystem level impacts of emerald ash borer on black ash wetlands: what does the future hold? Forests 9:179. https://doi.org/10.3390/f9040179

Laiho R, Prescott CE (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forest: a synthesis. Can J For Res 34:763–777

Littell RC, Milliken G, Stroup W, Wolfinger R, Schabenberger O (2006) SAS for mixed models, 2nd edn. SAS Institute Inc., Cary, NC

Looney CE, D'Amato AW, Palik BJ, Slesak RA (2015) Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened *Fraxinus nigra* forests in Minnesota, USA. Can J For Res 45:1728–1738

Looney CE, D'Amato AW, Palik BJ, Slesak RA (2017a) Canopy treatment influences growth of replacement tree species in *Fraxinus nigra* forests threatened by the emerald ash borer in Minnesota, USA. Can J For Res 47:183–192

Looney CE, D'Amato AW, Palik BJ, Slesak RA, Slater MA (2017b) The response of *Fraxinus nigra* forest ground-layer vegetation to emulated emerald ash borer mortality and management strategies in northern Minnesota, USA. For Ecol Manag 389:352–363

MacFarlane D, Meyer S (2005) Characteristics and distribution of potential ash tree hosts for emerald ash borer. For Ecol Manag 213:15–24

Magnússon RÍ, Tietema A, Cornelissen JHC, Hefting MM, Lalbitz K (2016) Tamm review: sequestration of carbon from coarse woody debris in forest soils. For Ecol Manag 377:1–15

Matthes JH, Lang AK, Jevon FV, Russell SJ (2018) Tree stress and mortality from emerald ash borer does not systematically alter short-term soil carbon flux in a mixed Northeastern U.S. forest. Forests 9:37. https://doi.org/10.3390/f9010037

Meyer L, Brischke C (2015) Fungal decay at different moisture levels of selected European-grown wood species. Int Biodeter Biodeg 103:23–29

Miao G, Noormets A, Domec JC, Fuentes M, Trettin CC, Sun G, McNulty SG, King JS (2017) Hydrology and microtopography control carbon dynamics in wetlands: implications in partitioning ecosystem respiration in a coastal plain forested wetland. Agric Forest Meteorol 247:343–355

Mosier SL, Kane ES, Richter DL, Lilleskov EA, Jurgensen MF, Burton AJ, Resh SC (2017) Interactive effects of climate change and fungal communities on wood-derived carbon in forest soils. Soil Biol Biochem 115:297–309

Nisbet D, Kreutzweiser D, Sibley P, Scarr T (2015) Ecological risks posed by emerald ash borer to riparian forest habitats: a review and problem formulation with management implications. For Ecol Manag 358:165–173

Noh NJ, Yoon TK, Kim RH, Bolton NW, Kim C, Son Y (2017) Carbon and nitrogen accumulation and decomposition from coarse woody debris in a natural regenerated Korean red pine (*Pinus densiflora* S. et Z.) forest. Forests 8:214. https://doi.org/10.3390/f8060214

Ohtsuka T, Shizu Y, Hirota M, Yashiro Y, Shugang J, Iimura Y, Koizumi H (2014) Role of coarse woody debris in the carbon cycle of Takayama forest, central Japan. Ecol Res 29:91–101

Perry KI, Herms DA, Klooster WS, Smith A, Hartzler DM, Coyle DR, Gandhi KJK (2018) Downed coarse woody debris dynamics in ash (*Fraxinus* spp.) stands invaded by emerald ash borer (*Agrilus planipennis* Fairmaire). Forests 9:191. https://doi.org/10.3390/f9040191

Pugh SA, Liebhold AM, Morin RS (2011) Changes in ash tree demography associated with emerald ash borer infestation, indicated by regional forest inventory data from the Great Lakes States. Can J For Res 41:2165–2175

Russell MB, Fraver S, Aakala T, Gove JH, Woodall CW, D'Amato AW, Ducey MJ (2015) Quantifying carbon stores and decomposition in dead wood: a review. For Ecol Manag 350:107–128

Ryan MG, Cavaleri MA, Almeida AC, Penchel R (2009) Wood CO_2 efflux and foliar respiration for Eucalyptus in Hawaii and Brazil. Tree Pysiol 29:1213–1222

Salomón RL, Valbuena-Carabaña M, Gil L, McGuire MA, Teskey RO, Aubrey DP, González-Doncel I, Rodríguez-Calcerrada J (2016) Temporal and spatial patterns of internal and external stem CO_2 fluxes in a sub-Mediterranean oak. Tree Physiol 36:1409–1421

SAS Institute (2012) SAS 9.4 for Windows, Cary, NC, USA

Schmid AV, Vogel CS, Liebman E, Curtis PS, Gough CM (2016) Coarse woody debris and the carbon balance of a moderately disturbed forest. For Ecol Manag 361:38–45

Shannon J, Van Grinsven M, Davis J, Bolton N, Noh NJ, Pypker T, Kolka R (2018) Water level controls on sap flux of canopy species in black ash wetlands. Forests 9:147. https://doi.org/10.3390/f9030147

Slesak RA, Lenhart CF, Brooks KN, D'Amato AW, Palik BJ (2014) Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can J For Res 44:961–968

Sorz J, Hietz P (2006) Gas diffusion through wood: implications for oxygen supply. Tree 20:34–41

Teskey RO, Saveyn A, Steppe K, McGuire MA (2007) Origin, fate and significant of CO_2 in tree stems. New Phytol 177:17–32

Trumbore SE, Angert A, Kunert N, Muhr J, Chambers JQ (2013) What's the flux? Unraveling how CO_2 fluxes from tree reflect underlying physiological processes. Tree Physiol 197:353–355

Ulyshen MD, Müller J, Seibold S (2016) Bark coverage and insects influence wood decomposition: direct and indirect effects. Appl Soil Ecol 105:25–30

Van der Wal A, Ottosson E, de Boer W (2015) Neglected role of fungal community composition in explaining variation in wood decay rates. Ecology 96:124–133

Van Grinsven MJ, Shannon JP, Davis JC, Bolton NW, Wagenbrenner JW, Kolka RK, Pypker TG (2017) Source water contributions and hydrologic responses to simulated emerald ash borer infestations in depressional black ash wetlands. Ecohydrology 1862:1–13. https://doi.org/10.1002/eco.1862

Van Grinsven MJ, Shannon JP, Bolton NW, Davis JC, Wagenbrenner JW, Kolka RK, Pypker TG (2018) Response of black ash wetland gaseous soil carbon fluxes to a simulated emerald ash borer infestation. Forests 9:324. https://doi.org/10.3390/f9060324

Warner DL, Villarreal S, McWilliams K, Inamdar S, Vargas R (2017) Carbon dioxide and methane fluxes from tree stem, coarse woody debris, and soils in an upland temperate forest. Ecosystems 20:1205–1216

Yoon TK, Han S, Lee DH, Han SH, Noh NJ, Son Y (2014a) Effects of sample size and temperature on coarse woody debris respiration from *Quercus variabilis* logs. J For Res 19:249–259

Yoon TK, Noh NJ, Han S, Lee J, Son Y (2014b) Soil moisture effects on leaf litter decomposition and soil carbon dioxide efflux in wetland and upland forests. Soil Sci Soc Am J 78:1804–1816

Yoon TK, Noh NJ, Kim S, Han S, Son Y (2015) Coarse woody debris respiration of Japanese red pine forests in Korea: controlling factors and contribution to the ecosystem carbon cycle. Ecol Res 30:723–734