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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

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Abstract Invasive species are widely recognized as altering species and community dynamics, but their impacts on biogeochemical cycling and ecosystem processes are less understood. The emerald ash borer (*Agrilus planipennis* Fairmaire) is a phloem feeding beetle that was inadvertently introduced to the US in the 1990s and relies solely on ash trees (*Fraxinus* spp.) to complete its life cycle. Ash trees have a wide geographic distribution and are an important component of many different forest types in the US. The larval feeding behavior of the emerald ash borer (EAB) effectively girdles the tree's phloem tissue resulting in tree mortality in as little as 2 years and stand mortality in as little as 5 years. Using the forest inventory and analysis database, we found that forest lands in the lower 48 states hold approximately 8.7 billion ash trees and saplings, which represent ~2.5 % of the aboveground forest carbon mass. Furthermore, we measured tree growth in 7 EAB impacted and 5 non-EAB impacted temperate forests in the Midwestern United States to quantify the impacts of EAB induced tree mortality on tree growth. We hypothesized that the initial C lost would be partly compensated for by the enhanced non-ash tree growth in EAB-impacted regions relative to non-EAB impacted regions. The EAB disturbance enhanced growth of non-ash trees in the EAB impacted region relative to the non-EAB impacted region. Results also indicate that in EAB impacted areas, growth of trees from the genera *Acer* and *Ulmus* responded most positively. Finally, we quantified annual biometric net primary productivity of the EAB impacted forests and compared these quantities to modeled growth of these forests in the absence of EAB and found that large scale ash tree mortality has reduced short term regional forest productivity. The loss of ash biometric net primary productivity is, in part compensated by enhanced growth of non-ash species. As expected, EAB disturbance severity was greater in forests with higher basal areas of ash. This study illustrates the ecosystem and regional scale impacts of invasive pest-induced disturbance on biogeochemical cycling and forest species composition.

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Introduction

Biotic and abiotic factors are critical to the functioning of forest ecosystems and govern combined carbon and nutrient cycling within them. Abiotic factors represent the principle drivers of terrestrial productivity at large spatial and temporal scales. These abiotic factors include mean annual temperature and precipitation (Churkina and Running 1998), and light radiation (Ogren and Sundin 1996). Biotic factors on the other hand include the ecological interactions that occur between species both above and belowground (e.g. competition for resource acquisition or herbivore-plant interactions). The impacts of biotic factors on ecosystem processes have long been recognized (Bolin 1977), but are less well understood because of inherent complexities of associated interactions (Chapin et al. 2000). Biotic effects on ecosystem processes are particularly unknown when considering the introductions of new species and pests (Ehrenfeld 2010). Untangling the effects of biotic variables on terrestrial forest ecosystems is important for predicting forest responses to pest outbreaks and may provide insight into future impacts of climate change on ecosystem dynamics and biogeochemical cycling.

Non-native pathogens and insect outbreaks have caused substantial damage to their host species. For example, the chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) largely extirpated the American chestnut (*Castanea dentata* (Marsh.) Borkh.) which was once a dominant component of North American temperate forests (Anagnostakis 1987; Hicke et al. 2012). Elm bark beetle-facilitated spread of Dutch elm disease (*Ophiostoma ulmi* (Buisman) Melin & Nannf. and *O. nova-ulmi* (Brasier)) resulted in considerable damage to elm trees across the eastern US (Karnosky 1979; Brasier 1991). While the consequences of non-native species for their host species are understood, their impacts on forest successional dynamics and forest productivity are less well known (Ehrenfeld 2010). The recent invasion of the emerald ash borer (*Agrilus planipennis* Fairmaire, EAB) in the US has the potential to impact forest ecosystems in a similar way via widespread tree mortality. This will likely have further impacts on the species composition and carbon cycling within these forests.

The EAB is a small, wood boring beetle, native to Asia (Bauer et al. 2003a; Wang et al. 2010). Inadvertently introduced to North America in the 1990s, EAB

has been identified as the agent responsible for the rapid and widespread decline of ash (*Fraxinus* spp.) trees in the Great Lakes region (Haack et al. 2002; McCullough and Katovich 2004; Siegert et al. 2007; Pugh et al. 2011). Feeding by EAB larvae in the cambial tissue severs nutrient and water transport between roots and shoots (Flower et al. 2010) resulting in high rates of tree mortality within 2–5 years (McCullough and Katovich 2004; Knight et al. 2008). The severity of this insect threat is compounded by the fact that EAB is capable of considerable dispersal distances ($\sim$32 km/year) and its rapid spread across the Great Lakes Region has been facilitated by human activities (Bauer et al. 2003b; Prasad et al. 2010). Although not all of the native *Fraxinus* spp. have been tested for susceptibility, all species within the current range of EAB (and tested in common garden studies) are known to be susceptible to EAB attack (Cappaert et al. 2005; Poland and McCullough 2006). Therefore, efforts to control EAB have focused on the removal of ash trees, the use of repeated insecticide applications to protect valuable urban trees and the introduction of biological control agents (Cappaert et al. 2005; McCullough et al. 2010; Fuester et al. 2010; Bauer et al. 2010). Despite these efforts, EAB continues to spread at an alarming rate across temperate forests of the Eastern United States resulting in the widespread mortality of ash, thereby affecting ecosystem fluxes and biogeochemical cycling. Annual forest carbon storage, a measure of net primary production (NPP), can be measured as the sum of gains in individual plant carbon pools (wood, leaf and root) and C lost to herbivory, less C lost to respiration over a specified period of time (Gough et al. 2008). Individual components of forest NPP, such as shifts in aboveground live wood C mass, can provide valuable information regarding shifts in carbon pools associated with disturbance events. The EAB outbreak in North America provides the opportunity to assess the impact of a unique pest outbreak on components of the carbon budget and forest ecosystems. A better understanding of the impacts of pest disturbances can inform forest managers and models predicting their impacts on ecosystems. Furthermore, despite the potential impacts of ash tree decline on forest C dynamics, the magnitude of these effects have not yet been quantified.

Globally forests store large quantities of C in wood and organic material and vary considerably in rates of

C storage (Goodale et al. 2002). Temperate forest ecosystems in North America, which represent the primary habitat for ash trees in the US, are regionally important carbon sinks, maintaining high rates of net ecosystem productivity (NEP) between 0.7 and 3.4 Mg C hectare^{-1} year^{-1} (Curtis et al. 2002). Aside from their substantial ecological impacts, native and non-native insect outbreaks have been causing unpredictable ecosystem C losses in forest ecosystems (Hicke et al. 2012). Forest pests directly impact the carbon cycling of forests via reduced carbon uptake and indirectly alter the remaining vegetation (Peltzer et al. 2010) as illustrated by the gypsy moth (*Lymantria dispar L.*) defoliation of an oak-dominated forest that reduced carbon sequestration by >44 % (Clark et al. 2010). Although the mechanism of EAB induced tree mortality is different than that of gypsy moth, the potential impacts on the C storage and dynamics of these highly productive systems may be considerable and remain largely unknown.

The objectives of this paper were threefold: first, we explore the potential impacts of the invasive EAB on standing ash C stocks in the United States; second, we quantify differences between the relative growth rates of non-ash trees in EAB impacted forests and non-EAB impacted forests in Ohio, USA; third, we quantify alterations to forest NPP associated with ash declines in temperate forests in Ohio, USA. This investigation relies on USDA Forest Inventory and Analysis data to evaluate the potential impacts of unimpeded EAB spread on *Fraxinus* spp. forest carbon stocks. To investigate tree growth responses which will inform our understanding of the successional trajectory of these temperate forests, we assessed the relative growth rates (RGR) of non-ash genera from seven heavily infested forests near Toledo, OH and five non-infested forests in Cleveland, OH from 2005 to 2011. We hypothesize that the non-ash trees in EAB impacted forests will exhibit a competitive release, and thereby higher RGR's, compared to trees in non-EAB impacted forests. For our test of EAB induced alterations in forest NPP, we hypothesize that the EAB disturbance will reduce forest NPP and the severity of this disturbance will relate to the basal area of ash in a forest. We also hypothesize that the EAB induced mortality will result in the compensatory growth of non-ash trees which will respond to the gaps opened by ash mortality.

Methods

Forest carbon inventory

Standing carbon stock data was generated using the Forest Inventory Data online application which draws from the US Forest Service's National Forest Inventory and Analysis (FIA) database (US Forest Service 2007). Briefly, the FIA program has been surveying forest land in the US since 1928 and periodically conducts tree inventories on randomly located plots in areas defined as forest land (i.e. greater than 1 acre, at least 120 ft wide, and exposed to particular management regimes) (Birdsey and Schreuder 1992; US Forest Service 2007). Forest land is defined as land at least 10 % stocked with trees of any size or formerly having had such tree cover and not currently developed for nonforest use (US Forest Service 2007). In this database, measurements are confined to aboveground live biomass on timberland in the contiguous US (i.e. the lower 48 states, excluding Alaska and Hawaii). See Pugh et al. (2011) for a more comprehensive discussion of FIA methodologies and research related to the use of this database to assess ash tree demography associated with EAB invasion in the Great Lakes States. The FIA database was used to generate statewide inventories on the standing *Fraxinus* spp. volume, which was converted to carbon content using a wood carbon fraction of 0.485, a carbon fraction derived from the elemental analysis of bole wood tissue from 20 ash trees (Gough et al. 2009). Inventory data from 2008 was used when it was available; otherwise the most recent data was utilized. This 2008 inventory represents the compilation of a 5 year window of plot measuring, i.e. 2003–2008, whereby 20 % of plots were visited each year. Due to the lack of FIA resolution, the authors did not use the FIA database to track ash decline, however we direct the readers to an analysis by Pugh et al. (2011) which used coarse FIA data and compared the inventory results to baseline information to track changes in ash mortality over time.

Site description and experimental design

Specific effects of EAB on the growth of non-ash trees and forest NPP were assessed by measuring diameter growth of trees (described in more detail later) in riparian forests in two regions (NW and NE) within the

Table 1 Summary characteristics of study areas located in non-EAB impacted (NI) and EAB impacted (I) regions of Ohio. Soil taxonomic characteristics derived from USDA NRCS

Region	Forest	Number of plots	Soil taxonomy	% Basal area ash (mean)
I	Maumee St. Forest	6	Granby loamy fine sand	43.1
I	Oak Openings	9	Sloan loam	60.9
I	Wildwood Metro Parks	3	Spinks fine sand	49.6
I	Fallen Timbers	6	St. Clair silty clay loam	36.8
I	Maumee Bay State Park	9	Toledo silty clay	78.6
I	Pearson Metro Parks	9	Latty silty clay	39.4
I	Goll Woods	3	Lenawee silty clay loam	11.2
NI	Bradley Woods	6	Mitiwanga silt loam	21.2
NI	Fowler Woods	3	Pewomo silty clay loam	33.5
NI	Holden Arboretum	6	Darian silt loam	67.4
NI	North Chagrin	5	Mahoning silt loam	49.1
NI	Rocky River	5	Chagrin silt loam	44.5

lake plains physiographic region in northern Ohio, USA (see Table 1 for additional site characteristics). The study area in NW Ohio (hereafter the EAB impacted region) is located ~60 mi from the epicenter of the EAB infestation in Detroit, MI and encompasses 45 plots (11.28 m radius) established across 7 forest stands. The study area in NE Ohio is located ~200 mi from the epicenter of the EAB infestation and encompasses 25 plots established across 5 forests. Due to the fact that none of the ash trees in the NE Ohio plots exhibited EAB symptoms (i.e. canopy decline, D shaped exit holes, and epicormic sprouting) during the study, this region was considered non-EAB impacted when the plots were established (although it is possible these stands were infested at very low, undetectable densities). Sites in NW Ohio, near Toledo, exhibited a mean annual temperature (MAT) of 9.2 °C and a mean annual precipitation (MAP) of 838 mm largely comparable to those in NE Ohio, near Cleveland, with a similar MAT of 9.7 °C and a MAP of 929 mm. Aside from the presence of ash in the canopy, plots were randomly established and placed at least 50 m from one another within the same forest stand. The study was initiated in 2005 and by 2006, >90 % of forests within the EAB impacted region (Toledo) exhibited EAB symptoms (i.e. epicormic sprouting, canopy dieback, and D shaped exit holes on ash trees). By 2011 ash tree mortality in the EAB impacted forests of NW Ohio exceeded 90 %. In contrast, the forests in the non-EAB impacted area of NE Ohio remained largely un-impacted by EAB

during the 2005 to 2011 study. Plots in NW Ohio were initially sampled in 2005 and re-sampled in 2011, while plots in NE Ohio were initially sampled in 2008 and re-sampled in 2011.

The forests within the study areas are secondary successional forests largely dominated by ash (*Fraxinus americana* L., *F. pennsylvanica* Marshall, *F. profunda* Bush, *F. nigra* Marshall). Other canopy species include sugar maple (*Acer saccharum* Marshall), silver maple (*Acer saccharinum* L.), American elm (*Ulmus americana* L.), cottonwood (*Populus deltoides* Bartram ex Marshall), basswood (*Tilia americana* L.), oak (*Quercus* spp.), hickory (*Carya* spp.), sycamore (*Platanus occidentalis* L.), American beech (*Fagus grandifolia* Ehrh.), and sweetgum (*Liquidambar styraciflua* L.).

Tree growth measurements

Fine-scale measurements of tree growth and mortality dynamics in specific sites are useful for understanding the rapidly changing C dynamics of forest ecosystems. Thereby, tree growth rates were quantified by measuring individual tree diameters (DBH, measured at breast height, 1.37 m), to the nearest 0.1 cm DBH, in 2005 and again in 2011 during June under similar weather conditions. Tree DBH was measured during mid-day over several days to minimize the likelihood that environmental factors such as the water-related expansion and shrinkage of sap would alter tree diameter (Baker et al. 2002; Zweifel et al. 2001). The

growth increment approach is appropriate for investigating patterns of tree growth and the production of wood (carbon accumulation) over longer periods such as the duration of this study (Condit et al. 2006; Zweifel et al. 2010; van Doorn et al. 2011). The relative growth rate (RGR, mm cm^{-1} year^{-1}) was calculated as the growth increment of an individual tree from 2005 to 2011 divided by the number of years between the measurement periods relative to the initial diameter of the tree (Garnier 1991). This approach allows us to standardize growth over a wide range of DBH's and to eliminate growth differences that arose prior to the initial sampling, thus encompassing canopy transitions during the EAB infestation. This approach, while coarse, is frequently used to compare growth differences in plants that arise from ontogeny, light environments, and between species (Walters et al. 1993). Here we used this method to assess differential growth responses of canopy trees in forests with EAB and those without EAB. Nearly 500 non-ash trees from the EAB impacted region and over 600 non-ash trees from the non-EAB impacted region were included in this analysis.

Canopy position classification

Initial tree canopy position (dominant, co-dominant, intermediate, and suppressed) was visually classified to assess differential growth rates between tree species in different canopy positions. It has been proposed that tree growth may be correlated with crown position (Korsgaard 1986) due to increased light availability for trees in canopy positions relative to those in understory positions (Ellsworth and Reich 1993). Tree canopy positions were classified according to Oliver and Larson (1996). Briefly, *dominant* trees were classified as those that extend their canopies above the general canopy level and were exposed to sunlight from above and on all sides, *co-dominant* trees had canopies that were at the average canopy level of the stand and the tops of their crowns and at least one side were exposed to light, *intermediate* trees occupied a position below the general crown canopy and only received sunlight directly from above, and *suppressed* trees were completely overtopped and receive no direct sunlight. Dominant and co-dominant canopy positions were pooled due to difficulties in assessing canopy position described by Nicholas et al. (1991).

Biometric NPP measurements

The impact of ash mortality on annual biometric NPP (NPP$_B$; live wood production) was measured by quantifying structural C mass contained in aboveground live wood biomass of trees from Toledo forests from 2005 to 2011. Wood production can represent a major component of forest NPP and standing biomass (Gough et al. 2008). NPP represents the carbon gain of living plants in an ecosystem less autotrophic respiration (carbon returned to the atmosphere by plant metabolism). Tree NPP$_B$ was calculated as the annual change in wood biomass (ΔB) between years derived from allometric equations relating stem DBH to aboveground wood dry mass developed specifically for deciduous hardwoods, aspen/alder/cottonwood/willow, soft maple, and hard maple/hickory/oak/beech by Jenkins et al. (2003). Forest annual NPP$_B$ was calculated as the sum of tree ΔB for each plot. Tree biomass was converted to carbon content using a wood carbon fraction of 0.5 (Vogt 1991). In June 2005 and 2011, over 1,300 trees (>10 cm DBH) were inventoried and DBH measured across 45 plots in 7 forests in Toledo, OH.

Because all of the ash trees in the NW Ohio plots had died by the end of the study, they did not contribute to the NPP$_B$ of these EAB impacted forests. Thus, annual NPP$_B$ in the EAB impacted forests was calculated using the observed RGR's of the non-ash trees. To assess the impact of EAB on these forests, we modeled the NPP$_B$ of these sites as if they were not impacted by EAB (henceforth referred to as non-EAB modeled forests). To do this we reincorporated the ash trees into the analysis and estimated their growth using the RGR calculated from ash trees in the non-EAB impacted forests of NE OH (25 plots in 5 forests, 609 trees >10 cm DBH). Because of the ash tree mortality, the non-ash trees in the EAB impacted forests have been exposed to reduced light competition and thus have grown at an accelerated rate. To correct for this we adjusted the RGR of non-ash trees using the rates calculated from non-EAB impacted forests in NE OH. The reduction in NPP$_B$ resulting from the EAB-induced mortality of ash was calculated as the sum of ash ΔB in the non-EAB modeled forests, i.e. adjusted using the RGR of ash from non-impacted forests in NE OH. Additionally, the quantity of NPP$_B$ in the EAB impacted forests which resulted from the enhanced growth of non-ash trees was calculated as the

difference between the NPP$_B$ of the non-ash trees in the non-EAB modeled forests and EAB impacted forests. Finally, we assessed the relationship between the percent of ash basal area in a forest and the change in forest NPP$_B$. The change in forest NPP$_B$ resulting from EAB was determined by subtracting plot level NPP$_B$ measurements of non-EAB impacted forests from those of EAB impacted forests.

Statistical analyses

To assess differences between the relative growth rates (RGR) of non-ash trees we used an analysis of covariance (ANCOVA) with the main effect of EAB impacted and non-EAB impacted forests (Toledo and Cleveland plots respectively, referred to as treatment) with basal area of ash in the stand as a covariate. Due to violations in normality, relative growth rates were rank order transformed prior to analysis, thereby differences detected via statistical methods represent differences in medians. Additionally, we used analysis of variance (ANOVA) to analyze RGR across genera, initial DBH, canopy position classes, and basal area of the Toledo plots to assess successional dynamics of EAB impacted forests. Relative growth rates were compared across genera and canopy position classes using Tukey's HSD, $\alpha = 0.05$. Both genera and canopy position were treated as categorical variables. Genera which represented a minor component of the canopy or lacked replication across canopy position classes were excluded from ad hoc comparisons. Differences in NPP$_B$ between EAB-impacted and simulated non-EAB impacted plots were tested using a student's t test. Finally, the relationship between the precent basal area of ash in a forest and the change in forest NPP$_B$ was assessed with a linear regression analysis. All statistical analyses were conducted using SYSTAT statistical software (v. 12, SYSTAT 2007).

Results

Potential impacts of EAB on standing *Fraxinus* spp. carbon stocks in the United States

Forest ecosystems in the contiguous 48 states store a substantial quantity of C in the aboveground biomass of live trees (~ 12.5 Pg C, 1 Pg $= 10^{15}$ g; Table 2). *Fraxinus* spp., which are widely dispersed across the

Table 2 Aboveground live C mass (MgC) categorized by genus in forests of the contiguous United States

Genus	Mg aboveground mass
Quercus	4,482,676,607
Pseudotsuga	4,094,698,084
Pinus	3,933,951,420
Acer	2,150,297,663
Populus	1,116,585,424
Tsuga	738,416,955
Carya	710,239,454
Fraxinus	607,511,991
Picea	473,270,314
Liquidambar	435,995,800
Fagus	326,100,951
Nyssa	303,461,129
Betula	200,992,593
Thuja	143,908,103
Callitropsis	143,846,601
Larix	123,354,685
Alnus	120,937,385
Sequoia	115,701,535
Tilia	104,944,094
Juglans	82,837,587
Calocedrus	70,115,954

US, represent ~ 2.5 % of this aboveground C mass, varying from 0–24 % depending on the state (Table 2; Fig. 1). The quantity of aboveground C stored in ash trees within the US (~ 0.303 Pg C) is equivalent to 1.7 to 2.9 times the quantity of C annually sequestered by forest vegetation in the US (Birdsey 1992; Birdsey and Heath 1995; Goodale et al. 2002). Ash reaches some of its highest densities in the Great Lakes region, where it represents ~ 5.5–9 % of the standing C mass depending on the state (Fig. 1). Current trapping programs indicate that EAB has been detected in 15 states all with high quantities of standing ash C mass (Fig. 1) accounting for 0.207 Pg C or nearly two-thirds of aboveground ash tree C mass.

Impacts on conspecific growth rates: a comparison between EAB impacted versus non-EAB impacted forests

The relative growth rates of non-ash trees were significantly higher in EAB impacted forests compared to the non-EAB impacted forests (Table 3;
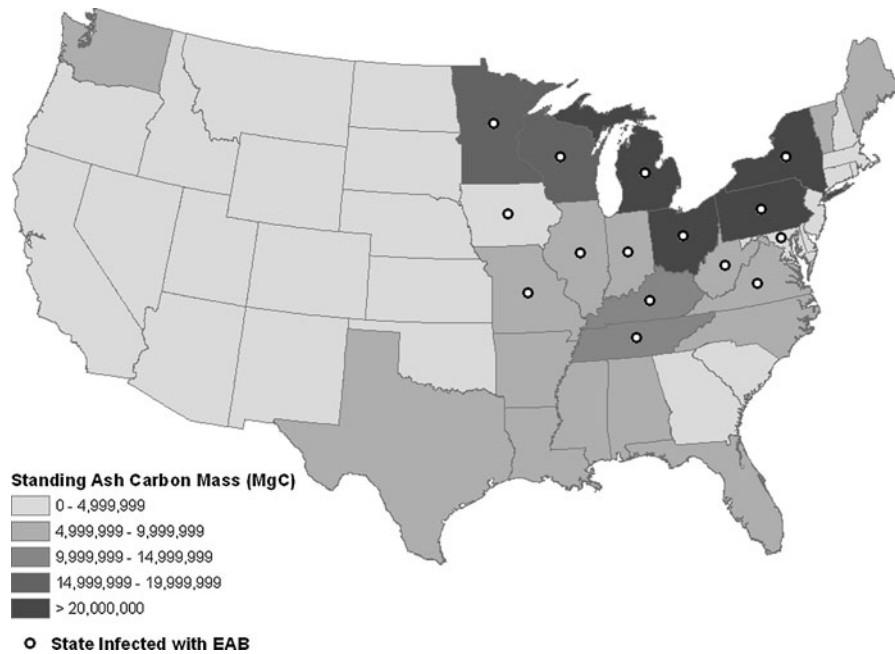
Fig. 1 Standing carbon mass of *Fraxinus* spp. in the contiguous United States. The density of *ash* is denoted by shading and the presence of EAB, as detected by the USDA Animal Plant Health Inspection Service EAB trapping program, is denoted with an *open circle*

Table 3 Analysis of variance statistics investigating the effect of treatment (EAB impacted vs. non-EAB impacted) and basal area of ash on rank transformed relative growth rates of non ash trees

| Source	Type III SS	df	MS	F-ratio	p value
Treatment	565,735	1	565,735	6.039	0.014
BA ash	10,641,678	1	10,641,678	113.599	<0.001
Treatment*BA ash	1,157,578	1	1,157,578	12.357	<0.001
Error	1.069×10^8	1,143	933,677		

$p = 0.014$). The basal area of ash in a forest stand also exhibited a significant positive correlation with tree RGR, indicating that increased ash density resulted in a higher RGR of non-ash trees (Table 3; $p < 0.001$). Additionally, ANOVA results revealed a significant interaction between EAB impacted and non-EAB impacted regions and the basal area of ash ($p < 0.001$). Therefore, the basal area of ash has a differential impact on non-ash tree RGR's between EAB and non-EAB impacted sites. Specifically, the slope of the regression was 15 % higher in EAB impacted compared to non-EAB impacted sites, with a more positive response in the RGR of non-ash trees from EAB impacted forests with higher basal areas of ash trees.

Conspecific growth rates in an EAB-impacted forest

Analysis of the RGR's of non ash trees from the EAB impacted forests reveals that trees from different genera exhibit significant differences in their RGR's as ash senesced (Table 4, $p < 0.001$). Overall, trees from the genera *Acer* and *Ulmus* exhibit some of the highest RGR's at 0.238 ± 0.012 (SE) and 0.224 ± 0.019 (SE) mm cm^{-1} year^{-1} respectively (Fig. 2). Between genera, trees from the genera *Acer, Ulmus* and *Quercus* had a significantly higher RGR's compared to *Liquidambar* (Fig. 2, $p = 0.001$, $p < 0.001$, and $p = 0.048$ respectively). Additionally, results indicate a significant negative correlation

Table 4 Analysis of variance statistics for the main effects of genera, DBH, basal area of ash, and canopy position on the rank order transformed relative growth rates of non ash trees in NW Ohio (Toledo)
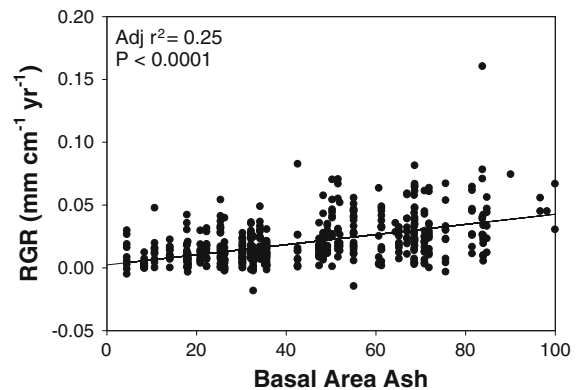
Source	Type III SS	df	MS	F-ratio	p value
Genera	501,023	8	62,267	4.529	<0.001
DBH	86,378	1	86,378	6.246	0.013
BA ash	1,858,841	1	1,858,841	134.421	<0.001
Canopy position	27,871	2	13,935	1.008	0.366
Error	6,720,649	486	13,828		
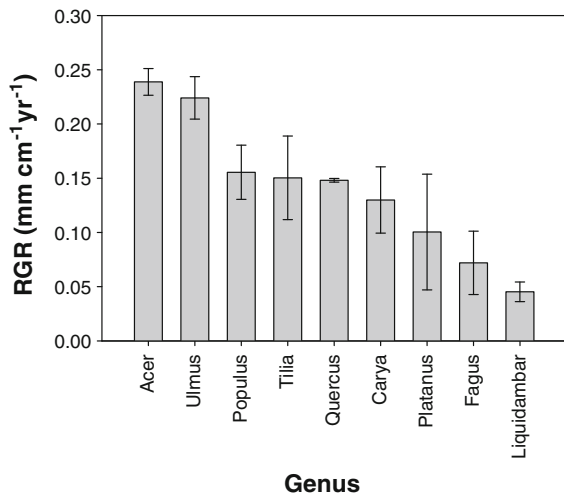
Fig. 2 The median relative growth rate of Genera from Toledo, OH, USA forests

Fig. 3 The relationship between the relative growth rate (RGR) of non *ash trees* and the basal area of *ash* per plot in EAB impacted forests of NW OH, USA

between the initial tree DBH and RGR, indicating the expected reduced RGR as trees age (Table 4, $p = 0.013$). Results also show a significant positive correlation between the initial basal area of ash in a plot and the RGR of non-ash trees (Table 4; Fig. 3; $p < 0.001$). Contrary to our hypothesis, tree RGR was not related to the initial canopy position of the tree (Table 4, $p = 0.366$).

Impacts of ash decline on annual forest biometric NPP

An analysis of annual biometric NPP from riparian forests in EAB-impacted sites (Toledo, OH, USA) indicates that EAB outbreaks can have substantial impacts on forest NPP_B. Modeled non-EAB impacted forests exhibited significantly higher NPP_B compared to EAB impacted forests (Fig. 4, $p < 0.001$). Results suggest that the EAB induced mortality of ash trees reduced average stand NPP_B in the Toledo forests by

about 31 % over the course of the study. In EAB impacted forests, reductions in annual NPP_B attributable to EAB-induced ash tree mortality were ~ 145 g C m^{-2} year^{-1}. The growth of non-ash trees accounted for ~ 197 g C m^{-2} year^{-1} in non-EAB impacted (modeled) sites compared to ~ 233 g C m^{-2} year^{-1} in EAB impacted sites, indicating a compensatory growth following ash tree mortality. Furthermore, our results indicate that at the plot level, the severity of the EAB disturbance on forest NPP_B was related to the ash basal area in a forest (Fig. 5).

Discussion

Fraxinus mortality affects forest carbon cycling

The rapid spread of the EAB-induced mortality of *Fraxinus* trees combined with the wide geographical distribution of ash (Fig. 1) is impacting the growth and C stocks of temperate forest ecosystems of the United States (Figs. 2, 3, 4). Standing live tree mass
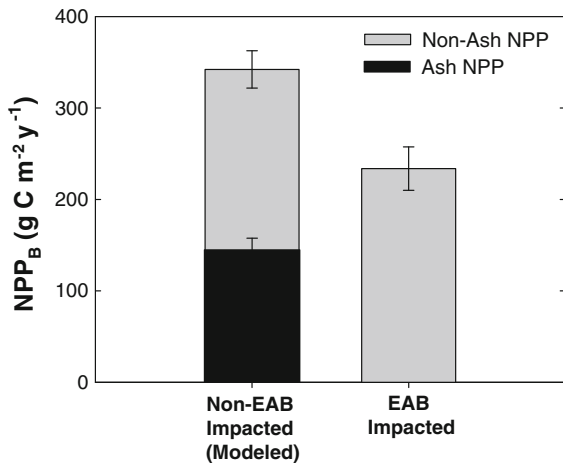
Fig. 4 Mean annual biometric net primary production (NPP_B) of non-EAB impacted (modeled) and EAB impacted forests in Toledo, OH. *Stacked bars* denote the contribution of NPP_B from *ash trees* (*black*) and *non-ash trees* (*grey*). The reduction in NPP_B of EAB impacted forests accounts for the loss of *ash trees* and the compensatory growth of *non-ash trees* following EAB induced tree mortality. Forest NPP_B for the non-EAB modeled Toledo sites was simulated using RGR's of trees from the non-impacted Cleveland forests
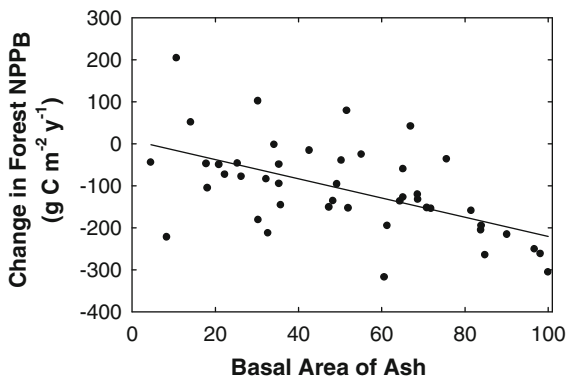

Fig. 5 The relationship between the basal area of ash (%) in a forest and the EAB induced change in forest annual biometric net primary production (NPP_B)

represents an important component of the biospheric C stock and the rapid release of part of this stored C could contribute to an increase in atmospheric CO_2 concentrations. Globally, C stored in terrestrial vegetation is nearly 80 % the size of the atmospheric C reservoir (Birdsey 1992) and temperate deciduous forests in the US have often been identified as an important net C sink, retaining more C than they release into the atmosphere (Brown and Schroeder 1999; Williams et al. 2012). The strength of this C sink

can be affected by the introduction of invasive pests as is the case of EAB that has reduced forest productivity (Fig. 4) limiting regional forest carbon sequestration and stored C stocks.

While *Fraxinus* spp. trees represent a small portion (~2.5 %) of the aboveground C mass in live trees in US forest lands; trees in the genus represent a substantially larger portion (~5.5–9 %) of the standing C mass in the Midwestern forests (Table 2). The contribution of ash trees to standing C mass varies depending on habitat type; in the forests included in this study *Fraxinus* spp. reaches ~10–100 % of the basal area. In other forest types, ash may be mixed with many other tree species and represent a smaller component of the ecosystem. Results from Gandhi (2007) and Smith (2006) suggest that there is no difference in *Fraxinus* spp. mortality across habitat type (i.e. xeric, mesic, hydric) or other stand-level variables such as ash density, ash basal area, total basal area, total tree density, or species diversity. This highlights the threat that EAB poses to all forests containing ash.

The EAB disturbance could represent a significant perturbation to the regional C budget of the Great Lakes States. Mortality of ash in the Great Lakes region could result in the decay of 0.156 Pg C in existing aboveground biomass, affecting the NPP of these EAB impacted forests (Fig. 1). Due to the fact that the FIA inventory excludes belowground biomass as well as urban and suburban ash trees, this analysis underestimates the quantity of C in ash trees. Our results indicate that a significant amount of C is sequestered in standing aboveground *Fraxinus* trees on forest lands (~0.3 Pg C). The impacts of EAB presented here are similar in magnitude to results of a study by Kurtz et al. (2008) who estimated the 20 year impact of the mountain pine beetle in a 374,000 km^2 forested region of British Columbia to be ~0.27 Pg C, which was severe enough to shift the region from a C sink to a C source. Similarly, Chambers et al. (2007) calculated that hurricane Katrina in 2005 had significant impacts on regional C budgets resulting in the mortality of ~320 million trees which became a carbon source of ~0.1 Pg C. These regional perturbations to the C cycle are also observed at smaller spatial scales by directly affecting annual forest NPP_B (Fig. 4). This study represents the first time the impact of the EAB on forest NPP_B has been estimated.

Our hypothesis that EAB impacted forests would exhibit reduced NPP_B compared to non-EAB impacted

forests was supported (Fig. 4). Our estimates of forest NPP_B (342 and 234 g C m^{-2} year^{-1} at non-EAB modeled and EAB impacted stands, respectively) are comparable to those found in other undisturbed temperate deciduous forests in the region (Reich et al. 1997). The observed NPP_B values were the result of an initial reduction of annual forest NPP_B caused by EAB induced tree mortality (Fig. 4), leading to reduced carbon storage and altered carbon sink strength. Results also indicate that the reduction of NPP_B associated with ash mortality ($\sim$145 g C m^{-2} year^{-1}) is partially offset by the compensatory growth of non-ash trees ($\sim$36 g C m^{-2} year^{-1}; Fig. 4). The effects of EAB on NPP are comparable to those reported by Nave et al. (2011) for aspen (*Populus* spp.) who observed a significant reduction in forest net ecosystem CO_2 exchange (NEE; a meteorologically based measure of NEP) (9 %) and soil respiration (39 %) following the artificially accelerated succession of aspen trees in a northern temperate forest. These results indicate that tree mortality leads to reduced canopy photosynthetic C uptake and thereby negatively impacts forest NEE and NPP. As NPP is correlated with soil respiration (Raich and Schlesinger 1992) these results suggest that tree mortality can negatively impact the amount of C allocated to belowground productivity, thereby impacting soil respiratory fluxes. Girdling experiments have also demonstrated that reduced basipetal carbon flow results in reduced soil respiration and concomitant declines in forest NPP (Högberg et al. 2001; Högberg and Högberg 2002). A study investigating the impacts of beech bark disease (BBD) on forests found that BBD correlated with the significant reduction of soil respiration rates, although they did not reveal a correlation between beech bark disease and reduced NPP (Hancock et al. 2008).

It is important to note that in our study, the decline in ash NPP_B was partially compensated for by the growth response of non ash trees (Table 3; Fig. 4), which was likely the result of increased availability of light, water and nutrients that will likely continue until canopy closure. Using a dendrochronological approach, Veblen et al. (1991) observed an abrupt increase in radial tree growth of non impacted trees in the subcanopy following spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks in the 1940's, indicating a release from suppression. Similarly, Lewis et al. (2005) observed a compensatory release of healthy

and lightly infected trees following the mortality of overstory spruce (*Picea* sp.) trees in Alaska, resulting from tomentosus root disease (*Inonotus tomentosus* (Fr.) Teng) and the spruce beetle. Furthermore, the higher compensatory growth rates achieved in non ash trees may only occur for a short period when they are experiencing a release from competition with ash. The magnitude of the reduction in NPP is expected to vary depending on the density of ash in the forest. Forest NPP in low ash density areas will be impacted less severely due to the loss of ash compared to high ash density areas, and thus may experience reduced non-ash tree compensatory growth (Figs. 3, 5). Because the growth response of non-ash trees was not uniform, the diversity and productivity of the resulting forest may not match pre-EAB conditions. However, the duration of these impacts remains uncertain.

Tree species responses to EAB infestation and impacts for carbon cycling

The results of this research highlight the potential impacts of the loss of the genera *Fraxinus* in temperate forests in North America through reductions in NPP_B (Fig. 4) and via altered successional dynamics (Table 4; Fig. 2). We examined whether the EAB disturbance impacted forest successional dynamics by altering the RGR of non-ash trees in EAB impacted and non-EAB impacted forests of northern Ohio. Our results suggest that EAB induced mortality of *Fraxinus* trees resulted in significant differences in RGR's of non-ash trees between EAB impacted and non-EAB impacted forests (Table 3, $p = 0.014$). The estimates of tree RGR's reported in this study (Fig. 2) were similar to those reported for other temperate deciduous forests (Jedlicka et al. 2004; Poulson and Platt 1996). The RGR's of non-ash trees in both EAB and non-EAB impacted regions was sensitive to the basal area of ash in the forest stand (Table 3, $p < 0.001$). Specifically, non-ash tree RGR's from forests with a high BA of ash was greater than forests with low BA of ash. Furthermore, the significance of the interaction term (treatment*BA ash) suggests that there is a differential response in the RGR of non-ash trees in EAB and non-EAB impacted regions as the basal area of ash in a stand increases. Specifically, the RGR's of non-ash trees exhibit a more positive response (+15 %) in EAB impacted forests with higher initial basal areas of ash trees relative to non EAB impacted

forests. This is likely the result of increased availability of light, nitrogen and moisture to the trees remaining in the expansive canopy gaps created by high densities of dying ash trees (Pedersen and Howard 2004; Prescott 2002). These results indicate that the EAB disturbance will differentially impact forest ecosystems at the landscape level depending on local ash density.

In highly EAB impacted forests, trees from different genera exhibit significantly different RGR's (Table 4). Trees from the genera *Acer* and *Ulmus* exhibited some of the highest RGR's observed in this study (Fig. 2). Relative growth rates for *Acer* and *Ulmus* trees were comparable to those previously reported in the literature (Safford 1973; Bell 1997; van Doorn et al. 2011). Relative differences in the RGR's between genera lead to shifts in the dominance of rapidly growing genera within EAB impacted forests. A similar release of subdominant maples, which subsequently increased in dominance, was observed following a gypsy moth outbreak in an oak-dominated Appalachian hardwood forests in Pennsylvania (Fajvan and Wood 1996). The RGR of non-ash trees in EAB impacted forests was significantly dependant on tree DBH with small trees exhibiting higher RGR's compared to larger trees (Table 4) as expected (Bruhn et al. 2000). Therefore, recruitment of small trees in the understory will determine the dominant canopy species in EAB impacted forests. Contrary to our hypothesis that trees in the co-dominant/dominant canopy position would exhibit higher RGR's compared to trees in suppressed and intermediate positions, there was no significant effect of the initial canopy position on tree RGR (Table 4). This indicates that the EAB disturbance is uniformly impacting the RGR of non-ash trees across all canopy positions and that the RGR responses are species-specific.

Our results indicate that the EAB disturbance will impact forest ecosystem NPP at various degrees, depending on local ash density (Fig. 5) and the distribution and responses of other tree species (Fig. 2), particularly juvenile trees (Table 4). In mixed species forests with low ash density, the impacts of EAB on forest NPP_B may be minimal, however, forests with a large density of ash will experience declines in NPP_B that are not likely to be offset by compensatory growth of non-ash species initially (Fig. 5). This will likely cause rapid successional and compositional change in these forests (Fig. 4).

NPP reductions could be further magnified in high ash density forests without adequate tree species available to respond, such as maple and elm (Fig. 2). However, the reduced canopy diversity in these forests may result in the increased severity of future disturbances, such as Dutch elm disease, invasive insects, or those resulting from expected climate change scenarios (Ayres and Lombardero 2000; Dale et al. 2001).

Conclusion

In summary, *Fraxinus* spp. are widely distributed across the US and represent ∼2.5 % of forest aboveground biomass (Fig. 1; Table 2) with 2–3 fold increases in regions currently affected by EAB. The widespread geographic distribution of *Fraxinus* and their high densities in riparian habitats, paired with the rapid disturbance effects of EAB are producing considerable impacts on C flux and storage. At the forest level, EAB induced ash decline can reduce NPP_B of impacted forests by ∼31 %, thereby negatively impacting the C sink strength of the region. The severity of EAB's impacts on forest NPP_B will vary based on the basal area of ash in a forest and will be partially mitigated by the compensatory growth of non-ash species. Additionally, ash tree mortality will result in a unique gap formation and lead to shifts in forest successional dynamics and species composition. *Acer* and *Ulmus* species which exhibited the highest relative growth rates in this study have the potential to become the dominant species in these forests. In general, biotic effects and the effects of invasive species on forest biogeochemistry and succession are poorly represented in models of the C cycle. The results presented here, show that the impacts of EAB on NPP and C storage capacity are substantial and occur rapidly and hence may modulate (by amplifying or even mitigating) the effects of climate change on the same processes. Thus, including the effects of such biotic interactions in climate change models may prove useful.

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References

Anagnostakis SL (1987) Chestnut blight: the classical problem of an introduced pathogen. Mycologia 79:23–37

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286

Baker TR, Affum-Baffoe K, Burslem DFRP, Swaine MD (2002) Phenological differences in tree water use and the timing of tropical forest inventories: conclusions from patterns of fry season diameter change. For Ecol Manag 171(3):261–274

Bauer LS, Haack RA, Miller DL, Petrice TR, Liu H (2003a) Emerald ash borer life cycle. In: Mastro V, Reardon R (eds) Abstracts of emerald ash borer research and technology development meeting. Forest Health Technology Enterprise Team. USDA FHTET-2004-02

Bauer LS, Miller DL, Taylor RAJ, Haack RA (2003b) Flight potential of the emerald ash borer. In: Mastro V, Reardon R (eds) Abstracts of emerald ash borer research and technology development meeting. Forest Health Technology Enterprise Team. USDA FHTET-2004-02

Bauer LS, Gould J, Liu H, Ulyshen M, Duan J, Sadof C, Ziegler A, Fraser I, Lelito J (2010) Update on emerald ash borer biological control research in the US In: Proceedings, emerald ash borer research and technology development meeting; 2009 October 21–22; Pittsburgh, pp 53–54

Bell DT (1997) Eighteen years of change in an Illinois streamside deciduous forest. J Torrey Bot Soc 124(2):174–188

Birdsey RA (1992) Carbon storage and accumulation in United States forest ecosystems. General technical report WO-59. USDA Forest Service, Washington

Birdsey RA, Heath LS (1995) Carbon changes in US forests. In: Joyce LA (ed) Productivity of America's Forest Ecosystems. General Technical Report RM-GTR-271. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, pp 56–70

Birdsey RA, Schreuder HT (1992) An overview of forest inventory and analysis estimation procedures in the Eastern United States with an emphasis on the components of change. General Technical Report RM-214. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins

Bolin B (1977) Changes of land biota and their importance for the carbon cycle. Science 196:613–615

Brasier CM (1991) *Ophiostoma novo-ulmi sp. nov.*, causative agent of the current Dutch elm disease pandemics. Mycopathologia 115:151–161

Brown SL, Schroeder PE (1999) Spatial patterns of aboveground production and mortality of woody biomass for eastern US forests. Ecol Appl 9:968–980

Bruhn D, Leverenz JW, Saxe H (2000) Effects of tree size and temperature on relative growth rate and its components of *Fagus sylvatica* seedlings exposed to two partial pressures of atmospheric CO2. N Phytol 146:415–425

Cappaert D, McCullough DG, Poland TM, Siegert NW (2005) Emerald ash borer in North America: a research and regulatory challenge. Am Entomol 51:152–165

Chambers JQ, Fisher JI, Zeng H, Chapman EL, Baker DB, Hurtt GC (2007) Hurricane Katrina's carbon footprint on US gulf coast forests. Science 318:1107

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 405:234–242

Churkina G, Running SW (1998) Contrasting climatic controls on the estimated productivity of global terrestrial biomes. Ecosystems 1:206–215

Clark KL, Skowronski N, Hom J (2010) Invasive insects impact forest carbon dynamics. Global Change Biol 16:88–101

Condit R, Ashton P, Bunyavejchewin S, Dattaraja H, Davies S, Esufali S, Ewango C, Foster R, Gunatilleke I, Gunatilleke C, Hall P, Harms KE, Hart T, Hernandez C, Hubbell S, Itoh A, Kiratiprayoon S, Lafrankie J, de Lao SL, Makana JR, Noor MN, Kassim AR, Russo S, Sukumar R, Samper C, Suresh HS, Tan S, Thomas S, Valencia R, Vallejo M, Villa G, Zillio T (2006) The importance of demographic niches to tree diversity. Science 313:98–101

Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agric For Meteorol 113:3–19

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayers MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BW (2001) Climate change and forest disturbance. Bioscience 51:723–734

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80

Ellsworth DS, Reich PB (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologica 96:169–178

Fajvan MA, Wood JM (1996) Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. For Ecol Manag 89:79–88

Flower CE, Knight KS, Gonzalez-Meler MA (2010) Using stable isotopes as a tool to investigate the impacts of EAB on tree physiology and EAB spread. In: Lanc D, Buck J, Binion D, Reardon R Mastro V (eds) Proceedings of the Emerald Ash Borer research and technology development meeting, Pittsburgh, PA, 20-21 October 2009, FHTET-2010-01. USDA Forest Service Health Technology Enterprise Team, Morgantown, WV, pp 53–54

Fuester RW, Duan JJ, Wildonger J, Taylor PB (2010) Biological control of emerald ash borers: the role of indigenous North American parasitoids. In: Proceedings, Emerald ash borer research and technology development meeting; 2009 October 21–22; Pittsburgh, pp 88–90

Gandhi, KJK, Smith A, Long RP, Herms DA (2007) Patterns of emerald ash borer induced ash decline and mortality in the forests of southeastern Michigan. In: Mastro V, Lance D, Reardon R, Parra G (eds) Proceedings of the emerald ash borer and Asian longhorned beetle research and technology development meeting; 2006 October 29–November 2; Cincinnati, pp 26–27

Garnier E (1991) Resource capture, biomass allocation and growth in herbaceous plants. Trends Ecol Evol 6:126–131

Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Jenkins JC, Kohlmaier GH, Kurz W, Liu S, Nabuus G-J, Nilsson S, Shvidenko AZ (2002) Forest carbon sinks in the northern hemisphere. Ecol Appl 12:891–899

Gough CM, Vogel CS, Schmid HP, Curtis PS (2008) Controls on annual forest carbon storage: lessons from the past and predictions for the future. Bioscience 58(7):609–622

Gough CM, Flower CE, Vogel CS, Dragoni D, Curtis PS (2009) Whole-ecosystem labile carbon production in a north temperate forest. Agric For Meteorol 149(9):1531–1540

Haack RA, Jendek E, Liu H, Marchant KR, Petrice TR, Poland TM, Ye H (2002) The emerald ash borer: a new exotic pest in North America. N Mich Entomol Soc 47(3&4):1–5

Hancock JE, Arthur MA, Weathers KC, Lovett GM (2008) Carbon cycling along a gradient of beech bark disease impact in the Catskill Mountains, New York. Can J For Res 38:1267–1274

Hicke JA, Allen CD, Desai AR, Deitze MC, Hall RJ, Hogg EH, Kashian DM, Moore D, Raffa KF, Sturrock RN, Vogelmann J (2012) Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Global Change Biol 18(1):7–34

Högberg MN, Högberg P (2002) Extramatrical ectomycorrhizial mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. N Phytol 154:791–795

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792

Jedlicka J, Vandermeer J, Aviles-Vazquez K, Barros O, Perfecto I (2004) Gypsy moth defoliation of oak trees and a positive response of red maple and black cherry: an example of indirect interaction. Am Midl Nat 152(2):231–236

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for United States tree species. J For Sci 49(1):12–35

Karnosky DF (1979) Dutch elm disease: a review of the history, environmental implications, control, and research needs. Environ Conserv 6:311–322

Knight KS, Long RP, Rebbeck J, Smith A, Gandhi K, Herms DA (2008). How fast will trees die? A transition matrix model of ash decline in forest stands infested by emerald ash borer. In: Mastro V, Reardon R, Parra G (eds) Proceedings of the emerald ash borer research and technology development meeting; 2007 October 23–4; Pittsburgh. FHTET 2008–2007. Morgantown, WV: US Forest Service, Forest Health Technology Enterprise Team, pp 29–30

Korsgaard S (1986) An analysis of the potential for timber production under conservation management in the tropical rainforest of South East Asia. Interim project status report. The Research Council for Development Research, Copenhagen, p 48

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990

Lewis K, Thompson RD, Trummer L (2005) Growth response of spruce infected by *Inonotus tomentosus* in Alaska and interactions with spruce beetle. Can J For Res 35:1455–1463

McCullough DG, Katovich SA (2004) Pest alert: emerald ash borer. United States Forest Service, Northeastern Area. NA-PR-02-04

McCullough DG, Poland TM, Anulewicz AC, Lewis P, Molongoski J (2010) Evaluation of emamectin benzoate and neonicotinoid insecticides: two-year control of EAB? In: Lanc D, Buck J, Binion D, Reardon R Mastro V (eds) Proceedings of the emerald ash borer research and technology development meeting, Pittsburgh, PA, 20-21 October 2009, FHTET-2010-01. USDA Forest service health technology enterprise team, Morgantown, WV, pp 68–70

Nave LE, Gough CM, Mauer KD, Bohrer G, Hardiman BS, Le Moine J, Munoz AB, Nadelhoffer KJ, Sparks JP, Strahm BD, Vogel CS, Curtis PS (2011) Disturbance and resilience of coupled carbon and nitrogen cycling in a north temperate forest. J Geophys Res 116:G04016. doi:10.1029/2011JG001758

Nicholas NS, Gregoire TG, Zedaker SM (1991) The reliability of tree crown position classification. Can J For Res-Rev Can de Res For 21:698–701

Ogren E, Sundin U (1996) Photosynthetic responses to variable light: a comparison of species from contrasting habitats. Oecologia 106:18–27

Oliver CD, Larson BC (1996) Forest stand dynamics, update edition. Wiley, New York

Pedersen BS, Howard JL (2004) The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. For Ecol Manag 196:351–366

Peltzer DA, Allen RB, Lovett GM, Whitehead D, Wardle DA (2010) Effects of biological invasions on forest carbon sequestration. Global Change Biol 16:732–746

Poland T, McCullough D (2006) Emerald ash borer invasion of the urban forest and the threat to North America's ash resource. J For 104:118–124

Poulson TL, Platt WJ (1996) Replacement patterns of beech and sugar maple in Warren Woods. Mich Ecol 77(4):1234–1253

Prasad AM, Iverson LR, Peters MP, Bossenbroek JM, Matthews SN, Snydor TD, Schwartz MW (2010) Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landsc Ecol 25(3):353–369

Prescott C (2002) The influence of the forest canopy on nutrient cycling. Tree Physiol 22:1193–1200

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

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus Ser B 44:81–99

Reich PB, Grigal DF, Aber JD, Gower ST (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology 78(2):335–347

Safford LO (1973) Fertilization increases diameter growth of birch-beech-maple trees in New Hampshire. In: US Department of Agriculture, Forest Service, Research Note NE-182. Upper Darby, Northeastern Forest Experiment Station, p 4

Siegert NW, McCullough DG, Liebhold AM, Telewski FW (2007) Resurrected from the ashes: as historical reconstruction of emerald ash borer dynamics through dendrochronological analysis. In: Mastro V, Reardon R (eds) Proceedings of the emerald ash borer research and technology development meeting; 2006 October 29–November 2; Cincinnati. FHTET 2007-04. Morgantown, WV: US Forest Service, Forest Health Technology Enterprise Team, pp 18–19

Smith A (2006) Effects of community structure on forest susceptibility and response to the emerald ash borer invasion of the Huron River watershed in southeast Michigan. A Thesis pp 1–134

SYSTAT (2007) SYSTAT 12.0 for windows. SPSS, Chicago

US Forest Service (2007) Forest inventory and analysis national core field guide, volume 1: field data collection procedures for phase 2 plots, version 4.0. Available from http://www.fia.fs.fed.us/library/field-guides-methods-proc/ Accessed 15 Sept 2009

van Doorn NS, Battles JJ, Fahey TJ, Siccama TG, Schwarz PA (2011) Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook Valley, New Hampshire. Can J For Res 41:1369–1379

Veblen TT, Hadley KS, Reid MS, Rebertus AJ (1991) The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72(1):213–231

Vogt K (1991) Carbon budgets of temperate forest ecosystems. Tree Physiol 9:69–86

Walters MB, Kruger EL, Reich PB (1993) Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. Oecologia 96:219–231

Wang XY, Yang ZQ, Gould JR, Zhang YN, Liu GJ, Liu ES (2010) The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. J Insect Sci 10:128

Williams CA, Collatz GJ, Masek J, Goward SN (2012) Carbon consequences of forest disturbance and recovery across the conterminous United States. Global Biogeochem Cycles 26, GB1005, doi:10.1029/2010GB003947

Zweifel R, Item H, Häsler R (2001) Link between diurnal stem radius changes and tree water relations. Tree Physiol 21:869–877

Zweifel R, Eugster W, Etzold S, Dobbertin M, Buchmann N, Häsler R (2010) Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. N Phytol 187:819–830