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Modeling respiration from snags and coarse woody debris before and after an invasive gypsy moth disturbance

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Key Points:
- Mortality increased the mass of snags and coarse woody debris fivefold
- Respiration rates from dead stems tripled after disturbance
- After disturbance, dead stem respiration was similar to NEE

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Modeling respiration from snags and coarse woody debris before and after an invasive gypsy moth disturbance

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Abstract Although snags and coarse woody debris are a small component of ecosystem respiration, disturbances can significantly increase the mass and respiration from these carbon (C) pools. The objectives of this study were to (1) measure respiration rates of snags and coarse woody debris throughout the year in a forest previously defoliated by gypsy moths, (2) develop models for dead stem respiration rates, (3) model stand-level respiration rates of dead stems using forest inventory and analysis data sets and environmental variables predisturbance and postdisturbance, and (4) compare total dead stem respiration rates with total ecosystem respiration and net ecosystem exchange. Respiration rates were measured on selected *Pinus* and *Quercus* snags and coarse woody debris each month for 1 year in a northeastern U.S. temperate forest. Multiple linear regression using environmental and biometric variables including wood temperature, diameter, density, species, and decay class was used to model respiration rates of dead stems. The mass of snags and coarse woody debris increased more than fivefold after disturbance and respiration rates increased more than threefold. The contribution of dead stems to total ecosystem respiration more than tripled from 0.85% to almost 3% and respiration from dead stems alone was approximately equal to the net ecosystem exchange of the forest in 2011 (fourth year postdisturbance). This study highlights the importance of dead stem C pools and fluxes particularly during disturbance and recovery cycles. With climate change increasing the ranges of many forest pests and pathogens, these data become particularly important for accurately modeling future C cycling.

1. Introduction

Following mortality, trees no longer sequester carbon (C), but continue to provide long-term C storage as dead standing trees (snags) and fallen logs (coarse woody debris). Snags and coarse woody debris (or collectively dead stems) also provide habitat for organisms [*Harmon et al.*, 1986], substrate for seedlings [*McGee and Birmingham*, 1997], and a storage reservoir for water and nutrients [*Forrester et al.*, 2012; *Schowalter*, 1992]. In forests across the United States, the Pacific Northwest generally contains the largest stocks of C in coarse woody debris [*Spies et al.*, 1988; *Woodall et al.*, 2008], with stocks in forested ecosystems generally increasing with increasing latitude [*Woodall et al.*, 2008]. Respiration from snags and coarse woody debris is generally a small component (<5%) of total ecosystem respiration compared with autotrophic respiration and respiration from soils [*Gough et al.*, 2007; *Liu et al.*, 2006; *Tang et al.*, 2008]. However, because many temperate forest ecosystems are modest sinks [*Goodale et al.*, 2002; *Pan et al.*, 2011], respiration from coarse woody debris becomes comparatively more important [*Forrester et al.*, 2012; *Gough et al.*, 2007; *Liu et al.*, 2006; *Valentini et al.*, 2000], and thus, increased respiration from snags and coarse woody debris could reduce the strength of the C sink in many forests.

In addition to background tree mortality that results from competitive exclusion, lightning strikes, disease and windthrow, larger-scale disturbances including insect attacks, intense storms, and fire can greatly increase the mass of snags and coarse woody debris in forests [*Franklin et al.*, 1987; *Hicke et al.*, 2012; *Vanderwel et al.*, 2013]. For example, *Bond-Lamberty et al.* [2003] found that more recently burned stands in boreal black spruce forests generally had significantly more coarse woody debris stocks than stands that had been burned 70 or more years ago. In tropical dry forests, *Harmon et al.* [1995] found that forests experiencing hurricanes had 1.6 times more coarse woody debris than undisturbed forests and forests experiencing fire had almost 4 times higher coarse woody debris amounts. Large-scale insect disturbances

have the potential to shift forests from C sinks to sources [*Clark et al.*, 2010; *Kurz et al.*, 2008; *Medvigy et al.*, 2012]. Likewise, climate change may increase the frequency of disturbances [*Dale et al.*, 2001] such as fire [*Flannigan et al.*, 2000, 1998] and severe storms [*Walsh and Pittock*, 1998] and may increase the range and frequency of tree pests and pathogens [*Ayres and Lombardero*, 2000; *Wilf and Labandeira*, 1999]. Therefore, it is important to determine the effects of disturbance on snags and coarse woody debris mass as well as their respiration rates in order to more fully understand the effects of disturbance on forest C balance.

Both native and nonnative insects can affect large areas of forests [*Dale et al.*, 2001; *Hicke et al.*, 2012; *Logan et al.*, 2003] and have exerted economic damage in excess of 1 billion dollars [*Aukema et al.*, 2011]. Likewise, forests impacted by insects can become more vulnerable to catastrophic fires, because they weaken and kill trees, increasing fuel loads and decreasing canopy cover which causes higher solar radiation on the forest floor [*Clark et al.*, 2012; *McCullough et al.*, 1998]. Increasing temperatures are also increasing the ranges of native and invasive insects that are strongly affected by minimum winter temperatures including mountain pine beetle (*Dendroctonus ponderosae* Hopkins) [*Carroll et al.*, 2003], southern pine beetle (*Dendroctonus frontalis* Zimmerman) [*Ungerer et al.*, 1999], and hemlock wooly adelgid (*Adelges tsugae* Annand) [*Dukes et al.*, 2009; *Orwig et al.*, 2002] in North America, and the pine processionary moth (*Thaumetopoea pityocampa* Denis and Schiffermüller) in Europe [*Battisti et al.*, 2005]. For forest insect pests such as gypsy moth (*Lymantria dispar* L.) whose life cycles are not severely impacted by minimum winter temperatures, predicting the effects of climate change on distribution and forest impact becomes more complex. *Williams and Liebhold* [1995] showed that an interaction between temperature and precipitation was important in predicting the forested area defoliated by gypsy moths as were early spring temperatures which caused moths to hatch before trees leafed out. Likewise, increasing atmospheric CO_2 concentrations require foliar feeders to ingest more leaf tissue to meet their nitrogen demand because leaves typically have higher C:N ratios in a high CO_2 environment [*Currano et al.*, 2008]. All of these environmental effects have the potential to increase the forested area currently affected by insect disturbance.

The objectives of this study were to (1) measure respiration rates from snags and coarse woody debris from individuals of *Quercus* and *Pinus* spp. throughout the year in an Atlantic coastal plain forest, (2) develop multiple linear regression models that estimate stand-level respiration rates of snags and coarse woody debris using meteorological and biometric parameters, (3) model respiration rates before and after a major gypsy moth defoliation using snag and coarse woody debris mass estimates from forest inventory and analysis (FIA)-type plots, and (4) compare daily and annual respiration from snags and coarse woody debris with total ecosystem respiration and net ecosystem exchange estimated by eddy covariance before and after defoliation. This is one of the first studies to estimate the effect of gypsy moth disturbance on dead stem respiration, and the findings will allow for more accurate predictions of C losses from snags and coarse woody debris respiration which will improve C cycling and ecosystem demographic (BIOME-BGC, ED2, etc.) models. This becomes especially important in light of climate change because models based on eddy covariance can only predict future C balance if stand structure and composition do not change significantly. Therefore, in order to include stand structural and compositional changes into models, characteristics of individual pools and fluxes need to be ascertained [*Chambers et al.*, 2001; *Tang et al.*, 2008]. Likewise, determining which meteorological variables most strongly affect the respiration of snags and coarse woody debris will allow for better predictions of how climate change will affect the long-term C storage pool of dead stems [*Chambers et al.*, 2001]. This becomes especially important as climate change and disturbance cycles interact to affect both the pools and fluxes of C from snags and coarse woody debris.

2. Materials and Methods

2.1. Site Description

This study was conducted at the Rutgers University Pinelands Field Station United States Forest Service (USFS) Silas Little Experimental Forest; 39°54′56.27″N, 74°35′44.00″W) which is located in the Pinelands National Reserve in southern New Jersey. The site is a naturally regenerated, oak-dominated forest containing mainly chestnut oak (*Quercus prinus* L.), black oak (*Quercus velutina* Lamb.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.), and post oak (*Quercus stellata* Wangenh.) with less abundant but codominant shortleaf pine (*Pinus echinata* Mill.) and pitch pine (*Pinus rigida* Mill.). The understory is comprised mainly of ericaceous shrubs including blueberry (*Vaccinium* sp.) and huckleberry (*Gaylussacia* sp.) as well as scattered

sedges, ferns, mosses, and lichens. The climate is cool temperate with an average summer temperature of 22.7°C and average winter temperature of 1.3°C. Precipitation is evenly distributed throughout the year and averages about 1120 mm annually [*Clark et al.*, 2012]. Soils are excessively well drained and comprised of >94% sand with low nutrient and water-holding capacity. Moisture content in the upper soil layer (0–30 cm) averaged around 8.6% during the study period and, over a longer time scale, ranges between 3% during summer droughts and approximately 11% at field capacity [*Schäfer*, 2011]. On a landscape scale, gypsy moths defoliated about 20% of upland forests in the New Jersey Pinelands in 2007 [*Clark et al.*, 2010]. From May to July 2007, the study site was completely defoliated by gypsy moths (*Lymantria dispar* L.). During the second part of the 2007 growing season, individuals leafed out again replacing about 50% of typical stand leaf area. The stand was partially defoliated again in 2008 resulting in a loss of stand leaf area of about 25% compared to typical values. Overall, this gypsy moth disturbance caused about 27% mortality of the overstory oak trees [*Schäfer*, 2011].

2.2. Stand Inventories

Snags and coarse woody debris were measured in an extensive network of FIA-type plots 4 times over a 7 year period. Sixteen FIA-type plots are located in the study area on a 1 km^2 grid and are arranged at regular intervals in a 4×4 arrangement. These plots were sampled twice before the gypsy moth disturbance (in 2004 and 2006) and twice after the disturbance (in 2009 and 2011). In 2006, coarse woody debris were not measured in this 4×4 grid but were instead measured in eight plots that were located approximately 1 km outside of the interior grid. Each FIA-type plot contained four 168 m^2 subplots, one center plot, and three plots located 36.6 m from the center point at azimuthal directions 0°, 120°, and 240°. Sampling protocols for FIA data sets can be found at http://fia.fs.fed.us. All snags larger than 12.7 cm in each subplot were measured including height, diameter at breast height, species, and decay class based on FIA protocol (http://fia.fs.fed.us/library/field-guides-methods-proc/). Briefly, decay classes for snags are defined as follows: (1) all branches and bark present with intact sapwood, (2) few limbs and variable amounts of bark with sapwood decaying but hardwood sound at the base, (3) only limb stubs and variable amounts of bark with sapwood and heartwood decaying at the base, (4) few or no limbs, variable amounts of bark and sapwood and heartwood in advanced decay, and (5) no limbs present, less than 20% bark, no sapwood and decaying heartwood [*O'Connell et al.*, 2013]. Mass and surface area of snags in each subplot were calculated using allometric equations for *P. rigida* and *Quercus* spp. from *Whittaker and Woodwell* [1968] using our measured wood densities (see section 2.4) and densities of live individuals to adjust snag mass.

Estimates of coarse woody debris size and abundance were also made for each FIA-type subplot, by measuring pieces of coarse woody debris crossing three 7.3 m long radial transects at azimuthal directions 30°, 150°, and 270°. A log is considered coarse woody debris if it measures larger than 7.6 cm in diameter and 0.9 m in length and is at an angle larger than 45° from vertical (any angle smaller than that is considered a snag). For each log crossing a transect, the small-end diameter, large-end diameter, transect diameter, length, species (if discernible) or genus, and decay class were recorded. Decay classes for coarse woody debris are defined in the FIA protocol as follows: (1) sound, freshly fallen logs with no rot, (2) sapwood partially soft but cannot be pulled apart, (3) sapwood can be pulled apart or is absent but heartwood is sound, (4) heartwood is decayed, and (5) piece no longer has a defined shape [*O'Connell et al.*, 2013]. Mass and surface area of coarse woody debris in each subplot were calculated based on line intersect sampling equations [*DeVries*, 1973; *Waddell*, 2002] as follows:

$$x_{\text{plot}} = \frac{\pi}{2L} \Sigma \frac{x_{\text{indiv}}}{l_{\text{indiv}}} \quad (1)$$

where x_{plot} is the variable of interest (mass or surface area) per unit area, L is the total length of measured transects in the plot, x_{indiv} is the variable of interest (mass or surface area) for each individual crossing a transect, and l_{indiv} is the length of that individual. Individual surface area was calculated using the average of small- and large-end diameters and did not include the surface area of the end faces. To calculate the mass of individuals, coarse woody debris volume was calculated based on small- and large-end diameters then multiplied by wood density. Wood densities from the respiration sample measurements (see section 2.4) were used to estimate densities of the various decay classes (Table 1).

2.3. Respiration and Stem Temperature Measurements

Point estimates of respiration rates on dead stems were measured with an infrared gas analyzer (IRGA; LI-6400XT; LI-COR Inc., Lincoln Nebraska, USA) with the soil CO_2 flux chamber attached (LI-6400-09). This

Table 1. Biometric Information for Snags and Coarse Woody Debris Measured for Monthly Respiration[a]

Species	Orientation	Decay Class	*N*	Diameter (cm)	Length/Height (m)	Sapwood Density (g cm^{-3})	Heartwood Density (g cm^{-3})
Q. prinus	coarse woody debris	2	4	14.5 (2.2)	8.5 (2.3)	0.39 (0.008)	0.51 (0.008)
		3	3	17.7 (1.2)	6.8 (1.2)	0.24 (0.02)	0.49 (0.02)
	snag	2	4	21.5 (2.3)	11.2 (2.3)	0.2 (0.01)	0.57 (0.02)
		3	2	23.2 (4.0)	11.7 (0.8)	0.2 (0.03)	0.45 (0.02)
Q. velutina	coarse woody	2	2	19.8 (0.3)	6.3 (1.5)	0.3 (0.03)	0.51 (0.01)
	debris	3	4	16.3 (1.0)	9.7 (0.6)	0.2 (0.01)	0.4 (0.01)
	snag	2	4	23.1 (2.7)	15.4 (1.3)	0.35 (0.02)	0.57 (0.02)
		3	2	21.2 (3.0)	11.3 (2.0)	0.18 (0.06)	0.52 (0.01)
Pinus spp.	coarse woody	1	1	33.0	19.4	0.45	
	debris	2	2	25.3 (7.7)	10.8 (1.1)	0.42 (0.01)	
	snag	1	1	36.0	18.8	0.46	
		2	2	28.8 (6.6)	13.9 (4.0)	0.44 (0.03)	

[a]Mean and standard error in parentheses; *N*, number of individuals in each category; diameter measured at the location of the respiration collar.

method was used because it allows for in situ, repeated measurements on individuals without destructive sampling which was not feasible for snags in particular. In order to attach the CO_2 flux chamber to dead stems, a piece of PVC pipe (collar), approximately 11.5 cm in diameter and 5.5 cm tall, was glued to each individual. Thirty-one snags and coarse woody debris were chosen for respiration measurements that were larger than 12 cm in diameter so that they would accommodate the respiration collars. Arcs were cut on one end of the collars so they would fit tightly to snags and coarse woody debris. To attach the collars to the individuals, waterproof glue was applied to the rim, and the collars were either strapped to the snags until the glue dried or placed on coarse woody debris. Collars were attached to areas with bark, if present. A silicone sealant was then applied to the inner and outer rim of the collars and also to any gaps or cracks in the bark or wood to prevent leakage points between the bark and the collar. We focused on three species (*Q. prinus*, *Q. velutina*, and *P. rigida*) which comprise about 80% of total basal area in this upland forest. The remaining basal area is comprised of other oak species whose dead wood respiration rates were modeled from an average *Q. prinus* and *Q. velutina* model. We chose snags and coarse woody debris ranging from decay class 1 to decay class 3 [*O'Connell et al.*, 2013] as these classes represent at least 70% of the dead wood in the forest following disturbance. Table 1 presents data for each measured individual.

The first round of respiration point measurements was performed in August 2012 and repeated monthly for 1 year. The IRGA was zeroed before each round of measurements. To begin, the IRGA chamber was placed on the PVC collar with a piece of foam inserted between the collar and the flux chamber to prevent CO_2 leakage. This system draws down the CO_2 concentration in the chamber, then records CO_2 accumulation in the chamber from the respiration occurring within each dead stem. The rate of CO_2 accumulation in the chamber is negatively correlated with the CO_2 concentration in the chamber, therefore an average respiration rate was calculated using this relationship and the average CO_2 concentration in the chamber. Three drawdown cycles for each individual were performed during each monthly measurement period and averaged. Concurrently with respiration measurements, a temperature probe attached to the LI-COR 6400 system was inserted into predrilled holes about 5 cm deep into the snags or coarse woody debris. After respiration measurements were made, a chisel was used to remove a wood sample from each individual for determination of wood density and moisture content. These samples were placed in plastic zip-top bags until further laboratory analysis was performed.

Stem temperatures measured during each round of respiration measurements were plotted versus respiration for each individual and an exponential function was fitted to the data (Sigmaplot; Systat Software Inc., Chicago, IL, USA). These exponential equations were then used to calculate Q_{10} values. In order to determine if Q_{10} values differed significantly between *Pinus* spp. and *Quercus* spp., snags and coarse woody debris, and decay classes, an analysis of variance (ANOVA) was performed in R version 2.5.1 (The R Foundation for Statistical Computing; http://ww.R-project.org). ANOVAs were also performed in R to determine if respiration rates differed between *Pinus* spp. and *Quercus* spp., snags and coarse woody debris, and between different decay classes within each species. A repeated measure design was employed where "subject within month" was used as an error term in each model.

To estimate continuous, half-hourly stem temperatures in order to model dead stem respiration, individuals of *Q. prinus* (three snags and three coarse woody debris), *Q. velutina* (six snags and four coarse woody debris), and *Pinus* spp. (one snag and one coarse woody debris) were fitted with copper constantan thermocouples that were made in the lab and inserted into 2 cm long hypodermic needles. Holes were drilled into each snag or coarse woody debris individual, and the thermocouples were inserted and connected to a CR3000 data logger and AM 16/32B multiplexer (Campbell Scientific Inc., Logan, UT, USA) which collected data every 30 s and averaged data every 30 min. These data were used to predict temperatures of snags and coarse woody debris for *Pinus* spp. and *Quercus* spp. using air temperature, orientation (snag or coarse woody debris), and decay class (for *Quercus* spp.) as explanatory variables (R version 2.5.1). Air temperatures were collected using a Vaisala HMP45C sensor (Campbell Scientific Inc.) located about 17.5 m aboveground and connected to a data logger (CR23X or CR1000, Campbell Scientific Inc.) which collected data every 10 s and averaged data every 30 min throughout the study period. Lagging air temperature data by 30 min intervals did not increase the r^2 value of the relationship with stem temperature, so nonlagged data were used. Because only one *Pinus* spp. snag and coarse woody debris was available for measurement in the immediate vicinity of the data logger, differences between decay classes were not included in the model estimating stem temperature from air temperature (adjusted $r^2 = 0.96$, residual SE = 1.7). For *Quercus* spp. coarse woody debris, *Q. velutina* and *Q. prinus* were combined, and a decay class term was included in the model (adjusted $r^2 = 0.94$, overall SE = 2.13). For *Quercus* snags, a species distinction was included in the model as well as a term to differentiate decay classes (adjusted $r^2 = 0.96$, overall SE = 1.93). A model for snag stem temperature with *Quercus* spp. combined was also included to predict stem temperatures for *Quercus* spp. (*Q. alba*, *Q. coccinea*, etc.) not being measured in this study (adjusted $r^2 = 0.94$, residual SE = 2.03).

2.4. Wood Density and Relative Water Content

Wood samples from each individual after each respiration measurement were returned to the lab and their fresh mass (M_f) immediately measured. The fresh volume (V_f) of each sample was then estimated using a water displacement method taking care to note the mass before water began filling void space in samples. Samples were then placed in a drying oven at 70°C for at least 48 h, and dry mass (M_d) was measured. Density of the wood samples (D; g cm^{-3}) was calculated as follows:

$$D = \frac{M_d}{V_f} \tag{2}$$

For *Pinus* spp., wood samples were assumed to be from sapwood due to their relatively deep sapwood. To determine if *Quercus* spp. wood samples were comprised of sapwood or heartwood, wood density data were combined in each species/decay class category for snags and coarse woody debris. Frequency distributions of wood density data were analyzed, and the bimodal distribution in the data was used to identify the sapwood: heartwood boundary (Table 1). Relative water content (RWC; %) was also calculated which represents the proportion of sample void space that is water-filled as follows [*Domec and Gartner*, 2002]:

$$\mathrm{RWC} = \frac{M_f - M_d}{V_f - V_s} \times 100 \tag{3}$$

where V_s is the volume of cell wall material in the sample calculated as dry mass (M_d) divided by the density of cell wall material (1.53 g cm^{-3}) [*Siau*, 1984] which is relatively constant across species [*Gartner et al.*, 2004].

2.5. Modeling Stand-Level Respiration From Snags and Coarse Woody Debris

Multiple linear regression models of respiration (μmol $CO_{2\ \mathrm{efflux}}$ m^{-2} $_{\mathrm{surface\ area}}$ s^{-1}) for snags or coarse woody debris were developed using the "regsubsets" function (Lumley and Miller. leaps: regression subset selection. R package version 2.7). This function compares models containing all possible combinations of variables in a full model and ranks them based on a given criteria (adjusted r^2, Akaike information criterion, etc.). Respiration rates were log-transformed prior to analysis to linearize relationships with explanatory variables. Explanatory variables included genus or species, decay class, stem diameter, wood density, relative water content, and stem temperature. Both genus/species and decay class were included individually as well as their interaction with biometric and meteorological variables. Since coarse woody debris of *Quercus* spp. were generally not distinguished to the species level in FIA data sets, only distinctions to the genus level were included.

Table 2. Wood Density for Each Species/Decay Class[a]

Species	Decay Class	Wood Density ($g\ cm^{-3}$) Snags	Coarse Woody Debris
Pinus spp.	1	**0.46**	**0.45**
	2	**0.44**	**0.42**
	3	0.26	0.26
	4	0.17	0.17
Q. prinus	1	0.51	0.54
	2	**0.39**	**0.45**
	3	**0.33**	**0.37**
	4	0.27	0.30
Q. velutina	1	0.53	0.51
	2	**0.46**	**0.41**
	3	**0.35**	**0.30**
	4	0.30	0.27
Quercus spp.	1	0.52	0.53
	2	**0.42**	**0.43**
	3	**0.34**	**0.33**
	4	0.29	0.29

[a]Bolded numbers were estimated from samples; nonbolded numbers were calculated from modeled data.

For snags, models having distinctions either to the genus or species level were included because snags were generally identified to the species level in FIA data sets. Respiration rates of snags and coarse woody debris were modeled separately and best models were selected based on adjusted r^2 values.

For both snags and coarse woody debris, six models with the highest adjusted r^2 were chosen for further analyses. To distinguish between these models, cross validation was performed using the Data Analysis and Graphics (DAAG) package [*Maindonald and Braun*, 2007] (R package version 0.95. http://www.stats.uwo.ca/DAAG). This procedure splits the overall data set into a training set and a testing set, uses the "training" observations and the specified model to calculate the beta parameters and then predicts respiration of the "testing" observations. Predicted values are compared with the testing observations to determine how well each model performed. This procedure was repeated 10 times with different, randomly selected training and testing observations from the data set and an overall residual mean square error (RMSE) term was calculated. The model with the lowest RMSE was chosen.

The developed models for snags and coarse woody debris were then used to estimate respiration rates ($\mu mol\ CO_2\ m^{-2}{}_{surface\ area}\ s^{-1}$) for each individual dead stem recorded during the FIA sampling years (2004, 2006, 2009, and 2011). Respiration rates were assumed to be zero if measured air temperatures were below freezing [*Bond-Lamberty et al.*, 2003; *Forrester et al.*, 2012]. To estimate respiration rates of *Q. alba*, *Q. coccinea*, and *Q. stellata* snags, a model derived from both *Q. prinus* and *Q. velutina* respiration data was used. Respiration rates of dead stems in decay class 4 were also not directly measured in this study and individuals in this decay class accounted for about 20% of coarse woody debris and 7% of snags. For snags and coarse woody debris in decay classes not directly measured in this study, the equation developed for the closest decay class was used with a wood density adjustment made. Wood densities of decay classes not directly measured in this study were estimated as follows: For *Pinus* spp., a sigmoidal function was fitted to the data of wood density versus decay class for *Pinus sylvestris* L. presented in *Harmon et al.* [2000]. The maximum of this sigmoidal function was adjusted slightly because our *Pinus* spp. in decay classes 1 and 2 had higher wood densities than *Pinus sylvestris*, and then this equation was used to estimate wood densities for *Pinus* spp. snags and coarse woody debris in decay classes 3 and 4. For *Q. prinus* and *Q. velutina* snags and coarse woody debris, exponential decay functions were fitted to the measured wood density data for decay classes 2 and 3. In order to anchor the exponential curve on both ends, wood densities of living *Q. prinus* and *Q. velutina* individuals were also included (as decay class 0) and individuals in decay class 5 were assumed to have a wood density of 0.25 (as estimated by *MacMillan* [1981] for *Q. alba* decay class 5). For all other *Quercus* spp., the average wood density of *Q. prinus* and *Q. velutina* in each decay class was used. Table 2 presents wood densities used to model respiration rates for all individuals. Coarse woody debris in decay class 5 were not included in the analysis, since they no longer have an identifiable structure. For 2011, about 8% of coarse woody debris individuals were in decay class 5.

Modeled respiration rates were scaled to daily C efflux ($g\ C\ d^{-1}$) by multiplying respiration rates by the surface area of each individual snag or coarse woody debris piece, multiplying by the molecular weight of C, then integrating half-hourly estimates to an entire day. The sum of respiration from snags and coarse woody debris in each subplot was calculated and divided by the area of the subplot to yield respiration rates per unit ground area ($g\ C\ m^{-2}\ d^{-1}$). Then, subplot respiration rates were averaged within each FIA-type plot, and total respiration rates for snags and coarse woody debris in each of the 16 FIA-type plots within the stand were averaged to estimate mean stand-level respiration rates. Error propagation in the modeled respiration rates was calculated as the sum of percent error in the carbon pool data (SE/mean) and percent error in the respiration model

Table 3. Parameters for Calculating Ecosystem Respiration Using Equation (4)[a]

	a	*b*	*n*	r^2	Model SE
		Growing Season			
2004	1.383 (0.068)	0.076 (0.003)	1705	0.432	2.533
2006	1.154 (0.032)	0.075 (0.001)	3348	0.457	1.854
2009	1.208 (0.037)	0.081 (0.002)	3668	0.493	2.172
2011	1.404 (0.047)	0.072 (0.002)	3680	0.397	2.702
		Dormant Season			
2004	0.838 (0.059)	0.101 (0.004)	1705	0.408	2.585
2006	0.858 (0.027)	0.091 (0.002)	3348	0.500	1.781
2009	0.778 (0.028)	0.107 (0.002)	3668	0.565	2.011
2011	0.853 (0.035)	0.101 (0.002)	3680	0.480	2.510

[a]Mean and standard error of estimates in parentheses; *n*, number of observations used to develop equation; and all models were significant at $P < 0.001$.

(calculated as model RMSE/the range of respiration input data). This overall percent error was then multiplied by daily and yearly respiration means to calculate an overall standard error term [*Taylor*, 1997].

2.6. Ecosystem Respiration and Net Ecosystem Exchange of CO_2

Net ecosystem exchange of CO_2 (NEE) was estimated using a closed-path eddy covariance system consisting of a 3-D sonic anemometer (Model 81000V, R. M. Young, Inc., Traverse City, MI, USA) mounted about 4 m above the canopy, a closed-path infrared gas analyzer (IRGA; LI-7000, LI-COR Inc., Lincoln, NE, USA), a 0.4 cm

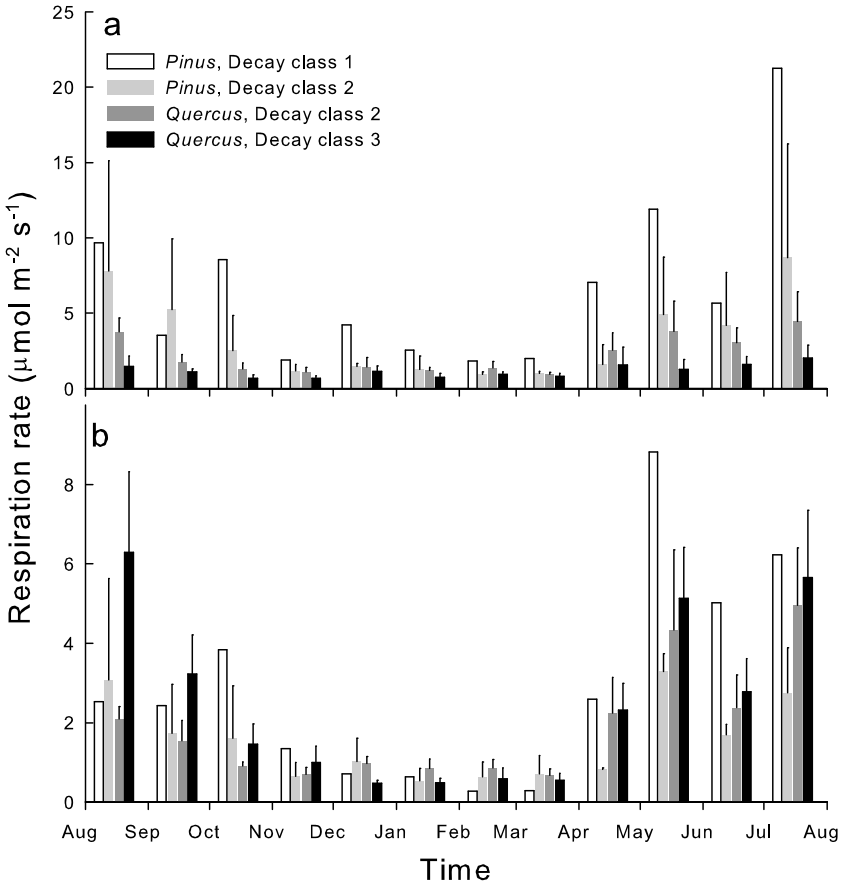

Figure 1. Monthly respiration rates (μmol CO_2 m^{-2} $_{surface\ area}$ s^{-1}; mean and standard error) for (a) snags and (b) coarse woody debris.

Table 4. Best Fit Equations to Calculate Respiration Rates of Snags and Coarse Woody Debris[a]

Species	Type	Decay Class	Equation	Adjusted r^2	RMSE
Pinus spp.	Snag	1	log(RESP) = −0.72 + 0.064*DIA − 2.99*DENS + 0.026*TEMP	0.56	0.085
Pinus spp.	Snag	2	log(RESP) = −0.14 + 0.0041*DIA − 0.96*DENS + 0.017*TEMP		
Q. prinus	Snag	2	log(RESP) = 0.11 + 0.0041*DIA − 0.96*DENS + 0.017*TEMP		
Q. prinus	Snag	3	log(RESP) = 0.73 − 0.056*DIA + 1.07*DENS + 0.0068*TEMP		
Q. velutina	Snag	2	log(RESP) = 0.34 + 0.0041*DIA − 0.96*DENS + 0.017*TEMP		
Q. velutina	Snag	3	log(RESP) = 0.45 − 0.056*DIA + 1.07*DENS + 0.0068*TEMP		
Quercus spp.	Snag	2	log(RESP) = 0.053 + 0.0013 *DIA − 0.46*DENS + 0.017*TEMP	0.52	0.090
Quercus spp.	Snag	3	log(RESP) = 1.00 − 0.046*DIA − 0.46*DENS + 0.0094*TEMP		
Pinus spp.	Coarse woody debris	1	log(RESP) = −1.16 + 0.032*DIA − 0.86*DENS + 0.044*TEMP	0.62	0.085
Pinus spp.	Coarse woody debris	2	log(RESP) = 0.35 + 0.032*DIA − 3.56*DENS + 0.023*TEMP		
Quercus spp.	Coarse woody debris	2	log(RESP) = 1.48 − 0.016*DIA − 3.56*DENS + 0.023*TEMP		
Quercus spp.	Coarse woody debris	3	log(RESP) = 0.45 − 0.016*DIA − 1.75*DENS + 0.034*TEMP		

[a]RESP (μmol CO_2 m^{-2} $_{surface\ area}$ s^{-1}), respiration rate; DIA (cm), diameter of snag or coarse woody debris; DENS (g cm^{-3}), wood density; and TEMP (°C), stem temperature.

ID Teflon-coated tube and an air pump, and a laptop PC [*Clark et al.*, 2010, 2012]. The IRGA was calibrated for CO_2 every 2–10 days using CO_2 tanks traceable to primary standards. Flux data were rejected at a friction velocity (u*) < 0.2 m s^{-1}, when measurable precipitation occurred, or when instrument malfunction occurred. The flux associated with the change in storage of CO_2 in the air column beneath the inlet was estimated using a profile system with inlets at 0.2, 2, 5, 10, 15, and 20 m height or 2 m height in the dormant season. Flux data are available at www.ornl.public.gov/ameriflux. Ecosystem respiration (R_{eco}) was calculated using continuous half-hourly air (growing season) or soil (dormant season) temperature data and the following equation:

$$R_{eco} = a \times e^{b*temp} \quad (4)$$

which was developed using nighttime temperature and net ecosystem exchange of CO_2 measurements (Table 3). Growing season was defined as the leaf-on period for overstory oaks (15 May to 31 October for this site). Half-hourly values were then gap-filled using equation (4), summed to daily and annual values, and compared with respiration rates of snags and coarse woody debris. Error terms for daily and annual NEE_C and R_{eco} were calculated as the maximum difference between mean values and values calculated using ± 1 standard error of the *a* or *b* coefficients in equation (4) (see Table 3).

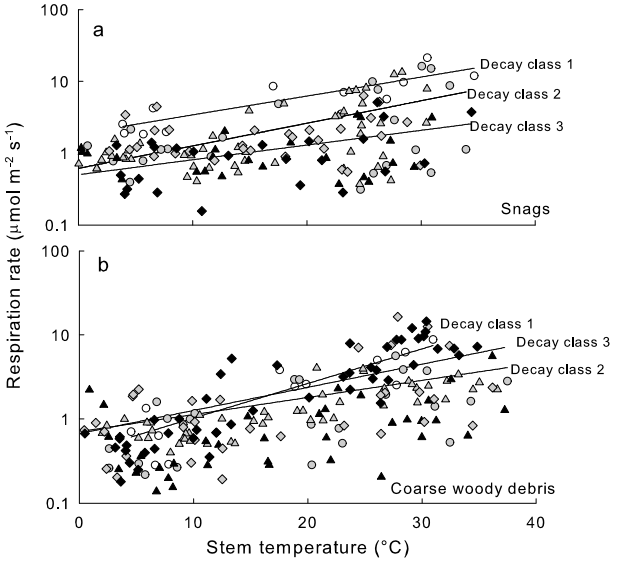

Figure 2. Respiration rates (μmol CO_2 m^{-2} $_{surface\ area}$ s^{-1}; note the log scale) versus stem temperature (°C) of (a) snags of *Pinus* spp. (circles), *Q. prinus* (triangles), and *Q. velutina* (diamonds). Equations were fitted to individuals in decay class 1 (open symbols; $y = 1.86 * 1.06^x$; $r^2 = 0.59$), decay class 2 (gray symbols; $y = 0.61 * 1.07^x$; $r^2 = 0.24$), and decay class 3 (black symbols; $y = 0.5 * 1.05^x$; $r^2 = 0.21$) and (b) coarse woody debris. Equations were fitted to individuals in decay class 1 ($y = 0.40 * 1.10^x$; $r^2 = 0.81$), decay class 2 ($y = 0.71 * 1.05^x$; $r^2 = 0.18$), and decay class 3 ($y = 0.67 * 1.07^x$; $r^2 = 0.32$).

3. Results

3.1. Respiration Rates of Snags and Coarse Woody Debris and Modeling

Overall, point measurement respiration rates from snags and coarse woody debris individuals followed a similar seasonal pattern, with highest rates in the summer and lowest rates in the winter (Figure 1). For *Pinus* spp., snags had significantly higher respiration rates than coarse woody debris ($p < 0.001$), while for *Quercus* spp., snags and coarse

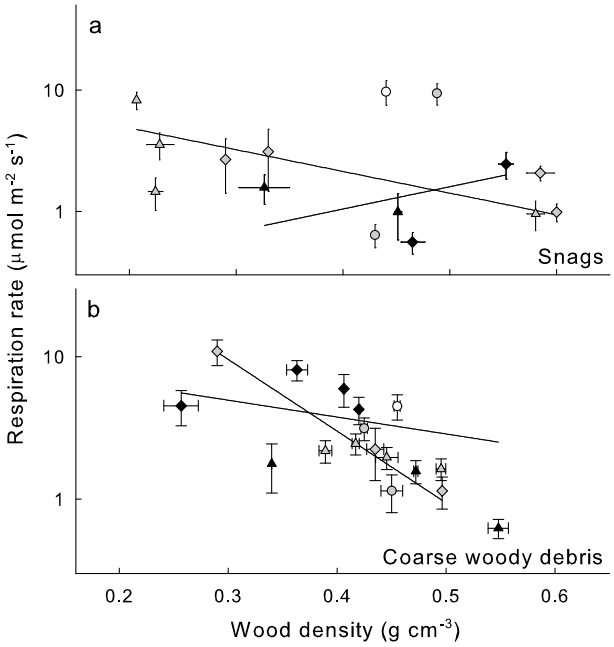

Figure 3. Average spring/summer respiration rates (μmol CO_2 m^{-2} surface area s^{-1}; note the log scale) versus average wood density (g cm^{-3}) for (a) snags of *Pinus* spp. (circles), *Q. prinus* (triangles), and *Q. velutina* (diamonds). Equations were fitted to individuals in decay class 2 (gray symbols; $11.05 * 0.016^{x}$; $r^2 = 0.41$) and decay class 3 (black symbols; $y = 0.19 * 69.23^{x}$; $r^2 = 0.19$) and (b) coarse woody debris. Equations were fitted to individuals in decay class 2 ($y = 311 * 9.04 \times 10^{-6x}$; $r^2 = 0.96$) and decay class 3 ($y = 11.22 * 0.07^{x}$; $r^2 = 0.18$). Error bars for wood density represent the standard error around the 12 monthly measurements, and error bars for respiration represent the error around seven spring and summer respiration measurements.

woody debris had similar respiration rates ($p = 0.24$). *Pinus* and *Quercus* spp. had similar respiration rates both for snags ($p = 0.07$) and coarse woody debris ($p = 0.92$). *Pinus* spp. in decay class 1 had higher respiration rates than *Pinus* spp. in decay class 2 ($p = 0.02$ for snags and 0.001 for coarse woody debris). For *Quercus* spp., snags in decay class 2 had significantly higher respiration rates than snags in decay class 3 ($p = 0.002$), while coarse woody debris in decay class 2 had significantly lower respiration rates than coarse woody debris in decay class 3 ($p = 0.03$).

Models for dead stem respiration rates tended to explain a greater amount of variation and had smaller RMSE when snags and coarse woody debris were considered separately. Additionally, distinguishing between *Q. prinus* and *Q. velutina* for snags yielded a better fitting model than when *Q. prinus* and *Q. velutina* were combined. For snags, the best fit multiple linear regression model included the following explanatory variables (listed in order of importance in the model): stem temperature, decay class*stem diameter, stem diameter, wood density, decay class*wood density, decay class*stem temperature, species, species*decay class, and decay class (Table 4). For coarse woody debris, the best fit multiple linear regression model included the following explanatory variables in order of importance: stem temperature, genus, genus*stem diameter, stem diameter, stem temperature*decay class, decay class, wood density*decay class, and wood density (Table 4).

Respiration rates significantly increased with the temperature of stems for both *Pinus* spp. and *Quercus* spp. of all decay classes (Figure 2). Because the temperature*decay class interaction was significant in the best fit respiration models, equations for temperature versus respiration were fitted by decay class (Figure 2). For snags, individuals in decay class 2 showed the largest increase in respiration for a given increase in temperature, followed by individuals in decay class 1, and then by individuals in decay class 3 (Figure 2a). For coarse woody debris, individuals in decay class 1 showed the largest increase in respiration for a given increase in temperature, followed by individuals in decay class 3, then by individuals in decay class 2 (Figure 2b). However, calculated Q_{10} values did not vary significantly between snags and coarse woody debris ($p = 0.86$), between *Pinus* and *Quercus* spp. ($p = 0.78$) or between decay classes ($p = 0.57$) and had an overall average (and SE) for all individuals of 2.36 ± 0.23. Yearly growing season ecosystem respiration Q_{10} values were about 2.14 ± 0.04 and also did not differ significantly from Q_{10} of snags and coarse woody debris ($p = 0.88$).

Snags had wood densities that ranged from 0.25 g cm^{-3} to 0.6 g cm^{-3} although *Pinus* spp. exhibited relatively small variation and averaged around 0.5 g cm^{-3} (Table 1 and Figure 3a). Coarse woody debris exhibited smaller variation in wood density ranging from 0.28 g cm^{-3} to 0.55 g cm^{-3} with *Pinus* spp. showing similarly small variation and averaging around 0.45 g cm^{-3} (Table 1 and Figure 3b). Again, since the interaction between decay class*wood density was significant in the best fit respiration models, equations for respiration versus wood density were fitted by decay class (except for decay class 1 which

Table 5. Stand-Level Estimates of Snag and Coarse Woody Debris Mass[a]

	Predefoliation		Postdefoliation	
	2004	2006	2009	2011
		Pinus *spp.*		
Coarse woody debris (Mg ha^{-1})	0.14 (0.1)	0.06 (0.04)	0.18 (0.1)	0.05 (0.04)
Snag (Mg ha^{-1})	0.14 (0.1)	0	0.08 (0.08)	0.08 (0.08)
		Quercus *spp.*		
Coarse woody debris (Mg ha^{-1})	1.5 (0.4)	0.76 (0.4)	1.7 (0.5)	2.2 (0.4)
Snag (Mg ha^{-1})	1.5 (0.6)	1.0 (0.3)	6.5 (1.8)	11.2 (2.2)
		Total		
Coarse woody debris (Mg ha^{-1})	1.6 (0.4)	0.82 (0.4)	1.9 (0.5)	2.3 (0.4)
Snag (Mg ha^{-1})	1.6 (0.6)	1.0 (0.3)	6.8 (1.9)	11.3 (2.2)
Overall total (Mg ha^{-1})	3.3 (0.9)	1.8 (0.3)	8.5 (2.0)	13.6 (2.4)

[a]Mean and standard error in parentheses; $N = 16$.

only contains a single individual; Figure 3). For both snags and coarse woody debris, individuals in decay class 2 exhibited a significant negative relationship between respiration rate and wood density, while individuals in decay class 3 exhibited a much weaker relationship than decay class 2 with snags exhibiting a slightly positive relationship (Figure 3a) and coarse woody debris exhibiting a slightly negative relationship (Figure 3b). The relative water content of either snags or coarse woody debris did not explain any of the variation in measured respiration rates and was not a significant variable in the best fit respiration models (data not shown). Snags tended to have relative water contents below 0.4, while the relative water contents of the measured coarse woody debris individuals varied from about 0.1 to 1.0. Likewise for coarse woody debris, *Pinus* spp. and *Quercus* spp. in all decay classes showed a similar degree of variability in relative water content.

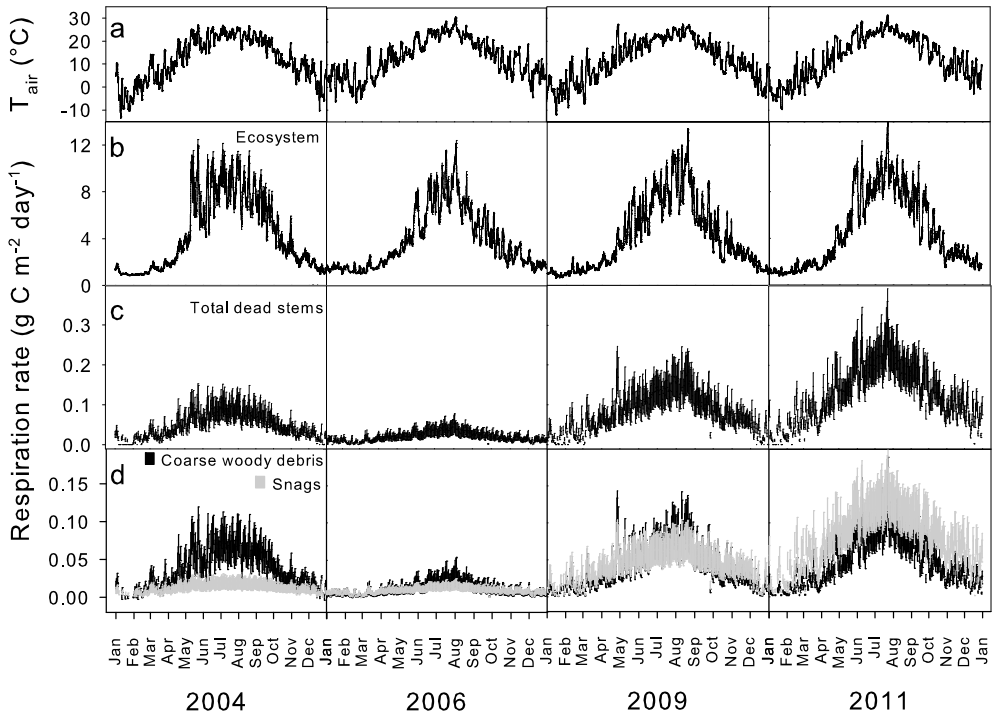

Figure 4. Yearly courses of (a) average daily air temperature (°C), (b) stand-level daily ecosystem respiration (mean ± standard error; g C m^{-2} $_{\text{ground area}}$ d^{-1}), (c) daily dead stem respiration (mean ± standard error; g C m^{-2} $_{\text{ground area}}$ d^{-1}), and (d) daily respiration of coarse woody debris (black lines; mean ± standard error; g C m^{-2} $_{\text{ground area}}$ d^{-1}) and snags (gray lines; mean ± standard error; g C m^{-2} $_{\text{ground area}}$ d^{-1}) during 2 years before the forest was defoliated by gypsy moths (2004 and 2006) and 2 years after defoliation (2009 and 2011).

Table 6. Yearly Net Ecosystem Exchange and Respiration From Snags, Coarse Woody Debris, and Ecosystem[a]

	Predefoliation		Postdefoliation	
	2004	2006	2009	2011
	Net ecosystem exchange (NEE; g C m^{-2} yr^{-1})[b]			
	−181 (26)	−140 (23)	−9 (25)	−49 (21)
	Respiration (g C m^{-2} yr^{-1})			
Snags	4.5 (1.9)	3.5 (1.2)	15.4 (4.9)	29.2 (7.1)
Coarse woody debris	13.4 (3.6)	4.1 (2.0)	14.3 (3.9)	16.9 (3.7)
Total dead stems	17.8 (5.5)	7.6 (3.2)	29.7 (8.6)	46.2 (10.8)
Ecosystem	1590 (78)	1390 (35)	1520 (41)	1650 (51)
	Ratio (%)			
Dead stem/Ecosystem	1.1 (0.39)	0.55 (0.25)	2.0 (0.63)	2.8 (0.74)
Dead stem/NEE	9.8 (4.4)	5.4 (3.2)	330 (1010)	94 (62)

[a]Mean and standard error in parentheses.
[b]Negative values represent carbon uptake by the ecosystem, positive values represent carbon flux to the atmosphere.

3.2. Stand-Level Pools of Snags and Coarse Woody Debris and Scaling of Respiration Rates

In general, mass of *Pinus* spp. snags and coarse woody debris were not significantly affected by the gypsy moth defoliation that occurred in 2007 and 2008 and averaged 0.09 Mg ha^{-1} across the four measurement periods (Table 5). Before gypsy moth defoliation, the mass of *Quercus* spp. snags and coarse woody debris was around 13 times larger than *Pinus* spp., and following defoliation, it was around 50 times larger (Table 5). Before gypsy moth defoliation, *Quercus* spp. total dead stem mass was similarly distributed between snags and coarse woody debris, but after defoliation, there was about 3 times greater mass as snags than coarse woody debris (Table 5). Overall, total dead stem mass increased from around 2.5 Mg ha^{-1} before defoliation to around 11 Mg ha^{-1} after defoliation (Table 5).

Before gypsy moth defoliation, respiration fluxes from dead stem pools were about 0.1 g C m^{-2} d^{-1} during the summers of 2004 and 2006 (Figure 4). Daily summer respiration rates from dead stems increased by almost 100% in 2009 compared to predefoliation levels, and then increased by an additional 25% in 2011 (Figure 4). However, total daily ecosystem respiration rates remained relatively constant both before and after gypsy moth defoliation averaging about 10 g C m^{-2} d^{-1} during the summer (Figure 4). In terms of yearly respiration rates, 2004 and 2006 had average respiration rates from snags and coarse woody debris of approximately 13 g C m^{-2} yr^{-1} (Table 6). In 2009, 2 years following gypsy moth defoliation, dead stem respiration rates had approximately doubled with snags and coarse woody debris contributing approximately equal amounts (Table 6). Between 2009 and 2011, yearly respiration rates from dead stems increased by about 50% which was attributed mostly to a doubling of the respiration from snags, although respiration from coarse woody debris also increased by about 18% (Table 6). Total ecosystem respiration increased by about 6% in 2009 and 2011 compared to predefoliation values and net ecosystem uptake of C (NEE) was only 5% of predefoliation values in 2009 and 30% of predefoliation values in 2011 (Table 6). The contribution of dead stem respiration to total ecosystem respiration was about 2.4 times higher in 2011 (about 2.8%) compared to predefoliation values of about 0.8% (Table 6). However, when compared to net ecosystem C uptake, dead stem respiration was approximately 3 times greater than NEE in 2009 and approximately equal to NEE in 2011 (Table 6).

4. Discussion

Following defoliation of an oak-dominated forest by gypsy moths, mass of snags and coarse woody debris increased more than fivefold from around 2.5 Mg ha^{-1} to about 13.6 Mg ha^{-1}. Likewise, the proportion of dead stem mass to live stem mass in this forest increased from about 3% before defoliation to more than 18% following disturbance. Annual respiration rates from snags and coarse woody debris were over 3.5 times larger than predefoliation levels and averaged 46 g C m^{-2} yr^{-1} approximately 4 years postdisturbance in 2011. This respiration rate from snags and coarse woody debris is approximately equal to the net uptake of C into the ecosystem for that year. Likewise, because pools of snags and coarse woody debris in this forest were over 5 times larger after defoliation, this suggests that there is a lag in the release of CO_2 after disturbance

and that disturbance effects will continue to impact ecosystem respiration and net ecosystem production well into the future. A simple calculation of postdefoliation C pools divided by respiration rate suggests that this forest will still contain dead stems 18 years postdefoliation, which is longer than the 5 to 10 year return interval of gypsy moth in many forests [*Allstadt et al.*, 2013]. In terms of partitioning between snags and coarse woody debris, in the predefoliation period (2004–2006) about 30% of snags fell in a 2 year period based on information from the FIA data set. From 2006 to 2009, only 5% of snags fell, largely due to the influx of new snags caused by the defoliation. From 2009 to 2011, about 10% of snags fell, increasing the coarse woody debris pool relative to the snag pool. Therefore, the coarse woody debris pool will continue to increase in this forest, postdefoliation, with the snag fall rate likely increasing with time since disturbance.

Predisturbance respiration rates from snags and coarse woody debris were generally lower than rates in other undisturbed forests including northern hardwood and conifer-dominated forests in the Great Lakes region [*Forrester et al.*, 2012; *Gough et al.*, 2007; *Tang et al.*, 2008] and New England [*Liu et al.*, 2006], coniferous forests in the Pacific Northwest [*Janisch et al.*, 2005] and southeastern oak-dominated forests [*Li et al.*, 2012]. This is likely because the sandy soils of this region limit productivity [*Pan et al.*, 2006] as well as the coarse woody debris pool compared with other temperate forests growing on more mesic soils. Likewise, little density-dependent mortality is occurring in this forest, and much of the coarse woody debris from a previous windthrow disturbance event in 1991 have largely decomposed [*Matlack et al.*, 1993]. However, postdefoliation coarse woody debris respiration rates in this forest were similar to [*Forrester et al.*, 2012; *Janisch et al.*, 2005; *Tang et al.*, 2008] or larger than [*Gough et al.*, 2007; *Liu et al.*, 2006] respiration rates measured in other forests. Postdefoliation respiration rates from dead stems were also similar to an oak forest in the Southeastern U.S., but much lower than oak forests that received either uneven-aged or even-aged harvest management [*Li et al.*, 2012]. In terms of dead stem C pools, both predisturbance and postdisturbance levels in this forest were lower than the average for forests in the Northeast [*Woodall et al.*, 2008] and postdisturbance levels were lower than dry tropical forest stands disturbed by fire or hurricanes [*Harmon et al.*, 1995]. However, defoliation caused the pool of biomass in snags and coarse woody debris to increase by more than fivefold which is proportionally higher than the increases caused by either fire (around threefold increase) or hurricane damage (around 50% increase at the most disturbed site) in a tropical dry forest [*Harmon et al.*, 1995].

There was a distinct increase in both the pools and respiration rates of snags and coarse woody debris from 2009 to 2011 even though the gypsy moth disturbance occurred in 2007 and 2008. This additional increase is likely due to widespread drought conditions in 2010 which caused additional mortality of trees that were likely already weakened by the gypsy moth disturbance. These newly deceased trees had not fallen yet and therefore significantly increased the pool of snags relative to coarse woody debris in 2011. Additionally, some of the difference in respiration rates between 2009 and 2011 may be attributed to differing summer temperatures because daily maximum temperatures in the summer of 2009 averaged 27.6 ± 0.4°C, and in 2011, averaged 29.9 ± 0.3°C. Therefore, additional environmental factors including drought and heat can have a comparatively greater effect on respiration rates of forests that have previously experienced a defoliation event compared to undisturbed forests given the weakened trees and larger dead stem pool.

In modeling respiration from either snags or coarse woody debris, we found that stem temperature, stem diameter, and wood density were the strongest predictors of respiration rates, with species and decay class distinctions also important. Stem temperature explained around 35% of the variation in respiration rates depending on the orientation (coarse woody debris versus snag) or decay class of the individual. Q_{10} values averaged around 2.36 and were similar to values measured for coarse woody debris in northern temperate forests in the Great Lakes region [*Gough et al.*, 2007], coarse woody debris from central Amazonia [*Chambers et al.*, 2000] and those measured for oak snags in Southeastern U.S. forests [*Li et al.*, 2007] but generally lower than values measured for oak coarse woody debris in Southeastern U.S. forests [*Li et al.*, 2007]. We also found that diameter of snags and coarse woody debris was a significant predictor of respiration rate with several other studies finding similar results [*Chambers et al.*, 2000; *Jomura et al.*, 2007; *Zell et al.*, 2009], while others finding that diameter was not a significant predictor [*Gough et al.*, 2007; *Mattson et al.*, 1987; *Russell et al.*, 2013]. Given that the surface to volume ratio is larger for smaller diameter stems, larger diameters should inhibit the access of fungal colonizers as well as the diffusion of oxygen into the individual [*Yatskov et al.*, 2003; *Zell et al.*, 2009]. Likewise, higher wood density should also limit access of fungi and oxygen diffusion, and we found that, particularly for decay class 2, individuals with higher wood density values had lower

respiration rates. *Chambers et al.* [2000, 2001] also found that wood density strongly affected respiration and decomposition rates of coarse woody debris.

Interestingly, moisture content of dead stems was not found to be a good predictor of respiration rates. While some studies have reported that coarse woody debris moisture content was not significantly correlated with respiration rates [*Mackensen and Bauhus*, 2003; *Tang et al.*, 2008], the majority found that moisture content explained a significant amount of the variability in respiration rates [*Barker*, 2008; *Bond-Lamberty et al.*, 2003; *Chambers et al.*, 2001; *Forrester et al.*, 2012; *Liu et al.*, 2006; *Wang et al.*, 2002; *Zell et al.*, 2009]. Studies finding a relationship between respiration rates and moisture content reported a quadratic [*Jomura et al.*, 2008; *Zell et al.*, 2009] or a threshold response [*Bond-Lamberty et al.*, 2003], where moisture contents generally below the fiber saturation point limited microbial activity and very high moisture contents limited oxygen diffusion [*Barker*, 2008]. Our study encompassed coarse woody debris with a wide range of moisture contents and therefore should have been able to detect a relationship between respiration rates and moisture content. Likewise, snags were generally found to have much lower moisture contents compared with coarse woody debris, but their respiration rates were similar (for *Quercus* spp.) or significantly higher (for *Pinus* spp.) than that of coarse woody debris. Therefore, the question remains as to why respiration of dead stems in this forest did not respond to changes in wood moisture content. One reason could be the sandy soils in this ecosystem having limited water- and nutrient-holding capacity. *Landesman and Dighton* [2010] found that soil microbial biomass and community composition were unaffected by rainfall manipulation treatments in this forest suggesting that decay organisms in this ecosystem may be adapted to a large range in moisture contents, and therefore, do not respond strongly to it. Likewise, nitrogen limitation, in particular, may limit decomposition rates in this forest [*Mackensen and Bauhus*, 2003].

Before disturbance, annual respiration from snags and coarse woody debris was about 0.8% of total ecosystem respiration. This is lower than reported values of around 1.4% for deciduous forests in the upper Great Lakes region of the U.S. [*Gough et al.*, 2007], 2% for a temperate forest in the New England region of the U.S. [*Liu et al.*, 2006], and 3 to 4% respectively for old growth hemlock (*Tsuga canadensis* (L.) Carrière) and sugar maple (*Acer saccharum* Marshall) stands in the Great Lakes region [*Tang et al.*, 2008]. While annual ecosystem respiration increased by about 6% in the years following the gypsy moth defoliation compared to predefoliation values, the contribution of dead stem respiration to total ecosystem respiration more than doubled. Although respiration from dead stems comprised only 2 to 3% of total ecosystem respiration after defoliation, this is a significant increase considering the relatively low postdisturbance productivity of the stand. Prior to defoliation, dead stem respiration accounted for only about 7% of net C uptake of this forest, while 4 years postdisturbance, the forest absorbed about 70% less C, and NEE was approximately equal to the respiration from dead stems alone. Therefore, although respiration from snags and coarse woody debris tends to be a relatively small source of C to the atmosphere, disturbances such as defoliation can significantly alter this C pool as well as its contribution to the overall C balance of the forest.

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References

Allstadt, A., K. Haynes, A. Liebhold, and D. Johnson (2013), Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect, *Oecologia*, *172*, 141–151.

Aukema, J., et al. (2011), Economic impacts of non-native forest insects in the continental United States, *PloS ONE*, *6*, e24587, doi:10.1371/journal.pone.0024587.

Ayres, M. P., and M. J. Lombardero (2000), Assessing the consequences of global change for forest disturbance from herbivores and pathogens, *Sci. Total Environ.*, *262*, 263–286.

Barker, J. (2008), Decomposition of Douglas-fir coarse woody debris in response to differing moisture content and initial heterotrophic colonization, *For. Ecol. Manage.*, *255*, 598–604.

Battisti, A., M. Stastny, S. Netherer, C. Robinet, A. Schopf, A. Roques, and S. Larsson (2005), Expansion of geographic range in the pine processionary moth caused by increased winter temperatures, *Ecol. Appl.*, *15*, 2084–2096.

Bond-Lamberty, B., C. Wang, and S. Gower (2003), Annual carbon flux from woody detritus for a boreal spruce fire chronosequence, *J. Geophys. Res.*, *107*(D3), 8220, doi:10.1029/2001JD000839.

Carroll, A., S. Taylor, J. Régnière, and L. Safranyik (2003), Effects of climate change on range expansion by the mountain pine beetle in British Columbia, *Rep. BC-X-399*, pp. 223–232, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Kelowna, British Columbia.

Chambers, J. Q., J. Schmel, and A. D. Nobre (2001), Respiration from coarse wood litter in central Amazon forests, *Biogeochemistry*, *52*, 115–131.

Chambers, J. Q., N. Higuchi, J. Schimel, L. Ferreira, and J. Melack (2000), Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon, *Oecologia*, *122*, 380–388.

Clark, K. L., N. Skowronski, and J. Hom (2010), Invasive insects impact forest carbon dynamics, *Global Change Biol.*, *16*, 88–101.

Clark, K. L., N. Skowronski, M. Gallagher, H. Renninger, and K. Schäfer (2012), Effects of invasive insects and fire on forest energy exchange and evapotranspiration in the New Jersey Pinelands, *Agric. For. Meteorol.*, *166-167*, 50–61.

Currano, E., P. Wilf, S. Wing, C. Labandeira, E. Lovelock, and D. Royer (2008), Sharply increased insect herbivory during the Paleocene-Eocene thermal maximum, *Proc. Natl. Acad. Sci. U. S. A.*, *105*, 1960–1964.

Dale, V., et al. (2001), Climate change and forest disturbances, *BioScience*, *51*, 723–734.
DeVries, P. (1973), A general theory on line-intersect sampling with application to logging residue inventory, in *Mededdlingen Landbouw Hogeschool No 73-11*, edited by H. Veenman, 23 pp., Wageningen, Netherlands.
Domec, J. C., and B. L. Gartner (2002), Age-and position-related changes in hydraulic versus mechanical dysfunction of xylem: Inferring the design criteria for Douglas-fir wood structure, *Tree Physiol.*, *22*, 91–104.
Dukes, J. S., et al. (2009), Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict?, *Can. J. For. Res.*, *39*, 231–248.
Flannigan, M., B. Stocks, and B. Wotton (2000), Climate change and forest fires, *Sci. Total Environ.*, *262*, 221–229.
Flannigan, M., Y. Bergeron, O. Engelmark, and B. Wotton (1998), Future wildfire in circumboreal forests in relation to global warming, *J. Vegetation Sci.*, *9*, 469–476.
Forrester, J., D. Mladenoff, S. Gower, and J. Stoffel (2012), Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps, *For. Ecol. Manage.*, *265*, 124–132.
Franklin, J., H. Shugart, and M. Harmon (1987), Tree death as an ecological process, *BioScience*, *37*, 550–556.
Gartner, B. L., J. R. Moore, and B. A. Gardiner (2004), Gas in stems: Abundance and potential consequences for tree biomechanics, *Tree Physiol.*, *24*, 1239–1250.
Goodale, C., et al. (2002), Forest carbon sinks in the Northern Hemisphere, *Ecol. Appl.*, *12*, 891–899.
Gough, C. M., C. S. Vogel, C. Kazanski, L. Nagel, C. E. Flower, and P. S. Curtis (2007), Coarse woody debris and the carbon balance of a north temperate forest, *For. Ecol. Manage.*, *244*, 60–67.
Harmon, M. E., O. Krankina, and J. Sexton (2000), Decomposition vectors: A new approach to estimating woody detritus decomposition dynamics, *Can. J. For. Res.*, *30*, 76–84.
Harmon, M. E., D. Whigham, J. Sexton, and I. Olmsted (1995), Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico, *Biotropica*, *27*, 305–316.
Harmon, M. E., et al. (1986), Ecology of coarse woody debris in temperate ecosystems, *Adv. Ecol. Res.*, *15*, 133–302.
Hicke, J., et al. (2012), Effects of biotic disturbances on forest carbon cycling in the United States and Canada, *Global Change Biol.*, *18*, 7–34.
Janisch, J., M. E. Harmon, H. Chen, B. Fasth, and J. Sexton (2005), Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest, *Ecoscience*, *12*, 151–160.
Jomura, M., Y. Kominami, M. Dannoura, and Y. Kanazawa (2008), Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan, *For. Ecol. Manage.*, *255*, 149–155.
Jomura, M., Y. Kominami, K. Tamai, T. Miyama, Y. Goto, M. Dannoura, and Y. Kanazawa (2007), The carbon budget of coarse woody debris in the temperate broad-leaved secondary forest in Japan, *Tellus*, *59*, 211–222.
Kurz, W. A., G. Stinson, G. Rampley, C. Dymond, and E. Neilson (2008), Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain, *Proc. Natl. Acad. Sci. U. S. A.*, *105*, 1551–1555.
Landesman, W., and J. Dighton (2010), Response of soil microbial communities and the production of plant-available nitrogen to a two-year rainfall manipulation in the New Jersey Pinelands, *Soil Biol. Biochem.*, *42*, 1751–1758.
Li, J., T. L. Powell, T. J. Seiler, D. P. Johnson, H. P. Anderson, R. Bracho, B. A. Hungate, C. R. Hinkle, and B. G. Drake (2007), Impacts of Hurricane Frances on Florida scrub-oak ecosystem processes: Defoliation, net CO_2 exchange and interactions with elevated CO_2, *Global Change Biol.*, *13*, 1101–1113.
Li, Q., J. Chen, and D. Moorhead (2012), Respiratory carbon losses in a managed oak forest ecosystem, *For. Ecol. Manage.*, *279*, 1–10.
Liu, W., D. Bryant, L. Hutyra, S. R. Saleska, E. Hammond-Pyle, D. Curran, and S. Wofsy (2006), Woody debris contribution to the carbon budget of selectively logged and maturing mid-latitude forests, *Oecologia*, *148*, 108–117.
Logan, J., J. Régnière, and J. Powell (2003), Assessing the impacts of global warming on forest pest dynamics, *Front. Ecol. Environ.*, *1*, 130–137.
Mackensen, J., and J. Bauhus (2003), Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*, *Soil Biol. Biochem.*, *35*, 177–186.
MacMillan, P. (1981), Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana, *Am. Midland Naturalist*, *106*, 335–344.
Maindonald, J., and W. J. Braun (2007), DAAG: Data Analysis And Graphics, R package version 0.95. [Available at http://www.stats.uwo.ca/DAAG.]
Matlack, G., S. Gleeson, and R. Good (1993), Treefall in a mixed oak-pine coastal plain forest: Immediate and historical causation, *Ecology*, *74*, 1559–1566.
Mattson, K., W. Swank, and J. Waide (1987), Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians, *Can. J. For. Res.*, *17*, 712–721.
McCullough, D., R. Werner, and D. Neumann (1998), Fire and insects in northern and boreal forest ecosystems of North America, *Annu. Rev. Entomol.*, *43*, 107–127.
McGee, G., and J. Birmingham (1997), Decaying logs as germination sites in northern hardwood forests, *Northern J. Appl. Forestry*, *14*, 178–182.
Medvigy, D., K. L. Clark, N. S. Skowronski, and K. V. R. Schäfer (2012), Simulated impacts of insect defoliation on forest carbon dynamics, *Environ. Res. Lett.*, *7*, 045703.
O'Connell, B., E. LaPoint, J. Turner, T. Ridley, D. Boyer, A. Wilson, K. Waddell, S. Pugh, and B. Conkling (2013), The forest inventory and analysis database: Database description and users manual version 5.1.6 for phase 2 *Rep.*, United States Department of Agriculture Forest Service.
Orwig, D., D. Foster, and D. Mausel (2002), Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid, *J. Biogeogr.*, *29*, 1475–1487.
Pan, Y., R. Birdsey, J. Hom, K. McCullough, and K. Clark (2006), Improved estimates of net primary productivity from MODIS satellite data at regional and local scales, *Ecol. Appl.*, *16*, 125–132.
Pan, Y., et al. (2011), A large and persistent carbon sink in the world's forests, *Science*, *333*, 988–993.
Russell, M., C. Woddall, S. Fraver, and A. D'Amato (2013), Estimates of downed woody debris decay class transitions for forests across the eastern United States, *Ecol. Model.*, *251*, 22–31.
Schäfer, K. V. R. (2011), Canopy stomatal conductance following drought, disturbance and death in an upland oak/pine forest of the New Jersey Pine Barrens, USA, *Frontiers Plant Sci.*, *2*, 1–7, doi:10.3389/fpls.2011.00015.
Schowalter, T. (1992), Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition, *Can. J. For. Res.*, *22*, 161–166.
Siau, J. (1984), *Transport Processes in Wood*, 245 pp., Springer-Verlag, New York.
Spies, T., J. Franklin, and T. Thomas (1988), Coarse woody debris in Douglas-fir forests of Western Oregon and Washington, *Ecology*, *69*, 1689–1702.
Tang, J., P. Bolstad, A. Desai, J. Martin, B. Cook, K. Davis, and E. Carey (2008), Ecosystem respiration and its components in an old-growth forest in the Great Lakes region of the United States, *Agric. For. Meteorol.*, *148*, 171–185.

Taylor, J. R. (1997), *An Introduction to Error Analysis: The Study of Uncertainties in Physical Measurements*, University Science Books, Sausalito, Calif.
Ungerer, M., M. Ayres, and M. J. Lombardero (1999), Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), *J. Biogeogr.*, *26*, 1133–1145.
Valentini, R., et al. (2000), Respiration as the main determinant of carbon balance in European forests, *Nature*, *404*, 861–865.
Vanderwel, M., D. Coomes, and D. Purves (2013), Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States, *Global Change Biol.*, *19*, 1504–1517.
Waddell, K. (2002), Sampling coarse woody debris for multiple attributes in extensive resource inventories, *Ecol. Indicators*, *1*, 139–153.
Walsh, K., and A. Pittock (1998), Potential changes in tropical storms, hurricanes, and extreme rainfall events as a result of climate change, *Clim. Change*, *39*, 199–213.
Wang, C., B. Bond-Lamberty, and S. Gower (2002), Environmental controls on carbon dioxide flux from black spruce coarse woody debris, *Oecologia*, *132*, 374–381.
Whittaker, R. H., and G. M. Woodwell (1968), Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York, *J. Ecol.*, *56*, 1–25.
Wilf, P., and C. Labandeira (1999), Response of plant-insect associations to Paleocene-Eocene warming, *Science*, *284*, 2153–2156.
Williams, D., and A. Liebhold (1995), Herbivorous insects and global change: Potential changes in the spatial distribution of forest defoliator outbreaks, *J. Biogeogr.*, *22*, 665–671.
Woodall, C., L. Heath, and J. Smith (2008), National inventories of down and dead woody material forest carbon stocks in the United States: Challenges and opportunities, *For. Ecol. Manage.*, *256*, 221–228.
Yatskov, M., M. E. Harmon, and O. Krankina (2003), A chronosequence of wood decomposition in the boreal forests of Russia, *Can. J. For. Res.*, *33*, 1211–1226.
Zell, J., G. Kändler, and M. Hanewinkel (2009), Predicting constant decay rates of coarse woody debris—A meta-analysis approach with a mixed model, *Ecol. Model.*, *220*, 904–912.