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Carbon storage in old-growth forests of the Mid-Atlantic: toward better understanding the eastern forest carbon sink

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Abstract. Few old-growth stands remain in the matrix of secondary forests that dominates the eastern North American landscape. These remnant stands offer insight on the potential carbon (C) storage capacity of now-recovering secondary forests. We surveyed the remaining old-growth forests on sites characteristic of the general Mid-Atlantic United States and estimated the size of multiple components of forest C storage. Within and between old-growth stands, variability in C density is high and related to overstory tree species composition. The sites contain 219 ± 46 Mg C/ha (mean \pm SD), including live and dead aboveground biomass, leaf litter, and the soil O horizon, with over 20% stored in downed wood and snags. Stands dominated by tulip poplar (*Liriodendron tulipifera*) store the most live biomass, while the mixed oak (*Quercus* spp.) stands overall store more dead wood. Total C density is 30% higher (154 Mg C/ha), and dead wood C density is 1800% higher (46 Mg C/ha) in the old-growth forests than in the surrounding younger forests (120 and 5 Mg C/ha, respectively). The high density of dead wood in old growth relative to secondary forests reflects a stark difference in historical land use and, possibly, the legacy of the local disturbance (e.g., disease) history. Our results demonstrate the potential for dead wood to maintain the sink capacity of secondary forests for many decades to come.

Key words: carbon sink; dead wood; eastern forests; Mid-Atlantic United States; old-growth forest; soil organic carbon.

INTRODUCTION

Forests and their associated soils store an estimated 45% of all terrestrial carbon (C) and contribute ~50% of total terrestrial net ecosystem production (NEP; Bonan 2008). Temperate forests in the eastern United States may sequester 0.11–0.15 Pg C/yr (Pacala et al. 2001), ~12–19% of the C emitted annually by fossil fuel combustion in the United States. (Ryan et al. 2010). Thus, forest C dynamics and storage emerge as important mitigating components of the global increase in atmospheric CO₂ concentrations. The main mechanism forming active C sinks in the Mid-Atlantic region of the eastern United States is forest recovery following abandonment of agropastoral lands in the mid-to-late 1800s, and an additional large-scale harvest of secondary forest in the late 1930s (Pan et al. 2004). Today 70% of eastern forests are aged between 50 and 100 years (Pan et al. 2011). Continued

forest growth is predicted to remain a major driving mechanism for C accumulation for decades to come (Thompson et al. 2011). The 1% of forests identified as old growth remaining in the eastern United States (Davis 1996) provides an empirical basis for estimating the long-term C storage potential of the recovering secondary (and tertiary) forests.

The scant remaining old-growth forests in the region offer an opportunity to empirically estimate the upper limit of C storage (Keeton et al. 2011). Classic “pattern and process” models (Watt 1947) of forest dynamics conclude that for forests of relatively similar growth and mortality rates, the live aboveground C (AGC) should rise to a maximum when all the trees of the initial cohort are large, then decline as the landscape becomes a mixed-age mosaic. However, a global synthesis of old-growth forests suggested that net primary productivity may be declining at lower rates than previously predicted in late succession, leading to a greater upper limit to C storage (Luyssaert et al. 2008). Within eastern North America, live AGC estimates from old growth range from 72 (Keeton et al. 2011) to 220 Mg C/ha

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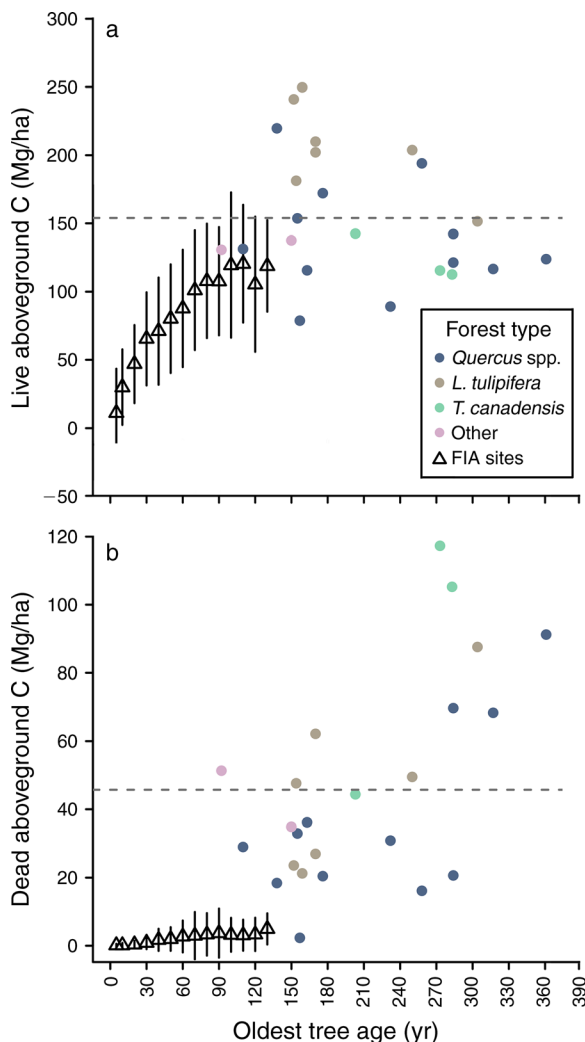


FIG. 1. Relationship between oldest tree age and (a) live aboveground carbon (AGC) and (b) dead AGC for U.S. Forest Service inventory (FIA) plots in 10-yr age class bins (triangles, mean \pm SD) and 25 old-growth stands (colored dots). Forest types reflect the dominant tree species composition (*Quercus* spp., *Liriodendron tulipifera*, *Tsuga canadensis*, or other) of each old-growth stand identified by a cluster analysis. The gray dashed lines indicate the mean live and dead AGC values, respectively, across old-growth sites.

(Busing and White 1993). Trends observed from chronosequences that include old growth suggest that C may continue to accumulate in stands for 200+ years (Tyrrell and Crow 1994, Brown et al. 1997, Ziegler 2000, Keeton et al. 2011). These studies propose that there are additional mechanisms governing C dynamics in old forests. Although tree death occurs quickly, decomposition of dead wood and subsequent release of CO₂ occurs at decade-to-century time scales (Luyssaert et al. 2008). The concentrations of soil organic carbon (SOC) stocks in old-growth forests can also increase (Zhou et al. 2006). However, not all second-growth chronosequences indicate continued accrual of live AGC as

stands reach maturity (Siccama et al. 2007), or an increase in SOC (Hamburg 1984, Fuller 2007). Improved estimates of C stocks in old-growth forests are important for informing strategies to predict long-term forest C dynamics in secondary forests.

This study examines C storage within the old-growth forests remaining at sites characteristic of the general Mid-Atlantic region and addresses the following questions: (1) What is the C density of these old-growth forests, and how is it allocated across pools? (2) What is the relationship between age of the oldest tree and C stocks during late succession? (3) What structural, compositional, and environmental variables are associated with C stocks in old-growth forests? (4) How do C stocks in the remaining old-growth forests compare to those in the matrix of secondary forests?

METHODS

Review of both academic and gray literature along with visits to several candidate sites throughout the study area (Virginia, Delaware, and Maryland, and parts of West Virginia, Pennsylvania, and New Jersey, USA; Appendix: Fig. A1) produced 25 sites that met a set of criteria for representative old-growth forest; most importantly, sites included could not show any evidence of having been cleared, could not be located on low-quality sites, and had a mature forest overstory (see Appendix for detailed methods).

Field sampling within these sites included a hierarchy of subplots that were designed to capture the variability of C stocks within and across major pools, including the live and dead tree biomass, leaf litter, and the soil organic (O) horizon. Live AGC was estimated using allometric equations developed by Jenkins et al. (2003) and Lambert et al. (2005). Dead wood volume was estimated for the various dead wood types (Harmon and Sexton 1996) and dead wood biomass was estimated from volume based on Waddell (2002). Leaf litter and soil O horizon C were estimated from six samples collected at each site. Oldest tree age was determined from tree cores using standard dendrochronological methods.

Relationships between C stocks, oldest tree age, and several environmental variables were modeled using linear regression. Total C stocks as well as individual C pools were examined for the complete set of old-growth sites and for four compositionally based subgroups delineated using an agglomerative clustering algorithm. Finally, the old-growth stands were put into the context of the younger forest mosaic by plotting live and dead AGC within an informal chronosequence using regional plot data obtained from the U.S. Forest Service Inventory and Analysis (FIA) program.

RESULTS

Mean age of the oldest trees measured in these forests was 208 ± 73 yr (all values reported as mean \pm SD, unless otherwise noted) and ranged from 72 to 361 yr

(Appendix: Table A1). Sites contained a mean of 219 ± 46 Mg C/ha in total measured C, 154 ± 47 Mg C/ha in live AGC, and 46 ± 30 Mg C/ha in dead AGC. Leaf litter and C in the soil O horizon contributed smaller amounts of total C stored (mean leaf litter = 6 ± 2 Mg C/ha; mean O horizon = 15 ± 13 Mg C/ha). At all sites, live AGC contributed nearly half or more to total C, with a mean of 68% (Appendix: Table A1). Dead AGC stored a mean of 21% of total C, and O horizon C and leaf litter C constituted 7.7% and 2.8% of total C, respectively. Among the FIA data, mean live AGC increased steadily until the 100-yr age category, where it approached an asymptote at 120 Mg C/ha (Fig. 1a), which is lower than 72% of the sampled old-growth sites. Dead AGC increased with age in the FIA sample, reaching a maximum of 5 Mg C/ha in the 130-yr age class (Fig. 1b). These patterns are consistent across forest types within the FIA sample (Appendix: Fig. A4). At 96% of old-growth sites, stored dead AGC was greater than the maximum estimate from the FIA bin averages. Dead AGC was on average 18 times greater in the old-growth sites than it was in the FIA bins.

The sites clustered into four groups based on tree species composition by basal area (m^2/ha ; Appendix: Fig. A3). The first group was largest ($n = 12$ sites), and was distinguished from the three other groups by its greater abundance of *Quercus alba* (white oak) and *Q. prinus* (chestnut oak) (Appendix: Fig. A3b). The predominance of one species defined the second and third groups (Appendix: Fig. A3c, d). *Liriodendron tulipifera* (tulip poplar) was 300% more abundant than the next most abundant species in the second group ($n = 7$ sites), and *Tsuga canadensis* (eastern hemlock) was the most abundant species in the third group ($n = 3$ sites). Due to the predominance of unique species in each group, species-specific forest type names were assigned to organize discussion of cluster groups: *Quercus* spp., *L. tulipifera*, and *T. canadensis*. In the remaining two sites *Acer saccharum* (sugar maple) and *Q. rubra* (northern red oak) were similarly prevalent, however there were only two such sites, and no species-specific forest type was assigned (other; Appendix: Fig. A3e).

Oldest tree age did not significantly relate to mean live AGC (colored points in Fig. 1a), leaf litter, O horizon C, or total C. The live AGC–oldest tree age relationship was significant ($P < 0.05$) after elevation was incorporated into the model ($r^2 = 0.31$, $F_{2,20} = 5.91$, $P = 0.009$). Elevation and site age had significant negative relationships with live AGC (live AGC = $237.86 - 0.14[\text{elevation}] - 0.24[\text{oldest tree age}]$; see Appendix for model derivation). The standardized, absolute regression coefficient of elevation ($\beta = 0.55$) was greater than that of oldest tree age ($\beta = 0.37$), indicating that elevation had greater influence in the model predicting live AGC than age. In contrast, oldest tree age explained considerable variation in dead AGC ($r^2 = 0.34$, $P = 0.002$; colored points in Fig. 1b). The relationship suggests a C

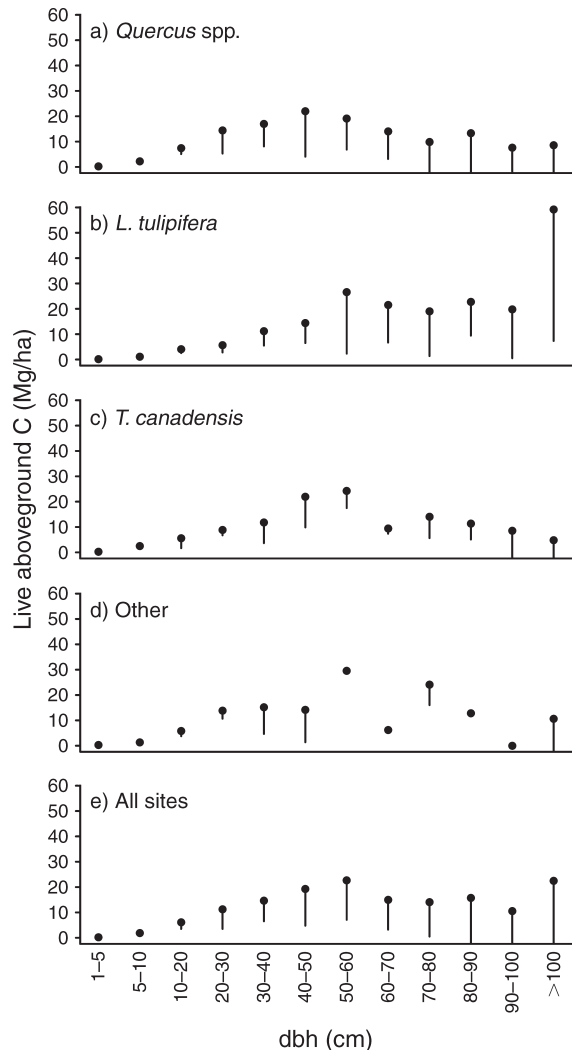


Fig. 2. Relationship between diameter at breast height size class (dbh; taken at 1.37 m aboveground) size class and live AGC for the 25 old-growth stands as grouped by their associated forest types: (a) *Quercus* spp., (b) *L. tulipifera*, (c) *T. canadensis*, and (d) other, as well as (e) across all old-growth sites. For all panels, dbh is binned by 5- and 10-cm increments. Forest types reflect the tree species composition of each old-growth stand identified by a cluster analysis. Error bars represent one SD, with only the lower SD shown to maximize the resolution of the y-axis. Large-diameter (>70 cm dbh) stems stored the most C across size classes for all sites, a trend that is most exaggerated in the *L. tulipifera* forest type.

accumulation rate in dead wood of $0.3 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for old-growth stands.

Additionally, relative dead AGC was nearly equivalent to or greater than live AGC among the older stands sampled. At Allen Seeger State Natural Area in Pennsylvania (273 yr) and Broad Creek Boy Scout Memorial Forest in Maryland (283 yr), dead AGC contributed 47% and 43%, respectively, to the total C stored, relative to 46% and 46% stored by live AGC. Across all sites as well as three of the four cluster groups,

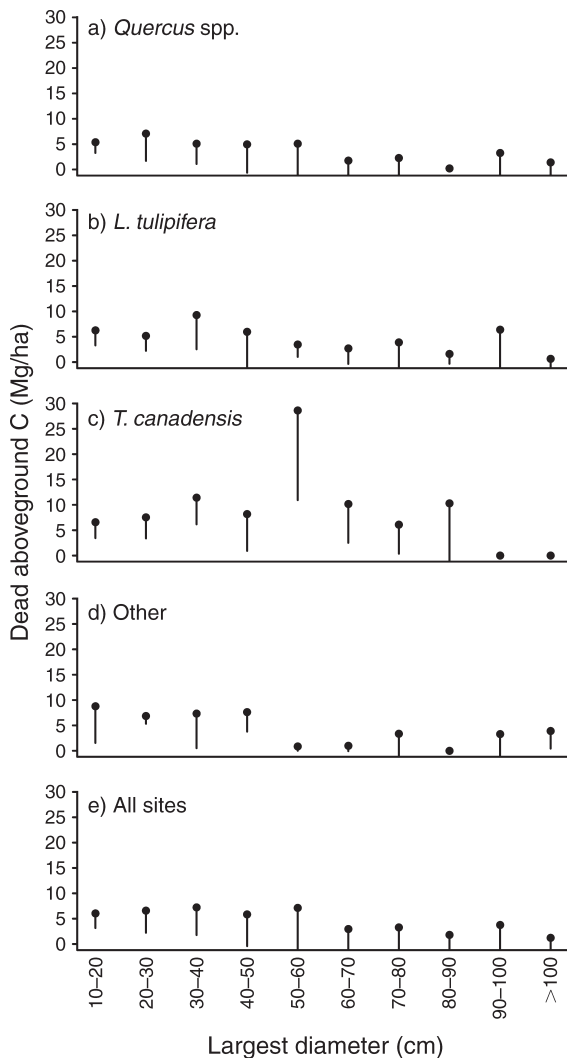


FIG. 3. Relationship between the largest diameter measured per piece of dead wood and dead AGC for the 25 old-growth stands as grouped by their associated forest types: (a) *Quercus* spp., (b) *L. tulipifera*, (c) *T. canadensis*, and (d) other, as well as (e) across all old-growth sites. The number of diameters measured for volume estimation varied with dead wood type. See Appendix for further explanation. Largest diameter is binned by 10-cm increments. Forest types reflect the tree species composition of each old-growth stand identified by cluster analysis. Bars represent one SD, with only the lower SD shown to maximize the resolution of the y-axis. Dead AGC was evenly distributed across size classes, with the exception of the *T. canadensis* forest type.

there was no relationship with live and dead AGC. However, there was a strong negative correlation in the seven stands dominated by *L. tulipifera* (dead AGC = $177.1 - 0.64[\text{live AGC}]$; $r^2 = 0.75$, $P = 0.007$).

Large-diameter stems (>70 cm dbh; taken at 1.37 m aboveground) contributed the majority of C to live AGC in 84% of the old-growth forests surveyed (Fig. 2e). On average, 60% of all live AGC was stored in large-diameter stems, 33% in stems 50–70 cm dbh, 8% in stems 5–20 cm dbh, and <0.1% in stems <5 cm dbh. Live

AGC distributed evenly across size classes in the *Quercus* spp., *T. canadensis*, and other forest types, with slightly greater C stores in the 40–60 cm dbh classes (Fig. 2a, c, d). The *L. tulipifera* forest type stored the majority of live AGC in stems >50 cm dbh, especially in stems >100 cm dbh (Fig. 2b). The mean live AGC stored in stems >100 cm dbh in the *L. tulipifera* forest type was 2.6 times greater than the all-site mean.

Across sites, 59% of dead AGC was stored in logs, 40% in snags, and 0.8% in stumps. Mean dead AGC distributed evenly across the largest-diameter size classes for all sites, with slightly greater C stores in pieces <60 cm diameter (Fig. 3e). Three of the forest types exhibited similar patterns, the exception being the *T. canadensis* forest type, with peaks of dead AGC storage in pieces with maximum diameters of 50–60 and 80–90 cm (Fig. 3c). Logs and snags contributed equally to dead AGC stores in the 50–60 cm diameter class, while dead AGC was exclusively composed of snags for the 80–90 cm diameter class.

DISCUSSION

Our findings add to a growing literature that suggests old-growth forests have greater C storage potential than previously realized (Luyssaert et al. 2008, Lichstein et al. 2009). The mean live AGC estimate for Mid-Atlantic old growth was 154 Mg C/ha, a near match to the IPCC (2006) cool temperate moist biome default value (155 Mg C/ha), but high (139 Mg C/ha; Burrascano et al. 2013) and low (377 Mg C/ha; Keith et al. 2009) relative to other global analyses of this biome. Notably, the Mid-Atlantic sites have exceptionally large pools of dead AGC relative to other old forests in the eastern United States (Fisk et al. 2002, Keeton et al. 2011, Hoover et al. 2012). The highest values previously reported in the East were 27 Mg C/ha in northern hardwood forests in Michigan, USA (Fisk et al. 2002). At 46 Mg C/ha, these Mid-Atlantic forests have dead wood stores close to the C-rich *Pseudotsuga* forests of the Pacific Northwest, USA (32–160 mg C/ha; Janisch and Harmon 2002, Smithwick et al. 2002) or *Nothofagus* forests in Chile (29–195 Mg C/ha; Carmona et al. 2002). These temperate moist forests share mechanisms that ultimately lead to high C densities, notably high-severity disturbances that transition large quantities of live biomass to dead, slow tree decomposition rates, and a long absence of land use (Keith et al. 2009).

O horizon C and leaf litter estimates were lower than observed in other temperate old-growth forests, and were relatively minor stores among the measured pools in the Mid-Atlantic. The mean C stock estimate for the leaf litter pool in the old-growth stands was slightly lower than that described for New England, USA old growth (6 vs. 9 Mg C/ha; Hoover et al. 2012). SOC estimates for other old-growth temperate forests were three to four times higher than our measurements (Mund 2004, Hoover et al. 2012); however these estimates were to 10–20 cm depths, versus an average

collected depth of 2.8 cm for the Mid-Atlantic sites. The O horizon is an important, but minor component of total SOC estimates, which average 228 ± 136 Mg C/ha for temperate deciduous forests globally (Jobbagy and Jackson 2000). We emphasize that the sum of C stocks measured in this study does not equate to total ecosystem C; rather, it is a characterization of several previously underestimated C pools.

Variation in C stores between old-growth sites is at least as important as the average in terms of understanding the C storage capacity. We observed high variability in both the live and dead AGC pools. Live AGC was more related to differences in morphological and physiological traits among dominant species than with maximum stand age. Indeed, forests dominated by *L. tulipifera* stand out as having the highest live AGC estimates and greatest density of large stems (Figs. 1a, 2). *L. tulipifera* trees are generally considered to be among the tallest and largest in eastern deciduous forests (Burns and Honkala 1990), and their mortality creates gaps large enough for conspecific recruitment. In so much as they are large, long-lived colonizers with rapid growth rates and a strong dependence on large gaps to regenerate, *L. tulipifera* in old growth is analogous to *Pinus strobus* L. in the northeastern U.S. (Frelich and Reich 1995), *Pseudotsuga menziesii* (Mirb.) Franco in the Pacific Northwest, USA (Franklin and Dyrness 1973), and *Eucalyptus regnans* in southeastern Australia (Keith et al. 2009). High productivity couples with low wood decomposition rates in these C-dense global forests (Keith et al. 2009); unlike those species, *L. tulipifera* has a high wood-decomposition rate (Harmon et al. 1986), which may explain why they had among the lowest dead AGC stores (Fig. 1b). The self-promotional regeneration and rapid decomposition rates of *L. tulipifera* as paired life-history traits offer an explanation for the negative relationship between live AGC and dead AGC. This forest type is characterized by multigenerational dominance of *L. tulipifera*, and so *L. tulipifera* likely both dominates the canopy as well the dead wood pool. The stands with high dead AGC and low live AGC capture a recent turnover in the canopy; conversely, stands with high live AGC but low dead AGC highlight the absence of a canopy disturbance and the *L. tulipifera* decay rate.

Dead AGC was also highly variable across the old-growth sites (Appendix: Table A1), representing the highest and the lowest published estimate of dead AGC for old growth in the eastern United States. The lowest value previously reported was 14 Mg C/ha in northern hardwoods in the Adirondack Mountains of New York, USA (Keeton et al. 2011). Unlike live AGC, dead AGC density was correlated to maximum age among the old-growth sites. Theoretical models suggest that dead AGC will increase with stand age as forests transition from mature to old growth. As the stand transitions into late succession, dead AGC increases because of canopy mortality (Harmon 2009). It is tempting to attribute a causal relationship between oldest tree age and dead

AGC; however, these sites do not represent a true chronosequence; rather a sample of primary forests, presumably at or near their maximum potential C storage. Chronologies of living trees provide age of one generation, making it difficult to capture the highly dynamic, non-static nature of old-growth forest ecosystems.

It is possible that these high dead wood estimates in certain stands are attributable to disturbances aside from typical gap dynamics. For example, chestnut blight (*Cryphonectria parasitica*) restructured the overstory composition in these forest in first half of the 1900s, by effectively eliminating adult *Castanea dentata* from a landscape once classified primarily as oak–chestnut (Braun 1950). Widespread mortality of *C. dentata* led to high volumes of dead wood, and what was not harvested still remains on the landscape today due to its remarkably slow decomposition rates (Wallace et al. 2001). The presence of dead *C. dentata* may explain the incongruence between stands with the lowest live AGC estimates also having the largest dead AGC pools (Fig. 1). Hemlock woolly adelgid (*Adelges tsugae*) outbreaks in certain old-growth stands dominated by *T. canadensis* are a modern analog to chestnut blight, causing canopy mortality and subsequent large dead wood C inputs (Fig. 3c) in stands with relatively low live AGC stores (Fig. 1). Pests and pathogens may also accelerate the flux into the dead wood pool in secondary forests by causing the mortality of prominent overstory species (e.g., *T. canadensis*, *Fraxinus* spp.; Poland and McCullough 2006).

To understand C trends in these dynamic old-growth forests, focus should be placed on the morphological and life-history characteristics that drive patterns in live AGC, the disturbance history that drives dead AGC, and environmental conditions that affect both pools (Keith et al. 2009). We must consider these mechanisms when comparing C stocks within current old-growth forests, as well as when considering the greater landscape potential. Unlike the old-growth stands, much of the surrounding secondary forests established in old fields with no legacy wood from previous stands. As such, dead wood will be one of the last C pools to develop within most of these secondary forests, especially where timber harvest is present.

Clearly, given the region's land-use legacy, dead wood will accumulate at a different rate in the matrix of maturing forests than it did in remnant old growth. Another less-appreciated factor determining the rate of C accumulation in eastern forests in the United States may be the proliferation of forest pests and pathogens that is occurring as a consequence of economic globalization and climate change (Liebhold et al. 2012, Weed et al. 2013); one upshot of which may be the expansion of the temperate forest C sink via the accelerated production of dead wood and the attendant maintenance of growing space for live C accumulation. In addition, the exceptionally large pools of dead C in

the Mid-Atlantic old-growth sites suggest at the high potential for a species-specific disturbance to transfer C from live to dead pools. Our findings corroborate a spate of recent studies (e.g., Luyssaert et al. 2008, Keeton et al. 2011) that have looked to remnant old growth to show that the broader landscape of secondary forest has the capacity to sequester and store C for many decades (Fig. 1). Our sites build on these studies by showing how different species associations accumulate and distribute C across pools using different strategies, even within a relatively small region, and that dead wood will be a major contributor to total C stores.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-1154.1.sm>