Detrital carbon pools in temperate forests: magnitude and potential for landscape-scale assessment

John Bradford, Peter Weishampel, Marie-Louise Smith, Randall Kolka,
Richard A. Birdsey, Scott V. Ollinger, and Michael G. Ryan

Abstract: Reliably estimating carbon storage and cycling in detrital biomass is an obstacle to carbon accounting. We examined carbon pools and fluxes in three small temperate forest landscapes to assess the magnitude of carbon stored in detrital biomass and determine whether detrital carbon storage is related to stand structural properties (leaf area, aboveground biomass, primary production) that can be estimated by remote sensing. We characterized these relationships with and without forest age as an additional predictive variable. Results depended on forest type. Carbon in dead woody debris was substantial at all sites, accounting for ~17% of aboveground carbon, whereas carbon in forest floor was substantial in the subalpine Rocky Mountains (36% of aboveground carbon) and less important in northern hardwoods of New England and mixed forests of the upper Midwest (~7%). Relationships to aboveground characteristics accounted for between 38% and 59% of the variability in carbon stored in forest floor and between 21% and 71% of the variability in carbon stored in dead woody material, indicating substantial differences among sites. Relating dead woody debris or forest floor carbon to other aboveground characteristics and (or) stand age may, in some forest types, provide a partial solution to the challenge of assessing fine-scale variability.

Résumé : La capacité d'estimer de façon fiable le stockage et le recyclage du carbone dans la biomasse détritique constitue un obstacle à l'établissement du bilan du carbone. Nous avons étudié les réservoirs et les flux de carbone dans trois paysages réduits de forêt tempérée pour évaluer l'ampleur du carbone emmagasiné dans la biomasse détritique et nous avons déterminé si le stockage du carbone dans les débris est relié aux propriétés structurales du peuplement (surface foliaire, biomasse aérienne, production primaire) qui peuvent être estimées au moyen de la télédétection. Nous avons caractérisé ces relations en incluant ou non l'âge de la forêt comme variable indépendante supplémentaire. Les résultats dépendaient du type de forêt. Dans toutes les stations, les débris ligneux contenaient une quantité appréciable de carbone qui représentait ~17 % du carbone aérien, tandis que la quantité de carbone dans la couverture morte était substantielle dans la zone subalpine des montagnes Rocheuses (36 % du carbone aérien) et moins importante dans les forêts de feuillus nordiques de la Nouvelle-Angleterre et dans les forêts mélangées de la partie nord du Midwest (~7 %). Les relations avec les caractéristiques aériennes expliquaient entre 38 et 59 % de la variation dans la quantité de carbone emmagasiné dans la couverture morte et entre 21 et 71 % de la variation dans la quantité de carbone emmagasiné dans les débris ligneux, indiquant qu'il y avait d'importantes différences entre les stations. Dans certains peuplements, la relation entre les débris ligneux ou la couverture morte et les autres caractéristiques aériennes, incluant ou non l'âge du peuplement, offre une solution partielle au défi que représente l'évaluation de la variation à échelle fine

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Introduction

Terrestrial vegetation is a central component of the global carbon cycle, storing over 600 Gt of carbon and annually exchanging approximately 10% of that carbon with the atmosphere (Schimel 1995). Forests contain more than 45% of terrestrial carbon (Bonan 2008), and minor alterations to forest carbon storage or cycling may have substantial impacts on atmospheric carbon dioxide concentrations (CO_2) and the global climate system. As a result, quantifying carbon dynamics in terrestrial systems is a central challenge for ecosystem scientists. Estimates of carbon pools and fluxes

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J. Bradford[1] and R. Kolka. USDA Forest Service, Northern Research Station, 1831 Hwy 169 E, Grand Rapids, MN 55744, USA.
P. Weishampel. University of Minnesota, Department of Soil, Water, and Climate, 1991 Upper Buford Circle, St. Paul, MN 55108, USA.
M.-L. Smith. USDA Forest Service, Legislative Affairs, 201 14th Street, SW, Washington, DC 20250-1130, USA.
R.A. Birdsey. USDA Forest Service, Northern Research Station, 11 Campus Boulevard, Suite 200, Newtown Square, PA 19073, USA.
S.V. Ollinger. Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03820, USA.
M.G. Ryan. USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Avenue, Fort Collins, CO 80523, USA.

[1] Corresponding author (e-mail: jbbradford@fs.fed.us).

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over large areas are essential for generating accurate estimates of carbon balance at scales relevant to management and policy. In its simplest form, net ecosystem carbon balance (NECB) is the difference between net carbon inputs into live biomass and carbon outputs from decomposition of dead biomass. Approaches to quantifying carbon inputs and outputs at large scales include remote sensing, simulation modeling, repeated inventories, and coupling atmospheric CO_2 measurements with simulation models. Remote sensing can provide good estimates of some variables such as aboveground live biomass (Schlerf et al. 2005), net primary production (Turner et al. 2005), and leaf area index (Hall et al. 2005). Furthermore, the resolution of these measurements continues to increase in the spatial (Koukoulas and Blackburn 2005), temporal (Running et al. 2004), and spectral (Ustin et al. 2004) domains. However, these components all focus on aboveground live biomass and production — processes that relate only to carbon inputs and provide limited insight into outputs of carbon, the other half of the NECB equation.

Estimating forest carbon dynamics for large areas will require accurate assessment of carbon cycling and storage in detrital biomass. Detrital carbon pools can be conceptually divided into three components: dead woody debris (DWD), consisting of all woody material both standing and down; forest floor (FF), consisting of litter and the organic layer of the soil; and carbon stored in mineral soil, encompassing soil carbon beneath the FF. Although mineral soil can hold substantial amounts of carbon and has high spatial variability, the size of this carbon pool typically changes very slowly (Schlesinger and Andrews 2000). By contrast, carbon storage and cycling in DWD and FF have been shown to vary substantially across space and time. Previous studies have found that the variation in DWD and FF carbon can relate to stand age (Sun et al. 2004), forest type (Currie and Nadelhoffer 2002), or disturbance history (Tinker and Knight 2000).

Attempts to account for this variability and assess forest NECB at large scales have often relied on simulation models to estimate inputs of carbon and outputs through decomposition of detrital carbon pools (Turner et al. 2004). Such models can be useful for estimating carbon balance but typically rely on site-specific variables, notably stand age and (or) disturbance history, that are not reliably available over large areas. Consequently, although these models may provide insight into very general patterns of carbon storage and cycling, they often do not have the spatial or temporal resolution necessary to accurately characterize spatially detailed carbon dynamics at landscape scales.

Repeated examination of forest inventories is an approach that is useful both for characterizing NECB and for validating remote sensing or modeling estimates of forest carbon balance (Goodale et al. 2002). However, the capacity of inventories to quantify large-scale carbon balance is limited by two factors: (1) although inventories can be spatially distributed over very large extents, they actually measure very small areas, potentially resulting in estimates with very high sampling errors as a consequence of widely distributed samples; and (2) despite some recent efforts to incorporate detrital pools into forest inventories (Bohl and Brandli 2007; Woodall et al. 2008), national-scale inventories are typically focused on quantifying potential timber production or biomass and thus often provide only limited insight into pools of nonlive carbon (Chojnacky and Heath 2002). Likewise, assessing carbon dynamics from direct monitoring of atmospheric CO_2 concentrations can provide insight into the overall balance but only limited information about the mechanisms behind the observed patterns or the specific pools or fluxes that account for important differences.

Because none of these approaches provide all the information necessary to accurately quantify the dynamics of detrital carbon pools, regional- or landscape-level carbon balance is often very roughly estimated. The difficulty of including detrital pools can introduce considerable uncertainty into landscape and regional estimates that could influence the overall assessment of carbon balance. Consequently, developing reliable methods for relating detrital biomass pools to other, more easily measured, forest attributes (including age) would dramatically simplify the challenge of estimating detrital biomass pools at large scales and would be an important advancement toward accurate carbon accounting.

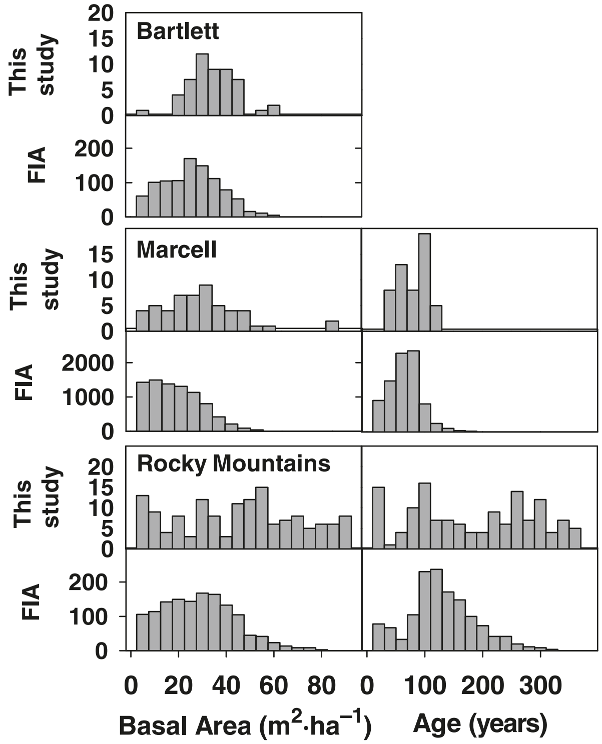
To address this challenge, we examined carbon pools in three temperate forest landscapes, located in Colorado, Wyoming, Minnesota, and New Hampshire, USA. Our objectives were (1) to assess the magnitude of carbon stored in dead woody debris (DWD) and forest floor (FF) by measuring the size of those carbon pools and comparing them with other carbon pools and fluxes, and (2) to determine whether the amount of carbon stored in DWD and FF pools is related to components that can be estimated via remote sensing and whether the size of these pools displays consistent relationships to stand age. Together, these two objectives provide insight into the challenge presented by detrital carbon pools. Objective 1 assesses how much influence variability in detrital carbon pools may have over total forest carbon balance, while objective 2 explores one logical approach to characterizing that variation over heterogeneous forest landscapes. If DWD and (or) FF are found to store substantial carbon and are not correlated with more easily measured processes, then the challenge of accounting for these carbon pools will be both important and difficult. If, on the other hand, detrital carbon pools are strongly linked to production, aboveground biomass, or litterfall, then those processes, which are amenable to estimation via remote sensing or successional forest models, can be used to estimate the dynamics of carbon stored in detrital pools.

Methods

Site description

We quantified carbon pools and fluxes in small landscapes in three temperate forest ecosystem types: northern hardwoods in central New Hampshire (Bartlett Experimental Forest), mixed forests of northern Minnesota (Marcell Experimental Forest), and subalpine Rocky Mountain forests in Colorado and Wyoming (three sites). These landscapes encompass a wide range of forest conditions, and comparison of basal area and age from these plots with data from the US Forest Service's Forest Inventory and Analysis program (FIA 2007) for nearby states indicates that these plots are generally representative of forests in their respective regions (Fig. 1).

Fig. 1. Comparing basal area and age of forest plots used in this study with histograms of Forest Inventory and Analysis (FIA) plots for nearby regions illustrates how plots included in this study are generally representative of forest conditions over a much larger area. FIA data include the following: for Bartlett, all forested FIA plots in New Hampshire and Vermont (*n* = 968); for Marcell, all forested plots in northern Minnesota and Wisconsin in the white–red–jack pine, spruce–fir, maple–beech–birch, and aspen–birch forest types (*n* = 8339); and for Rocky Mountains, all forested plots in Colorado and Wyoming in the fir–spruce and lodgepole pine forest types (*n* = 1372).



At each site, we identified a 1 km by 1 km area for study. Within this square kilometre, we established between 9 and 16 research plots at predetermined locations to avoid biased sampling of the landscape. Established to closely mimic USDA forest inventory and analysis plots, each of our plots consists of four subplots: a center subplot and three satellite subplots located 35 m away at 0°, 120°, and 240°. At the Rocky Mountain sites, we also included three additional plots at each site located just outside the square kilometre that were selected to represent younger forest types (Table 1).

Bartlett Experimental Forest

The Bartlett Experimental Forest consists primarily of old-growth northern hardwoods with *Fagus grandifolia* Ehrh. (American beech), *Betula alleghaniensis* Britt. (yellow birch), *Acer saccharum* Marsh. (sugar maple), and *Tsuga canadensis* (L.) Carrière (eastern hemlock) as the dominant species. Even-aged stands of *Acer rubrum* L. (red maple), *Betula papyrifera* Marsh. (paper birch), and *Populus tremuloides* Michx. (trembling aspen) occupy sites that were once cleared. *Picea rubens* Sarg. (red spruce) stands cover the highest slopes, and *Pinus strobus* L. (eastern white pine) is confined to the lowest elevations. Climate at Bartlett is characterized by warm summers with highs frequently above 32 °C and cold winters with lows often reaching –34 °C. Average annual precipitation is 127 cm, well distributed throughout the year, and snow typically accumulates to depths of 1.5 to 2 m in winter. Soils at Bartlett are Inceptisols and Spodosols, developed on glacial till derived from granite and gneiss. The soils are moist but generally well drained and shallow in places. In the late nineteenth century, the lower third of Bartlett (where this study was conducted) was heavily logged, while upper portions were only partially logged. Natural disturbances at Bartlett include hurricanes (1938) and ice storms (1998) and occasional small-scale wind storms. Variation in stand characteristics and annual net primary production across the Bartlett landscape have been reported by Ollinger and Smith (2005).

Marcell Experimental Forest

The Marcell Experimental Forest consists of a mosaic of upland forests and peatlands; plots in this project were limited to upland areas. Upland vegetation at Marcell is highly variable among watersheds depending on forest management practices and soils, is generally dominated by *Populus tremuloides* and *Populus grandidentata* Michx. (bigtooth aspen) but contains substantial components of northern hardwoods and other incidental species including *Betula papyrifera* and mixed pine stands of *Pinus resinosa* Ait. (red pine), *Pinus strobus* L. (white pine), and *Pinus banksiana* Lamb. (jack pine). The climate of the Marcell Experimental Forest is subhumid continental, with wide and rapid diurnal and seasonal temperature fluctuations. Forests at Marcell were generally logged in the early twentieth century, with the exception of lowland conifer forests. In the last several decades, disturbances at Marcell have consisted of occasional timber harvesting operations and infrequent wind storms that cause incomplete tree mortality on very small patches. The average annual air temperature is 3 °C, with extremes of –46 °C and 38 °C; average January and July temperatures are –15 °C and 19 °C, respectively. Upland soils at Marcell are mainly loamy sands or fine sandy loams (Nichols and Verry 2001).

Rocky Mountain forests

We examined three sites in the subalpine Rocky Mountains: The Fraser Experimental Forest, located near Fraser, Colorado; the Glacier Lakes Ecosystem Experiment Site, located near Centennial, Wyoming; and the Niwot Ridge AmeriFlux study site, located near Nederland, Colorado. Tree species consist primarily of *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) and *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) at higher elevations and *Pinus contorta* Dougl. ex Loud. (lodgepole pine) at lower elevations, with minor components of *Pinus flexilis* James (limber pine) and *Populus tremuloides* at Niwot. Climatic conditions at all sites are characterized by cold and relatively long winters (Table 1). Glacier Lakes boasts the highest elevation and precipitation, lowest temperatures, and largest average snowpack, whereas Niwot is the lowest, warmest, and driest of the three sites. Disturbance history varies among the sites. While only minor scattered logging occurred at Glacier Lakes over 100 years ago, Niwot was essentially clear-cut

Table 1. Climatic conditions, sample size, and general stand structure for forested landscapes in New Hampshire, Minnesota, Colorado, and Wyoming.

Site	Latitude	Longitude	Mean annual temp. (°C)	Mean annual precip. (mm)	Elevation (m)	Plots	Max. age (years)	Density (stems·ha^{-1})	Height (m)	LAI (m^2·m^{-2})
Bartlett, NH	44°2′39″N	71°9′56″W	6	1270	275	12	—	625	19	3.4
Marcell, MN	47°30′N	93°28′W	3	785	425	16	69	930	15.6	3.2
Fraser, CO	39°04′N	105°52′W	0	737	3100	12	200	832	11.4	4.3
Glacier Lakes, WY	41°22′N	106°15′W	–2	1000	3180	12	179	725	10.5	6.5
Niwot, CO	40°02′N	105°33′W	4	800	3050	12	133	1726	10.3	3.6

Note: Age, density, height, and leaf area index (LAI) estimates are based on all plots. Age was not measured at Bartlett.

between 1900 and 1910, and selective clearcuts were made at Fraser in the 1950s. Wildfires and insect outbreaks are important natural disturbances in these systems, and Fraser is the only site with evidence of large recent fires; Fraser experienced a widespread stand-replacing fire in approximately 1685. In addition, lodgepole pine trees in the lower region of the Fraser site are currently heavily invaded by mountain pine beetles (*Dendroctonus ponderosae*) and are experiencing severe mortality.

Data collection and compilation

Standing tree biomass

We recorded species, location, and diameter at breast height (DBH, 1.37 m) for all live and dead trees within 8–10 m (depending on site) of subplot centers. Aboveground biomass in foliage, branches, and stems was estimated from allometric equations at Bartlett (Ribe 1973; Whittaker et al. 1974; Hocker and Earley 1983), Marcell (Perala and Alban 1993), and the Rocky Mountain sites (Table S1[2]). Biomass was calculated for live and dead trees, saplings, and seedlings and converted to carbon by dividing by 2 (Schlesinger 1997; Fahey et al. 2005). Leaf area was estimated at Bartlett from litterfall collections (see below); at Marcell using a LAI-2000 Plant Canopy Analyzer under early morning, overcast conditions, above the understory vegetation at four locations on each subplot (values corrected for conifer component; LI-COR Biosciences, Lincoln, Nebraska); and at the Rocky Mountain sites from allometric equations for projected leaf area (Table S1[2]). Complete tree cores were collected from the three largest trees on each subplot at Marcell and the Rocky Mountain sites and averaged to estimate stand age. Age was not examined at Bartlett.

Dead woody debris

DWD carbon was calculated as the sum of carbon in coarse woody debris and carbon in standing dead trees (described above). Coarse woody debris was measured along three to four 7.5–15 m line intercept transects at each subplot. Diameter and decay class (Arthur and Fahey 1990) were recorded for all logs with diameter greater than 7.5 cm. Log diameters were transformed into cross-sectional areas by assuming that class I–III logs are circular, whereas class IV and V logs are oval shaped with ratios between short and long axis of 1:4 and 1:5, respectively (D. Tinker and D. Knight, unpublished data), and plot-level volume was corrected for angular distribution of logs (Brown 1971). Total down wood biomass per transect was estimated by multiplying volume by species-specific wood specific gravity for live wood and deadwood (Jenkins et al. 2003).

Forest floor

FF biomass was quantified by harvesting all organic material (other than standing biomass) above mineral soil within three 30 cm by 30 cm quadrats located 7 m from subplot center at 60°, 160°, and 300°. Only the organic soil layer was harvested in these FF samples, and the boundary between FF and mineral soil was determined by the presence of mineral-derived material, evaluated at each sampling location. Large tree roots (>3 mm) were not included in these samples, but fine roots were not removed. FF samples were dried at 65 °C to remove all moisture, weighed, and the entire sample was ground, mixed, and subsampled for analysis of total carbon and nitrogen content on a CHN analyzer. To calculate FF carbon, we multiplied the FF mass by the measured carbon concentration for each sample quadrat. Total area-based carbon stored in the FF was estimated by averaging the carbon content of the three samples in each subplot, corrected for the proportion of surface covered in boulders, which was estimated from boulder intercept measurements on the CWD transects.

Carbon fluxes

We calculated production as the sum of live tree and sapling biomass increment over the past 10 years, litterfall, and understory production. To quantify biomass increment, 5–10 trees in each subplot at Marcell and the Rocky Mountain sites were cored for increments spanning at least the past 10 years, and basal area increment was calculated from radial increments. At Bartlett, basal area increment was estimated by annually repeated DBH measurements of all trees greater than 10 cm in diameter, with measurement locations marked on each tree to ensure accuracy. Individual-tree biomass increments were calculated as the annual increase in above- and belowground biomass, and these values were summed to yield subplot-level estimates. Litterfall was estimated by collecting litter twice a year in three to five ~0.15 m^2 traps per subplot. Aboveground biomass of understory grasses and forbs was collected at peak biomass (late summer) from three 0.25 m^2 quadrats per subplot at the Rocky Mountain sites and three 0.5 m^2 quadrats at Marcell. Litterfall and understory samples were dried, weighed, and analyzed for carbon content. Net primary production was calculated as the sum of tree biomass increment, litter-

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[2] Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3922. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 2. Carbon pools (Mg C·ha^{-1}) in each small forested landscape with comparable previous estimates.

	Bartlett			Marcell			Rocky Mountains		
	This study			This study			This study		
	Mean	SE	Others	Mean	SE	Others	Mean	SE	Others
Aboveground live	95.6	4.6	120[a]	65.8	9.0	24–400[d]	81.1	8.4	25–126[g]
Snags	11.5	1.3	6.5[a]	9.6	2.2		14.0	4.2	7–64[h]
Coarse wood	9.0	0.7	3–20[b]	7.9	2.0	2–14[e]	13.5	1.7	
Forest floor	18.8	1.3	5–40[c]	6.6	0.6	7–20[f]	60.8	4.9	12–34[i]

[a] Fahey et al. (2005).

[b] Currie and Nadelhoffer (2002) and Chojnacky and Heath (2002).

[c] Gosz et al. (1976), Covington (1981), Federer (1984), Fahey et al. (2005), and Ollinger et al. (2002).

[d] Scheller and Mladenoff (2004).

[e] Grigal (2007).

[f] Bell et al. (1996), Grigal and Ohmann (1992), and Smith and Heath (2002).

[g] Pearson et al. (1984), Arthur and Fahey (1992), and Binkley et al. (2003).

[h] Fahey (1983), Arthur and Fahey (1992), Busse (1994), and Kueppers et al. (2004).

[i] Fahey (1983) and Arthur and Fahey (1992).

fall, and understory production, and did not include fine root production.

Statistical analysis

To quantify the relationship between net primary production, aboveground live biomass, leaf area index, and age (only at Marcell and Rocky Mountains) and the amount of carbon stored in DWD or FF we generated a set of candidate statistical regression models based on four different functional forms (Table S2[2]). These statistical models related DWD or FF carbon to independent variables using a linear function, a power function, an exponential rise to a maximum, and an equation that is a combination of exponential decay and exponential rise to a maximum that allows DWD or FF carbon to decline at young ages and increase at older ages, a result observed in some previous studies (Covington 1981; Duvall and Grigal 1999). To characterize the relationship between DWD or FF carbon and stand age, we also incorporated maximum age into the models as an independent variable (Table S2[2]). All independent variables were tested for colinearity, and combinations of independent variables with coefficient of determination >0.7 (tolerance <0.3) were not used simultaneously. Plots (each consisting of four subplots) were used as the experimental unit, and all variables were transformed as necessary to achieve normality.

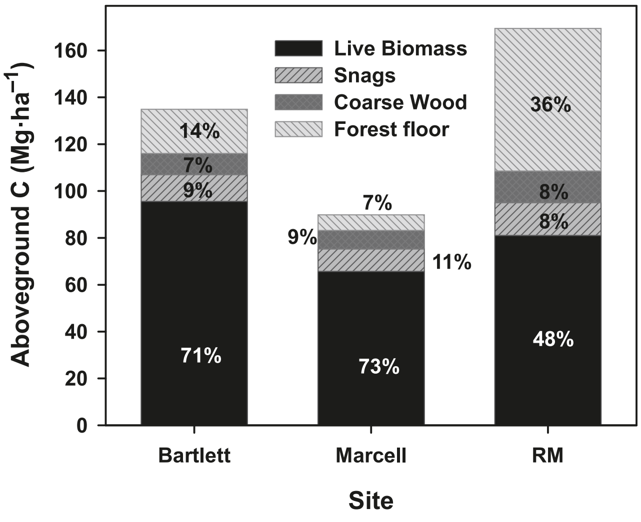
Each competing model for predicting the caron stored in DWD or FF can be conceptualized as a hypothesis about drivers of those detrital carbon pool dynamics. To compare these statistical models, we used a method that employs likelihood theory to determine the extent to which each model was supported by the data (Burnham and Anderson 2001). We used the corrected form of Akaike information criterion ($\mathrm{AIC_c}$) as an indicator of the information lost when a statistical model approximates truth. We ranked models according to the support for each model contained in the observed data and calculated model weights (w_i), which are interpreted as the weight of evidence in favor of the best model in comparison with other models in the candidate set of models. This model selection method has the advantage that it uses models created prior to data analysis and contains a penalty for each parameter included, thereby minimizing the chance of obtaining spurious results (Burnham and Anderson 2001). Because we were interested in examining the strength of relationships between either DWD or FF carbon and overstory attributes (leaf area, production, biomass, and age), we plotted the best model using each attribute individually, as long as the best model was statistically significant ($p < 0.1$) and accounted for at least 5% of the variation in the response variable. We also identified and discussed the overall best model for predicting either DWD or FF carbon from any combination of overstory attributes, both with and without age. Model selection results for all convergent models examined are presented in Table S3.[2]

Results

Objective 1: magnitude of carbon stored in DWD and FF

Aboveground live biomass was the largest carbon pool in all three forest types, storing roughly 81 Mg C·ha^{-1} at the Rocky Mountain sites, only 66 Mg C·ha^{-1} at Marcell, and 96 Mg C·ha^{-1} at Bartlett (Table 2). At Bartlett and Marcell, live biomass accounted for over 70% of total aboveground carbon, compared with only 48% at the Rocky Mountain sites (Fig. 2). In all forests DWD consisted of substantial components of both snags (standing dead trees) and down wood (fallen trees and branches), although carbon stored in snags was consistently slightly higher than that stored in down wood. At Bartlett, DWD stored approximately 20.5 Mg C·ha^{-1}, consisting of 11.5 Mg C·ha^{-1} from snags and 9.0 Mg C·ha^{-1} from down wood. Marcell contained 9.6 Mg C·ha^{-1} in snags and 7.9 Mg C·ha^{-1} in down wood, for a total of 17.4 Mg C·ha^{-1} in DWD. At the Rocky Mountain sites, DWD contained roughly 27.5 Mg C·ha^{-1}, of which 14.0 Mg C·ha^{-1} was in snags and 13.5 Mg C·ha^{-1} was in down wood. The mean proportion of aboveground carbon stored in DWD was quite consistent across these three forest types, ranging from 16% in the Rocky Mountains and Bartlett to 19% at Marcell. Unlike DWD, the amount of carbon stored in FF varied dramatically among sites. At Bartlett and Marcell, FF contained 18.8 and 6.4 Mg C·ha^{-1}, respectively, which accounted for an average of 14% and 7.4% of total

Fig. 2. Aboveground carbon in forested ecosystems partitioned into live biomass, standing dead trees, down coarse woody debris, and forest floor biomass. Percentages indicate mean proportion of total aboveground carbon stored in each component (not the proportion of means) and illustrate how the importance of detrital carbon pools (dead woody material and forest floor material) varies substantially among forest types.



aboveground carbon. By contrast, FF at the Rocky Mountain sites contained an average of 61 Mg C·ha^{-1}, accounting for 36% of total aboveground carbon.

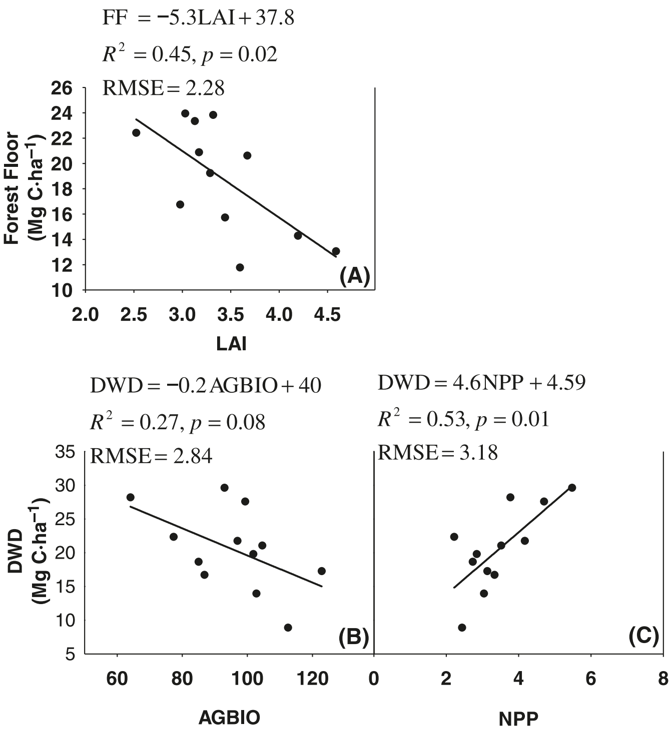
Live biomass increment was the largest carbon flux we measured, ranging from 1.4 Mg C·ha^{-1}·year^{-1} at the Rocky Mountain sites to 2.0 Mg C·ha^{-1}·year^{-1} at Marcell and 2.3 Mg C·ha^{-1}·year^{-1} at Bartlett. Annual litterfall rates were relatively consistent, from 0.8 Mg C·ha^{-1}·year^{-1} at the Rocky Mountain sites to 1.0 and 1.1 Mg C·ha^{-1}·year^{-1} at Marcell and Bartlett, respectively. Understory production, not measured at Bartlett, was 0.3 and 0.6 Mg C·ha^{-1}·year^{-1} at Marcell and the Rocky Mountain sites, respectively. Net primary production (NPP) can be approximated from the sum of live biomass increment, litterfall, and understory production, yielding estimates of 2.9, 3.4, and 3.5 Mg C·ha^{-1}·year^{-1} at the Rocky Mountain sites, Marcell, and Bartlett, respectively. Although this estimate of production does not include fine root production and is therefore an underestimation of total NPP, it does characterize the spatial patterns in NPP that can be related to DWD and FF.

Objective 2: relationship of carbon in DWD and FF to stand structure and age

Bartlett

The amount of carbon in FF at Bartlett was significantly related to leaf area (Fig. 3) in a linear model that accounted for 45% of the variability in FF carbon (p = 0.02); this model was identified as the best model for estimating FF carbon at Bartlett (Table 3). Other models for FF carbon at Bartlett that received substantial support from the data included a power function with leaf area and two models with both leaf area and aboveground biomass (Table S3[2]). The amount of carbon in DWD at Bartlett was linearly related to aboveground biomass (p = 0.08) and production (p = 0.01) in relationships that explained 27% and 53% of the variability in DWD carbon, respectively (Fig. 3). The best model for estimating DWD carbon at Bartlett used aboveground biomass in a power function modified by production (p = 0.006) to explain 71% of the variability in DWD carbon (Table 3). The data also indicate substantial support for other models of DWD carbon at Bartlett, notably linear models with leaf area, aboveground biomass, and production (Table S3[2]).

Fig. 3. Relationships at the Bartlett Experimental Forest between carbon stored in forest floor (FF) and leaf area (LAI) (A) and carbon stored in dead woody debris (DWD) and live biomass (AGBIO) (B) and net primary production (NPP) (C). Only relationships with $r^2 > 0.05$ and $p < 0.1$ are shown.



Marcell

At Marcell, stand structure was weakly related to the amount of carbon in both FF and DWD, and those relationships were not appreciably enhanced by including age. FF carbon was related to leaf area in a power functions accounting for 36% (p = 0.01) of the variability in FF carbon (Fig. 4). A power function with both leaf area and production generated the best model for predicting FF carbon from stand structure at Marcell, with a coefficient of determination of 38% (p = 0.01; Table 3). The amount of carbon in FF at Marcell was not significantly related to stand age alone, and the best age-related model for FF at Marcell used a power function with age, production, and leaf area to account for 39% (p = 0.01) of the variability in FF carbon — only a very minor increase over the best model without age. The data also suggested substantial support for models using leaf area and biomass in a power function, as well as models with leaf area alone (Table S3[2]).

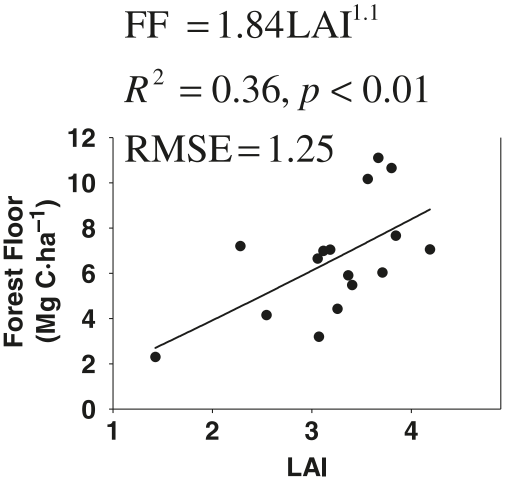
The amount of carbon stored in DWD at Marcell was not

Table 3. Best statistical regression models for the amount of carbon in forest floor (FF) and dead woody debris (DWD) as a function of aboveground biomass (AGBIO), leaf area index (LAI), net primary production (NPP), and stand age (AGE).

	Dependent variables	Model	AIC_C	w_i	p	RMSE	r^2
Bartlett							
FF	Aboveground characteristics	$FF = -5.265LAI + 36.7806$	34.7	0.36	0.02	2.28	0.45
DWD	Aboveground characteristics	$DWD = NPP \times 164.3AGBIO^{-0.735}$	36.3	0.31	0.006	3.53	0.71
Marcell							
FF	Aboveground characteristics	$FF = LAI \times 2.3NPP^{-0.1}$	28	0.23	0.01	1.07	0.38
	Including age	$FF = LAI \times 2.37AGE^{-0.01+NPP}$	28	0.47	0.01	1.07	0.39
DWD	Aboveground characteristics	$DWD = NPP \times 38.9LAI^{-1.78}$	80.3	0.31	0.07	6.29	0.21
	Including age	$DWD = 1.25AGE^{0.6}$	82.4	0.23	0.29	3.10	0.08
Rocky Mountains							
FF	Aboveground characteristics	$FF = AGBIO \times 1.6LAI^{-0.46}$	215	0.48	<0.0001	14.99	0.53
	Including age	$FF = AGBIO \times 1.7AGE^{-0.06NPP}$	225	0.45	<0.0001	20.20	0.59
DWD	Aboveground characteristics	$\ln DWD = 4.9\,e^{-0.09AGBIO} + 5.5(1 - e^{-0.008AGBIO})$	–12.1	0.85	<0.0001	0.54	0.50
	Including age	$\ln DWD = 4.27\,e^{(-0.03AGE)} + 40.7(1 - e^{-0.0003AGE})$	–20	1.00	<0.0001	0.50	0.60

Note: AIC_c, corrected Akaike information criterion; w_i, model weight; RMSE, root mean squared error; r^2, coefficient of determination.

Fig. 4. Relationship between carbon stored in forest floor (FF) and leaf area (LAI) at the Marcell experimental forest. Only relationships with $r^2 > 0.05$ and $p < 0.1$ are shown.



significantly related to any individual stand structural variables (Table S3[2]). The best DWD model at Marcell used leaf area in a power function modified by production to account for 21% of the variation in DWD carbon ($p = 0.07$; Table 3). Age was not related to the amount of carbon in DWD at Marcell, and incorporating age along with stand structure variables did not improve model performance.

Rocky Mountains

The carbon stored in FF at the Rocky Mountain sites was significantly related to both aboveground live biomass and leaf area with power functions explaining 53% and 36% of the variability in FF carbon, respectively ($p < 0.001$; Fig. 5). The best non-age model for FF carbon at the Rocky Mountain sites used a power function with leaf area modified by live biomass to explain 60% of the variability in FF carbon ($p < 0.001$; Table 3). Model weights suggest that other models using aboveground biomass and leaf area have some support in the data (Table S3[2]). Taken alone, stand age explained 25% of the variation in FF carbon ($p < 0.001$) at the Rocky Mountain sites in a power function, and the best age-related model incorporated both live biomass and production into that age relationship and accounted for 60% of the variation in FF carbon ($p < 0.001$), although alternative models with age and other independent variables received some support in the data (Table S3[2]).

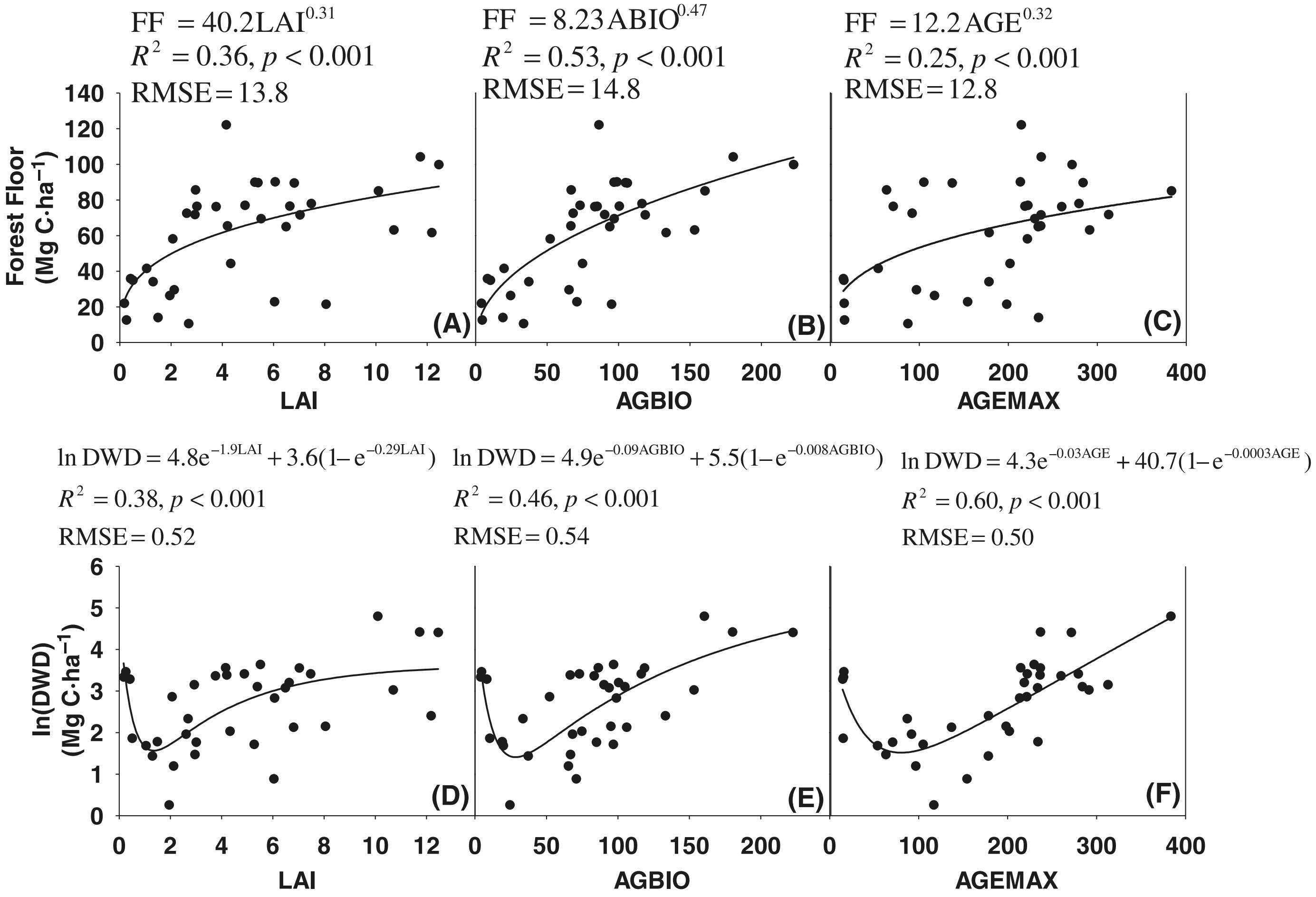
The carbon stored in DWD at the Rocky Mountain sites was related to both leaf area and aboveground biomass, as well as stand age (Fig. 5). Relationships between DWD carbon and leaf area, live biomass, and stand age were all best explained by the functional form containing terms for both exponential decay and exponential rise to a maximum. The leaf area and live biomass relationships accounted for 38% and 50% of the variability in DWD carbon ($p < 0.001$ for each), respectively, and the live biomass relationship was identified as the best non-age predictive model for DWD at the Rocky Mountain sites (Table 3). The age relationship was slightly stronger, accounting for 60% of the variation in DWD carbon ($p < 0.001$) and was the best age-related model that we examined (Table S3[2]). Alternative models for predicting DWD carbon at the Rocky Mountain sites, either without or with age, received only very limited support in the data (Table S3[2]).

Discussion

Influence of DWD and FF on net ecosystem carbon balance

Our results quantify detrital carbon pools in temperate forests and assess the potential for estimating these pools from more routinely measured variables. The size of detrital pools provides insight into the influence of each pool on total ecosystem carbon balance and thus on the need for accurately measuring that pool at landscape and larger scales. The amount of carbon released through decomposition of DWD and FF in comparison with estimates of carbon uptake via live biomass increment, litterfall, and understory production provides a measure of the potential for DWD and FF to influence the net ecosystem carbon balance (NECB). If DWD and FF decomposition is dramatically smaller than the other components of NECB, then it is reasonable to conclude that carbon release from these pools occurs primarily in episodic events such as fires or timber harvest and that

Fig. 5. Relationships between carbon stored in forest floor (FF) and leaf area (LAI) (A), live biomass (AGBIO) (B), and stand age (AGEMAX) (C), and carbon stored in dead woody debris (DWD) and leaf area (D), live biomass (E), and stand age (F) at three subalpine Rocky Mountain forest sites. Only relationships with $r^2 > 0.05$ and $p < 0.1$ are shown.



dynamics of these pools can be adequately estimated with simple models the remainder of the time. Our estimates of carbon stored in detrital pools are generally consistent with those of previous studies (Table 2) and indicate that substantial carbon is stored in DWD in all three forest types.

Combining these estimates of carbon stocks with previous work on DWD decay rates suggests that DWD decomposition has an important influence over NECB. Prior studies of DWD decomposition have reported decay rates ranging from near zero to more than 2 Mg C·ha^{-1}·year^{-1}, depending on forest type and time since disturbance (Harmon et al. 2004; Sun et al. 2004). Estimates of the decay rate for coarse wood in forests similar to Bartlett and Marcell may range between 0.02 and 0.05 year^{-1} (Laiho and Prescott 2004); this range of values, combined with our estimates of deadwood stocks, implies decomposition of 0.4–1.0 Mg C·ha^{-1}·year^{-1} at Bartlett and 0.3–0.8 Mg C·ha^{-1}·year^{-1} at Marcell. In subalpine forests, DWD decay rates range from 0.006 year^{-1} (Brown et al. 1998) to 0.05 year^{-1} (Laiho and Prescott 2004), suggesting decomposition of between 0.16 and 1.4 Mg C·ha^{-1}·year^{-1}. Although these decomposition estimates do not incorporate potential differences in decomposition rates as a consequence of tree species (Laiho and Prescott 2004; Sun et al. 2004), these general values for decomposition are substantial in comparison with the magnitude of carbon inputs by production in all three forest types, implying that these detrital pools have the potential to impact NECB and that assessing spatial and temporal variability in these pools would strengthen carbon accounting efforts.

Carbon stored in FF, by contrast, appears to be important in ecosystem carbon pools only in the Rocky Mountain forests. Published estimates of FF decay indicate a hypothetical range between 0.004 year^{-1} (Aber and Melillo 1991) for heavily decayed material and 0.05 year^{-1} for more recent leaf litter (Prescott et al. 2000*a*). This range would imply a FF decomposition of 0.08–0.94 Mg C·ha^{-1}·year^{-1} at Bartlett and 0.03–0.32 Mg C·ha^{-1}·year^{-1} at Marcell, compared with 0.24–3.0 Mg C·ha^{-1}·year^{-1} at the Rocky mountain sites. At Bartlett and Marcell, these estimates suggest that FF decay is relatively small compared with carbon inputs and DWD decomposition and is therefore unlikely to be a major driver of overall ecosystem carbon balance. FF carbon may be higher at the Rocky Mountain sites than at both Bartlett and Marcell because of a combination of low temperatures that inhibit decomposition during much of the year (Table 1) and low water availability during warm months than restricts decomposition when temperatures are warm (Monson et al. 2002). FF dynamics are influenced by the balance between the quality and quantity of litterfall inputs and climate-driven decomposition outputs (Prescott et al. 2000*b*). As a result, low decomposition rates could allow substantial FF accumulation over the long fire-free intervals observed in these subalpine forests, and other work has indicated that roughly 75% of the FF mass at our Rocky Mountain sites is substantially decayed humus material (Bradford et al. 2008). Low litter quality in the coniferous forests of the Rocky Mountains, compared with the deciduous or mixed forests of Marcell and Bartlett, may also contribute to the large FF carbon pool in the Rocky Mountain sites. In addition, earthworms are present at Marcell, likely contributing to the estimates of low carbon storage in FF (Alban and Berry 1994; Hale et al. 2005) and explaining why our estimates are lower than those of other published studies in similar forests (Table 2).

Estimating landscape-scale variation in detrital carbon pools

As landscape and ecosystem ecologists work to characterize ecosystems over large areas, spatial variability and spatial pattern have emerged as important determinants of how site-level observations should be scaled to larger areas. Consequently, identifying tools that characterize variability in ecosystem processes at intermediate scales within individual landscapes is a focal challenge. We examined the possibility of estimating the carbon stored in FF or DWD from stand structural characteristics, and our results indicate some potentially promising relationships between easily measured stand structure variables (leaf area, live biomass, and production) and either FF or DWD carbon. Our best models account for more than half of the variability in DWD carbon at Bartlett, and in both FF and DWD carbon at the Rocky Mountain sites.

On the other hand, some detrital pools were not well related to aboveground characteristics, notably DWD carbon at Marcell. An additional potential challenge illustrated by our data is the inconsistency in both the form of predictive relationships and the independent variables identified as most useful. At both Bartlett and Marcell, the best FF carbon model included leaf area, which is not surprising, since FF biomass is related to the balance between inputs from litterfall and outputs from decomposition (Prescott et al. 2000*b*). However, FF carbon displayed a positive relationship to leaf area at Marcell, in contrast to a negative relationship to leaf area at Bartlett, which may be a consequence of local fertility variations among plots impacting FF decomposition rates more than leaf production rates, thus creating low FF carbon stocks in areas with highest tree production and leaf area. At the Rocky Mountain sites both live biomass and leaf area were used to estimate FF carbon. The stand structural characteristics that were most related to DWD carbon also varied among sites; DWD carbon was most related to live biomass at the Rocky Mountain sites, compared with production and aboveground biomass at Bartlett and production and leaf area at Marcell.

Although DWD and FF are generally accepted as substantial carbon pools in forest systems, few previous studies have attempted to directly relate either pool to more easily measurable carbon pools or fluxes (although see Keane et al. 2006). Prior work has documented relationships between FF biomass and topographic position (Little et al. 2002), land management history (McGee et al. 1999; Prescott et al. 2000*a*), or stand age (Covington 1981; Yanai et al. 2003; Hall et al. 2006) but rarely stand structure. Our result of modest relationships between FF carbon and stand structure at all sites suggests that stand structure may be useful in characterizing spatial variability in FF carbon dynamics in some forest types. By contrast, we found only very marginal relationships between DWD carbon and stand structure at Marcell, a result that is consistent with previous work. Harmon et al. (2001) found no relationship between DWD biomass and other stand structural variables. Chojnacky and Heath (2002) used FIA plots in Maine to relate down deadwood biomass to basal area of standing live and dead trees and found a relationship explaining only 10% of down deadwood biomass, a finding that is in contrast to our results for estimating DWD at Bartlett ($r^2 = 0.71$). The weak relationships between DWD carbon and aboveground characteristics at Marcell indicates that DWD carbon at Marcell is effectively decoupled from current stand structure, perhaps as a consequence of variability in stand history (i.e., harvesting versus natural disturbance) within the landscape (Pregitzer and Euskirchen 2004).

The amount of carbon in both DWD and FF was moderately related to stand age at the Rocky Mountain sites, a result that has been documented in other studies for both FF (Covington 1981; Hall et al. 2006) and DWD (Fahey 1983; Carmona et al. 2002). However, FF and DWD carbon were essentially unrelated to age at Marcell. Our estimates of stand age were derived from tree cores, as opposed to historical disturbance information. Previous work at these sites has illustrated that age derived from cores is related to disturbance history, although tree cores tend to overestimate stand age in young stands and overestimate it in old stands (Bradford et al. 2008). Since FF and DWD may be influenced more by disturbance history than by the age of existing trees, this discrepancy may partially explain the disconnect between the amount of carbon in FF or DWD and age in this study. Alternatively, the weak relationships between DWD or FF carbon and age may be a consequence of plot selection; our plots were located on a systematic grid and were not selected from even-aged monocultures. Although this design potentially limits our ability to detect age- or stand-structure-related patterns, it does provide a realistic assessment of the capability of those variables to characterize landscape-scale variability in the uneven-aged, mixed forests that account for over 90% of global forest area (Dixon et al. 1994). Statistical models that estimate DWD or FF carbon based on age may work when applied to reasonably homogeneous stands selected across an extremely wide range of conditions, but we found only marginal relationships between DWD or FF carbon and tree age in mixed-age and mixed-species forests, potentially casting doubt on the utility of these commonly used relationships for detailed landscape-scale carbon accounting. The substantial differences we observed among the three sites suggests that forest type and possibly stand history play important roles in mediating the relationship between DWD or FF carbon and stand structural attributes. Developing useful general relationships will require further studies that are specifically designed to assess the influence of forest type and stand history.

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