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Late-successional and old-growth forest carbon temporal dynamics in the Northern Forest (Northeastern USA)

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ABSTRACT

Comprehensive data on the capacity and rates of change for carbon pools in managed and unmanaged forests is essential for evaluating climate change mitigation options being considered by policy makers at regional and national levels. We currently lack real and long-term data on forest carbon dynamics covering a wide range of forest management practices and conditions. Because of this, selecting the best policies for conserving forest carbon must rely on forest growth and yield models such as US Forest Service (USFS) Forest Vegetation Simulator (FVS) to predict the future forest carbon impacts of management actions. FVS may underestimate the capacity of older stands to accumulate carbon because the model relies on USFS Forest Inventory and Analysis data that lack data from late-successional and old-growth (LSOG) stands. Improving these models will increase the likelihood of selecting policies that successfully use forests to reduce atmospheric carbon. From 1995 to 2002, Manomet Center for Conservation Sciences conducted research on 65 10 m by 50 m permanent plots to evaluate forest structure (standing live and dead trees, and down coarse woody material) in LSOG stands across northern Maine. We re-measured these plots in 2011 to assess long-term carbon sequestration trends in LSOG stands of common forest types in the Northern Forest region for above ground alive, standing dead, and coarse woody material carbon pools. Late-successional (LS) and Old-growth (OG) aboveground live carbon (C) stocks were very high relative to regional mean C stocks (2.0–2.5 times the mean), LS plots were accumulating aboveground live C at a positive rate (0.61 Mg ha^{-1} year^{-1}), while C stocks on OG plots are declining ($-$0.54 Mg ha^{-1} year^{-1}). This change is driven by the presence of beech bark fungus (*Nectria* sp.) that is leading to mortality in larger diameter American beech (*Fagus grandifolia*) trees. We also found that the Northeast Variant of the Forest Vegetation Simulator is not a reliable predictor of aboveground live carbon accumulation rates in Northeastern LS and OG stands. This work provides important baselines for understanding the role of older forests and forest management within climate change mitigation strategies in the northeastern US. Late-successional and old-growth forests can play an important role in mitigating climate change, but understanding and quantifying natural disturbance risk to forest carbon stocks is critical for successful implementation of mitigation strategies. Further, regional forest carbon models will need calibration to accurately predict carbon accumulation rates in older forests.

1. Introduction

Global forests have a crucial role for addressing climate change because they store substantial amounts of carbon and are a leading source of emissions due to deforestation (Keith et al., 2009; Yingchun et al., 2012). In the US, the forest products sector also plays a key role by sequestering the equivalent of 10% of domestic greenhouse gas (GHG) emissions (Birdsey et al., 2006; Woodbury et al., 2007). Emerging carbon markets and regional climate change policies now allow emitters of GHGs to offset their emissions through carbon sequestration projects. Forest-based offsets hold great potential in the carbon marketplace, but their role has been limited by quantification uncertainty and concerns over risk of carbon (C) loss caused by natural disturbances (Galik and Jackson, 2009; Hurteau et al., 2009). There has also been the perception that mature forests are destined to achieve a steady state with respect to net exchange with the atmosphere (Jarvis, 1989). Recent studies, however, suggest that old forests may continue to serve as net carbon sinks for longer than previously thought (Luyssaert et al., 2008; Keith et al., 2009; Keeton et al., 2011); hence, the assumption that old forests in the northeastern US (including both late-successional (LS) and old-growth stands (OG)) are net emitters of

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C deserves reexamination. Unmanaged stands, and particularly late-successional and old-growth (LSOG) forests, may sequester an increasing amount of landscape C given the current age distribution of the northeastern U.S. forest.

Less than 1% of the northeastern forest is in an old-growth state (i.e., primary forest) (Davis, 1996) and long-term data on C stock changes over time within LSOG forests is lacking (Keeton et al., 2011). Our review of the stand establishment years (subtracting "stand age" from "measurement year") of the most recent measurement years (2008–2012) of US Forest Service (USFS) Forest Inventory and Analysis (FIA) data for New York and New England (USA) indicates that 0.4% (19 of 4921 plots) date from before 1862; with the oldest plot dating to an establishment around 1795. This small percentage of old forest plots represents a much smaller area than was present in the pre-settlement forest, and thus landscape C stocks are likely much lower now than 300 years ago. In Wisconsin (USA), the current forest C stocks in forests have only recovered to 49% of pre-settlement levels (Rhemtulla et al., 2009). The same conclusion would likely be made for the northeastern US forest, given an older, pre-settlement age-class distribution than current day (Lorimer, 1977; Keeton et al., 2011).

Forests younger than OG but beyond the typical rotation length of commercially managed forests of 50–100 years are often referred to as LS or "mature" forest (Frelich, 2002). LS forest stands represent a larger land area than OG in the northeastern US, but are still limited. In Maine, stand ages from 50–100 years are generally considered "economically mature" and stands over 100 years old are considered LS (Whitman and Hagan, 2007). However, Whitman and Hagan (2007) identified some stands over 80 years of age with LS structural characteristics. The fraction of FIA plots established between 80 and 150 years ago (i.e., representative of our study data) is 31% (1,534 of 4,921 plots). Of these plots, only 8% are greater than 100 years old, indicating that in the absence of harvest or stand-replacing disturbance a large number of plots will be entering a LS condition.

Comprehensive data on the storage capacity and rates of change of C in LSOG forests is essential for evaluating the full range of forest C mitigation and management options and as part of life cycle C accounting. Given the large forest area that may enter the LS class in the northeastern US, understanding the forest carbon dynamics within this age class becomes critical for forest management decision making. The work presented here builds on prior research in the region and provides a long-term (>15 years) evaluation of forest C stocks and rates of change using permanent sample plots in LS and OG stands in Maine (USA). These data are invaluable for assessing forest growth and yield models such as the USFS Forest Vegetation Simulator (FVS) to determine how well they predict the future forest C impacts of management actions. Most models like FVS may underestimate the capacity of older stands to accumulate carbon because data from old forest was lacking (Liu et al., 2011). Emerging forest carbon offset protocols also require field-based benchmarks to evaluate management trajectories. Our goals were to: (1) assess long-term carbon sequestration trends in LSOG stands of common forest types in the Northern Forest region of the northeastern USA; and (2) evaluate the ability of the USFS FVS model to predict carbon biomass accumulation in LSOG stands.

2. Material and methods

From 1995 to 2011, we measured and re-measured permanent plots to evaluate the impacts of harvest regimes on forest structure (standing live and dead trees, and down coarse woody material (DCWM)) on stands across Maine, including partially harvested, LS, and OG stands (Hagan and Grove, 1999; Gunn and Hagan, 2000). Re-measurement of these plots provided a unique opportunity to evaluate changes in carbon stocks to compare trends in carbon accumulation between LS and OG (LSOG) stands. LSOG plots were established in northern hardwood (hardwood) types and spruce-fir (softwood) types (Eyre, 1980). Northern hardwood plots were characterized by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). Spruce-fir plots were characterized by spruce (*Picea* spp., most *P. rubens*, with occasionally stems of *P. glauca*) and balsam fir (*Abies balsamea*).

OG plots were located in The Nature Conservancy's 2,000-ha Big Reed Forest Reserve, northern Piscataquis County, Maine (centered at 46°20′N and 69°5′W). Prior research by Fraver et al. (2009) on the Reserve determined there was no evidence of stand replacing disturbance on the plots they studied during the last 120–280 years (Fraver et al., 2009). LS plots were located in Kibby and Skinner Townships, northern Franklin County, Maine (centered at 45°25′N and 70°31′W) on private forestland with over 100 years of harvest history. Although these plots had evidence of prior logging, they were classified as LS stands because they lacked evidence of natural or human stand-replacing disturbances based on field observations (e.g., numerous tip-up mounds, fire scars, and even-aged distribution). Stand establishment for LS plots ranged from 80 to 150 years prior to the first measurement. Establishment dates are based on reviews of historical stand maps, logging records, and tree increment cores from the plots. Whitman and Hagan (2007) describe in greater detail the methods we used for distinguishing between LS and OG stands.

2.1. Aboveground forest carbon sampling

In 2011 we re-measured LS plots ($n = 23$) and OG plots ($n = 35$) at the two sites. The plots were permanently monumented and mapped by using GPS (±10 m) and recording nearby landmarks. OG plots were first measured in 1995. LS plots were first measured from 1998 to 2002. In 2011 we re-measured LS plots ($n = 23$) and OG plots ($n = 35$) at the two sites. The plots were permanently monumented and mapped by using GPS (±10 m) and recording nearby landmarks. OG plots were first measured in 1995. LS plots were first measured from 1998 to 2002. We established 10 m × 50 m plots in stands with large trees and a lack of obvious harvest disturbance evidence. The LS pots were established by choosing a starting point and a random cardinal direction for the orientation of the plot from the start point. We chose starting points that allowed the entirety of the plot to be >75 m from road and harvest block (existing and proposed) edges. Plots were large enough to encompass areas of closed canopy and natural tree fall gaps typical of LS and OG stands. Stand sizes in Kibby and Skinner Townships (for LS plots) were generally too small to allow for more than one plot per stand. OG plots were clustered in groups of six plots separated by at least 250 m. Six plot clusters were distributed throughout the 2000 ha forest reserve.

Except for diameters of down coarse woody material (DCWM), the original measurement methods were used in re-measurement (e.g., Gunn and Hagan, 2000): diameter of each live and dead trees (⩾8 cm DBH) was measured at breast height (DBH) and decay stage was assigned for the entire tree (Table 1); for each piece of DCWM (>10 cm mid-point diameter, >30 cm in length) length and mid-point diameter was measured and a decay stage and piece type (i.e., log, top, and whole tree) was assigned (Table 1). Initial DCWM diameters were measured using a linear tape measure held horizontally over the log. The re-measurements used calipers. The initial measurement method may overestimate mid-point diameter compared to the re-measurement method (see Section 3.2). Moreover, in 1995, the dimensions of the entire DCWM piece were recorded if any portion of it fell on the plot. Using the ordinary

Table 1
Qualitative decay class descriptions for standing trees and dead coarse woody material (adapted from Harmon et al., 1986).

Decay class	Standing trees	Down coarse woody material (DCWM)
1	Live and healthy	Bark firmly attached, exposed wood has fresh color (not weathered), wood beneath bark is solid, small twigs and branches intact, log elevated on support points/branches
2	Live but in decline	Bark flaking and not firmly attached, bare wood has weathered appearance, kicking the log may knock off bark but wood is solid, small twigs mostly absent, larger branches mostly intact, log elevated but may sag slightly
3	Dead, bark intact, small twigs and branches intact, wood solid	Bark mostly absent, surface of bare wood will flake off or shred when kicked, log is firm, but some areas of the wood are soft when pressed with a foot, large branches mostly absent, log sagging considerably, much of it on the ground
4	Dead, bark flaking, small twigs absent, large branches intact, wood solid	Log no longer a solid and intact piece, log will crush or break into large pieces when kicked, log shape becoming oval or flattened, wood is very spongy when presses with a finger, powder wood may be present, nearly all of log on ground
5	Bark mostly absent, nearly all branches absent, wood still fairly solid	Log oval or flat, generally powder wood, log very soft, can be easily broken up using your fingers, entire log is on the ground
6	Wood becoming soft in places, very top of tree has separated from bole, some flaking of bole will result from kicking tree	Not applicable
7	Bole considerably decomposed, mid-portion of tree has collapsed, kicking bole may result in large chunks falling from bole, wood generally soft	Not applicable
8	Most of bole has collapsed, wood generally soft and powdery, wood can be easily crumbled by hand	Not applicable

expansion factor of the reciprocal of plot area to scale biomass of each piece to a per hectare value would lead to biased estimates under the initial field protocol (Gove and Van Deusen, 2011). During re-measurement we measured both the full dimensions of each piece (e.g., the initial protocol) and the dimensions of the portion on the plot, but present the analysis using the full dimensions here for consistency. DCWM biomass volume per ha was then determined using new unbiased expansion factors described in detail in Appendix A.

2.2. Determining carbon stock change drivers

We compared aboveground C biomass stock changes between sampling periods by C pool type (Wilcoxon Rank Sum). We used coefficients from Jenkins et al. (2003) and Harmon et al. (2011) to convert species, volume, and decay class data to estimate C volume per ha (MgC ha^{-1}). Dead standing tree biomass estimates did not account for limb or top loss. We fit linear models to predict annual change in aboveground standing C storage using the following variables: stand age (LS vs. OG), stand type (softwood vs. hardwood), initial carbon stocks (total live C per ha), initial beech basal area, and mean DBH. We initially fit a full model containing simple effects of all variables listed, then used backward selection using the Akaike Information Criterion (AIC; Akaike, 1974; Burnham and Anderson, 2002) to select a final predictive model.

2.3. Forest carbon growth modeling

We used the USFS Forest Vegetation Simulator (FVS) to model carbon accumulation using the initial plot measurements to assess whether projected results from this model were consistent with our empirical results. FVS is the most widely accepted growth model within current forest carbon offset standards and relies on NE-TWIGS (Hilt and Teck, 1989) as the growth and yield model to derive carbon biomass estimates (Dixon, 2002). These growth and yield models are based on data collected by the USFS's Forest Inventory and Analysis (FIA) unit from the 1950s through the 1980s. FIA data for LS and OG forests in the northeastern US are scarce because LSOG forests are regionally scarce. Therefore, the forest growth models (i.e., FVS and NE-TWIGS) and remote sensing-derived maps (e.g., Zheng et al., 2008) currently used to guide decision-making regarding carbon stocks may underestimate the capacity of older stands to accumulate carbon because both depend on FIA data in which LSOG stands are scarce (Ingerson and Loya, 2008). Re-measured plot data allow rigorous model evaluation for LSOG stands. We used the Northeast Variant of the FVS growth and yield model to simulate growth from the initial measurement year to 2011. Because re-measurement periods were unequal between plots, and no other common divisor of re-measurement period existed, we used a one-year projection interval within the model. FVS includes extensive options for site-specific calibration. The need for calibration to obtain reliable projections has been widely documented both for conventional timber management purposes (Hamilton., 1994; Vandendriesche and Haugen, 2008; Ray et al., 2009) and for carbon estimation (MacLean et al., 2013). However, we lacked independent calibration data for LS and OG stands and so used the default parameter values for modeling. Modeled aboveground live tree carbon stocks (MgC ha^{-1}) and growth rates (MgC ha^{-1} year^{-1}) were compared with values from the field measurements. All statistical analyses were conducted in R (R Core Team, 2012; Wessa, 2013).

3. Results and discussion

3.1. Carbon stock change trends: standing carbon

In 2011, both LS and OG mean aboveground live carbon stocks were 2.0–2.5 times greater than the mean stocks for forest types typical of the region (Table 2). Individual stands exceeded the mean carbon stocking by as much as 5.2 times. Mean LS aboveground live C stocks in 2011 had increased since the initial inventories (Table 2; $W = 21$, $p < 0.001$). However, mean 2011 OG aboveground live C stocks had declined (but the median increased) since the initial inventory in 1995 (Table 2; $W = 439$, $p = 0.04$). Mean annual change in LS aboveground live C was 0.61 MgC ha^{-1} year^{-1} (SD = 0.69, Table 2), while C was lost from aboveground live OG stocks at a mean annual rate of −0.54 MgC ha^{-1} year^{-1} (SD = 1.31, Table 2). The observed decrease in dead standing C stocks on both LS and OG plots was not statistically significant (LS $W = 119$, $p < 0.58$; OG $W = 439$, $p = 0.66$) and remained constant as an overall percentage of the total standing C volume on OG plots (Table 2). Dead standing carbon stocks in 2011 represented 10.22%

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Table 2
Summary data (mean and SD) of late successional (LS) and old growth (OG) measured plots for historical (OG 1995; LS 1998–2002) and re-measurement (LS and OG 2011) periods. Regional low and high mean carbon (C) stocks are presented for comparison with measured plots (Climate Action Reserve Forest Project Protocol Version 3.2, Assessment Area Data, Northeast Supersection, based on USFS Forest Inventory and Analysis data; February 2, 2010).

Age class	Sample year (s)	Quadratic mean diameter (cm) (SD)	Mean trees ha^{-1} (SD)	Mean aboveground live MgC ha^{-1} (SD)	Mean aboveground dead standing MgC ha^{-1} (SD)	Mean aboveground DWM MgC ha^{-1} (SD)	Mean total aboveground MgC ha^{-1}	Mean annual MgC ha^{-1} AGL C stock change[a]	Low regional mean C stock (MgC ha^{-1})	High Regional Mean C Stock (MgC ha^{-1})
Old growth	1995	22.47 (3.17)	661.14 (164.78)	111.25 (36.01)	20.09 (17.61)	16.69 (11.31)	148.03	–	44.6	45.63
Old growth	2011	21.44 (3.33)	596.00 (143.72)	102.63 (34.49)	18.71 (13.10)	11.48 (4.70)	132.82	−0.54	44.6	45.63
Late successional	1998–2002	20.15 (4.56)	922.61 (490.73)	89.53 (29.91)	14.44 (15.78)	6.17 (3.34)	110.14	–	44.6	45.63
Late successional	2011	21.73 (4.75)	837.39 (486.56)	96.79 (30.55)	11.02 (7.32)	5.05 (3.13)	112.86	0.61	44.6	45.63

[a] AGL, aboveground live.

of total aboveground standing stocks in LS plots compared to 15.42% in OG.

Backward selection using AIC led to a final linear model that included only initial carbon stocks and initial American beech basal area as predictors:

$$\Delta C = 1.237 - 0.0008C_0 - 0.1249B$$

where ΔC is annual carbon accumulation (MgC ha^{-1} $year^{-1}$), C_0 is initial carbon stock (MgC ha^{-1}), and B is initial basal area of American beech (m^2 ha^{-1}). High plot-to-plot variability led to a rather low R^2 (0.368). Although model selection was information-theoretic, we note that the model would be highly significant if judged by frequentist standards ($p < 0.0001$ for the overall model, and both effects individually significant at $p = 0.01$). This model result indicates that starting American beech volume was an important predictor of lost C volume over time, corroborating that aboveground live tree carbon stock decline in OG is likely a result of a large portion of American beech trees in the region infected with the *Nectria* sp. fungus. Old growth aboveground live C volume of American beech declined on the study plots from 15% to 7% of total C volume. Statewide in Maine, live tree volume of American beech has declined 14% since 2003 (McCaskill et al., 2011). Beech bark disease (BBD), the result of sap feeding by an introduced beech scale insect (*Cryptococcus fagisuga*) that allows lethal fungal infections by *Neonectria ditissima* and *Neonectria faginata*, reached the Big Reed study area between 1935 and 1945 (Morin et al., 2007). An episode of high mortality in American beech occurred in northern Maine (including the Big Reed study area) from 2003 to 2006, likely the result of a combination of drought and BBD (Kasson and Livingston, 2012). Mortality within the OG plots was likely exacerbated by the presence of larger diameter trees that often experience greater decline and mortality from BBD (see Morin et al., 2007). We did not evaluate regeneration within the plots, but such an evaluation would be necessary to understand the long-term forest C response to this disturbance event. If American beech reclaims the space created by the mortality, then it is unlikely that forest stocks would recover to 1995 levels. The presence and relative abundance of sugar maple and other shade tolerant species within these plots will play a role in the future structure of these stands. The risk of C loss from a known disturbance agent like BBD emphasizes the importance of either planning for that possibility in forest carbon project development (e.g., contributing to C buffer pools or buying insurance) or managing to mitigate that risk (Galik and Jackson, 2009; Hurteau et al., 2009).

LSOG forest C stocks of the plots sampled in 2011 were greater than the regional mean for all stands types and ages (Table 2). Even with the recent C volume lost from the aboveground live pools, OG plots were 2.3 times greater than the regional mean for similar forest types. Our measured aboveground live C stocks are consistent with recent measurements by Hoover et al. (2012) of old-growth forest C stocks in northern hardwood stands in Maine. Hoover et al. (2012) reported mean stocks of 114 MgC ha^{-1} ($n = 4$) compared to our mean of 102 MgC ha^{-1}. We measured dead standing stocks in OG plots that were more than two times the mean measured by Hoover et al. (2012). When the aboveground live and dead standing pools are considered together, total mean C was comparable to Hoover et al. (2012) at 121 MgC ha^{-1}. This shows that the carbon carrying capacity for these stands is quite high (and on par with other regional estimates) even with a recent disturbance. Keeton et al. (2011) report regional (Maine, New Hampshire, and New York) means for OG biomass volumes that were generally higher than our data and Hoover et al. (2012). Though Keeton et al. (2011) acknowledge the wide range of biomass volumes they observed across the region, particularly for OG plots in Maine ($n = 17$). However, our LS data are within the reported

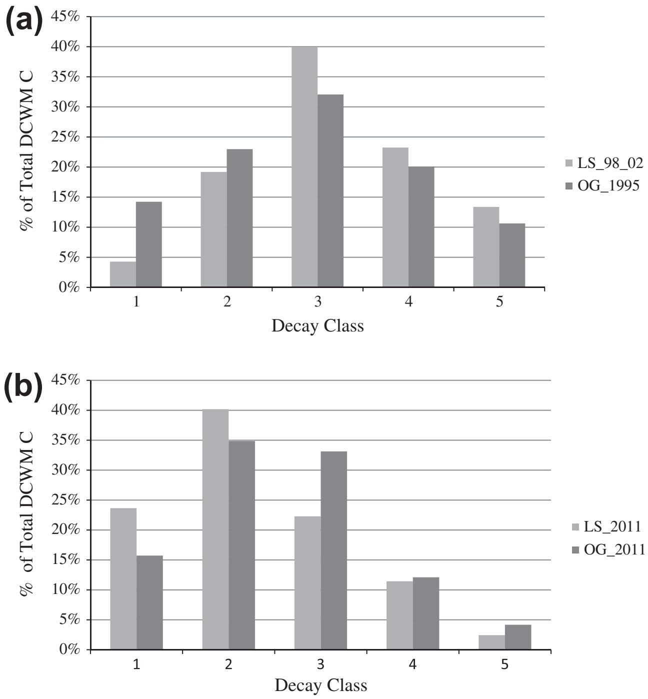

Fig. 1. Decay class distribution (% of total) for down coarse woody material (DCWM) carbon (C) volumes for (1b) historical LS (LS_98_02) plots measured between 1998 and 2002 and OG (OG_1995) plots measured in 1995; and (1b) re-measured LS (LS_2011) and OG (OG_2011) plots measured in 2011. See Table 1 for description of decay classes.

values for "mature" forests in Maine and more broadly within the region.

3.2. Carbon stock change trends: dead and down carbon

Total DCWM C pools declined in OG plots from the initial measurements to 2011 ($W = 481$, $p = 0.005$) but did not significantly change on LS plots ($W = 193$, $p = 0.09$). DCWM C pools represented 9% of OG and 4% of LS aboveground total carbon volume in 2011 compared to 12% and 6% in the initial measurements (Table 2). Mean total DCWM C volume in OG plots was more than two times greater than the mean total volume LS plots within measurement periods (Table 2). However, methodological differences are likely responsible for some of the difference in DCWM C pools between measurement years. Initial measurements from 1995 to 2002 were made using diameter tape measures held over the width of a DCWM piece, whereas final measurements in 2011 were made using calipers. Ocular estimates made with a tape measure held over the DCWM piece are biased toward overestimating the piece diameter compared to a caliper (A. Whitman, pers. obs), which led to higher C volume estimates (Table 2). Additionally, earlier crews tended to identify more DCWM pieces than the 2011 field crew sampled, particularly on OG plots (e.g., 1520 pieces in 1995 vs. 1138 pieces in 2011). Hence, we have high confidence about within year comparisons and less confidence about between measurement comparisons.

The pattern of C distribution across decay stages differed between measurements and varied slightly between LS and OG. For both LS and OG, the initial measurements had a greater percentage of total C biomass in Decay Classes 4 and 5 than the re-measurements in 2011 (Fig. 1a and b), perhaps which may also be a result of the potential observer bias described above. For the initial measurements, the decay class distribution on LS plots was similar to OG plots, with the exception of Decay Class 1. Most of the C volume for both age classes was contained in Decay Class 3. In the re-measured plots from 2011, a greater percentage of LS DCWM C volume was in Decay Class 1 (24%) and a greater percentage OG DCWM C volume increased in Decay Class 2 and decreased in Decay Classes 4 and 5 (Fig. 1a and b).

Properly accounting for C stocks in the dead standing and DCWM pools should show how the dead above-ground C mitigates near-term loss of aboveground live C stocks, particularly when the disturbance does not involve combustion. However, the between-year methodological differences make it difficult to confidently evaluate whether accounting for DCWM C pools could demonstrate a mitigating effect for the above ground live pools. Since the BBD disturbance does not result in combustion, and there was no harvest salvage, most of the resulting mortality probably remains on the forest floor or has been incorporated into below-ground C pools.

3.3. FVS model and old forest dynamics

LS aboveground live C stocks increased since the initial measurements. The USFS FVS growth model was consistent with the increasing trend, but the modeled growth was poorly correlated with observed changes in carbon stocks for both LS and OG stands (LS stands, Spearman's $r = 0.05$, $p = 0.83$; OG stands, Spearman's $r = 0.16$, $p = 0.37$; Fig. 2). FVS generally over-predicted increases in carbon stocks for LS plots and greatly overestimated increases in carbon stocks for OG plots (Fig. 2). The somewhat better predictive output for LS stands was likely because only 3 of 23 LS plots had American beech present. Hence, the LS plots would not have been susceptible to the species-specific disturbance that led to mortality on the OG plots. Even so, the tendency for FVS to over predict carbon accumulation in LS plots was counter to our initial hypothesis, and to the results of MacLean et al. (2013) who found that uncalibrated FVS tended to under predict carbon accumulation for FIA plots across the northeastern United States. Local calibration of FVS is often necessary to achieve high accuracy estimates even in common forest types and age classes (e.g. Ray et al., 2009; MacLean et al., 2013), so it is unsurprising that predictions of carbon stocks of LSOG forest would be inaccurate without

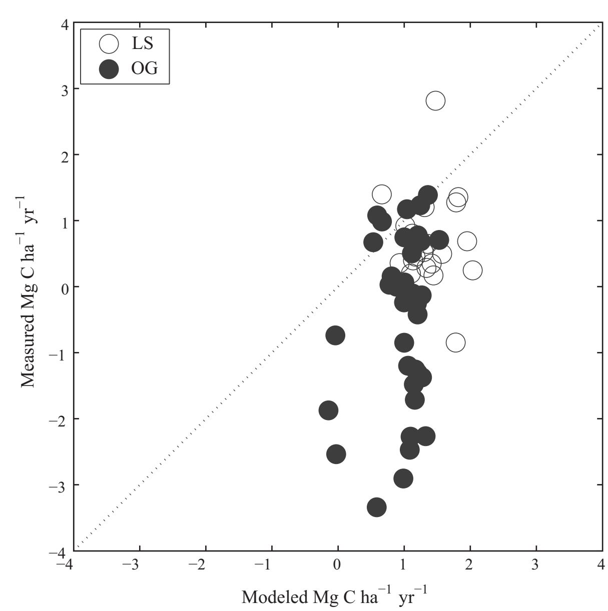

Fig. 2. Late-successional (LS) and old-growth (OG) measured aboveground live carbon accumulation rates (MgC ha^{-1}) plotted against modeled accumulation rates using the Northeast Variant of FVS.

calibration. However, because of the relative rarity of the LS and OG development stages, there is a lack of calibration data available for LSOG forests. Enhancement of the projection ability of FVS may require targeted data collection on re-measured plots in such forests, especially if the age distribution of the northeastern forest shifts toward older stands on some ownerships and projection of stands into older age classes becomes necessary to model short- to mid-range business-as-usual scenarios for forest carbon offset projects.

Explicit incorporation of natural disturbance risk is essential for potential carbon losses to be appropriately accounted for in models. For example, if the *Nectria* spp. fungus remains common throughout the northeastern U.S., the capacity of Northern Hardwood LS and OG stands to sustain prolonged carbon gain could be reduced if American beech is abundant in a given stand. To accurately describe LSOG carbon dynamics, FVS would require modifications that include beech bark disease scenarios.

4. Conclusions

Our results show that the capacity for older forests to store C is more than two times the current average stocking. LS stands were continuing to accumulate aboveground C, though OG stands declined largely because of a widespread natural disturbance. Recent harvest trends (from 2003 to 2008) in Maine have reduced average stand diameters for maple/beech/birch forests (McCaskill et al., 2011), so LS and OG forest area is not likely to increase without additional incentives for private landowners to create such structure (Maine's forests are 96% privately-owned). Even though FIA plot data shows large number of plots in 80–100 year range, timber harvests will target those stands. Encouraging the development of LSOG forests will likely improve the climate change mitigation benefits of forests in the northeastern US (Seidl et al., 2012; Burrascano et al., 2013). Such a forest management strategy will be beneficial even when the full emissions implications of the full forest product sector are taken into account in a life cycle analysis (Gunn, Unpublished Data).

Increasing aboveground forest C stocks through the conservation of older forests also comes with risk that might not be detected by current modeling tools such as FVS, particularly in LSOG forests. Natural disturbance can lead to significant C loss, but is not necessarily catastrophic (Goetz et al., 2012). The risk of forest C loss is influenced by at least three factors: 1) the severity, duration, and frequency of natural disturbances, including fire, insect damage and severe weather; 2) the response of trees to increasing atmospheric CO_2 concentrations and changes in climatic conditions; and, 3) landowner behavior (Galik and Jackson, 2009). While landowner behavior can be addressed through legal mechanisms, greater understanding of C loss risk based on changing natural disturbance regimes in a warming climate (e.g., increased risk of ice storms, microbursts, and fire related to severe summer droughts) will support both carbon offset project development and policies that seek to use forests as part of a regional climate mitigation strategy.

Natural disturbance regimes and climate change could greatly enhance or reduce the carbon storage capacity of northeastern US forests (Groffman et al., 2012). Quantification of this risk for different forest types and age classes will be an important area of climate change mitigation research. Calibration and improvement of existing forest growth and yield models will help us better predict possible carbon storage trajectories. Continued monitoring of LSOG forests using permanent plots will provide vital data for model calibration and evaluation, and for detecting impacts of disease and climate change on existing and future potential carbon sinks.

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Appendix A. DCWM volume calculations

As Gove and Van Deusen (2011) show, when DCWM attributes are measured for an entire log, and the log is included in a sample whenever any portion of the log is included in a fixed-area plot, estimates of the DCWM attributes are biased if the usual fixed plot estimators are used to expand the attributes of the sample to per hectare values. Gove and Van Deusen (2011) present an unbiased estimator appropriate to this protocol (their "sausage method") when the fixed-area plot is circular. Here, we develop an unbiased estimator that can be used when the fixed-area plot is any convex polygon (including a rectangle as used in the field work for this study).

Consider the situation in Fig. A1. A piece of DCWM of length L_i (m) and orientation θ_i is tallied on a plot of area $a_{nominal}$ (ha). We assume only that the plot is of a convex shape, with its area and configuration fixed in advance, and with its center (or other unique point) located at random. Now, consider the shape, area, and orientation of the inclusion zone for this piece, defined as the region where the plot center can land and the piece will be included. This inclusion zone evidently has an area a_i equal to $a_{nominal}$, plus the length of the piece multiplied by the projection of the plot onto an axis perpendicular to θ_i:

$$\alpha_i = a_{nominal} + \frac{L_i proj(a \perp \theta_i)}{10,000}$$

where the factor of 10,000 converts m^2 to ha. Following logic similar to that employed in derivations for line intersect sampling, we either make the design-based assumption that the orientation of the plot is determined at random (Kaiser, 1983), or that the

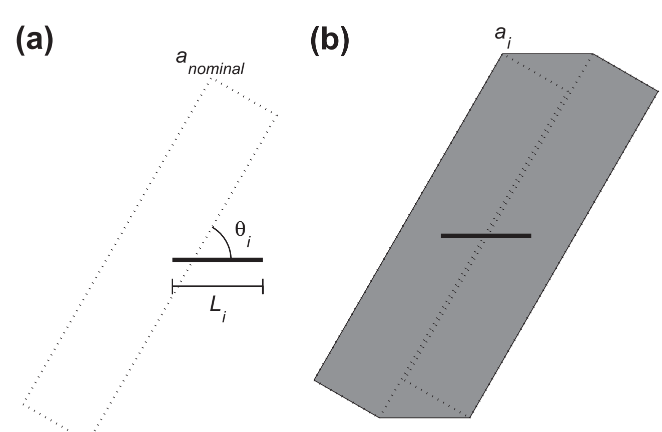

Fig. A1. A piece of down coarse woody material intersected by a rectangular plot (a), and its corresponding inclusion zone (b).

pieces of DCWM are oriented at random (De Vries, 1973, 1986). Now, a powerful result in geometry states that the expectation over θ_i of the projection of the plot equals the circumference of the plot c divided by π (Kendall and Moran, 1963, p. 58). Therefore, we may calculate the expected value of the inclusion zone area for the DCWM piece as:

$$E[a_i] = a_{nominal} + \frac{cL_i}{10,000\pi}$$

and $1/E[a_i]$ provides an unbiased expansion factor for the piece, akin to the "unconditional" estimator of Kaiser (1983) for line intersect sampling. In the field protocol used in this study, which employed a 10×50 m plot, $a_{nominal}$ = 0.05 ha and c = 120 m.

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