Forest Ecology and Management 266 (2012) 108–114

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Benchmark carbon stocks from old-growth forests in northern New England, USA

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ARTICLE INFO

Article history:
Received 6 September 2011
Received in revised form 3 November 2011
Accepted 4 November 2011
Available online 1 December 2011

Keywords:
Old-growth forests
Forest carbon stocks
Second-growth forests

ABSTRACT

Forests world-wide are recognized as important components of the global carbon cycle. Carbon sequestration has become a recognized forest management objective, but the full carbon storage potential of forests is not well understood. The premise of this study is that old-growth forests can be expected to provide a reasonable estimate of the upper limits of carbon storage for similar forest types in comparable site conditions. We sampled old-growth stands in Maine, Vermont, and New Hampshire to establish benchmark values for carbon storage in the forests of northern New England. Our specific objectives were: (1) develop estimates of carbon stocks in key live and dead biomass carbon pools of hardwood and softwood forests in northern New England, (2) compare these values to other estimates of carbon stocks in old-growth forests, and (3) compare data collected from mature second-growth forests to the old-growth benchmark values. Twelve sites in Vermont, New Hampshire, and Maine were sampled to estimate total carbon stocks in aboveground live and dead biomass, down dead wood, forest floor, and soil to 20 cm. Total carbon stocks averaged 216 t/ha for northern hardwoods and 267 t/ha in softwood sites, with 116 and 125 t/ha in the aboveground live tree biomass for hardwoods and softwoods, respectively. Our results showed old-growth softwood averaged about 25% more carbon than old-growth hardwood, primarily due to the higher carbon amounts in the thick forest floors characteristic of old-growth softwood. Old-growth hardwoods supported live biomass carbon stocks similar to those in mature hardwood stands (about 80–120 years old), although forest floor stocks in old-growth were about twice as high (a non-significant difference). Overall carbon stocks in mature second-growth hardwoods were 89% of those in old-growth stands; this difference was not statistically significant. Additional work is needed in mature second-growth softwoods; data were not available for comparison to the benchmarks.

Published by Elsevier B.V.

1. Introduction

The role of forests in the global carbon cycle has been a topic receiving increasing attention (Dixon, 1994; Malhi et al., 2002) and more recently, the role of old-growth forests has been a topic of some debate. Following the ecosystem development theory of Odum (1969), the widely held view in ecology has been that production slows and eventually reaches a steady state or declines over time; this was further elaborated in a review by Ryan et al. (1997). This view of old-growth forests as carbon neutral and therefore unimportant as sinks has recently been challenged with reports describing continued carbon accumulation (Luyssaert et al., 2008; Carey et al., 2001; Phillips et al., 1998); further work provides re-analyses and suggests that the findings of Phillips et al. (1998) are the result of methodological artifacts (Clark, 2002). A recent volume by Wirth et al. (2009a) explores the functions of old-growth forest systems, synthesizing the most recent research results and examining a number of topics related to ecosystem structure and function, including carbon sequestration.

Field and Kaduk (2004) present a comprehensive look at the carbon balance of the Wind River old-growth forest (*Pseudotsuga menziesii–Tsuga heterophylla*) using multiple approaches including eddy flux, biometric measurements, ecosystem process models, and leaf-based models. Each approach showed a forest with high rates of gross primary production and respiration, although estimates of net production from the eddy flux method were higher than those based on biometric measurements. This difference illustrates a key challenge when comparing estimates developed from different approaches: the temporal scales of the measurements are different. Eddy flux observations capture carbon exchange data in real time, while biometric measurements quantify net changes and are often made on time intervals of 5 years or longer. Eddy flux measurements can detect a large sink in a year where production is higher (or respiration is lower) than average due to deviations from average annual precipitation patterns, while biometric measurements integrate this variability over multiple years and decades. Gough et al. (2008) found that while biometric and eddy flux estimates of net ecosystem production differed in any given year in a

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0378-1127/$ - see front matter Published by Elsevier B.V.
doi:10.1016/j.foreco.2011.11.010

deciduous forest in Michigan, with each succeeding year of data the estimates converged; they reasoned that the long-term convergence cross-validated the independent estimates. Field and Kaduk (2004) concluded that the forest may be a substantial sink in any given year, depending on environmental conditions, but that sustained high rates of carbon accumulation were improbable. They argue that it is unlikely that old-growth forests are important for their rate of carbon storage, but rather for their high existing stocks. Because of their high carbon stocks and the likelihood of low accumulation rates, old-growth forests can provide an estimate of the probable upper bound of carbon storage in a given forest type (see Smithwick et al., 2002 for an example of this approach).

The purpose of this study is to use old-growth forest stands as an opportunity to establish benchmark values for forest carbon storage in the forests of northern New England. While numerous studies of old-growth forest remnants exist in the literature (e.g., Tyrrell and Crow, 1994; Orwig et al., 2001; Hale et al., 1999), the majority focus on community structure and rarely provide measurements of standing biomass, and so cannot be used to estimate carbon stocks. Examples of the benchmarking approach that include data on biomass or carbon are Mroz et al. (1985), who characterized two old-growth northern hardwood stands in Michigan, and Smithwick et al. (2002), who collected data from a number of old-growth sites in Oregon and Washington. The premise of these studies is similar: old-growth forests can be expected to provide a reasonable estimate of the upper limits of carbon storage for similar forest types in comparable site conditions. The objectives of this study are to: (1) establish estimates of carbon stocks in the main carbon pools of old-growth hardwood and softwood forests in northern New England, (2) test the validity of these estimates as benchmarks by comparing them to estimates of carbon stocks in other old-growth forests, and (3) use the benchmark values to assess the carbon stocks of mature second-growth northern hardwood forests.

2. Methods

2.1. Site description

The definition of old-growth is problematic and has been well-discussed (e.g., Wirth et al., 2009b). Definitions generally fall into two categories: those based on structural characteristics and those focused on successional processes. A variety of characteristics is used to distinguish old-growth forests under these definitions, including disturbance history. In the eastern United States, the occurrence of old-growth stands is quite limited; such stands often survived because the sites were inaccessible or of low productivity. Eastern tree species are often shorter lived than those that dominate western old-growth forests, and so the "typical" picture of old-growth forests with large trees and an abundance of large decaying logs is not always applicable. Mosseler et al. (2003) developed a definition of old-growth for the Acadian forest type that considers temperate old-growth forests to be in the final stages of stand development, containing old trees, and largely free of evidence of human activity. Mosseler et al. (2003) provide a list of structural and process characteristics that are considered to be attributes of old-growth; age criteria include an average age of ≈150 years for shade tolerant species, with some trees approaching maximum age (300+ years). We applied Mosseler et al.'s broad definition and list of criteria in the site selection process. In some cases (The Bowl, Gifford Woods), past publications report tree ages of 250–400+ years from increment cores, while for other sites no age information is available and records of land use history and site examinations were used to establish that harvesting had not occurred in the past ≈150 years; actual forest age may be quite older.

The objective in site selection was to find the best available and reasonably accessible old-growth northern hardwood and spruce-fir or spruce-hemlock stands in New Hampshire, Vermont, and Maine. The stands were to be well-stocked, containing trees of near-maximum age for the species, and with no evidence of harvesting or major area-wide natural disturbance. Sufficient area was required to easily accommodate two 0.2 ha plots, which were located so as to represent the average conditions of the site. All study stands are located on public lands, although this was not a selection requirement. General site characteristics for the study stands are given in Table 1, while Fig. 1 shows the approximate study locations. It is worth noting that Leak (1987) described climax stands of spruce-fir and northern hardwoods in this region containing about 41 and 30 m^2/ha, respectively, of basal area, a criterion met by about half the stands in this study.

The northern hardwood stands in New Hampshire were classic old-growth: The Bowl Natural Area (elevation 610 m, 43°57′ lat.) and Mountain Pond (a proposed natural area, elev. 518 m, 44°10′ lat.); each supported typical old-growth beech-birch-sugar maple and had no known history of harvesting. The softwood stands were in the Gibbs Brook Natural Area (primarily spruce-fir, elev. 762 m, 44°12′ lat.) and on the Bartlett Experimental Forest (the so-called Picnic Grove, elev. 305 m, 44°04′ lat., a 4 ha area of old hemlock-spruce with an occasional white pine). This latter area apparently was a reserve stand along the Louisville Brook, water supply for the town of Bartlett. Soils in the hardwood stands were stony, well-drained tills derived from granite. The softwoods at Gibbs Brook were partly influenced by shallow-to-bedrock soils. The Picnic Grove occurred on a fine-textured soil with some evidence of slack-water deposition. Average annual temperature for the area is 6.9 °C, and precipitation averages 1270 mm annually.

In Vermont, the northern hardwood stands included Gifford Woods (elev. 475 m, 43°40′ lat.), a classic, rich northern hardwood old-growth reserve (Vermont State lands) with a high proportion of sugar maple. This area was unusual in that it had a high population of earthworms which resulted in rapid incorporation of the forest floor into a mull-like structure (this is not a recent development, see Bormann and Buell, 1964). The remaining sites in Vermont were on the Green Mountain National Forest where there had been no record of harvesting since establishment of the Forest in 1932. The Stone Farm site (elev. 486 m, 43°16′ lat.) was rich northern hardwoods, including a proportion of white ash, with no obvious signs of anthropogenic disturbance. Spruce Meadow (elev. 478 m, 43°12′ lat.) and French Hollow (elev. 450 m, 43°11′ lat.) were spruce-fir with a strong Eastern hemlock component. Soils were generally derived from glacial till and were well drained and acidic, often with a spodic horizon. Average annual temperature for the area is 7.6 °C, and precipitation averages 993 mm annually.

The Maine stands were located in Evans Notch (elev. app. 457 m, 44°18′ lat.), an area of high recreation value, therefore with very little disturbance. One northern hardwood stand (Royce) was on a bench above a steep incline with very limited possibilities of any harvest, and exhibiting typical old-growth characteristics. The other hardwood stand (Caribou) was on a gentler slope, but near the main road and with no known signs or history of harvest. The Maine spruce-fir stands (Moose Creek, Haystack) were classic old-growth spruce-fir with a high proportion of large-sized spruce and a minimum of fir. The hardwoods grew on stony, well-drained tills probably derived from crystalline schists (Goldthwaite, 1948), while the softwood soils were underlain with shallow basal till (well- to moderately-well drained) and ortstein, a cemented spodic horizon. Average annual temperature for the area is 6.1 °C, and precipitation averages 1118 mm annually.

Table 1
General characteristics of old-growth stands sampled. See text for additional details.

Site	State	Forest type	BA (m^2/ha)	Trees/ha (>2.5 cm)	QMD (>7.5 cm)
Caribou Trail 1	ME	N. hardwood	33.4	74	23.6
Caribou Trail 2	ME	N. hardwood	36.0	136	14.2
Royce 1	ME	N. hardwood	25.2	96	19.3
Royce 2	ME	N. hardwood	33.7	138	16.0
Gifford Woods 1	VT	N. hardwood, *A. saccharum*	33.4	93	31.0
Gifford Woods 2	VT	N. hardwood, *A. saccharum*	34.4	94	31.0
Stone Farm 1	VT	N. hardwood	45.1	105	22.1
Stone Farm 2	VT	N. hardwood	25.0	95	30.5
Mountain Pond 1	NH	N. hardwood	27.7	117	15.5
Mountain Pond 2	NH	N. hardwood	26.1	120	18.5
The Bowl 1	NH	N. hardwood	26.8	121	19.1
The Bowl 2	NH	N. hardwood	21.1	83	25.9
		Hardwood mean	**30.7**	**106**	**22.2**
		Standard error	**1.9**	**5.9**	**1.8**
Moose Creek 1	ME	Spruce-fir	45.3	177	16.5
Moose Creek 2	ME	Spruce-fir	55.9	170	15.5
Haystack 1	ME	Spruce-fir	54.5	237	13.7
Haystack 2	ME	Spruce-fir	51.1	128	16.5
French Hollow 1	VT	Hemlock-spruce	31.8	72	34.0
French Hollow 2	VT	Hemlock-spruce	44.9	73	31.5
Spruce Meadow 1	VT	Hemlock-spruce-fir	31.1	110	13.7
Spruce Meadow 2	VT	Hemlock-spruce-fir	35.0	157	10.4
Picnic Grove 1	NH	Hemlock	57.9	109	24.4
Picnic Grove 2	NH	Hemlock	56.1	173	15.2
Gibbs Brook 1	NH	Spruce-fir	30.2	159	13.5
Gibbs Brook 2	NH	Spruce-fir	31.1	141	10.2
		Softwood mean	**43.7**	**142**	**17.9**
		Standard error	**3.3**	**13.6**	**2.3**

BA = basal area; QMD = quadratic mean diameter.

Fig. 1. Map showing approximate locations of study sites.

2.2. Field and laboratory methods

Two temporary plots 0.2 ha in size were established at each site for a study-wide sample size of 24 plots, 12 hardwood and 12 softwood. Sampling occurred prior to leaf-off in 2007 and 2008. All live and dead stems >2.5 cm dbh and over were sampled by diameter and species (stems <10 cm were tallied on a 0.1 ha central subplot); large stems with obvious signs of rot were evaluated for soundness. Aboveground biomass was calculated according to Jenkins et al. (2003). Biomass values for live trees with rot were reduced based on the estimate of sound volume; biomass for standing dead trees was adjusted to reflect actual snag height using tables of the proportion of volume by 2.4 m (8 ft) bolts. Down dead wood (>7.5 cm) was inventoried using the line-intercept method as described by Harmon and Sexton (1996) on two 30.5 m (100 ft) transects at right angles (crossing at plot center). Decay classes used are as described in Heath and Chojnacky (2001). For all woody biomass, carbon was assumed to be 50% of dry weight.

Forest floor samples included all organic material above the mineral soil, and were collected on a systematic grid across the plot using a 25 cm^2 sampling frame, following the general method outlined by Harmon et al. (1999). Six samples were taken at each plot and were not composited; all material was air dried and weighed, then coarsely ground. Carbon concentrations were determined on homogenized subsamples by dry combustion. Mineral soil samples were collected on a systematic grid of twelve points across the plot, using a slide impact hammer corer following the methods used by the US Forest Service Forest Inventory and Analysis Program (2010). Each sample was 5 cm $\times$ 20 cm. Soils were oven dried at 105 °C and analyzed by dry combustion for carbon concentration. Separate samples were taken at each site to determine bulk density for use in calculating carbon stocks; due to the spatial variability of coarse fragments and the difficulty of obtaining accurate site specific values for this property, no adjustments were made for coarse fragment volume and all calculations were made based on rock-free soil volume. Although this results in stock estimates that are likely to be higher than actual values, estimates of coarse fragment volume can have a large effect on estimates and introduce a sizeable amount of error.

Significance testing was conducted using *t*-tests to compare carbon stocks in hardwood and softwood types; values met the assumptions for parametric testing. Plot values were pooled across states since the contrast of interest was hardwood vs. softwood and the study purpose was to develop estimates of upper bounds of carbon storage in northern hardwood and softwood types in northern New England, rather than for individual sites or states. Therefore, although carbon stock values are presented by state for the reader's information, each hardwood and softwood plot was considered a replicate for that type, for a sample size of 12 for each type. Comparisons of mean carbon stocks in old-growth hardwood and mature second-growth hardwood stands were also conducted using *t*-tests. For the pools that did not meet the test assumption of heterogeneous variance, Welch's correction was applied.

3. Results and discussion

3.1. Carbon stocks in hardwood and softwood stands

Total carbon stocks (aboveground live and dead biomass, down dead wood, forest floor, and soil to 20 cm) in hardwood stands were similar across the three states, and averaged 216 t/ha. Total carbon stocks in softwood stands were more variable, ranging from 234 t/ha in Vermont to 293 t/ha in Maine, with an overall mean of 267 t/ha (Table 2). Overall carbon storage was significantly different between hardwood and softwood stands ($p < 0.001$), which was driven by the forest floor pool. Carbon in aboveground live biomass was not significantly different between hardwood and softwood stands, averaging between 94 and 143 t/ha. The standing dead and down dead carbon pools were of similar magnitude and not significantly different between the hardwood and softwood sites, varying from 6 to 20 t/ha, with most sites between 6 and 12 t/ha. Forest floor carbon was significantly different between hardwood and softwood forests ($p < 0.001$), with an overall mean of 18 t/ha for the hardwood stands and 52 t/ha in softwoods, exceeding the estimates for the down dead and standing dead pools at most sites (Table 2). Soil carbon stocks (to 20 cm) were not significantly different between forest types, with mean values of 63 t/ha for hardwoods and 68 t/ha in the softwood sites.

3.2. Validity of measured values as benchmarks

Our measurements yield estimates of carbon stocks that are comparable to those reported for other old-growth forests of similar forest types, as shown in Table 3. The mean value of 116 t/ha for the aboveground live tree carbon pool is within the scope of values reported for northern hardwoods in New Hampshire, the Upper Peninsula of Michigan, and Northern Ontario, which range from 89 to 134 (Table 3). Mroz et al. (1985) report somewhat higher values of 162 and 141 t/ha for two old-growth sites dominated by sugar maple (*Acer saccharum*) in Michigan, while Spetich and Parker (1998) estimated this pool to be 106 t/ha in an old-growth oak-hickory dominated forest in Indiana. Considering the range of site characteristics and stand histories, these estimates are fairly consistent. Examples of similar studies in eastern temperate old-growth softwood forests were difficult to locate; to give context to our results, Table 3 shows results from some western forests. Our mean value of 125 t/ha for the softwood stands is similar to that reported for old-growth spruce-fir in British Columbia (137 t/ha).

The "classic" definition of old-growth forest includes large quantities of down and standing woody debris. However, this expectation may be the result of the larger extent of old-growth forests on the coast of the Pacific Northwest. Smithwick et al. (2002) report values of 48 t/ha in the down dead wood carbon pool in forests in Coastal Oregon, and 25 t/ha for standing dead. We did not find significant differences between hardwood and softwood stands for the down dead or standing dead carbon pools (Table 2), and mean values for each were 8–13 t/ha. This is comparable to estimates of 13–15 t/ha reported elsewhere (Table 3) for northern hardwood forests. McGee et al. (1999) report a higher value of 23 t/ha of carbon in down dead wood in an Adirondack northern hardwood forest, however, this value includes pieces as small as 2.5 cm diameter. Tyrrell and Crow (1994) found values of 1–14 t/ha for down dead carbon in hemlock-hardwood forests, while Goodburn and Lorimer (1998) estimated this pool to be 14 and 10 t/ha for northern hardwood and hemlock-hardwood stands, respectively. Goodburn and Lorimer also report values of 4 (northern hardwood) and 10 (hemlock-hardwood) t/ha for carbon in standing dead stems, which agrees with our results.

Forest floor carbon is generally regarded as an unimportant pool in many forest types. However, our value of 18 t/ha for the northern hardwood sites was higher than either the down dead or standing dead wood carbon stocks, and similar to values from northern hardwood sites in Michigan (13 and 9 t/ha, Table 3). Higher values have been reported for forest floor carbon in northern hardwood sites in northern Ontario (28 and 32 t/ha, Table 3) and hardwood-hemlock forests in Michigan (38 t/ha, Scharenbroch and Bockheim, 2008). Mean forest floor carbon in softwood stands in our study was 52 t/ha, although values for individual sites were

Table 2
Carbon stocks in old-growth hardwood and softwood forests.

			AG live	AG dead	Down dead	Forest floor	SOC (20 cm)	Total
			Metric tons of carbon/ha					
Hardwood	ME	Mean	114 (8.0)	7 (2.8)	7 (2)	20 (8.9)	68 (8.3)	217 (18.2)
	VT	Mean	139 (14.9)	6 (1.7)	12 (2.7)	6 (2.1)	55 (2.1)	218 (14)
	NH	Mean	94 (2.7)	9 (2.5)	16 (6.4)	27 (8.8)	67 (7.3)	214 (15.4)
			116 (7.6)	**8 (1.3)**	**12 (2.5)**	**18 (4)**	**63 (3.9)**	**216 (8.4)**
Softwood	ME	Mean	143 (3.6)	6 (1.2)	7 (2.5)	73 (7.6)	63 (5.4)	293 (7.8)
	VT	Mean	111 (12.7)	12 (2.3)	11 (3)	29 (3.1)	70 (6)	234 (10)
	NH	Mean	120 (27)	20 (10.7)	10 (1.8)	54 (11.9)	72 (7)	275 (24.7)
			125 (9.9)	**13 (3.7)**	**9 (1.4)**	**52 (6.9)**	**68 (3.4)**	**267 (11.2)**
p value; all hardwood vs. all softwood			$p = 0.485$	$p = 0.225$	$p = 0.337$	$p < 0.001$	$p = 0.331$	$p < 0.001$

AG live = aboveground live tree biomass; AG dead = aboveground dead tree biomass; SOC = soil organic carbon in top 20 cm of mineral soil. *p* values are from *t*-tests comparing mean carbon stocks in old growth hardwood and softwood stands by carbon pool. Standard error of the mean is given in parentheses. Values in bold type are overall means for each forest type.

Table 3
Mean estimates of carbon pools (t/ha) in select old-growth forests. Ages are estimates; all studies report no evidence of anthropogenic disturbance.

Location	N. New England	N. New England	New Hampshire	Michigan	Michigan	N. Ontario	British Columbia	Oregon (Coast/East)	Montana	Rocky Mountains
Approx. lat./long.	43–44°N 71°W	43–44°N 71°W	45°57′N 71°W	46°14′N 89°19′W	48°03′N 88°38′W	47°03′N 84°25′W	54°03′N 122°03′W	44°N 122°W	47°N 113°W	39°04′N 105°52′W
Forest type	Northern hardwoods	*Tsuga*, *Picea*, *Abies*	Northern hardwoods	Northern hardwoods	Northern hardwoods	Northern hardwoods (2 sites)	*Picea-Abies*	Mixed conifers	*Larix*, mixed conifers	*Pinus*, *Picea-Abies*
Age	150–400+	150–400+	400+	200–300	Not given	>120	>140	150–450+	185	111–210
AG live tree	116	125	131, 104	131	134	104, 89	137	454/84[b]	144	91
AG dead tree	8	13		14				25/9		
DDW	12	9	15[a]	13			30	48/10	20[c]	37
Forest floor	18	52		13	9	28, 32	57	23/10	24	72
Soil	63 (20 cm)	68 (20 cm)				212, 226 (1 m)			76 (1 m)	61 (15 cm)
Study	This study	This study	Martin (1977), Martin and Bailey (1999), Gore and Patterson (1986)	Fisk et al. (2002)	Rutkowski and Stottlemyer (1993)	Morrison (1990)	Fredeen et al. (2005)	Smithwick et al. (2002)	Bisbing et al. (2010)	Bradford et al. (2008)

AG = aboveground; DDW = down dead wood. Numbers in parentheses are sampling depths.
[a] Value is for pieces >7.5 cm diameter only; same threshold value used in this study.
[b] First value is for coastal forest, second value is for forest east of the Cascades.
[c] Includes aboveground dead (snags) and down dead wood.

as high as 85 t/ha. Softwood forest floor carbon stocks in our study exceeded values for spruce-fir and mixed conifers in other regions, but were less than the average reported by Bradford et al. (2008, Table 3) from a variety of Rocky Mountain subalpine forests. These results suggest that the forest floor carbon pool in older forests is substantial and may warrant greater attention, since this pool can easily be lost through disturbance. A comprehensive meta-analysis of harvesting impacts on forest floor and soil carbon by Nave et al. (2010) found that after harvest, carbon stocks declined by 20% in conifers and 36% in hardwoods.

Estimates of soil carbon are rare in the old-growth literature, and are difficult to compare due to the many different sampling depths and methods used. Due to the high prevalence of coarse fragments in northern forest soils, we sampled to a depth of 20 cm. Soil carbon stocks were 63 and 68 t/ha for hardwood and softwood sites, respectively, which is consistent with the estimates of 51 t/ha (to a depth of 25 cm) for northern hardwood-hemlock forests reported by Scharenbroch and Bockheim (2008), and 61 t/ha (to a depth of 15 cm) measured by Bradford et al. (2008) in Rocky Mountain subalpine forests. It is unclear if carbon storage in soils reaches equilibrium at some theoretical maximum value, or continues to increase over time. Reichstein et al. (2009) examined this issue using a variety of modeling approaches, but did not reach a firm conclusion and state that further work to understand the long-term stabilization mechanisms for soil carbon is required. However, the values measured in this study compare well with those from similar depth increments, and are likely reasonable estimates of the upper range of expected values for surface soil carbon.

Based on the agreement of our measurements with other values reported in the literature for similar old-growth forest types, the values in Table 2 represent reasonable estimates of the upper bounds of carbon stocks in old-growth northern hardwood and old-growth softwood forests in northern New England, and can be used as benchmarks against which assess the carbon storage potential of other softwood and northern hardwood stands in the region.

3.3. Using the benchmarks: comparisons to mature northern hardwood second-growth forests

The USDA Forest Service maintains a network of experimental forests throughout the United States (Adams et al., 2004). The history of these sites is generally well documented and a variety of ongoing experiments provides research opportunities. Using the methods described previously, soil and forest floor data were collected from long-term experimental plots on the Fernow Experimental Forest in West Virginia, the Middle Mountain Research Area on the Monongahela National Forest, West Virginia, the Kane Experimental Forest in Pennsylvania, and the Argonne

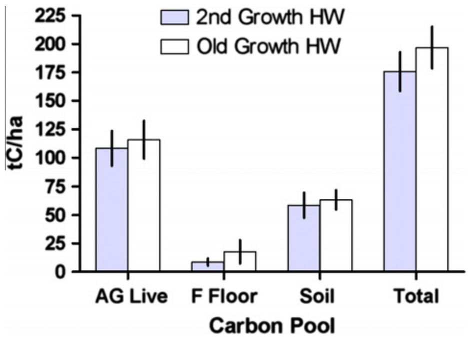

Fig. 2. Mean stocks (t/ha) and 95% confidence intervals for selected carbon pools in mature second-growth and old-growth northern hardwood stands.

Experimental Forest in Wisconsin (down and standing dead wood was not sampled). Inventory data collected as part of ongoing research studies was used to calculate carbon in aboveground live biomass according to the equations used in this study. All of these sites are second-growth naturally-stocked northern hardwood stands used as control plots for silvicultural studies, and were about 80–120 years old at the time of sampling.

Mean carbon stocks and 95% confidence intervals are shown in Fig. 2 for the aboveground live tree, forest floor, and soil (to 20 cm) pools in mature second-growth and old-growth northern hardwood sites. For the aboveground live tree carbon pool, the mature second-growth estimate of 108 t/ha was not significantly different from those in the old-growth sites (93% of old-growth value), which echoes the findings of Fisk et al. (2002) who reported no significant differences in aboveground live overstory carbon between old growth (131 tC/ha) and mature second-growth (115 tC/ha) forests. Although forest floor carbon stocks in second-growth hardwood stands were 49% of those in the old-growth sites (9 and 18 t/ha, respectively), this difference was not statistically significant. If the values for the Gifford Woods site, which had a very thin forest floor relative to all other hardwood sites (likely due to the presence of a large earthworm population) are removed, the forest floor carbon stock in second-growth sites averages 42% of that in old-growth, a significant difference ($p = 0.0459$). Soil carbon stocks in second-growth forests averaged 59 t/ha (92% of old-growth value), and were not significantly different from those in the old-growth stands. Total (aboveground live tree, forest floor, mineral soil to 20 cm) carbon stocks in second-growth forests averaged 176 t/ha, or 89% of the total stock found in old-growth northern hardwood sites (197 t/ha); this difference was not statistically significant.

4. Conclusions

The important role of forestland in the global/regional carbon cycle is well recognized. Nevertheless, questions remain on the effects of stand age, species composition, and management as well as the relative importance of the major forest components including live/dead trees, dead wood, soils, and forest floor. Better information would provide not only improved means for estimating carbon stocks, but would also help in the development of improved management directions and techniques.

This study established benchmark carbon stocks in old-growth softwood and hardwood stands in three New England states and used those estimates to assess the carbon storage of mature (about 80–120 years old) second-growth unmanaged hardwood stands. Old-growth softwood averaged about 25% more carbon than old-growth hardwood, primarily due to the higher carbon amounts in the thick forest floors characteristic of old-growth softwood. Old-growth hardwoods supported similar carbon stocks to mature hardwood stands (mature second-growth stands averaged 89% of the carbon stored in old-growth hardwood stands), although forest floor stocks were about twice as high (a non-significant difference). Old-growth softwoods averaged about 40% higher in total carbon than the second-growth hardwoods.

In the old-growth stands, aboveground live trees supported about 45–55% of the total carbon; surface mineral soils accounted for 25–30%; dead trees and deadwood each about 3–6%, and the forest floor 7–19% (significantly higher in softwoods).

In terms of management direction, maintenance of softwood stands to older age classes offers some gain in carbon storage, primarily due to the forest floor component. During any management activity, protection of the forest floor is an important precaution.

Our recommendation is that the benchmark estimates for the upper bounds of carbon stocks in northern New England for northern hardwoods are: 116 t/ha for aboveground live biomass, 8 t/ha in aboveground dead biomass, 12 t/ha for down dead wood, 18 t/ha for forest floor, and 63 t/ha in surface mineral soils. For softwood stands, these values are as follows (tC/ha): aboveground live biomass, 125; aboveground dead biomass, 13; down dead wood, 9; forest floor, 52; surface mineral soil, 68.

Acknowledgments

This research was supported by a grant from the Northeastern States Research Cooperative. The authors would like to thank the staff of Gifford Woods State Park, Green Mountain National Forest, and White Mountain National Forest for facilitating access to study sites, and Elizabeth LaPoint for preparing the map. The manuscript benefitted from thoughtful comments from Linda Heath, Jim Smith, and two anonymous reviewers.

References

Adams, M.B., Loughry, L., Plaugher, L., (Comps.), 2004. Experimental forests and ranges of the USDA Forest Service. US Department of Agriculture, Forest Service, General Technical Report NE-321.
Bisbing, S.M., Alaback, P.B., DeLuca, T.H., 2010. Carbon storage in old-growth and second growth fire-dependent western larch (*Larix occidentalis* Nutt.) forests of the Inland Northwest, USA. For. Ecol. Manage. 259, 1041–1049.
Bormann, F.H., Buell, M.F., 1964. Old-age stand of hemlock-northern hardwood forest in central Vermont. Bull. Torrey Bot. Club 91, 451–465.
Bradford, J.B., Birdsey, R.A., Joyce, L.A., Ryan, M.G., 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. Glob. Change Biol. 14, 2882–2897.
Carey, E.V., Sala, A., Keane, R., Callaway, R.M., 2001. Are old forests underestimated as global carbon sinks? Glob. Change Biol. 7, 339–344.
Clark, D.A., 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. Ecol. Appl. 12, 3–7.
Dixon, R.K., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.
Field, C.B., Kaduk, J., 2004. The carbon balance of an old-growth forest: building across approaches. Ecosystems 7, 525–533.
Fisk, M.C., Zak, D.R., Crow, T.R., 2002. Nitrogen storage and cycling in old-and second-growth northern hardwood forests. Ecology 83, 73–87.
Fredeen, A.L., Bois, C.H., Janzen, D.T., Sanborn, P.T., 2005. Comparison of coniferous forest carbon stocks between old-growth and young second-growth forests on two soil types in central British Columbia, Canada. Can. J. For. Res. 35, 1411–1421.
Goldthwaite, L., 1948. Glacial till in New Hampshire. NH State Planning and Development Comm., Mineral Resources Survey, Part 10.
Goodburn, J.M., Lorimer, C.G., 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. Can. J. For. Res. 28, 427–438.
Gore, J.A., Patterson III, W.A., 1986. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. Can. J. For. Res. 16, 335–339.
Gough, C.M., Vogel, C.S., Schmid, H.P., Su, H.-B., Curtis, P.S., 2008. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agric. Forest Meteorol. 113, 158–170.
Hale, C.M., Pastor, J., Rusterholz, K.A., 1999. Comparison of structural and compositional characteristics in old-growth and mature managed hardwood forests of Minnesota, USA. Can. J. For. Res. 29, 1479–1489.

Harmon, M.E., Sexton, J., 1996. Guidelines for measurements of woody detritus in forest ecosystems. US LTER Network Office Publication Number 20. University of Washington, Seattle.

Harmon, M.E., Nadelhoffer, K.J., Blair, J.M., 1999. Measuring decomposition, nutrient turnover, and stores in plant litter. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard soil methods for long-term ecological research. Oxford University Press, New York, pp. 202–240.

Heath, L.S., Chojnacky, D.C., 2001. Down dead wood statistics for Maine timberlands, 1995. US Department of Agriculture, Forest Service, Resource Bulletin NE-150.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. For. Sci. 49, 12–35.

Leak, W.B., 1987. Characteristics of five climax stands in New Hampshire. US Department of Agriculture, Forest Service, Research Note NE-336.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. Nature 455, 213–215.

Malhi, Y., Meir, P., Brown, S., 2002. Forests, carbon and global climate. Philos. Trans. R. Soc. Lon. A 360, 567–1591.

Martin, C.W., 1977. Distribution of tree species in an undisturbed northern hardwood-spruce-fir forest, The Bowl, NH. US Department of Agriculture, Forest Service, Research Note NE-244.

Martin, C.W., Bailey, A.S., 1999. Twenty years of change in a northern hardwood forest. For. Ecol. Manage. 123, 253–260.

McGee, G.G., Leopold, D.J., Nyland, R.D., 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecol. Appl. 9, 1316–1329.

Morrison, I.K., 1990. Organic matter and mineral distribution in an old-growth *Acer saccharum* forest near the northern limit of its range. Can. J. For. Res. 20, 332–1342.

Mosseler, A., Lynds, J.A., Major, J.E., 2003. Old-growth forests of the Acadian Forest Region. Environ. Rev. 11, S47–S77.

Mroz, G.D., Gale, M.R., Jurgensen, M.F., Frederick, D.J., Clark III, A., 1985. Composition, structure, and aboveground biomass of two old-growth northern hardwood stands in Upper Michigan. Can. J. For. Res. 15, 78–82.

Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2010. Harvest impacts on soil carbon storage in temperate forests. For. Ecol. Manage. 259, 857–866.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Orwig, D.A., Cogbill, C.V., Foster, D.R., O'Keefe, J.F., 2001. Variations in old-growth structure and definitions: forest dynamics on Wachusett Mountain. Massachusetts Ecol. Appl. 11, 437–452.

Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Núñez, P.V., Vásquez, R.M., Laurance, S.G., Ferriera, L.V., Stern, M., Brown, S., Grace, J., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282, 439–442.

Reichstein, M., Ågren, G.I., Fontaine, S., 2009. Is there a theoretical limit to soil carbon storage in old-growth forests? A model analysis with contrasting approaches. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), Old Growth Forests: Function, Fate, and Value. Springer-Verlag, Berlin, pp. 267–281.

Rutkowski, D.R., Stottlemyer, R., 1993. Composition, biomass and nutrient distribution in mature northern hardwood and boreal forest stands. Michigan Am. Midl. Nat. 130, 13–30.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27, 213–262.

Scharenbroch, B.C., Bockheim, J.G., 2008. Gaps and soil C dynamics in old growth northern hardwood-hemlock forests. Ecosystems 11, 426–441.

Smithwick, E.A., Harmon, M.E., Remillard, S.M., Acker, S.A., Franklin, J.F., 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecol. Appl. 12, 1303–1317.

Spetich, M.A., Parker, G.R., 1998. Distribution of biomass in an Indiana old-growth forest from 1926–1992. Am. Midl. Nat. 139, 90–107.

Tyrrell, L.E., Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75, 370–386.

U.S. Department of Agriculture, Forest Service, 2010. Forest Inventory and Analysis Phase 3 Indicator Field Guide Version 5.0. Unpublished report available at <http://fia.fs.fed.us/library/field-guides-methods-proc/>.

Wirth, C., Gleixner, G., Heimann, M. (Eds.), 2009a. Old Growth Forests: Function, Fate, and Value. Springer-Verlag, Berlin.

Wirth, C., Messier, C., Bergeron, Y., Frank, D., Fankhanel, A., 2009b. Old-growth forest definitions: a pragmatic view. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), Old Growth Forests: Function, Fate, and Value. Springer-Verlag, Berlin, pp. 11–33.