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Carbon Stocks in Managed Conifer Forests in Northern Ontario, Canada

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Carbon pools and net primary productivity (aboveground) were measured in managed stands of jack pine (Pinus banksiana Lamb.) and black spruce (Picea mariana [Mill.] B.S.P.), ranging in age from 10 to 53 years, in the Lake Nipigon area of northern Ontario. Organic carbon in the forest floor and surface mineral soil (top 15 cm) ranged from 13 to 46 Mg C ha^{-1} and 10 to 29 Mg C ha^{-1}, respectively. Carbon in aboveground tree biomass ranged from 11 to 74 Mg C ha^{-1} in crop trees, and 0 to 11 Mg C ha^{-1} in non-crop trees. Coarse woody debris (downed woody debris and snags) contained between 1 and 17 Mg C ha^{-1}. Understory vegetation rarely represented more than 1% of total ecosystem carbon accumulation, but was responsible for a larger proportion of aboveground net primary productivity (ANPP). Rates of ANPP (expressed as carbon) ranged from 0.8 to 3.5 Mg C $ha^{-1}\,y^{-1}$. Carbon stocks in managed stands were compared with published values from similarly aged fire-origin stands in the North American boreal region. Carbon stocks in our study stands generally exceeded those in unmanaged fire-origin stands of the same age, due to larger tree and forest floor carbon pools.

Keywords boreal forest, carbon sequestration, carbon stocks, jack pine, black spruce, plantations, forest management

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1 Introduction

As the demand for forest products from the boreal region increasingly warrants the use of intensive management, the area of natural forest in Canada converted to managed forest will likely increase (Nelson and Vertinsky 2003). With this trend comes the need to understand the carbon and nutrient budgets of the managed forest estate, in light of global warming and carbon dynamics, demand for bioenergy from forest residues, and trends towards ecosystem-based management approaches.

Studies have suggested that silviculturally managed forests, particularly plantations, store less carbon over their lifetimes than natural forest stands (Cooper 1983, Harmon et al. 1990, Fleming and Freedman 1998), and the idea that young, aggrading plantation forests may be desirable over old-growth in terms of carbon sequestration has been widely refuted (e.g. Vitousek 1991, Cannell 1999). Managed forests have been found to have less detrital biomass than most natural forests (Fleming and Freedman 1998), and smaller live-tree biomass, as trees are often felled when the mean annual growth increment is maximized but before maximum biomass accumulation is achieved (Cannell 1999). Nonetheless, plantations and other forms of managed stands, especially those composed of boreal conifer species, are becoming an increasingly dominant landscape feature, although they remain relatively unstudied, particularly in Canada. In addition, as plantation forestry is still relatively new in many parts of Canada (e.g. Neilson et al. 2007), few opportunities have existed to study managed forests of advanced ages. Thus, information on the carbon sequestration and storage capabilities of managed forests in Canada's boreal region is relatively scarce and mostly limited to very young stands.

Previous studies investigating the impacts of harvesting and other management activities on carbon dynamics in northern forests have focused on comparing young managed stands to unlogged mature or old-growth stands. Unsurprisingly (especially given that most of these studies involve managed stands 20 years old or younger) these studies have found that young managed stands store less carbon than old forests (e.g. Fredeen et al. 2005), a pattern that will have implications for global (or at least national) carbon budgets if forest management alters the age class structure over the landscape by skewing it towards younger stands. In the North American boreal forest, where stands are subjected to frequent stand-replacing disturbance (i.e. wildfire), comparisons between managed stands and naturally disturbed stands of similar age may be more meaningful than those made between relatively young managed stands and 'old-growth' or mature stands, if the purpose is to understand the ecological impacts of forest management at the stand level and how these differ from those of natural disturbances.

Boreal forests play an important role in the global carbon (C) cycle (Price and Apps 1995, Fyles et al. 2002, Kang et al. 2006, Bond-Lamberty et al. 2007, Luyssaert et al. 2007, Bonan 2008, Kurz et al. 2008, Sun et al. 2008). Many of the studies investigating this role are based on simulation models. Empirical data on stand-level C stocks are valuable for validating these models. In this paper, we report on measured C stocks and aboveground net primary production (ANPP) in silviculturally managed forests of jack pine (Pinus banksiana Lamb.) and black spruce (Picea mariana [Mill.] B.S.P) in northern Ontario, Canada. We make comparisons between species and site types, and assess our measurements against other North American boreal upland conifer forests, managed and unmanaged, in the age range of our study stands.

2 Materials and Methods

2.1 Site Description

The stands investigated in this study were located within a 50 km radius around the town of Beardmore, Ontario (49.5° N Lat., 88° W Long.) in the Central Plateau and Superior forest regions of northwestern Ontario and within Ontario site region 3W (Hills 1961, Rowe 1972, Racey et al. 1989). The climate is humid sub-boreal characterized by cool short summers and long cold winters, with a mean annual temperature and precipitation of 0.2 °C and 784.0 mm respectively (Environment Canada 1982). The average length of the frost-free period is 75 to 100 days (Chapman and Thomas 1968).

Of the 17 selected stands, 12 were plantations established after clearcut harvesting, 2 were established post-harvest by aerial seeding, and 3 were naturally regenerated after fire (and some form of harvest or salvaging) and then thinned to desired spacing. Details of stand management histories can be found in Table 1. The 12 jack pine and 5 black spruce stands ranged in age from 10 to 53 years since establishment (as of 1998). All were located on upland sites, with well-drained to rapidly drained soils. Pine stands were located on deep sands of both outwash and windblown origin, and occasionally on silty sands. Spruce stands were found on silty sands of till origin and deep, silty lacustrine clays. Two general site types, based mainly on soil texture, were identified: stands on deep sands were labelled "dry", while those on finer-textured soils were considered "mesic" (soil nutrient content was also lower in the dry compared to the mesic sites; unpublished data).

2.2 Study Design

For the purposes of this study, each stand was treated as a case study representing a unique combination of species, management history, and site conditions. While this study did include stands of a range of ages, we decided against using a chronosequence approach to make inferences about temporal changes in carbon pools in these managed forests. This was due to 1) variable management histories; 2) the small number of suitable stands at either age extreme, and, particularly with respect to soil carbon; 3) the sensitivity of soil carbon accumulation to the presence of finer-textured soils in the profile,

Table 1. Management history of jack pine (P) and black spruce (S) stands in the Lake Nipigon region of northern Ontario.

Stand code	History of silvicultural activities
P13	Salvage harvested in 1986 after budworm infestation; prescribed burn; planted in 1988
P16	Planted 1984
P2	Cut early 1960s; planted 1967, with some natural regeneration
P3	Cut early 1960s; humus layer completely removed (by blading); seeded 1964; thinned to 1.2 by 1.2 m spacing in 1969
P4	As in P3, but not thinned
P15	Planted 1963
P5	Cut late 1950s; planted 1962; cleaned of aspen and birch 1966, 1970, 1974, sprayed with brushkill 1970
P7	Original stand burned in 1956 wildfire; salvaged 1958–1959; natural regeneration thinned in 1961–1962 to 0.9 by 1.2 by 1.5 m variable spacing; cleaned of aspen 1963
P8	Burned in 1956 wildfire; salvaged 1958; planted 1959; supplemented with strong natural regeneration
P6	Cut 1951; burned in 1956 wildfire; sparse natural regeneration with some black spruce underplanting
P10	Cut early 1940s; burned by escaped prescribed burn in 1946; planted spring 1951
P11	Burned mid-1940s; natural regeneration cleaned and thinned in winter 1962 to 1.2 by 1.5 m spacing
S10	Planted 1986
S7	As in P5
S1	Cut 1951 with some birch left standing; burned 1956; planted 1961
S5	As in S2, but planted 1961
S2	Cut 1930–1938; burned 1940, 1948; planted 1960 in variable 1.2 by 1.2, 1.5 by 1.5, and 1.8 by 1.8 m spacing; manual removal of aspen and birch 1966, 1970, 1974; sprayed with herbicide 1970

Table 2. Site and mensurational characteristics of the study stands (P = jack pine, S = black spruce).

Stand code	Age [a] (yr)	Density (stems ha^{-1})	Mean (s.d.) [b] dbh [c] (cm)	Mean (s.d.) height (m)	Basal area (crop trees) (m^2 ha^{-1})	Basal area (non-crop trees) (m^2 ha^{-1})	Surface soil texture [d] and site type [e]
P13	10	2459	5.8 (1.5)	4.2 (0.5)	7.0	0.0	vfS (dry)
P16	14	2237	8.5 (2.4)	6.6 (0.9)	13.7	1.4	SivfS (mesic)
P2	31	3467	10.6 (3.3)	13.5 (1.8)	33.5	2.6	fS (dry)
P3	34	3698	8.3 (4.0)	10.7 (2.3)	23.2	1.5	fS (dry)
P4	34	2322	12.6 (4.0)	13.9 (2.1)	31.7	2.7	fS (dry)
P15	35	2022	13.0 (2.9)	15.6 (1.9)	28.3	5.2	Si (mesic)
P5	36	2116	13.4 (3.3)	15.1 (1.3)	32.0	0.8	LvfS (mesic)
P7	38	2489	11.9 (3.1)	15.0 (1.6)	29.6	1.4	SivfS (mesic)
P8	39	2344	12.9 (3.0)	15.5 (1.2)	32.3	1.8	SiL (mesic)
P6	40	1351	15.9 (4.4)	15.9 (1.8)	24.6	0.9	SifS (dry)
P10	47	1164	16.7 (3.0)	18.1 (1.7)	24.7	0.2	fS (dry)
P11	53	1789	15.2 (3.5)	19.2 (1.8)	34.3	0.2	SiL (mesic)
S10	12	2830	4.0 (2.0)	4.1 (1.1)	4.4	5.7	Si (mesic)
S7	36	2500	12.5 (2.8)	10.1 (1.9)	32.0	1.4	SiS (mesic)
S1	37	2811	12.1 (2.7)	10.8 (1.7)	34.0	5.2	SiC (mesic)
S5	37	3400	10.4 (3.6)	7.7 (1.9)	32.1	0.3	SiS (mesic)
S2	38	3200	12.9 (3.0)	11.0 (2.0)	44.2	0.9	SivfS (mesic)

[a] Time since stand establishment
[b] Standard deviation
[c] Diameter at breast height (1.3 m above the ground)
[d] fS = fine sand; LvfS = loamy very fine sand; Si = silt; SiC = silty clay; SifS = silty fine sand; SiL = silty loam; SiS = silty sand; SivfS = silty very fine sand; vfS = very fine sand
[e] General stand classification based on soil texture: dry = pure sands, mesic = finer-textured soils

making it difficult to attribute differences in soil carbon pools to changes over time (Johnson and Miyanishi 2008). See Table 2 for information on the characteristics of all 17 stands.

2.3 Vegetation and Soil Sampling

2.3.1 Canopy Vegetation

Within each stand, three to five 0.0225 ha plots (15 m × 15 m) were established. Within each plot, diameter at breast height (dbh; 1.3 m) was measured on all trees with a dbh greater than or equal to 2 cm (including dead trees; these were treated separately in the data analysis), and height was measured on 50% of the trees (every second tree encountered), using standard methods. A breast height increment core was collected from a minimum of 10 trees (randomly chosen from those used for height measurements) per plot.

Three trees (of the “crop” species) of average diameter for a given plot were selected for destructive sampling; these were located outside plot boundaries, usually about one tree length away. Samples of foliage, branches, stemwood and stembark were collected from each felled tree. Representative subsamples of each component of interest from each tree were taken, ensuring the inclusion of material from throughout the crown (needles and branches) and from the full length of the trunk (wood and bark).

In the lab, tree tissues were then ground in a Wiley mill to pass through a 2 mm mesh screen; ground samples were then dried at 65 °C to a constant weight (usually 48 hours), and cooled in a desiccator directly prior to carbon analysis. Carbon concentration of tree tissues was determined by dry combustion using a Leco CR-12 Carbon Determinator (Leco Corporation, St. Joseph, Michigan).

Aboveground tree biomass was estimated with species-specific allometric equations based on dbh (or dbh and height) measurements. Biomass was calculated, by component, for each measured tree, then summed over all trees per plot to give biomass per unit area. Carbon pool sizes in the different crop tree components were calculated using the carbon concentrations determined in the lab, and the biomass values for each component. The equations were developed for prior studies of jack pine and black spruce in northern Ontario (unpublished; Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources), and were the most geographically proximate equations available for these species. Equations are as follows, where the mass (in kilograms) of each tree component is a function of diameter at breast height (dbh, in centimetres) or dbh and height (ht, in metres):

Black spruce:

$$\text{Foliage} = 0.287 + 0.071 * \text{dbh}^{1.256} \qquad (1)$$

$$\text{Branches (live)} = 0.627 + 0.011 * \text{dbh}^{1.812} \qquad (2)$$

$$\text{Branches (dead)} = 0.229 + 0.042 * \text{dbh}^{1.313} \qquad (3)$$

$$\text{Stemwood} = 3.490 + 0.015 * \text{dbh}^{2.941} \qquad (4)$$

$$\text{Stembark} = 0.017 + 0.016 * \text{dbh}^{2.247} \qquad (5)$$

Jack pine:

$$\text{Foliage} = 0.017637 * \text{dbh}^{1.882059} \qquad (6)$$

$$\text{Branches (live)} = 0.0010405 * \text{dbh}^{2.931628} \qquad (7)$$

$$\text{Branches (dead)} = 0.000756 * \text{dbh}^{2} * \text{ht} \qquad (8)$$

$$\text{Stemwood} = 0.1359444 * \text{dbh}^{2.236943} \qquad (9)$$

$$\text{Stembark} = 0.0050741 * \text{dbh}^{2.6819} \qquad (10)$$

Carbon in dead standing trees (snags) and non-crop trees was estimated from biomass values (also calculated using the above equations; snags were assumed to be composed of stemwood and bark only) at an estimated carbon concentration of 50%.

Stem incremental growth (for ANPP estimations) was estimated using annual growth rings measured on the increment cores using a TRIM (Tree Ring Increment Measurement) system apparatus developed by the Ontario Ministry of Natural Resources. Stem increment measurements were then applied to ANPP estimations described below.

2.3.2 Understory Vegetation

To measure the aboveground biomass of each layer of understory vegetation, destructive sampling was carried out within one 1 m × 1 m quadrat per study plot (i.e. 3 to 5 per plantation). The size of area sampled depended on the vegetation layer: 1 m × 1 m for shrub biomass, 0.5 m × 0.5 m for herbaceous biomass (prostrate shrubs, e.g. Epigaea repens, were included in this category), and 0.25 m × 0.25 m for moss/lichen biomass. All aboveground biomass within each sampling category was clipped and oven dried at 65 °C to a constant weight before weighing.

Carbon content of the understory vegetation was determined by sampling the dominant species from each of the shrub, herbaceous, and moss/lichen layers from each of the inventory quadrats. Carbon pool sizes are therefore based on the collective biomass of all species of vegetation within a given layer, but on the carbon concentrations for only one (the dominant) species in each layer. Samples of understory vegetation were processed and analysed for total C, as described above for tree tissues.

2.3.3 Forest Floor and Mineral Soil

Within each of the 3 to 5 plots per stand, samples of forest floor material (L, F, and H horizons combined) and mineral soil were taken from small pits at three random sampling points. Forest floor depth (to the top of the mineral soil) was measured. Mineral soil was sampled from between 10 and 15 cm below the organic-mineral interface. This depth, which always fell within the B horizon, was chosen as the standard sampling depth for mineral soil. One large soil pit (1 m depth) per stand was excavated for sampling by horizon; this revealed that the A (Ae) horizon was relatively thin and discontinuous in most stands, reinforcing our decision to use a sample from the more consistent B horizon to represent the top 15 cm of mineral soil in these stands. For bulk density estimation, one sample each of forest floor and mineral soil per plot (i.e. 3 to 5 per stand) was obtained using a sampler of known volume. Samples were kept on ice and then frozen until they could be air dried and subsequently processed in the lab.

Forest floor and mineral soil samples were air dried, and the contents of each individual sample bag thoroughly mixed; a subsample from each bag was then passed through a 1 mm sieve (forest floor samples were ground before sieving). Total carbon was determined by dry combustion as above. To test for the presence of inorganic carbon, and assess the importance of its contribution to total carbon values, one subsample per plot was divided in two, with one portion being combusted at 500 °C prior to total carbon analysis. The amount of inorganic carbon detected was negligible in mineral soil and forest floor samples, and so total carbon is taken to represent organic carbon for the purpose of this study. To express results on an oven-dry basis, a moisture content correction factor for each sample was determined by weighing a separate subsample before and after oven drying to a constant weight (at 65 °C for forest floor samples, and 105 °C for mineral soil samples; all subsamples were cooled in a desiccator before weighing). Bulk density samples were oven dried at 105 °C, cooled in a desiccator and then weighed.

2.3.4 Coarse Woody Debris (Downed Woody Debris and Snags)

Within each plot, every piece of downed woody debris (DWD) with a minimum diameter of 5 cm at the base (wider end) was included for measurement. Two diameter measurements (one at each end) and a length measurement were made on each piece. Volumes were estimated using the length and average of the two diameter measurements. Pieces of DWD completely covered by feathermoss were not counted or measured; these were considered to be part of the forest floor, and were assumed to be accounted for in the random measurements of forest floor depth and biomass described above. Each piece of DWD encountered was assigned to a decay class based on the observed extent of decomposition; these ratings varied on a scale from 1 to 5, with 1 being sound wood and 5 being highly friable wood with little structural integrity remaining. Within each plot, one piece of DWD representing each decay class present was sampled (by handsaw) and kept cool until it could be returned to the lab. These samples were used to determine the average density of wood in each decay class. First, fresh volume estimates were made of each DWD sample by calculations based on measured dimensions for regularly shaped samples (disks), and by water displacement for irregularly shaped samples (samples were wrapped in a thin layer of stretched Parafilm™, which was delicately applied so that it adhered tightly to the contours of sample and sealed it against water absorption, but did not alter sample dimensions through compression). Parafilm™ was then removed and samples were oven dried at 65 °C to a constant weight (generally for several days), cooled in a desiccator, and weighed. Subsamples of DWD pieces were processed and analyzed for carbon concentration as described above for vegetation samples.

2.3.5 Aboveground Net Primary Productivity (ANPP)

Aboveground net primary productivity (ANPP) was estimated in a subset of 5 jack pine stands (P13, P16, P3, P5, and P10) and 2 black spruce stands (S10 and S7). Stands were selected to enable comparisons between species and site types (adjacent spruce and pine stands were chosen where possible).

ANPP was estimated using a combination of litterfall and stem increment measurements, as well as annual understory vegetation production. Aboveground tree litterfall was collected over a three-year period (1998–2000). Square wooden littertraps measuring 0.5 m × 0.5 m in surface area were used; these had nylon mesh bottoms and were raised approximately 10 cm above the ground on wooden legs. Within each of the selected stands, traps were randomly placed within each of 3 plots, resulting in a total of 9 traps per stand (jack pine) or 6 traps per stand (black spruce).

Litter was collected monthly during the field seasons of 1998 and 1999, and every 6 weeks during the 2000 field season, from late May until early October. Overwinter litterfall was collected in the first spring collection of each year; the final collection date was late May, 2001, for a total of 3 full years of collected litterfall. Litter was air dried and stored in paper bags until sorted. Litter from each trap at each collection time was sorted into components: foliage of the planted species; foliage of any other species; structural tissue (bark, twigs); reproductive tissue (cones;

seeds); and miscellaneous (anything too small to be otherwise categorized). Litter was then oven-dried at 65 °C to a constant weight, cooled in a desiccator, and weighed.

For ANPP estimates, only foliar litterfall was used (this is discussed further below). Crop-tree foliar litterfall samples from each trap in each of three collection times (overwinter, midsummer, fall) from one collection year (1999) were analysed for carbon content as described above for vegetation samples. For non-crop foliar litterfall, one sample per plot at one collection time (overwinter, as this was usually the only collection with sufficient biomass of this component for analysis) was analysed. The size of the annual carbon flux in litterfall was calculated by applying the carbon concentration values to the foliar litterfall mass from all three collection years.

The 5-year stem increment ending in 1998 (when the increment cores were taken) was used to estimate the dbh of each cored tree 5 years prior to sampling (e.g. Doyon and Bouchard 1998). This value was then applied to a species-specific biometric equation (developed for jack pine and black spruce in northern Ontario; Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources) to derive an estimate of the stem (including bark) biomass 5 years prior to sampling, which was subtracted from the similarly derived current stem biomass, giving a 5-year increment in stem biomass. The 5-year increment was then divided by 5 to obtain an average annual increment in stem biomass growth representative of the last several years of growth (e.g. Doyon and Bouchard 1998, Jenkins et al. 2001).

Annual stem biomass increment values for the 10 cored trees in each plot (in the subset of stands used in the litterfall study) were added together, then corrected to account for the density of trees in each plot; the resulting value was used as an estimate of the total annual production of stem biomass in each plot. The total annual foliar litterfall weights for each plot were added to the total stem production estimates to obtain estimates of tree ANPP in each plot. This method of tree ANPP estimation incorporates those components that constitute the largest proportion of ANPP (i.e. stem increment and foliar production) (e.g. Comeau and Kimmins 1989) and is commonly used as a simple, direct measurement of forest productivity (e.g. Whittaker et al. 1974, Smith et al. 2002). It does not, however, include below-ground NPP, and disregards other components which contribute to total ANPP, namely annual branch/twig increment, tree mortality, and biomass lost to herbivory. Under non-infestation conditions, herbivory is generally responsible for a relatively small amount of biomass loss in forests, on the order of 1.5% to 2.5% of total NPP (Kimmins 1997). Gower et al. (1999) recommend excluding tree mortality from NPP estimations when using the approach taken in this study (i.e. using increment cores to back-calculate annual woody biomass increment).

Estimating foliar NPP using litterfall as a surrogate for new foliage production may also underestimate actual new foliage production, since an assumption of steady state is required which may not be met in young, aggrading stands (Gower et al. 2001). However, this method is preferred over the use of non-site-specific allometric equations to estimate annual foliar biomass increment, since foliar biomass for a given parameter such as tree dbh can vary widely (Crow and Schlaegel 1988, Gower et al. 1999). All of the stands in the current study had reached or were nearing crown closure, with the exception of the 12-year-old spruce stand, so we felt that the assumption of steady-state foliar biomass was largely appropriate. However, it must be noted that the ANPP estimates for the young stands, especially the young black spruce stand, may be underestimated.

A conservative estimate of the understory vegetation ANPP was made by summing the carbon stocks of the herb layer and of the shrub foliage component, both of which are produced on an annual basis. Estimates do not include moss and lichen NPP, which was not directly measured. Annual increment of shrub stems was also not included. Estimates of non-crop tree ANPP were also conservative, as stem increment was not measured for these species.

2.4 Analysis of Error Components

There are 3 key sources of variability embedded in the estimate of stand-level carbon stocks. These include the field measurements (i.e., within- and between-site variability), lab analysis (i.e., % C of each tissue component subsample), and the allometric equations (i.e., confidence intervals for each model parameter). To examine these error components and their effects on carbon estimates, we used data from the 4 mid-aged black spruce stands (S1, S2, S5, S7). Each component was isolated by using its measured range (i.e., 95% confidence intervals) while applying the overall mean values for the other two components.

2.5 Literature Review: Comparisons with Other Boreal Conifer Forests

We searched the literature for carbon stock data from North American boreal upland conifer forests, managed and unmanaged, in the age range of our study stands. We included aboveground tree biomass, CWD, and forest floor stocks, as these were most widely reported, and are comparable to our study. We did not include mineral soil C stocks as these were less frequently reported in studies of forest carbon; when soil carbon was reported, sampling depths tended to vary among studies, making comparisons tenuous. Where only tree biomass values were reported in the literature, these were converted to C using a factor of 0.5 (Pregitzer and Euskirchen 2004); where only forest floor mass was reported, a factor of 0.4 was used to convert to C (this is a rough average of the carbon concentrations in the forest floors of our study stands; this value is similar to the conversion factor used by Wang [2003]). For expediency, we use the term "natural" to refer to fire-origin, naturally regenerated stands, and "plantation" to refer to our study stands, even though some originated from thinning (to desired spacing) of natural regeneration on post-fire, salvage-logged sites.

3 Results

3.1 Carbon Stocks

Total carbon stocks (including surface mineral soil) ranged from 47 Mg C ha^{-1} in the youngest black spruce stand to 151 Mg C ha^{-1} in the oldest jack pine stand (both on mesic sites) (Table 3).

Among young stands, the 14-year-old jack pine stand on the mesic site contained substan-

Table 3. Carbon stocks (Mg C ha^{-1}) in ecosystem components of managed jack pine and black spruce stands (see Tables 1 and 2 for site information and management history of each stand).

Stand code	Crop trees	Non-crop trees	Understory vegetation	Snags	DWD	Forest floor	Mineral soil (top 15 cm)	Total
P13	11.0	0.00	0.77	0.01	5.01	24.8	17.5	59.1
P16	24.3	2.78	0.36	0.13	1.93	25.2	24.3	79.0
P2	65.6	5.03	0.41	6.88	0.35	25.8	12.0	116.1
P3	38.7	2.80	0.91	1.54	0.20	30.5	8.82	83.5
P4	65.2	5.16	0.62	5.18	0.33	35.8	14.6	126.9
P15	57.3	10.7	0.79	2.48	0.91	20.0	12.7	104.9
P5	69.2	1.85	0.64	6.48	1.15	38.1	21.7	139.1
P7	58.8	3.42	0.63	9.30	2.31	36.1	18.9	129.5
P8	65.1	0.33	0.53	9.85	2.86	39.8	14.5	133.0
P6	52.4	1.92	1.29	1.02	0.17	18.1	9.9	84.8
P10	58.2	0.53	1.10	2.71	1.01	23.9	10.0	97.5
P11	73.7	0.35	0.45	11.2	5.92	45.8	13.2	150.6
S10	10.5	7.05	0.73	0.68	1.20	13.0	14.1	47.3
S7	51.8	2.85	0.37	1.82	0.83	16.1	20.7	94.5
S1	53.7	9.99	0.18	1.78	0.14	36.5	28.5	130.8
S5	50.8	0.66	0.47	0.72	0.06	22.4	24.3	99.4
S2	72.2	2.04	0.17	1.37	n/a	33.2	22.8	131.8

n/a: Data not available

tially more carbon overall compared to either the 12-year-old black spruce stand growing adjacent to it, or the 10-year-old jack pine stand on the dry site (Table 3). Differences among the youngest stands were mainly due to differences in tree biomass, though the smaller carbon pools in forest floor and mineral soil in the young black spruce stand (somewhat compensated for by a larger carbon pool in non-crop trees) represent important differences between the pine and spruce on mesic sites in this age group. In the oldest (47–53 years old) stands, more carbon had accumulated in the mesic jack pine stand compared to the dry stand, due to greater amounts in crop trees, snags, downed woody debris, and the forest floor.

In mid-aged stands (31–40 years old), C stocks in aboveground tree biomass ranged from 39–72 Mg C ha^{-1}, but did not differ appreciably between species or site types (Table 3). One stand (P3) had appreciably lower crop tree C compared to the others (39 Mg C ha^{-1}); this stand also experienced a greater level of organic matter removal during its management history (blading and early thinning). Woody debris was most abundant in jack pine stands on mesic sites, and scarcest in black spruce stands. C stocks in understory vegetation were lowest in black spruce stands and highest in jack pine stands on dry sites. Forest floor C stocks in this age group ranged from 16–40 Mg C ha^{-1} and tended to be highest in jack pine stands on mesic sites, while mineral soil C was lowest in jack pine stands on dry sites. Differences in both bulk density and carbon concentration influenced the differences seen in mineral soil carbon stocks (Table 4). Mineral soil (top 15 cm) in the mesic black spruce stands had lower bulk density and hence lower mass, but high enough carbon concentrations to compensate for this, resulting in significantly higher carbon stocks compared to jack pine stands. Dry jack pine stands had the highest mineral soil bulk density, but the lowest carbon concentrations, and the lowest soil carbon stocks overall. These results illustrate the overriding importance of carbon concentration as the driver of soil carbon stock size.

In mid-aged and older jack pine plantations on mesic sites, carbon in crop tree biomass (aboveground) constituted slightly over 50% of the total amount of carbon in all measured ecosystem components (Table 3). In jack pine stands on dry sites, the proportion in trees was higher, at 55 to 60%. Black spruce stands on mesic sites contained similar but slightly lower proportions of ecosystem carbon in crop tree biomass compared to jack pine on mesic sites. In mid-aged and older stands on all site types, the largest pool of carbon was found in crop tree stem biomass (not shown).

Understory vegetation, downed woody debris (DWD), snags, and non-crop trees represented only small contributions to overall carbon accumulation in these stands. Even when taken together, these components generally accounted for less than 5% of total measured ecosystem carbon.

Table 4. Characteristics of the forest floor (O horizon; L, F, H horizons combined) and mineral soil (top 15 cm) in managed jack pine and black spruce stands (see Tables 1 and 2 for site information and management history of each stand).

Stand code	Depth (cm)	Forest floor Bulk density (g cm^{-3})	Forest floor C (%)[a]	Mineral soil[b] Bulk density (g cm^{-3})	Mineral soil[b] C (%)[a]
P13	4.2	0.24	25.6	1.20	0.98
P16	5.9	0.10	35.2	1.03	1.72
P2	5.7	0.12	35.5	1.27	0.72
P3	5.2	0.13	45.9	1.24	0.53
P4	6.5	0.13	39.5	1.17	0.86
P15	3.4	n/a	37.6	1.12	0.75
P5	6.0	0.17	38.2	1.19	1.23
P7	6.2	0.11	46.9	1.07	1.19
P8	6.1	0.16	42.1	0.92	1.05
P6	3.5	n/a	36.0	1.10	0.60
P10	4.3	0.12	46.6	1.27	0.53
P11	7.7	0.13	45.6	1.20	0.74
S10	3.8	0.11	32.8	1.06	0.91
S7	4.4	0.11	35.1	1.02	1.33
S1	6.8	0.13	44.7	0.99	2.13
S5	4.7	0.14	34.1	1.03	1.58
S2	6.7	0.10	48.8	0.89	1.70

[a] Organic carbon concentration based on oven-dry weight
[b] Top 15 cm
n/a: Data not available

3.2 Aboveground Net Primary Productivity (ANPP)

In this paper, ANPP is reported as mass of carbon, rather than biomass, and both crop tree ANPP

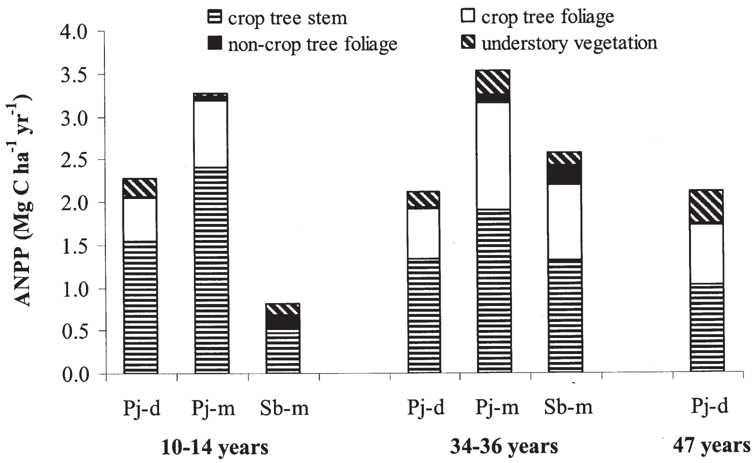

Fig. 1. Components of aboveground net primary productivity (ANPP; expressed as C) in managed jack pine and black spruce forests in northern Ontario, Canada. "Pj" = jack pine; "Sb" = black spruce; "d" = dry site; "m" = mesic site.

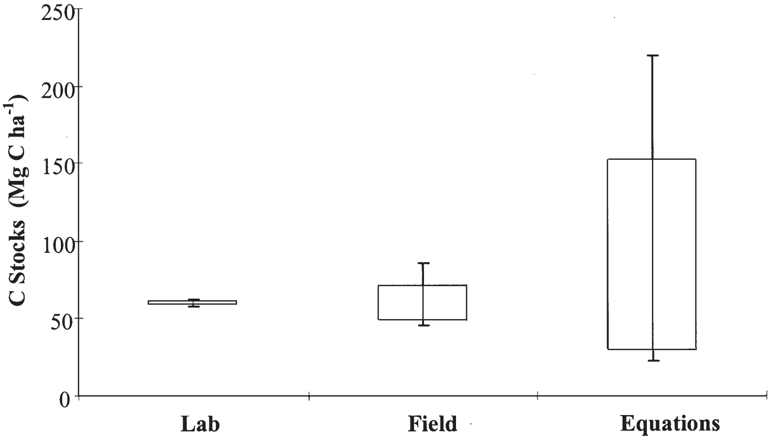

Fig. 2. The partitioned sources of error (laboratory analyses, field measurements, allometric equations) associated with estimating stand-level carbon stocks in 4 different black spruce plantations (36–38 years old; all on upland, mesic sites). "Boxes" cover ± 1 standard deviations; "whiskers" represent the range of values.

(stem biomass increment plus crop tree foliar litterfall) and total ANPP (the former plus understory vegetation increment and foliar litterfall from non-crop trees) will be considered. Rates of ANPP ranged from 0.8 to 3.5 Mg C ha^{-1} y^{-1}, and were found to vary by stand species, age, and site type (Fig. 1). Young jack pine stands had higher ANPP than young black spruce, with the ANPP of the mesic jack pine stand significantly greater than that of the mesic black spruce stand. Among mid-aged stands, the dry jack pine stand had the lowest ANPP (Fig. 1). At most, the understory vegetation contributed about 20% of ecosystem ANPP, and most often 10% or less. The lower rates of ANPP in the dry stands are reflected in the lower rates of both litterfall and stemwood production compared to the stands on mesic sites (Fig. 1).

In terms of species differences, the results suggest that the tree ANPP of black spruce will peak at a later stand age than that of jack pine. The 12 year old black spruce plantation had accumulated much less crop tree biomass than either of the pine plantations by this time, and crowns had not yet started to close. In terms of overall ANPP, the low ANPP observed in the crop trees in the young black spruce stand was compensated for by a productive non-crop tree/tall shrub component that was negligible in the other stands (ANPP of this component was not measured, but see Table 3 for the carbon stocks in non-crop trees). Foliar litterfall from the crop trees in the young spruce stand was exceeded by foliar litterfall from other species over the course of the study (Fig. 1).

3.3 Error Analysis

The box (± 1 standard deviation) and whisker (max. and min.) diagram (Fig. 2) clearly indicates the primary source of error in estimating stand level carbon stocks is related to the inherent error associated with the model parameters within the allometric equations. In this example, five different equations (for different tree components; see Eqs. 1–5 for black spruce), each with 3 parameters, were applied to the field inventory data. When the 95% confidence interval for each parameter was inserted into the model and applied to the field data, it generated a mean of 90 Mg C ha^{-1}, compared to 60 Mg C ha^{-1} for the other two error components and a range from 23 to 219 Mg C ha^{-1}. The laboratory analysis error component, on the other hand, had little influence on the overall estimate suggesting that the application of the 50% C assumption used in many other studies would still provide reasonable estimates. In the presented example for the mid-aged, mesic black spruce plantations, the mean % C for all sampled components and subsamples was 49.8% with a coefficient of variation of 2.83%.

3.4 Comparisons with Other Boreal Conifer Forests

We found only a dozen studies reporting on carbon (or biomass) stocks in North American boreal forests in the age range of our stands. Results of the literature review are shown in Table 5.

4 Discussion

4.1 Carbon Stocks in Trees, CWD, and Forest Floor

At a given age, pine stands on mesic sites had accumulated more carbon than either pine on dry sites or spruce on mesic sites. Although aboveground tree biomass C in mid-aged stands did not differ dramatically by species or site type (an unexpected result, given the range of substrate types, i.e. from silty clay to pure fine sand), it did tend to be higher in pine stands on mesic sites. Greater amounts of CWD (snags and downed woody debris) put these same stands ahead in total carbon stocks.

Our exploratory analysis of the error associated with tree biomass C stock estimates revealed that the allometric equations contributed the most uncertainty to estimates, as others have found (e.g. Chave et al. 2004). The uncertainty is related to the residuals from the model parameters themselves; we did not investigate the error associated with the choice of allometric equation. The equations used in this study were specific to our tree species and geographic region, and were developed from a relatively large dataset (for black spruce, 80 trees spanning the range of tree diameters found in our study sites). Although they were not developed explicitly for silviculturally managed forests, we judged these equations to be the most suitable given the lack of better alternatives; however, there is sure to be error associated with this choice. We may have been able to reduce the amount of uncertainty in our estimates had we chosen to use just one equation (for total tree biomass) for each tree; however, as we were interested in analyzing the carbon content of each tree component separately (foliage, stemwood, etc.), we chose to use multiple equations per tree,

Table 5. C stocks in managed and unmanaged North American boreal conifer forests grouped by age range. All stands chosen for inclusion here were on upland sites, on soils ranging from sands to clays. Values were rounded to the nearest Mg C ha^{-1} to facilitate interpretation. Totals represent the included components only. Trees = aboveground parts only (total of crop and non-crop trees); woody debris = snags and downed logs; forest floor = O horizon (L, F, H layers combined); Pj = jack pine; Sb = black spruce.

Source	Stand species (dominant)	Stand age (years)	Stand origins and site information	Trees	C stocks (Mg C ha^{-1})		Total
					Woody debris	Forest floor	
		10–20					
This study	*P. banksiana*	10–14	clearcut, planted; sand to silty sand	11–27	2–5	25	41–54
Howard et al. (2004)	*P. banksiana*	10	clearcut, nat. regen.; sand	3	4	11	18
Rothstein et al. (2004)	*P. banksiana*	12–14	fire, nat. regen.; sand	3–10	7–9	1–2	14–19
Nalder and Wein (1999)	*P. banksiana*	16–19	fire, nat. regen.; sand to loamy sand	8–27	1 c)	8–10	17–38
MacLean and Wein (1976)	*P. banksiana*	13–16	fire, nat. regen.; sandy loam	0–1			
Hegyi (1972)	*P. banksiana*	20	fire, nat. regen.; site class 1–2	3–8			
This study	*P. mariana*	12	clearcut, planted; silt	18	2	13	32
Wang et al. (2003)	*P. mariana*	12	fire, nat. regen.; clay	2–3	48–89	7–11	62–94
Fleming and Freedman (1998)	*P. mariana*	13–21	clearcut, planted; loam	9–29	0–3	21–31	40–51
Wang et al. (2003)	*P. mariana*	20	fire, nat. regen.; clay	2–5	8–30	6–69	41–79
		25–40					
This study	*P. banksiana*	31–40	clearcut, planted (or thinned nat. regen.); sand to silt loam	41–71	1–13	18–40	74–118
Rothstein et al. (2004)	*P. banksiana*	22–27	fire, salvaged, nat. regen.; sand	24–25	1	3–4	28–29
Reich et al. (2001)	*P. banksiana*	25–40	clearcut, nat. regen.; sandy loam	17			
Reich et al. (2001)	*P. banksiana*	25–40	fire, nat. regen.; sandy loam	22			
Howard et al. (2004)	*P. banksiana*	29	clearcut, nat. regen.; sand	19	2	11	32
MacLean and Wein (1976)	*P. banksiana*	29–40	fire, nat. regen.; sandy loam	18–46			
Nalder and Wein (1999)	*P. banksiana*	30	fire, nat. regen.; sand to loamy sand	19–22	1 c)	10–13	30–36
Hegyi (1972)	*P. banksiana*	30	fire, nat. regen.; site class 1–2	31–50			
Foster et al. (1995)	*P. banksiana*	35	fire, nat. regen.; sand	48			
Alban et al. (1978)	*P. banksiana*	40	clearcut, planted; sandy loam	74		13	
This study	*P. mariana*	36–38	clearcut, planted; silty sand, silty clay	52–74	1–3	16–37	73–109
Reich et al. (2001)	*P. mariana*	25–40	clearcut, nat. regen.; organic	11			
Wang et al. (2003)	*P. mariana*	37	fire, nat. regen.; clay	14–15	3–6	5–11	26–28
		40–60					
This study	*P. banksiana*	47–53	clearcut, planted (or thinned nat. regen.); sand to silt loam	59–74	4–17	24–46	86–137
Rothstein et al. (2004)	*P. banksiana*	36–52	fire, nat. regen.; sand	40–44	5	12–13	58–60

Source	Stand species (dominant)	Stand age (years)	Stand origins and site information	Trees	C stocks (Mg C ha^{-1})		Total
					Woody debris	Forest floor	
MacLean and Wein (1976)	*P. banksiana*	44–57	fire, nat. regen.; sandy loam	29–42			
Preston et al. (2006)	*P. banksiana*	42[a]	fire, nat. regen., xeric site	31	5	14	50
Doucet et al. (1976)	*P. banksiana*	44	fire, nat. regen.; sand	31–53			
Foster et al. (1995)	*P. banksiana*	45	fire, nat. regen.; silt loam	53			
Nalder and Wein (1999)	*P. banksiana*	46–55	fire, nat. regen.; sand to loamy sand	14–70	2[c]	8–21	30–93
Foster et al. (1995)	*P. banksiana*	56	fire, nat. regen.; sand	80		20	
Preston et al. (2006)	*P. mariana*	55[a]	fire, nat. regen., mesic site	49	9	18	76
Gordon (1983)	*P. mariana*	48	fire, nat. regen., sand	70	3[c]	43	116
		60–80					
Nalder and Wein (1999)	*P. banksiana*	62–80	fire, nat. regen.; sand to loamy sand	26–72	4[c]	7–18	38–91
Hegyi (1972)	*P. banksiana*	65	fire, nat. regen.; site class 1–2	22–53			
Foster et al. 1995	*P. banksiana*	68	fire, nat. regen.; silt loam	68		25	
Rothstein et al. (2004)	*P. banksiana*	72	fire, nat. regen.; sand	49	8	12	69
Howard et al. (2004)	*P. banksiana*	79	fire, nat. regen.; sand	32	10	9	51
Preston et al. (2006)	*P. banksiana*	73–78[a]	fire, nat. regen., xeric site	25–51	3–6	5–9	33–63
Wang et al. (2003)	*P. mariana*	71	fire, nat. regen.; clay	27–50	1–2	23–27	51–79

[a] Age at breast height (1.3 m)
[c] DWD only
[c] Snags only

each with its own parameters and associated error. Even so, the large amount of uncertainty associated with the equation parameters points to a need for more precision in converting tree diameter and height measurements into biomass estimates. This would require that more attention be given to the hazards involved with extrapolation of stand-level C stock data to the landscape or regional levels without a firm grasp of the uncertainties associated with the stand-level measurements. More awareness of this problem may provide better incentive to expend the significant amounts of time and resources needed to gather adequately large datasets for equation development.

Comparisons of carbon stock data between our study stands and similarly-aged stands obtained from the literature (mainly fire-origin but including some managed stands) (Table 5) are discussed in the following few paragraphs.

In the youngest age group (10–20 years), our jack pine plantations held more carbon in aboveground tree biomass than all other stands, except for one natural stand in northern Alberta (Nalder and Wein 1999) (Table 5). This is not surprising, given that stand development in plantations is often accelerated during the early stages. Our 10-year-old jack pine plantation had almost four times more aboveground tree carbon than a naturally regenerated 10-year-old clearcut in Saskatchewan, even though both were on sandy soils. Woody debris was only reported in a few of the studies of young stands. This limited information shows natural stands to contain roughly twice as much CWD as harvested stands in this age group; again, this is not surprising given that natural disturbances tend to leave behind large amounts of CWD, while one effect of forest harvesting is the removal of this material for commercial use. Forest floor carbon stocks were much higher in our young plantations compared to natural stands, due to the lack of consumption by fire, the persistent presence of logging slash, and the already substantial foliar litter production in these young stands (500–800 kg C ha^{-1} yr^{-1}). Overall, total aboveground carbon stocks (including forest floor) were larger in our young jack pine plantations than in natural stands of similar age.

Young black spruce plantations (10–20 years old), both from our study and from a New Brunswick study (Fleming and Freedman 1998), contained much larger carbon stocks in trees compared to natural stands (Table 5). On the other hand, the natural stands contained vastly more woody debris carbon than did the plantations (up to ~40 times as much). Trends in forest floor carbon stocks were less clear, with values varying by an order of magnitude even within one study. Overall, the woody debris had an overriding effect on total aboveground carbon stocks, resulting in the natural stands being associated with higher maximum values. The woody debris component in the young natural stands represents a ‘legacy’ from the pre-disturbance stands. The greater amounts of woody debris found in the young, natural spruce compared to the young, natural jack pine stands probably reflects higher pre-disturbance productivity and perhaps age in the black spruce (which were found on upland, fine-textured soils [Wang et al. 2003]), leading to larger, unburned boles left behind.

In the mid-aged category (25–40 years), jack pine stands originating from clearcutting and planting contained larger carbon stocks in aboveground tree biomass than most, but not all, natural stands in the same category. Natural jack pine stands with comparable tree carbon stocks tended to be located in more southerly locations in the boreal or near-boreal regions (New Brunswick, Minnesota, etc.). Black spruce plantations from our study, in this age range, contained 3 to 5 times more carbon in aboveground tree biomass than natural stands. For both species, stands that were clearcut and planted had much larger carbon stocks in aboveground tree biomass than stands that were naturally regenerated after clearcutting, again demonstrating the accelerated tree biomass accumulation in plantations.

In mid-aged stands, forest floor carbon stocks, when reported, were highest in plantation stands compared to natural stands, as was the trend in the younger stands. Many studies of stands in the mid-aged group did not include estimates of CWD carbon stocks or biomass, so it is difficult to make any conclusions about this ecosystem component. Our mid-aged jack pine stands varied widely in CWD carbon stocks; the stands on mesic sites were beginning to self-thin and produce considerable amounts of CWD, while the stands on dry sites had not yet reached this phase of development and contained very little CWD.

In the black spruce stands, CWD tended to be found in greater amounts in the natural stands, but data was sparse.

The oldest plantation stands (47–53 years; jack pine only) also contained more carbon in aboveground tree biomass than most, but not all, of the natural stands. The difference in forest floor carbon stocks (generally higher in the plantations compared to the natural stands) was maintained in this age group; when reported, forest floor values from natural jack pine stands were always lower than those from the plantations. Only a natural black spruce stand, also from the Nipigon area (Gordon 1983), had similar forest floor carbon stocks to our jack pine plantations.

We could find no information on North American boreal conifer plantations older than 53 years; however, we included in our compilation natural stands 60–80 years old (not yet "old growth", but older than stands in our study) to illustrate that the plantation carbon stocks, in all measured ecosystem components, generally exceeded even those in natural stands a decade or more older. We did not include "old growth" natural stands since the purpose of the exercise was to compare the plantations with natural stands of similar ages and/or stages of development, and we do not yet have plantations old enough to compare with ~100-year-old-plus natural stands on this basis. It remains uncertain whether plantations will ultimately accumulate more biomass and carbon than natural forests by the end of a rotation, or whether they simply accumulate carbon at a faster rate and hence reach their maximum value sooner.

In addition to total ecosystem stocks, the distribution of carbon within forest stands is important to consider when trying to understand the effects of forest management disturbances on carbon accumulation and dynamics in forests. Although harvesting (either stem only or full tree) of the oldest dry jack pine stand in this study would remove a smaller absolute amount of carbon compared with the old mesic jack pine stand, a greater proportion of the total site carbon capital would be lost from the dry stands. Dead and living organic matter (including in surface mineral soil) were each of similar importance proportionally in mid-aged and older plantations. In terms of carbon storage, the effects of management (and other perturbations such as climate change) on forest floor and soil organic matter will therefore be as important as effects on living trees.

4.2 Mineral Soil Carbon

We found that our oldest jack pine stands had lower mineral soil carbon stocks than our younger stands in both the dry and mesic categories, with the mid-aged stands somewhere in between; however, we cannot regard these stands as chronosequences due to the lack of adequate replication in the youngest and oldest age categories. The differences among stands in soil carbon may be due to management effects (e.g. Harmon and Marks 2002), to differences in site-specific features such as soil texture (Grigal and Ohmann 1992), or to a combination of factors. While studies have shown that forest management has little effect on mineral soil carbon (Johnson and Curtis 2001, Johnson et al. 2002, Howard et al. 2004, Fredeen et al. 2005), studies from northern North America are not numerous, and there remain few opportunities to assess impacts over multiple rotations in this region. In the boreal forest, there have been no long-term studies of forest management effects on soil carbon even through the first rotation; because of the removal of large amounts of organic matter from the ecosystem during harvesting, it would be wise to monitor soil carbon over time in managed stands to gauge the true impact.

Management-induced soil carbon declines have been documented in warmer-climate forests. Turner and Lambert (2000) observed patterns of decline in soil organic carbon under both Eucalyptus grandis and Pinus radiata plantations in Australia: soil carbon appeared to stabilize after several years of loss, but showed no evidence of increasing throughout the rotation period (Turner and Lambert 2000). Declines in soil carbon were attributed to net carbon losses caused by high rates of soil organic matter decomposition following harvesting disturbance, that were not replaced by soil carbon inputs, for example, from root turnover (Turner and Lambert 2000). Sandy soils in particular may be vulnerable to organic matter (and hence carbon) loss due to management activities. Nambiar (1996), referring to the decline in mineral soil carbon concentrations in young P. radiata plantations on sandy soils, suggested that the dynamics of carbon in coarse-textured forest soils are not well understood, and that these soils may be particularly sensitive to changes in carbon inputs and decomposition rates. Both of these can be affected by harvesting and site preparation, especially with practices such as forest floor removal for seedbed enhancement.

4.3 ANPP

There was little information available on rates of NPP for natural stands of comparable ages to our stands. We did find higher ANPP values in our managed stands compared to those summarized for mature boreal forest by Gower et al. (2001), which were between 0.65 to 1.3 Mg C $ha^{-1}\,y^{-1}$ in black spruce (115 to 200 years old), and about 1 Mg C $ha^{-1}\,y^{-1}$ in jack pine (63 to 65 years old). However, ANPP values in our stands are at the low end of the range reported by Cannell (1982; as cited in Perry 1994) for boreal forests worldwide, and for pine forests (Pinus resinosa, P. strobus, and jack pine) in the mid-Atlantic U.S. region (Jenkins et al. 2001). The latter study did not include values for black spruce forests, but did report ANPP values in Picea glauca/Abies balsamea forests to range from 2.2 to 4.8 Mg C $ha^{-1}\,y^{-1}$ (values converted to carbon, using a factor of 0.5, for comparative purposes). The ANPP of the Beardmore black spruce plantations corresponds with the low end of this range.

ANPP values reported by Gordon et al. (2000) for 27-year-old black spruce plantations in central Ontario were very similar to those of the 36-year-old plantation in the current study (2.3 Mg C $ha^{-1}\,y^{-1}$). For jack pine, Morrison and Foster (2001), in north central Ontario, estimated the ANPP of natural stands 20 to 65 years old to range from 2.5 to 3.5 Mg C $ha^{-1}\,y^{-1}$ (including understory vegetation) depending upon stand age. This compares well with the ANPP estimates for jack pine plantations in our study, (2.1 to 3.5 Mg C $ha^{-1}\,y^{-1}$) with the jack pine stands on dry (sandy) sites occupying the low end of this range. Foster (1974), working in a 30 year old natural jack pine stand in central Ontario, found a much higher rate of litterfall (3729 kg $ha^{-1}\,y^{-1}$) than in the dry jack pine stand in our study (1662 kg $ha^{-1}\,y^{-1}$), despite similar age, stocking, and site type. The more southerly location of Foster's study may partially explain the difference, but the hampered productivity in our stand may also stem from the drastic removal of organic matter (blading treatment, which removed slash and forest floor) that occurred during site preparation. Sandy, nutrient poor sites are more susceptible to decreased productivity from organic matter removal and associated nutrient depletion (e.g. Bhatti et al. 1998); the low productivity in our 34-year-old dry jack pine stand (P3) may be evidence of this, as the blading treatment in this stand was particularly severe (personal observation).

In fast-growing plantation forests in warm climates, where productivity changes over several rotations have been measured, increases in productivity have generally been attributed to greater inputs of management resources, including the planting of tree species with inherently high rates of productivity in short rotation situations (e.g. Samuelson et al. 2001). In northern forests, less information is available on management-related changes to NPP, especially with reference to long-term effects of intensive management. Reich et al. (2001), working in the southern boreal forest region in Minnesota, compared ANPP in logged versus burned stands of jack pine, and found that 31 to 33-year-old logged (naturally regenerated) stands had lower ANPP than fire-regenerated stands of the same age, although not significantly lower. The authors concluded that logging had not affected ANPP differently than wildfire. The ANPP estimations for the jack pine stands in the current study compare well with their values for similarly aged jack pine, falling somewhere in between their logged and burned stands. The ANPP of the mesic jack pine plantation in this study, however, surpasses that of Reich et al. (2001).

Whether or not the alteration of forest structure through management will lead to a reduction in sustainability or future productivity cannot be directly addressed in this paper. However, given the susceptibility of poor sites to productivity declines due to management-related organic matter removal (e.g. Carlyle and Nambiar 2001), further investigation of the dynamics of organic matter in managed boreal forests is encouraged. To ensure that managed forests retain the capacity to produce biomass and sequester carbon in amounts comparable to naturally disturbed and regenerating forests, we need to determine under what circumstances and by what mechanisms soil disturbance and removal of biomass in harvesting may result in soil organic matter deficiencies and impacts on long-term productivity (e.g. Morris 1997). To gain a more complete understanding of carbon dynamics in these managed ecosystems, more information is also needed on carbon outputs (e.g. soil respiration and leaching) as well as below-ground allocations of NPP.

5 Summary and Conclusions

Carbon stocks and fluxes were estimated in managed stands of jack pine and black spruce ranging in age from 10 to 53 years. Ecosystem carbon stocks (including surface mineral soil, forest floor, and all aboveground biomass and woody debris) ranged from 47 to 151 Mg C ha^{-1}, and were highest in jack pine stands on mesic sites. Understory vegetation, DWD, snags, and non-crop trees represented minor quantities of carbon relative to crop trees, forest floor, and mineral soil.

The ability of managed stands to accumulate carbon will depend upon species, site type, the degree to which site resources have been depleted by management practices, and rotation length. The age-class structure of the managed forest landscape will also be important for higher-level processes relevant to carbon sequestration. The results of this study suggest that crop species selection and age distribution of the regenerating forests created through the conversion of natural forests to intensively managed, single-species plantations will influence carbon pools and fluxes and hence carbon sequestration rates in northern Ontario forests. At the stand level, the accumulation of carbon may be accelerated by plantation forestry, at least through the first rotation, although the amount of carbon sequestered by maturity may not differ appreciably between managed and unmanaged forests of similar ages. Although we made useful comparisons between managed stands and similarly-aged unmanaged stands using data from the literature, investigations directly comparing developing plantations with natural forests developing after stand-replacing fire are necessary to further elucidate the magnitude and nature of changes to carbon stocks induced by forests management.

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Total of 62 references