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Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada

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Abstract

We calculated carbon budgets for a chronosequence of harvested jack pine (*Pinus banksiana* Lamb.) stands (0-, 5-, 10-, and ~29-year-old) and a ~79-year-old stand that originated after wildfire. We measured total ecosystem C content (TEC), above-, and belowground net primary productivity (NPP) for each stand. All values are reported in order for the 0-, 5-, 10-, 29-, and 79-year-old stands, respectively, for May 1999 through April 2000. Total annual NPP (NPP_T) for the stands ($Mg\,C\,ha^{-1}\,yr^{-1} \pm 1$ SD) was 0.9 ± 0.3, 1.3 ± 0.1, 2.7 ± 0.6, 3.5 ± 0.3, and 1.7 ± 0.4. We correlated periodic soil surface CO_2 fluxes (R_S) with soil temperature to model annual R_S for the stands ($Mg\,C\,ha^{-1}\,yr^{-1} \pm 1$ SD) as 4.4 ± 0.1, 2.4 ± 0.0, 3.3 ± 0.1, 5.7 ± 0.3, and 3.2 ± 0.2. We estimated net ecosystem productivity (NEP) as NPP_T minus R_H (where R_H was calculated using a Monte Carlo approach as coarse woody debris respiration plus 30–70% of total annual R_S). Excluding C losses during wood processing, NEP ($Mg\,C\,ha^{-1}\,yr^{-1} \pm 1$ SD) for the stands was estimated to be -1.9 ± 0.7, -0.4 ± 0.6, 0.4 ± 0.9, 0.4 ± 1.0, and -0.2 ± 0.7 (negative values indicate net sources to the atmosphere.) We also calculated NEP values from the changes in TEC among stands. Only the 0-year-old stand showed significantly different NEP between the two methods, suggesting a possible mismatch for the chronosequence. The spatial and methodological uncertainties allow us to say little for certain except that the stand becomes a source of C to the atmosphere following logging.

Key words: boreal forest, carbon sequestration, forest management, net ecosystem productivity, net primary productivity, *Pinus banksiana*

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Introduction

Understanding boreal carbon dynamics requires that we understand the effects of disturbance. Boreal forests play an important role in the global climate system (Chapin *et al.*, 2000) through the storage of several hundred petagrams of carbon in soils and detritus (Post *et al.*, 1982; Meentemeyer *et al.*, 1985; Goulden *et al.*, 1998, Hobbie *et al.*, 2000), through the biophysical control of vegetation on albedo (Bonan *et al.*, 1992; Foley *et al.*, 1994), and through the release of millions of tonnes of CO_2 to the atmosphere as a result of large-scale fires (Cahoon *et al.*, 1994; Goldammer & Furyaev, 1996; Cofer *et al.*, 1998; Harden *et al.*, 2000; Amiro *et al.*, 2001; Wang *et al.*, 2001). There is evidence that the boreal forest biome's status as a C sink or source varies from year to year (Wang & Polglase, 1995; Bousquet *et al.*, 2000), and research has generally measured low average rates of sequestration in boreal forests compared with temperate and tropical biomes (Valentini *et al.*, 2000; Prentice *et al.*, 2001). The low long-term rates of sequestration in boreal forests are at least partly due to disturbance.

The boreal forest is dominated by stand-renewing fires (average return intervals ~ 50–500 years) and by periodic insect outbreaks (Bonan & Shugart, 1989;

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Payette, 1993). Eddy covariance and inventory studies suggest that the annual net C exchange of some boreal forest stands changes between sink and source because of temperature sensitivity or disturbance history (Goulden *et al*., 1998; Lindroth *et al*., 1998; Arain *et al*., 2002). Diverse methods (Kurz & Apps, 1999; Harden *et al*., 2000; Goodale *et al*., 2002; Gurney *et al*., 2002) provide evidence that a recent surge in fire and insect disturbance rates (Auclair & Carter, 1993; Kurz & Apps, 1996), combined with increased temperatures, has caused Canada's boreal forest to become a small net source of C in recent decades.

In addition to these natural processes, human activity also impacts boreal forest structure and function, yet we have little understanding of how wood harvesting affects C dynamics and climate. In the past century, logging has contributed to only a small fraction of disturbance effects on boreal forests, trailing behind wildfires and insect outbreaks (Kurz & Apps, 1996). However, as demand for forest products continues to rise in the next century, many countries will experience greater pressure to harvest more of their boreal forests. Approximately 1 million ha of Canadian forest are logged annually (20 000 in Saskatchewan), the largest proportion of which is boreal (Canadian Forest Service, 1999). Understanding how logging impacts the C balance of Canadian boreal forests is critical for determining appropriate management scenarios.

The primary objective of this study was to quantify the changes in C content and annual sequestration for a jack pine (*Pinus banksiana* Lamb.) logging chronosequence using ground-based measurements of biomass, detritus, and C fluxes. The chronosequence approach 'trades space for time' as a way to observe longer-term successional patterns than is possible in most studies. Limitations of this approach will be discussed.

Methods and experimental design

Site description

The study area was located approximately 100 km northeast of Prince Albert, Saskatchewan, Canada, near the southern limit of the boreal forest in the mid-boreal upland ecoregion (Acton *et al*., 1998). It was part of the Southern Study Area (SSA) of the BOReal Ecosystem-Atmosphere Study (BOREAS) (Gower *et al*., 1997), and falls within Weyerhaeuser Canada's Forest Management Licence Agreement area.

The jack pine ecosystem is an important component of Canadian boreal upland forests, and similar ecological equivalents exist in Scandinavia and Eurasia. This study focused on the jack pine–lichen forest subtype, which dominates poor quality outwash sands in even-aged cohorts with a relatively frequent fire return interval (Majcen *et al*., 1980). The typical forest harvest practice for jack pine stands (Rudolph & Laidly, 1990) is clear-cutting with branches and foliage left on site, followed by mechanical site preparation (scarification) to improve natural regeneration (Weber *et al*., 1995).

We selected five jack pine stands of different ages to form a chronosequence (Table 1). Prior to harvest, they were mature jack pine stands that originated after wildfire. The premise of the chronosequence approach is that the stands have similar environmental conditions and past history (Amundson & Jenny, 1997). The five stands differed, theoretically, only in harvest year and represented the jack pine community at critical stages during succession. We identify stands by the age of the overstory in 1999, estimated from ring count at the soil surface (5–10 trees per stand). Since seedling establishment may lag disturbance for several years, and since in-seeding in an 'even-aged' stand can span more than a decade, the designation of stand age is somewhat arbitrary and may differ from other studies conducted at the same locations. The mature stand was ~79 years old, originated after a catastrophic fire in the early 1920s, and served as an example of preharvest conditions. The 0-, 5-, 10-, and 29-year-old stands represented a recent clear-cut, stand reinitiation, and early and late aggradation stages of stand development, respectively. The three youngest stands had been disc trenched, with no apparent thinning or planting. The BOREAS SSA young and old jack pine stands (Gower *et al*., 1997) were the 29- and 79-year-old stands, respectively.

All stands were on coarse, excessively drained, nutrient-poor, sandy, permafrost-free, upland Brunisols with an organic layer of varying thickness (Gower *et al*., 1997; Steele *et al*., 1997; Acton *et al*., 1998). Stands were located in flat portions of the glacial outwash plain, within 7 km of each other.

Average growing seasons last approximately 150 days (Rowe, 1972) from May to October. Mean air temperatures are −19.8 °C for January and 17.6 °C for July, with mean annual precipitation of 405 mm (Environment Canada, 1993).

The primary groundcover was a mixture of reindeer lichen (*Cladina* spp.), which dominated the older stands, and bearberry (*Arctostaphylos uva-ursi*), which dominated the younger stands. Infrequent, scattered clumps of green alder (*Alnus crispa*) co-occurred with feathermoss (*Pleurozium* spp.). Grasses were present at all four logged stands, and were prevalent at the two youngest stands. However, the 0-year-old clear-cut had little vegetation until the summer of 2000 because of the logging disturbance. Other common forbs and shrubs

Table 1 Stand locations, plot sizes (m × m), tree height (m) stem diameters (cm), stem densities (ha^{-1}), basal area ($m^2 ha^{-1}$), and overstory leaf area index ($ha\,ha^{-1}$) at the five stands for the 1999 and 2000 growing seasons

	Stand age				
	0-year-old	5-year-old	10-year-old	29-year-old	79-year-old burn
Latitude (decimal °)	53.853°N	53.908°N	53.911°N	53.876°N	53.916°N
Longitude (decimal °)	104.625°W	104.655°W	104.652°W	104.645°W	104.692°W
Plot size (m × m)	15 × 15	10 × 10	15 × 15	10 × 10	25 × 25; 20 × 20[§]
Tree height (approx.) (m)	None	0–3	2–4	No data	12–15
DBH (cm)*					
Mean	None	None	2.3	3.7	13.1
Range	None	None	0.3–8.0	0.2–13.1	3.9–22.9
D_0 (cm)[†]					
Mean	None	1.4	1.5	0.9	None
Range	None	0.4–6.7	0.4–3.8	0.3–1.7	None
Live stems (ha^{-1})					
1999	0	4925 (3481)	5789 (2687)	13050 (3465)	1196 (146)
2000	0	8625 (6232)	6111 (2751)	12575 (3211)	1160 (138)
Dead stems (ha^{-1})[‡]					
1999	0	0	22 (25)	475 (550)	776 (301)
2000	0	0	189 (179)	800 (678)	808 (312)
Basal area ($m^2 ha^{-1}$)*					
1999	0	0	2.0 (0.7)	16.5 (3.1)	17.4 (3.0)
2000	0	0	3.6 (1.1)	19.0 (3.0)	17.6 (3.2)
Overstory LAI ($ha\,ha^{-1}$)[‡]					
1999	0	0.1 (0.1)	0.6 (0.2)	2.6 (0.5)	1.3 (0.3)
2000	0	0.6 (0.4)	1.1 (0.4)	2.9 (0.4)	1.3 (0.3)

Values in parentheses are ± 1 standard deviation ($n = 4$).

*Only for trees 1.37 m tall or taller.

[†] Only for trees shorter than 1.37 m. D_0 refers to the stem diameter at the soil surface.

[‡] For all trees, including seedlings and saplings.

[§] Three of the four replicate plots were 25 × 25 m; the fourth was 20 × 20 m. These were previously sited plots from BOREAS.

were bog cranberry (*Vaccinium vitis-idaea*), blueberry (*Vaccinium myrtilloides*), willow (*Salix* spp.), and red-osier dogwood (*Cornus stolonifera*). There were no seedlings or saplings in the understory of the 79-year-old stand.

Experimental design

We established four representative, replicate square plots in random locations in each stand in May 1999. Plot size varied depending on stand age and density and ranged from 10 m × 10 m in the younger stands to 25 m × 25 m in the oldest stand (Table 1). Measurements were taken in and near these plots between May 1999 and November 2000 to characterize the stands and to determine ecosystem C content and fluxes. Throughout the text, biomass refers to live vegetation biomass only. All values for ecosystem components (i.e. biomass, detritus, and mineral soil) are always expressed in terms of C content in Mg C.

Biomass, leaf area index (LAI), and net primary productivity (NPP)

Allometry. Tree biomass, NPP, and one-half total surface LAI were estimated using allometric regression equations developed specifically for boreal jack pine (after Gower *et al.*, 1997; Gower *et al.*, 1999; Bond-Lamberty *et al.*, 2002a; Wang *et al.*, submitted for publication). Equations were of the form $\log_{10} M = a + b(\log_{10} D)$, where M is component biomass or area and D is stem diameter at 1.37 m (DBH) or 0 m (D_0) above the soil surface. We used site-specific equations for saplings and larger trees (Gower *et al.*, 1997; S. J. Steele, unpublished data; and this study (data not shown)). Equations developed for jack pine seedlings near Thompson, Manitoba were used for smaller-diameter trees (Bond-Lamberty *et al.*, 2002a).

Before needle elongation in May 1999, all trees were tagged, and the DBH of each tree taller than 1.37 m (or, for shorter trees, the D_0) was measured in each replicate plot. After two growing seasons (October 2000), the diameters were remeasured (for all trees with DBH <3.0 cm) or calculated from radial increment cores (for all trees with DBH >3.0 cm), and new seedling D_0s were measured for the first time.

We calculated dry biomass of each tissue component for each tree for May 1999 and October 2000. Unless otherwise noted, C content of all tissue components was estimated as the product of dry biomass and an assumed C concentration of 0.45 for foliage and herbaceous tissues, and 0.50 for wood and roots (Atjay *et al.*, 1977).

Aboveground biomass. We estimated aboveground tree biomass as the sum of stem, branch, and foliage biomass for each tree in each measurement year using allometry. We estimated vascular understory biomass (AB_U) in July 1999 using four 0.71 m × 0.71 m clipped subplots, which were randomly located in each replicate plot (16 subplots per stand) (Gower *et al.*, 1997).

Belowground biomass. Coarse root (>5 mm diameter) biomass (B_{CR}) was calculated using allometry. Fine root biomass (B_{FR}) (understory plus jack pine roots <5 mm diameter) was estimated using soil cores (Steele *et al.*, 1997). Ten soil cores (10 cm diameter × 30 cm deep) were collected from each plot (40 per stand) between May 13 and 18, 1999. This depth was judged to be sufficient because our field experience and previous work by Strong & Roi (1983) suggest that more than 90% of root biomass generally occurs within 20 cm of the forest floor. Sieved roots were dry-ashed at 450 °C for 24 h to correct for mineral soil contamination (Steele *et al.*, 1997).

Aboveground NPP. We estimated aboveground tree NPP ($ANPP_{JP}$) using allometric equations for stem biomass, branch biomass, and new foliage production. Average annual $ANPP_{JP}$ was calculated for the 1999 and 2000 growing seasons as

$$\mathrm{ANPP}_{\mathrm{JP}} = \Delta B_{\mathrm{w}} + D_{\mathrm{w}} + \mathrm{NF} + H \approx \Delta B_{\mathrm{w}} + \mathrm{NF}, \qquad (1)$$

where ΔB_W is the change in woody biomass, D_W is woody detritus production (not measured), NF is annual new foliage production, and H is herbivory (Gower *et al.*, 1999). Herbivory was assumed to be negligible, but we accounted for tree mortality by assuming that trees that died during the study had negligible NPP and calculating annual B_W and NF only for the trees alive at the end of the study (Clark *et al.*, 2001).

We estimated aboveground understory NPP ($ANPP_U$) using clipped subplots (described above). $ANPP_U$ was calculated as the sum of annual herbs plus new twig and new foliage biomass of perennials. Three $ANPP_U$ components were neglected because they were too small to measure reliably: radial stemwood increment, lichen (Ipatov & Tarkhova, 1983), and feathermoss (which only covered 0–1% of the ground surface).

Belowground NPP. Coarse root NPP (NPP_{CR}) was calculated as the annual increment in B_{CR} using allometry. We neglected CR turnover (detritus production of live trees), but accounted for CR mortality (of dead trees) in the snag pool (see below).

Fine root NPP (NPP_{FR}) (jack pine plus understory) was determined using the ingrowth core method (Steele *et al.*, 1997). Five soil cores (10 cm diameter × 30 cm deep) were removed from each plot (20 per stand) between May 13 and 18, 1999, sieved, and composited by plot and horizon. The root-free soil and forest floor were replaced in the holes by horizon. This method probably underestimates NPP_{FR}, because it excludes production and turnover between measurements (although reduced competition among roots may stimulate growth, having the opposite effect). Steele *et al.* (1997) showed that soil disturbance from this method depresses root growth in the first year, so we take the average growth from the first two years to minimize disturbance effects. These ingrowth cores were sampled after two growing seasons (on October 31, 2000) using a 4.9 cm × 30 cm deep corer, and were treated as described above for B_{FR}.

Detritus and mineral soil

Forest floor. Forest floor samples were collected at five random locations in each plot using a 25.2 cm diameter ring. Material within the ring was collected down to mineral soil, including moss and lichen biomass, fine litter (<1 cm diameter), and buried coarse woody debris (CWD) (>1 cm diameter). Live vascular plants and coarse roots were excluded. Samples were dried at 70 °C, weighed, and ground. Subsamples were analyzed for total % C and % N (results not shown) on a Carlo Erba elemental analyzer (CE Instruments, Wigan, UK) coupled to a Europa 20-20 tracemass (PDZ Europa, Cheshire, UK).

Coarse woody debris and snags. C content of CWD (downed wood and stumps) was estimated using three 1 m × 10 m transects for each stand, plus either one (for the 0-, 5-, and 29-year-old stands) or two (for the 10- and 79-year-old stands) 1 m × 50 m transects for each stand. All visible CWD >1.0 cm diameter was collected from these randomly oriented transects adjacent to the biomass plots and sorted by size and decay class (Bond-Lamberty *et al.*, 2002b).

Standing dead wood (snag) mass was estimated for each plot using stem diameters and allometric equations for old stem, branch wood, and coarse roots. Dead/dying coarse roots at the 0-year-old stand were estimated as equal to the live CR component at the 79-year-old stand.

Mineral soil. Three randomly located mineral soil samples of known volume were collected from each plot at each of two soil depths (0–10.2 cm and 10.2–20.4 cm). Each of these samples was dried and weighed for calculation of bulk density (Elliott *et al*., 1999), ground, and analyzed for total % C and % N (results not shown). We installed one representative soil pit at each stand to characterize the profile to the C horizon (~1 m). Data from Vogel & Gower (1998) were used for the 79-year-old stand.

Soil surface CO_2 flux (R_S) and CWD respiration (R_{CWD})

Soil surface CO_2 flux (R_S). R_S (the sum of root respiration (R_R) and heterotrophic respiration (R_H) (Raich & Schlesinger, 1992)) were measured four to five times per year in 1999 and 2000. Four 15.3 cm diameter PVC collars were randomly located in each plot (16 total per stand) and inserted about 2 cm deep into the soil, minimizing disturbance. R_S was measured in each of the collars using a LI-6200 closed, dynamic infrared gas analyzer system (LI-COR, Inc., Lincoln, NE, USA) fitted with a clear, 15 cm diameter soil respiration chamber (see Norman *et al*., 1997 for complete description).

We developed site-specific empirical regression models for daily R_S (Striegl & Wickland, 1998) using gravimetric soil moisture samples (Gardner, 1986) and 2 and 10 cm soil temperatures taken adjacent to each of the collars at the time of measurement. These models were used with continuous 60 min averages of soil temperature and moisture from each of the stands to estimate annual R_S. Data loggers fitted with thermocouples and CS615 soil water reflectometers (Campbell Scientific, Inc., Logan, UT, USA) were used at the harvested stands. Soil temperature and moisture data for the 79-year-old stand were obtained from the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (unpublished data).

CWD respiration (R_{CWD}). The small size of the R_S chambers could not accommodate most CWD, which was shown to be a significant CO_2 source for some stands in a previous boreal study (Bond-Lamberty *et al*., 2002b; Wang *et al*., 2002b). Therefore, to estimate total annual R_{CWD} at each stand, we used estimates from the literature (some interpolated) for CWD decomposition rates (k_{CWD}), applied them to our measured CWD amounts (mean ± 3 standard deviations of among-plot variability), and developed six different scenarios for a Monte Carlo analysis: k was constant at 0.034 per year (the average value for jack pine CWD in well-drained stands in a burn chronosequence (Bond-Lamberty *et al*., 2002b; Wang *et al*., 2002b)); or k varied (between 0.005 and 0.1 per year) with time since disturbance, CWD size class, and decomposition class. Minimum and maximum annual R_{CWD} estimates from these scenarios for each stand were used as limits for a Monte Carlo model to generate an estimate of the mean and standard deviation of annual R_{CWD}. We neglected respiration of snags, which was assumed to be small compared with R_{CWD}. Respiration of dead coarse roots was accounted for in R_S.

Net ecosystem productivity (NEP) and heterotrophic respiration (R_H)

Flux estimate approach. NEP is the net annual exchange of C for an ecosystem. We adopt the sign convention that positive NEP denotes a sink and negative NEP denotes a source. We estimated annual NEP as

$$\mathrm{NEP} = \mathrm{NPP}_T - R_H, \tag{2}$$

$$R_H = R_S - R_R + R_{CWD} \approx f(R_S) + R_{CWD}, \tag{3}$$

where f varied from 0.3 to 0.7, and where NPP_T is total net primary productivity (the sum of ANPP_{JP}, ANPP_U, NPP_{FR}, and NPP_{CR}). We assumed other losses from the ecosystem (e.g. leaching, erosion, and volatilization) were negligible.

Accurately partitioning the measured R_S flux into R_R and R_H is problematic. Previous work suggests that live R_R contributes between 30% and 70% of the annual flux (Schlesinger, 1977; Ewel *et al*., 1987; Raich & Nadelhoffer, 1989; Haynes & Gower, 1995; Ryan *et al*., 1997b; Striegl & Wickland, 1998; Hogberg *et al*., 2001), with ~ 50% cited most commonly as a 'best guess' for forests (see Anderson, 1992; Landsberg & Gower, 1997; Hanson *et al*., 2000; Wang *et al*., 2002a). This number could vary with ecosystem structure, successional stage, fertility, microbial community, seasonality, and microenvironment.

To calculate NEP, we used a Monte Carlo approach (Law *et al*., 2003). We randomly varied all components of NPP_T according to a normal distribution within ± 3 standard deviations of the mean, among-plot values. We set maximum and minimum values for R_H (before adding R_{CWD}) as ($0.3R_S - 3\,\mathrm{SD}(R_S)$) and ($0.7R_S + 3\,\mathrm{SD}(R_S)$), respectively, for each stand to account for uncertainty in partitioning R_H and for among-plot spatial variation in R_S. We randomly varied R_H within this interval according to a uniform distribution. These results were summed together with R_{CWD} according to Eqns (2) and (3) to derive NEP at each stand.

Stocks approach. As a check against the flux budget method, we also calculated NEP between pairs of stands using a change in stocks approach:

$$\mathrm{NEP}\,(\mathrm{stand}\,x\,,\mathrm{stand}\,y) = \frac{\mathrm{d}C(x,y)}{\mathrm{d}t(x,y)} \approx \frac{\mathrm{TEC}(x) - \mathrm{TEC}(y)}{\mathrm{Age}(x) - \mathrm{Age}(y)}, \quad (4)$$

where TEC is total ecosystem C content for a stand and Age is the number of years since stand establishment. This approach complements the flux estimate approach to calculating NEP, which can only estimate NEP for an individual year. The stocks approach calculates the average annual rate of change in TEC that would be necessary to account for the difference in measured TEC between two stands in a chronosequence. Using the two approaches helps to constrain the instantaneous annual NEP flux estimates by determining whether they are realistically representative of the ecosystem's rate of change over time. We calculated NEP for each pair of stands using Monte Carlo simulation, with limits based on the among-plot spatial variability in TEC and the uncertainty in stand age.

Statistical analysis

Values for each of the stands are averages for the four replicate plots ± 1 standard deviation unless otherwise noted. The standard deviations reported for Monte Carlo analyses take into account both among-plot spatial variability and a measure of uncertainty in parameter choice. We repeated Monte Carlo simulations 4000 times to ensure that variance of the estimate had stabilized.

We used nested one-way mixed model analysis of variance (ANOVA) to determine the effect of stand (fixed), plot (random), and the interaction between the two on ecosystem characteristics after checking assumptions and correcting for heteroscedasticity (Sokal & Rohlf, 1995). ANOVA uses *F*-ratios, ratios of mean squares (MS), to indicate whether groups are significantly different from each other. We tested for differences among replicate plots, within the stands, using $F = \mathrm{MS}_{\mathrm{stand:plot}}/\mathrm{MS}_{\mathrm{residuals}}$ (where $\mathrm{MS}_{\mathrm{stand:plot}}$ is variation among plots, but within stands, and has 15 degrees of freedom). When an ecosystem characteristic differed among the five stands (based on $F_{4,15} = \mathrm{MS}_{\mathrm{stand}}/\mathrm{MS}_{\mathrm{plot}}$), we used Fisher's protected least significant difference (LSD) test to determine significant differences ($\alpha = 0.05$) among stands (Sokal & Rohlf, 1995). For summary quantities that could not be calculated below the plot level (e.g. total ecosystem C, NPP, NEP) we used one-way ANOVA without nesting.

Linear regression parameters for allometric equations and R_S models were tested using the appropriate *F*-tests, and log transformations were used to correct for heteroscedastic variance (Chatterjee & Price, 1991; Sokal & Rohlf, 1995).

We attempted to minimize the variability in state factors among these stands, other than age. Inference should only be drawn for these five stands comprising the chronosequence, since the stands themselves are unreplicated, and not necessarily representative of all clear-cut jack pine stands of similar ages (*sensu* Hurlbert, 1984).

Results and discussion

Carbon content and accumulation

Biomass and LAI. Total live C content increased significantly with stand age ($F = 212.8$; $P < 0.001$) (Table 2). Jack pine foliage biomass increased with stand age through the 29-year-old stand, but the 79-year-old stand had 45% less foliage biomass than the 29-year-old stand. Annual biomass accumulation in jack pine (rate of increase in aboveground plus coarse root biomass) decreased with stand age. Fine root biomass (woody plus herbaceous) showed no consistent pattern with stand age, LAI, or foliage NPP. Carbon content of the understory differed significantly among stands ($F = 4.49$, $P = 0.014$), and peaked early in the chronosequence at the 5- and 10-year-old stands (which had significantly more C than all but the 29-year-old stand). Understory C content was very sparse ($0.03 \pm 0.04\,\mathrm{Mg\,C\,ha^{-1}}$) at the 0-year-old clear-cut in 1999 – the season immediately following harvest and the only year we measured. However, there was significantly more understory at that stand in summer 2000, probably a similar amount to that at the 5-year-old stand. Similar patterns in biomass accumulation have been observed for a black spruce fire chronosequence in Manitoba (Bond-Lamberty *et al.*, 2002c; Wang *et al.*, 2003), for a mixedwood logged chronosequence in Manitoba (Plaut, 2002), and for lichen-type Scots pine chronosequences in Siberia (Wirth *et al.*, 2002b). LAI followed the expected pattern of increasing rapidly following disturbance, approaching an asymptote, and declining (Gower *et al.*, 1996a).

Detritus and mineral soil

The total C content of the detritus and mineral soil was significantly greater at the 0-year-old clear-cut, and

Table 2 Above- and belowground carbon distribution (Mg C ha^{-1}) by ecosystem component for the five jack pine stands in 1999 and 2000

	0-year-old		5-year-old		10-year-old		29-year-old		79-year-old*	
Mg C ha^{-1}	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000
Living vegetation										
Jack pine stem	0.0	0.0	0.1 (0.0)	0.6 (0.4)	1.4 (0.5)	2.2 (0.8)	14.6 (3.4)	17.0 (3.6)	26.6 (5.4)	26.8 (5.7)
Jack pine branch	0.0	0.0	0.0 (0.0)	0.2 (0.1)	0.6 (0.2)	1.0 (0.3)	2.5 (0.5)	3.0 (0.5)	4.2 (1.1)	4.3 (1.2)
Jack pine foliage	0.0	0.0	0.1 (0.0)	0.3 (0.2)	0.8 (0.3)	1.4 (0.5)	2.0 (0.4)	2.3 (0.3)	1.1 (0.2)	1.1 (0.2)
Understory (aboveground)	0.0 (0.0)	–	0.5 (0.3)	–	0.8 (0.7)	–	0.1 (0.1)	–	0.1 (0.1)	–
Jack pine coarse root	0.0	0.0	0.0 (0.0)	0.2 (0.1)	0.3 (0.1)	0.7 (0.2)	3.8 (0.9)	4.5 (0.9)	6.0 (1.2)	6.0 (1.3)
Fine root	1.2 (0.1)	–	0.7 (0.2)	–	1.1 (0.2)	–	1.3 (0.3)	–	0.8 (0.1)	–
Total jack pine (aboveground)	0.0	0.0	0.1 (0.1)	1.1 (0.8)	2.8 (1.1)	4.5 (1.6)	19.2 (4.1)	22.3 (4.2)	31.8 (6.7)	32.1 (7.1)
Total live (aboveground)	0.0 (0.0)	–	0.6 (0.3)	–	3.6 (0.5)	–	19.3 (4.1)	–	31.9 (6.7)	–
Total live (belowground)	1.2 (0.1)	–	0.7 (0.2)	–	1.4 (0.2)	–	5.1 (0.6)	–	6.8 (1.3)	–
Total live	1.2 (0.1)	–	1.4 (0.4)	–	5.0 (0.5)	–	24.4 (4.7)	–	38.7 (8.0)	–
Detritus/mineral soil										
Standing dead[†]	0.0	0.0	0.0	0.0	0.0 (0.0)	0.0 (0.0)	0.4 (0.8)	0.4 (0.8)	6.7 (2.4)	7.3 (2.3)
Dead/dying roots from harvest[‡]	6.0 (~1.2)	–	–	–	–					
Coarse woody debris[§]	6.8 (2.5)		7.1 (3.3)		3.8 (2.7)		2.0 (0.1)		3.2 (1.2)	
Forest floor[¶]	26.9 (11.9)		12.4 (2.8)		10.9 (2.3)		11.0 (3.6)		8.6 (1.2)	
Mineral soil	32.1 (6.1)		22.0 (5.8)		27.9 (13.4)		27.8 (10.7)		20.9 (3.0)	
Total detritus/mineral soil	71.8 (17.7)		41.4 (6.6)		42.6 (14.9)		41.1 (10.3)		39.4 (7.4)	
Total ecosystem carbon	**73.0 (17.6)**	–	**42.8 (6.9)**	–	**47.6 (14.4)**	–	**65.5 (12.8)**	–	**78.2 (10.6)**	–

Values in parentheses are ± 1 standard deviation ($n = 4$).

*Seventy-nine-year-old stand was established after wildfire.

[†] Includes stem, branch, and coarse roots.

[‡] C content of dead and dying jack pine coarse roots at the clear-cut is estimated to be equivalent to the C content of live jack pine coarse roots at the 79-year-old stand. Value in parentheses is 1 standard deviation ($n = 4$) of the among-plot measurements for the 79-year-old stand.

[§] Includes CWD > 1 cm diameter visible at the surface.

[¶] Includes soil O horizon, live lichen and moss, and all CWD within the O horizon, but not visible at the surface.

essentially equal at the other four stands ($F = 7.59$; $P = 0.0015$; LSD($\alpha = 0.05$) = 23.3). Forest floor C content was largest at the 0-year-old clear-cut (two to three times larger than the other stands), and there was no significant difference among the other stands ($F = 8.51$; $P = 0.0009$; LSD($\alpha = 0.05$) = 0.20 for log-transformed values). Mineral soil C content differed significantly among the five stands according to ANOVA ($F = 3.06$; $P = 0.0496$); however, the LSD at $\alpha = 0.05$ showed no significant difference (LSD = 0.37 for log-transformed values). The 0-year-old clear-cut had the largest mean mineral soil C content, while the 79-year-old stand had the smallest.

A chronosequence of burned jack pine stands in the same eco-climatic region had similar forest floor C values and slightly smaller mineral soil C values (Nalder & Wein, 1999). For a chronosequence of harvested boreal mixedwood stands in Manitoba, Plaut (2002) measured 25–44 $\mathrm{Mg\,C\,ha^{-1}}$ in the forest floor (about 2.5–4.5 × as much as in the present study) and 46–53 $\mathrm{Mg\,C\,ha^{-1}}$ in the mineral soil (about 1.5–2.5 × as much as in the present study). As in the present study, none of these studies found evidence that C accumulated in the forest floor with age. These studies do not support the empirical relationship described by Covington, who also used a chronosequence approach, showing a rapid 50% loss of forest floor mass postharvest, followed by slow recovery (Covington, 1981). Yanai *et al.* (2000, 2003) caution strongly against using a chronosequence approach to predict changes in forest floor C.

The slightly larger mineral soil C content at the 0-year-old clear-cut could be attributed to some combination of three factors: the more fertile preharvest conditions associated with a jack pine–feathermoss–lichen stand (Vogel & Gower, 1998) (see section Chronosequence site matching); the amount of mechanical mixing between forest floor and mineral soil layers during logging; or simply the heterogeneity of mineral soil C storage throughout the stand. We would not expect harvesting to significantly affect the mineral soil C content of a flat, sandy system such as this. A meta-analysis of previous studies also found little evidence that harvest affected soil C content (Johnson & Curtis, 2001).

CWD C content was greatest for the 0- and 5-year-old stands, and smallest for the 29-year-old stand. Snags were only a significant proportion of TEC (9%) for the mature stand. Plaut (2002) found a similar amount of C in CWD for a Manitoba mixed-wood logging chronosequence.

Dynamics of CWD following logging are very different than after fire in many ways. However poor statistical power and high variability in logging practices and fire intensity prevent us from identifying systematic differences in CWD patterns between logged and burned sites in the region. For both the logged stands and the one burned stand, this study found up to four times as much C in CWD as did Nalder & Wein (1999) for comparably aged burned jack pine stands. Bond-Lamberty *et al.* (2002b) measured highly variable amounts of CWD in their wildfire chronosequence with up to 88.8 $\mathrm{Mg\,C\,ha^{-1}}$ at an 11-year-old stand – an order of magnitude more than in the present study. Wirth *et al.* (2002b) also found significantly larger amounts of CWD in most of their burned Scots pine stands, mostly left over from previous disturbance cycles.

In the present study, most logging slash was left flat on the ground, which speeds up its rate of decomposition by several decades compared with burn residues (Nalder & Wein, 1999). So we expect CWD C content to peak immediately following logging, to fall due to decomposition, then to increase again with tree mortality. While the pattern observed roughly approximates this heuristic, we are aware that interstand variance and differences in logging practices among stands within a chronosequence can mask general successional patterns (Yanai *et al.*, 2000). Also, because CWD is very spatially heterogeneous, we have probably undersampled, but we cannot quantify the magnitude or direction of this error.

Total ecosystem C content and distribution. Excluding the 0-year-old clear-cut, TEC increased with age from 42.8 to 46.8, 65.5, and 78.2 $\mathrm{Mg\,C\,ha^{-1}}$ at the 5-, 10-, 29-, and 79-year-old stands, respectively (Table 2; Fig. 1). The 5- and 10-year-old stands had significantly less C than the 79-year-old stand, and the 5-year-old stand had significantly less C than the 0-year-old stand ($F = 8.18$; $P = 0.0010$; LSD($\alpha = 0.05$) = 26.0). Wirth *et al.* (2002b) found similar qualitative trends and similar amounts of C in TEC in their Scots pine study. Because of the large amount of detritus and soil C, the 0-year-old clear-cut contained almost as much C (73.0 $\mathrm{Mg\,C\,ha^{-1}}$ – *after harvesting and removals*) as did the mature stand. This signals that the 0-year-old clear-cut was probably a more productive site prior to harvest than others in the chronosequence (implications discussed below.) The relative distribution of C within each stand also differed significantly. Except for the mature stand, mineral soil comprised the largest fraction of TEC for each stand (42–60%). For the mature stand, the overstory fraction (41%) exceeded the mineral soil fraction (27%).

NPP and allocation

$\mathrm{NPP_T}$ and relative allocation differed among the stands (Table 3; Fig. 2). $\mathrm{ANPP_{JP}}$ and $\mathrm{NPP_{CR}}$ peaked at the 29-

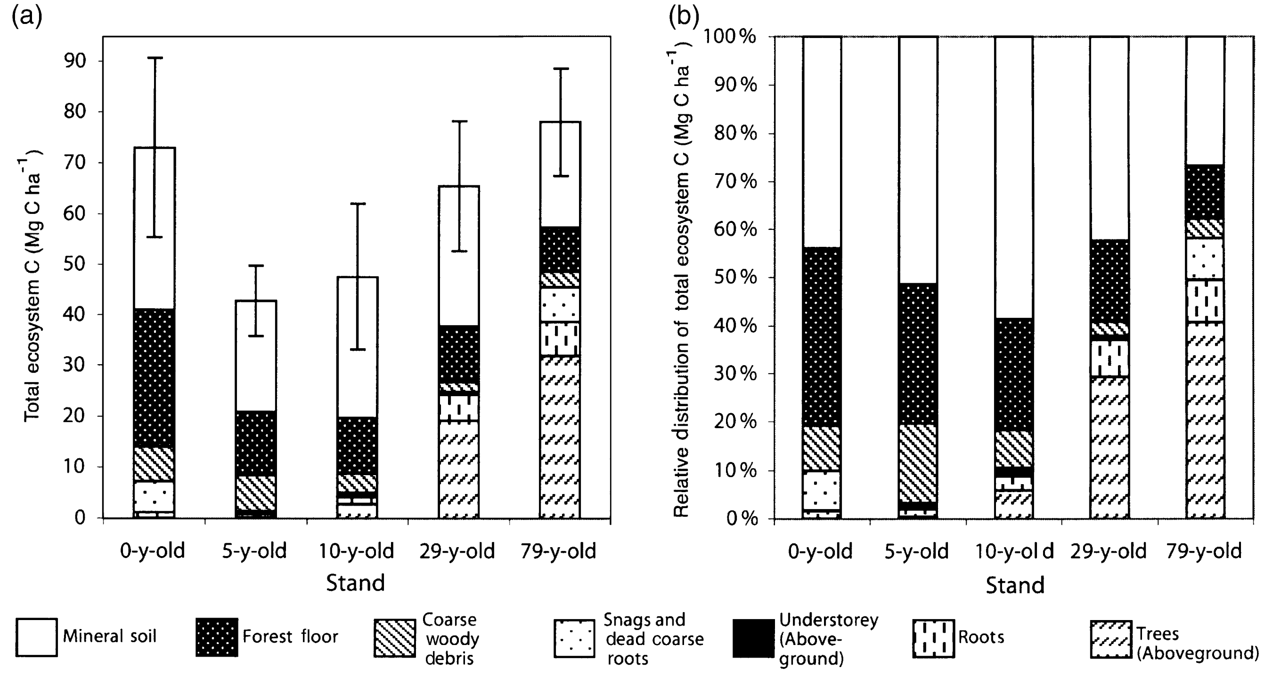

Fig. 1 Total ecosystem carbon content for each stand in 1999. (a) Total C amount by stand and component. (b) Relative C distribution at each stand. Bars represent ± 1 standard deviation, calculated as the difference among plots within each stand. Forest floor includes soil O horizon, live moss and lichen, and buried coarse woody debris. Root biomass includes coarse and fine roots of trees and understory. Dead/dying coarse roots at the 0-year-old clearcut are estimated from the biomass of live coarse roots at the 79-year-old stand. There were no aboveground snags at the 0-year-old stand. Coarse woody debris includes surface CWD > 1 cm in diameter.

year-old stand, which was also the stand with the highest LAI. Total ANPP increased linearly with overstory LAI, although not with NPP_T because NPP_{FR} peaked earlier, at the 10-year-old stand (Fig. 3). NPP_T was significantly higher at the 29-year-old stand than at all other stands except for the 10-year-old stand, which had greater belowground allocation ($F = 33.7$; $P < 0.001$; $LSD(\alpha = 0.05) = 1.58$).

NPP_T increased linearly for approximately the first 15 years, then peaked and leveled off approximately 30 years following disturbance. This pattern was qualitatively similar to the NPP pattern seen following fire in the Albertan boreal plains (Amiro *et al.*, 2000). NPP_T values for the ≥10-year-old jack pine stands were similar to average values for mature evergreen needle-leaf boreal forests (2.42 Mg C ha^{-1} yr^{-1} for *Pinus*, Gower *et al.*, 1997). $ANPP_{JP}$ at the 29-year-old stand was about 113% higher than during BOREAS, while at the 79-year-old stand it was about 25% lower (calculated from Gower *et al.*, 1997). However, the change in NPP between measurements in 1994–1995 and in 1999–2000 cannot be attributed solely to age-related stand dynamics, since interannual climate variability also plays a role (e.g. Arain *et al.*, 2002).

An increase in allocation to belowground tissues has been posited as being associated with age-related decline in aboveground tree tissues (Gower *et al.*, 1996a; Ryan *et al.*, 1997a), however the $BNPP : NPP_T$ ratio did not exhibit a consistent pattern during succession in this study. BNPP comprised 43–67% of NPP_T, except at the 0-year-old clear-cut where it was 98%. The average $BNPP : NPP_T$ for the stands (excluding the clear-cut) was 0.47 – a value that is very similar to the 0.41 reported for all boreal evergreen needle-leaf forests (Gower *et al.*, 1999; Gower *et al.*, 2001). Since we did not separate woody and herbaceous roots, we cannot say whether there was a pattern in jack pine allocation. It is clear, however, that with around 50% of NPP occurring belowground, it is critical to account for belowground processes in quantifying C sequestration.

Soil surface CO_2 flux (R_S) and heterotrophic respiration (R_H)

Soil surface CO_2 flux. Site-specific models that regressed the natural logarithm of R_S on 10 cm soil temperature explained the largest amount of the observed variation and produced acceptable residual plots (adjusted r^2 ranged from 0.73 to 0.88; $P < 0.0001$ for all coefficients) (Table 4). Soil moisture did not improve the regression models.

Table 3 Major annual carbon fluxes for the five jack pine stands (Mg C ha^{-1} y^{-1}) for 1999 (May 1999–April 2000) and 2000 (May 2000–April 2001)

Flux approach	0-year-old		5-year-old		10-year-old		29-year-old		79-year-old*	
Mg C ha^{-1} y^{-1}	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000
NPP										
JP stem	0.0	0.0	0.3 (0.2)	0.3 (0.2)	0.4 (0.1)	0.4 (0.1)	1.2 (0.2)	1.2 (0.2)	0.6 (0.0)	0.6 (0.0)
JP branch	0.0	0.0	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)	0.3 (0.0)	0.3 (0.0)	0.1 (0.0)	0.1 (0.0)
JP foliage[†]	0.0	0.0	0.0 (0.0)	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)	0.5 (0.1)	0.5(0.1)	0.2 (0.0)	0.2 (0.0)
Understory	0.0 (0.0)	–	0.2 (0.0)	–	0.1 (0.1)	–	0.0(0.0)	–	0.0 (0.0)	–
JP coarse root	0.0	0.0	0.1 (0.0)	0.1 (0.0)	0.2 (0.0)	0.2 (0.0)	0.3 (0.0)	0.3 (0.0)	0.1 (0.0)	0.1 (0.0)
Fine root	0.8 (0.3)		0.6 (0.2)		1.7 (0.6)		1.1 (0.4)		0.7(0.4)	
ANPP	0.0 (0.0)	–	0.6 (0.3)	–	0.9 (0.2)	–	2.0 (0.2)	–	0.9 (0.1)	–
BNPP	0.8 (0.3)	–	0.7 (0.2)	–	1.8 (0.6)	–	1.5 (0.4)	–	0.8 (0.4)	–
NPP_T	0.9 (0.3)	–	1.3 (0.1)	–	2.7 (0.6)	–	3.5 (0.3)	–	1.7 (0.4)	–
Respiration										
R_S	4.4 (0.1)	4.3 (0.1)	2.4 (0.0)	2.3 (0.0)	3.3 (0.1)	3.2 (0.1)	5.7 (0.3)	5.5 (0.2)	3.2 (0.2)	3.2 (0.2)
R_{CWD}[‡]	0.4 (0.3)		0.5 (0.3)		0.4 (0.3)		0.1 (0.0)		0.2 (0.1)	
R_H[‡] (without R_{CWD})	2.3 (0.6)		1.2 (0.3)		1.7 (0.5)		3.0 (0.9)		1.7 (0.5)	
R_H[‡] (with R_{CWD})	2.7 (0.6)		1.7 (0.5)		2.1 (0.6)		3.1 (0.9)		1.9 (0.6)	
R_H (after Bisbee)[§]	1.9	–	1.0	–	1.5	–	2.3	–	1.5	–
NEP[¶] [‖]										
= (NPP−R_H[‡])[‡]	−1.9 (0.7)		−0.4 (0.6)		+ 0.4(0.9)		+ 0.4 (1.0)		−0.2 (0.7)	
= (NPP−R_H) (after Bisbee)[§]	−1.5 (0.5)	–	−0.2 (0.4)	–	+ 0.9 (1.3)	–	+ 1.1 (0.4)	–	+ 0.0 (0.5)	–

Stocks approach Mg C ha^{-1} y^{-1}	0–5 year	5–10 year	10–29 year	29–79 year*
NEP[¶]				
= (d*TEC*)/(d*Age*)[‡]	−5.9 (3.9)	+ 0.8 (1.1)	+ 1.0 (1.0)	+ 0.2 (0.3)

Values in parentheses are ± 1 standard deviation. For fluxes calculated directly from measurements, this represents the among-plot spatial variation ($n = 4$). For fluxes estimated using Monte Carlo simulation, the uncertainty value represents the standard deviation of all simulation runs ($n = 4000$), taking into account both among-plot spatial variation of the components and uncertainty in parameter estimation.

Abbreviations: JP, jack pine; ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity; NPP_T, total net primary productivity (aboveground + belowground); R_S, soil surface CO_2 flux; R_{CWD}, coarse woody debris respiration; R_H, heterotrophic respiration; NEP, net ecosystem productivity; TEC, total ecosystem carbon content.

*Seventy-nine-year-old stand was established after wildfire.

[†] Foliage NPP is calculated from allometric equations for jack pine new foliage.

[‡] Calculated using Monte Carlo simulation.

[§] Calculated after Bisbee (2001).

[¶] Net ecosystem productivity (NEP) and net ecosystem exchange (NEE) are interchangeable terms.

[‖] Flux-based calculations of NEP include R_{CWD} as part of the R_H term.

Total annual R_S rates (Mg C ha^{-1} yr^{-1}) for the period May 1, 1999–April 30, 2000 were highest for the 29-year-old stand (5.71 ± 0.26), followed by the 0-year-old clear-cut (4.43 ± 0.11), and lowest for the 5-year-old stand (2.45 ± 0.04) (Table 3). R_S fluxes were 3–5% lower for the second year (2000–2001) because of lower soil temperatures. The high R_S rate at the 29-year-old stand could be attributed to the high NPP driving R_R, or to higher decomposition rates. The 29-year-old stand had less CWD than the other stands, and the CWD present was more decomposed, implying elevated decomposition.

Logging is often hypothesized to result in a pulse of increased respiration, because of increased growing season soil temperatures, changed soil moisture regimes, and increased resource availability to microbes. However, in summarizing several previous studies of R_S in paired clear-cut/control studies, Raich & Schlesinger (1992) found no clear pattern – R_S could increase, decrease, or remain the same. One factor contributing to this ambiguity is the fact that respiration in the reviewed studies was measured at differing intervals after disturbance; waiting too long following harvest could miss a short-lived, elevated R_S

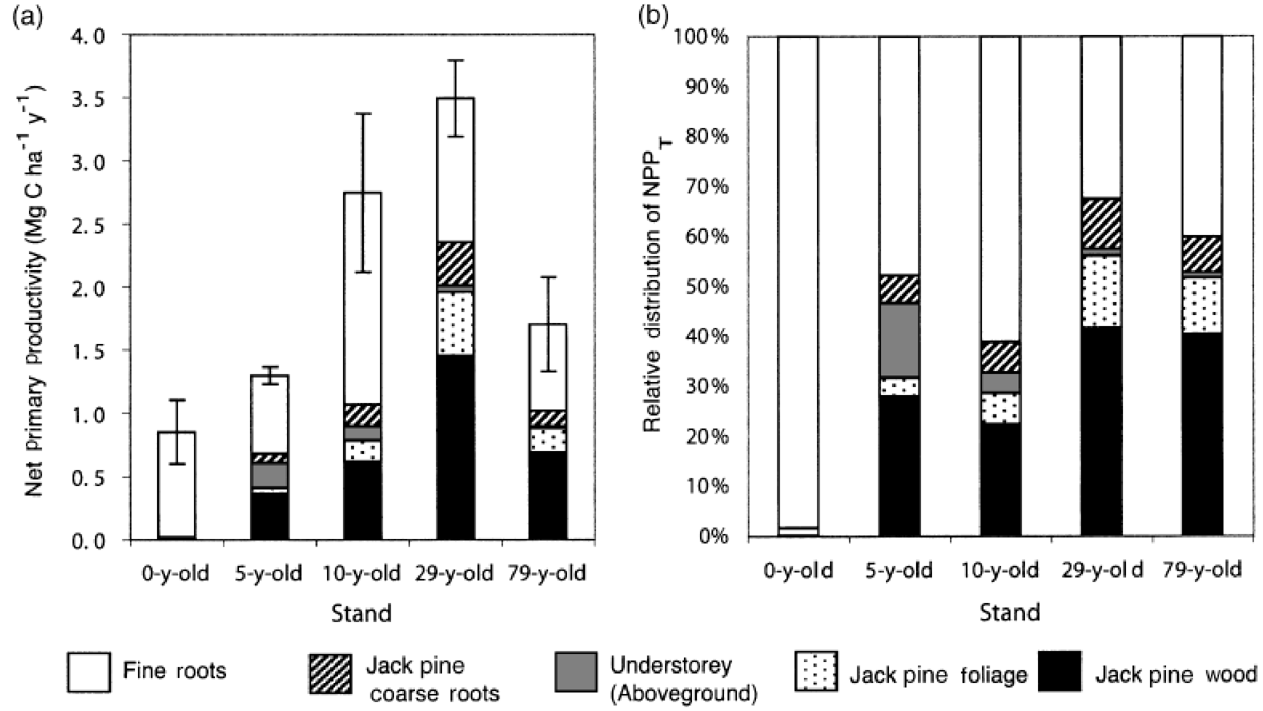

Fig. 2 Total net primary productivity (NPP$_T$) at each stand in May 1999–April 2000. (a) NPP$_T$ by stand and component. (b) Relative allocation of NPP$_T$ among tissues at each stand. Bars represent ± 1 standard deviation, calculated as the difference among the plots within each stand. Foliage NPP is estimated from allometric equations. Fine root NPP may be underestimated, because the ingrowth core method misses turnover between measurements (Steele *et al*., 1997).

pulse. However, another factor, which instead reflects a real property of forests, is that these patterns result from the competitive dynamics between microbes and roots, which vary among systems. In this study, high resource availability to microbes plus continued tree root respiration (since roots may take months to die following harvest) may have caused the high R_S rate at the 0-year-old clear-cut, followed by depressed annual R_S at the 5-year-old stand. In other systems, where (a) the microbial pool and its access to resources differ; (b) tree roots die more or less quickly; and (c) new vegetation takes more or less time to establish, we would expect to see the timing and strength of respiration response following disturbance to be different.

A third complicating factor, however, is the evidence showing that the 0-year-old clear-cut may have been a more fertile stand with more feathermoss in the forest floor and therefore with a different decomposition substrate than the other stands. If this site were a good match for the chronosequence, we could infer that annual R_S increased as a result of harvest, then declined by almost half (to the value of the 5-year-old stand) within less than 5 years. However, it is perhaps more likely that the increased R_S flux resulted from the larger amount of organic substrate at this site supporting microbial metabolism, combined with quick recovery of R_R due to alder sprouting. Implications will be discussed below.

Looking only at our four established stands, we found that, just as in two other boreal chronosequence studies for logged jack pine (Striegl & Wickland, 2001) and burned black spruce (Wang *et al.*, 2002a), R_S decreased for several years following disturbance and increased during aggradation (compared with mature stands), although the timing of peak R_S differed among the studies. Wang *et al*. proposed that peak R_S would occur before canopy closure, when soil temperatures are highest. However, peak R_S for our study occurred after canopy closure. We found that $\ln(R_{S,\text{annual}})$ was significantly positively correlated with fine root biomass (Pearson's r correlation coefficient = 0.934; $n = 5$; $r_{\text{crit}}(\alpha = 0.05) = 0.878$), although not with NPP$_{FR}$ ($r = 0.267$; $n = 5$; NS) (Fig. 4). R_S values for the stands in this study were comparable with values reported for annual R_S fluxes from previous studies in upland boreal evergreen forests, most of which ranged from 2 to 6 Mg C ha^{-1} yr^{-1}, with a few up to 9 Mg C ha^{-1} yr^{-1} (see summaries by Raich & Schlesinger, 1992; Wang *et al.*, 2002a).

Heterotrophic respiration. Monte Carlo estimates of R_{CWD} (Mg C ha^{-1} yr^{-1}) were 0.4 ± 0.3, 0.5 ± 0.3, 0.4 ± 0.3, 0.1 ± 0.0, and 0.2 ± 0.1 for the 0-, 5-, 10-, 29-, and 79-year-old stands, respectively. Annual R_{CWD} for Bond-Lamberty *et al.*'s (2002b) black spruce fire chronosequence ranged from 0.1 to 2.0 Mg C ha^{-1} yr^{-1}.

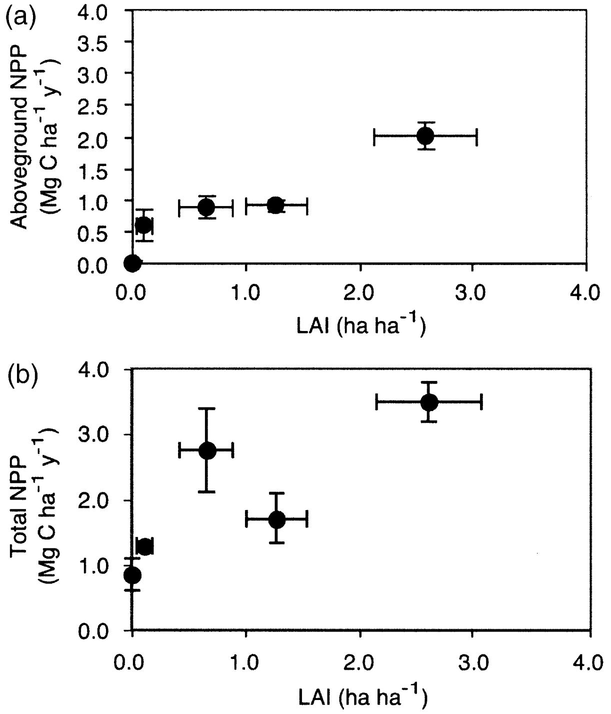

Fig. 3 The relationship between (a) aboveground net primary productivity (ANPP), (b) total net primary productivity ($\mathrm{NPP_T}$) and one-half total leaf area index of the overstory (LAI). ANPP and LAI are well correlated, however this relationship breaks down when BNPP is included. Bars represent ± 1 standard deviation, calculated as the difference among plots at each stand.

Monte Carlo estimates of annual R_{H} (including R_{CWD}; see Eqn (3)) ranged from 1.7 ± 0.5 Mg C ha^{-1} yr^{-1} for the 5-year-old stand to 3.1 ± 0.9 Mg C ha^{-1} yr^{-1} for the 29-year-old stand (Table 3). For comparison only, using measured soil temperatures and equations derived from trenched plot experiments in a nearby black spruce community (Bisbee, 2001), we calculated estimates of R_{H} that were about 40–46% of R_{S} (Table 3). This is well within our envelope for R_{H}.

Net ecosystem productivity

We estimated NEP (Mg C ha^{-1} yr^{-1} ± 1 SD) according to Eqn (2) from May 1, 1999 to April 30, 2000 as −1.9 ± 0.7, −0.4 ± 0.6, 0.4 ± 0.9, 0.4 ± 1.0, and −0.2 ± 0.7 for the 0-, 5-, 10-, 29-, and 79-year-old stands, respectively (Table 3). Qualitatively, NEP for this chronosequence followed the expected pattern (Fig. 5). The 0-year-old clear-cut and the 5-year-old stand were C sources. The 10- and 29-year-old stands were probably small C sinks. The wildfire-established 79-year-old stand was close to equilibrium during the study. However, NEP was only significantly different (lower) at the 0-year-old clear-cut compared with the other four stands, none of which were significantly different from each other. Interannual variability of climate, NPP, and R_{H} constitute another level of uncertainty in these numbers that is beyond the scope of this study.

Clark *et al.* (2001) caution that neglecting branch and coarse root turnover systematically underestimates NPP. We were unable to find appropriate empirical literature values for these terms to quantify this error. Li *et al.* (2003) state that coarse root turnover is set to 2% in the Carbon Budget Model of the Canadian Forest Sector. Applying this value to our branch and coarse root biomass measurements would result in an increase in NEP of 0–5% for the stands (magnitude increases with biomass).

Table 4 Soil surface CO_2 flux regression equations and corresponding sample sizes (*n*), adjusted r^2 (coefficient of determination), *F*-statistics, and *p*-values for the five jack pine stands

Stand	Regression equation	*n*	r^2	*F*	*p*
0-year-old	$\log_e R_s = -1.20005 + 0.1635\,(T_{\mathrm{soil}})$	143	0.78	507	<0.0001
5-year-old	$\log_e R_s = -1.65280 + 0.1328\,(T_{\mathrm{soil}})$	145	0.73	377	<0.0001
10-year-old	$\log_e R_s = -1.33644 + 0.1509\,(T_{\mathrm{soil}})$	151	0.78	514	<0.0001
29-year-old	$\log_e R_s = -1.23751 + 0.1963\,(T_{\mathrm{soil}})$	136	0.88	967	<0.0001
79-year-old	$\log_e R_s = -1.44210 + 0.1670\,(T_{\mathrm{soil}})$	194	0.73	531	<0.0001

R_s is the surface CO_2 flux measured in μmol m^{-2} s^{-1}, where a positive flux is from the surface to the atmosphere. T_{soil} is the soil temperature measured 10 cm below the surface of the soil O horizon. The regressions were based on hand-held temperature probe measurements of instantaneous T_{soil} measured simultaneously with (and adjacent to) point measurements of R_{S}. All regression parameters were significant ($P < 0.01$). The equations were used with the daily averages of continuously recorded, 1 min thermocouple measurements of T_{soil} to estimate total annual R_{S}.

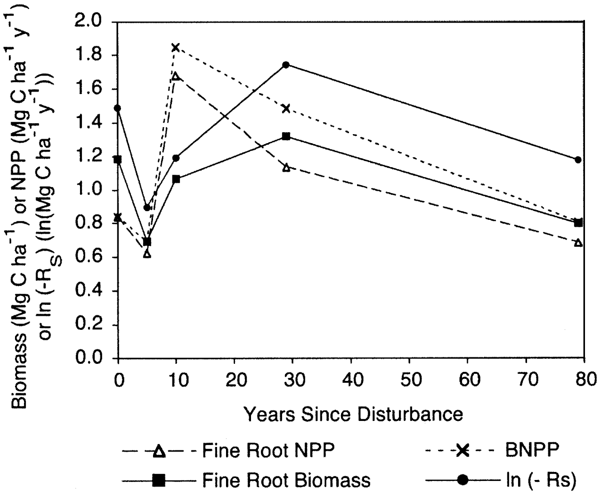

Fig. 4 The patterns of fine root biomass (B_{FR}), fine root NPP ($\mathrm{NPP_{FR}}$), belowground NPP (BNPP), and $\ln(-R_{\mathrm{S}})$ throughout the chronosequence. While B_{FR}, $\mathrm{NPP_{FR}}$, and BNPP might all be expected to be correlated with R_{S}, only B_{FR} follows the same pattern as R_{S} and $\ln(R_{\mathrm{S}})$ over time. R_{S} (Pearson's $r = -0.916$) and $\ln(R_{\mathrm{S}})$ ($r = -0.934$) are well correlated with B_{FR} for the five stands, but not with $\mathrm{NPP_{FR}}$ or BNPP.

Overall, the magnitude of spatial and methodological uncertainties allows us to say little for certain about NEP patterns except that the stand becomes a net source of CO_2 to the atmosphere following logging. Considering only NPP and R_{H}, it is possible that the chronosequence switched from source to sink around 7 years after disturbance, however the uncertainties associated with NEP are so high that the chronosequence may actually *never* have become a sink.

Another caveat regarding NEP is that if one includes emissions from wood harvest and processing, this extends the length of time the chronosequence would remain a net source of carbon to the atmosphere – or possibly negates the sink potential altogether. If we apply values from an Albertan case study (Price *et al.*, 1996) and assume that 100% of stemwood was removed from the site during clear-cutting (26.8 Mg C ha^{-1}), we estimate that ~16% (4 Mg C ha^{-1}) was directly emitted as CO_2 during processing (excluding bio-fuel), while another 17% (5 Mg C ha^{-1}) was emitted during biomass burning at the mill (possibly replacing fossil fuel emissions). The remaining C was split between lumber, pulp, and landfill pools, resulting in further emissions to the atmosphere over a span of decades. Probably only up to 10–15 Mg C ha^{-1} could be assumed to remain in storage long-term (beyond 100 years) in products and landfills. A full treatment of this topic depends on analysis of actual product life-cycle chains, should include emissions due to transportation, and is beyond the scope of this study.

Results of the stocks approach to estimating NEP (Eqn (4)) are also shown in Fig. 5. The flux and stocks-based approaches to estimating NEP provided values that were not significantly different from each other, except between the 0- and 5-year-old stands (see below).

The bulk of published eddy covariance data for temperate and boreal forests shows net C sequestration in undisturbed forests (most figures up to ~2.7 Mg C ha^{-1} yr^{-1} for boreal), but there is almost no annual tower flux data yet available from recently disturbed forests (Lindroth *et al.*, 1998; Arneth *et al.*, 1999; Berbigier *et al.*, 2001; Law *et al.*, 2001). Although they did not report annual NEP values, Schulze *et al.* (1999) found a net release of C to the atmosphere during the summer of 1996 at three disturbed stands: a 7- and a 13-year-old logged *Pinus sylvestris* stand in Siberia, and a 2-year-old windthrow of *Picea abies* NW of Moscow. Six out of seven of their undisturbed forest stands (43–215 years old) were C sinks during the measurement period. Arneth *et al.* (1999) found 8-year-old logged *Pinus radiata* in New Zealand to be a net C sink, and Amiro (2001) found a 10-year-old burned mixed boreal in Saskatchewan to be a sink also.

Our understanding of NEP dynamics is still weakest for the years immediately following disturbance. There is at least one notable example of a mature boreal forest being a strong C source in some years (Lindroth *et al.*, 1998), probably because of disequilibrium conditions and management history. However the majority of data show mature, undisturbed boreal forests to be sinks, even at advanced ages. The sparse published data for recently disturbed forests, which are likely to be more variable, are far less conclusive. Determining the strength and duration of net C emissions following disturbance will be one of the biggest challenges to any effort to quantify the effects of land use on C sequestration. Only after this is accomplished will we be able to make accurate assessments of net biome productivity (NBP), which integrates NEP over timescales that include disturbances (decades to centuries).

Chronosequence site matching

One concern with the chronosequence approach is that there is no measure of variability for different harvested stands of the same successional stage. We have taken care to minimize variation in other confounding factors, including distance, slope, edaphic characteristics, and climate. However, given this limitation, it is important to view the apparent patterns in ecosystem properties with a critical eye, and to consider each stand as one example of a successional community of that age.

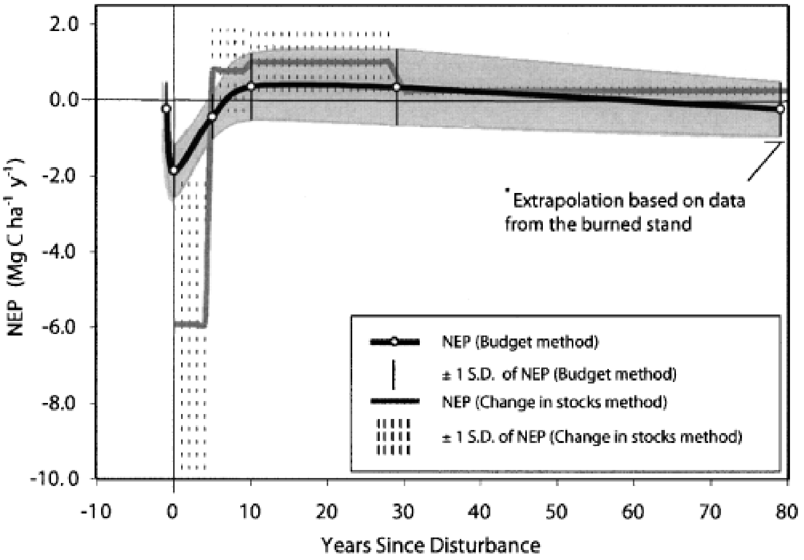

Fig. 5 Net ecosystem productivity (± 1 standard deviation of 4000 Monte Carlo iterations) throughout the chronosequence for May 1, 1999–April 30, 2000. The lines represent the hypothetical pattern of change in NEP following disturbance, calculated using two different methods. The envelopes describe a range of values that is likely to include the actual NEP. Positive NEP means that C is being sequestered by the forest; negative NEP means that the net balance of C is to the atmosphere. *Flux budget method:* The heavy, black line and its surrounding envelope (shaded light grey) show NEP calculated as $NPP_T - R_H$, where R_H was estimated as 30–70% of R_S, plus R_{CWD}. The uncertainty term includes (a) uncertainty in the partitioning of R_H, (b) spatial variability in measured R_S, and (c) uncertainty in the decay rate of CWD. *Change in stocks method:* The heavy, grey line and its surrounding envelope (shaded with dashed lines) show NEP estimated from the difference in total ecosystem C content between pairs of stands, divided by the difference in dominant tree age. The uncertainty term includes (a) spatial variability in TEC, and (b) uncertainty in length of time since disturbance. The 79-year-old stand established after wildfire is plotted both at the beginning and end of the chronosequence, since no data were available for a mature, logged stand; therefore, lines connecting the 29- and 79-year-old stands are speculative. A mature, logged stand of this age may have had more positive NEP, because CWD tends to decay more quickly in logged stands than in burned stands. There are also other important differences in the effects of wildfire and logging.

Comparing values for NEP derived from the flux budget approach and the stocks approach showed that the 5-, 10-, 29-, and 79-year-old stands were plausibly matched for comparing their C budgets (Fig. 5) (i.e. integrating the measured rates of NEP from 5 to 79 years can account for the observed changes in TEC). However, at observed flux rates, it is unlikely that TEC at the 0-year-old clear-cut could fall to the amount observed at the 5-year-old stand in only 5 years. This is primarily because of the large amount of forest floor present at the 0-year-old clear-cut (more than double the amount at some of the other stands).

Much of this 'extra' forest floor was fine litter left as a result of logging. This small-diameter, relatively labile C will degrade quickly in the coming years (Harmon *et al.*, 1987). However, this stand contained a continuous layer of dead feathermoss, and stump-sprouting green alder began to appear at a higher density than the other stands (where its presence was minimal) in the second summer following harvest. These characteristics suggest a more fertile site (Vogel & Gower, 1998) that may not have been a perfect match for the chronosquence.

Implications

This area of research has important implications for C accounting. Although parties to the Kyoto Protocol have agreed to assign C credits for certain land-use practices that result in C sequestration (Watson *et al.*, 2000; Schulze *et al.*, 2002), developing an accurate accounting system is problematic. As this study and others have demonstrated, determining NEP is costly, time-consuming, and highly uncertain (Malhi *et al.*, 1999; Chapin *et al.*, 2000; Coomes *et al.*, 2002), particularly with respect to belowground processes (Gower *et al.*, 1996b; Malhi *et al.*, 1999; Grigal, 2000; Hobbie *et al.*, 2000; Chapin & Ruess, 2001; Hogberg *et al.*, 2001; Johnson & Curtis, 2001). Moreover, intensive management may be hindered by soil impoverishment and climate change, but these effects are not easy to predict (Kimmins, 1996; Brais *et al.*, 2000; DeLuca &

Zouhar, 2000; Falkowski *et al*., 2000; Grigal, 2000; Simard *et al*., 2001).

Furthermore, there is broad skepticism that forest carbon sequestration schemes will result in a net benefit for the global environment once all C flows are considered, since it is the large-scale spatial and temporal integrals of NEP – including the fate of harvested wood – that matter for global C cycling (Harmon *et al*., 1990; Malhi *et al*., 1999; Schulze *et al*., 1999; Chapin *et al*., 2000; Harden *et al*., 2000; Hobbie *et al*., 2000; Kellomaki, 2000; Schulze *et al*., 2000; Goodale *et al*., 2002; Janisch & Harmon, 2002; Randerson *et al*., 2002; Schulze *et al*., 2002). Another important consideration is that managing forests for C sequestration, even if possible, will not always maximize other values such as wildlife and watershed protection, and human needs (Bondrup-Nielsen, 1995; Duinker, 1996; Kimmins, 1996; Niemela, 1999; Kellomaki, 2000; Noss, 2001; Schulze *et al*., 2002).

Conclusions

This study found that a clear-cut jack pine forest stand was a significant annual net source of C to the atmosphere in the two years following harvest. A clear-cut stand with ~5-year-old trees was a smaller net source. A ~10-year-old and a ~29-year-old stand were probably small net sinks. A ~79-year-old stand was either in equilibrium or a small source during the study.

Uncertainties in belowground fluxes hinder us most in determining NEP. This study highlights the need to understand R_S patterns in disturbed forests, especially in the months immediately following disturbance. It also underlines the need to develop methods to accurately partition and model root and microbial respiration. We can seldom accurately predict or measure the length of time over which a disturbed forest remains a C source – knowledge crucial for accurate accounting.

While we recognize that chronosequence studies are an important interim step in understanding long-term ecosystem dynamics, especially in areas of research critically relevant to ecosystem modeling and policy-making, our analysis highlights the problematic nature of the approach. Continuous, long-term ecological research following ecosystems over time is an essential complement to chronosequence studies (Powers & Vancleve, 1991; Wirth *et al*., 2002a). Likewise, eddy flux tower data comparing pre- and postharvest conditions are critical.

Some important factors are outside the scope of our analysis. Our results quantify only the local ecosystem fluxes and not the significant effects of wood processing and natural landscape fire dynamics. More research is necessary to compare the effects of timber management and natural fire regimes within ecosystems and across landscapes. There is an urgent need for major research initiatives integrated over multiple scales to combine bottom-up techniques with top-down approaches in order to understand the C dynamics of human-impacted terrestrial ecosystems (Running *et al*., 1999; Canadell *et al*., 2000). Future research should put these results in the context of the boreal landscape mosaic, forest management, and global climate change policy.

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