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Loss and recovery of ecosystem carbon pools following stand-replacing wildfire in Michigan jack pine forests

David E. Rothstein, Zhanna Yermakov, and Allison L. Buell

Abstract: We used a 72-year chronosequence to study the loss and recovery of ecosystem C pools following stand-replacing wildfire in Michigan, USA, jack pine (*Pinus banksiana* Lamb.) forests. We quantified the amount of C stored in aboveground plant biomass, standing dead timber, downed dead wood, surface organic soil, and mineral soil in 11 jack pine stands that had burned between 1 and 72 years previously. Total ecosystem C ranged from a low of 59 Mg C·ha⁻¹ in the 4-year-old stand to 110 Mg C·ha⁻¹ in the 72-year-old stand. Changes in total ecosystem C across the chronosequence conformed to theoretical predictions, in which C stocks declined initially as decomposition of dead wood and forest-floor C exceeded production by regenerating vegetation, and then increased asymptotically with the development of a new stand of jack pine. This pattern was well described by the following "gamma" function: total ecosystem C (Mg·ha⁻¹) = 112.2 - 39.6 × age^{0.751} × exp(-0.053 × age^{0.039}); mean-corrected R² = 0.976. Using the first derivative of this parameterized gamma function, we estimated that jack pine stands function as a weak source of C to the atmosphere for only ca. 6 years following wildfire, and reach a maximum net ecosystem productivity of 1.6 Mg C·ha⁻¹·year⁻¹ by year 16. We attribute the rapid transition from carbon source to carbon sink in these ecosystems to two factors: (i) stand-replacing wildfires in these xeric forests leave behind little respirable substrate in surface organic horizons, and (ii) jack pine is able to rapidly reestablish following wildfires via serotinous cones. Jack pine stands remained net sinks for C across the chronosequence; however, net ecosystem productivity had declined to 0.12 C ha⁻¹·year⁻¹ by year 72. Carbon sequestration by mature jack pine ecosystems was driven primarily by continued growth of overstory jack pine, not by accumulation of detrital C.

Résumé : Nous avons utilisé une chronoséquence de 72 ans pour étudier la perte et la récupération des pools de C dans l'écosystème après un feu qui a entraîné le remplacement du peuplement dans les forêts de pin gris (*Pinus banksiana* Lamb.) du Michigan, aux États-Unis. Nous avons quantifié la quantité de C emmagasiné dans la biomasse aérienne des plantes, les arbres morts debout, le bois mort au sol, le sol organique en surface et le sol minéral dans 11 peuplements de pin gris qui avaient brûlé entre un et 72 ans auparavant. La quantité totale de C dans l'écosystème variait de 59 Mg C·ha⁻¹ dans le peuplement âgé de quatre ans à 110 Mg C·ha⁻¹ dans le peuplement âgé de 72 ans. Les variations dans la quantité totale de C dans l'écosystème pour l'ensemble de la chronoséquence correspondaient aux prédictions théoriques selon lesquelles la quantité de C diminue initialement alors que la décomposition de C dans le bois mort et la couverture morte excède la production par la végétation qui se régénère et elle augmente par la suite de façon asymptotique avec le développement d'un nouveau peuplement de pin gris. Ce comportement était bien décrit par la fonction gamma suivante : quantité totale de C dans l'écosystème (Mg·ha⁻¹) = 112,2 - 39,6 × âge^{0,751} × exp(-0,053 × âge^{0,039}); R² moyen corrigé = 0,976. À l'aide de la première dérivée de cette fonction gamma paramétrée, nous avons estimé que les peuplements de pin gris constituent une faible source de C pour l'atmosphère pendant approximativement six ans après un feu et atteignent une productivité nette de l'écosystème maximum de 1,6 Mg C·ha⁻¹·an⁻¹ vers l'âge de 16 ans. Dans ces écosystèmes, nous attribuons la transition rapide de source à puits de C à deux facteurs : (i) après être passés dans ces forêts xériques, les feux qui entraînent le remplacement d'un peuplement laissent peu de substrat respirable dans les horizons organiques de surface et (ii) le pin gris est capable de s'établir à nouveau rapidement après un feu à cause de ses cônes sérotineux. Les peuplements de pin gris sont demeurés un puits net de C pour l'ensemble de la chronoséquence. Cependant, la productivité nette de l'écosystème avait diminué à 0,12 Mg C·ha⁻¹·an⁻¹ rendu à 72 ans. La séquestration du carbone par les peuplements matures de pin gris était surtout due à la croissance continue des pins gris dans l'étage dominant, non à l'accumulation de C dans les déchets.

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Introduction

The role of forests and forest management in the global carbon cycle is increasingly of concern to scientists and policy makers (Dixon et al. 1994; Houghton 1996; Murray et al. 2000; Schulze et al. 2000). In particular, the advent of international agreements to regulate total C emissions places a greater emphasis on our ability to accurately quantify: (i) re-

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regional and national C stocks in forest ecosystems, (ii) regional and national fluxes of C between forest ecosystems and the atmosphere, and (iii) the effects of disturbance (natural and anthropogenic) on C stocks and fluxes.

Fire is the predominant natural disturbance agent across much of the temperate and boreal region (Spurr 1964), and researchers are increasingly recognizing the potential for changing fire regimes to impact global patterns of C cycling (Kasischke et al. 1995; Fearnside 2000; Harden et al. 2000). Fire influences stand-level C dynamics directly by converting biomass to atmospheric C, and indirectly by initiating successional changes in the balance between production and decomposition. At the landscape scale, fire regime determines net C storage and exchange through its control over the distribution of stand ages (Kasischke et al. 1995). To accurately predict the effects of changing fire regimes on future stocks and fluxes of C from fire-dependent ecosystems, we need a better understanding of the direct and indirect effects of fire on stand-level C dynamics.

At the stand level, fire produces an immediate transfer of a portion of total ecosystem C to the atmosphere through direct combustion. However, the amount of C directly lost to combustion is typically small relative to total ecosystem C, but can range from 5% to 25% depending on ecosystem type and fire conditions (Auclair 1985; Stocks 1989; Dixon and Krankina 1993; Kasischke et al. 2000a). Fire also results in indirect emissions of C by altering the balance between production and decomposition, thus converting forest ecosystems from C sinks to C sources. Vegetation mortality associated with wildfire drastically reduces net primary productivity (NPP) and creates a large pool of detrital C susceptible to decomposition. Furthermore, removal of the forest canopy can increase soil temperature, reduce transpiration, and produce a flush of nutrients stimulating decomposition of wildfire-generated detritus and soil organic matter (Dixon and Krankina 1993; Kasischke et al. 2000b; O'Neill et al. 2002). The rate of C flux after wildfire, as well as the duration over which a burned forest functions as a C source, will depend on the amount of organic matter retained, changes in postfire microclimate, and the lag time in NPP as a new stand regenerates. Many modeling studies assume that C release from postfire decomposition exceeds that released by direct combustion (Dixon and Krankina 1993; Kasischke et al. 1995; Fearnside 2000); however, empirical data quantifying the long-term effects of wildfire on total ecosystem C budgets are scant (cf. Wirth et al. 2002).

At the landscape level, fire affects C dynamics primarily through its control over stand age distribution. Traditional ecological theory holds that mature forest ecosystems reach a steady state with respect to biomass in which gross primary production = autotrophic + heterotrophic respiration (Odum 1969; Chapin et al. 2002). This suggests that fire may be viewed as a rejuvenating factor, increasing the sink strength of forest ecosystems by replacing old, slow-growing stands with young, actively growing ones. However, more recent research has shown that older forests may remain active sinks for C, if they continue to accumulate C in woody debris, forest-floor detritus, and soil organic matter (Schulze et al. 2000; Harmon 2001). The net effect of fire frequency

on landscape C balance will depend on the balance between the loss of C due to direct combustion and accelerated decomposition, and increased rates of sequestration due to enhanced NPP.

We used a 72-year chronosequence to elucidate successional patterns of C loss and recovery following wildfire in the jack pine forests of northern Lower Michigan, USA. The jack pine forests of this area provide an ideal environment for chronosequence studies, because climatic, edaphic, and floristic variation is held to a minimum. We used this chronosequence to address the following specific research questions:

- What is the net loss of C in the years immediately following wildfire?
- For how long after wildfire are jack pine ecosystems a net source of C to the atmosphere?
- What is the role of detrital pools in driving ecosystem C balance through stand recovery?
- Do older jack pine stands continue to sequester C?

Materials and methods

Study sites

All of our study sites were located within a 240-km² area in the Highplains district of northern Lower Michigan (Table 1). This region is characterized by a harsh, continental climate with a short growing season (82 days) and cold temperatures (mean annual temperature = 6.3 °C) (Albert et al. 1986). The landscape of this region consists of glaciofluvial features including broad, outwash plains interspersed with steep ridges composed of finer-textured ice-contact deposits (Albert et al. 1986). Soils in the outwash plain are dominated by acidic, excessively drained, poorly developed sands of the Grayling series (Werlein 1998). Jack pine has been the dominant vegetation of the outwash plains since prior to European settlement (Comer et al. 1995). The combination of exceedingly dry conditions, flat topography, and highly flammable vegetation resulted in a presettlement return interval of stand-replacing wildfires of 30–80 years (Simard and Blank 1982; Whitney 1986).

In April and May 2002, we developed a chronosequence of 11 wildfire-regenerated jack pine stands that burned in 2001, 2000, 1998, 1995, 1990, 1988, 1980, 1975, 1966, 1950, and 1930. We used fire reports from the United States Department of Agriculture – Forest Service and Michigan Department of Natural Resources to develop a list of candidate fires of at least 80 ha that occurred within the previous 40 years. We then used field scouting to eliminate areas that showed evidence of planting, salvage logging, or that were less than 90% jack pine basal area. However, we were unable to locate sites in the 20- to 30-year range that had not been salvage logged following wildfire (see Discussion below). The two oldest stands were located using United States Department of Agriculture – Forest Service compartment maps followed by field surveys to validate that stands were even-aged jack pine with no evidence of planting (i.e., tree rows or furrows), which we assume to have been of wildfire origin. Jack pine's extreme shade intolerance and dependence on wildfire for regeneration (Eyre 1938; Simard and Blank 1982; Cayford and McRae 1983), together with the high frequency of wildfires in this area, suggests that any

Table 1. Age, location, vegetation, and soil properties of chronosequence sites.

Age (years)	Lat. (N)	Long. (W)	% jack pine ^a	Stem density ^b	A horizon pH ^c	Gravel band ^d	Silt + clay (%) ^e
1	44°31'	84°16'	ND	ND	4.23	No	11
2	44°36'	84°00'	ND	ND	4.19	No	10
4	44°28'	84°20'	ND	ND	4.33	No	7
7	44°30'	84°18'	97	10 741	4.24	Yes	18
12	44°43'	84°29'	89	2 755	4.05	Yes	7
14	44°27'	84°16'	100	2 585	4.26	Yes	10
22	44°36'	84°3'	100	7 040	4.34	No	9
27	44°43'	84°25'	100	1 564	4.27	No	8
36	44°26'	84°14'	100	4 149	4.11	Yes	8
52	44°33'	84°21'	98	1 326	3.86	No	8
72	44°34'	84°24'	99	1 530	3.77	No	9

Note: ND, no data.

^a(Jack pine basal area / total stand basal area) × 100.

^bLive, overstory trees (no. ha⁻¹).

^cIn 1:2, soil-water paste.

^dYes indicates the presence of at least one subsurface horizon with >10% coarse fragments by mass.

^eIn upper B horizon.

other scenario for stand establishment is exceedingly unlikely. At each site, we identified an area (between 1 and 2.5 ha) of uniform terrain, with no evidence of human disturbance, which contained no unburned patches of forest, and that met all of the criteria outlined above, which we hereafter refer to as a stand. Within each stand, we located three parallel, 60-m transects using random start points (stratified along the long axis of the stand) for all soil and vegetation sampling.

Vegetation C pools

We quantified C associated with vegetation in the following pools: live overstory, understory shrubs and herbs, fine roots, standing dead trees, and dead wood (standing and downed). We estimated dry biomass for each pool using a variety of techniques and then converted biomass to C stocks using a constant carbon:biomass ratio of 0.5 (Linder and Axelsson 1982; Coomes et al. 2002). We quantified C pools in living trees only for stands aged 7 years and older. Jack pine regeneration in stands less than 7 years old was all under 30 cm in height and was not accounted for in our C budgets. At stand age 7, jack pine regeneration ranged from 50 to 120 cm in height. At this stand, we measured heights of all trees within three 3 m × 6 m plots. We then harvested five trees ranging in height from 42 to 134 cm to develop a regression equation predicting dry biomass from height (biomass (kg) = 0.0014 × exp(0.039 × height (cm)); R² = 0.994). For sites aged 12, 14, 22, 27, 36, 52, and 72 years, we measured diameter at breast height (DBH; 1.37 m) for all trees located within three 7 m × 14 m plots (located at random points along each transect). We used allometric equations from the literature to estimate total aboveground biomass as a function of DBH for each living tree. We used the equations of Perala and Alban (1993) to estimate total aboveground biomass of jack pine and the few red pine (*Pinus resinosa*) we encountered. These are composite equations derived from three sites in Minnesota and one in Upper Michigan (Perala and Alban 1993). We used a general hardwood equation from Whittaker and Marks (1975) to estimate biomass of northern pin oak (*Quercus ellipsoidalis*).

We collected three soil cores (5.08 cm in diameter × 10 cm deep) per transect in July 2002 for the determination of fine root biomass. We hand picked all roots <2 mm in diameter, brushed them free of soil particles, and determined their oven-dry (65 °C) mass. We sampled understory vegetation in August 2002, by clipping the aboveground portion of all grasses, forbs, shrubs, ferns, mosses, and lichens from two 0.25-m² plots randomly located along each transect. Samples were composited by transect and oven-dried and weighed to determine mass per unit area.

We measured every standing dead tree and every piece of downed wood in three 7 m × 14 m plots in each stand. We estimated the mass of standing dead trees from their DBH as total aboveground biomass less foliage mass from the allometric equations of Perala and Alban (1993). This approach assumes that the little or no branch or bark biomass is consumed by fire (Stocks 1989) and that all foliage is killed. We did not attempt to account for changes in mass associated with decomposition of standing dead trees, so that our results likely err on the side of overestimating standing dead biomass.

We measured every piece of downed wood in each plot that was >5 cm in diameter at the largest end. For each piece, we measured total length, and made two, orthogonal diameter measurements at each end. For any piece that extended outside of the plot, we measured length and diameter at the plot border. We assigned each piece to one of three decay classes: (1) bark intact, (2) bark and twigs lost, but wood sound, and (3) shape maintained, but wood yielding to pressure. Woody debris whose shape was lost was considered forest-floor material and sampled as described below. Diameter and length measurements were converted to volumes using the formula for a frustum of a cone (Wenger 1984). We cut samples of each decay class from each plot to determine density using volumetric displacement of water and oven-dry mass (65 °C). Densities of downed wood decay classes were 378.5 (±38.4), 330.4 (±26.5), and 145.4 (±14.3) kg·m⁻³ for decay classes 1, 2, and 3, respectively. Total dry biomass of each plot was calculated as the sum of the volume of each piece multiplied by the appropriate density conversion.

Soil C pools

We separated soil into three pools for our C inventories: forest floor (O horizons), mineral soil to a depth of 10 cm (A horizon), and mineral soil from 10 to 100 cm. We sampled the forest floor in November 2002 using a 625-cm² sampling frame, at three or four random locations per transect. This material was composited by transect and oven-dried and weighed to determine mass per unit area. A ca. 50-g subsample of each composited sample was ground in a Wiley mill to pass a 20-mesh screen, and then further subsampled and analyzed in duplicate for C concentration on a Carlo-Erba NA1500 elemental analyzer (Carlo-Erba, Milan, Italy). We collected three soil cores (5.08 cm in diameter × 10 cm deep) per transect in July 2002 for the determination of A horizon C concentration. Soil cores were composited by transect, subsampled, pulverized in a ball mill, and then analyzed in duplicate for C concentration on the NA1500. Additional cores (one per transect) were collected using a sleeve-core sampler (Soilmoisture Equipment Corp., Santa Barbara, Calif.) for the determination of A horizon bulk density in November 2002. Total C in the top 10 cm was calculated for each transect as the product of C concentration and mass of soil contained in that layer. We estimated C stored in subsurface mineral soil by digging a single soil pit at each site. Within each soil pit, we distinguished genetic horizons, based primarily on variation in color, to a depth of 1 m. We measured the thickness of each horizon, collected samples for the determination of bulk density (sleeve-core sampler), and collected additional samples for the determination of C concentration. We passed C concentration samples through a 2-mm sieve to determine the percentage of coarse fragments (by mass), and determined texture on sieved soil using the Bouyoucos hydrometer method (Gee and Bauder 1986). Subsamples of sieved soil from each horizon were pulverized in the Kieco ball mill and analyzed for C concentration in duplicate using the NA1500 elemental analyzer. We calculated C storage (g·m⁻²) for each horizon individually, based on C concentration and bulk density (corrected for coarse fragments), and then summed these to estimate total subsurface soil C.

Data analysis

Stand was the level of replication, with an *n* of 3 for within-stand replication (transect) for all C pools except subsurface soil. Changes through time in C sequestration in particular pools and in the entire ecosystem were analyzed by regressing stand means against age since stand-replacing wildfire. Where data conformed to a priori theoretical predictions, we specified model equations using least-squares nonlinear regression. We specified the Richard's function (Cooper 1983) to describe the recovery of live overstory biomass as

$$[1] \quad OB_t = OB_{max} [1 - \exp(-at)]^b$$

where OB_t represents the overstory biomass at time t , OB_{max} represents the potential maximum overstory biomass, t is time (years) since stand-replacing wildfire, a is a parameter controlling the rate of biomass accumulation, and b is a parameter controlling the inflection point of the curve. We

specified the gamma function (Covington 1981) for forest-floor C and total ecosystem C as

$$[2] \quad C_t = a + bt^c \exp(dt^e)$$

where C_t is the amount of C stored at time t , t is time in years since stand-replacing fire, and a , b , c , d , and e are parameters defining the shape of the curve. Essentially, the term bt^c determines the rate of decline in C stock immediately following disturbance, then, as the term $\exp(dt^e)$ approaches zero, C stock increases towards the asymptote, a (Covington 1981). All regression analyses were conducted using SYSTAT (version 10) for personal computers.

Results

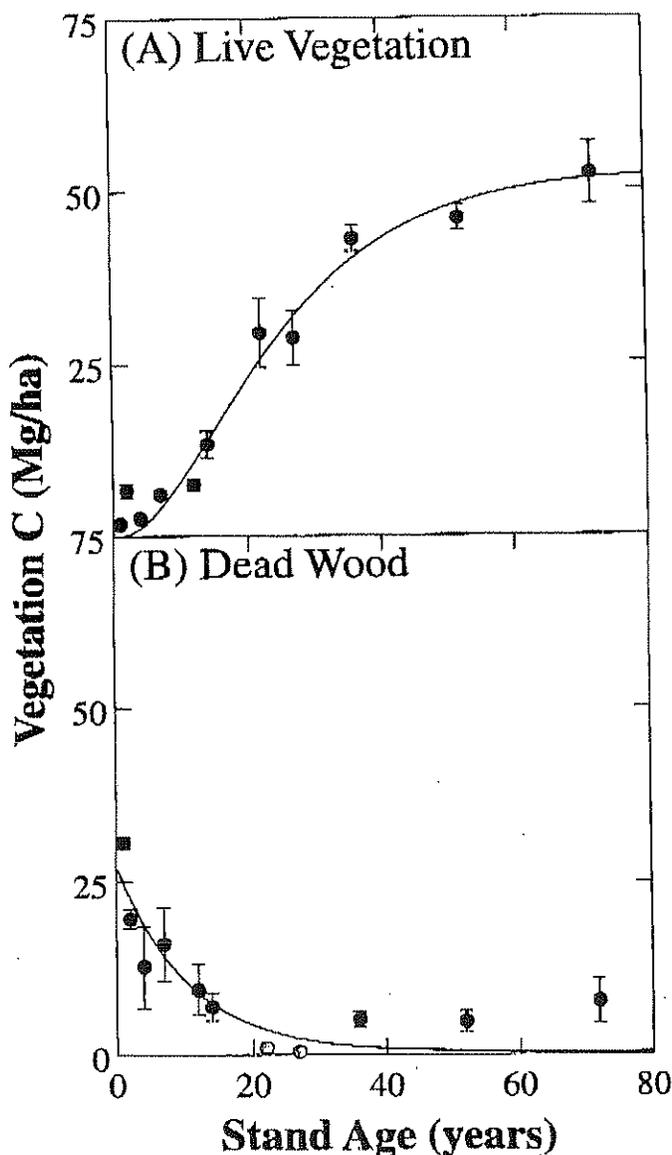
Chronosequence characteristics

The successful application of any space for time substitution requires that all factors other than age are held as constant as possible. Overall, we found stands along this chronosequence to be nearly uniform in vegetation and soil characteristics (Table 1). All stands were dominated by jack pine, with some scattered individuals of northern pin oak (*Quercus ellipsoidalis*) and red pine (*Pinus resinosa*). Soils across the chronosequence were excessively well drained, acidic sands of the Grayling series (Typic Udipsamments; Werlein 1998). We did observe variation among stands in the presence or absence of gravel bands within the profile (Table 1). These textural discontinuities result from variations in the velocity of water during parent material deposition and may slow drainage from the profile, potentially improving soil water holding capacity. The 7-year-old stand was distinct from all others in that it had both gravel banding and markedly finer texture than the other stands (Table 1). We also observed variation among stands in the density of the jack pine stand that regenerated postfire (Table 1). Clearly, the general decline in jack pine density with stand age reflects self-thinning processes; however, within this general decline we observed three stands (12, 14, and 27 years), which had densities markedly lower than others of similar age.

Vegetation C pools

The accumulation of C in living vegetation across our chronosequence followed a classic sigmoidal pattern with slow accumulation in the establishment phase, a period of rapid accumulation between ca. 10 and 30 years, and then a decline in the rate of accumulation approaching an asymptote of 53 Mg C·ha⁻¹ (Fig. 1A). This pattern of C storage by living vegetation conformed well to the Richards function for logistic growth: vegetation C (Mg·ha⁻¹) = 53.05 × (1 - exp(-0.063 × age))^{2.507}; mean-corrected $R^2 = 0.973$; $P < 0.001$. Herbaceous plants and shrubs dominated vegetation early in the chronosequence, but overstory trees accounted for >90% of all C in live vegetation from year 14 onward (Table 2). Ground vegetation was dominated by small-statured shrubs such as *Vaccinium angustifolium*, *Comptonia peregrina*, *Prunus pumila*, and *Arctostaphylos uva-ursi*. In addition, we found large amounts of *Carex pennsylvanica*, *Pteridium aquilinum*, and assorted mosses and lichens. At

Fig. 1. Carbon content in (A) living vegetation and (B) dead wood as a function of time since stand-replacing wildfire. Dead wood includes both standing dead trees and downed dead wood. Symbols represent stand means (± 1 SE; $n = 3$), and the curves represent nonlinear regression lines described in the text. Dead wood C for stands aged 22 and 27 are represented in gray to indicate that these points were excluded from our regression analysis.



no point along the chronosequence did we observe regeneration by shade-tolerant tree species.

Carbon storage in dead wood followed a pattern opposite that of live vegetation, declining from a peak value of 31 $\text{Mg}\cdot\text{ha}^{-1}$ at year 1 to a minimum of 0.5 $\text{Mg}\cdot\text{ha}^{-1}$ at year 27, and then increasing slightly in mature stands (Fig. 1B). Dead wood in young stands was dominated by trees killed in the stand-originating fire, whereas dead wood of postfire origin did not accumulate in appreciable quantities until ca. 30 years after stand establishment. Downed wood dominated the dead wood C pool in the middle of the chronosequence

(years 7–36), whereas C in standing dead trees exceeded that in downed wood in young (<7 years) and old (>36 years) stands. The extremely low values for dead wood at stands aged 22 and 27, coupled with the presence of cut stumps (lacking fire scars) at stand age 27, suggested that salvage logging occurred at these sites. We described the decline in dead wood C storage (excluding salvage logged stands 22 and 27) through time using an exponential decay model: dead wood C ($\text{Mg}\cdot\text{ha}^{-1}$) = $27.39 \times \exp(-0.096 \times \text{age})$; mean-corrected $R^2 = 0.683$; $P < 0.001$.

Soil C pools

Forest-floor C followed the general pattern outlined by Covington (1981), in which forest-floor mass declines early in stand development as the rate of decomposition exceeds the rate of litter production and then accumulates towards an asymptote later in stand development (Fig. 2A). We found a very low amount of C in forest floor in the 1-year-old stand (ca. 1/3 that of mature stands), suggesting significant consumption by wildfire. Forest-floor C continued to decline until ca. 12 years, at which time forest-floor C increased rapidly towards an asymptotic value of 12.5 $\text{Mg}\cdot\text{ha}^{-1}$. The single exception to this general pattern was the 7-year-old stand, which had a forest-floor C content equivalent to that of the mature stands on this chronosequence. This stand apparently differed from all others in terms of moisture relations, as indicated by the presence of gravel bands and finer soil texture (Table 1). More mesic conditions may have influenced current forest-floor mass by limiting initial losses to combustion, increasing the rate of recovery due to greater shrub production, or some combination of the two. Thus, we excluded this stand to fit patterns of forest-floor C storage to the gamma function of Covington (1981): forest-floor C ($\text{Mg}\cdot\text{ha}^{-1}$) = $12.59 - 9.04 \times \text{age}^{0.147} \times \exp(-0.00004 \times \text{age}^{3.027})$; mean-corrected $R^2 = 0.926$; $P < 0.001$.

In contrast with the forest-floor pool, we observed a weak decline in surface soil C content across the chronosequence (Fig. 2B). Despite higher stand means at intermediate-aged sites, this decline was best described (lowest sum-of-squares residual) with a simple linear regression: C ($\text{Mg}\cdot\text{ha}^{-1}$) = $24.17 - 0.0617 \times \text{age}$; $R^2 = 0.295$; $P = 0.049$. Carbon storage in the subsurface soil also peaked at intermediate stand ages, but in this case we found no statistically significant linear or nonlinear trend with time (Fig. 2C). A second-order polynomial model did provide a marginally significant fit to the data: C ($\text{Mg}\cdot\text{ha}^{-1}$) = $15.749 + 0.466 \times \text{age} - 0.0064 \times \text{age}^2$; $R^2 = 0.401$; $P = 0.053$. Thus, total C storage in soil increased slightly through the first ca. 15 years of secondary succession, while the proportion stored in surface organic horizons increased from that point forward with little or no change in total soil C storage (Fig. 3).

Net ecosystem C dynamics

The sum of changes in individual C pools across the chronosequence gave rise to a pattern of total ecosystem C storage that was well described by the gamma function of Covington (1981) (excluding stand age 7): total ecosystem C ($\text{Mg}\cdot\text{ha}^{-1}$) = $112.2 - 39.6 \times \text{age}^{0.351} \times \exp(-0.053 \times \text{age}^{1.039})$; mean-corrected $R^2 = 0.976$; $P < 0.001$. Total ecosystem C decreased from 75 $\text{Mg}\cdot\text{ha}^{-1}$ at year 1 to an estimated mini-

Table 2. Pools of C found along 72-year jack pine chronosequence.

Age (years)	Soil (20–100 cm)	Soil (0–10 cm)	Forest floor	Dead wood	Fine roots	Understory	Overstory
1	14.3	23.7±1.4	4.2±0.7	30.6±1.0	1.3±0.6	0.5±0.2	ND
2	16.8	23.7±3.0	1.4±0.5	19.6±1.8	5.2±1.3	1.2±0.1	ND
4	21.0	21.1±2.4	1.5±0.7	12.7±7.2	1.6±0.2	1.0±0.2	ND
7	14.9	23.5±1.5	10.1±3.3	16.0±6.6	3.6±0.3	2.0±0.4	0.4±0.2
12	20.6	26.0±2.6	1.2±0.5	9.4±4.4	3.2±0.1	1.2±0.2	2.9±0.8
14	23.3	27.0±4.6	1.9±0.2	6.9±2.5	2.3±0.6	0.6±0.2	10.4±1.9
22	21.5	22.3±3.2	3.2±0.3	1.0±0.4	3.9±0.4	0.6±0.2	25.1±5.3
27	28.7	22.1±0.5	3.8±0.5	0.5±0.3	2.4±0.4	2.4±0.5	24.0±4.6
36	19.1	21.0±1.7	12.9±0.4	5.1±1.3	2.2±0.3	0.5±0.1	40.4±1.7
52	23.2	19.2±2.6	11.8±1.4	4.8±1.8	1.8±0.8	0.7±0.3	43.5±3.0
72	16.1	20.8±3.1	12.4±2.0	7.7±3.8	1.9±0.6	1.7±0.3	48.8±8.2

Note: Values are means \pm 1 SE, and all values are in units of Mg C ha⁻¹. No error estimation is given for mineral soil owing to a sample size of 1. ND, no data.

imum of 59 Mg·ha⁻¹ by year 6 (Fig. 4A). From this point forward, jack pine stands accumulated C across the chronosequence, approaching an estimated maximum storage potential of 112 Mg C·ha⁻¹. The large amount of C in the forest floor at stand age 7 had a strong influence on our estimated minimum value for ecosystem C storage, and so this data point was excluded from parameterization of the gamma function. Including stand age 7 resulted in a slightly poorer fit to the data ($R^2 = 0.953$) and increased the estimated minimal C storage to 64 Mg C·ha⁻¹. We took the first derivative of the parameterized gamma function to describe the rate of change of ecosystem C storage across the chronosequence, yielding an estimate of net ecosystem productivity (NEP) through time (Fig. 4B). This indicates that jack pine stands along this chronosequence were a source of C to the atmosphere for the first 6 years following wildfire. From this point forward, NEP was positive, reaching a maximum value of 1.6 Mg C·ha⁻¹·year⁻¹ at year 16 and then declining to a low of 0.12 Mg C·ha⁻¹·year⁻¹ by year 72.

Discussion

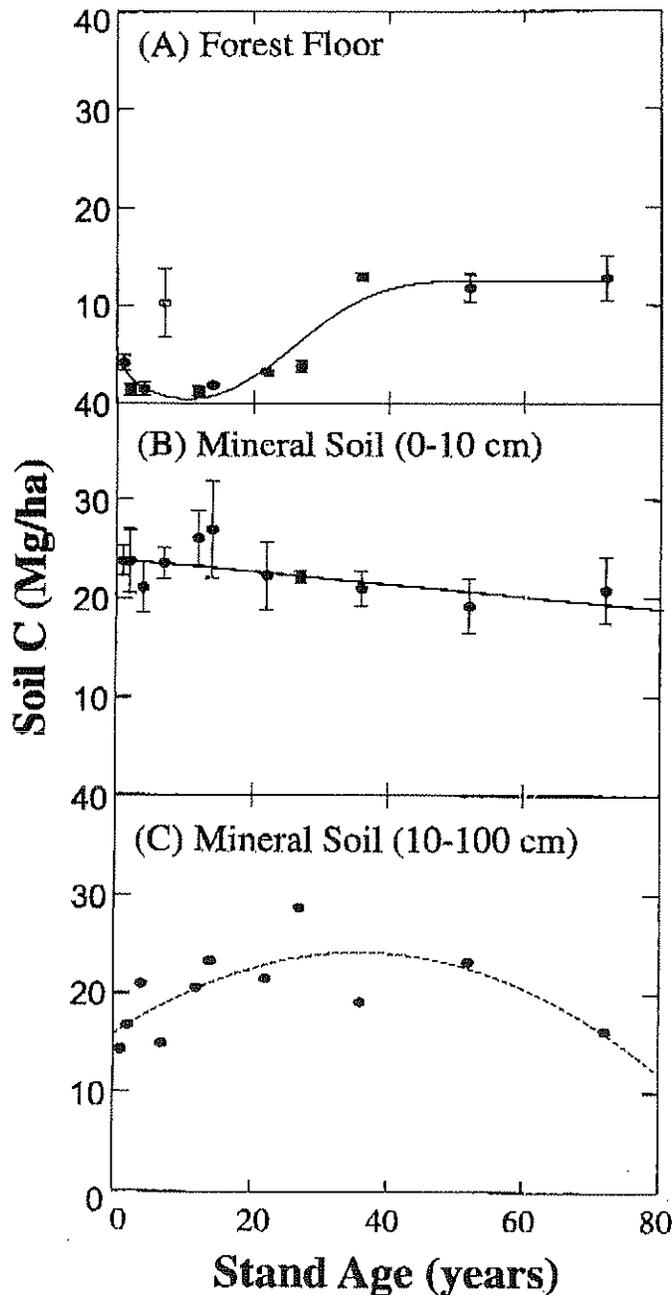
Overall we found that patterns of ecosystem C storage following wildfire conformed well to theoretical predictions (Odum 1969; Chapin et al. 2002): jack pine ecosystems were initially a C source following wildfire as decomposition exceeded production, they then transitioned to strong C sinks as young stands grew vigorously, and then sequestration slowed as stands matured. Based on our regression analysis of total ecosystem C against stand age, we estimate that jack pine stands along this chronosequence remain a net source of C to the atmosphere for only 6 years following wildfire, losing a total of 16 Mg C·ha⁻¹ over this period. Although we do not have estimates of direct losses of C to combustion, Simard et al. (1983) estimated an average consumption of 10.6 Mg C·ha⁻¹ from mature jack pine in northern Lower Michigan, and Stocks (1989) estimated an average consumption of 5.9 Mg C·ha⁻¹ for mature jack pine in Ontario, Canada. Thus our chronosequence data support the idea that C losses from postfire decomposition can exceed direct losses from combustion (Dixon and Krankina 1993; Kasischke et al. 1995; Fearnside 2000; Wirth et al. 2002).

As expected, this loss of C early in our chronosequence was driven by the loss of C from dead wood left behind following fire. We observed only a slight decline in C stored in surface organic horizons (Fig. 2A), presumably owing to near complete combustion by wildfire (Simard et al. 1983). While we did observe a weak decline in C stored in A horizon soil over the entire chronosequence (Fig. 2B), this likely reflects a redistribution of C through succession, rather than a net loss. Early in the chronosequence soil pH is elevated, graminoid biomass is high (Abramovsky 2003), A horizons are thicker, and there is little accumulation of surface organic matter. As the jack pine stands develop, pH drops (Abramovsky 2003), A horizons become thinner, and organic matter accumulates in surface horizons (Oe and Oa; Fig. 3). In contrast with soil, we observed a large (ca. 20 Mg C·ha⁻¹) and rapid loss of C from dead wood pools over the first 14 years of the chronosequence.

This rapid loss of C is of concern, however, because it appears to greatly exceed the decay rate of woody material in a direct study of jack pine log decomposition in northern Minnesota (Alban and Pastor 1993). In fact, the exponential decay constant of -0.096 from our regression of dead wood C against stand age is more than double the -0.042 empirically determined by Alban and Pastor (1993). However, the decay rates we observed are not unprecedented in the literature — compare the 71% mass loss after 14 years observed in lodgepole pine logs (Laiho and Prescott 1999) with the 77% decline in dead wood C from stand age 1 to stand age 14 (Table 2). Overestimation of wood decay rates in this study could have resulted from either systematic differences in overstory biomass of preburn stands across our chronosequence, or systematic errors in our methodology for determining dead wood C pools.

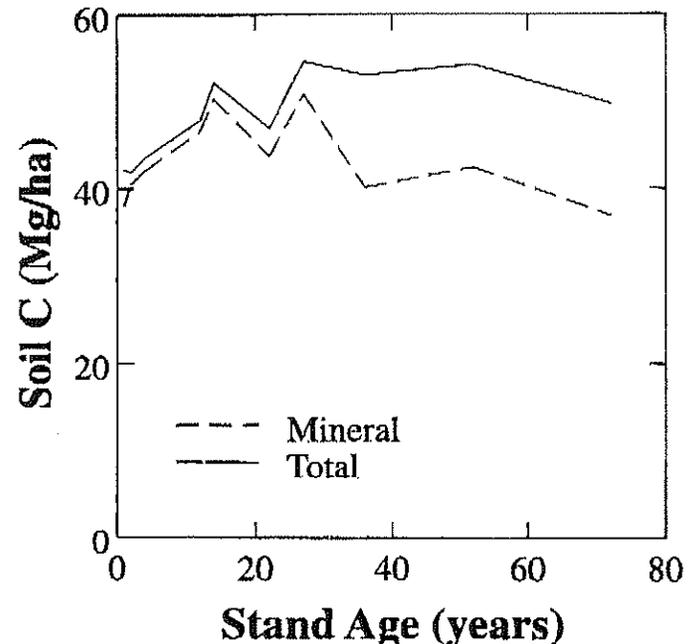
Our fundamental assumption is that declines in C stored in dead wood over the first 14 years of our chronosequence reflect the decay of fire-generated detritus over time. In general, the older the preceding stand at the time it was burned the more dead wood will be left following fire (i.e., Fig. 1A). Thus a systematic decrease in preburn stand age along the chronosequence could result in an overestimation of C losses from dead wood decay. To gain insight into preburn stand conditions, we compared the diameter distributions of all standing and downed dead trees in stands aged

Fig. 2. Soil C content in (A) forest floor, (B) surface mineral soil, and (C) subsurface mineral soil as a function of time since stand-replacing wildfire. Symbols represent stand means (± 1 SE; $n = 3$), and curves represent regression lines described in the text. Forest-floor C for stand age 7 is represented in gray to indicate that this point was excluded from our regression analysis. Subsurface soil C estimates are from a single soil pit per stand, therefore there are no estimates of within-stand variation.



1–14 years (Fig. 5). Clearly, stand age 2 burned at a much younger age (we know this to be 20 years) than the other stands; however, there is no obvious trend among the remaining stands (in terms of median diameter they increase in the order $1 < 14 < 4 < 12 < 7$ years). This suggests that

Fig. 3. Changes in the amount and distribution of soil C with stand age. Mineral soil C includes both surface (0–10 cm) and subsurface (10–100 cm) horizons. The difference between total and mineral soil C corresponds with the amount of forest-floor C.

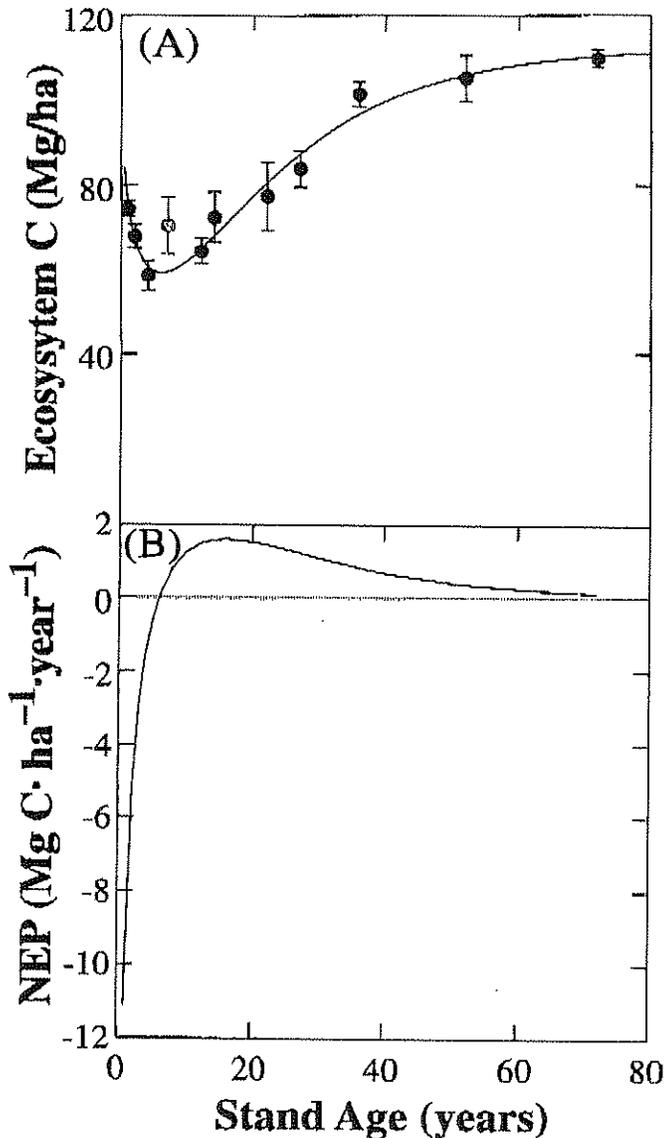


variation in preburn stand age is unlikely to have systematically biased our estimates of C losses from dead wood pools.

Two aspects of our methodology for calculating dead wood C may have resulted in an overestimation of woody debris decomposition: (i) our use of discrete decay classes described by a single density, and (ii) our failure to sample downed wood that had lost its shape. Whereas a single piece of wood will lose biomass continuously through the decomposition process, our use of average densities for particular decay classes necessarily resulted in a stepwise decline through time. Thus we would have underestimated the density of material that had recently entered a particular decay class and overestimated the density of material that had long been in a particular decay class. This could have resulted in a large underestimate of dead wood C in stands aged 12 and 14, where significant amounts of decay class 3 first appeared (data not shown). Another concern is that woody debris that had lost its shape (i.e., beyond class 3) would have been incompletely sampled with our sampling frame for surface organic horizons. Thus it is likely that errors associated with estimating dead wood biomass at least partially explain the rapid loss of dead wood C through the first 14 years of our chronosequence.

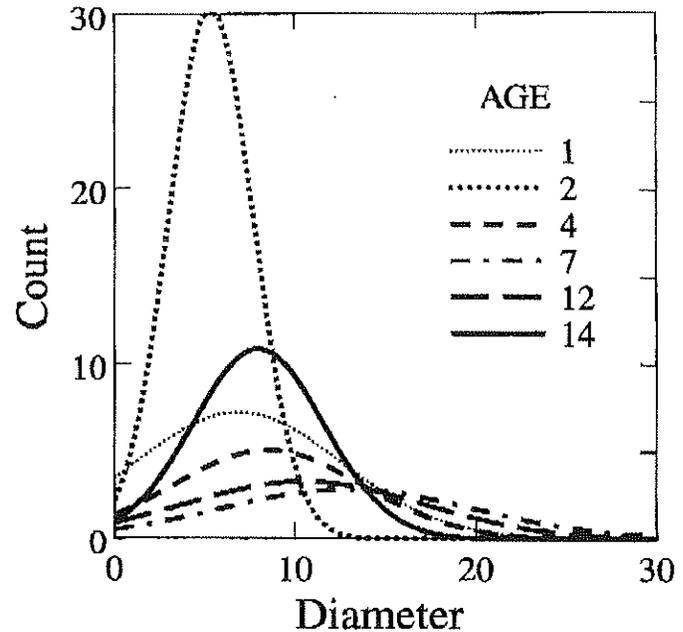
How might any overestimation of dead wood decay have affected our calculation of C loss early in secondary succession? To quantify this we used the k value of -0.042 empirically determined by Alban and Pastor (1993), and the amount of dead wood in stand age 1, to model C loss over time based on exponential decay. Even under this slower decay scenario, stands remained a net source of C to the atmo-

Fig. 4. (A) Total ecosystem C content and (B) net ecosystem productivity (NEP) as a function of time since stand-replacing wildfire. Symbols in 4A represent stand means (± 1 SE; $n = 3$), and the curve represents the nonlinear regression line described in the text. Total ecosystem C for stand age 7 is represented in gray to indicate that this point was excluded from our regression analysis. The curve in 4B represents rates of NEP through time estimated from the first derivative of the gamma function described in the text.



sphere for 6 years, but declined to a minimum of only 65 Mg C·ha⁻¹, or a net loss of 10 rather than 16 Mg C·ha⁻¹. However, stand-replacing wildfire would also generate belowground detritus in the form of dead coarse roots, which would represent a source of C loss unaccounted for in our methodology. To estimate potential error associated with not accounting for coarse root decomposition, we estimated the amount of dead roots in stand age 1 using the allometric equation of Morrison (1974; 9 Mg C·ha⁻¹). We then modeled C loss from this pool using the decomposition constant

Fig. 5. Diameter distributions for all standing and downed dead trees in stands from 1 to 14 years of age.



of -0.0415 determined for coarse roots of lodgepole pine by Yavitt and Fahey (1982). Again, these calculations do not change the timing of transition to a net C sink, but rather indicate an additional loss of 2 Mg·ha⁻¹ over this period.

Overall, these calculations reinforce our conclusion that postfire losses of C from northern Michigan jack pine forests are relatively small and of short duration. Pearson et al. (1987) came to a similar conclusion for lodgepole pine (*Pinus contorta*) forests in Wyoming, USA, where they argued that net negative C balance would only last a few years following wildfire. In contrast, Wirth et al. (2002) found that Siberian Scots pine (*Pinus sylvestris*) stands remained a net C source for 12–24 years following stand-replacing wildfire. Similarly, Kasischke et al. (1995) predicted that boreal forests will remain net C sources for 25–37 years following wildfire, depending on climatic conditions.

Why should Rocky Mountain lodgepole pine and Michigan jack pine ecosystems have lower net C losses following disturbance than these boreal forests? Janisch and Harmon (2002) have argued that the timing of transition from C source to C sink depends on both the amount of respirable substrate left on site, and the rate of growth by the regenerating stand. Boreal forests will retain large amounts of C in surface organic horizons that is susceptible to decomposition, which should lead to large and sustained losses of C following disturbance (O'Neill et al. 2002, 2003). Although jack pine is a boreal species, it occurs at the southern limit of its range in Michigan on extremely xeric, sandy soils with little capacity to store C. Thus the brief period over which jack pine stands served as a weak source of C can, in part, be attributed to the loss of much of the easily respirable substrate to direct combustion (Fig. 2A). In addition, jack pine and lodgepole pine are both strongly fire-adapted species with serotinous cones allowing them to quickly reoccupy a site following fire, thus minimizing the duration of any lag

phase in NPP. In contrast, for species without serotinous cones, reestablishment is dependent on seed dispersal from unburned patches of forest, potentially extending the lag period for NPP.

Rapid establishment of jack pine seedlings, followed by rapid accumulation of biomass in the developing jack pine stands, drove the transition to positive NEP early in our chronosequence. Thus we found that jack pine ecosystems in Michigan reached a maximum NEP of $1.6 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ at the relatively young age of 16 years, compared with Siberian Scots pine ecosystems, which took over 50 years to reach a maximum NEP of $0.6 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (Wirth et al. 2002). Whereas jack pine NEP was much higher than that of Siberian Scots pine, it was lower than the $2.1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ reported by Hooker and Compton (2003) for *Pinus strobus* ecosystems in New England, and equivalent to the $1.7 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ reported by Law et al. (2003) for *Pinus ponderosa* ecosystems in Oregon, USA.

Harmon (2001) and Schulze et al. (2000) have argued that older forest stands may remain strong sinks for C because of accumulation in soil and woody debris. Whereas the rapid accumulation of forest-floor C between years 10 and 36 made an important contribution to C sequestration during the period of exponential jack pine growth, we found that total soil C (including forest floor) reached a steady state by year 36 and did not contribute to net C sequestration by older stands. Accumulation of dead wood C appeared to increase in the older stands but made only a small contribution to total ecosystem C storage by age 72 (7%). Thus NEP declined from year 16 forward, so that older jack pine stands were a relatively weak sink for C (NEP = $0.12 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ at age 72). However, it is important to note that, because these ecosystems occur only on extremely droughty and nutrient-poor sites, there was essentially no advanced regeneration by shade-tolerant tree species able to take advantage of gaps formed by jack pine mortality. Thus we would urge caution in extrapolating these results to other environments. In more mesic sites, we would expect to find significant amounts of advanced regeneration by shade-tolerant species, which would provide an important sink for C as overstory trees begin to senesce.

Our estimates of NEP are based on substituting space for time, thus they depend on the critical assumption that sites are equivalent in all biophysical, ecological, and historical characteristics other than age. Because this assumption is never fully met, it is important to evaluate factors that may confound our estimation of successional changes in NEP. Despite the apparent uniformity of soils in this area, previous research has shown that subtle differences in texture in outwash sands can strongly affect jack pine productivity (Walker et al. 2003; Kashian et al. 2003) and thus successional changes in C accumulation. Ten of our 11 stands fell within the range of 7%–11% silt + clay; however, stand age 7 appeared to be an outlier having 18% silt + clay. To evaluate the effects of this unintended variation in soil texture on ecosystem C storage, we analyzed the residuals from our non-linear regression of total ecosystem C against stand age. We found that B horizon texture explained nearly 50% of the residual variation from our regression including stand age 7, but less than 5% of the residual variation when we excluded stand age 7. These results suggest that stand age 7 truly is an

outlier, and that variation in soil texture among the remaining stands is unlikely to confound our space for time substitution.

Whereas the broad outwash plains in this landscape provide little obvious topography, several ecosystem classification studies have shown that landscape position can have a strong effect on jack pine growth rates (Kashian and Barnes 2000; Walker et al. 2003; Kashian et al. 2003). These studies have shown that jack pine height growth is ca. 20% greater on higher-level outwash terraces compared with lower-level terraces, despite the fact that total elevation change may be less than 20 m. Kashian and Barnes (2000) attributed these productivity differences to cold air drainage, which creates significantly colder microclimate in lower-level terraces. Thus microclimatic variation associated with landscape position could potentially confound our quantification of temporal changes in NEP. However, all of these studies have demonstrated a strong relationship between forest composition and microclimate, whereby northern pin oak is an important component on warmer sites and is virtually absent from colder microsites (Kashian and Barnes 2000; Walker et al. 2003; Kashian et al. 2003). Thus we argue that by explicitly avoiding sites with a significant northern pin oak component, we have likely avoided confounding variation in microclimate. However, this does suggest that our estimates of NEP may be at the low end for jack pine forests of this area, because we selected stands more likely to occupy colder microsites.

Stand density is another important factor that is known to affect productivity and thus patterns of C accumulation through secondary succession. We found wide variation in stand density along our chronosequence (Table 1). Clearly some of this variation is deterministic, i.e., an overall decline in jack pine density through succession due to self-thinning. However, there also appears to be a substantial amount of stochastic variation in density, likely related to cone crop on the preceding stand at the time of wildfire, conditions for seedling establishment following wildfire, etc. In particular, the six young stands, in which we quantified jack pine C pools, fall clearly into low-density (12, 14, and 27 years) and high-density (7, 22, and 36 years) groupings (Table 1). Previous studies on jack pine (Hegyi 1972) and the closely related lodgepole pine (Litton et al. 2003) have shown that total biomass of young stands increases markedly with increases in stocking density. The variation in stocking density that we observed will not affect our interpretation of C losses in the first years after fire, because tree C is an insignificant portion of total ecosystem C (i.e., <1% at age 7). However, uncontrolled variation in density may influence our estimation of C accumulation later in secondary succession. Note that the exponential phase of jack pine growth is anchored at the low end by a low-density stand (12 years) and at the high end by a high-density stand (36 years). This suggests that our estimate of the rate of C accumulation during this phase (Fig. 4B) may be biased high.

A final source of potential error in our estimation of successional changes in NEP comes from our use of regional, rather than locally derived, allometric biomass equations. To assess the potential error associated with this, we compared jack pine C pools across our chronosequence calculated using six different allometric equations for jack pine

derived from areas throughout the northeastern USA and Canada (in Ter-Mikaelian and Korzukhin 1997). We found that the coefficient of variation among all six equations for tree biomass declined across the chronosequence from 18% at stand age 12 to 16% at stand age 72. This suggests that the potential error associated with using an incorrect allometric equation would be at most 0.06 Mg C·ha⁻¹ at stand age 12 (0.1% of ecosystem total) to 7.5 Mg C·ha⁻¹ at stand age 72 (7% of ecosystem total). Our actual error from not using a site-specific biomass equation is likely to be less, however, because much of the variation in estimates came from a single equation from New Brunswick (MacLean and Wein 1976), which was consistently lower than all others. Dropping this equation reduced the coefficient of variation to 9% at stand age 72.

Conclusions

The uniform soils, climate, and vegetation of these northern Lower Michigan jack pine forests provide an excellent environment to utilize space for time substitution to test theoretical predictions of ecosystem response to disturbance. Overall, we found that jack pine ecosystems along this chronosequence function as a weak source of C following wildfire, but rapidly switched to a net sink after ca. 6 years. Regenerating jack pine ecosystems reached their maximal rate of NEP at a relatively young age of 16 years, and then C sequestration declined from that point forward. Mature jack pine ecosystems remained weak net sinks for C; however, sequestration was driven primarily by continued growth of overstory jack pine, not by accumulation of detrital C.

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