

Carbon stocks across a chronosequence of thinned and unmanaged red pine (*Pinus resinosa*) stands

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Abstract. Forests function as a major global C sink, and forest management strategies that maximize C stocks offer one possible means of mitigating the impacts of increasing anthropogenic CO₂ emissions. We studied the effects of thinning, a common management technique in many forest types, on age-related trends in C stocks using a chronosequence of thinned and unmanaged red pine (*Pinus resinosa*) stands ranging from 9 to 306 years old. Live tree C stocks increased with age to a maximum near the middle of the chronosequence in unmanaged stands, and increased across the entire chronosequence in thinned stands. C in live understory vegetation and C in the mineral soil each declined rapidly with age in young stands but changed relatively little in middle-aged to older stands regardless of management. Forest floor C stocks increased with age in unmanaged stands, but forest floor C decreased with age after the onset of thinning around age 40 in thinned stands. Deadwood C was highly variable, but decreased with age in thinned stands. Total ecosystem C increased with stand age until approaching an asymptote around age 150. The increase in total ecosystem C was paralleled by an age-related increase in total aboveground C, but relatively little change in total belowground C. Thinning had surprisingly little impact on total ecosystem C stocks, but it did modestly alter age-related trends in total ecosystem C allocation between aboveground and belowground pools. In addition to characterizing the subtle differences in C dynamics between thinned and unmanaged stands, these results suggest that C accrual in red pine stands continues well beyond the 60–100 year management rotations typical for this system. Management plans that incorporate longer rotations and thinning in some stands could play an important role in maximizing C stocks in red pine forests while meeting other objectives including timber extraction, biodiversity conservation, restoration, and fuel reduction goals.

Key words: carbon dynamics; carbon storage; Chippewa National Forest, Minnesota, USA; forest management; *Pinus resinosa*; red pine; stand age; thinning.

INTRODUCTION

A growing awareness of the role anthropogenic CO₂ emissions play in regulating global climate (IPCC 2007), and the importance of forests as a global C sink (Pregitzer and Euskirchen 2004) have led to suggestions that forest managers incorporate C storage and sequestration into their planning process (Birdsey et al. 2006, IPCC 2007). Our understanding of how forest management influences standing C stocks, however, is limited because many forest C studies have focused on quantifying trends in unmanaged forests (Gough et al.

2008). Those studies that have addressed the influence of forest management on C stocks have often focused on individual components (whole tree, bole wood, soil C, dead organic material, or other components) rather than total ecosystem C. Further, while C stocks in forests clearly vary with stand age or time since disturbance (Law et al. 2004, Pregitzer and Euskirchen 2004), direct comparisons of age-related trends in managed and unmanaged forests are extremely limited. Studies that quantify and compare total ecosystem C in stands of various ages are needed to better understand C storage potentials in different ecosystems and to inform forest managers about opportunities to increase C stocks in managed forests (Gough et al. 2008).

In unmanaged forests, total ecosystem C stocks generally increase with stand age as pools of living biomass, forest floor material (organic soil horizons), and mineral soil C accumulate through stand development before ultimately leveling off in older stands (Law et al. 2004, Peltoniemi et al. 2004, Pregitzer and Euskirchen 2004). Deadwood C, however, is highly

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variable during stand development (Pregitzer and Euskirchen 2004, Bradford et al. 2009). In temperate forests, deadwood typically represents a large C pool following stand-replacing natural disturbance, declines with age in young stands as existing deadwood pools decompose, and begins to increase with age in middle-aged to old stands as senescence and minor disturbances increase the rate of deadwood additions (Spies et al. 1988, Duvall and Grigal 1999, Bradford et al. 2009).

Forest management activities have a number of potential influences on these general trends in C stock dynamics. Thinning and selection harvesting periodically remove leaf area, which is the physiological basis for tree productivity and a key driver of ecosystem productivity (Chapin et al. 2002). Thus, thinned forests might be expected to have lower rates of C accumulation than unmanaged forests. Direct removal of live tree biomass during harvesting generally reduces total ecosystem C stocks (Finkral and Evans 2008, Chatterjee et al. 2009, Davis et al. 2009, North et al. 2009). Some studies, however, report little difference in live tree C when stands that were thinned from below are compared with unmanaged stands (Hoover and Stout 2007, Hurteau and North 2009). These contrasting results demonstrate the importance of ecosystem-specific studies that examine the impact of a variety of silvicultural options on total ecosystem C stocks.

Forest management activities have well-documented impacts on deadwood pools. Timber harvesting removes live woody biomass before the opportunity for mortality, so managed forests typically have less deadwood biomass or volume than unmanaged forests (Duvall and Grigal 1999, Hura and Crow 2004, Gibb et al. 2005, Burton et al. 2009). As a result, managed stands generally have smaller deadwood C pools than unmanaged stands (Seidl et al. 2007, Chatterjee et al. 2009, Swanson 2009).

Timber harvesting can also impact soil C stocks. Harvesting influences soil temperature, soil moisture, root chemistry, and living root biomass, which all affect soil respiration rates, which in turn influence soil C cycling (Burton et al. 2002, Ryu et al. 2009). Increases in soil temperature and moisture following thinning are correlated with increased heterotrophic respiration rates, but reduced live root biomass leads to lower autotrophic respiration rates (Ryu et al. 2009). Thus, total soil CO₂ efflux may be higher (Concilio et al. 2006, Selig et al. 2008) or lower (Sullivan et al. 2008) in thinned stands than unmanaged stands when compared at ambient temperatures. In practice, these opposing factors can contribute to either increases in soil C following thinning (Skovsgaard et al. 2006, Selig et al. 2008), or have little impact on soil C (Boerner et al. 2008, North et al. 2009). C in forest floor layers may also be impacted by harvesting, but there is considerable uncertainty regarding the cause (Yanai et al. 2000, 2003).

We sampled all major ecosystem C pools across a 300-year chronosequence of thinned and unmanaged red

pine (*Pinus resinosa* Ait.) stands to compare age-related trends in C stocks between these two conditions. Our objective was to understand how thinning affects the dynamics of total ecosystem C as well as each of its component pools over time. We focused on thinning because it is a common management technique used for a variety of purposes across both public and private ownerships in many forest types and regions. A simple literature search on ISI's Web of Knowledge using the key words "thinning" and "forest management," for instance, returns results from 46 countries spanning six continents. Additionally, our chronosequence encompasses typical rotations (60–100 years) for red pine management (Gilmore and Palik 2005), as well as estimated return intervals for stand-replacing wildfires (120–250 years) in this system prior to widespread European settlement (Heinselman 1973, Whitney 1986, Palik and Pregitzer 1992). As such, our findings provide benchmarks for estimating C stocks in red pine stands managed for a variety of objectives, and should represent C pool dynamics across the full range of stand development for this forest type.

METHODS

Study sites

The study was located primarily on the Chippewa National Forest in northern Minnesota, USA. The chronosequence included 24 thinned stands, and 33 stands with no history of harvesting after establishment (unmanaged). The unmanaged chronosequence includes stands from an existing study (Bradford and Kastendick 2010), but we remeasured C pools in several of these stands and roughly doubled the chronosequence length for this study. For the thinned chronosequence, we selected only stands that were last harvested at least five years prior to data collection. Thinning in red pine on the Chippewa National Forest typically begins around age 40, so we do not have any thinned stands younger than this age. We considered our younger unmanaged stands to be representative of C dynamics for both the thinned and unmanaged conditions for ages <40 years. To minimize the potential effects of site productivity on C storage, all stands were located on sandy, outwash-derived Entisols with low fertility and water-holding capacity (Nyberg 1987). These soils are typical of native red pine forests in the Great Lakes region for both the presettlement and modern eras (Whitney 1986, Gilmore and Palik 2005). Site index calculated from tree cores taken in each stand ranged mostly from 17 to 20 m at 50 years, although a few of the younger stands (<50 years) had higher calculated values (23–25 m). Most stands were located within an area of ~30 × 30 km, with the majority of stands located within a 5 km radius of one another.

Red pine was the dominant overstory species, representing 86% of the total basal area across all stands, with eastern white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* L.), and northern red oak (*Quercus rubra* L.) each representing

1–4% of the remaining basal area. The study area has an average annual temperature of 3.9°C and average annual precipitation of 70 cm. Stand age was determined from USDA Forest Service records and validated with increment cores taken from dominant trees in each stand. Because detailed records of management do not exist for many of the older stands in our chronosequence, stands were labeled as thinned if they showed any evidence of partial cutting (either cut stumps or harvest records). The oldest stands in the thinned and unmanaged chronosequences (approximate ages 193–306 years) were old growth with no history of logging (prior to the initiation of thinning in the mid-20th century for the thinned stands), while the intermediate-aged stands (approximate ages 60–162 years) were primarily naturally regenerated second-growth forests that developed after the first logging in this area, and younger stands (under 60 years of age) were mostly plantation origin. Although the number of entries in individual thinned stands varied, the youngest thinned stands (ages 40–60 years) had generally been thinned only once, the oldest thinned stands (ages 200–245 years) had been thinned three to five times, and intermediate-aged thinned stands had been thinned from one to three times.

Data collection and C content calculation

Three 0.02-ha sampling plots were randomly located in each stand. All live and dead woody stems ≥ 2.5 cm diameter at breast height (dbh; 1.37 m) were measured and tallied in each plot. Woody stems < 2.5 cm dbh and > 15 cm in height were measured and tallied in a 10-m² plot nested within each 0.02-ha plot. Regionally derived, species-specific allometric equations were used to calculate biomass of all components (leaves, branches, stems, and roots > 5 mm in diameter) of both live and dead woody stems (Perala and Alban 1994). For standing dead stems, biomass was calculated as total live biomass minus leaves and live branches. Although we did not account for changes in wood density associated with different decay classes for standing dead stems, the vast majority of dead stems fell into the first two decay classes defined by Duvall and Grigal (1999), which differ in wood density by only 0.05 g/cm³ for red pine. Biomass of woody species was converted to C content using published values for the woody tissue C content of most tree species in the data (Lamloom and Savidge 2003). Published values or direct measurements from local stands were used for calculating the C content of foliage and roots of any tree species that represented $> 1\%$ of the total basal area. A generic value of 50% C was used for all components of shrubs and poorly represented trees.

Stump diameter, species, and decay class were recorded for all stumps within each 0.02-ha tree plot. Decay classes were defined based on structural integrity, wood texture, wood color, and the presence of invading roots (Chojnacky et al. 2004). Stump and root biomass

was estimated using locally derived, species-specific allometric equations for decay-free trees, then multiplied by a correction factor based on decay class (Chojnacky et al. 2004). Stump (and the associated roots) C was calculated by assuming stumps were 50% C by mass.

Downed deadwood was sampled using a line intersect sampling method developed to inventory fuels (Brown 1974). Three 8-m sampling transects were established across permanent 0.02-ha plots at 0, 180°, and 270° from plot center. The 8-m transects included three smaller nested transects. In the first 1 m of each transect, 0.0–0.6 cm diameter deadwood was tallied. In the first 2 m of each transect, 0.6–2.5 cm diameter deadwood was tallied. In the first 4 m of each transect, 2.5–7.6 cm diameter deadwood was tallied. Down deadwood > 7.6 cm in diameter was measured along the entire 8-m transect. Species, diameter, and decay class (Sollins 1982, FIA 2007) were recorded only for down deadwood > 7.6 cm diameter.

Fine woody debris (diameter < 7.6 cm) biomass was calculated using the equation:

$$\text{FWD} = 2.241722 \sum_{i=1}^3 \frac{f T_i (\text{dia}_i^2) \rho d c a}{L_i}$$

where FWD is fine woody debris biomass in Mg/ha, 2.241722 is a conversion factor from tons/acre to Mg/ha, i is the three diameter classes of FWD, f is a constant (11.64), T is the number of pieces of wood for each diameter class and species, dia is the diameter class of an individual piece of wood in inches ($\text{dia}_1^2 = 0.0151$, $\text{dia}_2^2 = 0.289$, and $\text{dia}_3^2 = 2.76$), r is wood specific gravity for a given species (Perala and Alban 1994), d is a decay modifier, c is a slope correction factor ($c = 1$ for our analyses because slopes were level or nearly level in all plots), a is a correction factor equal to 1.13 for material not lying flat on the ground (Brown 1974), and L is transect length (in feet; Brown 1974, Chojnacky et al. 2004).

Coarse woody debris biomass was calculated using the equation:

$$\text{CWD} = 2.241722 \sum_{i=1}^n \frac{f (\text{dia}_i^2) \rho d c}{L_i}$$

where CWD is coarse woody debris (diameter > 7.6 cm) biomass in Mg/ha, n is the number of pieces of wood in each transect, d is a decay class modifier calculated as class 1, 1.0; class 2, 0.84; class 3, 0.71; class 4, 0.45; and class 5, 0.35 for conifers or class 1, 1.0; class 2, 0.78; class 3, 0.45; class 4, 0.42; and class 5, 0.35 for hardwoods (Chojnacky et al. 2004), and all other terms are defined as described before for FWD. The C concentration of down deadwood biomass was assumed to be 50%.

Herbaceous vegetation and woody stems < 15 cm in height were sampled in three 0.25-m² clip plots nested within each 0.02-ha tree plot. All herbaceous material (forbs, graminoids, and club mosses) in each plot was clipped at peak biomass, oven-dried to a constant mass at 70°C, weighed, bulked by tree plot, ground on a Wiley mill,

and analyzed for C concentration using a Leco TruSpec (model 630-100-400; Leco, St. Joseph, Michigan, USA).

Forest floor (O horizon) material was sampled in three 0.05 m² circular plots nested within each 0.02-ha tree plot. Forest floor samples were collected after removing all herbaceous and down woody material from each forest floor plot. After collection, forest floor samples were oven-dried to a constant mass at 70°C, weighed, ground on a Wiley mill, and analyzed for C concentration using a Leco TruSpec (model 630-100-400).

Mineral soil and medium-sized roots (diameter <5 mm and >2 mm) were sampled from one 6.4 cm diameter, 30 cm deep soil core in each 0.02-ha tree plot. Soil cores were dried and passed through a 2-mm sieve to remove rocks and roots > 2 mm in diameter. Mineral soil mass was calculated as oven-dried soil core mass minus root mass and rock mass. Fine roots < 2 mm diameter were included in the mineral soil mass. Roots between 2 and 5 mm diameter were sorted out during sieving and weighed separately (roots > 5 mm diameter were accounted for in the allometric equations for woody species). Mineral soil and root material were ground on a Wiley mill and analyzed for C concentration using a Leco TruSpec (model 630-100-400). Although the 30-cm core depth did not capture C stocks in deeper mineral soil or deeper fine to medium-sized roots, soil C declines rapidly with depth in pine stands (Conkling et al. 2002), so our 30 cm depths should capture the majority of the dynamic soil C pool.

Statistical analysis

C sources were grouped into five pools for analysis: live tree C (woody plants ≥ 2.5 cm dbh including all roots > 2 mm diameter), live understory C (woody plants < 2.5 cm dbh and all herbaceous plants), deadwood (standing dead woody plants, down deadwood, and stumps), forest floor, and mineral soil (including fine roots < 2 mm diameter). Total ecosystem C (the sum of all pools), total aboveground C (live stems, foliage, standing dead stems, and down deadwood), and total belowground C stocks (forest floor, mineral soil, live roots, and deadwood in roots and stumps) were also calculated. All data were averaged across the plots in each stand to create stand-level values for analysis.

Relationships between stand age, management (thinned or unmanaged), and C stocks were analyzed using linear and nonlinear regression. We also analyzed age-related trends in the percentage of total ecosystem C stored in aboveground pools compared to belowground pools. Models were constructed using a variety of functional forms including linear ($Y = \beta_1 x$), power ($Y = \beta_1 x^{\beta_2}$), negative exponential decay ($Y = \beta_1 e^{-\beta_2 x}$), Chapman-Richards increase to an asymptote ($Y = \beta_1 (1 - e^{-\beta_2 x})^{\beta_3}$), and negative exponential decay followed by an increase to an asymptote ($Y = \beta_1 e^{-\beta_2 x} + \beta_3 (1 - e^{-\beta_4 x})^{\beta_5}$) to capture the variety of trends characteristic of different C pools. These

five functions were chosen based on previous studies describing age-related changes in various C pools. C in overstory trees, for instance, frequently increases rapidly following stand establishment, but the rate of increase can slow to approach an asymptote as stands age (Law et al. 2004, Pregitzer and Euskirchen 2004). In contrast, deadwood pools are often quite high during stand establishment, followed by a decline as existing deadwood decomposes, and may increase again as forests age and new deadwood is recruited (Spies et al. 1988, Duvall and Grigal 1999, Bradford et al. 2009). Because thinning captures some of the potential deadwood recruitment as stands age, however, thinned stands may show a rapid decline in deadwood pools following stand establishment, with no apparent increase as stands age.

We used Akaike Information Criterion (AIC) scores to select the best model from each of the five functional forms described previously, including models with and without intercepts for all of our C pools. All models were initially constructed with parameters to account for differences between thinned and unmanaged stands, and a sum-of-squares reduction test was performed after selecting the best functional forms for the thinned and unmanaged stands to determine whether thinning had a significant impact on age-related trends in each C pool. A pseudo- R^2 value ($1 - SS_{\text{error}}/SS_{\text{tot}}$, where SS_{tot} refers to the corrected total) was calculated to quantify the amount of variability captured by each of our final models. In some cases, the best (lowest) AIC score was associated with a model that included different functional forms for thinned and unmanaged stands, but the sum of squares reduction test was not significant. In these cases, we selected the model with the lowest AIC score for our analyses to preserve implications about differences in age-related trends in C stocks between thinned and unmanaged stands, but we have noted all such instances in the text and attempted to interpret results from these models cautiously.

Because we had relatively few very young (<20 years) and very old (>200 years) stands, there was potential for a small number of stands on the ends of the age distribution to have a large effect on our regression model parameter estimation. To guard against this, we calculated bootstrapped estimates, standard errors, and 95% confidence intervals for all regression coefficients and significance tests. We also recalculated our pseudo- R^2 values using bootstrapped estimates of SS_{err} and SS_{tot} . Although our original regression coefficients were similar to the bootstrapped coefficients in all cases, there were some instances in which convergence problems arose while fitting models to the resampled data sets. In these cases, we selected the next-best fitting functional form and reran our analyses until convergence problems were eliminated. Model assumptions were evaluated with residual plots, and all analyses were performed using SAS version 9.2 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Individual C pools and total ecosystem C

Live tree C increased rapidly for the first 60 years of the chronosequence in unmanaged stands, then gradually reached an asymptote in middle-aged unmanaged stands, but continued to increase at a somewhat slower rate in thinned stands across the entire chronosequence ($P < 0.001$; Fig. 1). The best model for live tree C included a Chapman-Richards function for unmanaged stands and a power function for thinned stands (Table 1). Although this model included parameters to describe different behavior in thinned stands, the effect was only marginally significant ($P = 0.038$).

Live understory C declined rapidly in young stands, but the rate of decline slowed between ages 30 and 60 years, and there was little change in live understory C pools of middle-aged to older stands ($P < 0.001$; Fig. 1). Live understory C was best modeled with a power function (Table 1). Thinning did not have a significant impact on live understory C.

Deadwood C increased somewhat with age in unmanaged stands, but decreased with age in thinned stands ($P < 0.001$; Fig. 1). However, deadwood C was highly variable across the chronosequence in both thinned and unmanaged stands. Deadwood C was best modeled with an exponential growth function for unmanaged stands and an exponential decay function for thinned stands (Table 1). The thinning effect was marginally significant ($P = 0.040$).

In unmanaged stands, forest floor C increased to an asymptote in middle-aged stands and changed little thereafter, but forest floor C decreased with age in thinned stands ($P < 0.001$; Fig. 1). The best model for forest floor C included a Chapman-Richards function for unmanaged stands and a negative exponential decay function for thinned stands (Table 1). The thinning effect was highly significant ($P < 0.001$).

Mineral soil C declined rapidly in young stands, but the rate of change dropped considerably between ages 25 and 75 years, and there was little additional change in mineral soil C for middle-aged to older stands ($P < 0.001$; Fig. 1). Mineral soil C was best modeled with a power function (Table 1). Thinning did not have a significant effect on mineral soil C.

Total ecosystem C increased rapidly with age in young stands, but the rate of increase slowed in middle-aged stands, and approached an asymptote around age 150 years ($P < 0.001$; Fig. 1). The best model for total ecosystem C was a Chapman-Richards function (Table 1). Thinning did not have a significant effect on total ecosystem C.

Partitioning between aboveground and belowground pools

Total aboveground C increased rapidly with age in young stands followed by a more gradual increase with age in middle-aged stands, until approaching an asymptote in older stands ($P < 0.001$; Fig. 2). Total

aboveground C was best modeled with a Chapman-Richards function (Table 1). Thinning did not have a significant effect on total aboveground C.

Belowground C pools changed little across the chronosequence, but our models did indicate a negligible increase with age ($P < 0.001$; Fig. 2). Total belowground C was best modeled as an exponential increase (Table 1). Thinning did not have a significant effect on total belowground C.

When these data were partitioned into above- and belowground pools, and expressed as percentages, belowground pools were the dominant source of C in young stands, but the percentage of total ecosystem C stored in aboveground pools increased rapidly as stand age increased. The percentage of C stored in aboveground pools reached a maximum of ~60% of total ecosystem C around age 60 in unmanaged stands, while the percentage of C stored in aboveground pools increased more gradually in thinned stands, but continued to increase throughout the chronosequence ($P < 0.001$; Fig. 2). The percentage of C stored in aboveground pools was best modeled using a Chapman-Richards function for unmanaged stands and a power function for thinned stands (Table 1). The thinning effect was highly significant ($P < 0.001$).

DISCUSSION

These results suggest that thinning had limited impacts on total ecosystem C, although age-related trends in some individual C pools and the distribution of total ecosystem C between aboveground and belowground pools, when expressed as percentages of total ecosystem C, were modestly affected by thinning. Thinning reduced forest floor C stocks in older stands, slowed the rate of increase in live tree C and the proportional rate of increase in aboveground C pools, and may have affected deadwood pools, but there were no significant thinning effects on total ecosystem C, total aboveground C, or total belowground C. These findings have a number of implications for C management in red pine forests and likely for C management in many forests dominated by shade-intolerant conifers.

Our results support the positive relationships between stand age and both live C and total ecosystem C characteristic of forests worldwide (Pregitzer and Euskirchen 2004). Our total ecosystem and live tree C pools for young-middle-aged stands are similar in both magnitude and rate of increase to those of similar-aged stands reported (or estimated from biomass data) in shorter red pine chronosequence studies (King et al. 2007, Ouimet et al. 2007, Bradford and Kastendick 2010). No previous studies in this system, however, have provided data on C stocks in old (160+ year) stands to provide a complete picture of C stock dynamics over either the 120–250 years estimated for historical fire return intervals in this system (Heinselman 1973, Whitney 1986, Palik and Pregitzer 1992), or the 300+ years estimated for red pine's potential life span (Burns

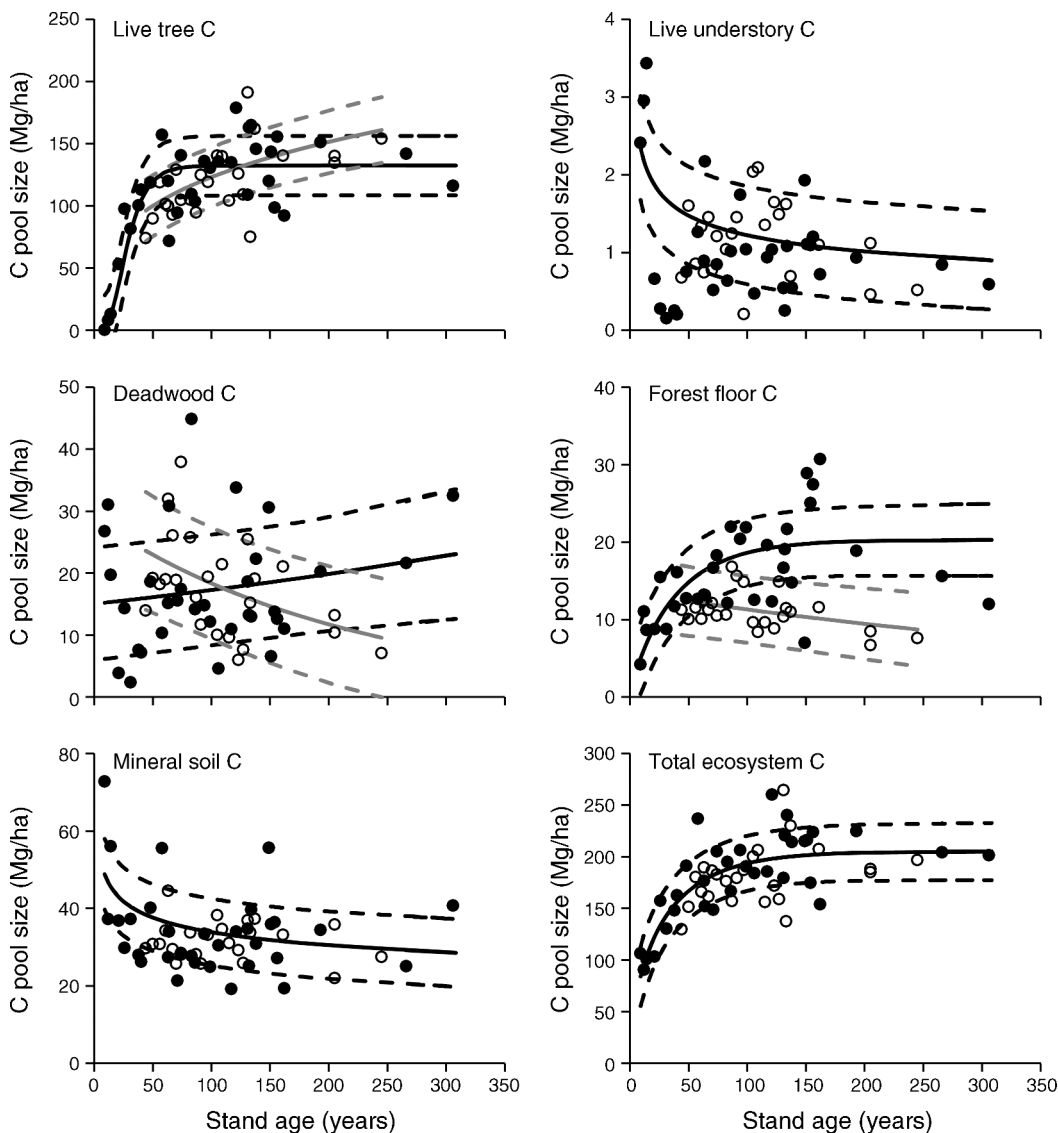


FIG. 1. Relationships between various C pools, stand age, and thinning in a Minnesota, USA, red pine (*Pinus resinosa*) forest. Solid circles represent unmanaged stands; open circles represent thinned stands. Black lines represent regression predictions for unmanaged stands or all stands combined when the thinning effect was not significant, and gray lines represent regression predictions for thinned stands in models with significant thinning terms. Dashed lines represent bootstrapped standard error estimates for the predicted values.

and Honkala 1990). Few studies in any system have provided C chronosequence data for managed stands (Gough et al. 2008) to provide a basis for comparison of thinning impacts, but our total ecosystem C trendline for unmanaged stands fell roughly in the middle of the range of available data for other temperate pine forests (Law et al. 2003, Peichl and Arain 2006, Noh et al. 2010), suggesting our C pool estimates are reasonable in both magnitude and rate of change.

Live tree C increased with age until approaching a maximum around 100 years in unmanaged stands, but continued to increase with age across the entire chronosequence in thinned stands. However, the ab-

sence of significant thinning effects on total ecosystem C strongly indicates that thinning did not produce the reduction in C stocks suggested in other studies (Finkral and Evans 2008, Chatterjee et al. 2009, North et al. 2009). Long-term thinning studies indicate that red pine stands maintain similar levels of productivity across a wide range of stocking levels (Liechty et al. 1986, Bradford and Palik 2009); thus, our finding that thinning did not affect total ecosystem C stocks may be reflective of the study system's underlying capacity to compensate for lost potential productivity (leaf area) resulting from timber harvesting with rapid increases in the growth of residual trees after harvest, even in old age

TABLE 1. Regression models relating C pools and stand structural attributes to stand age and management history in a Minnesota, USA, red pine (*Pinus resinosa*) forest.

Dependent variable	Model form†	β_1	β_2	β_3	Model <i>P</i>	Pseudo- <i>R</i> ²	SSR <i>P</i> ‡
Live tree C	if TH	31.0459	0.299		<0.001	0.969	0.038
	then PWR	(8.510)	(0.059)		(<0.001, <0.001)	(0.954, 0.980)	
	else CR	132.448	0.084	6.790			
		(6.759)	(0.038)	(10.297)			
Live understory C	PWR	4.248	-0.270		<0.001	0.781	0.112
		(2.414)	(0.160)		(<0.001, <0.001)	(0.706, 0.855)	
Deadwood C	if TH	28.757	0.005		<0.001	0.824	0.040
	then NE	(6.323)	(0.002)		(<0.001, <0.001)	(0.766, 0.877)	
	else NE	15.026	-0.001				
		(2.958)	(0.001)				
Forest floor C	if TH	13.499	0.002		<0.001	0.932	<0.001
	then NE	(1.152)	(0.001)		(<0.001, <0.001)	(0.903, 0.958)	
	else CR	20.297	0.023	0.844			
		(3.871)	(0.025)	(2.686)			
Mineral soil C	PWR	68.117	-0.152		<0.001	0.945	0.242
		(22.700)	(0.079)		(<0.001, <0.001)	(0.925, 0.969)	
Total ecosystem C	CR	205.163	0.023	0.528	<0.001	0.982	0.245
		(7.908)	(0.009)	(0.184)	(<0.001, <0.001)	(0.974, 0.988)	
Total aboveground C	CR	125.887	0.030	1.288	<0.001	0.971	0.121
		(6.050)	(0.011)	(0.555)	(<0.001, <0.001)	(0.958, 0.981)	
Total belowground C	NE	75.356	-0.000		<0.001	0.980	0.087
		(3.069)	(0.000)		(<0.001, <0.001)	(0.972, 0.986)	
Percentage of C aboveground	if TH	29.627	0.150		<0.001	0.996	<0.001
	then PWR	(4.134)	(0.029)		(<0.001, <0.001)	(0.993, 0.998)	
	else CR	60.237	0.129	10.212			
		(0.925)	(0.069)	(34.957)			

Notes: Values in parentheses indicate bootstrapped standard error estimates for regression coefficients (β_1 – β_3) and bootstrapped 95% confidence intervals for significance tests and pseudo-*R*². Abbreviations are: PWR, power function; CR, Chapman-Richards function; and NE, negative exponential function.

† TH indicates thinned stands; PWR = $\beta_1(\text{age}^{\beta_2})$; CR = $\beta_1(1 - \exp^{-\beta_2\text{age}})$; NE = $\beta_1(\exp^{-\beta_2\text{age}})$.

‡ Sum of squares reduction test comparing a full (with thinning terms) model to a reduced (no thinning terms) model.

(D'Amato et al. 2010, Powers et al. 2010). This seems particularly likely since we did not include stands that were thinned in the very recent past (less than five years prior to measurement) in our study. Thus, while thinning had no apparent impact on total ecosystem C storage in our data, results from a landscape populated by many recently thinned stands may be different.

A casual interpretation of our results also suggests that the rate of C storage (i.e., the slope of the total ecosystem C stocks curve) slows to nearly zero by the middle of the chronosequence. Thus, while C stocks are maintained in old red pine stands, these stands gain little additional C over time. This finding is consistent with estimates of C fluxes from a variety of forest types (Law et al. 2004, Pregitzer and Euskirchen 2004, Gough et al. 2008), and emphasizes the need to carefully consider landscape-scale age distributions in C management.

Our results for live tree C also suggest that, while thinning may have the anticipated impact of modestly reducing the rate of C accumulation in live biomass compared to unmanaged stands, thinned red pine stands can ultimately store as much or more C in the live tree pool in old age because thinned stands continue to build live tree C stores decades after unmanaged stands have reached their peak. The youngest thinned stands in our study (ages 40–60 years) had only been thinned once,

while the oldest stands (ages 200–245 years) had been thinned up to five times, so the continued accrual of live tree C across the thinned chronosequence occurred over an increasing number of thinning entries as well. This finding is consistent with the widely reported phenomenon of delayed culmination of mean annual increment in repeatedly thinned stands (Assman 1970, Curtis 1995, Stinson 1999, D'Amato et al. 2010). Although the live tree C trend we observed in thinned stands is consistent with our understanding of thinning impacts, differences between the thinned and unmanaged live tree C trendlines at any given stand age were quite small relative to the size of total ecosystem C pools. This fact is underscored by the absence of a significant thinning effect on total ecosystem C, and suggests that the cumulative effects of multiple thinnings are negligible over long rotations. Rigorous stocking control with relatively short thinning cycles, however, can reduce total ecosystem C stocks (Powers et al. 2011).

Deadwood C stocks have been related to stand age and harvesting (Duvall and Grigal 1999, Bradford et al. 2009, Chatterjee et al. 2009). Our results do suggest that thinning reduced deadwood C stocks over time, which agrees with studies from a variety of forest types that indicate forest management reduces deadwood pools (Kirby et al. 1998, Duvall and Grigal 1999, Fridman and

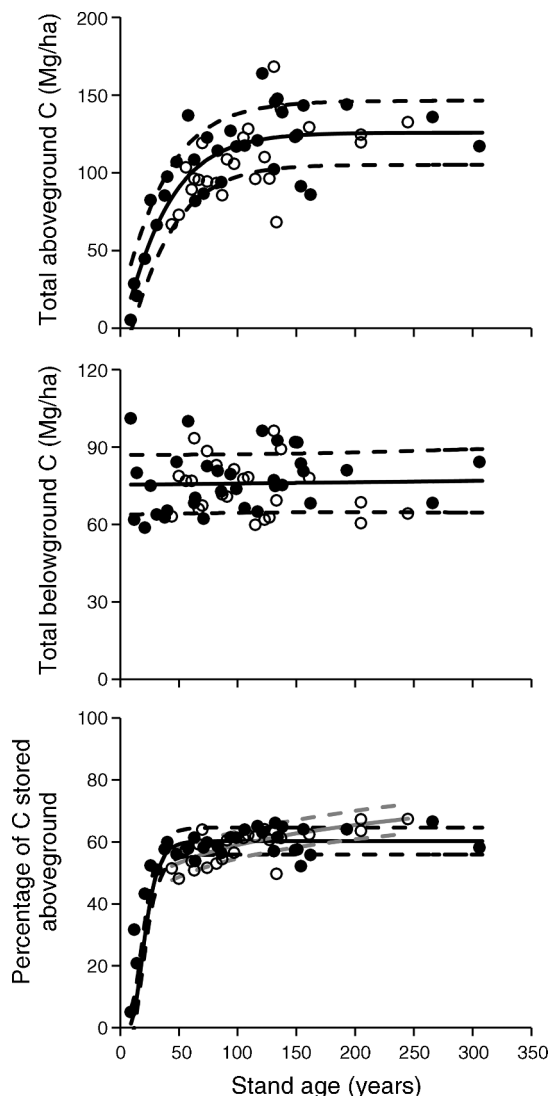


FIG. 2. Relationships between C stocks in aboveground or belowground pools, stand age, and thinning in a Minnesota red pine forest. Solid circles represent unmanaged stands; open circles represent thinned stands. Black lines represent regression predictions for unmanaged stands or all stands combined when the thinning effect was not significant, and gray lines represent regression predictions for thinned stands in models with significant thinning terms. Dashed lines represent bootstrapped standard error estimates for the predicted values.

Walheim 2000, Hura and Crow 2004, Gibb et al. 2005). We did not find evidence of the U-shaped temporal pattern of deadwood biomass and C stocks described for many temperate forests (Spies et al. 1988, Duvall and Grigal 1999, Janisch and Harmon 2002, Pregitzer and Euskirchen 2004, Bradford et al. 2009), although our deadwood data were highly variable, and our regression model forms were not selected with this pattern in mind. Pregitzer and Euskirchen (2004) suggest that high variability in deadwood pools is common in temperate forests and attribute this variability to the influence of

different forest management activities on deadwood pools sizes in young stands. If we control for some of the differences in stand origins and management by, for instance, comparing deadwood pools in our three oldest thinned stands (which were in an old-growth condition at the time of their initial thinning in the mid-20th century) to deadwood pools in our three oldest unmanaged stands (which are currently in an old-growth condition), we find that deadwood C pools were, on average, more than twice as large in the unmanaged stands than in the thinned stands.

Increases in forest floor or detrital C with stand age are common (Covington 1981, Pregitzer and Euskirchen 2004, Peichl and Arain 2006, Bradford et al. 2008, 2009). However, our finding that forest floor C declines with age in thinned stands contrasts with reports that thinning has little impact on forest floor C stocks (Boerner et al. 2008, Chatterjee et al. 2009). The abrupt halt and age-related decline of forest floor C accumulation we observed for thinned stands could be triggered by a variety of harvest-related factors including reduced litter inputs, increased decomposition rates associated with higher soil temperature or moisture, or mixing of surface materials into the mineral soil during harvesting operations (Yanai et al. 2000, 2003). There was no evidence of a difference in mineral soil C in thinned stands relative to unmanaged stands, so we have no support for the hypotheses that mixing or increased decomposition rates could have reduced forest floor C stocks following harvesting by transferring organic C into the mineral soil (Covington 1981), and the idea of accelerated decomposition following harvesting is not well supported by experimental studies (Yanai et al. 2003). Reduced litter or branch inputs after harvesting remain possible explanations for the trends in forest floor C we observed, but we have no direct evidence to support these explanations. Regardless of the cause, age-related differences in forest floor C stocks between thinned and unmanaged stands in our study were not large enough to create significant management-related differences between total ecosystem or belowground C pools across the chronosequence, although the thinning effect on forest floor C combined with the thinning effect on live tree C likely explain the difference in age-related patterns of the percentage of total ecosystem C stored in aboveground pools.

The pattern of rapid decline in mineral soil C stocks of young stands followed by a phase of very gradual decline in mineral soil C as stand age increased beyond ~75 years contrasts with the trend of increasing soil C with stand age reported in some studies (Hooker and Compton 2003, Pregitzer and Euskirchen 2004, Sun et al. 2004). The marginal decline in soil C that followed our initial, rapid drop is, however, consistent with findings from some pine-dominated forests (Rothstein et al. 2004, Ouimet et al. 2007). Age-related effects on mineral soil C stocks are highly variable, and other studies report no significant relationships between stand age and soil C (Peichl and Arain 2006, Bradford et al. 2008). It is worth noting that the

maximum mineral soil C value observed in our youngest stand (73 Mg/ha) was very similar to the average for total belowground C for all stands across the chronosequence (76 Mg/ha). This could imply that the high mineral soil C stocks in our youngest stands were largely the result of a legacy effect due to C inputs from the decomposition of dead root biomass in the years immediately following harvesting. Further, the mineral soil trend is largely shaped by the three youngest stands in the chronosequence (ages < 15 years). When these stands are omitted, our models predict virtually no change in mineral soil C across the remaining stands in the chronosequence. While it is regrettable that we could not sample more of these very young stands, the pattern of rapid soil C decline following clearcutting that we observed has been documented in other systems (Diochon et al. 2009, Tang et al. 2009), and could result from increased C mineralization rates following harvest (Diochon et al. 2009).

Although we caution that limitations of the data (e.g., few very young stands and no stands that were thinned less than five years prior to measurement) reduce our ability to generalize these findings over space and time, our results provide some important information that can only be derived from long, well-replicated chronosequences that compare stands which have been thinned repeatedly (in the case of our older thinned stands) throughout their development to unmanaged stands. There are few field studies comparing temporal trends of C pools in managed and unmanaged stands (Gough et al. 2008). This has hindered our understanding of how temporal changes in C dynamics of a “typical” managed stand compare to those of a typical unmanaged stand. While long-term silvicultural studies provide a window into these types of questions for live tree C pools (e.g., Hoover and Stout 2007), these studies generally do not have long-term records of the variables needed to estimate changes in C stocks in the forest floor, mineral soil, understory vegetation, or downed deadwood over time. Although marginal in size, the different temporal trajectories of live tree C, forest floor C, and aboveground–belowground C allocation we observed, for instance, could not be detected from data sets that represent responses to only one thinning in older stands, from chronosequences that are truncated at the end of a traditional management rotation, or from long-term tree growth and survival data sets that lack information needed to determine non-tree C dynamics. More importantly, our results indicate that the modest differences between thinned and unmanaged stands that may occur in some individual C pools had little impact on total ecosystem C stocks over the course of stand development in red pine.

Our analyses suggest that appropriate rotations to maximize C stocks in red pine (150 years or more), are significantly longer than the 60–100 year rotations conventionally used in this system (Gilmore and Palik 2005), and our estimate of appropriate rotations for maximizing C stocks in managed red pine are quite

similar to recent recommendations of 130–140 year rotations for maximizing wood production in thinned stands (D’Amato et al. 2010). We must note, however, that our analysis only considered C stored on site, and C stocks in wood products derived from harvested timber can also be a significant C stock (Birdsey et al. 2006). Because total C stocks in thinned red pine stands were similar to total C stocks in unmanaged stands across the chronosequence, it is possible that total C stocks in older stands that have been thinned repeatedly could be slightly higher than total C stocks in older unmanaged stands if C in end-use wood products and landfills was also accounted for. Further studies are clearly needed to address this point directly, but the concept could have significant implications for carbon management in systems where other objectives that require timber harvesting (fiber extraction, fuels treatments, or restoration) have equal or greater importance.

MANAGEMENT IMPLICATIONS

Our findings have several potential implications for forest managers and policymakers. First, thinning did not appear to have a significant impact on maximum ecosystem C stocks in the red pine forest we studied, although repeated thinning may reduce C stocks in this system (Powers et al. 2011). This suggests that intermediate treatments designed to improve growing conditions for residual trees, control fuels or wildfire behavior, or increase structural complexity for restoration and conservation objectives may all be accommodated to some extent when managing to maximize C stocks. Second, although C in live biomass of unmanaged stands appears to peak near the end of a conventional management rotation, total ecosystem C continues to increase with stand age for several decades beyond the peak in live biomass, and C in live biomass does not appear to reach a peak in thinned stands, even after nearly 250 years. Managing a portion of the landscape on longer rotations of 120–150 years or more could simultaneously increase C stocks, reduce the proportion of the landscape characterized by young stands that act as C sources rather than sinks (Pregitzer and Euskirchen 2004), and meet conservation goals that call for longer intervals between regeneration harvests (Gilmore and Palik 2005). Third, the forest floor and deadwood pools combined to represent 20–30% of total ecosystem C across our chronosequence. Harvesting logging debris for biofuels and site preparation practices that directly reduce forest floor or deadwood pools will have significant, negative effects on C stocks that should be weighed against any potential benefits. Finally, contemporary forest management guidelines often focus on management of live C pools; however, other pools (deadwood, forest floor, and mineral soil) represented the bulk of C in young stands, and 30–40% of C in middle-aged and older stands in our study. This underscores the importance of considering management impacts on all ecosystem C pools if C storage is an objective.

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