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Age-related patterns of forest complexity and carbon storage in pine and aspen–birch ecosystems of northern Minnesota, USA

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Abstract: Forest managers are seeking strategies to create stands that can adapt to new climatic conditions and simultaneously help mitigate increases in atmospheric CO_2. Adaptation strategies often focus on enhancing resilience by maximizing forest complexity in terms of species composition and size structure, while mitigation involves sustaining carbon storage and sequestration. Altered stand age is a fundamental consequence of forest management, and stand age is a powerful predictor of ecosystem structure and function in even-aged stands. However, the relationship between stand age and either complexity or carbon storage and sequestration, especially trade-offs between the two, are not well characterized. We quantified these relationships in clearcut-origin, unmanaged pine and aspen chronosequences ranging from <10 to >130 years in northern Minnesota. Complexity generally increased with age, although compositional complexity changed more over time in aspen forests and structural complexity changed more over time in pine stands. Although individual carbon pools displayed various relationships with stand age, total carbon storage increased with age, whereas carbon sequestration, inferred from changes in storage, decreased sharply with age. These results illustrate the carbon and complexity consequences of varying forest harvest rotation length to favor younger or older forests and provide insight into trade-offs between these potentially conflicting management objectives.

Résumé : Les aménagistes forestiers cherchent des stratégies pour créer des peuplements capables de s'adapter aux nouvelles conditions climatiques tout en contribuant à atténuer l'augmentation de CO_2 atmosphérique. Les stratégies d'adaptation sont souvent axées sur l'amélioration de la résilience en maximisant la complexité de la forêt en termes de composition et de structure de dimension des espèces tandis que les mesures d'atténuation visent l'accumulation et la séquestration soutenues du carbone. La modification de l'âge du peuplement est une conséquence fondamentale de l'aménagement forestier et l'âge du peuplement est un puissant prédicteur de la fonction et de la structure de l'écosystème dans les peuplements équiennes. Cependant, les relations entre l'âge et la complexité de la forêt ou l'accumulation et la séquestration du carbone et plus particulièrement les compromis entre les deux ne sont pas bien caractérisés. Nous avons quantifié ces relations dans des chronoséquences non aménagées de pin et de peuplier issues de coupes à blanc et allant de <10 à >130 ans dans le nord du Minnesota. La complexité de la forêt augmentait généralement avec l'âge, quoiqu'avec le temps la complexité compositionnelle variait plus dans les forêts de peuplier alors qu'avec le temps la complexité structurelle variait davantage dans les peuplements de pin. Bien que les réservoirs individuels de carbone aient montré différentes relations avec l'âge du peuplement, l'accumulation totale de carbone augmentait avec l'âge tandis que la séquestration du carbone, déduite à partir des changements dans l'accumulation, diminuait brusquement avec l'âge. Ces résultats illustrent les conséquences sur le carbone et la complexité de différents âges d'exploitabilité selon qu'on favorise des forêts plus jeunes ou plus vieilles et donnent une idée des compromis entre ces objectifs d'aménagement potentiellement contradictoires.

[Traduit par la Rédaction]

Introduction

As the reality of climate change becomes increasingly apparent (IPCC 2007), forest managers are urgently seeking strategies to create stands that can both adapt to new climatic conditions and help mitigate increases in atmospheric CO_2 (Bosworth et al. 2008). Managers must facilitate adaptation by creating stands that are capable of sustaining forest productivity, habitat quality, and other ecosystem services under changing, and increasingly variable, climatic conditions (IPCC 2007). One conceptual approach to adaptation involves maximizing forest complexity within stands (Millar

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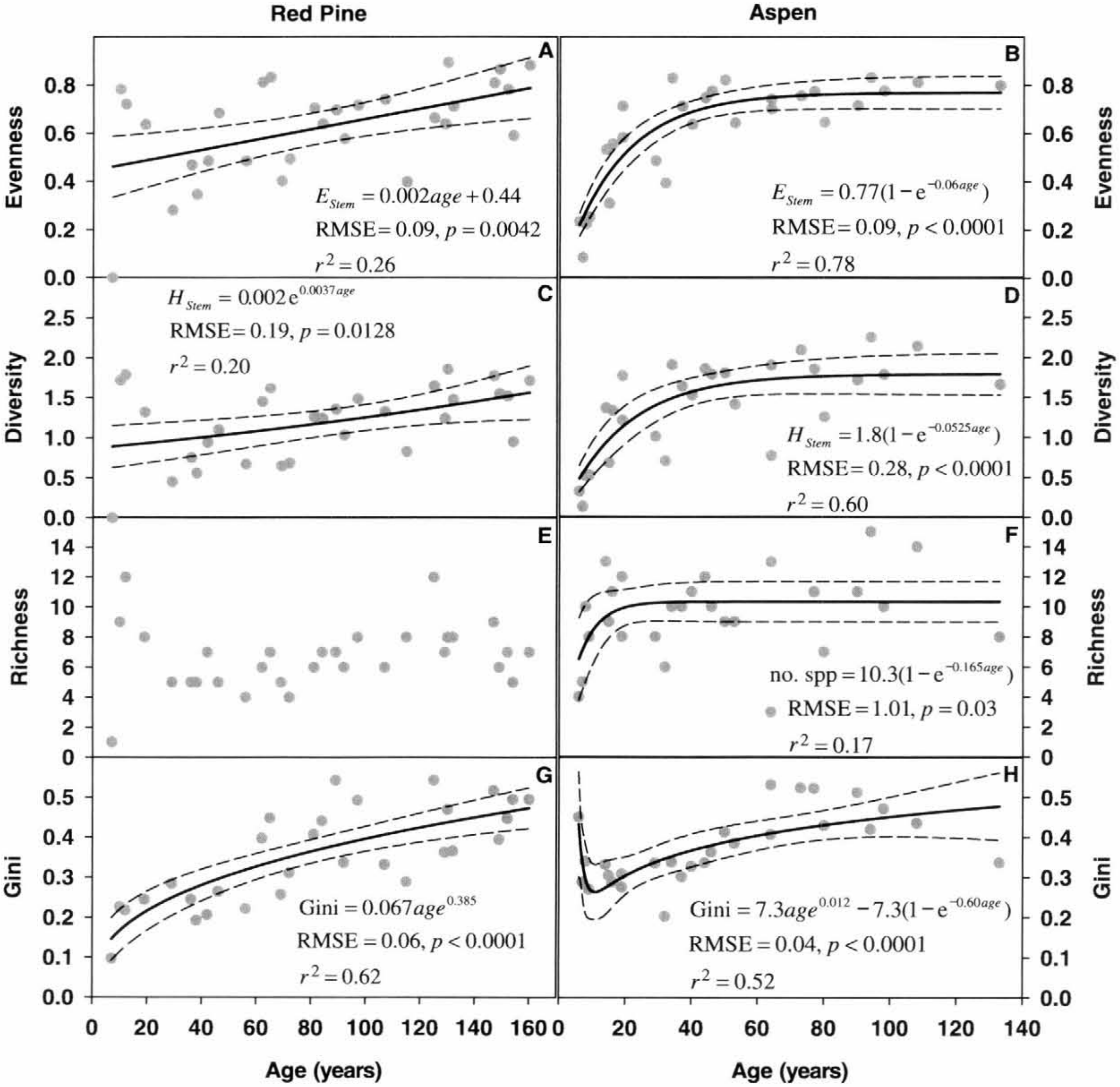
Fig. 1. Forest complexity as a function of stand age in pine and aspen chronosequences from northern Minnesota. Each point represents a single stand, solid lines are the best-fit regression results of the highest performing regression model (see Supplemental Tables S2A and S2B)^2, and dashed lines are upper and lower 95% confidence intervals of the regression. Text within each panel provides model form and parameter estimates as well as significance level (p), root mean squared error of the model (RMSE), and coefficient of determination (r^2). Measures of complexity include tree species evenness (E_{Stem}) (A and B), tree species diversity (H_{Stem}) (C and D), tree species richness (no. spp.) (E and F), and the Gini index of dispersion in tree diameters (Gini) (G and H.) Panels without a regression line indicate nonsignificant relationships.



et al. 2007), where complexity can be either compositional diversity in tree species or structural diversity in tree sizes (McElhinny et al. 2005; Smith et al. 2008). Complexity may enhance forest adaptability to new conditions because more complex stands may have higher functional diversity, i.e., different species and (or) sizes may respond differently to new or variable conditions, creating more overall stability in ecosystem function and enabling complex forests to sustain ecosystem services in the context of changing conditions. In addition, because rising atmospheric CO_2 is a major driver of climate change (IPCC 2007), forest managers are being asked to mitigate climate change by maintaining the ecosystem service provided by continued carbon storage and sequestration in forest ecosystems (Birdsey et al. 2006).

One of the simplest and yet most dramatic impacts of forest management is manipulation of stand age as a result of harvesting. Manipulation of stand age is especially influential in forests managed by even-aged rotations, which remain very common in the United States (US) and worldwide. Consequently, it is essential to understand the relationship between stand age and both forest complexity and carbon storage and sequestration. Forest complexity has long been expected to increase with stand age (Odum 1969), and studies have observed very high levels of complexity in mature or old-growth stands (Spies and Franklin 1988).

However, few studies have characterized the more subtle variations in forest complexity that may exist within the more narrow range of stand ages in managed forests (Brassard et al. 2008).

Numerous studies have identified a link between stand age and aspects of the forest carbon cycle (Pregitzer and Euskirchen 2004; Magnani et al. 2007), suggesting that altering the distribution of forest age structures may be a feasible mechanism for influencing carbon storage and sequestration (Heath and Birdsey 1993; Depro et al. 2008). Stand age is an especially powerful predictor of carbon storage in even-aged forests resulting from traditional forest management (Smith et al. 1997). Although the importance of stand age is well recognized, many studies of age-related forest carbon storage focus on only a subset of forest carbon pools, notably live-tree biomass or bole biomass, and fewer studies have identified useful relationships between age and other components of ecosystem carbon storage, particularly carbon stored in non-tree components and detrital material (Bradford et al. 2009). As a result, the carbon consequences of alterations to stand age that result from management actions remain unclear, underscoring the need for studies examining whole-ecosystem carbon storage across a range of ages (Anderson et al. 2008; Hudiburg et al. 2009).

Our objective was to characterize how stand age influences both forest complexity and carbon storage and sequestration in chronosequences of even-aged red pine and aspen–birch stands in northern Minnesota. These results provide insight into the impact of age-related management strategies on carbon storage and sequestration and forest complexity in these two widespread forest types of mid-continental North America that are typically managed using even-aged methods. Although chronosequences have long been recognized as a useful tool for assessing ecological patterns and processes (Odum 1969) and continue to contribute to our understanding of pattern and process in forest ecosystems (Hudiburg et al. 2009), the method hinges on the important and often overlooked assumption that all sites within a chronosequence are essentially identical in climatic and edaphic conditions (Johnson and Miyanishi 2008). To meet this assumption, we established upland pine and aspen–birch chronosequences, each utilizing sites within close proximity, on a consistent soil order and with nearly identical management and disturbance history.

Methods

Study area

The pine chronosequence ranged from 7 to 160 years and included 30 pine-dominated stands on the Cutfoot Experimental Forest in northern Minnesota (47.549N, 94.092W). Measured in 2007, pine stands occurred on low-fertility outwash plains in the Entisol soil order with rapid permeability, low available water capacity, and slow surface runoff (Nyberg 1987), typical soil conditions for red pine in the northern Lake States. Red pine (*Pinus resinosa* Aiton) comprised about 81% of the total basal area, with lesser species (comprising 16%) consisting of jack pine (*Pinus banksiana* Lamb.), Eastern white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill.) (see Supplemental Table S1)[2]. The aspen chronosequence ranged from 6 to 133 years and included 28 aspen-dominated stands on the Marcell and Pike Bay experimental forests (47.549N, 94.092W and 47.549N, 94.092W, respectively). Measured in 2008, aspen stands occurred on moraine and till and (or) outwash plains in the Alfisol soil order, which is very typical for aspen–birch forests in the northern Lake States, with moderate to rapid permeability, high to moderate available water capacity, and moderate surface runoff (Nyberg 1987). Trembling aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.) comprised 67% of total basal area, with lesser species (comprising 23%) consisting of sugar maple (*Acer saccharum* Nutt.), paper birch, red maple (*Acer rubrum* L.), American basswood (*Tilia americana* L.), and balsam fir (Supplemental Table S1)[2]. Stands in both chronosequences have strongly continental climates, with an average annual temperature of 3.9 °C and an average annual precipitation of 70 cm (MRCC 2006).

Stand selection and data collection

Pine and aspen stands were selected from the United States Forest Service inventory database of stand origin date, management history since origination (i.e., no thinning, which was confirmed in the field), and size (a minimum of 3 ha). Within each chronosequence, stands had similar management and disturbance histories and were selected to be on extremely similar soil conditions (see soil descriptions above). To the best of our knowledge, all stands were clearcut at the time of stand origin, and pine stands were subsequently planted while aspen–birch stands were naturally regenerated; no thinning, management treatments, or catastrophic disturbances have occurred since stand origination and no additional site preparation occurred on any stands. Age-related patterns inferred from this chronosequence are strengthened by this consistency in climate, stand history, and soil conditions (Johnson and Miyanishi 2008).

In each chronosequence stand, three 0.02 ha sampling plots were randomly located at least 30 m from surrounding stands and roads. Although relatively small, these three plots sampled sufficient area to include an average of 80 trees per stand in red pine and >200 trees per stand in aspen while also providing three estimates of carbon storage as a measure of within-stand variability. In addition, this sampling regime was fast enough to allow measurement of a total of 58 stands. All woody stems ≥2.5 cm diameter at breast height (DBH; 1.37 m) were inventoried in each plot. We tallied species and DBH for all stems on each plot and height for a subset of stems (20%). Increment cores were taken from two dominant trees per plot and used in conjunction with inventory data to verify stand age. The biomass of live and standing dead trees was calculated using regionally derived species-specific allometric equations (Perala and Alban

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[2] Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5353. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 2. Forest carbon cycling as a function of stand age in pine and aspen chronosequences in northern Minnesota. Each point represents a single stand, error bars are standard error between plots within each stand, solid lines are the best-fit regression results of the highest performing regression model (see Supplemental Tables S2A and S2B)^2, and dashed lines are upper and lower 95% confidence intervals of the regression. Text within each panel provides model form and parameter estimates as well as significance level (p), root mean squared error of the model (RMSE), and coefficient of determination (r^2). Carbon storage (in Mg C·ha^{-1}) is shown for carbon in live trees (A and B), dead woody material (C and D), understory vegetation (E and F), forest floor material (G and H), mineral soil (I and J), and total (K and L.) Carbon sequestration (in Mg C·ha^{-1}·year^{-1}) was estimated from differentiating the equation for total ecosystem carbon storage (M and N). Panels without a regression line indicate nonsignificant relationships.

1993). Woody stems <2.5 cm DBH were measured in a circular 10 m^2 plot nested within each tree plot. Species and stem diameter at 15 cm height were measured on all live and dead woody species, and biomass was calculated using species-specific allometric equations (Perala and Alban 1993). Herbaceous (herbs, graminoids, and club mosses) biomass was harvested at peak standing crop biomass (July–August) from 0.25 m^2 clip plots nested within the sample plots (three clip plots per plot in pine stands sampled in 2007; one per plot in aspen stands sampled in 2008 after observation of low within-plot variability) and was then ovendried at 70 °C to a constant mass and weighed. Herbaceous samples were ground using a Wiley mill in the laboratory and subsamples were analyzed for total carbon. Carbon content for woody species was assumed to be 50% of total biomass (Heath et al. 2003), while laboratory-analyzed samples were computed as the total ovendry mass multiplied by the percentage of carbon in the sample.

Estimates of downed woody debris were obtained from three line intersect transects per plot (8 m in pine stands, 12 m in aspen stands) at 0°, 120°, and 240° from each plot center. All fine woody residues along the transects were separated into diameter classes of 0–0.6, 0.6–2.5, and 2.5–7.6 cm and tallied along 1, 2, and 4 m transects, respectively (Brown 1971). Coarse woody debris >7.6 cm diameters along the entire respective transect lengths were identified to species, measured for diameter (cm) and decay class (Sollins 1982; FIA 2007) to provide estimates of downed wood biomass (Brown 1971; Brown and Roussopoulos 1974) and carbon pools.

Forest floor and mineral soil were sampled following protocols similar to the Forest Inventory and Analysis Phase 3 protocols (FIA 2007). Forest floor samples were collected 4 m from the plot center (at 0°, 120°, and 240°) by harvesting the O horizon from a 25 cm diameter plastic cylinder. All forest floor samples were oven-dried at 70 °C to a constant mass then weighed to determine total biomass.

One 6.4 cm diameter, 30 cm deep (likely to encompass any alterations in soil carbon storage as a result of harvesting; Johnson and Curtis 2001), mineral soil core was collected on each plot from inside one of the three forest floor sample locations. Soil samples were oven-dried (105 °C) to constant mass, weighed, and passed through a 2 mm sieve to remove rocks and roots >2 mm. We calculated soil mass for each section as total ovendry mass minus the >2 mm rock and root fractions. Root fractions greater than 2 mm but less than 5 mm (>5 mm accounted for in allometric equations) were then ground, homogenized by stand, and analyzed for CHN concentrations. All herbaceous material, forest floor, mineral soil, and root fraction samples were analyzed for total carbon with a Leco TruSpec (model 630-100-400).

Carbon and complexity response variables

We compiled our field measurements into five carbon pools: carbon in live trees greater than 2.5 cm DBH, including stems, branches, foliage and roots; carbon in live understory material, including herbaceous plants and woody plants <2.5 cm DBH; carbon in dead woody material, including standing dead trees, down dead woody debris, and dead tree roots; carbon in forest floor material; and carbon in mineral soil. Total ecosystem carbon was calculated as the sum of these five pools. To characterize forest complexity, we focused only on trees ≥2.5 cm DBH and calculated three response variables to assess compositional complexity and one response variable to assess structural complexity. All complexity variables were calculated at the stand level using the combined tree list from all three plots. For compositional complexity, we calculated Shannon's diversity index (H) as

$$H = -\sum_{i=1}^{s} \frac{n_i}{N} \ln \left(\frac{n_i}{N}\right)$$

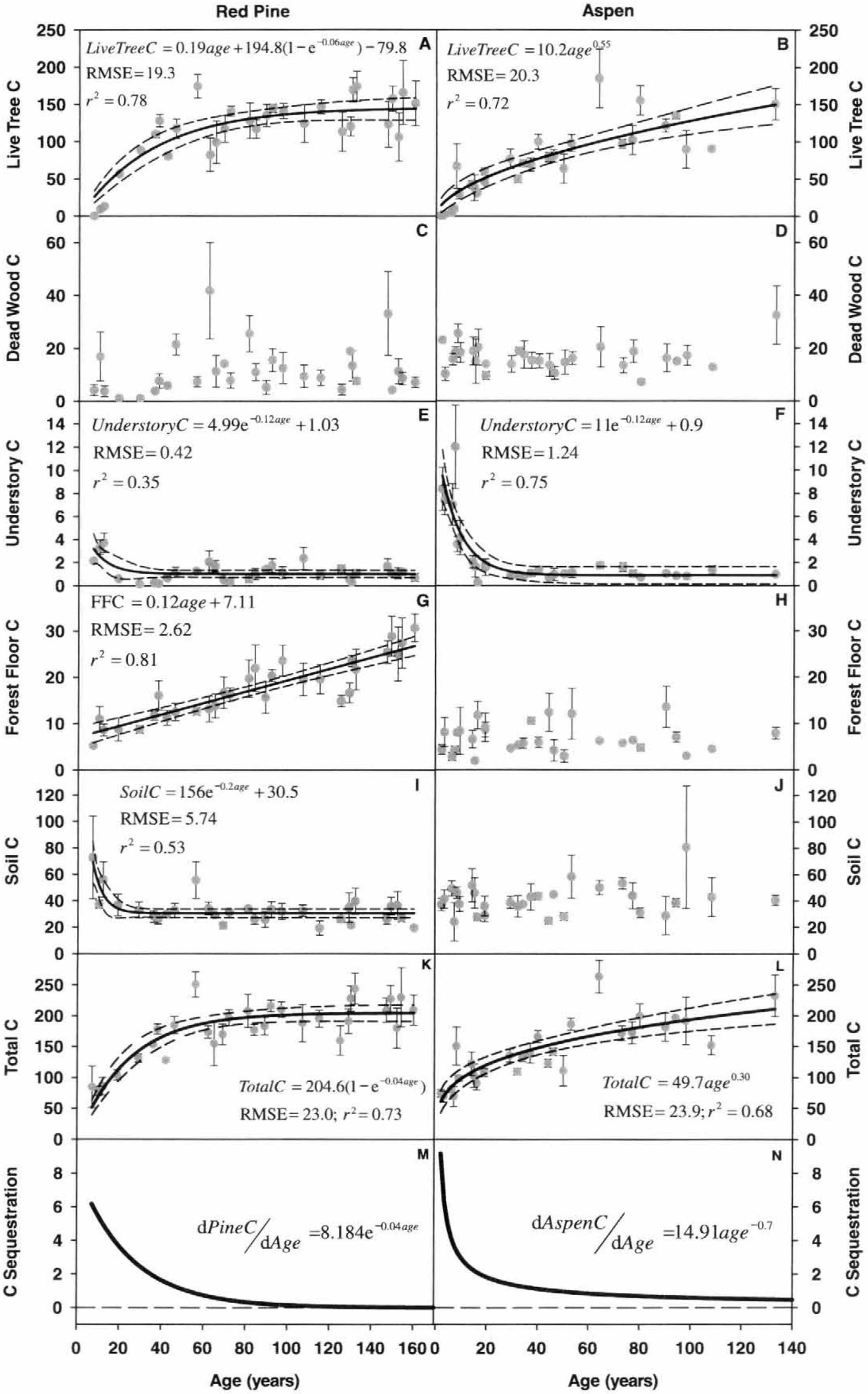
where S is the total number of species in the stand, N is the total number of stems on the stand, and n_i is the number of stems of species i. We also calculated species evenness (E) as $E = H/\ln(S)$. The final compositional variable was species richness, simply the average number of species observed per stand. To assess structural complexity, we calculated the gini coefficient of statistical dispersion of tree diameters (G), which provides a general measure of the magnitude of spread in tree sizes and serves as a metric of live-tree structural complexity. Within each stand, G was calculated from the tree list ordered by ascending diameter as

$$G = \frac{\sum_{i=1}^{n}(2i - n - 1)x}{n^2\mu}$$

where n is the number of trees in the stand, x is the diameter of tree i, and μ is the mean tree diameter for each stand.

Data analysis

All carbon storage variables were averaged within each stand (n = 3 plots per stand), and stands were treated as the experimental unit for regression analysis. Once response variables were tested for normality we compared a set of candidate statistical regression models based on four functional forms to quantify the relationship between each response variable and stand age. These statistical models related each carbon pool to stand age using a linear function, a power function, an exponential increase, and an exponential rise to a maximum. Each of these general equation forms can fit data that increase or decrease with


Red Pine
Aspen
Live Tree C
Dead Wood C
Understory C
Forest Floor C
Soil C
Total C
C Sequestration
Age (years)
A
$LiveTreeC = 0.19age + 194.8(1 - e^{-0.06age}) - 79.8$
RMSE=19.3
$r^2 = 0.78$
B
$LiveTreeC = 10.2age^{0.55}$
RMSE= 20.3
$r^2 = 0.72$
C
D
E
$UnderstoryC = 4.99e^{-0.12age} + 1.03$
RMSE= 0.42
$r^2 = 0.35$
F
$UnderstoryC = 11e^{-0.12age} + 0.9$
RMSE=1.24
$r^2 = 0.75$
G
$FFC = 0.12age + 7.11$
RMSE= 2.62
$r^2 = 0.81$
H
I
$SoilC = 156e^{-0.2age} + 30.5$
RMSE= 5.74
$r^2 = 0.53$
J
K
$TotalC = 204.6(1 - e^{-0.04age})$
RMSE= 23.0; r^2= 0.73
L
$TotalC = 49.7age^{0.30}$
RMSE= 23.9; $r^2 = 0.68$
M
$dPineC/dAge = 8.184e^{-0.04age}$
N
$dAspenC/dAge = 14.91age^{-0.7}$
0 20 40 60 80 100 120 140 160
0 20 40 60 80 100 120 140
0 50 100 150 200 250
0 20 40 60
0 2 4 6 8 10 12 14
0 10 20 30
0 20 40 60 80 100 120
0 50 100 150 200 250
0 2 4 6 8

age, and each was run with and without an intercept term. To allow response variables to have intermediate maxima or minima, a result observed in some previous studies (Covington 1981; Duvall and Grigal 1999), we also examined all possible combinations of two functional forms combined into a single predictive equation. Once the best model for total ecosystem storage was selected, temporal patterns of carbon sequestration was estimated by differentiation.

Models were tested for homoscedasticity and compared using likelihood theory to determine which model was most supported by the data (Burnham and Anderson 2001). We calculated Akaike's information criterion ($\mathrm{AIC_C}$), ranked models based on $\mathrm{AIC_C}$, and calculated model weights (w_i), which are interpreted as the weight of evidence in favor of the best model in comparison to other models in the candidate set of models.

Results

Complexity

Forest complexity was positively related to stand age in all of the response variables that we examined except species richness in the pine chronosequence. Tree species evenness was positively related to stand age in both forest types (Figs. 1A and 1B). The best models were a linear relationship ($p = 0.004$, $w_i = 0.25$, $r^2 = 0.26$) with age in pine and a combination of linear and exponential functions ($p < 0.0001$, $w_i = 0.30$, $r^2 = 0.78$) in aspen. Tree species diversity was positively related to age in both forest types (Figs. 1C and 1D), although in pine stands the relationship was exponential ($p = 0.013$, $w_i = 0.26$, $r^2 = 0.20$), and in aspen stands the best model was an exponential rise to a maximum ($p < 0.0001$, $w_i = 0.35$, $r^2 = 0.60$). Mean tree species richness per plot was positively related to age in aspen stands (Fig. 1F, $p = 0.03$, $r^2 = 0.17$), and the best model was an exponential rise to a maximum ($w_i = 0.34$). In contrast, richness was not significantly related to age in pine stands (Fig. 1E). Structural complexity (Gini coefficients) increased with age in both forest types (Figs. 1G and 1H, $p < 0.0001$). The best model was a power function ($w_i = 0.33$, $r^2 = 0.62$) in pine forests and a combination of a power function and an exponential rise to a maximum ($w_i = 0.28$, $r^2 = 0.52$) in aspen forests.

Carbon storage

Both live carbon pools we examined (live trees and live understory vegetation) were significantly related to stand age. Carbon stored in live trees increased with age in both pine and aspen forests ($p < 0.001$, Figs. 2A and 2B). In both forest types, live-tree carbon increased quickly at young ages and gradually leveled off at older ages. In pine, the best model was a combination of the linear and exponential rise to a maximum functional forms ($w_i = 0.31$, $r^2 = 0.78$), whereas the best model in aspen forests was a power function ($w_i = 0.29$, $r^2 = 0.72$). Carbon stored in live understory biomass was negatively related to stand age in both forest types ($p < 0.001$, Figs. 2E and 2F). In both pine and aspen forests, the best model for live understory carbon was a negative exponential decline (pine: $w_i = 0.33$, $r^2 = 0.35$; aspen: $w_i = 0.80$, $r^2 = 0.75$) demonstrating rapid decreases in understory carbon at young ages followed by consistently low levels of understory carbon in older forests.

None of the three detrital carbon pools that we quantified (dead woody material, forest floor, and mineral soil) were significantly related to stand age in aspen forests, and in pine forests only forest floor and mineral soil were related to stand age. Carbon content in forest floor material increased linearly with stand age ($w_i = 0.29$, $r^2 = 0.81$) in the pine forests ($p < 0.001$, Fig. 2G). Mineral soil carbon was negatively related to stand age in pine forests ($p < 0.001$, Fig. 2I). The best model for explaining this relationship was a negative exponential ($w_i = 0.67$, $r^2 = 0.53$).

Total ecosystem carbon was positively related to stand age in both forest types ($p < 0.001$, Figs. 2K and 2L). The best model for total carbon in pine forests utilized an exponential rise to a maximum ($w_i = 0.41$, $r^2 = 0.73$), whereas the best model in aspen forests utilized a power function ($w_i = 0.42$, $r^2 = 0.68$). Our estimates of carbon sequestration rates as a function of stand age suggest that the highest sequestration rates occur in very young forests, and that these rates rapidly decrease with age in both forest types (Figs. 2M and 2N). Sequestration in aspen forests is higher than pine forests in very young stands and in stands older than roughly 60 years, whereas pine stands displayed higher sequestration during intermediate ages. Perhaps more importantly, these data suggest that aspen–birch forests may continue to sequester carbon at low rates even at older ages, a finding that warrants further investigation.

Many of the best models for both carbon storage and complexity displayed low model masses, implying some uncertainty about the optimal functional form of the equation relating either carbon storage or complexity to stand age. This uncertainty does not undermine the strength and validity of the best models reported here, and alternative models were often functionally similar to the best models identified in a given set, in some cases only differing in the presence or absence of an intercept term (see Supplemental Tables S2A, S2B, S3A, and S3B)[2]. As such, these models collectively support the general age-related patterns in carbon storage described by the best models.

Discussion

Our results indicate moderately strong, positive relationships between structural complexity (Gini coefficient) and stand age, a finding consistent with previous work that examined forests across a similar range of ages (Larson et al. 2008). In contrast, relationships between compositional complexity (evenness, diversity, and richness) and stand age appear to depend on forest type and the specific index of compositional complexity. In pine, stand age was not significantly related to species richness and displayed only moderate positive relationships with species diversity and evenness. The best models for compositional complexity in aspen typically accounted for more of the observed variability than the best models in red pine, suggesting that compositional complexity may be more dependent on age in aspen than in pine forests. However, much of the relationship between stand age and compositional complexity in aspen stands occurs in the first 50 years following stand initiation. During this time, species richness, diversity, and evenness all increase rapidly, whereas these measures of complexity show relatively little change after approximately age 50. This suggests that while structural complexity in aspen stands may continue to increase beyond the typical management rotation in aspen forests (30–60 years, depending on site quality), our data do not suggest that compositional complexity will continue to increase in these older stands.

In both forest types, our data support the strong, positive relationships between live-tree carbon and stand age (Pregitzer and Euskirchen 2004). Understory carbon initially decreased in young forests and stabilized at low levels by approximately 40 years, suggesting that even the older stands in these chronosequences appear not to be experiencing substantial decreases in canopy cover that would cause increases in understory biomass (Franklin et al. 2002). Although age-related patterns of dead wood have been described (Chojnacky and Heath 2002) and some previous studies have supported those patterns (Carmona et al. 2002), other studies have not observed a consistent relationship between age and dead wood (Harmon et al. 2001; Fraver et al. 2002; D'Amato et al. 2008). Our observation of no relationship between carbon in dead woody material and stand age in either forest type may be a result of these stands being depleted in woody material at stand initiation (i.e., the vast majority of woody material was removed via harvesting). This result underscores the continued challenge of characterizing dead woody material for carbon accounting efforts across the range of ages and conditions found in managed forests (Bradford et al. 2009).

The relationship between age and forest floor carbon appears to depend on forest type. Unlike some previous studies in deciduous forests (Yanai et al. 2003), we found that aspen leaf litter did not accumulate substantially as the stand develops, perhaps because the higher quality litter was rapidly decomposed (Prescott et al. 2000). In contrast, we found a strong positive relationship between forest floor carbon and age in pine stands, a finding consistent with other coniferous chronosequence results (Sun et al. 2004; Bradford et al. 2008). Lower forest floor biomass and therefore lower forest floor carbon in young forests may be a consequence of forest harvesting activities or stand-replacing natural disturbances that can cause physical disturbance and accelerate forest floor decomposition (Jandl et al. 2007). In addition, young pine stands often contain a substantial component of pioneer hardwoods (Supplemental Table S1)[2], which produce more decomposable litter. Although mineral soil carbon is typically much less responsive to stand age than other carbon pools (Jandl et al. 2007), in pine stands we observed elevated levels of mineral soil carbon that decreased by approximately 30–40 years. These higher soil carbon levels may be a result of harvest operations adding needle litter to the soil profile and (or) physically mixing the forest floor and mineral soil, which can stimulate forest floor decomposition and integration into the mineral soil (Johnson and Curtis 2001; Silver and Miya 2001).

By quantifying the relationship between stand age and both forest complexity and carbon storage, these results provide insight into the overall costs and benefits of forest management strategies that favor younger or older forests. We found that both total carbon storage and most complexity indices generally increase with stand age. The strong relationship between total ecosystem carbon storage and stand age in both forest types suggests that age plays an important role in influencing overall ecosystem carbon storage and can provide insight into carbon sequestration (Pregitzer and Euskirchen 2004). Consistent with other studies (Gough et al. 2008), we found the highest carbon sequestration rates in young stands. Although carbon sequestration rates may be adversely impacted by changing climatic conditions (Leonelli et al. 2008), the higher sequestration rate in younger stands suggests a probable trade-off between management strategies that favor older versus younger forests. The benefits of longer rotations favoring older forests, i.e., enhanced forest complexity and carbon storage for adaptation and mitigation, respectively, will need to be balanced against the benefits of shorter rotations favoring younger forests, i.e., higher carbon sequestration rates and rapid generation of forest products. Sequestration rates are relatively level after 60 years in both forest types, but aspen sequesters carbon at a higher level beyond current recommended management rotations of 30–60 years, suggesting that increasing the rotation length of aspen would have a greater effect on total ecosystem carbon storage than increasing the rotation length of pine forests.

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