Thinning, Age, and Site Quality Influence Live Tree Carbon Stocks in Upland Hardwood Forests of the Southern Appalachians

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Abstract: This study examines the effects of thinning, age, and site quality on aboveground live tree carbon (ATC) (Mg/ha) stocks in upland hardwood forests of mixed-species composition in the southern Appalachian Mountains. In 1974, 80 plots ranging in size from 0.06 to 0.1 ha were established in even-aged, mixed-hardwood forests throughout the southern Appalachians. All trees >2.54 cm dbh within each plot were tagged and measured. Sixty-two plots received a low thinning to a broad range of residual basal areas (BAs) (m^2/ha) whereas 18 of the 80 plots remained unthinned and served as controls. Remeasurement of plots occurred every 5 years through 2005. Individual tree volumes were converted to stand-level estimates of ATC stocks for each inventory cycle. The average net annual rate of carbon (C) storage in aboveground live tree biomass was significantly greater in thinned versus unthinned stands. We found that light low thinnings had a neutral to slightly positive effect on net ATC stocks over the long-term relative to unthinned stands of similar age and initial BA. Relative differences, however, varied with age when ingrowth data were excluded from the analysis and with age and BA when ingrowth data were included in the analysis. In general, the gains in net ATC stocks in thinned verses unthinned stands were minor. The increased rate at which thinned stands stored C coupled with substantial mortality in unthinned stands was probably responsible for this "crossover" effect of thinning on ATC stocks. FOR. SCI. 58(5):407–418.

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IT IS WELL ESTABLISHED that the conversion of old-growth forests to young forests via intensive management (e.g., clearcutting) decreases stand-level carbon (C) storage primarily due to the removal of C stored in aboveground biomass (Harmon 1990). However, the effect that less-than-stand-replacing disturbances, including intermediate stand management activities such as thinning, have on C storage remains unclear. Thinning has been customarily used to capture and remove volume that would have been lost due to mortality during stand development as well as to increase and concentrate future growth on more economically valuable trees (Nyland 2002). Whereas more traditional objectives associated with thinning are related to timber production, today thinning treatments are designed and implemented to achieve numerous objectives including the creation and maintenance of wildlife habitat, wildfire hazard reduction, and ecosystem restoration, with benefits to timber production often considered a positive byproduct.

Past research examining the effects of thinning have focused on traditional individual-tree or stand-level volume growth and yield variables with little to no regard for the effects of thinning on C uptake and storage. Many factors influence the stand-level response to thinning including the method of thinning (Emmingham et al. 2007, Bradford and Palik 2009), stand structure (Oliver and Murray 1983, Marquis and Ernst 1991), species composition (Nowak 1996), age (Beck and Della-Bianca 1975, Medhurst et al. 2001, Juodvalkis et al. 2005), and site quality (Skovsgaard 2009). Given the factors that influence postthinning production, it is reasonable to assume that the response of C uptake and storage to thinning is not uniform across a forested landscape; rather C uptake and storage after thinning likely varies across forest types, age classes, edaphoclimatic gradients, and thinning prescriptions.

Relative to information regarding volume production after thinning, there is a paucity of information pertaining to response of C storage to thinning across the various forest types in the United States. In general, studies have shown the response of the aboveground live tree C pool is negatively affected by thinning in the short- and long-term, and this result appears to be consistent across both western (Finkral and Evans 2008, Campbell et al. 2009) and eastern US forest types (Taylor et al. 2007, Chiang et al. 2008, Keyser 2010, D'Amato et al. 2011). Although these studies suggest that total C storage decreases with thinning, postthinning C storage is significantly influenced by thinning method and subsequent stand structure (Hoover and Stout 2007), age at the time of thinning (Schroeder 1991), and site quality (Kranabetter 2009, Keyser 2010, Gonzalez-Benecke et al. 2010), making it difficult to generalize the C consequences of thinning. Inconsistent results from these studies emphasize the need to account for various physical stand attributes when the consequences of thinning on C storage are interpreted.

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Of the studies that have addressed the effects of alternative silvicultural treatments on C storage, many have used data collected from previously established growth and yield studies (e.g., Skovsgaard et al. 2006, Hoover and Stout 2007, Nilsen and Strand 2008). Although long-term growth and yield studies may be useful for addressing aspects of some contemporary issues, such as C storage, the original objectives associated with these studies limits many of these data sets to information regarding net C production (e.g., Keyser 2010, Horner et al. 2010), with limited details on gross C production, deadwood C dynamics (unless deadwood dynamics are modeled as performed by Hoover and Stout 2007), and ex situ C storage (i.e., C stored in forest products).

Upland hardwood forests of the southern Appalachians are capable of storing a substantial amount of C in aboveground biomass (Brown et al. 1999). Here, as elsewhere, C storage in aboveground live biomass varies with stand age (Brown et al. 1997). Current and past land-use patterns have had a substantial impact on age class structure of upland hardwood forests of the southern Appalachian Mountains. The age class distribution within this complex landscape, where minor changes in topography have a significant influence on site productivity, will likely influence the response of the aboveground live tree C pool at the stand-level. In this article, we use 30 years of individual tree growth data to quantify the effect of thinning on long-term C storage across a broad range of site qualities, stand ages, and postthinning stand structures in upland hardwood forests of mixed-species composition throughout the southern Appalachian Mountains. Specifically, we test whether C storage in aboveground live tree biomass increases over that observed in comparable unthinned stands. Specific hypotheses were the following: net C storage in aboveground tree biomass is positively related to stand age and site quality; regardless of thinning intensity, net aboveground live tree C stocks in unthinned stands will exceed net aboveground live tree C stocks in thinned stands for any given age and site quality combination; and although total standing aboveground live tree C stocks will be greater in unthinned stands 30 years postthinning, the average net annual rate at which C is stored in aboveground live tree biomass in thinned stands will exceed net C storage rates in comparable unthinned stands.

Materials and Methods

Study Area

This study uses long-term data collected as part of a study examining the growth and yield of mixed-hardwood stands throughout the southern Appalachians. The original objective of this study was to examine the effects of postthinning residual basal area, site quality (i.e., site index), and stand age on timber production. Since this study was initiated, three publications have been produced using the original study design, including a model predicting forage production as a function of postthinning stand structure (Beck 1983), an individual tree growth model created using only treated plots (Harrison et al. 1986), and a stand-level growth model produced using only a subset of the treated plots (Bowling et al. 1989). In 1974, 80 permanent plots ranging in size from 0.06 to 0.1 ha were established in upland hardwood stands throughout the Blue Ridge and northern Ridge and Valley Provinces of the southern Appalachian Mountains (Figure 1). Plots were located in northern Georgia ($n = 3$), western North Carolina ($n = 46$), eastern Tennessee ($n = 24$), and southern Virginia ($n = 7$). Forestland within the study region is dominated by various upland hardwood forest types. However, the majority of the study area is dominated by oak (*Quercus*) species or is of mixed-oak composition. Plots were located in a variety of topographic positions with slopes between 6 and 65% and elevations ranging from 600 to 1,350 m. All plots were established in even-aged stands of mixed-species composition. Stands originated as a result of heavy cutting and varied in age between 19 and 78 years (Table 1).

Data Collection

At the time of plot establishment and before the thinning treatment, all live trees >2.54 cm dbh (1.37 m aboveground line) within each plot were tagged and stem-mapped. For all tagged trees, species, dbh, and height were recorded. One increment core at stump height (0.3 m above ground line) along with total tree height (m) was obtained from six dominant/codominant yellow-poplar and/or oak trees per plot. Age at stump height was obtained from the increment cores in the laboratory and under magnification. With use of the age and height data, an estimate of site index (SI) (base age 50) for each of the six trees per plot was calculated for yellow-poplar using SI equations developed by Beck (1962) and subsequently converted to oak SI using Doolittle's (1958) conversion equations and for oak using SI equations developed by Olson (1959). Plot-level SI was calculated as the average SI of the six sample trees. SI values in this study encompassed the variability observed across the mixed-hardwood forest type in the southern Appalachians ranging from 18.9 to 33.8 m.

In 1974, after plot establishment and the prethinning inventory, 62 plots received a low thinning or thinning from below (Nyland 2002, p. 409) to a residual basal area (BA) (m^2/ha) that was at least one 6 m^2/ha BA class less than the prethinning BA, where the number of BA classes the prethinning BA was reduced were chosen at random. Before thinning, stand BA averaged 25.9 m^2/ha but varied between 19.1 and 44.3 m^2/ha (Table 1). BA was reduced to an average of 13.8 m^2/ha but ranged from 6.4 to 24.6 m^2/ha. As a percentage of prethinning BA, the thinnings reduced BA between 10 and 73%. The range in thinning intensities ranged from a grade A thinning, in which only suppressed trees were removed, to a grade D or heavy thinning, in which the majority of codominant trees were removed. Eighteen of the 80 plots remained unthinned and served as controls. Initial BA in unthinned plots varied between 16.8 and 33.9 m^2/ha. Remeasurement of all thinned and five of the unthinned plots occurred during the dormant season every 5 years after thinning up through 2005 for a total of seven inventories. Because of time constraints and limited resources, the remaining unthinned plots were inventoried less frequently with measurements occurring in four of the

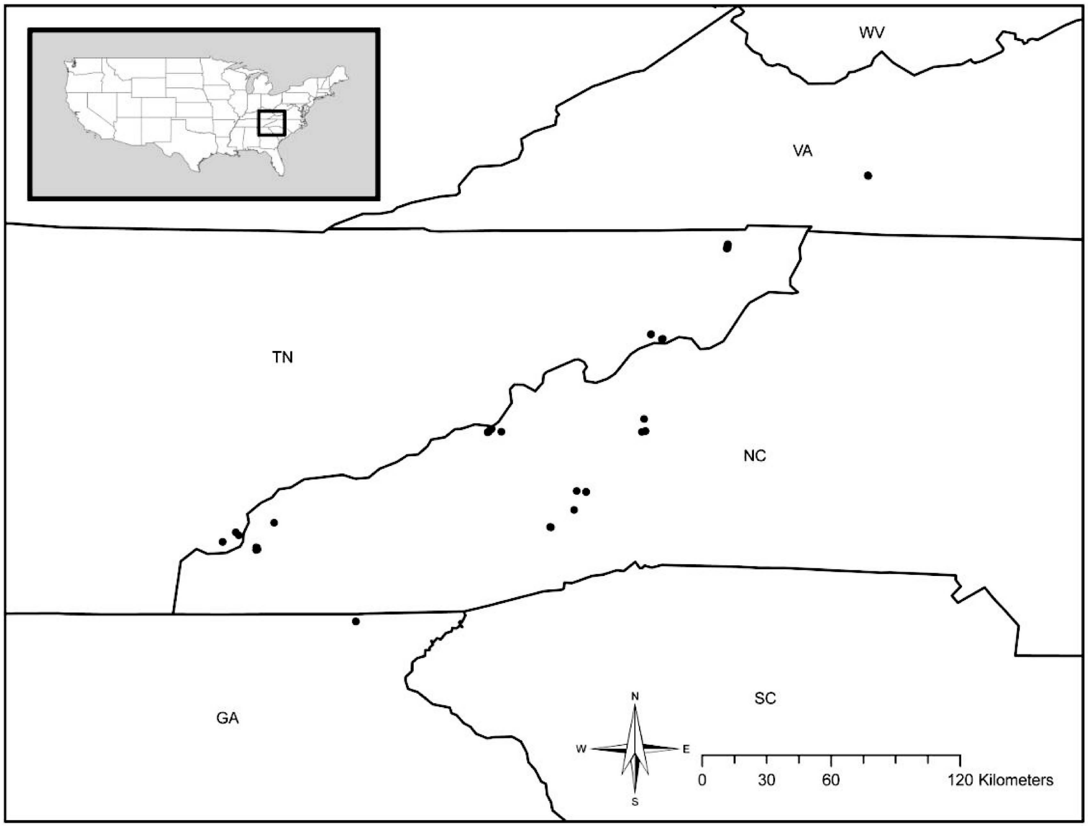

Figure 1. Map of the study area displaying location of study plots used in this article (solid circles). Because of scale, symbols represent more than one study plot.

seven inventory cycles. During each inventory cycle, the status of all tagged trees was assessed (e.g., live/dead), and dbh was recorded on all live trees. Beginning in 1995, ingrowth trees (trees >11.4 cm dbh) were tagged, and species and dbh were recorded. When tagged trees were recorded as "dead" during a given inventory cycle, individual tree data including dbh and status (e.g., standing dead versus dead and down) was not recorded in the current nor in any subsequent inventory cycles. Consequently, deadwood C dynamics are not reported.

We used the carbon submodel (Reinhardt et al. 2007) within the Fire and Fuels Extension (Reinhardt and Crookston 2003) to the Forest Vegetation Simulator (FFE-FVS) (version 6.21; revision date Sept. 19, 2008) (Crookston and Dixon 2005) to calculate and convert individual tree volume (calculated using equations from the National Volume Estimator Library maintained by the USDA Forest Service, Forest Products Measurements group in the Forest Management Service Center) to estimates of individual tree C stocks. The FFE-FVS was used only as a volume and C compiler of individual tree data collected during this study and was not used to model or simulate the effects of treatments on C pools over time. Stand-level estimates of aboveground live tree C (ATC) (Mg C) stocks were obtained by summing individual tree C estimates and then scaled to a per hectare basis (Mg/ha). Because size and status of mortality (i.e., standing versus dead and down and decay status) were not recorded during the inventories, mortality was not included in the ATC biomass pool.

Statistics

Prethinning data were used to test the hypothesis that ATC stocks in undisturbed, upland hardwood forests are largely a function of stand age. We used linear regression (PROC GLM; SAS Institute 2003) to examine the relationship between prethinning ATC stocks and stand age. Prethinning ATC values were $\log_e$-transformed to achieve normality and homoscedasticity.

Analysis of covariance (ANCOVA) was used to assess the effects of thinning and various postthinning stand attributes on C storage in the aboveground live tree pool (ATC) over time. To assess how ingrowth affects ATC stocks, we developed models of ATC storage separately using data sets that estimated ATC stocks based on the exclusion (ingrowth-excluded scenario) and inclusion (ingrowth-included scenario) of ingrowth data. The full model for both scenarios contained independent continuous variables including the inverse of stand age (1/A), SI, and stand-level basal area (ln BA), and a categorical variable for thinning (yes, no) along with all possible interactions between the categorical and continuous variables. Models were simplified by systematically removing covariate terms that had significance levels <0.05 as suggested by Milliken and Johnson (2002). Models were fitted using PROC MIXED (SAS Institute 2003). The covariance structure used to account for the autocorrelation among measurements that occurred on each independent plot was modeled using a first-order autoregressive structure. We report r^2 values for

Table 1. Pre- and postthinning stand attributes of thinned and unthinned upland hardwood stands in the southern Appalachian Mountains.

Stand attribute	Thinned ($n = 62$)				Unthinned ($n = 18$)			
	Mean	Minimum	Maximum	SD	Mean	Minimum	Maximum	SD
Site index (m)	24.2	18.9	29.2	2.2	28.2	20.1	33.8	3.7
Initial stand age (yr)	40	19	58	12	53	20	78	16
BA (m^2/ha)								
Prethinning	25.9	19.1	44.3	4.4	28.7	16.8	33.9	5.5
Immediately postthinning	13.8	6.4	24.6	4.5	28.7	16.8	33.9	5.5
30 yr postthinning (no ingrowth)	26.6	13.1	55.1	7.3	35.7	28.5	51.4	5.8
30 yr postthinning (ingrowth)	31.5	19.7	59.2	6.7	37.5	28.9	52.3	5.6
Density (trees/ha)								
Prethinning	1,003	375	3,732	625	612	375	1,815	442
Immediately postthinning	322	99	966	189	612	375	1,815	442
30 yr postthinning (no ingrowth)	269	86	800	86	381	141	916	208
30 yr postthinning (ingrowth)	502	237	1,050	142	453	170	916	193
RD (%)								
Prethinning	82	53	123	13	77	58	95	11
Immediately postthinning	41	19	75	13	77	58	95	11
30 yr postthinning (no ingrowth)	66	33	125	19	84	62	114	12
30 yr postthinning (ingrowth)	81	46	135	17	89	65	116	12
Quadratic mean diameter (cm)								
Prethinning	19.8	8.6	31.9	4.4	28.1	12.8	53.2	9.3
Immediately postthinning	25.2	12.0	37.7	5.5	28.1	12.8	53.2	9.3
30 yr postthinning (no ingrowth)	37.7	23.3	49.1	6.3	37.1	21.3	60.0	9.1
30 yr postthinning (ingrowth)	28.7	22.6	38.2	3.5	34.2	21.3	54.8	7.1
Aboveground live tree C (Mg/ha)								
Prethinning	60.9	38.7	102.5	13.5	76.4	36.0	147.5	24.8
Immediately postthinning	35.0	13.7	66.1	12.3	76.4	36.0	147.5	24.8
30 yr postthinning (no ingrowth)	78.7	40.8	172.2	20.7	105.5	74.5	154.6	21.9
30 yr postthinning (ingrowth)	87.0	52.8	178.6	19.9	108.7	79.4	155.3	21.6

As presented, RD is calculated based on Reineke's stand density index (SDI) (Reineke 1933) and calculated as outline by Ducey and Knapp (2010).

the ATC models as a goodness-of-fit measure where $r^2 = 1 -$ (residual sum of squares/corrected total sum of squares) (Monserud and Marshall 1999). ATC stocks and BA were $\log_e$-transformed to achieve normality and homoscedasticity.

The final models developed during the ANCOVA procedure produced what we refer to as "static" models of ATC storage in that they are point-in-time estimates of observed ATC values as a function of the point-in-time values of the independent variables. These static models do little to address how any given stand responds to a particular thinning relative to a comparable unthinned stand over time. To assess how ATC stocks responded to changes in stand-level BA that occurred after the thinning, models that project BA through time after thinning were incorporated into the static ATC models.

We used the nonlinear form of the BA projection model presented by Bowling et al. (1989) to model BA through time for unthinned and thinned stands (Equation 1):

$$\mathrm{BA}_{ij} = b_0\left(\mathrm{BA}_{ij-1}^{\left(\frac{\mathrm{A}_{ij-1}}{\mathrm{A}_{ij}}\right)}\right)e^{\left(\left(1-\left(\frac{\mathrm{A}_{ij-1}}{\mathrm{A}_{ij}}\right)\right)\times(b_1+b_2\times SI_i)+b_3\times yst_{ij}\right)} \tag{1}$$

where BA_{ij} is BA of plot i at inventory j, BA_{ij-1} is BA of plot i at inventory $j - 1$, A_{ij} is stand age of plot i at inventory j, A_{ij-1} is stand age of plot i at inventory $j - 1$, SI_i is SI of plot i, yst_{ij} is the number of years since thinning for plot i at inventory j, and b_0, b_1, b_2, and b_3 are empirically derived model parameters. This model (Equation 1) (Bowling et al. 1989) was initially fit to data from 44 of the 62 thinned plots used in this study from the first and second postthinning inventory cycles. The full model was reduced by systematically removing independent variables that had significance levels <0.05.

Parameter estimates were obtained using PROC NLIN (SAS Institute 2003) and were considered significant if the confidence interval did not contain zero. We report r^2 values for the BA projection models as a goodness-of-fit measure where $r^2 = 1 -$ (residual sum of squares/corrected total sum of squares) (Monserud and Marshall 1999). Once BA growth models were developed, we incorporated BA projections into the selected ATC static models (Table 2), which then allowed for the estimation of ATC for any SI, age, and thinning (i.e., no thinning verses various thinning intensities) combination. These "dynamic" C models were used to test the hypothesis that regardless of thinning intensity, total ATC stocks in unthinned stands would exceed total ATC stocks in thinned stands for any given age and site quality combination.

Table 2. Parameter estimates (SE) associated with the final static ATC models for the ingrowth-excluded and ingrowth-included scenarios.

	b_0 (intercept)	b_1 (thin)	b_2 (ln BA)	b_3 (thin × ln BA)	b_4 (1/A)	b_5 (thin × l/A)	b_6 (SI)	r^2	CF
Ingrowth excluded	0.8565	−0.0268	1.0990		−6.4235	−2.8816		0.97	1.003
	(0.0342)	(0.0267)	(0.0085)		(0.3963)	(0.5509)			
Ingrowth included	1.4940	−0.8984	0.8441	0.2272	−14.7176	6.1505	0.0108	0.97	1.002
	(0.0901)	(0.1889)	(0.0107)	(0.0484)	(0.6211)	(1.5153)	(0.0034)		

Parameters associated with the categorical variable "thin" are applicable to unthinned stands. The $\log_e$ bias correction factor (CF) used to correct for bias when back-transforming $\log_e$ transformed data was calculated as $e(\text{SEE}^2/2)$ (Baskerville 1972), where SEE is the SE of the estimate of the regression.
* Parameter was not significant at $\alpha = 0.05$, but was included in the final model because of the significant interaction between thin and age.

We used ANCOVA to test the hypothesis that rates of C storage were greater in thinned than in unthinned stands (PROC MIXED; SAS Institute 2003). Average annual ATC increment was calculated as

$$(\text{ATC}_{ij+30} - \text{ATC}_{ij})/30$$

Here ATC_{ij} is the ATC stock of plot i immediately postthinning and ATC_{ij+30} is the ATC stock of plot i 30 years postthinning. Thinning (yes, no) was the categorical variable and age at the time of thinning and/or SI were included as covariates. As in the development of the static ATC models, the covariate portion of the model was reduced following procedures outlined by Milliken and Johnson (2002). Average annual ATC increment data were $\log_e$-transformed to achieve normality and homoscedasticity in the ingrowth-included scenario. The 0.05 level was used to test for significance in all analyses.

Results

Prethinning Carbon Stocks

ATC stocks in all 80 plots before thinning were variable and ranged from 38.7 to 147.5 Mg/ha. The analysis confirmed our hypothesis that stand age is a significant predictor ($P < 0.0001$) of ATC stocks in upland hardwood stands of the southern Appalachian Mountains. Although significant, the strength of stand age alone in predicting ATC was relatively low ($r^2 = 0.52$, root mean square error = 0.178). Including SI in the model, which was positively related to ATC stocks, only slightly improved the ability to predict prethinning ATC stocks ($r^2 = 0.57$, root mean square error = 0.171). When any single measure of prethinning stocking levels (Table 1) was included in the model (e.g., BA, trees/ha, or relative density [RD]), r^2 values increased, suggesting that density is an important predictor of stand-level ATC stocks in upland hardwood forests. In order of increasing importance, measures of stand structure including prethinning trees/ha ($r^2 = 0.61$, root mean square error = 0.1640), RD ($r^2 = 0.88$, root mean square error = 0.0907), and BA ($r^2 = 0.94$, root mean square error = 0.0625) provided the greatest improvement in the prediction of prethinning ATC stocks (final model ln ATC=0.3935 + 0.0094(age) + 0.0049(SI) + 0.9843(ln BA).

Static ATC Models

As a result of the thinning, ATC stocks in thinned stands, which averaged 61 Mg/ha before thinning, were reduced by an average of 43% immediately after the thinning. Regardless of thinning or residual basal area, ATC stocks in thinned stands based on either the inclusion or exclusion of ingrowth 30 years postthinning exceeded ATC stocks before thinning. At the end of the 30-year sampling period, ingrowth accounted for an average of 9.5% of total stand-level ATC in thinned stands, but varied greatly between 0 and 35%. In unthinned stands, ingrowth accounted for an average of 3% of total stand-level ATC and varied between 0 and 15%. Using the most recent inventory data (i.e., 30 years postthinning), significant ($P < 0.05$) negative correlations between the percentage of ATC due to ingrowth and residual BA ($r = -0.54$) and SI ($r = -0.31$) were observed.

The static models of ATC are point-in-time estimates of observed ATC values as a function of the thinning treatment (thinned or unthinned), stand age, stand BA, and SI based on the observed inventory data. BA was selected as the density measure of interest because of the influential effects observed on prethinning ATC stocks. The final static ATC model under the ingrowth-excluded scenario modeled ATC as a function of thinning (yes, no), ln(BA), 1/A, and the interaction between thinning and 1/A (Table 2). Interestingly, SI was not a significant predictor ($P > 0.05$) of ATC stocks under the ingrowth-excluded scenario. For a given age and stand BA, ATC stocks in unthinned and thinned stands did not differ. However, the significant thinning × 1/A interaction suggests that the slopes describing the effect of age on postthinning ATC stocks between unthinned and thinned stands were not equal.

The final static ATC model after reduction of the covariate portion of the model under the ingrowth-included scenario modeled ATC as a function of thinning, ln(BA), thinning × ln(BA), 1/A, thinning × 1/A, and SI (Table 2). The parameter estimate for the thinning variable under the ingrowth-included scenario indicated that unthinned stands have smaller ATC stocks than thinned stands for a given age and stand BA (Table 2). The significant interaction between thinning and age suggests that the slopes describing the effect of age on ATC stocks between thinned and unthinned stands were not equal. Similarly, the significant interaction between thinning and BA suggests that the relationship between ingrowth-included ATC stocks and BA was not equal. Unlike the ingrowth-excluded scenario, the positive parameter estimate associated with SI was significant, suggesting that ATC stocks for thinned and unthinned stands increase with increasing SI.

Postthinning BA Projections

BA projection models for the ingrowth-excluded scenario suggest different growth trajectories for thinned and unthinned stands. Under the ingrowth-excluded scenario, SI was not a significant predictor of BA for either the unthinned or thinned stands. The final, reduced model used to project BA through time under the ingrowth-excluded scenario for both unthinned and thinned stands had the form

$$BA_{ij} = b_0\left(BA_{ij-1}^{\left(\frac{A_{ij-1}}{A_{ij}}\right)}\right)e^{\left(1-\left(\frac{A_{ij-1}}{A_{ij}}\right)(b_1)\right)} \quad (2)$$

BA projection models explained a significant amount of the variation in the data with r^2 values of 0.94 for the ingrowth-excluded unthinned model and 0.97 for the ingrowth-excluded thinned model (Table 3). Total BA increased through time in all stands, regardless of thinning treatment or thinning intensity, stand age, and prethinning BA. Although total BA increased through time, the rate at which BA accumulated in unthinned stands was less than that in thinned stands, regardless of stand age and initial stocking. The 5-year periodic BA increment of both thinned and unthinned stands in the ingrowth-excluded scenario was greatest in young stands but decreased as stands matured.

Unlike the ingrowth-excluded scenario, years since thinning was a significant predictor of total BA for thinned stands in the ingrowth-included scenario. Again, SI was not a significant predictor of total BA for either unthinned or thinned stands under the ingrowth-included scenario. Unthinned stands were, therefore, modeled using the BA model used to project BA under the ingrowth-excluded scenario (Equation 2), whereas the reduced model used to project BA for thinned stands under the ingrowth-included scenario had the form

$$BA_{ij} = b_0\left(BA_{ij-1}^{\left(\frac{A_{ij-1}}{A_{ij}}\right)}\right)e^{\left(1-\left(\frac{A_{ij-1}}{A_{ij}}\right)(b_1)+b_2\times yst_{ij}\right)} \quad (3)$$

Basal area projection models for the ingrowth-included scenario explained a significant amount of the variation with r^2 values ranging from 0.94 for the unthinned model to 0.92 for the thinned model (Table 3).

Dynamic ATC Models

BA projections for the ingrowth-excluded and ingrowth-included scenarios were incorporated into static models of ATC (Table 2) to provide estimates of ATC stocks for any SI, age, and thinning combination and used to examine relative differences in ATC stocks under alternative thinning scenarios. When ingrowth was excluded from the dynamic C models, we found that light low thinning had a neutral to slightly positive effect on ATC stocks over the long-term relative to that on unthinned stands of similar age and initial BA, but relative differences varied with age at the time of thinning because of the significant interaction between stand age and thinning treatment apparent in the ANCOVA (Table 2). For example, in a stand possessing an initial BA of 20 m^2/ha, a low thinning that removed 10 and 25% of prethinning BA at 30 years of age resulted in a neutral to positive response in ATC stocks relative to that for an unthinned stand of similar age and initial BA stocking levels after 30 years (Figure 2a). As age increased, the proportion of BA that could be removed without adversely affecting long-term ATC stocks (i.e., where thinning caused a decrease in ATC stocks relative to those in comparable unthinned stands) decreased (Figure 2b). The lack of a significant interaction between stand BA and thinning treatment in the static ATC model (Table 2) suggests that relationships between thinned and unthinned ATC stocks remain similar across the range of stand BA observed in this study (Figure 2c and d).

Under the ingrowth-included scenario, relative differences between ATC stocks in thinned and unthinned stands varied not only with age, as was observed under the ingrowth-excluded scenario, but also with stand BA as suggested by the static models of ATC (Table 2; Figure 3). Unlike the ingrowth-excluded scenario, the time required for ATC stocks in thinned stands to approximate that of unthinned stands increased as age increased under the ingrowth-included scenario. The proportion of BA that could be removed without adversely affecting long-term ATC stocks varied across the range of BAs observed in this study because of the interaction between BA and unthinned stands (Table 2). In general, as initial BA increased, the proportion of BA that could be removed before the breakeven point between ATC stocks in thinned and unthinned stands was achieved decreased (Figure 3).

Under the ingrowth-included scenario, SI explained a significant amount of variation in ATC stocks. The positive parameter estimate associated with SI (Table 2) indicates an increase in ATC stocks with increased SI. For example, ATC stocks on a site of average quality (e.g., SI 24) would be expected to be approximately 4.5% lower than ATC stocks observed on a higher-quality site (e.g., SI 28). The effect of SI was similar between unthinned and thinned

Table 3. Parameter estimates (SE) associated with the BA growth models for the ingrowth-excluded and ingrowth-included scenarios for both thinned and unthinned stands.

	b_0	b_1	b_2	r^2
Ingrowth excluded				
Equation 2: unthinned	1.0266 (0.0206)	3.6701 (0.2306)	NA	0.94
Equation 2: thinned	1.0628 (0.0104)	3.5744 (0.1022)	NS	0.97
Ingrowth included				
Equation 2: unthinned	1.0472 (0.0209)	3.5425 (0.2236)	NA	0.94
Equation 2: thinned	1.0462 (0.0295)	3.2681 (0.2056)	0.0039 (0.0007)	0.93

NA, not applicable; NS, not significant.

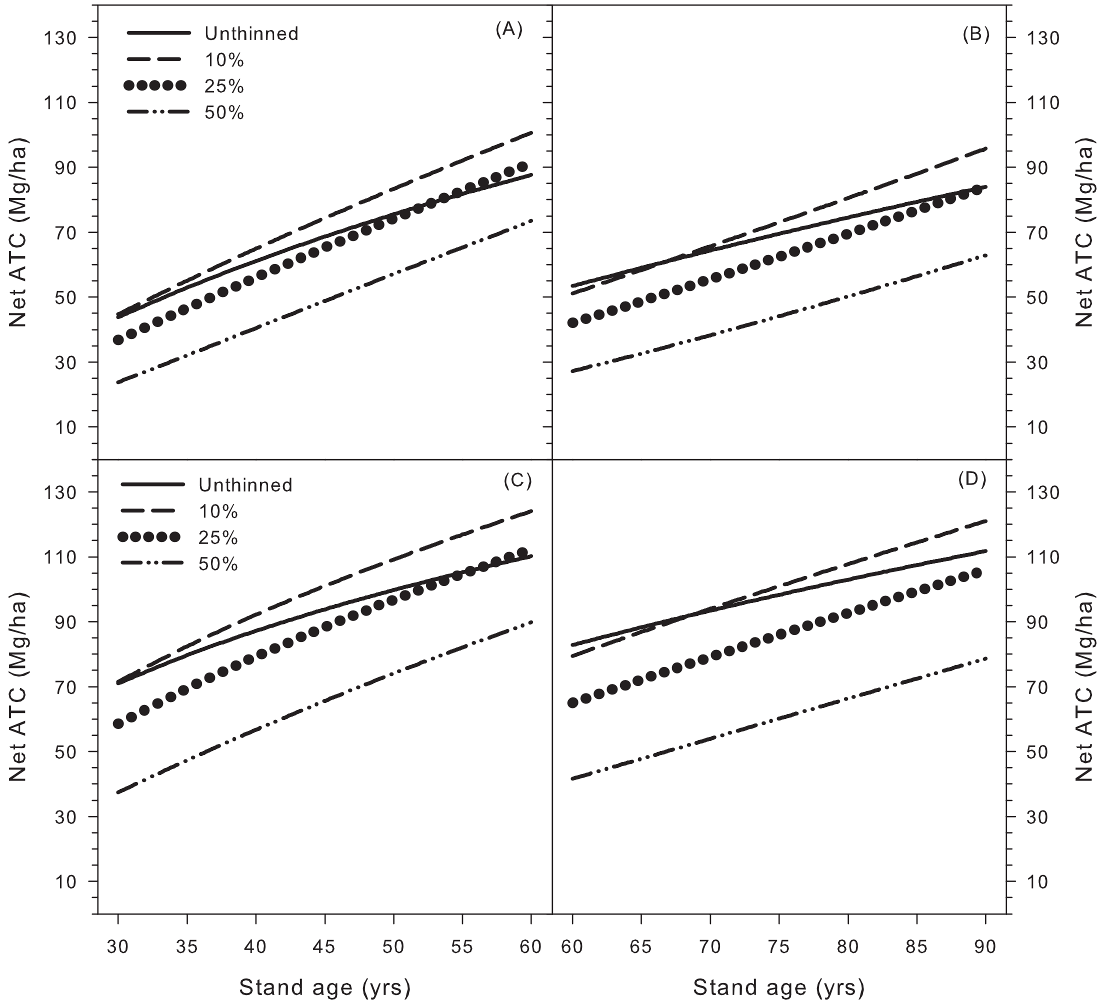

Figure 2. A and B. Projected net ATC stocks (Mg/ha) under the ingrowth-excluded scenario for an unthinned stand with initial BA of 20 m²/ha and comparable stands that had 10, 25, and 50% of initial BA thinned from below at 30 and 60 years of age, respectively. C and D. Analogous projections under an initial BA of 30 m²/ha. Stand-level basal area was projected for 30 years using equation 2 and subsequently used in models of net ATC storage over time.

stands because no significant interaction between SI and thinning treatment was observed.

ATC Storage Rates

Although ATC stocks increased in all stands, the rate at which thinned and unthinned stands accumulated ATC differed. Between 1975, immediately postthinning, and 2005, unthinned stands accumulated ATC at a net rate of 38 and 42% when ingrowth was excluded and included, respectively (Table 1). This rate is markedly slower than that for the thinned stands for which ATC stocks increased at an average net rate of 125% when ingrowth was excluded and 148% when ingrowth was considered over the 30-year period. Average net annual ATC increment adjusted for the effect of age at the time of thinning observed in the ingrowth-excluded static ATC model was significantly greater in thinned than in unthinned stands ($P = 0.0001$) with least-squares means (lsmeans ±SE) of 1.46 (0.08) and 0.77 (0.15) Mg/ha/year, respectively. Similarly, after adjustment for the effects of age and SI in the ingrowth-included static ATC model, net annual ATC increment in thinned stands was significantly greater than that in unthinned stands ($P = 0.0042$) with back-transformed lsmeans averaging 1.63 (1.04) and 1.19 (1.09) Mg/ha/year, respectively.

Discussion

The age and stage of stand development of all 80 plots are within the range of the majority of the land base in the southern Appalachians (Smith et al. 2009) insofar as they are in the stem exclusion or early stages of the understory reinitiation (Oliver and Larson 1996) and are still aggregating C in aboveground biomass (Bolstad and Vose 2005). Similar to chronosequence studies in both eastern (Bradford and Kastendick 2010) and western (Jansich and Harmon 2002) US forest types, we found support for our hypothesis that stand age is positively related to ATC stocks in upland hardwood stands of the southern Appalachian Mountains. Although significant, the strength of stand age alone in predicting ATC stocks in forest stands was relatively low compared with other studies (Law et al. 2003, Taylor et al. 2007, Bradford and Kastendick 2010). The significance of site productivity in predicting the prethinning ATC stocks confirms the results of Kranabetter (2009) and Keyser (2010), who found significantly greater C storage on sites

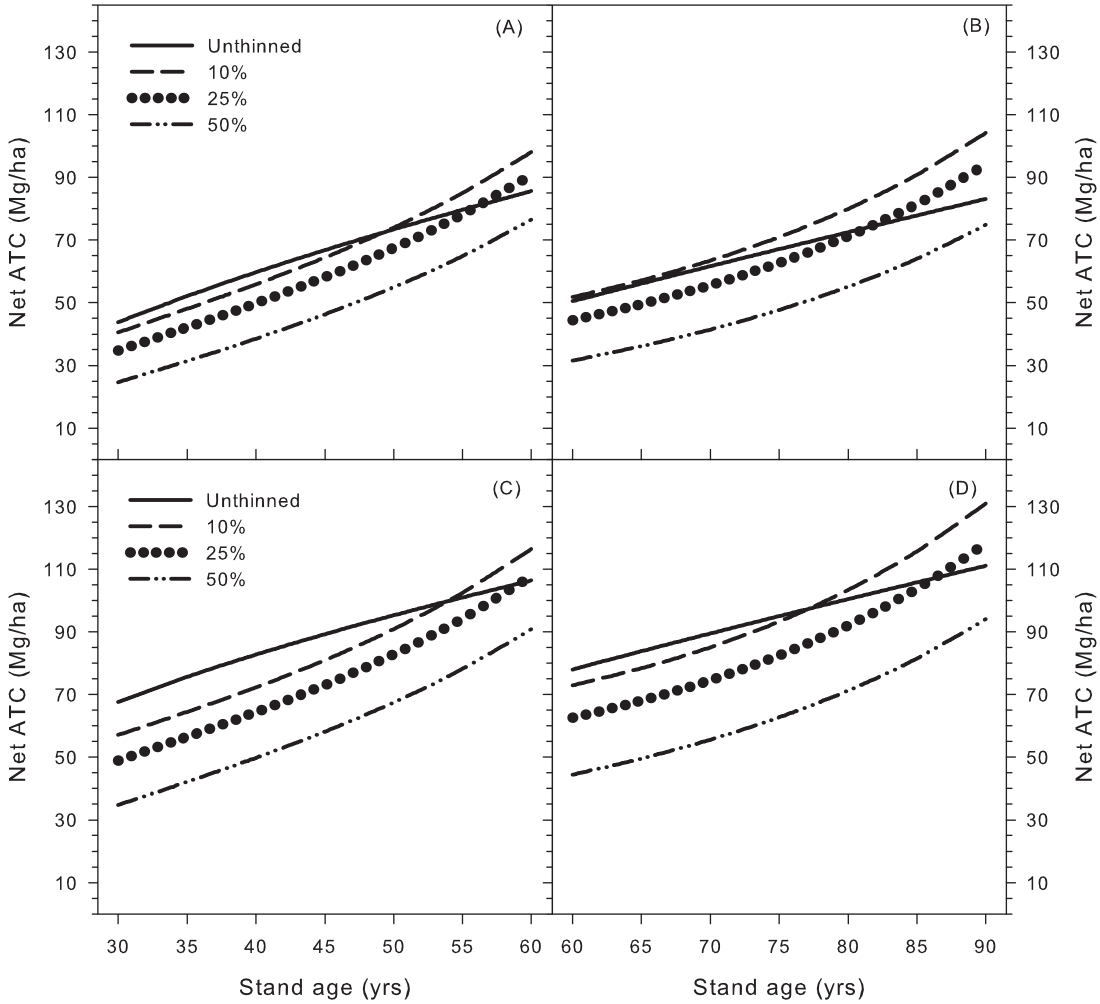

Figure 3. A and B. Projected net ATC stocks (Mg/ha) under the ingrowth-included scenario for an unthinned stand of average quality (SI 24) with initial BA of 20 m^2/ha and comparable stands that had 10, 25, and 50% of initial BA thinned from below at 30 and 60 years of age, respectively. C and D. Analogous projections under an initial BA of 30 m^2/ha. Stand-level basal was projected for 30 years using Equation 2 for unthinned stands and Equation 3 for thinned stands and subsequently used in models of net ATC storage over time.

with higher SI. Although SI was positively related to ATC stocks, it only slightly improved the ability to predict pre-thinning ATC stocks, suggesting that other stand attributes including size, density, and/or species composition (Martin et al. 2005, Hoover and Stout 2007) play a significant role in determining ATC stocks in second-growth upland hardwood forests.

Contrary to our hypothesis that thinning would decrease long-term ATC stocks relative to unthinned stands, we found that upland hardwood forests of mixed-species composition are fairly resilient in their ability to recover the C stored in aboveground live tree biomass removed during thinning. In general, relatively light levels of low thinning had a neutral to slightly positive effect on long-term post-thinning ATC stocks relative to their unthinned counterparts regardless of whether or not ingrowth data were included in the estimation of ATC stocks. Although the literature suggests that C is maximized by reducing disturbance events (Harmon 2001), when the results of the present studies are put in the context of past growth and yield research, the outcomes from this study are not overly surprising. Although not the most common outcome, small increases in standing volume (from which the conversion to live tree C is relatively straightforward) after light to moderate levels of thinning have been reported in a variety of growth and yield studies (e.g., Mäkinen and Isomäki 2004, Pitt and Lanteigne 2008, Curtis and Marshall 2009). Numerous model simulation studies have examined the potential long-term impacts of alternative management scenarios on stand-level C stocks (e.g., Harmon and Marks 2002, Davis et al. 2009, Harmon et al. 2009, Nunery and Keeton 2010, Reinhardt and Holsinger 2010); however, there is a paucity of data-driven research that specifically addresses the effects of thinning and other intermediate stand management activities on long-term changes in C uptake and storage. In one data-driven study in northern hardwood forests in Pennsylvania, Hoover and Stout (2007) documented a slightly positive effect of light low thinning on ATC stocks over a 25-year period. Similarly, in bottomland forests of southeastern Australia, thinning early in stand development increased net C storage in aboveground live biomass between 4 and 21% of that in unthinned stands (Horner et al. 2010).

In contrast, in a study that examined the effects of thinning on live tree C storage in pure yellow-poplar stands in the southern Appalachian Mountains, Keyser (2010) observed that ATC storage decreased as thinning grade increased even after 35 years of postthinning growth. Because of the lack of unthinned controls, however, examination of a potential crossover effect in yellow-poplar stands was not possible, making the results of this study somewhat limited in interpreting the C tradeoffs between active versus passive management.

Our hypothesis that younger stands would respond more positively to thinning in terms of their ability to recapture a proportion of the C removed during the thinning was true under the ingrowth-excluded scenario. The age at which thinning was implemented had a significant effect on the level of removal that could occur without negatively affecting long-term ATC stocks. When thinned at a young age (e.g., 30 years of age), thinning, without considering ingrowth, increased ATC stocks by a greater degree than when thinning was delayed until 60 years of age. The negative effect of stand age on postthinning ATC storage is not surprising. Numerous studies have documented a decrease in total stand production (e.g., BA and volume) after thinning with increasing age across a broad range of forest types and geographic regions (e.g., Knoebel et al. 1986, Hasenauer et al. 1997, Medhurst et al. 2001, Juodvalkis et al. 2005, del Rió et al. 2008). Whether measured in terms of standing volume or C storage, the differential response of thinning across ages is due to the ability of an individual to recapture the growing space created by the removal of competing individuals. In general, after the creation of growing space, crown expansion and, therefore, an increase in leaf area occurs quickly in young trees compared with older individuals for which crown width may already be at or near the biological maximum (Miller 1997, 2000, Juodvalkis et al. 2005). Consequently, when thinnings are conducted in young stands, closed-canopy conditions can recur quickly, whereas thinning when stands are older and probably already in understory reinitiation often fails to recapture the newly created growing space and return to full-site occupancy (Oliver and Larson 1996). Of interest, the relationship between stand age and long-term ATC stocks for a given level of thinning was reversed when ingrowth data were incorporated in the estimation of ATC stocks. Under the ingrowth-included scenario, a greater proportion of the prethinning BA could be removed without negatively affecting ATC stocks in older versus younger stands. This is simply an artifact of the inability of older trees to recapture growing space after thinning. In these cases, growing space created by crown shyness (Goudie et al. 2009) and mortality-induced canopy gaps is filled with the ingrowth from new seedlings that establish postthinning, stump sprouts from cut trees, and/or advance reproduction. Lack of growing space in high-density stands in particular limits the establishment and development of ingrowth (Strong and Erdmann 2000).

Although ATC stocks increased in all stands throughout the study period, the net rate at which thinned and unthinned stands accumulated C differed substantially. Without taking into consideration the influence of ingrowth on C dynamics, over the course of the 30-year study period, unthinned and thinned stands accumulated ATC at an average net rate of 0.77 and 1.46 Mg/ha/year, respectively, after controlling for the negative effect of stand age on average net annual ATC increment. Similarly, when considering ingrowth into estimates of ATC, unthinned and thinned stands stored C at an average net rate of 1.19 and 1.63 Mg/ha/year. Average net annual ATC increments observed in this study are substantially greater than C uptake storage rates reported for northern hardwood forests in the eastern United States (Hoover and Stout 2007, Nunery and Keeton 2010), emphasizing the variability in landscape-level C uptake and storage potential known to occur among forest types and physiographic regions (Wofsy et al. 1993, Greco and Baldocchi 1996). Although only a few studies detail the response of C increment to thinning (e.g., Hoover and Stout 2007, Campbell et al. 2009, Horner et al. 2010, Keyser 2010), many studies have documented a positive effect of light to moderate levels of thinning on net annual wood/volume increment relative to unthinned counterparts with older stands being less responsive to thinning than younger stands (Knoebel et al. 1986, Strong and Erdmann 2000, Medhurst et al. 2001, Juodvalkis et al. 2005, del Rió et al. 2008, Curtis and Marshall 2009). Whereas light to moderate thinnings appear to stimulate production, heavy thinnings can decrease overall production (e.g., del Rió et al. 2008), suggesting that an optimum level or optimal range of growing stock conditions may exist for maximizing volume and/or C production.

The increased rate at which thinned stands stored C in aboveground biomass coupled with substantial overstory tree mortality in unthinned stands was probably responsible for the crossover effect of thinning on ATC stocks. Although stand-level BA increased in both unthinned and thinned stands over time, average trees/ha was substantially reduced. During the 30 years after thinning, average trees/ha decreased by 38% in unthinned stands compared with only 16% in thinned stands when ingrowth was excluded. When ingrowth was included, trees/ha decreased by 26% in unthinned stands, whereas thinned stands experienced an increase in trees/ha estimates of 56% above those observed immediately postthinning. The range of RD in unthinned stands 30 years postthinning was well within the zone in which density-dependent mortality occurs (e.g., average RD for unthinned stands = 0.85 versus 0.66 for thinned stands).

Although data from long-term growth and yield studies have proven valuable for providing insight into contemporary issues (e.g., D'Amato et al. 2011), the current study also brings to attention the limitations of using studies that were not originally designed to conduct detailed analyses of some of these emerging issues, such as forest C storage in relation to silvicultural activities. In this study, data collection protocols were designed to meet the original objective (i.e., growth and yield in response to thinning). Consequently, the data required to conduct more holistic and thorough analyses of forest C storage in response to thinning were not collected, resulting in knowledge gaps surrounding the complete C consequences of thinning. For example, because net production as opposed to gross production was the primary variable of interest in the original study (Harrison et al. 1986, Bowling et al. 1989), dbh was not measured on individual trees that died between inventory cycles. Neglecting the growth increment that occurred between inventory cycles in this study, as well as in other studies using growth-and-yield data sets to address C dynamics in relation to silvicultural prescriptions (e.g., Keyser 2010, Horner et al. 2010, D'Amato et al. 2011), discounts C fixed and stored by individual trees before death (i.e., gross increment) and therefore stand-level C increment and production in stands experiencing mortality are underestimated. Data regarding C storage in the deadwood biomass pool coupled with net aboveground live tree production could be used to compensate for the lack of information on gross C production and provide a more accurate description of the effects of thinning on forest C storage. However, again, the original objectives associated with previously established growth and yield studies did not often include quantifying the accumulation and longevity of the deadwood biomass pool, making this type of analysis difficult, if not impossible, with the existing data.

This study provides information about the effects of partial or intermediate silvicultural disturbances on C dynamics on the aboveground live tree biomass pool across a varied and complex landscape and may be used to quantify the tradeoffs between thinning and live tree C storage across upland hardwood forest types of the southern Appalachians. In the southern Appalachians, the greatest proportion of total ecosystem C is found in the aboveground live biomass pool and mineral soil (Bolstad and Vose 2005). Because there is little change in mineral soil C associated with varying silvicultural prescriptions (Johnson and Curtis 2001), ATC is considered the most dynamic and most easily manipulated of the C pools (Fahey et al. 2010). The present age structure of many of the stands comprising this data set has exceeded that which is typical of the traditional rotation age. Conclusions made using data from only the earliest of the postthinning inventory data sets may not have resulted in similar conclusions because the mortality observed in unthinned stands is a relatively recent phenomenon. It appears from this study that thinning coupled with an extended rotation age is a management action that may be used to increase live tree C stores (e.g., Harmon et al. 2009, Ryan et al. 2010). Lack of data on gross C production, deadwood, and ex situ C pools limits our ability to analyze the impacts of thinning on C storage outside of the relatively narrow measure of net C production and increment. A more complete and detailed description of C dynamics after thinning and other silvicultural prescriptions could be attained by obtaining an inventory of all ecosystem C components including small trees, shrubs, standing dead trees, dead and down coarse woody debris, forest floor, mineral soil, and ex situ C pools through time.

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