# Effects of timber harvest on carbon pools in Ozark forests

**Qinglin Li, Jiquan Chen, Daryl L. Moorhead, Jared L. DeForest, Randy Jensen, and Rachel Henderson**

**Abstract:** We quantified and compared carbon (C) pools at a Missouri Ozark experimental forest 8 years after different harvest treatments. Total C pools were 182, 170, and 130 Mg C·ha$^{-1}$ for the control (no-harvest management; NHM), single-tree, uneven-age management (UAM), and clearcut even-age management (EAM) stands, respectively. Harvesting reduced the live tree C pool by 31% in the UAM, 93% in EAM stands, and increased the coarse woody debris (CWD) C pool by 50% in UAM and 176% for EAM, compared with NHM stands. UAM significantly ($p = 0.02$) increased the mineral soil C pool by 14%, whereas EAM had no effect. More interestingly, the distribution of C among various components (i.e., live, dead wood, CWD, litter, and soil) ranged from 0.7% to 29% on NHM stands and from 0.1% to 43% on EAM stands. Soil nitrogen (N) (%) was significantly correlated with soil C (%) in the UAM stands, whereas soil temperature was negatively related to live tree C. Soil N (%) and canopy cover were significantly correlated with live tree and soil C (%) pools at EAM stands. Our results revealed that the largest C pool in these forests was living trees. The soil and CWD C pool sizes suggest the importance of dynamics of decaying harvest debris, which influences N retention.

**Résumé :** Nous avons quantifié et comparé les réservoirs de carbone (C) dans une forêt expérimentale située dans les monts Ozark au Missouri huit ans après que différents traitements de récolte eurent été appliqués. La quantité totale de carbone dans les différents réservoirs de carbone atteignait respectivement 182, 170 et 130 Mg C·ha$^{-1}$ dans le traitement témoin (aménagement sans récolte), avec un aménagement inéquienne par pied d'arbre (AIPA) et avec un aménagement équienne et une coupe à blanc (AECB). La récolte a réduit le réservoir de C des arbres vivants de 31 % dans le système AIPA et de 93 % dans le système AECB et augmenté le réservoir de C dans les débris ligneux grossiers (DLG) de 31 % dans le système AIPA et de 176 % dans le système AECB comparativement aux peuplements non récoltés. Le système AIPA a significativement ($p = 0{,}02$) augmenté le réservoir de C du sol minéral de 14 % tandis que le système AECB n'a eu aucun effet. Il était plus intéressant de constater que la distribution de C parmi les diverses composantes (c.-à-d. le bois vivant, le bois mort, les DLG, la litière et le sol) variait de 0,7 % à 29 % dans les peuplements non coupés et de 0,1 % à 43 % dans les peuplements coupés à blanc. L'azote (N) (%) dans le sol était significativement corrélé avec le C (%) dans le sol dans le système AIPA. Nos résultats révèlent que le plus important réservoir de C dans ces forêts est constitué des arbres vivants. La dimension des réservoirs de C du sol et des DLG montre l'importance de la dynamique de la décomposition des déchets de coupe qui influence la rétention de N.

[Traduit par la Rédaction]

## Introduction

Carbon (C) pools in terrestrial ecosystems are receiving increasing attention partly because terrestrial ecosystems have some potential to store C and, thus, help offset increases in atmospheric carbon dioxide ($CO_2$) (Agren and Hyvonen 2003). In particular, temperate forests have high potential to sequester C (Gifford 1994; Cox et al. 2000; Post and Kwon 2000) and may be managed to enhance sequestration (Smithwick et al. 2002). For example, C losses following harvest can be reduced by modifying harvesting methods to maintain a minimal leaf area (Chen et al. 2004). However, forest ecosystems are dynamic, and their ability to sequester C is affected by many factors, such as fires, harvesting, windthrow, insects, diseases, and modified microclimate, aside from management (Guyette and Larsen 2000; Bresee et al. 2004; Chen et al. 2005). Moreover, forest regrowth does not immediately balance C loss from harvest and subsequent decay of harvest debris (Abbott and Crossley Jr. 1982; Aerts 1997). Indeed, intense timber harvesting would turn forests into a major C source as important as fossil fuel combustion immediately after the disturbance (Post et al. 1990; Sarmiento and Gruber 2002). Unfortunately, gaps in our knowledge about forest C dynamics hamper efforts to accurately predict the effects of disturbances and management alike (Lee et al. 2002). Quantifying the consequences of different timber harvesting methods on subsequent C pools, including live trees, coarse woody de-

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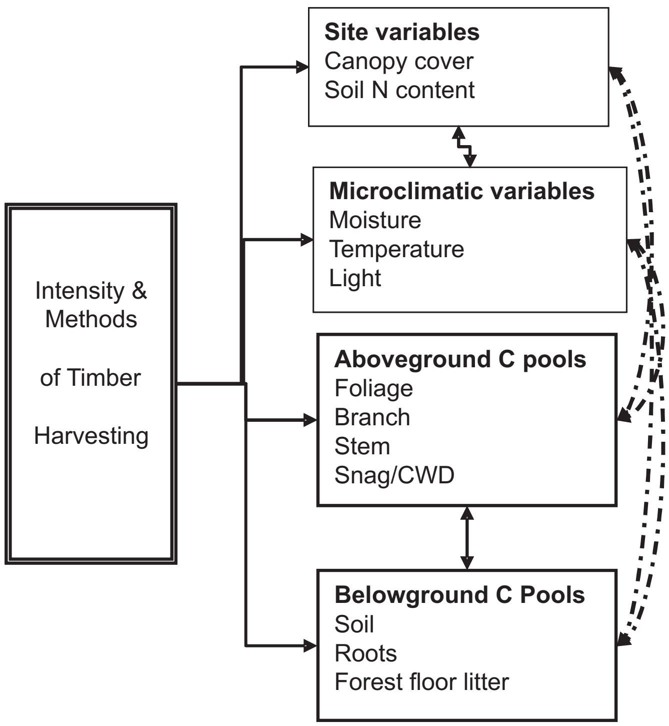
**Fig. 1.** A conceptual model of intercorrelation between carbon pools and microclimatic and site variables for timber harvest treatments at the Missouri Ozark forest ecosystem. The broken arrow lines are intercorrelations between carbon (C) pools and their affected and (or) affecting factors. The solid arrow lines are timber harvest effects, the interactions among carbon pools, and interactions among microclimatic and site variables (CWD, coarse woody debris; N, nitrogen).




bris (CWD), roots, forest floor litter, and soil, would provide much needed data.

Carbon storage and its distribution within a forest vary with many factors including disturbance history (Sah et al. 2004). For example, clear-cutting immediately decreases aboveground C (Johnson 1992; Grigal and Berguson 1998; Chen et al. 2005) but can also initiate a long-term decline in forest floor litter organic matter over decades following harvesting (Aber et al. 1978). It is not clear how different intensities and methods of harvest may interact with environmental conditions (soil moisture (SM) and soil temperature (ST)) and site factors (soil nitrogen (N) content and canopy cover (CC)) to affect the dynamics of C pools in forest ecosystems. Here we propose a conceptual model that links differences in environmental and site factors following different harvest regimes on subsequent allocations of C in forest stands (Fig. 1).

Timber harvesting will reduce aboveground biomass, which consequently would change stand and environmental conditions. However, ecosystem processes respond to changed environments differently. Our model suggests that timber harvest increases solar radiation penetrating the canopy; promotes understory photosynthesis, which may increase stand productivity; and warms soils, possibly accelerating decomposition (Lloyd and Taylor 1994; Lavigne et al. 2003; Ma et al. 2005). Faster decomposition can increase N mineralization from dead organic matter, as well as reduce soil C pools. Nitrogen uptake by plants is lower when aboveground biomass is reduced, so that soil N availability may increase, which in turn, has the potential to promote biomass production (Baker et al. 1986; Nohrstedt et al. 1989). Moreover, soil moisture may increase from reduced canopy evapotranspiration (Pitacco and Gallinaro 1996; Lu et al. 2003), despite warmer soils, further promoting decomposition (Lloyd and Taylor 1994; Lavigne et al. 2003; Ma et al. 2005). Lastly, the effects of aboveground harvest can either increase or decrease belowground biomass (Aber et al. 1978; Kranabetter and Coates 2004). These complex interactions between changing production, decomposition, microclimate, and nutrient regimes following harvest make it very difficult to predict impacts on C dynamics. Thus, empirical studies are necessary to elucidate how timber harvest alters microclimatic and site factors, as well as C pools in manipulated forest ecosystems.

The primary objective of this study was to quantify the effects of different silvicultural treatments on C pool sizes in forest stands by sampling aboveground biomass of live trees, roots, CWD, and total soil C content, 8 years after a large-scale harvesting experiment. The Missouri Ozark Forest Ecosystem Project (MOFEP) has a well-documented preharvest data set to compare changes in stand stem density, basal area, and species composition between pre- (1995) and post-treatment (2003) dates. These data can be used to infer the effects of forest harvesting on C pools. We expected that all C pools, except CWD, would be higher in control stands than in harvested stands. A second objective was to determine the relationships between variations in C pool sizes among treatments and environmental variables (i.e., soil moisture, soil temperature, soil N content, and canopy coverage). We hypothesized that differences in soil moisture, soil temperature, soil N content, and canopy cover could explain a significant portion of the variation in C pools.

## Study site

The MOFEP (Fig. 2) was initiated in 1989 to examine the impacts of timber harvest on multiple ecosystem characteristics of Missouri Ozark forests (Brookshire and Shifley 1997; Shifley and Brookshire 2000; Shifley and Kabrick 2002). The MOFEP is located in the southeastern Missouri Ozarks (91°12′W, 37°06′N). This area is primarily mature upland oak, oak–hickory, and oak–pine communities (Brookshire and Shifley 1997; Xu et al. 2004). *Quercus alba* L. (white oak), *Quercus velutina* Lam. (black oak), and *Quercus coccinea* Muenchh. (scarlet oak) are the dominant oak species, and *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory) and *Carya glabra* (Mill.) Sweet var. *odorata* (Marsh.) Little (pignut hickory) are the dominant hickory species, and *Pinus echinata* P. Mill. (shortleaf pine) is the only pine species in this area. The region receives an annual mean of 1120 mm of precipitation and has a mean annual temperature of 13.3 °C (Guyette and Larsen 2000). The soils are mostly Alfisols and Ultisols (Kabrick et al. 2000).

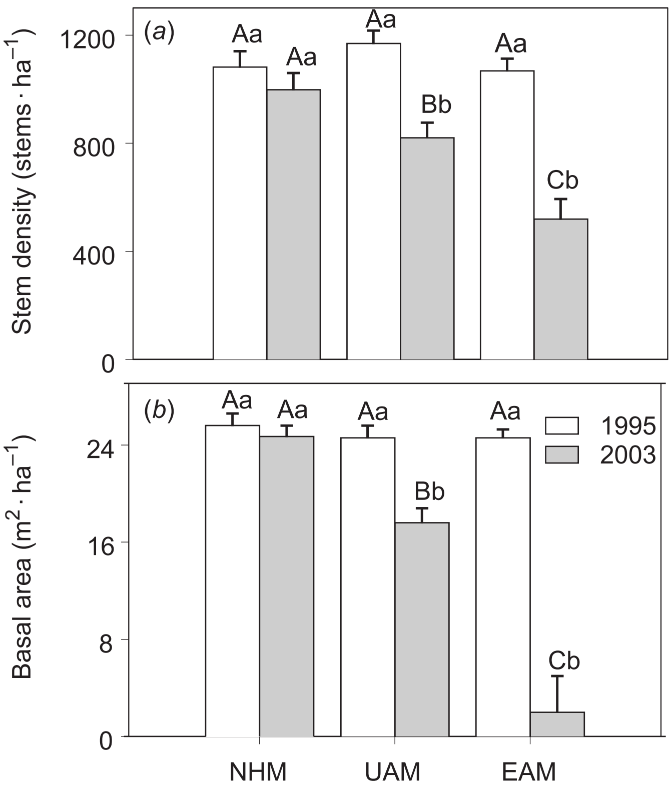
The timber harvest treatments selected for MOFEP were even-age management (EAM), uneven-age management

**Fig. 2.** Locations and types of timber harvest treatments for the Missouri Ozark Forest Ecosystem Project (MOFEP).


(UAM), and no-harvest management (NHM), for nine forested experimental sites, ranging in size from 266 to 527 ha. Treatment sites were chosen based on similarities in forest age, vegetation, and soil characteristics, as described by Brookshire and Shifley (1997) and Sheriff and He (1997). In brief, the experimental sites were randomly assigned one of the three timber harvesting regimes: EAM, UAM, and NHM (Fig. 2). Sites were subdivided into stands, averaging 4 ha in size, with similar ecological land types (ELT) defined by slope, aspect, vegetation composition, and soil type. About 10% of the forest biomass was removed from each site during each harvest entry, producing a landscape of both harvested and unharvested patches. Approximately 10% of both EAM and UAM sites were defined as "old growth" and not available for harvest. The remaining 90% of the sites were available for experimental treatments. The forests (at the end of the rotation that is about 100 years using a 15 year cutting cycle) would consist of 10% seedlings, 20% of trees with a diameter at breast height (DBH) of 6–14 cm, 30% of trees with a DBH of 14–29 cm, and 40% of trees with a DBH > 29 cm. At UAM sites, the goal for the largest diameter trees was the same as the goal for sawtimber size at EAM sites, and the target tree size-class distribution was identical to the composition size-class distribution at EAM sites (Brookshire and Shifley 1997). To achieve these class distributions, some stands were clearcut, and others received intermediate cutting following Missouri Department of Conservation Forest Land Management Guidelines (Missouri Department of Conservation 1986). At UAM sites, trees were removed in small groups, individually, or girdled and left standing. The NHM sites were not subjected to manipulation, but the wildfires and large-scale insect outbreaks would be suppressed. These sites resembled old-growth forests and served as an experimental control for this project (Sheriff and He 1997). Prior to the MOFEP treatment, no harvesting had occurred on these sites since 1950, and most of the overstory trees were 50–70 years old (Forkner and Marquis 2004).

A total of 648 permanent forest vegetation plots (0.2 ha) were distributed across the nine MOFEP sites to document forest vegetation response to treatment. Plots were randomly allocated within stands with each stand receiving at least one plot. The percentage of plots in each ELT was similar to the proportion of the ELTs within the sites (Brookshire and Shifley 1997). A complete, pretreatment set of vegetation data was collected on all plots from June 1994

**Fig. 3.** The comparison of (*a*) the mean stem density (trees·ha$^{-1}$, DBH > 3.8 cm) and (*b*) the mean basal area (m$^2$·ha$^{-1}$, DBH > 3.8 cm) at the Missouri Ozark Forest Ecosystem Project (MOFEP) between pre- and post-harvest. Harvest treatments were no-harvested management (NHM), single-tree, uneven-aged management (UAM), and clearcut, even-aged management (EAM). The preharvest year was 1995, and the postharvest year was 2003. Error bars are SEs. Bars with the same uppercase letters (i.e., A, B, and C) or lowercase letters (i.e., a and b) are not significantly different ($p$ > 0.05, Tukey's test) among treatments or between pre- and post-harvest within each treatment, respectively.




to November 1995 (Brookshire and Shifley 1997). The data were used as pretreatment forest vegetation baseline information to compare postharvest effects on stem density, basal area, and species composition in the current study.

## Methods

### Study design

In this study, we selected six sites (sites 1–6) with two sites in each treatment (Fig. 2). The plots of each site were pooled by treatment. Within each treatment, 12 forest vegetation plots were selected with similar soil types, species composition, and ELT, for a total of 36 plots. Field data were collected during 2002–2003, unless otherwise stated.

### Data collection

Carbon pools examined were (*i*) live-tree biomass, with DBH > 3.8 cm, including stems (hardwood, sapwood, and bark), branches, and foliage, (*ii*) coarse and fine roots, including both live and dead portions, (*iii*) CWD, including standing (i.e., snags) and down dead trees, (*iv*) forest floor litter, and (*v*) mineral soil. The C content was estimated as 50% of biomass values (Prichard et al. 2000; Smith and Heath 2002).

Live tree C was quantified using a species-based allometric eq. 1 to estimate C pools (foliage, branch, and stem with bark) for live trees, either developed for the local species or from the nearest geographical location (Ter-Mikaelian and Korzukhin 1997):

$$[1] \qquad M = aD^b$$

where $M$ is the oven-dry mass of the biomass component of a tree (kg), $D$ is the DBH (cm), and $a$ and $b$ are empirical coefficients estimated through regression analysis. In some cases, species-specific equations were not available, so we used the equation as developed for the same genus as first priority, then family, and lastly, a similar species. We tested the effects of these substitutions while retaining observed DBH distributions. Generally, equation replacements within a family generated very small variations in biomass (e.g., 2.0% when *Q. coccinea* was substituted for *Quercus stellata* Wangenh. (post oak)). Between family substitutions produced higher variations (e.g., 11% when *Ulmus americana* L. (American elm) replaced *Morus rubra* L. (red mulberry)), but were rare.

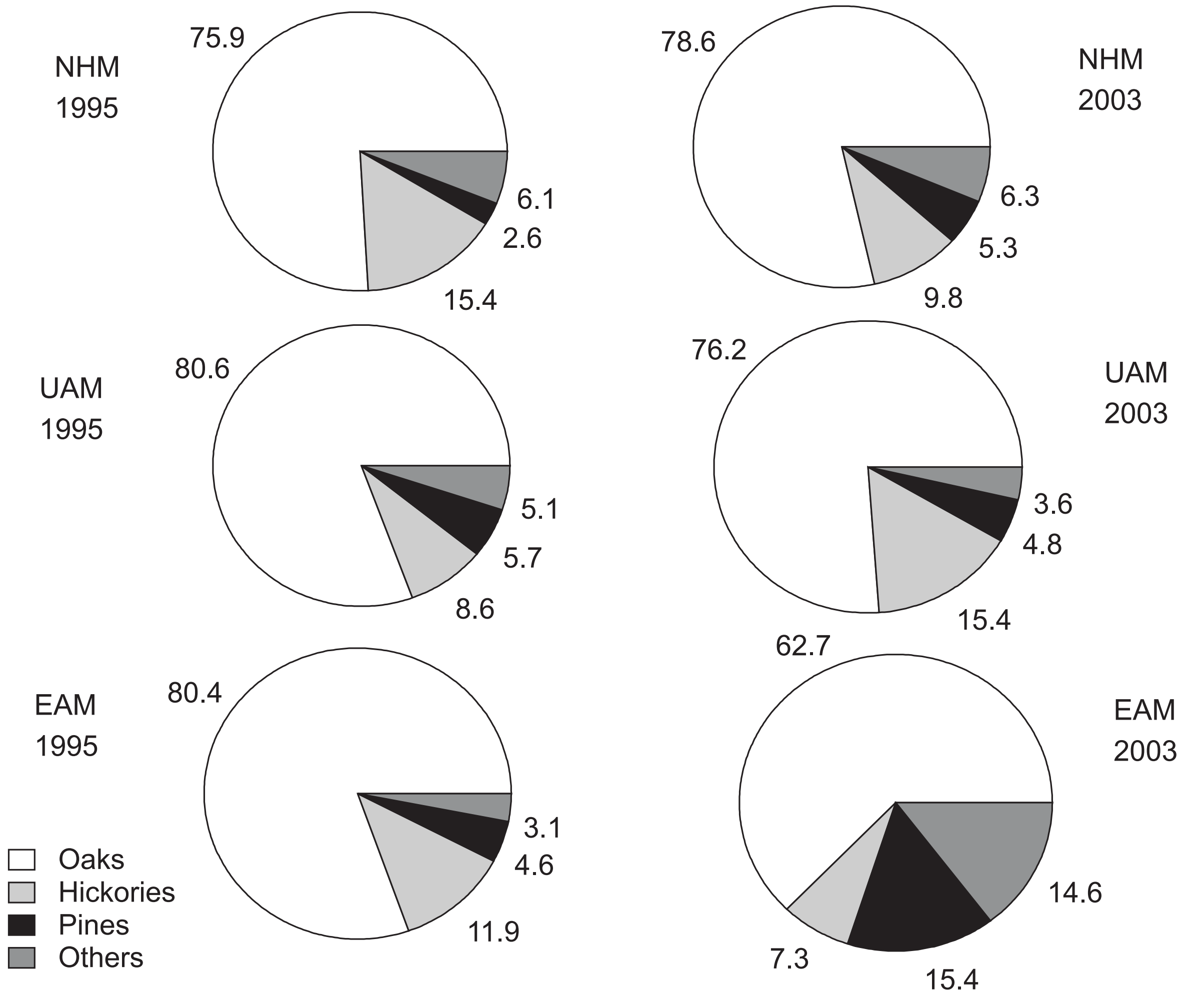
Coarse root C (≥2 mm in diameter, including dead and live) was sampled with soil pits (1 m × 1 m), with depth determined by root zone (60–120 cm). Three soil pits were dug at each treatment, representing forest types with the same soil class, aspect, elevation, and slope, for a total of nine samples. Pits were located 50 m east of vegetation plot centers. Fine root C was quantified from four root cores (81 cm$^2$ and 30 cm depth) taken near each soil pit, for a total of 36 samples. Each core was washed, and all roots <2 mm in diameter were sorted and measured. Both coarse and fine roots (including both dead and live) were oven-dried at 65 °C to obtain a constant mass. We tested our soil pit data against the regression model of Cairns et al. (1997), which predicts total root biomass from aboveground biomass. We found close agreement between estimates and our observations for the NHM and UAM sites, but a significant difference existed for the EAM site (see Discussion). Hence, we assumed that our direct field measurements reasonably represent the root biomass in our study sites.

Coarse woody debris C was estimated by the transect method (Van Wagner 1968; Martin 1976)

$$[2] \qquad W = \frac{\pi^2 S \sum d^2}{8L}$$

where $W$ is the mass per unit area (Mg·ha$^{-1}$), $S$ is the specific gravity of the log (Mg·m$^{-3}$), $d$ is the diameter of the log intersected (cm), and $L$ is the length of the transect (m). A 100 m transect in each of the 36 vegetation plots was surveyed during the summer of 2003, for a total of 36 transects. All CWD was recorded by species and decay class for logs >5 cm in diameter that intersected the transect (Shifley et al. 1997; Spetich et al. 1999). Snags (species and DBH) were recorded in each of the 36 vegetation plots by species and decay class, during the live tree survey. The specific gravity of both CWD and snags by decay class was used to convert volume to mass (Adams and Owens 2001).

**Fig. 4.** The percentages of pre- (1995) and post-harvest (2003) basal area that consisted of oaks (*Quercus* spp.), hickories (*Carya* spp.), shortleaf pine (*Pinus echinata*), and other species at the Missouri Ozark Forest Ecosystem Project (MOFEP). Harvest treatments were no-harvested management (NHM), single-tree, uneven-aged management (UAM), and clearcut, even-aged management (EAM).




Forest floor litter C was collected during the summer of 2003 using a 0.25 m$^2$ (0.5 m × 0.5 m) frame at 20 m intervals along a 100 m CWD transect, for a total of six samples in each plot ($N$ = 216). All CWD less than 5 cm in diameter were included as litter. All litter was oven-dried at 65 °C to constant mass.

Understory plant C was not evaluated in this study because we could not harvest the long-term vegetation plots. Rochow (1974) reported that the understory was only about 1% of the total aboveground biomass near our study sites, on sites with similar species composition. This omission should have little effect on our estimates of total C storage.

Four samples of mineral soil C were sampled (top 15 cm depth and organic layer excluded) at each plot using a soil core (81 cm$^2$) during the summer of 2003, for a total of 144 samples. Soil samples were oven-dried for 48 h at 65 °C, ground, oven-dried for another 48 h at 65 °C, and then analyzed for total C and N contents using a CHN analyzer (PerkinElmer 2400 CHN/O analyzer; PerkinElmer, Waltham, Massachusetts). Soil bulk density and rock content of each plot were provided by the earlier studies of Shifley and Brookshire (2000).

We also monitored ST (of the top 15 cm) and SM (at 15 cm depth). One HOBO data logger (Onset Computer Corp., Pocasset, Massachusetts) with four temperature sensors recorded soil temperature at each plot for a total of 36 data loggers and 144 sensors. The data loggers recorded 0.5 h mean soil temperature from January to December 2003. Three groups of time dominant refectrometer (TDR; Campbell Scientific Inc., Logan, Utah) rods were permanently installed in each plot at the center, north and south of the center ~2 m apart, for a total of 108 groups. The moisture readings were taken every 2 weeks from May to October 2003. All the readings were calibrated by one soil moisture sensor (CS616; Campbell Scientific Inc.) at each treatment, for a total of three sensors, recorded 0.5 h mean soil moisture for the same time period as the HOBO data loggers. The CC was measured at each of the 36 plots by taking fisheye images at 5 m intervals along a 100 m CWD transect for a total of 21 images per plot every month from May to October 2003. All images were analyzed by gap light analyzer software (GLA; www.rem.sfu.ca).

### Statistical analysis

Means and standard errors were calculated for N (%), CC (%), ST, and SM by treatment. All variables were checked

**Table 1.** Carbon pool sizes (Mg C·ha$^{-1}$) by harvest treatments at the Missouri Ozark Forest Ecosystem Project (MOFEP) study area.

| Type of carbon pool | NHM | UAM | EAM | *N* |
|---|---|---|---|---|
| Live trees | | | | |
| Foliage | 1.3 (0.1)a | 1.0 (0.1)b | 0.1 (0.0)c | 36 |
| Branch | 18.4 (1.1)a | 13.0 (1.0)b | 1.2 (0.3)c | 36 |
| Stem | 60.4 (3.2)a | 41.1 (3.7)a | 4.0 (1.2)c | 36 |
| Sum | 80.2 | 55.1 | 5.4 | |
| Roots | | | | |
| Coarse | 17.5 (7.5)a | 11.0 (6.0)a | 9.3 (2.3)a | 9 |
| Fine | 2.1 (0.3)a | 4.4 (0.4)a | 5.0 (1.5)a | 36 |
| Sum | 20.0 | 15.3 | 14.3 | |
| Coarse woody debris (CWD) | | | | |
| Snags | 5.2 (1.0)a | 6.2 (1.8)a | 0.3 (0.2)b | 36 |
| Dead down trees | 17.7 (4.5)a | 26.5 (6.5)a | 48.9 (5.7)b | 36 |
| Sum | 22.9 | 32.8 | 49.2 | |
| Forest floor litter | 5.9 (0.4) a | 6.0 (0.6)a | 5.7 (0.5)a | 216 |
| Soil (top 15 cm) | 53.7 (2.9)a | 62.0 (3.4)b | 55.4 (2.8)ab | 144 |
| **Total** | 182.2 | 170.0 | 130.0 | |

**Note:** Values are means with SEs given in parentheses. Treatments include no-harvest (NHM), uneven-age management (UAM), and even-age management (EAM). Values with the same letters are not significantly different ($p > 0.05$, Tukey's test). *N*, number of samples.

**Table 2.** Summary of mean total soil nitrogen content (N, %), canopy coverage (CC, %), soil moisture (SM, %), and soil temperature (ST, 5 cm, °C) at the Missouri Ozark Forest Ecosystem Project (MOFEP) study area.

| Harvest treatment | N (%) | CC (%) | SM (%) | ST (°C) |
|---|---|---|---|---|
| NHM | 0.13 (0.01)a | 90.3 (0.4)a | 14.9 (1.1)a | 18.1 (0.1)a |
| UAM | 0.14 (0.01)a | 91.2 (0.4)ab | 13.3 (0.7)a | 20.7 (0.3)b |
| EAM | 0.18 (0.01)b | 92.03 (0.3)b | 19.3 (1.2)b | 20.9 (0.2)b |

**Note:** Treatments include no-harvest (NHM), uneven-age management (UAM), and even-age management (EAM). Values are means with SEs given in parentheses. Values with the same letters are not significantly different ($p > 0.05$, Tukey's test).

**Table 3.** The overall results of canonical correlation analysis of carbon (C) pool variables versus microclimatic and site for all the components.

| Pair of canonical components | Canonical correlation | Total variance explained | *P* |
|---|---|---|---|
| $U_1$, $V_1$ | 0.92* | 0.78 | <0.001* |
| $U_2$, $V_2$ | 0.76* | 0.21 | 0.001* |
| $U_3$, $V_3$ | 0.08* | 0.008 | 0.75 |
| $U_4$, $V_4$ | 0.02* | 0.002 | 0.91 |

*Significant canonical correlation at the 95% level.

for normal distribution with Shapiro–Wilk tests, and data were log transformed to normalize them for statistical analysis. All analyses were conducted using SAS software (version 9.1; SAS Institute Inc., Cary, North Carolina), and an $\alpha$ value of 0.05 was used to determine statistical significance.

Pretreatment (1995) data on stem density, basal area, and species composition allowed us to use a two-way analysis of variance (ANOVA) to test differences between treatment and time. We did not have pretreatment C pools (stem, foliage, branch, snag, CWD, forest floor litter, and soil), microclimatic (SM and ST), or site factor (N% and CC) data. Therefore, these posttreatment (2003) data were analyzed by one-way ANOVA to test differences among treatments. Differences between treatment means were compared using a Tukey's test.

Relationships between C pools (live tree stem, foliage, and branch C; snag, CWD, and forest floor litter; and soil C, microclimatic, and site variables) were examined by canonical correlation analysis (CCA) for the entire data set and within each treatment. This analysis constructed a linear combination of C pool variables

$$[3] \qquad U_i = a_{i1}X_1 + a_{i2}X_2 + a_{i3}X_3 + a_{i4}X_4$$

where $X_1$ is the live tree C variable, $X_2$ is the detritus variable, $X_3$ is the forest floor litter varaible, and $X_4$ is the soil variable, and a linear combination of microclimatic and site variables

$$[4] \qquad V_i = b_{i1}Y_1 + b_{i2}Y_2 + b_{i3}Y_3 + b_{i4}Y_4$$

where $Y_1$ is the SM variable, $Y_2$ is the ST variable, $Y_3$ is the N variable, and $Y_4$ is the CC variable, which produced the strongest correlation between $U_i$ and $V_i$ ($i$ = 1–4), where $a_{ij}$ and $b_{ij}$ are coefficients. These analyses were performed to evaluate relationships between C pools and environmental

**Table 4.** The intercorrelation of the carbon pool variables versus microclimatic and site variables.

| Variable | NHM | UAM | EAM | Overall |
|---|---|---|---|---|
| Soil N (%) | Soil C (+) | Soil C (+) | Forest floor litter (+) | Soil C (+) |
| Canopy coverage (%) | Forest floor litter (–) | ns | Live tree (+) | ns |
| Soil temperature (°C) | ns | Live tree (–) | ns | ns |
| Soil moisture (%) | ns | ns | ns | ns |

**Note:** Treatments include no-harvest (NHM), uneven-age management (UAM), and even-age management (EAM). Plus and minus signs in parentheses give significant postive and negative correlations, respectively, between the two variables at the 95% level. C, carbon; N, nitrogen; ns, no significant correlation at the 95% level.

**Table 5.** Stem density and basal area of different forest types measured at (*a*) diameter breast height (DBH) and (*b*) measured for live tree carbon (C) ($Mg \cdot ha^{-1}$) relative to this study.

(*a*) Stem densities and basal area for different forest types measured at DBH.

| Forest type | DBH (cm) | Stem density ($N \cdot ha^{-1}$) | Basal area ($m^2 \cdot ha^{-1}$) | Reference |
|---|---|---|---|---|
| Old-growth forest (Kentucky) | >2.5 | 1246 | 27.0 | (Muller 1982) |
| Second old growth (Kentucky) | >2.5 | 1761 | 23.5 | (Muller 1982) |
| Ozark old-growth forests (Tennessee) | >6.6 | 547 | 9.2 | (Weaver and Ashby 1971) |
| Old-growth forest (Missouri) | >10.0 | 401 | 23.1 | (Shifley et al. 1997) |
| Second old growth (Missouri) | >11.4 | 396 | 8.9 | (Shifley et al. 1997) |
| Second growth (Missouri) | >3.8 | 997 | 24.7 | This study |
| Uneven age management (Missouri) | >3.8 | 820 | 17.6 | This study |
| Eight-year-old stands (Missouri) | >3.8 | 519 | 2.0 | This study |

(*b*) Live tree C for different forest types and ages.

| Forest type and age | Live tree C ($Mg\ C \cdot ha^{-1}$) | Reference |
|---|---|---|
| Oak–hickory, 35–92 years (Missouri) | 51 | (Rochow 1974) |
| Conterminous United States | 61 | (Turner et al. 1995) |
| Oak–hickory, 70–90 years | 80 | This study |
| Oak–hickory, 70–90 years (uneven age) | 55 | This study |
| Oak–hickory, 8 years | 5 | This study |

factors ($V_i$, microclimatic, and $U_i$ site variables (Manly 2004).

## Results

### Stem density and species composition

There were no significant differences in mean stem density and mean basal area (DBH >3.8 cm) among preharvest (1995) treatments ($p$ = 0.67; Fig. 3). Harvesting significantly reduced stand density in the UAM and EAM stands by 30% and 53%, respectively ($p$ = 0.001; Fig. 3*a*). Harvesting also significantly reduced mean basal area in UAM stands by 29% and in EAM stands by 99% ($p$ = 0.001; Fig. 3*b*). There were no significant differences in mean stem density and mean basal area in NHM stands between pre- and post-harvest treatment (Fig. 3).

Harvesting did not significantly change the major species composition between pre- and post-harvest ($p$ = 0.15, Fig. 4). Oaks (*Quercus* spp.) were the dominant species in all stands at both pre- and post-harvest treatment. The next most abundant species were hickories (*Carya* spp.) at both pre- and post-harvest stands, except for postharvest EAM stands, where pines (*Pinus* spp.) were more abundant than hickories.

### Carbon pool sizes and harvest effects

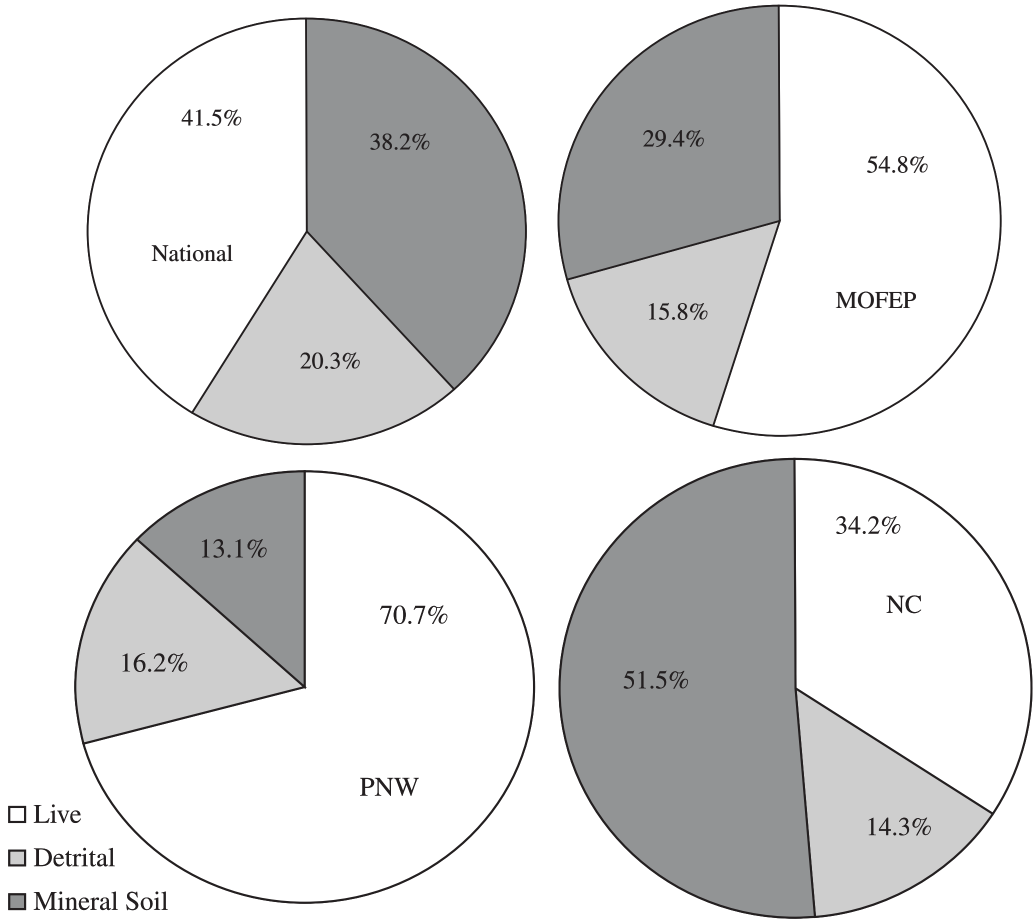
The total C pool was 182, 170, and 130 $Mg\ C \cdot ha^{-1}$ in the NHM, UAM, and EAM stands, respectively (Table 1). In the NHM stands, C was allocated as follows: 44% in the live trees, 11% in the roots, 13% in the CWD, 3% in the forest floor litter, and 29% in the mineral soil. In the UAM stands, 32% of the C was in the live trees, 9% was in the roots, 19% was in the CWD, 4% was in the forest floor litter, and 36% was in the mineral soil. In the EAM stands, the C allocation was 4% in the live trees, 11% in the roots, 38% in the CWD, 4% in the forest floor litter, and 43% in the mineral soil.

Harvesting significantly reduced live tree C ($p < 0.01$; Table 1) and increased CWD ($p < 0.01$) and mineral soil C ($p < 0.02$). Live tree C fell by 31% and 93% in UAM and EAM stands, respectively, with tree C in NHM > UAM > EAM. Harvest increased CWD by 115% in EAM stands and mineral soil C by 14% in UAM stands compared with NHM. Finally, harvesting had no detectable impact on forest floor litter ($p$ = 0.47), fine root ($p$ = 0.59), or coarse root ($p$ = 0.14) C pool sizes (Table 1).

### Harvest affects environmental and site factors

Timber harvest increased soil N content, SM, and ST in EAM over NHM stands by 0.05% ($p$ = 0.002), 4% ($p$ = 0.007), and 3 °C ($p$ = 0.001), respectively (Table 2). The CC in EAM stands was 2% ($p$ = 0.003) higher than that of NHM stands. There were no significant differences between UAM and NHM, except for ST, which was 3 °C higher in

**Fig. 5.** A comparison of the Missouri Ozark Forest Ecosystem Project (MOFEP) relative carbon (C) pool allocation to that of other studies: National, national mean (Turner et al. 1995); MOFEP, this study; PNW, Pacific Northwest (Smithwick et al. 2002); NC, North Central region mean (Turner et al. 1995).




NHM stands ($p$ = 0.001). Soil N content and SM in EAM stands was 0.04% ($p$ = 0.03) and 6% ($p$ = 0.001) higher, respectively, than that of UAM stands, but there were no significant differences in CC and ST between UAM and EAM stands (Table 2).

### Factors relating to C pools

Significant correlations existed between C pools and the environmental variables ($p$ = 0.001; Table 3). The first two pairs of significant canonical components explained 99% of the variation between these two sets of variables. The first component explained 78% of total variance and the second component explained 21% (Table 3). Both microclimatic and site variables were significantly intercorrelated with C pool variables, and these relationships differed with treatment (Table 4). Soil N was positively correlated with soil C in NHM and UAM stands and with the forest floor litter in EAM stands. Canopy cover was negatively correlated with forest floor litter at NHM stands, but positively correlated with live tree C in EAM stands. Soil temperature was negatively correlated with live tree C at UAM stands (Table 4).

## Discussion

In general, our study results were consistent with expected changes in C pool allocations, soil N, and microclimate characteristics of stands following timber harvest. An earlier, preharvest study (1993–1996) showed no significant differences among study plots in total soil C pools at MOFEP (Spratt Jr. 1997), but we found that stand density, basal area, and live tree C were all lower on harvested sites (Fig. 3 and Table 1), despite the fact that stand composition was not affected (Fig. 4). Also, as expected, the EAM treatment reduced live tree C pools more than UAM. These results provide relatively little insight to live tree dynamics aside from confirming that reductions by both harvest treatments persisted across the 8 year period.

Effects of treatment on belowground biomass were more interesting because harvesting had no detectable impact on C pool sizes of either fine roots or coarse roots (Table 1). It is possible that fine-root biomass recovered in the 8 year span and that living and dead coarse roots persisted during this period. However, we found discrepancies in comparing our empirical observations with estimates of root biomass calculated from aboveground biomass measures. As mentioned above, Cairns et al. (1997) evaluated the root biomass allocation across upland forests by relating it to aboveground biomass for forests ranging from 2 to 340 years old. We had good agreement with their model for NHM (19.6 versus 18.6 Mg C·ha$^{-1}$) and UAM (15.3 versus 14.7 Mg C·ha$^{-1}$)

stands. However, it disagreed with our observations for the EAM stands (14.3 versus 1.6 Mg C·ha$^{-1}$), suggesting that Cairn's model may not consider legacy root effects for young regenerating stands, and care should be used when the model is applied in this manner.

We also found that CWD and mineral soil C were higher at harvested sites, but litter pools showed no differences, 8 years after harvesting. Leaf litter in these forests has a turnover time of approximately 3–5 years (personal observations), suggesting that litter accumulations affected by harvest would soon disappear as production by young trees increased and possibly with windblown inputs from adjacent, intact stands. In contrast, harvesting significantly increased CWD by 115% in EAM stands and mineral soil C by 14% in UAM stands, compared with NHM. It is not surprising that CWD increased with harvesting, because a large amount of residual tree slash is typically left on-site (Harmon et al. 1990; Hoff et al. 2004; Houghton 1996). However, we were surprised that only the EAM sites showed this increase at MOFEP. Apparently, coarse logging debris on UAM sites was insufficient to make a persistent difference.

The increase in the mineral soil C pool in UAM stands was similar to responses of another northern temperate forest (Kranabetter and Coates 2004). Possible explanations for this finding may be that there is a greater initial incorporation of debris into soils on UAM sites by logging activities (Kranabetter and Coates 2004) and the generation of greater fine, medium, and coarse woody debris on soil surfaces (see the following). These factors could produce greater soil organic matter (SOM) as they decayed and are consistent with our observation of no differences in litter layer between treatments (above). In contrast, other studies have shown that intensive timber harvesting may significantly reduce forest soil organic C, perhaps because SOM loss is stimulated by changes in microclimate and edaphic characteristics. For example, Oliver et al. (2004) found a reduction of 3.1 Mg·ha$^{-1}$ in mineral soil C stocks to a 0.1 m depth after harvesting a forest in New Zealand. Such differences between studies illustrate different dynamics of SOM among forests, as pulses of logging debris are processed by the system. In our study, the 14% increase in the soil C pool in UAM sites represents about 1788 Mg $CO_2$ sequestered from the atmosphere over 8 years since the harvest, when projected to the whole MOFEP study area (3484 ha). How long this pool will persist is unknown, but it likely represents C retention of debris produced by harvest. In contrast, the increase in CWD on EAM sites seems not to have yet entered the SOM pool, although the higher soil N content, SM, and STs in EAM sites would be expected to increase decay rates (Table 2).

Intercorrelation between the C pool variables and environmental factors (Fig. 1 and Table 3) appears to be very complex. First, soil N was positively related to mineral soil C, as reported in several other studies (Baker et al. 1986; Nohrstedt et al. 1989; Johnson 1992; Johnson and Curtis 2001). This is consistent with classical studies of forest ecosystems in which harvesting directly affected N retention as a function of biomass and organic matter (Likens et al. 1970), and illustrates the important role that C has on N dynamics. Next, CC was positively correlated with live tree C in EAM stands, probably resulting from the establishment and growth of saplings (Claus and George 2005). Third, live tree C was negatively correlated to ST at UAM stands, probably because decreasing biomass and density allowed more solar radiation to impact and warm the soil surface (Brown et al. 1997; Chen et al. 1999). Finally, CC was negatively correlated with forest floor litter at NHM stands, likely because self-thinning generates more gaps and reduces canopy depth as forests age (Palik and Pregitzer 1993). When forests mature, mechanical and intercrown abrasions (Putz et al. 1984) produce less twig or branch litter (Reiners and Lang 1987) and less leaf litter. Evidently, implication of CCA elucidated the complicated relationships between ecosystem processes and their controlling factors (Table 4). Future efforts should be made to design controlled experiments to understand the mechanistic regulations and feedbacks among the biological and physical variables (Fig. 1).

The primary goal of our study was to evaluate the impacts of harvest on sizes and allocation of C pools within forests of the Missouri Ozarks. Indeed, the stem density (401–1761 individuals·ha$^{-1}$) and basal area (8.9–27.0 m$^2$·ha$^{-1}$) fell within the ranges of values reported by other studies of similar forests in this region (Weaver and Ashby 1971; Muller 1982; Shifley et al. 1997). Unfortunately, comparisons of our C pool components to other studies were hampered because C pool estimates are differently influenced by site-specific disturbance regimes and the definitions of some major C pools vary, especially for dead organic matter (Grier and Logan 1977; Matthews 1997; Schlesinger 1977). Fortunately, live tree C has a relatively clear definition and comparable methodologies among the studies (Table 5). The mean live tree C in MOFEP forests was 25% higher than for a similar ecosystem in Missouri (Rochow 1974).

Another goal of our study was to use our new knowledge of the Missouri Ozark forests to gain broader insights into general forest C dynamics. However, both sizes and allocation of C among pools in forest ecosystems vary greatly across regions (Fig. 5). For example, the mean live tree C pool at MOFEP was approximately 17% and 21% higher than the national mean and mean for the north-central United States, respectively (Turner et al. 1995), but it was 16% lower than the mean for Pacific Northwest forests (Smithwick et al. 2002). The mean soil C at MOFEP was about 16% higher than the Pacific Northwest mean (top 15 cm; Smithwick et al. 2002) but 12% and 22% lower than the means for the nation and north-central United States, respectively (top 15 cm; Turner et al. 1995). These allocation patterns suggest different capacities for C sequestration. For example, mineral soils contain the largest C pools on average in both the nation and north-central United States, representing approximately 42% and 52% of total forest C, respectively (Turner et al. 1995). In contrast, live trees represented the largest C pool in MOFEP and the Pacific Northwest, which accounted for about 55% and 71% of total forest C, respectively. Therefore, managing an ecosystem to increase C sequestration should consider the allocation patterns of C, because management activities and disturbances can reconfigure ecosystem C pools. Thus, the relatively larger live tree C pool in MOFEP suggests that these forests may be most amenable to storing C through management and conservation efforts, whereas other systems that store more C in the mineral soil may benefit from management plans focusing on soil C retention. Clearly, a similar effort to this study should be made to monitor the changes of various C pools as the MOFEP study moves to the future — allowing us to understand the long-term dynamic of C pools following these experimental manipulations.

## Conclusions

We found that timber harvests at the MOFEP experiment affected some, but not all major C pools in the forests of the Missouri Ozarks 8 years after harvest, with a greater variation related to the harvest method (EAM versus UAM). Aside from expected changes in live-tree biomass, there were no significant impacts of harvesting on forest floor litter or root C pools. Soil N was more positively correlated with soil C at both UAM and EAM stands than that of the controls. The mineral soil C pool was 14% higher in UAM stands, whereas CWD was 176% greater in EAM stands. This suggests a possible flow of C through the system initiated by a pulse of logging debris and mediated by harvest regime, but more detailed analyses of soil C pools over time with treatment is needed to explore long-term logging-induced changes in soil C storage and associated N pools. As new data become available from MOFEP's long-term monitoring program and additional manipulative experiments, we will be able to extrapolate our findings for revising current forest management plans to increase the C sequestration strength of the forests.

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