A Dissertation

Entitled

CARBON STORAGE AND FLUXES IN A MANAGED OAK FOREST LANDSCAPE

By

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Submitted as partial fulfillment of the requirements for

The Doctor of Philosophy in Biology

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August 2006

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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An Abstract of
Carbon Storage and Fluxes in a Managed Oak Forest Landscape

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Carbon (C) storage and fluxes were investigated for the Missouri Ozark Forest Ecosystem Project (MOFEP) in southeastern Missouri, USA, to determine the effects of timber harvesting regimes (non harvest: NHM, uneven age management: UAM, and even age management: EAM) on carbon storage and related ecological processes. The central hypothesis was that harvesting regimes would alter major forest ecosystem processes and thus affect the magnitude of C sequestration within the system. Specifically, from 2003 to 2005, I used biometric and empirical modeling approaches quantified the C pool sizes, examined the contribution of microclimate variables to the variation of the C pool sizes. I further examined the rates of mixed leaf litter mass loss under different harvesting regimes. Finally, I measured ecosystem component respiratory C losses and examined their responses to the harvesting regimes. Total C pools were 182, 170, and 130 Mg C ha^{-1} for the NHM, UAM, and EAM stands, respectively. Harvest significantly reduced C

pools in live tree biomass and increased the pool sizes of coarse woody debris. I found significant correlations between C pools and soil nitrogen, soil temperature, and canopy coverage. Harvest also significantly increased mixed oak and oak-hickory leaf litter decomposition. The oak-hickory litter mixtures decay faster than that of either oak or oak-pine litter mixtures. The decay constant over the 32-month of field incubation ranged between 0.39 and 0.51 y^{-1} at my study sites, and had linear relationships with initial litter C chemistry and cellulose to nitrogen ratio and the nitrogen concentration in remaining litter also had a linear relationship to cumulative mass loss. Lastly, timber harvesting reduced by 27.7% annual ecosystem respiration in the EAM stands compared to that in the NHM stands. The annual ecosystem respiratory carbon losses were 1642, 1691, and 1285 g C m^{-2} y^{-1} in the NHM, UAM, and EAM stands, respectively. The harvesting activities affected ecosystem processes by removing biomass, and changed the magnitude of component respiration.

Acknowledgements

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Table of Contents

List of Tables

List of Figures

Chapter 1 Introduction

1.1 Background

Forests occupy about 30% of the global land surface and hold 77% of the global carbon (C) pool found in vegetation (Gifford 1994, Cox et al. 2000, Post and Kwon 2000). Managing forests to enhance C sequestration is one possible means of reducing CO_2 concentration in the atmosphere (Vitousek 1991, Smithwick et al. 2002). Recent studies suggests that C may be sequestered in terrestrial ecosystems in northern temperate latitudes (Ciais et al. 1995), especially northern forests (Myneni et al. 2001). However, the forest contributions to the global C budget remain uncertain because processes controlling net C uptake vary with physiological differences in forest functional groups, developmental stages, disturbance regimes, management practices, climate, and nutrition status (McMurtrie and Wolf 1983, Houghton et al. 1999, Amundson 2001, Brye et al. 2002). Thus field studies of ecosystem-level CO_2 exchange must be integrated with smaller-scale studies of physiological and biophysical processes to link organisms, stand, and regional components of C cycles (Post et al. 1990, Gifford 1994, Schlesinger 2000, Lal 2005). At present, there is little data available to support predictions of net C exchange under different harvest regimes or at different stages of forest development (Chen et al. 1999, Clark et al. 1999).

Measuring C pool sizes between two points in time is the most obvious means of quantifying C storage in forest ecosystems (Turner et al. 2000). The main C pools are: (1) live tree biomass, including stems (sapwood and bark), branches, and foliage, (2) coarse and fine roots, including both live and dead portions, (3) coarse woody debris (CWD), including standing (i.e., snags) and down dead trees, (4) understory vegetation, (5) forest floor litter, and (6) soil (Figure 1.1). Total C in forests of the conterminous US was estimated at 36.7 Pg C ($1x10^{15}$ g), with about 50% of that in the soil (Turner et al. 1995). Trees represented 33% of the total, including roots, followed by CWD (10%), forest floor litter (6%), and understory (1%). However, the size of each component varies with forest types, age, disturbance history, and location (Smithwick et al. 2002). Harvesting reduces live tree biomass, but how it affects other C pools remains unclear. For example, Johnson (1992) concluded that there was no general trend of forest harvesting either reducing or increasing soil C storage (Johnson 1992). Kranabetter and Coates (2004) reported an increase in belowground biomass, whereas Aber et al., (1978) found a decrease. Clearly, further investigation into the effect of harvesting on C pools is necessary. In particular, it is unclear how alternative harvesting regimes will affect C pool sizes within forest ecosystems.

Two dynamic ecological processes, photosynthesis and respiration, control C pool gains and losses within forested ecosystems. The main C fluxes are computed by gross primary production (GPP), autotrophic respiration (R_a), and heterotrophic respiration (R_h) (Figure 1.2). R_h fluxes nearly equal the input from photosynthesis, and are more important than photosynthesis in determining the variability of an ecosystems net C storage or loss at a given latitudinal gradient (Valentini et al. 2000). R_h is comprised of

respiratory C losses by organisms. Heterotrophic respiration is about 60% of soil surface CO_2 efflux (Hanson et al. 2000), of which 30% comes from soil microbes, and another 30% comes from leaf litter and CWD respiration (i.e., decomposition) (Bowden et al. 1993). Live roots account for about 40% of soil surface CO_2 efflux (Hanson et al. 2000). Therefore, to estimate changes in the C cycle in forest ecosystems accurately, this study was designed to obtain precise ecosystem component respiration. So far, only a few studies have examined all of these components (Law et al. 1999, Curtis et al. 2005, Reichstein et al. 2005).

Leaf litter decomposition is an important component of heterotrophic respiration (R_h) and of the global C budget (Aerts 1997). Recent studies have shown inconsistent responses in litter decomposition to timber harvest. Some studies have reported increased decay (Gadgil and Gadgil 1978, Prescott et al. 1993), others showed decreased decay (Yin et al. 1989, Prescott et al. 2000), and yet others reported no effect (Wallace and Freedman 1986, Prescott 1997). Timber harvest can change litter decomposition by altering microclimatic conditions of the forest floor (Brosofske et al. 1997), leaf litter biochemistry (Forkner and Marquis 2004), and composition of the microorganism community (Salminen and Haimi 1997, Cortez 1998). Indeed, climate, litter chemistry, and soil organisms have been considered, in order of declining effect, the major factors controlling decomposition (Meentemeyer 1978, Lavelle et al. 1993). Within this context, the effect of timber harvest on decomposition partly depends on alteration of either microclimate or litter biochemistry (Yin et al. 1989). However, few studies have explicitly examined the combined effects of selective timber harvest and leaf litter mixture on decomposition within a particular climatic regime.

1.2 Objectives and study overview

The central hypothesis of this research is that harvesting regimes alter major forest ecosystem processes and thus affect the magnitude of C sequestration. Specifically, three sub-hypotheses are: (1) fluctuations in microclimate are responsible for a significant portion of the variation in C pool sizes; (2) rates of leaf litter mass loss are greater in harvested stands than in non-harvested stands; and (3) timber harvesting reduces ecosystem respiratory C losses. The goal of the research described in the following chapters is to further understanding of C fluxes under different timber harvesting regimes. In Chapter 2, I quantified C pool sizes 8 years after timber harvesting and compared managed and control stands. In Chapter 3, I examined rates of mixed leaf litter mass loss under different harvesting regimes across the landscape. Finally, in Chapter 4, ecosystem respiratory C losses were quantified and compared under different harvesting regimes. The results from this research will enhance our understanding of C storage and fluxes in response to harvesting regimes.

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Figure 1.1 Components of the carbon pools in a managed forest ecosystem (adopted from Lal, 2005).

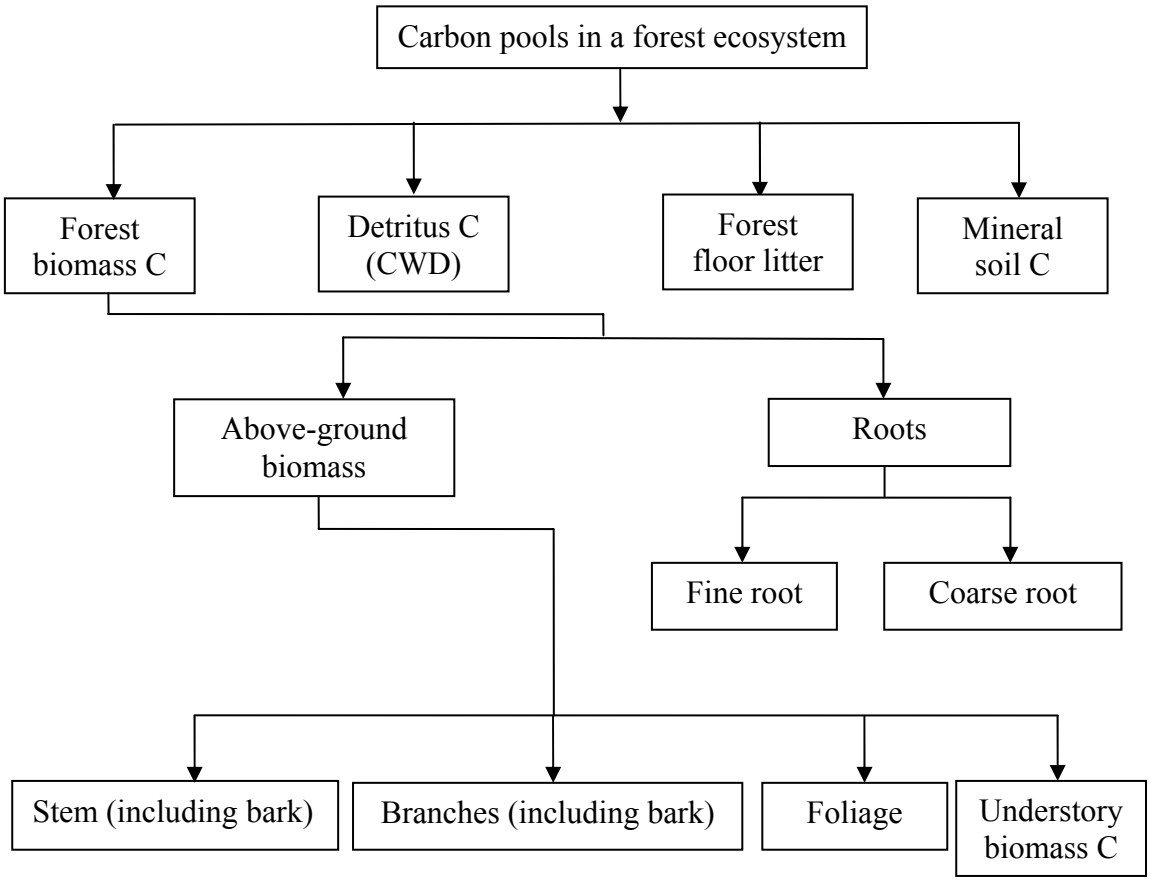
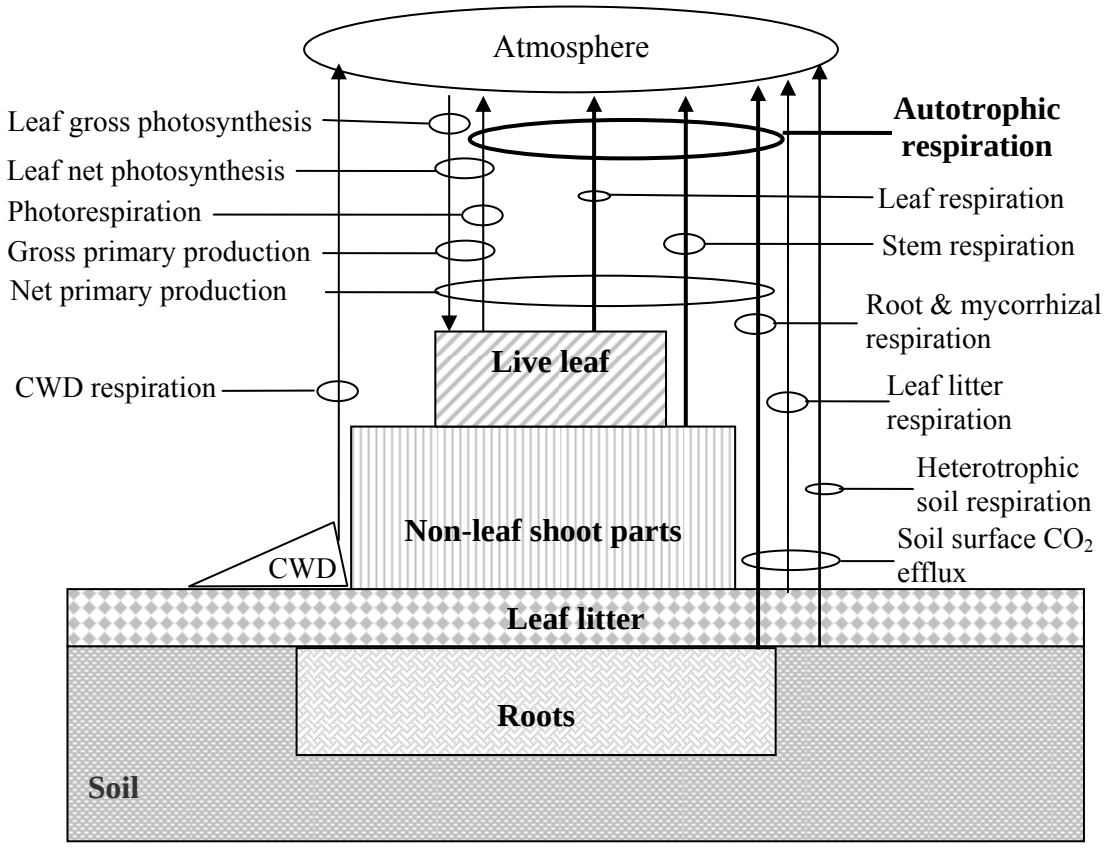


Figure 1.2 Diagram of major ecosystem respiratory carbon losses in a forested ecosystem (not scaled to their sizes; adopted from Gifford, 2003).



Chapter 2 Alterations of Tree Removals on Carbon Pools in Ozark Forests

Abstract

I quantified carbon (C) pools at a managed Missouri Ozark experimental forest. Total C pools were 182, 170, and 130 Mg C ha^{-1} for the control non harvest management (NHM), singletree uneven age management (UAM), and clear-cut even age management (EAM) stands, respectively. Harvests reduced C pools in live tree biomass by 31% in the UAM, and 93% in the EAM stands, and increased the coarse woody debris (CWD) C pool by 50% in UAM and 176% for the EAM compared to the NHM stands. UAM significantly ($p = 0.02$) increased the mineral soil C pool by 13.5% after the first 8 years timber harvest, while EAM did not increase the mineral soil C pool. I observed a significant ($p = 0.001$) positive relationship between total soil nitrogen (N) and C pools. Canopy coverage showed negative correlation with forest floor litter in the NHM and live tree in the EAM stands. Soil N was significantly correlated with soil C, while soil temperature was negatively related to live tree C in the UAM stands. Soil N and canopy coverage were significantly correlated with live tree and soil C pools in the EAM stands. Results improve our understanding of landscape level C pools and can support better management strategies for C sequestration in other central hardwood forests such as CWD management strategies after clear cutting.

2.1 Introduction

Quantifying terrestrial C pools has received increasing attention due to high capacity of the terrestrial ecosystems to store C and its potential ability to help offset rising atmospheric C dioxide (CO_2) concentration (Agren and Hyvonen 2003). One emphasis has been placed on temperate forests because of the large amounts of C stored and high capacity to sequester anthropogenically derived C (Gifford 1994, Cox et al. 2000, Post and Kwon 2000). Thus, managing forests to increase C sequestration is one potential means of offsetting anthropogenic CO_2 input (Smithwick et al. 2002). For example, alternative management practices have been sought to reduce the C loss by maintaining minimal leaf area (Chen et al. 2004b). However, forest ecosystems are rarely stable, for example, temperate forests are subjected to disturbances (i.e., fires, harvesting, wind throw, insects, and diseases) during the past few decades (Guyette and Larsen 2000, Bresee et al. 2004, Chen et al. 2005). Human disturbances can significantly disrupt the C sequestration strength of a forest (Chen et al. 2004a). Following a major disturbance, forest re-growth does not immediately balance C loss from both harvest and subsequent decomposition at a site (Abbott and Crossley Jr. 1982, Aerts 1997). Several recent studies had shown that intensive timber harvesting would turn forests into a major C source -- potentially as important as fossil fuel combustion (Post et al. 1990, Sarmiento and Gruber 2002). Therefore, knowledge gaps about biological processes in forest ecosystems pamper efforts to accurately predict effects of disturbance on C cycle (Lee et al. 2002). Clearly, additional information is needed about changes following timber harvesting in forest ecosystem C pools, including live trees, coarse woody debris, roots,

forest floor, and soil. Quantifying C pools under different management regimes is also a necessitation to determine the effectiveness of management practices.

The C storage and its distribution within a forest vary with disturbance history (Sah et al. 2004) and species composition (Rothstein et al. 2004, Barrio Anta et al. 2006). Several studies documented that clearcutting decreased C pools sizes on live tree biomass and mineral soil at temperate deciduous forests (Johnson 1992, Grigal and Berguson 1998, Chen et al. 2005). For example, forest floor organic matter declined for 15-30 years following cutting and required 60-80 years to recover to precut levels in northern hardwood forest ecosystem (Aber et al. 1978). Timber harvesting also decreased total ecosystem C and soil C storage in the boreal forest region of central Canada (Peng et al. 2002). However, it is not clear how environmental conditions (soil moisture: SM, soil temperature: ST) and site factors (soil N content: N, canopy coverage: CC) associated with multiple intensity levels of timber harvesting will affect the accumulation, allocation, and changes of C pools in these ecosystems. Thus, we proposed a conceptual model to link the C pool changes with microclimatic and site factors (Figure 2.1). Timber harvests increase solar radiation penetrating the canopy, promote photosynthesis which may increase productivity. Meanwhile, an open canopy can warm soils thus accelerating soil decomposition and therefore potentially decreasing soil pools (Lloyd and Taylor 1994, Lavigne et al. 2003, Ma et al. 2005). While increased soil N availability, by decreases in aboveground biomass uptake, has the potential to promote biomass production (Baker et al. 1986, Nohrstedt et al. 1989). Moreover, soil moisture may increase because of reducing canopy evapotranspiration (Pitacco and Gallinaro 1996, Lu et al. 2003). The increased soil moisture can promote soil decomposition and

likely decreasing soil pools (Lloyd and Taylor 1994, Lavigne et al. 2003, Ma et al. 2005). Lastly, timber harvest decrease aboveground C pools which can increase or decrease belowground biomass (Aber et al. 1978, Kranabetter and Coates 2004). Therefore, the microclimatic and site factors affected by timber harvest can be predictors of the C pools in a managed forest ecosystem.

One objective of this study was to evaluate the effects of different silvicultural treatment on C pool sizes through field sampling of live trees aboveground biomass, roots, coarse woody debris (CWD), and total soil C content based at a large-scale experiment (i.e., MOFEP) executed 8 years before this study. Missouri Ozark Forest Ecosystem Project (MOFEP, see study site for detailed information) had well documented pre-harvest data for us to compare the changes of stand stem density, basal area, and species composition between pre- (1995) and post-harvest (2003). These data can be used to infer the effects of forest harvests on the C pool sizes. We expect that that all C pool sizes except CWD will be higher in control stand than in the harvested stands. Our second objective was to determine the causes of the variation of C pool sizes within each management by correlating environmental variables (i.e., soil moisture, soil temperature, soil N content, and canopy coverage) with C pool sizes. We hypothesized that spatial variation of soil moisture, soil temperature, soil N content, and canopy coverage contributed to a significant portion of the variation of the C pool sizes.

2.2 Study site

The MOFEP (Figure 2.2) was initiated in 1989 to examine the impacts of timber harvest on multiple ecosystem components (Brookshire and Shifley 1997, Shifley and

Brookshire 2000, Shifley and Kabrick 2002). MOFEP is located in the southeastern Missouri Ozarks (91°12′ W and 37° 06′ N). This area is primarily mature upland oak, oak-hickory and oak-pine communities (Brookshire and Shifley 1997, Xu et al. 2004). *Q. alba* (white oak), *Q. velutina* (black oak), and *Q. cocinea* (scarlet oak) are the dominant oak species, while *C. cordiformis* (bitternut hickory) and *C. glabra* (pignut hickory) are dominant hickory species, and *P. echinata* (shortleaf pine) is the only pine specie in this area. MOFEP receives an annual average of 1120 mm of precipitation and experiences a mean annual temperature of 13.3°C (Guyette and Larsen 2000). The soils are mostly Alfisols and Ultisols (Kabrick et al. 2000).

The overall timber harvest treatments selected for MOFEP were even age management (EAM), uneven age management (UAM), and non harvest management (NHM), which includes nine forested sites, ranging in size from 266 to 527 ha. Sites were chosen based on similarities in forest age, vegetation, and soil composition. Specifics of site selection are detailed in Brookshire et. al. (1997) and Sheriff and He (1997). In brief, the entire sites were randomly assigned one of the three timber harvesting regimes: EAM, UAM, and NHM (Figure 2.2). Sites were subdivided into stands, averaging 4 ha in size, of similar ecological land types (ELTs) defined by slope, aspect, vegetation composition, and soil type. At each timber harvest, 10% of forest biomass was removed, which resulted in landscapes having both harvested areas and no-harvested forest. Ten percent of the area of each EAM and UAM sites was designed as "old-growth" and not available for harvest. The remaining area was designed as: 10% seedlings, 20% trees 6-14 cm in DBH, 30% trees 14-29 cm in DBH, and 40% was greater than 29 cm in DBH as saw timber in the EAM sites. In the UAM sites, the largest

tree diameter objective was the same as saw timber size objective for EAM sites and the target tree size class distribution was identical to the composition size class distribution in EAM sites (Brookshire and Shifley 1997). To achieve these class distributions in EAM sites, some stands were clear-cut and others were treated with intermediate cutting following Missouri Department of Conservation Forest Land Management Guidelines (1986), while in UAM sites, trees were removed in small groups, individually, or girdled and left standing. NHM sites were not subjected to manipulation, except that wildfires and large-scale insect outbreaks. This treatment resembled "old growth" management and served as an experimental control treatment in this project (Sheriff and He 1997). Prior to MOFEP, no harvesting had occurred since 1950 and most of the overstory trees were 50-70 years old (Forkner and Marquis 2004).

A system of 648 permanent forest vegetation plots (0.2 ha) was distributed across the nine MOFEP sites to document forest vegetation response to treatment. Plots were allocated among stands based on stands size with the constraint that each stand receives at least one plot. Location of the plots within stands was random (Brookshire and Shifley 1997). A complete vegetation plot data set was collected from June 1994 to November 1995 (Brookshire and Shifley 1997). The data were used as pre-treatment forest vegetation baseline information to compare post-harvest effects on stem density, basal area, and species composition in this study.

2.3 Methods

2.3.1. Study design

In this study, we selected six sites (site 1 to 6) and grouped same management type as one group for a total of three groups (Figure 2.2). Within each group, twelve forest vegetation plots were selected with similar soil types, species composition, and ELT for a total of 36 plots. The plots in the EAM stands were clear cuts, while the plots in the UAM stands were single tree selective harvest.

2.3.2 Data collection

C pools are divided into: (1) live tree biomass, with diameter at breast height (DBH) > 3.8 cm, including stems (hardwood, sapwood, and bark), branches, and foliage, (2) coarse and fine roots, including both live and dead portions, (3) CWD, including standing (i.e. snags) and down dead tree, (4) forest floor litter, and (5) 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 species-based allometric equation (2.1) to estimate C pools (foliage, branch, stem with bark) for live trees, either developed for the local species or from the nearest geographical location (Ter-Mikaelian and Korzukhin 1997).

$$M = aD^b \qquad (2.1)$$

where M is the oven-dry weight of the biomass component of a tree (kg), D is DBH (cm), and a and b are parameters. Species not present in the literature were

grouped by genus or similar species. The species and DBH data were collected between the fall of 2002 and the spring of 2003.

Root C was measured by a soil pit (1 m x 1 m x 0.6 m) method (Hughes et al. 1999). Three soil pits were dug in each management type with the same soil type, aspect, elevation, and slope for a total of 9 samples. The pits were located 50 meters east from a vegetation plot center. The pits were used to quantify coarse roots (≥ 2 mm in diameter, including both dead and live) during the summer of 2003. Four fine root cores (81 cm^2) were taken near each soil pit for a total of 36 samples to quantify fine root C. Each root core was washed, sorted, and measured for all roots < 2 mm in diameter. The coarse and fine roots (including both dead and live) were oven dried at 65^oC to obtain a constant oven dried weight.

CWD C was estimated by transect method (Wagner 1964, Martin 1976):

$$W = \frac{\pi^2 S \sum d^2}{8L} \qquad (2.2)$$

where W is weight per unit area (Mg ha^{-1}), S is specific gravity of the log (Mg m^{-3}), d is diameter of the log intersected with transect (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. 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 classes while the live trees were surveying. Specific gravity of CWD and snag by decay classes was used to convert volume to mass (Adams and Owens 2001).

Forest floor litter C was collected using a 0.25 m^2 (0.5 m x 0.5 m) frame at 20 m intervals along a 100 m CWD transect for a total of 6 samples in each plot (N = 216) during the summer of 2003. CWD less than 5 cm in diameter was included as litter. All litter was oven dried at 65^oC to obtain a constant oven dried weight.

Understory C was not evaluated in this study, because we could not harvest understory in long-term monitored vegetation plots. The literature reported that the understory was only about 1% of total above ground biomass nearby our study sites, which has similar species composition (Rochow 1974). It would minimally affect the estimates of total C storage at MOFEP.

Mineral soil C was sampled (top 15 cm depth and organic layer excluded) with 4 replications at each plot for a total of 144 samples during the summer of 2003 using a soil core (81 cm^2). Soil samples were oven dried for 48 hours at 65^oC and ground, oven dried for another 48 hours at 65^oC, and then analyzed for total C and N contents using CHN (PerkinElmer 2400 CHN/O Analyzer). Soil bulk density and rock contents of each plot were obtained from previous on site studies (Shifley and Brookshire 2000).

Microclimatic variables include measuring soil moisture (SM, at top 15 cm) and temperature (ST, 5 cm depth) in each of the 36 plots by using Time-Domain Reflectrometry (TDR, Campbell Scientific Inc., USA.) and Taylor portable thermometer (Forestry Supplier Corporation, USA.), respectively. SM and ST were taken two times a month from May to October of 2003. Canopy coverage (CC) were measured at each of the 36 plots by taking fisheye images along 100 m CWD transect in 5 m interval for a total 21 images per plot every month from May to October 2003. All the images were analyzed by gap light analyzer software (GLA, www.rem.sfu.ca).

2.3.3 Statistical analysis

Means and standard errors were calculated for N (%), CC (%), ST, and SM by managements. All variables were checked for normal distribution with Shapiro-Wilk tests. All analyses were conducted using SAS software (V9.1, SAS Institute Inc., Cary, North Carolina, USA) and a p-value of 0.05 was used to determine statistical significance.

Harvest effects on stem density, basal area, and species composition were quantified by comparing these variables in plots between pre- and post-harvest by using two-way analysis of variance (ANOVA) to test differences between the managements and year. While harvest effects on C pools (stem, foliage, branch, snag, CWD, forest floor, and soil) and microclimatic (SM and ST) and site factors (N% and CC) were quantified by one-way ANOVA to test differences among managements. Significant differences between means were compared with Tukey's test.

Relationships between C pools (live tree, including stem, foliage, branch; detritus, including snag and CWD; forest floor; and soil C %) and microclimatic (SM and ST) and site (N% and CC) variables were examined by using canonical correlation analysis (CCA) for the whole data set and within each management. CCA takes to answering this question is to search for a linear combination of C pools variables (X_1: live tree C, X_2: detritus, X_3: forest floor, and X_4: soil)

$$U_i = a_{i1}X_1 + a_{i2}X_2 + a_{i3}X_3 + a_{i4}X_4 \qquad (2.3)$$

and a linear combination of microclimatic and site variables (Y_1: SM, Y_2: ST, Y_3: N, and Y_4: CC)

$$V_i = b_{i1}Y_1 + b_{i2}Y_2 + b_{i3}Y_3 + b_{i4}Y_4 \qquad (2.4)$$

where these are chosen to make the correlation between U_i and V_i (i = 1, …, 4) as large as possible and a_{ij} and b_{ij} are coefficients. The pairs of canonical variables (U_1, V_1), …, (U_4, V_4) then represents an independent dimension in the relationship between the two set of variables (X_1, …, X_4) and (Y_1, …, Y_4). The first pair (U_1, V_1) has the highest possible correlation and is therefore the most important, and second pair (U_2, V_2) has the second highest correlation and is therefore the second most important, etc. CCA provides the correlation analysis between C pool variables and their canonical variables (U_i), microclimatic and site variables with their canonical variables (V_i). CCA also offers the inter-correlation analysis between C pool variables and V_i, microclimatic and site variables with U_i (Manly 2004).

2.4 Results

2.4.1 Stem density and species composition

There was not significant difference in mean stem density (DBH > 3.8 cm) among pre-harvest (1995) managements (p = 0.67). The mean stem density was 1082, 1169, and 1106 trees ha^{-1} in 1995 in the NHM, UAM, and EAM stands, respectively. However, harvest significantly reduced 30% and 53% stem density in both the UAM and EAM stands, respectively (p = 0.001). While there was no significant difference in mean stem density in the NHM stands between pre- and post-harvest management (Figure 2.3a).

The mean basal area (DBH > 3.8 cm) was not significantly different among pre-harvest treatments (p = 0.77). The mean basal area was 25.6, 24.6, and 24.6 m^2 ha^{-1} in 1995 in the NHM, UAM, and EAM stands, respectively. As expected harvest significantly reduced mean basal area in the UAM by 29% and EAM by 99% (p = 0.001).

There was no significant difference in mean basal area in the NHM stands between pre- and post-harvest management (Figure 2.3b).

Harvesting did not significantly change the major species composition between pre- and post-harvest ($p = 0.15$, Figure 2.4). Oaks (*Quercus spp*) were the dominant species in all stands at both pre- and post-harvest management. The next most abundant species were hickories (*Carya. spp*) in both pre- and post-harvest stands, but pines (*Pinus. spp*) in post-harvest EAM stands.

2.4.2 C pool sizes and harvest effects

The total C pool was 182, 170, and 130 Mg C ha^{-1} in the NHM, UAM, and EAM stands, respectively (Table 2.1). In the NHM stands, C pools were allocated as: 44% in live trees, 11% in roots, 13% in CWD, 3% in forest floor litter, and 29% in mineral soil. In the UAM stands, 32% was in live trees, 9% in roots, 19% in CWD, 4% in the forest floor litter, and 36% in mineral soil. In the EAM stands, 4% in live trees, 11% in roots, 38% in CWD, 4% in forest floor litter, and 43% in mineral soil.

As expected, harvest significantly reduced live tree C ($p < 0.01$; Table 2.2), and increased CWD ($p < 0.01$) and mineral soil ($p < 0.02$) C pools. First, harvest significantly reduced live tree C by 31% and 93% in the UAM and EAM stands, respectively; the NHM had the highest live tree C pool, followed by UAM and EAM. Secondly, CWD increased by 115% in the EAM stands. Lastly, the C pool in mineral soil was 14% higher in the UAM stands than in NHM stands. Finally, harvest did not have a detectable impact on forest floor litter ($p = 0.47$), fine roots ($p = 0.59$), and coarse roots ($p = 0.14$) C pool sizes (Table 2.2).

2.4.3 The factors affecting C pool sizes

Timber harvest significantly increased soil N content, canopy coverage, soil moisture, and soil temperature in the EAM stands by 0.05 ($p = 0.002$), 2 ($p = 0.003$), 4% ($p = 0.007$), and 3°C ($p = 0.001$), respectively (Table 2.3). There was no significant difference between UAM and NHM except soil temperature. Soil temperature in the UAM stands was 3°C higher than that of NHM stands ($p = 0.001$). While soil N content and soil moisture in the EAM stands were 0.04 ($p = 0.03$) and 6% ($p = 0.001$) significantly higher than that of UAM stands, respectively. There were no significant difference in canopy cover and soil temperature between the UAM and EAM stands (Table 2.3).

Significant correlations existed between C pool and microclimatic and site variables ($p = 0.001$; Table 2.4). The first two pairs of canonical components explained 99% variation of these two set of variables. The first component of soil N content (0.99) was positively correlated with the first component of soil C content (0.98, $r = 0.91$), while there was no significant correlation at the second component between the two set of variables (Table 2.4).

The microclimatic and site variables were significantly inter-correlated with C pool variables and changed by managements (Table 2.5). The first component of soil N content was positively correlated with the first component of soil C in the NHM and UAM stands, but it was positively correlated with the first component of forest floor litter in the EAM stands. In contrast, the second component of canopy cover negatively correlated with forest floor litter in the NHM stands, while the second component of soil

temperature negatively correlated with live tree in the UAM stands. The second component of canopy cover was negatively correlated with live tree in the EAM stands (Table 2.5).

2.5 Discussion

A three-year pre-harvest study (1993-1996) showed no significant differences among study plots in total soil C pools at MOFEP (Spratt Jr. 1997). However, we found increased (13.5%) mineral soil C pools 8 years after harvest in the UAM stands, similar finding was noted at other northern temperate forest (Kranabetter and Coates 2004). The possible reasons may be UAM having minor disturbances through ground skidding of logs, which would have incorporated some organic matter into the upper soil horizons (Kranabetter and Coates 2004). Furthermore, after a harvest the input of tree slash would increase CWD pools and the C would eventually be incorporated into soil C pools. For example, forest harvest did increased CWD in the UAM (49.9%) stands above the levels in the NHM stands, due to the large amount of residual tree C that was typically left on site to decompose (Harmon et al., 1990; Houghton, 1996; Hoff et al., 2004). Moreover, open canopy reduced light competition may promote aboveground productivity, which can increase belowground productivity. Additionally, intensive timber harvesting activities may significantly reduce forest soil organic C. Hart and Sollins (1998) reported that 13 years of root exclusion trench manipulation experiments had little effect on soil C pools at old-growth conifer forest, while Oliver et al. (2004) found that a further reduction of 3.1 Mg C ha^{-1} in mineral soil C stocks to 0.1 m depth before and after harvesting, comparing to former research at the same location and same depth with a

reduction of 3.6 Mg C ha^{-1} at New Zealand. Therefore, mineral soil C pool may have little effect if site clearing or burning followed after timber harvest (Johnson 1992, Hart and Sollins 1998). Nevertheless, I observed that soil C pool was 13.5% higher in the UAM stands than that of the NHM stands. If this difference were projected to the whole MOFEP study area (3484 ha), it would represent 1533 Mg CO_2 sequestered from the atmosphere over the first 8 years of management.

Estimating root biomass from aboveground biomass in recently disturbed forests should be used with caution. Cairns et al. (1997) evaluated the global root biomass allocation across upland forests by relating it to aboveground biomass with forest ages ranging from 2 to 340 years old. I had good agreement with their model for the NHM (19.55 versus 18.35 Mg C ha^{-1}) and UAM (13.80 versus 13.11 Mg C ha^{-1}) stands. However, it was in disagreement in the EAM stands (11.20 versus 1.60 Mg C ha^{-1}). This suggests that the limitation of Cairn's model may be more pronounced at young stands. Results also indicate that harvests change existing above- and below-ground C allocation relationships. As shown in my hypothesis (Fig. 2.1), C allocation is regulated by many biotic and abiotic variables through regulating various processes (e.g., photosynthesis due to change in leaf area or canopy coverage) and interactions between soil microclimate and respirations. My results from this study are limited to only two kinds of sivilcultural treatments in southeast Ozarks. Although I have no evidence showing simple extrapolations to other forests is feasible, such effort is urgently needed by pooling together published and ongoing research toward a synthetic conclusion.

I found that soil N was positively related to mineral soil C pools, as also reported in several studies (Baker et al. 1986, Nohrstedt et al. 1989, Johnson 1992, Johnson and

Curtis 2001). Harvests directly affected the ecosystem N budgets at Hubbard Brook, because deforestation caused lack of nitrification and vegetation uptake, which increased stream nitrate concentrations 41-fold higher than the undisturbed condition the first year and 56-fold higher the second (Likens et al. 1969). Canopy coverage was negatively correlated with forest floor litter in the NHM stands, because as forests age, mechanical and intercrown abrasions between trees created more gaps (Putz et al. 1984), which produced more twig and branch litter (Reiners and Lang 1987). While canopy coverage negatively correlated with live tree C in the EAM stands, this maybe from large openings facilitated new species establishment and tree growth (Claus and George 2005). Live tree C was negatively correlated to soil temperature in the UAM stands, it is reasonable that harvest reduced stem density increasing larger openings where solar radiation can warm the soil (Brown et al. 1997).

The stem density and basal area of this study was in the range of the values reported by other studies with similar vegetation around this region (Table 2.6). The stem density and basal area varied according to the starting DBH, ranging from 401 to 1761 n ha^{-1}, and 8.9 to 27.0 m^2 ha^{-1}, respectively (Weaver and Ashby 1971, Muller 1982, Shifley et al. 1997). Unfortunately, comparisons of C pool components in our study to that in other studies were hampered because C pool estimates often reflect the influences of disturbances, and because the definitions of major C pools (i.e., detrital and soil) differ (Grier and Logan 1977, Matthews 1997, Schlesinger 1997). Fortunately, the live tree C has a relatively clear definition and comparable methodologies among the studies (Table 2.6). The average live tree C at MOFEP second growth forests was 10% higher than the

average in the conterminous United States (Turner et al. 1995) and 25% higher than a similar ecosystem in Missouri (Rochow 1974).

The proportion of C pool components in an ecosystem varied greatly across regions. For example, the mean live tree C pool at MOFEP was around 23 and 25% higher than the national average and north central United States, respectively (Turner et al. 1995), but it was 10% lower than the Pacific Northwest average (Smithwick et al. 2002). While the mean soil C at MOFEP was about 11% higher than the Pacific Northwest average (Smithwick et al. 2002), but it was 21 and 26% lower than the national average and north central United States, respectively (Turner et al. 1995). Furthermore, the relative proportion of C pool component in an ecosystem indicates the capacity of C allocation. For example, the largest C pool component in national average and north central United States was in mineral soil C pool, which accounted for about 50 and 55%, respectively (Turner et al. 1995), in contrast, the largest C pool component in MOFEP and Pacific Northwest was in live tree C pool, which accounted for about 55% and 63%, respectively. Therefore, managing an ecosystem for increasing C sequestration should consider the relative bigger proportion of the C component in an ecosystem, because any management activities and disturbances such as fire can cause the ecosystem C pools reconfiguration. Thus, the large live tree C pool in MOFEP ecosystem, relative to the other part of the north central United States, suggests that MOFEP may be more amenable to storing C through management and conservation efforts than other systems that store more C in live tree.

2.6 Conclusions

Forest harvest affected major C pool sizes in Missouri Ozarks. Currently, mineral soil C pool increased 13.5% in the UAM stands, while detritus increased 176% in the EAM stands. However, there were no significant impacts of forest harvesting on forest floor and roots C pools. Soil N was positively correlated with soil C in the UAM and EAM stands, while soil temperature was negatively correlated with live tree C in the UAM stands. Nonetheless, our initial data showed that mineral soil C in the UAM stands was higher than other treatments, which indicated that detailed soil C chemistry studies with replication across a greater range of forest ages would be useful to determine the effects of timber extraction on C quality. Moreover, knowledge of C fraction pool sizes (e.g., acid soluble and/or acid insoluble) is needed to explore long-term logging-induced changes in C storage and C and N cycling.

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Table 2.1 Summary of mean total soil nitrogen content (N %), canopy coverage (CC %), soil moisture (SM %), and soil temperature (ST 5cm, ºC) at Missouri Ozark Forest Ecosystem Project (MOFEP) study area (one standard error in parenthesis). Managements include non harvest (NHM), uneven age management (UAM), and even age management (EAM). Statistically similar means ($p > 0.05$, Tukey's test) between managements have the same lowercase superscripts (i.e., a, and b).

Harvests	N (%)	CC (%)	SM (%)	ST (ºC)
NHM	0.13[a]	90.3[a]	14.9[a]	18.1[a]
	(0.01)	(0.4)	(1.1)	(0.1)
UAM	0.14[a]	91.2[ab]	13.3[a]	20.7[b]
	(0.01)	(0.4)	(0.7)	(0.3)
EAM	0.18[b]	92.03[b]	19.3[b]	20.9[b]
	(0.01)	(0.3)	(1.2)	(0.2)

Table 1.2 The mean C pool sizes (Mg C ha^{-1}) by harvest managements at Missouri Ozark Forest Ecosystem Project (MOFEP). Management abbreviations are same as table 2.1. One standard error is in parenthesis.

		NHM	UAM	EAM
Live trees	Foliage	1.32 (0.06)	1.04 (0.10)	0.14 (0.02)
	Branch	18.44 (1.14)	12.96 (0.95)	1.22 (0.26)
	Stem	60.42 (3.15)	41.05 (3.74)	4.01 (1.17)
	Sum	80.18	55.05	5.37
Roots	Coarse	17.50 (7.50)	10.96 (5.94)	9.31 (2.31)
	Fine	2.09 (0.28)	4.38 (0.38)	4.99 (1.50)
	Sum	19.59	15.34	14.30
Coarse woody debris (CWD)	Snags	5.18 (1.01)	6.21 (1.78)	0.28 (0.19)
	Dead down tree	17.70 (4.51)	26.54 (6.53)	48.92 (5.73)
	Sum	22.88	32.75	49.20
Forest floor litter		5.91(0.36)	5.96 (0.63)	5.73 (0.49
Soil	Top 15cm	53.66(2.91)	60.91(3.43)	55.41 (2.80)
	Grand total	182.22	170.01	130.01

Table 2.2 The analysis of variance of carbon pools at Missouri Ozark forest ecosystem (P = 0.05, N is number of samples).

		Management		
		F-value	P value	N
Living tree	Foliage	54.51	<0.01	36
	Branch	58.57	<0.01	36
	Stem	55.96	<0.01	36
Coarse woody debris (CWD)	Snag	3.25	0.06	36
	Dead down tree	8.99	<0.01	36
Forest floor		0.19	0.82	216
Roots	Coarse	2.83	0.14	9
	Fine	0.58	0.59	36
Soil	Top 15 cm	4.63	<0.02	144

Table 2.3 The overall results of canonical correlation analysis of C pool variables verses microclimatic (soil moisture (SM %) and soil temperature (ST ºC)) and site (canopy coverage (CC %) and soil nitrogen content (N %)) variables and standardized canonical coefficients of the first (U_1, V_1) and second (U_2, V_2) components.

Pair of Canonical Components	Canonical correlation	Total variance explained	P value
(U_1, V_1)	0.92*	0.78	< 0.001*
(U_2, V_2)	0.76*	0.21	0.001*

C pool variables	Live tree	Detritus	Forest floor	Soil C
U_1	-0.11	-0.08	0.01	0.98†
U_2	-0.99	0.01	0.08	-0.16

Microclimatic and site variables	Soil N (%)	CC (%)	SM (%)	ST (ºC)
V_1	0.99†	-0.16	-0.18	-0.31
V_2	0.25	0.31	0.36	0.63

* denotes significant canonical correlation at the 95% level;

† denotes significant inter-correlation between C pool and microclimatic and site variables at the 95% level;

Table 2.4 The standardized canonical coefficients of C pool variables verses microclimatic and site variables for the first and second components by management. Management abbreviations are same as table 2.1. Microclimatic and site variables' abbreviations are same as table 2.4.

	C pool variables	Live tree	CWD	Forest floor	Soil C
NHM	U_1	0.02	0.13	-0.06	1.00†
	U_2	0.83	-0.38	-1.08†	0.22
UAM	U_1	-0.07	-0.06	-0.20	1.03†
	U_2	1.31†	0.40	0.11	0.45
EAM	U_1	-0.39	-0.06	0.78†	0.24
	U_2	0.60†	-0.11	-0.42	0.77

	Microclimatic and site variables	Soil N (%)	CC (%)	SM (%)	ST (ºC)
NHM	V_1	1.07†	0.20	0.38	0.02
	V_2	0.78	1.33†	-0.56	0.68
UAM	V_1	0.80†	-0.12	-0.18	-0.26
	V_2	-0.45	0.54	-0.21	-0.66†
EAM	V_1	0.67†	0.93	-0.35	0.73
	V_2	0.46	-0.95†	-0.12	-0.41

† denotes significant inter-correlation between C pool and microclimatic and site variables at the 95% level.

Table 2.5 Stem density and basal area of different forest types measured at diameter breast height (DBH) and live tree C (Mg C ha^{-1}) relative to this study

Forest type	DBH (cm)	Stem density (N ha^{-1})	Basal area (m^2 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
8 years old stands (Missouri)	>3.8	519	2.0	This study
Forest type/age	Live tree C (Mg C ha^{-1})			
Oak-hickory, 35-92 years Missouri		51		Rochow 1974
Conterminous U.S.		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

Figure 2.1 The conceptual model of inter-correlation between carbon pools and microclimatic and site variables under timber harvest regimes at a Missouri Ozark forest ecosystem. The dished arrow lines are inter-correlation between carbon pools and their affected/affecting factors. The solid arrow lines are the interactions among carbon pools, and interactions among microclimatic and site variables.

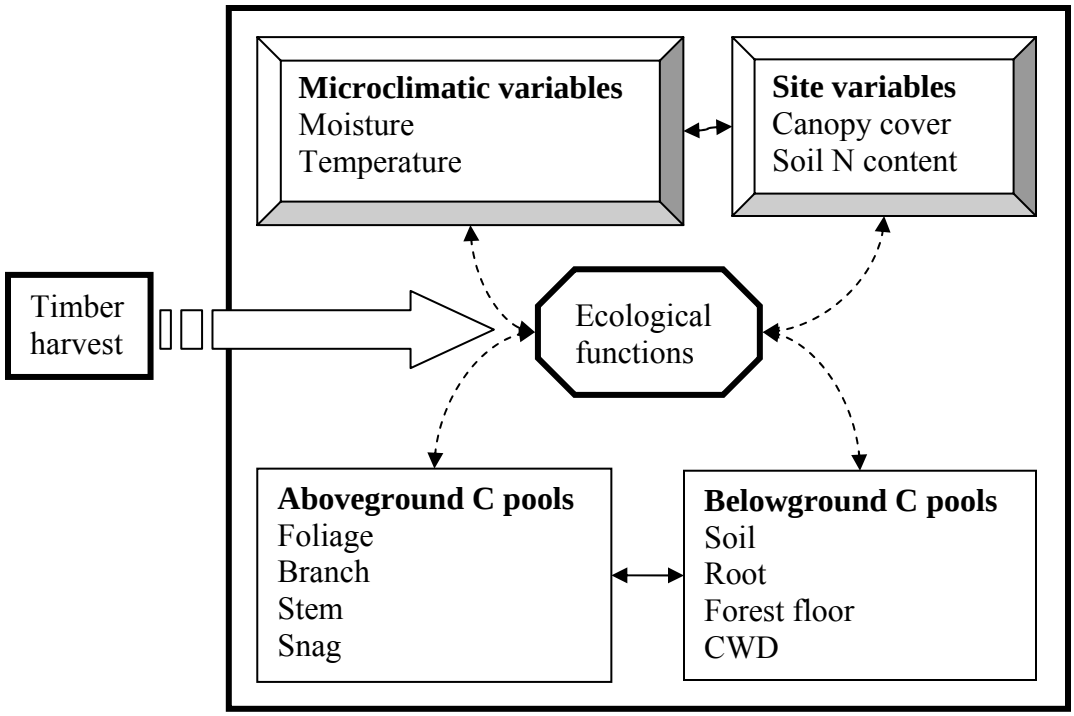


Figure 2.2 The location and timber harvest management in the Missouri Ozark Forest Ecosystem Project.

Figure 2.3 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 MOFEP between pre- and post-harvest. Harvests were non harvest management (NHM), singletree - uneven age management (UAM), and clear cut - even age management (EAM). The pre-harvest year was 1995, and the post-harvest year was 2003. Error bars are ± one standard error. Statistically similar means ($p > 0.05$, Tukey's test) are represented with identical uppercase letters (i.e., A, B, and C) and lowercase letters (i.e., a, and b) for among managements and between pre- and post-harvest within each management, respectively.

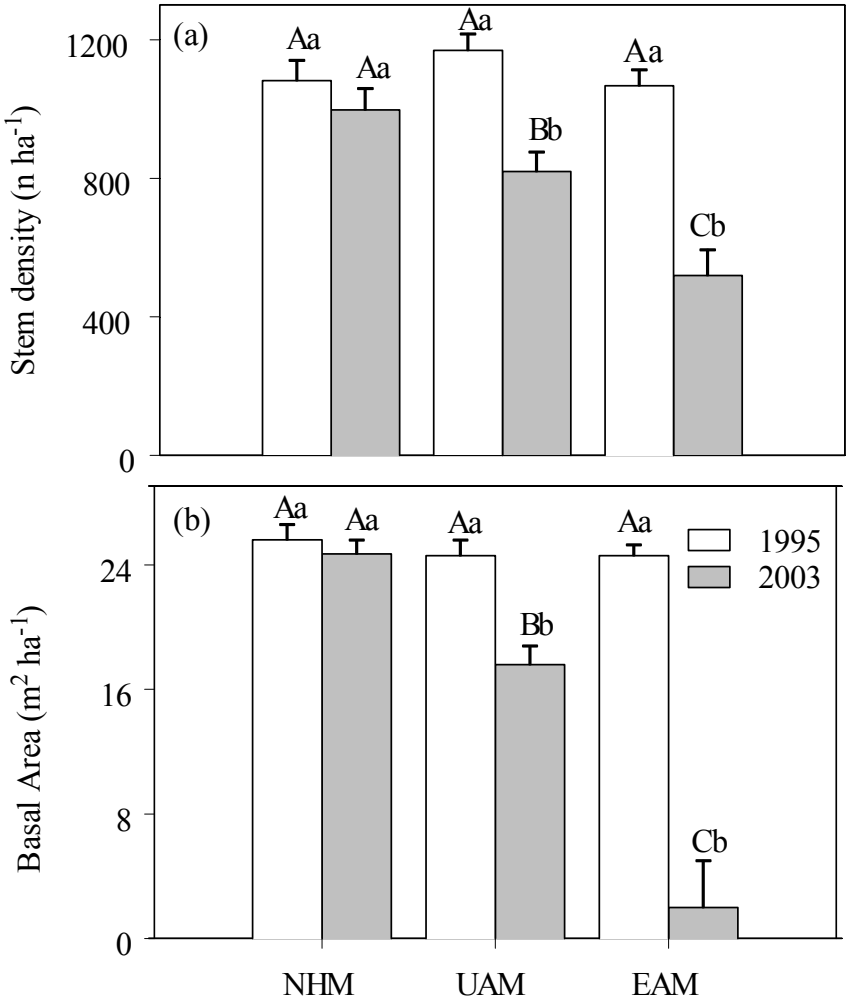
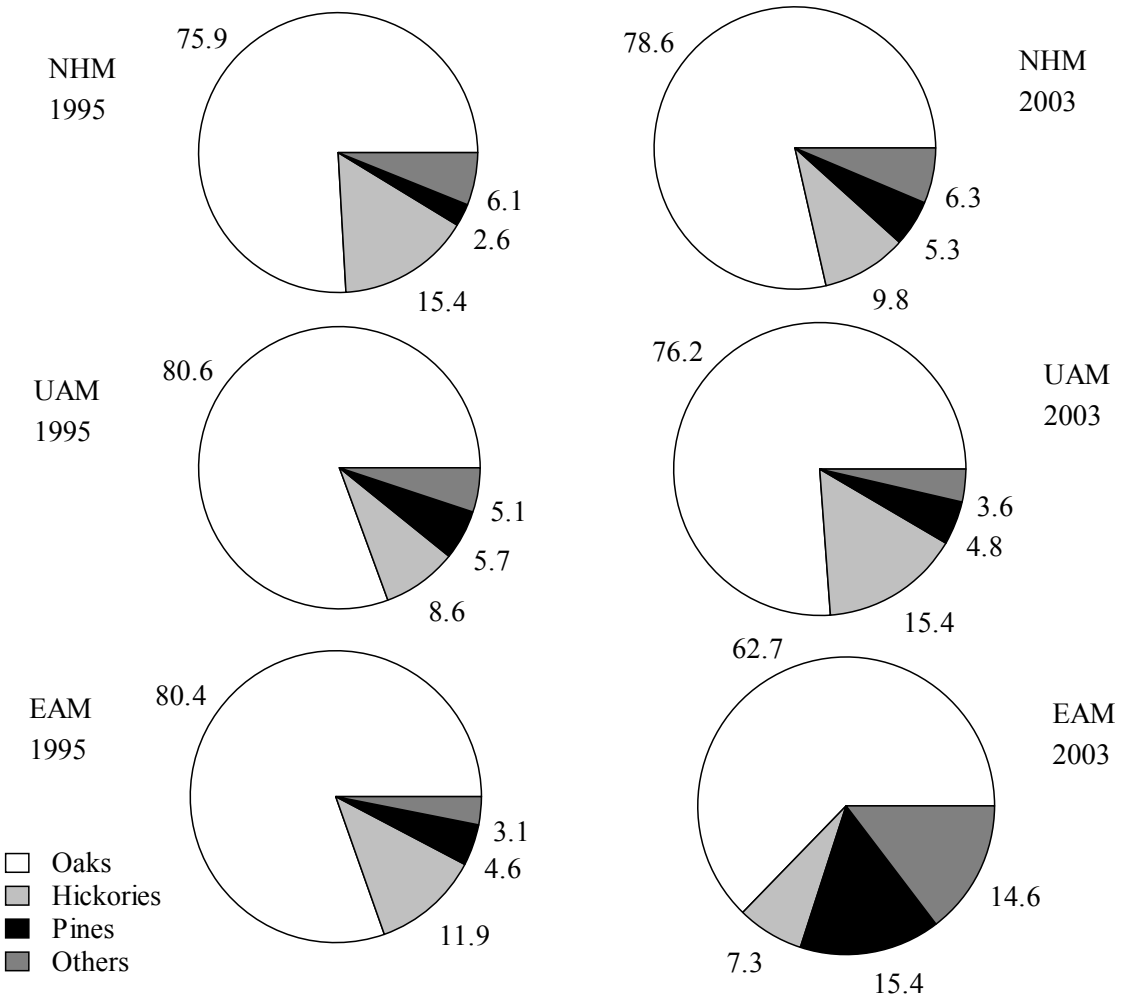


Figure 2.4 The percentage of pre- (1995) and post-harvest (2003) species basal area composition distributed at MOFEP. Management abbreviations were same as Figure 2.3. Species groups are oaks (*Quercus spp*), hickories (*Carya spp*), shortleaf pine (*Pinus echinata*) and others.



Chapter 3 Mixed Litter Decomposition in a Managed Missouri Ozark Forest Ecosystem

Abstract

I monitored the decomposition of mixed leaf litter (*Quercus spp, Carya spp, and Pinus echinata*) in a Missouri Ozark forest 8 years after experimental manipulation. Leaf litter mass losses and changes in carbon chemistry (extractive, acid soluble, and acid insoluble fractions) of litter were measured after 32 months in field incubations to determine the effects of litter composition and stand manipulation on decomposition and nitrogen (N) concentration in the remaining litter. The coefficient of decay (*k*) over this period ranged between 0.39 (±0.006) and 0.51 (±0.009) yr^{-1} for oak, oak-hickory, and oak-pine litter. There were significant main effects of stand manipulation ($p = 0.03$) and litter type ($p < 0.01$) on decay. Mass losses of oak and oak-hickory litter were 7% ($p = 0.02$) and 4% ($p = 0.04$) higher on harvested stands than controls, respectively. Mass loss of oak-hickory litter was 3% faster than oak-pine ($p = 0.03$), and 6% faster than oak ($p = 0.02$) litter on control stands, whereas the oak-hickory litter mass loss was 5% higher than that of oak litter in harvested stands ($p = 0.01$). The decay constant (*k*) had a linear relationship with initial leaf litter nitrogen content cellulose to N ratio. The nitrogen concentration in remaining litter had a linear relationship to cumulative mass loss. In summary, this study demonstrated significant effects of timber harvest and litter

composition on decomposition and N dynamics in a managed Missouri Ozark forest.

3.1 Introduction

Recent studies have shown inconsistent responses in litter decomposition to timber harvest. Some studies have reported increased decay (Gadgil and Gadgil 1978, Prescott et al. 1993), others showed decreased decay (Yin et al. 1989, Prescott et al. 2000), and yet others reported no effect (Wallace and Freedman 1986, Prescott 1997). Timber harvest can change litter decomposition by altering microclimatic conditions of the forest floor (Brosofske et al. 1997), leaf litter biochemistry (Forkner and Marquis 2004), and composition of the microorganism community (Salminen and Haimi 1997, Cortez 1998). Indeed, climate, litter chemistry, and soil organisms have been considered, in order of declining effect, the major factors controlling decomposition (Meentemeyer 1978, Lavelle et al. 1993). Within this context, the effect of timber harvest on decomposition partly depends on the regional climate (Yin et al. 1989). In a cold climate, warmer soil temperatures following a timber harvest may facilitate decomposition, whereas timber harvest in a warm climate may hamper decomposition by reducing the moisture content of surface organic matter (Keenan and Kimmins 1993, Antos et al. 2003). However, few studies have explicitly examined the combined effects of selective timber harvest and leaf litter mixture on decomposition within a particular climatic regime.

The decomposition of leaf litter mixtures recently has become an active research area because it mimics the nature of leaf litter in most forests (Blair et al. 1990) and provides insight to leaf litter interactions during decomposition (Gartner and Cardon

2004). Experimental tests, however, have not shown consistent results (Rustad and Cronan 1988, Taylor et al. 1989, Fyles and Fyles 1993). Some researchers reported that mixing litter types in mixed wood forests hasten decomposition. For example, Taylor et al. (1989) reported faster decomposition (after the initial leaching phase) of aspen (*Populous tremuloides*) litter when mixed with green alder (*Alnus crispa*). Fyles and Fyles (1993) found red alder (*Alnus rubra*) leaves facilitated Douglas-fir (*Pseduotsuga menziesii*) needles decomposition, whereas Rustad and Cronan (1988) reported that mixtures of white pine (*Pinus strobes*), red spruce (*Picea rubens*), and red maple (*Arcer rubrum*) decomposed faster than pure litter of any of these species. In contrast, Thomas (1968) found no difference in the 1st year decomposition rate of loblolly pine (*Pinus teada*) needles when mixed with flowering dogwood (*Cornus florida*) leaves. Klemmedson (1992), also reported no effect of mixing litters of gambel oak (*Quecus gambelii*) and ponderosa pine (*Pinus ponderosa*) on decomposition rate. Similarly, Prescott et al. (2000) found that mixing needle litter of white spruce (*Picea glauca*), Douglas-fir (*Psudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) with broadleaf litter of trembling aspen (*Populus tremuloides*) and red alder (*Alnus rubra*) was unlikely to hasten decomposition in mixed wood forests of British Columbia. Finally, Gartner and Cardon (2004) concluded that interactions of litter from different species in an ecosystem not only affected composite decomposition rates, but also influenced the structure and activity of the decomposer community. Thus, patterns of mixed litter decomposition are not predicable, but a better understanding of the factors affecting mixed litter decomposition is needed to better manage forest floor litter.

General models of litter decay predict that decomposition rate is determined by the quality of litter (soluble fraction, cellulose, and lignin) and nitrogen availability under comparable climatic regimes (Berg and Cortina 1995, Osono and Takeda 2004, Fioretto et al. 2005, Osono and Takeda 2005). For example, initial lignin-to-N ratio is regarded as one of the most important factors that mediate decay (Melillo et al. 1982, McClaugherty et al. 1985, Limpens and Berendse 2003), but this relationship is highly variable between litter types and even during decomposition within a single litter type. Thus, a detailed investigation of high lignin content litter decomposition may provide insight to interactions between controlling factors and litter types during decay.

Of importance to both site fertility and decomposition, the dynamics of N in decaying litter varies by plant species and with initial N concentration (Berg and Staaf 1980, Berg and Cortina 1995). In the past decade, a number of models have been proposed to predict the amount of nitrogen released from decaying litter (Melillo et al. 1982, Staaf and Berg 1982, Aber et al. 1990). For example, Berg and Staaf (1980) noted a linear increase in N concentration with litter mass loss, and Berg and Cortina (1995) found that the initial N concentration had a profound influence on the rate of increase in N concentration. Holub and Lajtha (2003) found a quadratic linear relationship between N concentration and cumulative mass loss of epiphytic lichen, whereas McClaugherty et al. (1985) found no pattern in the amount of N accumulated in decomposing sugar maple leaves under different N fertilized stands. These observations have been largely from studies of decomposition of single-species of needles and deciduous leaves. However, patterns of nitrogen release could be very different from leaf litter mixtures. Thus, investigating N dynamics during decomposition of mixed litter may increase

understanding of nutrient dynamics under more realistic conditions for mixed species forests.

The purpose of the present study was to (1) evaluate the mass loss patterns of litter mixes and their C fractions during decay, (2) investigate the effects of timber harvest on subsequent, mixed litter decay, and (3) evaluate changes in N concentration during mixed litter decay.

3.2 Study site

This study was conducted at the Missouri Ozark Forest Ecosystem Project (MOFEP) (Brookshire and Shifley 1997, Shifley and Brookshire 2000, Shifley and Kabrick 2002) site, on single-tree selected harvest and control stands. MOFEP is located in the southeastern Missouri Ozarks (91°12′ W and 37° 06′ N). This area is primarily mature upland oak, oak-hickory and oak-pine communities (Brookshire and Shifley 1997, Xu et al. 2004). Dominant oak species are *Q. alba* (white oak), *Q. velutina* (black oak), and *Q. cocinea* (scarlet oak), whereas *C. cordiformis* (bitternut hickory) and *C. glabra* (pignut hickory) are dominant hickory species, and *P. echinata* (shortleaf pine) is the only pine species in this area. MOFEP receives an annual average 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).

3.3. Methods

3.3.1. Timber harvest treatment

The single-tree harvest treatment was implemented at MOFEP on uneven age management sites in the fall of 1996. These sites ranged from 266 to 527 ha, and were chosen according to forest age, vegetation, and soil composition. Specifics of site selection are detailed in Brookshire et. al. (1997) and Sheriff and He (1997). In brief, the harvest goal was to generate a stand composition of 10% seedlings, 20% of trees 6-14 cm DBH, 30% trees of 14-29 cm DBH, and 40% of trees >29 cm DBH (Brookshire and Shifley 1997). The control sites were not subjected to harvest, but still experience wildfires and large-scale insect outbreaks, and resemble "old growth" management in this project (Sheriff and He 1997). Prior to MOFEP, no harvesting had occurred on these sites since 1950 and most of the overstory trees were 50-70 years old (Forkner and Marquis 2004).

3.3.2 Litter bag experiments

Three stands of oak, oak-hickory, and oak-pine were selected at each of three replicated harvest and control stands, for a total of 18 stands. Leaf litter was collected in the autumn of 2002 with litter traps. The litter for our study was mixed according to average basal area of each stand, i.e., litter was 100% oak leaves, oak-hickory litter was 80% oak leaves and 20% hickory leaves, and oak-pine litter was 70% oak leaves and 30% pine needles. The litter bags (10 x 10 cm) were constructed of fiber-glass window screening and filled with 5 grams of air dried mixed leaf litter. About 10 grams of each

mixed litter type was sub-sampled to calculate an oven vs. air dry weight ratio and to perform an initial chemical analysis. Litter bags (a total of 360) were deployed during the autumn of 2002, in the same stands of litter collection. Four bags at each plot were collected in February, May and August 2003, May 2004, and June 2005. The remaining litter in each bag was oven-dried at 65ºC to a constant weight.

3.3.3 C chemistry assays

The oven dried litter was ground in a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 0.5mm sieve. A modification of methods described by Moorhead and Reynolds (1993) was used to determine the fraction of each sample that was: (1) soluble in water and ethanol, (2) removed by sulfuric acid digestion, and (3) acid insoluble. Although not precisely accurate, for convenience we will herein refer to these chemical fractions as the soluble, cellulose, and lignin fraction, respectively. In brief the procedure was to place approximately 0.25 g oven-dried sample into a preweighed 25-ml centrifuge tube, add about 15-ml distilled water and place the tube in a sonicating water bath at 60 ºC for 30 min. The tube was spun at 30,000 rpm for 15 min in a high-speed centrifuge. The supernate was suctioned and the procedure repeated six times. Following water extraction, the process was repeated six times with 98% ethanol. The samples were then oven dried at 60ºC for 24 hr and weighed. The soluble content of the litter was estimated as the difference between original and extracted sample weights. To the remaining dried sample was added 2-ml 72% sulfuric acid. The sample was incubated for 1 hr at 30 ºC and 56-ml of distilled water used to transfer the material to a 125-ml flask. The flasks were autoclaved for 1 hr at 120 ºC, the sample was suctioned

onto a preweighed Millipore filter and oven dried at 60 ºC for 24 hr. The cellulose content of the sample was estimated as the difference between pre- and postacid digestion dry sample weight. The residue was put in a preweighed, aluminum tin and placed in a muffle furnace at 500 ºC for 24 hr. Containers were then weighed and ash mass recorded. The lignin content of the sample was estimated as the difference between pre- and combusted dry sample weight. The total N and C content of litter was determined with a CHN analyzer (Perkin Elmer 2400 Series II) for sub-samples from each litter bag.

3.3.4 Calculations and statistical analysis

Mass loss data for each litter type were fit to an exponential decay function for each stand:

$$M_t = M_0 e^{-kt} \qquad (3.1)$$

where M_t and M_0 are litter mass at time t and time 0, respectively, k is the decomposition constant (yr^{-1}), and t is time (yr). A value of k was computed for each plot over the complete incubation period (32 months).

Litter bags collected at subsequent dates for a given site were considered as repeated measures (Cortet et al. 2006). Mass remaining was analyzed using a two-way MANOVA (Analysis of variance with multiple variables), with stands (oak, oak-hickory, and oak-pine) and treatments (harvest and control) being fixed factors, and dates being the multiple variable (five sampling dates). Two-way ANOVA (mixtures and treatments) with comparison between means by adjusted Tukey's test was used to compare k values. Two-way ANOVA with multiple comparisons between means by adjusted Tukey's test was also used to test the initial differences in litter chemistry between litter mixes and

between treatments. Regression analysis examined the relationship between the decay constant *k* and initial nitrogen (N) concentration, C/N ratio, and cellulose/N ratios. Regressions also examined relationships between litter nitrogen concentration and cumulative mass loss. All statistical analysis were performed with SAS 9.1 (2003, Cary, NC, USA).

3.4 Results

3.4.1 Litter mass loss and initial chemistry

After 32 months of field incubation, the mixed oak-hickory and oak litter mass losses were 4 and 7% higher on harvested stands than on control stands ($p = 0.03$; Figure 3.1; Table 3.1). On the control stands, oak-hickory litter decayed significantly faster than oak and oak-pine litter over the full 32-month field incubation ($p < 0.01$); mass loss of the oak-pine litter was 5% and 9% faster than oak litter at the second (05/2003, 6-month incubation, $p = 0.02$) and last retrieval (06/2005, 32 months, $p = 0.02$). In contrast, on the harvested stands, oak-hickory litter decayed 7, 5, and 8% faster than oak litter at the first (02/2003, 3-month incubation, $p = 0.04$), third (08/2003, 9-month incubation, $p = 0.02$), and last retrieval (06/2005, 32- month incubation, $p = 0.01$; Figure 3.1). Additionally, the overall decay constant (*k*) of oak-hickory litter was 0.04 yr^{-1} greater on harvested stands than control stands ($p = 0.04$), whereas the decay constants of oak litter were 0.06 and 0.09 yr^{-1} smaller than oak-hickory litter on both control ($p = 0.04$) and harvested ($p = 0.05$) stands (Table 3.2).

The initial soluble fraction of oak-hickory litter was 9% higher at harvested than control stands ($p = 0.03$), whereas the cellulose fraction was 13% lower at harvested than

control stands ($p < 0.01$; Table 3.3). Other litter types showed no differences in chemistry between treatments. At control stands, the soluble fraction of oak-pine litter was 10% higher than oak-hickory litter ($p = 0.05$), and the cellulose fraction of oak-hickory litter was 13 and 10% higher than oak ($p = 0.04$) and oak-pine ($p = 0.01$) litter, respectively.

The initial N content of oak-hickory litter was 0.26% higher than oak-pine litter ($p = 0.04$) on control stands, but the initial chemistry of the three litter types was very similar ($p > 0.05$) at harvest stands. The cellulose/N ratios were 31.2, 30.8, and 29.1 for oak, oak-hickory, and oak-pine litter, respectively (Table 3.3).

The regression analysis of decay rate as a function of initial litter N concentration (Figure 3.2a), cellulose/N ratio (Figure 3.2b), and C/N ratio (Figure 3.2c) showed that the cellulose/N ratio was a significant predictor for all three litter types, with R^2 values of 0.84, 0.95, and 0.85 for oak, oak-hickory, and oak-pine litter, respectively (Table 3.4). The initial N concentration was a good predictor of *k* for oak litter ($R^2 = 0.94$, $p = 0.01$), while C/N ratio was a significant predictor for *k* in oak ($R^2 = 0.85$, $p = 0.01$) and oak-pine litter ($R^2 = 0.75$, $p = 0.02$; Figure 3.2; Table 3.4).

3.4.2 Carbon fraction dynamics

The changes in mass and C fractions of each litter type showed similar trends during decay (Figure 3.3). First, loss of the soluble fraction dominated overall mass loss at the beginning of incubations. For example, the total mass loss of oak litter was 29% after 9-months, of which 24% was from the soluble fraction (Figure 3.3a). In oak-hickory litter, the soluble fraction contributed 15% of the total of 17% mass loss after 3-

months (Figure 3.3b). Finally, in oak-pine litter the soluble fraction contributed 17% of a total of 22% mass loss after 6-months (Figure 3.3c). After rapid loss of soluble fraction, loss of the cellulose fraction dominated litter mass loss over longer periods. In oak litter, the cellulose fraction declined 13% between 9 and 19-months, which accounted for 63% of the total mass loss. In oak-hickory litter, both the soluble and cellulose fractions made the same contribution to the total mass loss between 3 and 19-months (41%). However, in oak-pine litter, the loss of cellulose loss constituted about 41% of the total mass loss between 6 and 19-months. Finally, the lignin fraction slowly degraded during the 32-month field incubation, declining about 9, 9, and 10% from oak, oak-hickory, and oak-pine litters, respectively, during the 32-month field incubation (Figure 3.3).

3.4.3 Nitrogen concentration dynamics

The concentration of N in remaining litter increased throughout decomposition, increasing as much as 2.5 times from the initial values to final concentrations (Figure 3.4). The N concentration in remaining oak, oak-hickory, and oak-pine litter showed strong linear relationships with cumulative mass loss (Table 3.5). Furthermore, the three litter types showed similar trends in N accumulation (Figure 3.4; Table 3.5).

3.5 Discussion

In this study we found that mixed oak and oak-hickory litter decayed faster in harvested stands than control stands. This is consistent with earlier reports that timber harvest enhances litter decomposition by altering temperature and moisture conditions at the forest floor (Keenan and Kimmins 1993, Antos et al. 2003). In our study sites, higher

soil moisture content or greater leaching may have occurred at harvested than control stands, but both types of stands had similar soil and air temperatures during the field incubation (Li et. al., unpublished data). Indeed, oak-hickory litter had significantly higher soluble content on harvested than control stands (Table 3.3), which may have resulted in greater leaching losses. Furthermore, harvest-induced canopy removal may increase physical impacts of heavy throughfall drops on the forest floor litter, which can mechanically disrupt litter and result in faster decomposition, as observed at harvested stands (Yin et al. 1989). In contrast, neither the soluble content nor mass loss of oak-pine litter was significantly different between the control and harvested stands. Therefore, the physical structure of pine needles may be more resistant to mechanical disturbance.

Mixed oak-hickory litter decomposed faster than that of oak and oak-pine litter mixtures in our study sites This agreed with previous studies that litter mixtures could generate synergistic effects (Gartner and Cardon 2004). Gartner and Cardon (2004) attributed the interactions among adjacent litters from different species during decomposition to the physical, chemical, and biological processes individually or in combination. The specific leaf area of hickory leaves (142.7 cm^2 g^{-1}) was higher than oak leaves (125.5 cm^2 g^{-1}; Martin et al. 1998), the mixing would increase the total oak-hickory mixed litter leaf area. While the litter surface where decomposition is occurring was physically altered and increased by the hickory and oak litter mixing (Hector et al. 2000). In contrast, the pine needles have less leaf area, but they have different chemical contents than the oak and/or the hickory leaves (Berg and Staaf 1980, Berg et al. 1982). The mixing of pine needles with broadleaves may directly influence decomposition rates through relocating the nutrients and secondary chemicals among litter types or by

enhancing decomposer activity (Taylor et al. 1989, Fyles and Fyles 1993, McTiernan et al. 1997). Furthermore, some researchers also reported that nutrients released from rapidly decaying, higher quality litter could stimulate decay in adjacent, more recalcitrant litters (Fyles and Fyles 1993, McTiernan et al. 1997). However, the oak leaves have the similar leaf area with the same weight of leaves among species, and they also have the similar chemical contents. Therefore, the mixing of oak litter did not enhance decay rate. Furthermore, some researchers also found that the litter mixing affected decomposers abundance and activity (Hansen and Coleman 1998, Hansen 1999, Wardle 2002). Thus, physical changes in leaf mixes would influence decomposition rates both directly or indirectly through the decomposer community and its activities.

Not surprisingly, we found that litter decomposition rates were significantly related to initial cellulose/N ratios. This agreed with many reports that cellulose content was a facilitator of litter decomposition (McClaugherty and Berg 1987, Fog 1988). In contrast, the initial lignin/N ratio exerts a strong negative influence on the rate of decomposition (Melillo et al. 1982), with an initial lignin to N ratio of about 29:1 considered critical for tissue decomposition (Melillo et al. 1982). If lignin/N ratios were greater than 29:1, decomposition would not likely occur without N input via fixation, absorption of atmospheric ammonia, throughfall, dust, insect frass, green litter, and/or fungal translocation (Melillo et al. 1982). However, we found no significant correlation between decomposition rate and lignin/N ratio. This may suggest that the major factor affecting decomposition shifts from lignin to cellulose in high lignin content litters.

I found that the N concentration in remaining litter increased about 0.21 to 0.23 mg g^{-1} mass loss in all three litter types. This increase was within the range reported by

Berg et al. (1999), in a synthesis of studies performed on 54 different sites with 6 different litter types, i.e., the N concentration increased between 0.08 and 0.23 mg g^{-1} litter mass loss. However, the reasons for such a strongly linear relationship between N concentration and moss lost are not clear (Berg and McClaugherty 2003), but possible explanations include an increasing N–rich microbial biomass while litter decays (Grgorich et al. 1991, Aikio et al. 2000), and/or recalcitrant tissues like lignin bind N during the late stages of decay and reduce N leaching (Berg et al. 1982). However, we were not sure which mechanism attributed to our study site, and suggest that a comprehensive, long-term experiment would be needed to evaluate the mechanisms underlying increasing N concentration with progressive litter mass loss.

3.6 Conclusions

We found that mixed oak and oak-hickory litter decomposition was increased during 32-month field incubation in a managed forest ecosystem due to timber harvest and speculate that this was the result of modified microclimatic factors (i.e., litter moisture). Furthermore, the mean decay constant of mixed oak, oak-hickory, and oak-pine was 0.41, 0.49, and 0.43 yr^{-1}, respectively, and significantly related to initial cellulose to N ratios. The oak-hickory litter had higher decomposition rate largely due to that the litter mixing increased mixed litter total leaf area, whereas oak-pine litter had a higher decomposition rate maybe due to the chemical contents mixtures between oak leaves and pine needles. The N concentration in remaining litter was a linear function of mass loss in all three mixed litter types. Therefore, both litter decay and nitrogen dynamics are affected by timber harvest and litter type in Missouri Ozark forests.

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Table 3.1 Results of MANOVA comparing litter mass remaining at different times, between treatments, and among litter types (oak, oak-hickory, and oak-pine; two way MANOVA with repeated measures on 54 samples, litter types and treatments were varying factors for each sampling date)

	df	F	P
Between subject			
Litter type	10	5.14	<0.01
Management	5	2.69	0.03
Litter type x managment	10	5.02	<0.01
Within subject			
Time	4	1072	<0.01
Time x litter type	8	2.25	0.03
Time x management	4	1.58	0.20
Time x litter type x management	8	4.89	<0.01

Analysis of variance with multiple variables (see text for more explanation).

Table 3.2 Estimates of decay rate coefficient (k, yr^{-1}) for the oak, oak-hickory, and oak-pine mixed litter decomposing on control and harvested stands at the Missouri Ozark mixed forest ecosystem. One standard error was in parenthesis. Statistically similar ($p > 0.05$) means with the same lowercase letter are not different between litter types within the treatment, whereas statistically similar means with the same upper case letter are not different for a litter type between treatments.

	Oak	Oak-hickory	Oak-pine
Control	0.39^{Aa}	0.47^{Ab}	0.41^{Aab}
	(0.006)	(0.006)	(0.037)
Harvest	0.42^{Aa}	0.51^{Bb}	0.44^{Aab}
	(0.027)	(0.009)	(0.028)

Table 3.3 Percentage nutrient content and chemical fractions of initial oak, oak-hickory, and oak-pine mixed litter at the Missouri Ozark forest ecosystem. One standard error was in parenthesis. Statistically similar ($p > 0.05$) means with the same lowercase letter are not different between litter types within the treatment, whereas statistically similar means with the same upper case letter are not different for a litter type between treatments.

	Control			Harvest		
	Oak	Oak-hickory	Oak-pine	Oak	Oak-hickory	Oak-pine
Solubles *	40.89^{Aab}	36.61^{Aa}	47.04^{Ab}	43.83^{Aa}	45.37^{Ba}	45.33^{Aa}
	(4.17)	(3.08)	(2.64)	(2.21)	(1.74)	(2.76)
Cellulose †	31.76^{Aa}	41.74^{Ab}	28.55^{Aa}	32.20^{Aa}	29.04^{Ba}	30.67^{Aa}
	(2.50)	(1.69)	(2.29)	(0.49)	(0.68)	(2.16)
Lignin ‡	27.35^{Aa}	24.65^{Aa}	24.40^{Aa}	24.00^{Aa}	25.59^{Aa}	24.00^{Aa}
	(1.69)	(1.41)	(2.64)	(2.01)	(1.36)	(0.70)
C	49.59^{Aa}	49.10^{Aa}	50.61^{Aa}	48.84^{Aa}	47.87^{Aa}	49.85^{Aa}
	(0.73)	(0.99)	(0.39)	(0.36)	(0.09)	(0.85)
N	1.00^{Aab}	1.20^{Ab}	0.94^{Aa}	1.08^{Aa}	1.11^{Aa}	1.22^{Aa}
	(0.01)	(0.07)	(0.06)	(0.13)	(0.11)	(0.28)

Note: values are given as mean, with one standard error in parentheses (n = 3).

* Soluble (%) in hot water and ethanol.

† Soluble (%) in sulfuric acid (72%), ~cellulose.

‡ Insoluble (%) in sulfuric acid (72%), ~lignin.

Table 3.4 Regression analyses for decay constant *k* (yr^{-1}) versus initial litter nitrogen concentration (mg g^{-1}), cellulose/N ratio, and C/N ratio by litter types at the Missouri Ozark mixed forest ecosystem.

		Slope	Intercept	F	R^2	P
Oak	Initial [N]	0.216	0.180	59.54	0.94	0.01
	Cellulose/N	-0.006	0.591	21.54	0.84	0.01
	C/N	-0.004	0.607	23.34	0.85	0.01
Oak-hickory	Initial [N]	0.033	0.452	0.24	0.06	0.65
	Cellulose/N	-0.004	0.603	84.37	0.95	0.01
	C/N	-0.001	0.534	0.25	0.06	0.64
Oak-pine	Initial [N]	0.119	0.299	6.32	0.61	0.06
	Cellulose/N	-0.007	0.626	72.44	0.85	0.01
	C/N	-0.004	0.620	11.76	0.75	0.02

Table 3.5 Regression analyses for nitrogen concentration (mg g^{-1}) and cumulative mass loss (%) in remaining litter by litter types at the Missouri Ozark mixed forest ecosystem.

	slope	Intercept	F	R^2	P
Oak	0.231	9.24	251.33	0.88	<0.01
Oak-hickory	0.213	10.57	130.11	0.79	<0.01
Oak-pine	0.211	8.68	187.59	0.85	<0.01

Figure 3.1 Percent of original oak, oak-hickory, and oak-pine litter mass remaining in the control and harvested stands at each collection date (mean ± one standard error). The same upper case letters represent statistically similar ($p > 0.05$) means between treatments within the same retrieval date, whereas the same lowercase letters represent statistically similar means within the same retrieval date between litter types.

Figure 3.2 Linear relationships between decay constant k (yr^{-1}) and initial litter N concentrations (mg g^{-1}; a), cellulose/N ratio (b), and C/N ratio (c). Solid, long-dashed, and short-dashed lines represent oak, oak-hickory, and oak-pine litter mixes, respectively. Bars represent one standard error.

Figure 3.3 Stack plot of percent original mass of lignin + cellulose + soluble = total litter mass remaining (LMR) in oak (a), oak-hickory (b), and oak-pine (c) litter during decomposition. Bars indicate one standard error.

Figure 3.4 Linear regression represents the litter N concentration as a function of cumulative litter mass loss. Solid, long-dashed, and short-dashed lines represent oak, oak-hickory, and oak-pine litters, respectively.

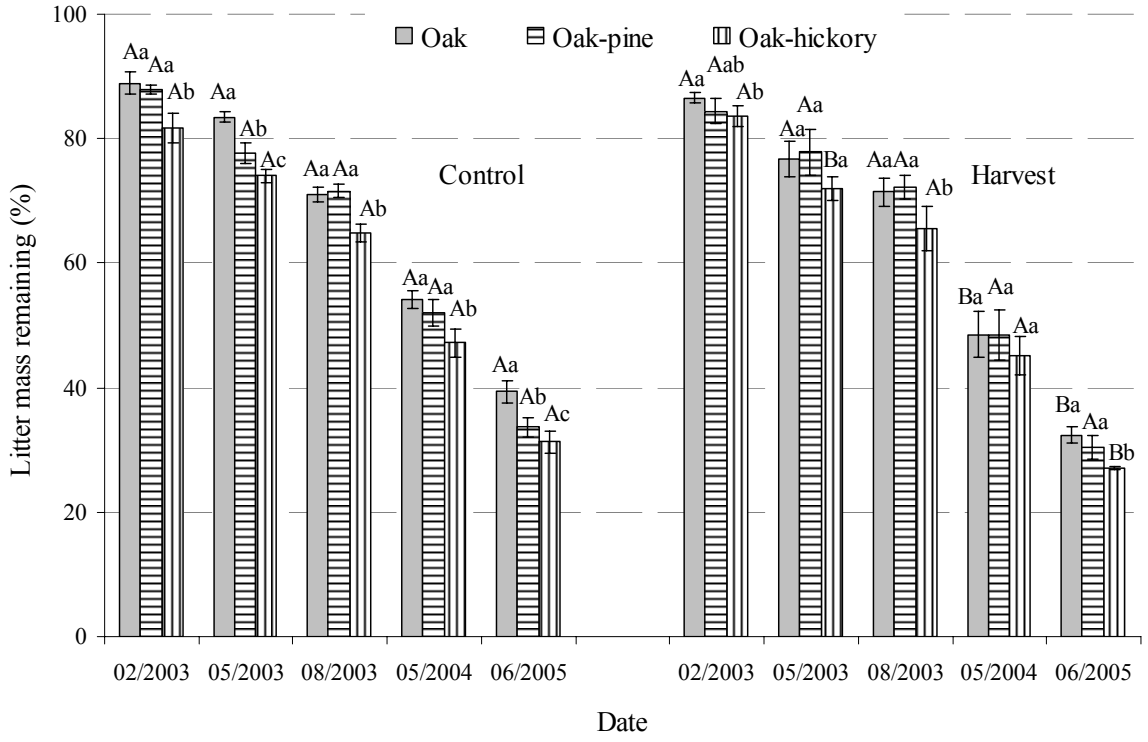
Oak
Oak-pine
Oak-hickory
Control
Harvest
Litter mass remaining (%)
Date
100
80
60
40
20
0
02/2003
05/2003
08/2003
05/2004
06/2005
Aa Aa Ab
Aa Ab Ac
Aa Aa Ab
Aa Aa Ab
Aa Ab Ac
Aa Aab Ab
Aa Aa Ba
Aa Aa Ab
Ba Aa Aa
Ba Aa Bb

Figure 3.1

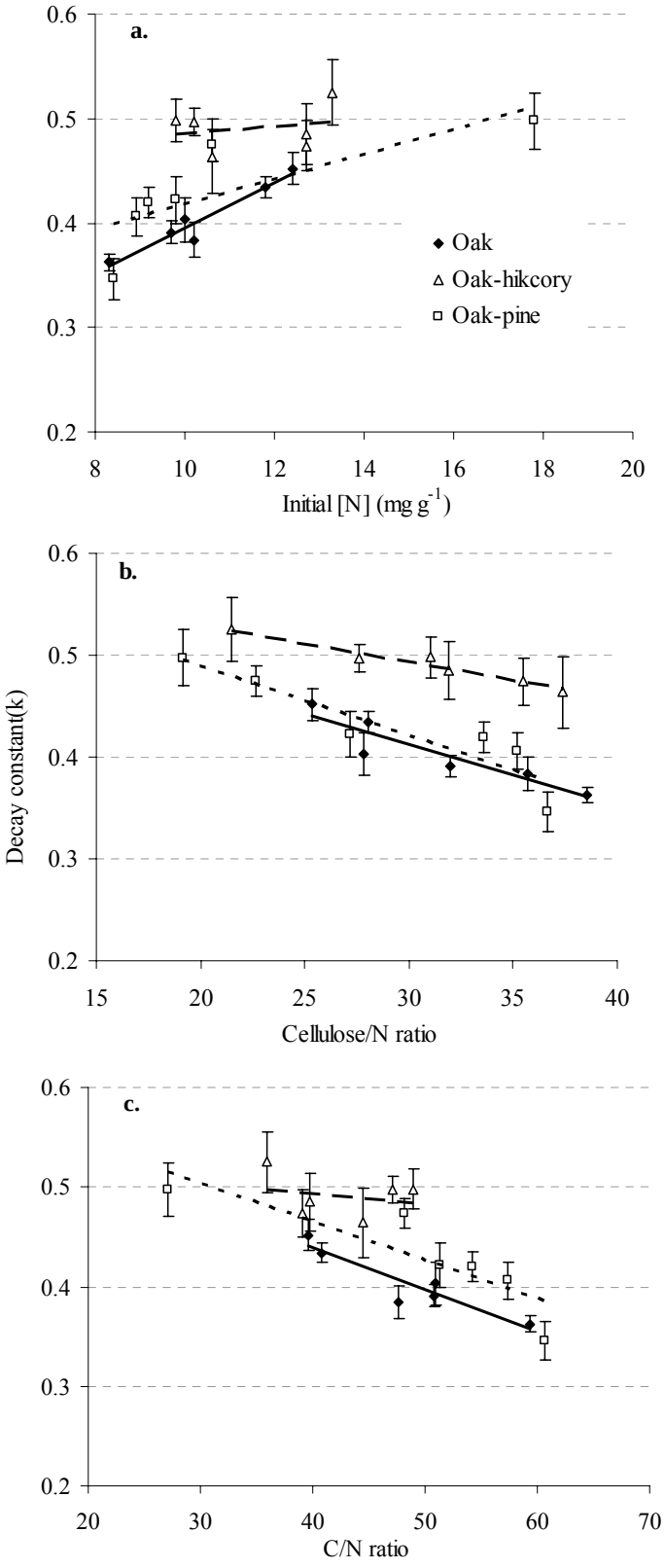
a.
0.6
0.5
0.4
0.3
0.2
8
10
12
14
16
18
20
Initial [N] (mg g-1)
Oak
Oak-hikcory
Oak-pine
b.
Decay constant(k)
15
20
25
30
35
40
Cellulose/N ratio
c.
20
30
40
50
60
70
C/N ratio

Figure 3.2

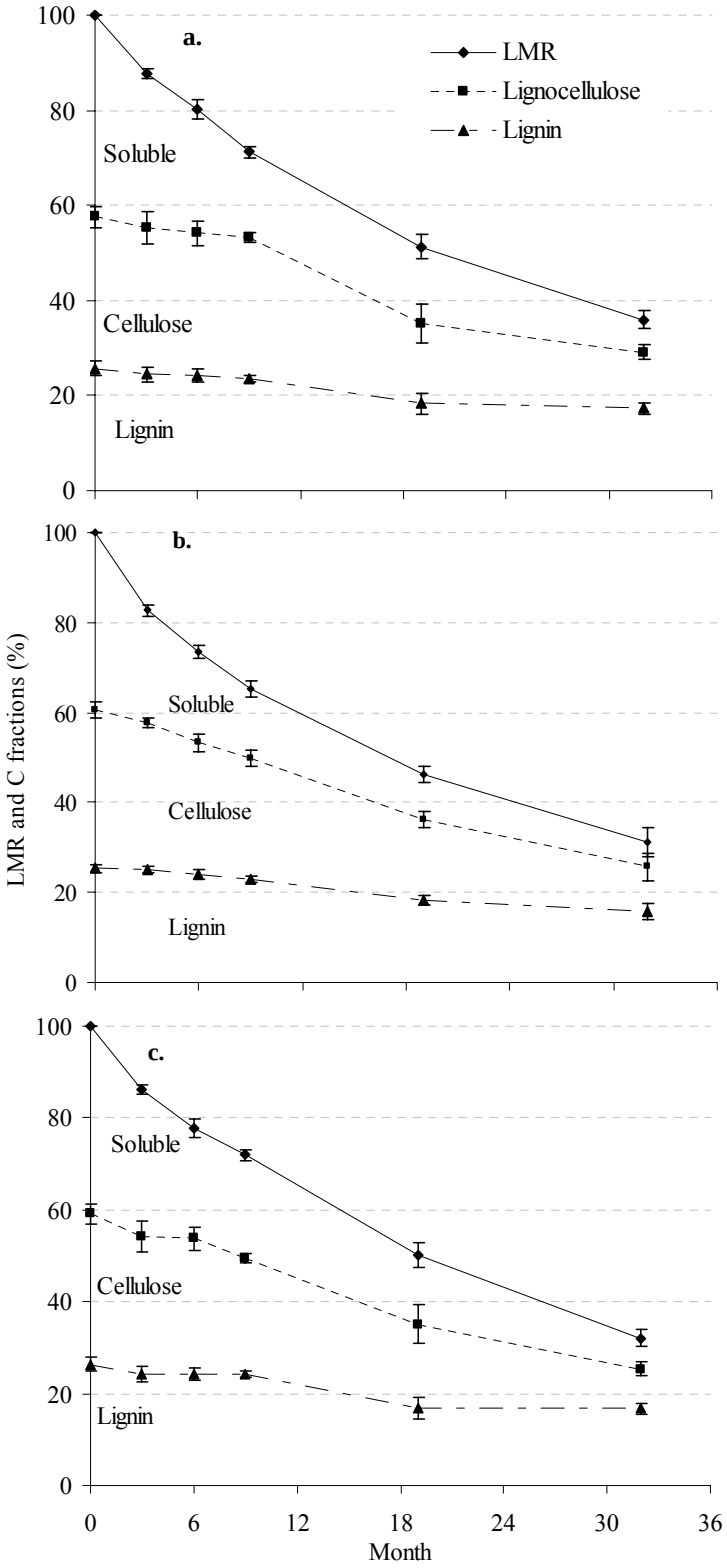
a.
b.
c.
LMR
Lignocellulose
Lignin
Soluble
Cellulose
Lignin
LMR and C fractions (%)
Month
0
20
40
60
80
100
0
6
12
18
24
30
36

Figure 3.3

1

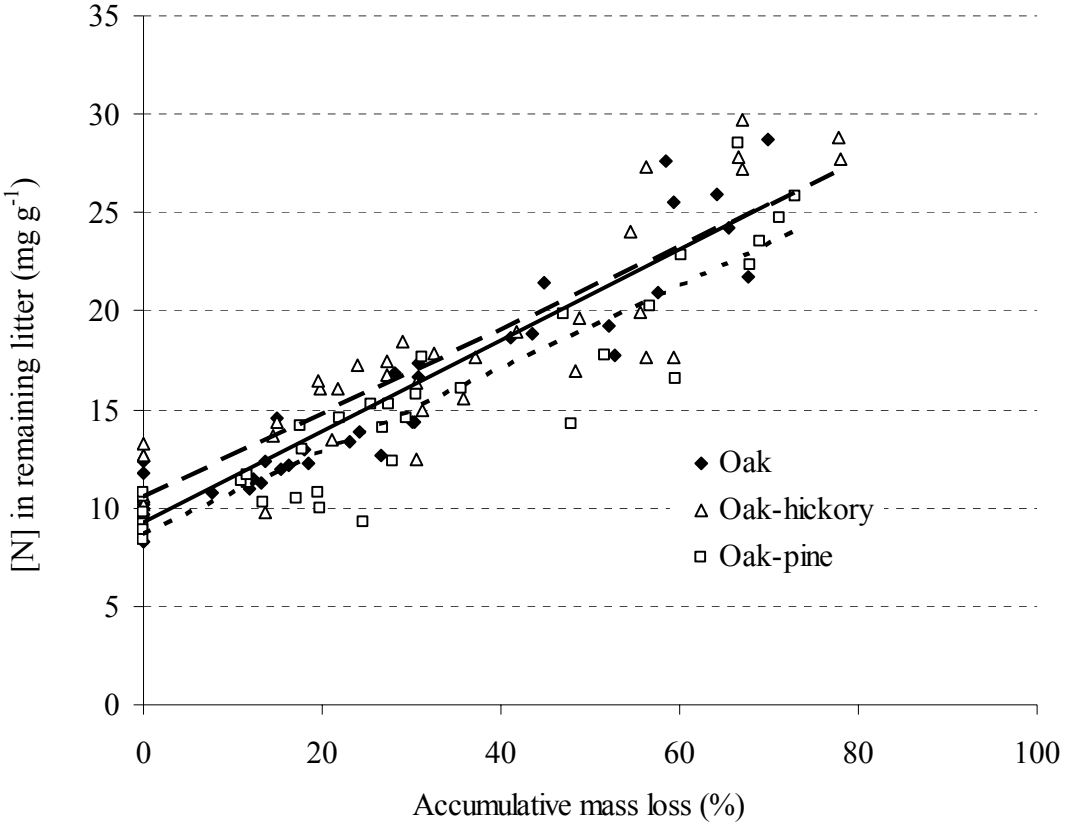
35
30
25
20
15
10
5
0
[N] in remaining litter (mg g-1)
0
20
40
60
80
100
Accumulative mass loss (%)
Oak
Oak-hickory
Oak-pine

Figure 3.4

Chapter 4 Ecosystem Respiration and its Components in a Managed Oak Forest Ecosystem

Abstract

The chamber-based method was used to collect ecosystem respiration component (i.e., leaf, sapwood, snag, down dead wood, and soil) data at varies stands in a managed oak forest ecosystem 8 years after a timber harvesting event. Three timber harvesting regimes were: non-harvest management (NHM), uneven-age management (UAM), and even-age management (EAM). I discovered that components' respiration responded exponentially to temperature. In order to estimate annual ecosystem and its components respiration, I linked environmental variables (i.e., temperature) with ecological processes to derive process based respiration models for my study site. The annual ecosystem respiration rates were 1641.7, 1690.9, and 1285.6 g C m^{-2} y^{-1} in the NHM, UAM, and EAM stands, respectively. Timber harvesting reduced annual ecosystem respiration in the EAM stands compared to that in the NHM stands by 27.7% ($p = 0.001$). Soil respiration was the largest component and contributed between 72 to 85% of the total ecosystem respiration. In the NHM stands, leaf respiration and sapwood (both about 10%) were the next largest component, followed by snag (5%) and down dead wood (2%). In the UAM stands, the second largest component was leaf respiration

(7%), and followed by stem sapwood (7%), snag (6%), and down dead wood (2%), while in the EAM stands, down dead wood (12%) was the second largest component, followed by sapwood (2%), leaf (1%), and snag (0%) because of young regrowth. The results indicted that harvesting activities influenced ecosystem processes by removing biomass, and changing the magnitude of component respiration.

4.1. Introduction

Forests are a critical component in the global carbon (C) cycle and in the process of climate change (Tans et al. 1990, Fan et al. 1998). Scientists are discovering considerable variability regarding the role of forests in the global C budget (Houghton, 1999). Forest ecosystem and its component C fluxes vary depending on vegetation age, species composition, disturbance, and local climate (Tang and Baldocchi 2005, Vogel et al. 2005, Wu et al. 2006). A forest ecosystem's net C gain or loss is represented by the small difference between the two large fluxes of photosynthesis and respiration (Goulden et al. 1996, Law et al. 1999, Curtis et al. 2005). Respiration fluxes nearly equal the input from photosynthesis, and are more important than photosynthesis in determining the variability of an ecosystems net C storage or loss at a given latitudinal gradient (Valentini et al. 2000). Therefore, to estimate changes in the C cycle in forest ecosystems accurately, this study was designed to obtain precise ecosystem component respiration. So far, only a few studies have examined all of these components (Law et al. 1999, Curtis et al. 2005, Reichstein et al. 2005).

Timber harvesting has been identified as a major influence on forest ecosystem processes (Chen et al. 2005, Amiro et al. 2006). An understanding of the ecological role

of anthropogenic disturbance regimes in the context of the C cycle will help us in the design of sustainable forest management strategies (Matthew and Grigal 1999). Furthermore, studying C fluxes with disturbance helps us to understand the changes in the functional responses of the ecosystem components (Raich et al. 2006, Sampson et al. 2006). Although a significant amount of research has been conducted in North America over the past decades, to examine the impacts of management practice on soil respiration, few studies have quantified ecosystem component respiration under different harvesting regimes. Therefore, this study quantified and compared ecosystem respiration and its components in a managed forest ecosystem.

Temperature is the primary variable driving the respiration of each ecosystem component, but additional variables may also affect respiration. For example, soil moisture is an important regulator of soil respiration when the ecosystem is under water stress conditions (Xu and Qi 2001b, Tang et al. 2005). Soil respiration may be controlled by photosynthesis in addition to environmental variables (Hogberg et al. 2001, Tang et al. 2005). Precipitation frequency and duration may affect soil respiration during and after a drought (Xu et al. 2004). Leaf respiration may be driven by temperature and related to species and leaf nitrogen content (Bolstad et al. 1999). Snags and down dead wood respiration may be driven by temperature, moisture, and decay class (Pyle and Brown 1998, Wilcke et al. 2005). It is very difficult to measure and estimate respiration components by considering all the variables, thus I used temperature as our predicting variable.

The overall objectives of this study were to quantify ecosystem respiration within a managed oak dominated mixed deciduous forest, and to partition this respiratory CO_2

flux into its primary source components of soil, sapwood, leaf, snag, and down dead wood respiration. I was interested in how different harvesting regimes affected these sources of respiratory CO_2 and how these fluxes varied inter-annually. Specifically, I wanted to: 1) measure respiration components from each stand with similar dominant species within each treatment; and 2) estimate the annual ecosystem respiration and estimate the percentage of each component at each treatment; and 3) compare ecosystem respiration components among treatments.

4.2. Study site

The study was carried out at the Missouri Ozark Forest Ecosystem Project (MOFEP) for examining the impacts of timber harvest on multiple ecosystem components (Brookshire and Shifley 1997, Shifley and Brookshire 2000, Shifley and Kabrick 2002). MOFEP is located in the southeastern Missouri Ozarks (91°12′ W and 37° 06′ N). This area is primarily mature upland oak, oak-hickory and oak-pine communities (Brookshire and Shifley 1997, Xu et al. 2004). *Q. alba* (white oak), *Q. velutina* (black oak), and *Q. cocinea* (scarlet oak) are the dominant oak species, while *C. cordiformis* (bitternut hickory) and *C. glabra* (pignut hickory) are dominant hickory species, and *P. echinata* (shortleaf pine) is the only pine specie in this area. MOFEP receives an annual average of 1120 mm of precipitation and experiences a mean annual air 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-aged management (EAM), uneven-aged management (UAM), and non-harvest management (NHM), which

includes nine forested sites, ranging in size from 266 to 527ha. Sites were chosen based on forest age, vegetation, and soil composition. Specifics of site selection are detailed in Brookshire et. al. (1997) and Sheriff and He (1997). In brief, the entire sites were randomly assigned one of the three timber harvesting regimes: EAM, UAM, and NHM. Sites were subdivided into stands, averaging 4 ha in size, of similar ecological land types (ELTs) defined by slope, aspect, vegetation composition, and soil type. At each timber harvest, 10% of forest biomass was removed, which resulted in landscapes having both harvested areas and no-harvested forest. Ten percent of the area of each EAM and UAM sites was designed as "old-growth" and not available for harvest. The remaining area was designed as: 10% seedlings, 20% trees 6-14cm in diameter at breast height (DBH), 30% trees 14-29cm in DBH, and 40% was greater than 29cm in DBH as saw timber at EAM sites. At UAM sites, the largest tree diameter objective was the same as saw timber size objective for EAM sites and the target tree size class distribution was identical to the composition size class distribution in EAM sites (Brookshire and Shifley 1997). To achieve these class distributions in EAM sites, some stands were clear-cut and others were treated with intermediate cutting following the Missouri Department of Conservation Forest Land Management Guidelines (Missouri Department of Conservation 1986), while in UAM sites, trees were removed in small groups, individually, or girdled and left standing. NHM sites were not subjected to manipulation, except for wildfires or large-scale insect outbreaks. This treatment resembled "old growth" management and served as an experimental control treatment in this project (Sheriff and He 1997). Prior to MOFEP, no harvesting had occurred since 1950 and most of the overstory trees were 50-70 years old (Forkner and Marquis 2004).

A system of 648 permanent forest vegetation plots (0.2 ha) was distributed across the nine MOFEP sites to document forest vegetation response to treatments. Plots were allocated among stands based on stands size with the constraint that each stand received at least one plot. Location of the plots within stands was random (Brookshire and Shifley 1997).

4.3. Methods

4.3.1. Study design

In this study, I selected six sites (site 1 to 6) and grouped same management type as one group for a total of three groups. Within each group, twelve forest vegetation plots were selected with similar soil types, species composition, and ELT for a total of 36 plots. The plots in EAM were clear cuts, while the plots in UAM were single tree selective harvest.

4.3.2. Data collection

Soil respiration (R_{soil}, g CO_2 m^{-2} hr^{-1}) was measured using an EGM4 (PP Systems, Amesbury, MA, USA) at each of 36 plots. Six soil collars, each with a height of 4.4 cm and a diameter of 10 cm, were inserted into the soil in each plot groups of two collars in three random locations. Surface efflux was measured during summer and fall 2003, summer 2004, and early spring and summer 2005. Soil temperature at 5 cm and 10 cm was measure adjacent to each respiration collar with a portable temperature probe. The measurements were made every 2 to 4 weeks in the 2003, 2004, and 2005 growing

season, late fall of 2003, and early spring of 2005. In addition to periodic measurements of soil temperature coinciding with respiration measurements, continuous soil temperature was measured at 5 cm, averaged every hour, by using HOBO dataloggers (Onset computer Corporation, Pocasset, MA, USA; Figure 4.1), starting at Nov. 11, 2002. The exponential equation (4.1) was used to analyze the relationship between respiration and temperature:

$$R = R_0 * e^{\beta T} \qquad (4.1)$$

where R is component respiration (soil, down dead wood, snag, sapwood, or leaf; Table 4.1), T is temperature of each component, R_0 and β are fitted parameters. The Q_{10} can be derived from equation (4.2):

$$Q_{10} = e^{10\beta} \qquad (4.2)$$

The estimated parameters were used to predict component respiration for every hour over three years based on temperature measurements.

Down dead wood respiration was measured on five soil collars at each plot for a total of 60 down dead logs in each treatment. The collars, the dimension was the same as soil respiration collar, were inserted into randomly selected, large-diameter woody debris in each plot by decay class. The measurements protocols were similar to soil respiration. Temperature sensors were inserted into the log near the collar at 5 cm depth, hourly mean down dead wood temperature was recorded from November 11, 2002. The frequency of down dead wood respiration measurements was the same as for soil respiration. The same exponential equation as soil respiration was used to analyze the relationship between the down dead wood respiration and temperature. The volume based measurement of down dead wood respiration can be up scaled to the stand level based on

the estimation of the total volume of down dead wood and continuous temperature measurements. The down dead wood volume was estimated according to equation (4.3) (Wagner 1964, Martin 1976) along one-hundred meter transect in each plot for a total of 36 transects. Each down dead wood piece greater than 5 cm in diameter on transects was recorded according to decay classes, length, and diameter, to estimate the volume of down dead wood.

$$V = \frac{\pi^2 \sum d^2}{8L} \qquad (4.3)$$

where V is volume per unit area (m^3 ha^{-1}), d is diameter of the log intersected with transect (cm), and L is the length of the transect (m).

Snag respiration was measured on seven snags at each plot for a total of 84 snags in each treatment. Collars, the dimension was the same as soil respiration collar, were mounted on each snag by decay class with silicon sealant at an approximately 137 cm height and a random azimuth. The measurements, equipment, and frequency were the same as for soil respiration. Upscale the chamber measurements to stand level, snag surface area was estimated by allometric equation (4.4) (Martin et al. 1998):

$$\log_{10} Y = a + b * \log_{10} x \qquad (4.4)$$

where x is the stem DBH (cm), Y is the stem volume, and a and b are species specific parameters. The mean surface area of each class was projected to per ground area. Temperature sensors were inserted into the snag near the collar at 5 cm depth, hourly mean snag temperature was recorded from November 11, 2002.

Sapwood respiration was measured on four trees (white oak, hickory, black oak and short leaf pine) at each plot for a total of 48 trees in each treatment. Collars, the dimension was the same as soil respiration collar, were mounted on each tree with silicon

sealant at an approximately 137 cm height and a random azimuth. The measurements, equipment and frequency are the same as for soil respiration. Temperature sensors were inserted into the stem near the collar at 5 cm depth, hourly mean sapwood temperature was recorded from November 11, 2002. Sapwood volume was calculated by allometric equation (4.4) by species. Measured stem respiration rates per unit area were converted to rates per unit of sapwood volume based on tree DBH measurements, assuming a wedge-shape volume that contributed to the respiration rates. The same exponential equation as for soil respiration was used to analyze the response of stem respiration per unit of sapwood volume by each species to stem temperature. To upscale chamber measurements of stem respiration to stand level, total sapwood volume per unit of ground area in each stand was estimated. One assumption was taken that branch respiration per volume had the same rate as stem respiration, similar to the assumption made by Law et al. (1999) and Bolstad et al. (2004).

Leaf respiration was estimated from the exponential response function (4.1), and species specific parameters were adopted from published literature (Bolstad et al., 1999). The canopy temperature and leaf biomass per ground area were used to estimate annul leaf respiration. Canopy temperature per hour was approximated by air temperature in the canopy at the height of 2 m. Ground-based leaf biomass of each species was estimated from allometric equation (4.4). The time between leaf expansion and leaf senescence for deciduous trees was between 100 and 285 days a year.

4.3.3 Statistical analysis

A two-way ANOVA (Analysis of variance) by treatments (NHM, UAM, and EAM) and years (2003, 2004, and 2005) with comparison between means adjusted with the Tukey's test, was used to compare soil and ecosystem respiration. A three-way ANOVA by treatments, years, and species with comparison between means adjusted with the Tukey's test, was used to compare leaf and sapwood respiration, while a three-way ANOVA by treatments, year, and decay class, with comparison between means adjusted with the Tukey's test, was used to compare down dead wood and snag. All statistical analysis were performed with SAS 9.1 (2003, Cary, NC, USA).

4.4. Results

4.4.1 Soil respiration

Soil respiration strongly correlated with soil temperature. Plots of spatially averaged soil respiration against average soil temperature show a strong exponential relationship between soil respiration and soil temperature (Figure 4.2). The parameters in equation 4.1 for soil respiration are summarized in Table 4.1. Q_{10} was derived as 1.68 for the NHM, 1.60 for UAM stands, and 2.22 for EAM stands. The three fitted lines indicated that the temperature sensitivity in the EAM stands was larger than that of NHM and UAM stands, while the reference respiration (R_0) at UAM stands was larger than that of NHM and EAM stands.

The annual soil respiration in the UAM stands was 8.8 ($p = 0.003$) and 16.1% ($p = 0.001$) significantly higher than that of NHM and EAM stands, respectively, while the annual soil respiration in the NHM stands was 8.1% significantly higher than that of the

EAM stands ($p = 0.007$; Table 4.2). Cumulative soil respiration summed to be 1191.1, 1309.5, and 1097.5 g C m^{-2} y^{-1} in the NHM, UAM, and EAM stands, respectively (Table 4.3). The average of annual soil respiration over the three stands was 1199.4 g C m^{-2} y^{-1}.

4.4.2 Down dead wood respiration

Down dead wood volume was estimated as 507.5, 554.2, and 2028.7 m^3 ha^{-1} in the NHM, UAM, and EAM stands, respectively, for diameters greater than 5 cm (Table 4.4). Spatially averaged down dead wood respiration and down dead wood temperature at 5 cm in the wood were used to estimate parameters in equation 4.1 (Figure 4.3).

The annual down dead wood respiration at EAM stands was 74.8 ($p = 0.001$) and 75.0% ($p = 0.001$) significantly higher than that of NHM and UAM stands, respectively. While the annual down dead wood respiration varied significantly among decay classes ($p = 0.015$). Decay class 3 had the highest annual respiration, followed by decay class 2, 4, 5, and 1. Cumulative down dead wood respiration per unit of ground area was estimated as 39.7, 39.5, and 156.3 g C m^{-2} $year^{-1}$ in the NHM, UAM, and EAM stands, respectively (Table 4.5).

4.4.3 Snag respiration

Snag surface area was estimated as 2060.5, 2199.2, and 0 m^3 ha^{-1} at the NHM, UAM, and EAM stands, respectively, for diameter at breast height greater than 3.8 cm (Table 4.6). Spatially averaged snag temperature at 5 cm in the snag was used to estimate

parameters in equation 4.1 (figure 4.4). The parameters and Q_{10} values by decay classes were shown in the Table 4.1.

The annual snag respiration at the NHM stands was similar to that of UAM stands, while there were no snags in the EAM stands. The annual snag respiration varied significantly among decay classes (p= 0.001; Table 4.2). The decay class 2 had the highest annual respiration, followed by decay class 4, 6, 3, 1, 5, and 7. Cumulative snag respiration per unit of ground area was estimated as 87.5 and 105.4 g C m^{-2} y^{-1} in the NHM and UAM stands, respectively. The average annual snag respiration was 96.4 g C m^{-2} y^{-1} (Table 4.7).

4.4.4 Sapwood respiration

Total sapwood volume of the four species in NHM stands was greater than that of UAM, and it was greater than that of EAM stands. Black oak had the largest volume int the NHM and UAM stands, while the short leaf pine had the largest volume at EAM stands (Table 4.8).

Changes in sapwood respiration exponentially correlated with sapwood temperature (Figure 4.5). The parameters for the exponential equation and Q_{10} values were shown in Table 4.1. Annual sapwood respiration varied significantly among species (p = 0.001; Table 4.2). The annual sapwood respiration of black oak was 67.9 (p = 0.001) and 74.9% (p = 0.001) significantly higher than that of hickory and short leaf pine, respectively, while the annual sapwood respiration of white oak was 64.3 (p = 0.002) and 72.1% (p = 0.001) significantly higher than that of hickory and short leaf pine, respectively.

Annual sapwood respiration also decreased according to the severity of harvesting. For example, the annual sapwood respiration in the NHM stands was 85.3% ($p = 0.001$) significantly higher than that of EAM stands, while the annual sapwood respiration in the UAM stand was 79.9% ($p = 0.001$) significantly higher than that of EAM stands. The annual sapwood respiration in the NHM and UAM stands was primarily from black and white oak trees, while the annual sapwood respiration in the EAM stands was mainly from white oak and short leaf pine trees. The order of the magnitude of sapwood respiration in the NHM stands was white oak, black oak, hickory, and short leaf pine, while the order of the magnitude of sapwood respiration in the UAM stands was black oak, white oak, hickory, and short leaf pine. In the EAM stands, however, the order of the magnitude of sapwood respiration was short leaf pine, white oak, black oak, and hickory. These patterns did not change inter-annually. The average of annual sapwood respiration was 39.6, 28.5, and 5.8 g C m^{-2} $year^{-1}$ in the NHM, UAM, and EAM stands, respectively (Table 4.9).

4.4.5 Leaf respiration

The leaf dry mass of the four main tree species was the largest in the NHM stands, followed by UAM and EAM stands. In the NHM stands, white oak leaf dry mass was the greatest, followed by short leaf pine, black oak, and hickory. In the UAM stands, white oak was the greatest, followed by short leaf pine, hickory, and black oak, respectively. In the EAM stands, black oak leaf dry mass was the greatest, followed by short leaf pine, white oak, and hickory (Table 4.10).

The leaf respiration in the NHM stands was 94.8% ($p = 0.001$) higher than that of the EAM stands, while leaf respiration in the UAM stands was 93.1% ($p = 0.009$) higher than that of the EAM stands (Table 4.2). There was no significant inter-annual difference in leaf respiration among species ($p = 0.9$). In the NHM and UAM stands, white oak leaf respiration was the greatest, followed by black oak, hickory, and short leaf pine, while in the EAM stands, the short leaf pine was the highest, followed by hickory, black oak, and white oak. The average annual leaf respiration was 162.2 g C m^{-2} $year^{-1}$ at NHM stands, 122.3 g C m^{-2} $year^{-1}$ at UAM stands, and 8.4 g C m^{-2} $year^{-1}$ at EAM stands (Table 4.11).

4.4.6 Ecosystem respiration

Ecosystem component respiration had seasonal and daily variation in three stands (Figure 4.6a, b, and c). Daily mean ecosystem respiration varied between 0.39 – 0.87 g CO_2 m^{-2} hr^{-1} in the NHM stands. It varied between 0.42 – 0.89 g CO_2 m^{-2} hr^{-1} in the UAM stands and between 0.23 – 0.78 g CO_2 m^{-2} hr^{-1} in the EAM stands. The annual ecosystem respiration was 1641.7, 1690.9, and 1285.6 g C m^{-2} y^{-1} in the NHM, UAM, and EAM, respectively. Ecosystem respiration was the lowest in January – March, and rapidly increased after mid April. It peaks in early July. The change of peak time over three years corresponded with inter-annual variability in local climate. Ecosystem respiration dropped in mid-November. Component respiration demonstrated the same seasonal variations as ecosystem respiration.

The annual ecosystem respiration in the EAM stands was 27.7 ($p = 0.001$) and 31.5% ($p = 0.001$) significantly lower than that of NHM and UAM stands (Table 4.2). Soil respiration was the largest component in three stands and contributed between 72 to

85% of the ecosystem respiration. In the NHM stands, leaf respiration (10%) was the next largest component, followed by stem sapwood (10%), snag (5%), and DDW (2%). In the UAM stands, the second largest component was leaf respiration (7%), and followed by stem sapwood (7%), snag (6%), and down dead wood (2%), while in the EAM stands, down dead wood (12%) was the second largest component and followed by stem sapwood (2%), leaf (1%), and snag (0%; Table 4.3). Aboveground autotrophic respiration (stem + leaf respiration) comprised 20, 14, and 3% in the NHM, UAM, and EAM stands, respectively, with leaf respirations slightly higher than stem respirations in the NHM and UAM stands. While dead wood debris respiration (snag + down dead wood respiration) comprised 7, 8, and 12% of ecosystem respiration in the NHM, UAM, and EAM stands respectively, with snag respiration higher than down dead wood in the NHM and UAM stands (Table 4.3).

4.5. Discussion

4.5.1 Comparison in respiration among treatments

Our direct measurements of respiration in a temperate forest demonstrate that oak-hickory forest ecosystem respiration and its components will be affected by timber harvesting. MOFEP timber harvesting removed 235.5m^3 ha^{-1} in EAM stands and 113.5 m^3 ha^{-1} in UAM stands (Kabrick et al. 2004), which substantially reduced live tree biomass. Therefore, autotrophic respiration (stem + leaf respiration), the cost for tree growth and maintenance in stems and leaves, was 320.8 g C m^{-2} $year^{-1}$ in the NHM stands, and decreased to 236.6 and 31.8 g C m^{-2} $year^{-1}$ in the UAM and EAM stands, respectively.

4.5.2 Temperature controls on respiration

Temperature is a key factor affecting ecosystem respiration and its components in this temperate oak-hickory forest ecosystem, and an exponential response function appears to explain most of the observed temporal variation (Chimner and Welker 2005). Temperature sensitivity (Q_{10}) to respiration was regarded as temperature-dependent (Lloyd and Taylor 1994, Fang and Moncrieff 2001), and Q_{10} may vary with soil moisture in certain areas (Xu and Qi 2001a, Tang et al. 2005), while fixed Q_{10} values over years provide useful estimates for ecosystem respiration and its components at our study site.

Some recent findings at arid sites found that soil water had some impact on respiration relative to temperature (Ma et al. 2005). In arid or semi-arid ecosystems, soil water is the major factor limiting ecosystem activities (i.e., respiration) and its sensitivity to temperature, particularly in the summer (Xu and Qi 2001a). Water appears to be sufficient at our site to retain microbial activity and plant physiology with an annual average of 16% in the top 15 cm of soil. However, a summer drought in a dry year was found to reduce the annual soil respiration in a mature forest found in Northern Wisconsin (Martin and Bolstad 2005). The sufficient soil moisture at our study site may mean that soil moisture was not a limiting factor on respiration. In addition, soil moisture typically had only a small effect (8% on average) in improving regressions between eddy-flux measured ecosystem respiration and soil temperature for 14 sites in Northern Wisconsin and Michigan (Noormets et al. 2005). Thus, soil temperature was a major determinant for soil respiration at our study site.

Temperature also appears to be the control on leaf, sapwood, down dead wood, and snag respiration. The other potential controlling factors for down dead wood and snag respiration include decay status (Robertson and Daniel 1989, Harmon et al. 1995, Kruys et al. 2002) and moisture. At our study site, the moisture was not an important control, but the decay status was important in explaining the spatial variation of measurements.

Soil temperature measurements indicated that the soil temperature at 5 cm is typically above freezing during the winter. Thus, the soil respiration could be from microbial decomposition from unfrozen soils and from root maintenance respiration occurring in deep soils (Curiel Yuste et al. 2004, Larionova 2005, Vogel et al. 2005). Sapwood and pine needles also release CO_2 in the winter non-growing season as maintenance respiration (Ryan 1990, Ryan and Waring 1992, Ryan et al. 1996). Temperature in large down dead wood and snags was above 0 °C and thus resulted in down dead wood and snag respiration in the winter. However, we used a fixed date for deciduous tree leaf development and therefore leaf respiration only peaks during the growing season.

4.5.3 Comparison with other forest ecosystems

We could not find other studies in similar ecological zones, which used chamber methods to estimate total ecosystem respiration from second growth forests. However, a recent study about component respiration in a mature northern hardwood forest using chamber and biometric measurement methods, Curtis et al. (2005) reported 1425, 1003, 166, and 256 g C m^{-2} $year^{-1}$ of ecosystem respiration, soil respiration, stem respiration,

and leaf respiration, respectively. These were higher than our second growth oak-hickory stands. Furthermore, the magnitude of our cumulative respiration is comparable to other studies in different ecosystems. For example, Ryan et al. (1997) used a biometric approach in several Canadian forests and estimated that annual autotrophic respiration ranged from a low of 535 g C m^{-2} $year^{-1}$ in *Pinus banksiana* forests to a high of 908 g C m^{-2} $year^{-1}$ in *Populus tremuloides* stands. Law et al. (1999) reported the first full annual assessment of ecosystem respiration as 894 g C m^{-2} $year^{-1}$ in the mixed age *Pinus ponderosa* forest. But Bolstad et al. (2004)reported comparatively high annual ecosystem respiration up to 1469 g C m^{-2} $year^{-1}$ in a mature *P. tremuloides* stand, while Wang et al. (2004) estimated annual ecosystem respiration in a Finnish *Pinus sylvestris* forest using both modeling and meteorological approaches showed an average ecosystem respiration of 611 g C m^{-2} $year^{-1}$, which did not differ significantly from meteorological estimates.

Ecosystem respiration form our site is also much lower than that of mature Amazon tropical forests with estimations of 2337.6 g C m^{-2} $year^{-1}$ (Lloyd et al. 1996), and of 3070 g C m^{-2} $year^{-1}$ (Carswell et al. 2002). Higher temperature, longer growing seasons, and higher photosynthesis and growth rates in tropical forests may explain the higher respiration than that found at our study site.

Our results showed that ecosystem respiration and its components in a temperature oak forest ecosystem are strongly influenced by management regimes coupled with local temperature. This has implications for modeling changes to the large pools of carbon stored in temperate oak forest from changes in management regimes and variation in local climate. It also indicates that we must look at projected changes in both

management activities and climatic conditions such as temperature gradients if we are to understand these ecosystem process controls on the ecosystem functions.

4.6. Conclusions

Our chamber-based flux measurements coupled with spatial and temporal scaling allowed us to estimate ecosystem and its components respiration. Harvesting regimes affected ecosystem component respiration and temperature was the major climatic factor affecting respiration in the temperate oak forest ecosystem. Exponential functions between respiration and temperature explained most of the observed spatial and temporal variation. The annual ecosystem respiration was 1641.7, 1690.9, and 1285.6 g C m^{-2} y^{-1} in the NHM, UAM, and EAM stands, respectively. Soil respiration was the largest component, which accounted for between 72 to 85% of total ecosystem respiration. Our data indicated that harvesting regimes affected ecosystem processes and local climatic conditions such as temperature can be used to predict variation of the ecosystem functions within different harvesting regimes.

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Table 4.1. Parameters in the temperature response function (Eq. 4.1) for soil respiration (R_{soil}, g CO_2 m^{-2} hr^{-1}) from three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM), down dead wood respiration (R_{ddw}, g CO_2 m^{-3} hr^{-1}) from five decay classes, snags (R_{snag}, g CO_2 m^{-2} hr^{-1}) from seven decay classes, stem (R_{stem}, g CO_2 m^{-3} hr^{-1}), and leaf (R_{leaf}, g CO_2 m^{-2} hr^{-1}) from four species. The unit of temperature is °C.

		R_0	B	Q_{10}	R^2
R_{soil}	NHM	0.4970	0.0518	1.6779	0.74
	UAM	0.5407	0.0468	1.5962	0.74
	EAM	0.3937	0.0796	2.2176	0.74
R_{ddw}	Decay class 1	0.2942	0.0277	1.3196	0.58
	Decay class 2	0.2494	0.0541	1.7169	0.54
	Decay class 3	0.3237	0.0489	1.6313	0.49
	Decay class 4	0.3399	0.0414	1.5122	0.52
	Decay class 5	0.2954	0.0446	1.5619	0.55
R_{snag}	Decay class 1	0.3141	0.0955	2.5990	0.68
	Decay class 2	0.7818	0.0158	1.1707	0.59
	Decay class 3	0.3896	0.0455	1.5754	0.48
	Decay class 4	0.3965	0.0028	1.0281	0.50
	Decay class 5	0.1325	0.0639	1.8953	0.73
	Decay class 6	0.3056	0.0347	1.4151	0.62
	Decay class 7	0.3846	0.0224	1.2513	0.74
R_{stem}	White oak	2.4163	0.0298	1.3470	0.72
	Hickory	1.2754	0.0367	1.4430	0.64
	Black oak	1.9264	0.0357	1.4297	0.65
	Short leaf pine	1.2651	0.0463	1.5882	0.60
R_{leaf}	White oak	1.3533	0.0200	1.2211	0.65
	Hickory	1.2554	0.0221	1.2473	0.68
	Black oak	1.2988	0.0344	1.4101	0.71
	Short leaf pine	1.2628	0.0214	1.2391	0.53

Table 4.2. Analysis of variance of soil, down dead wood, snag, sapwood, leaf, and ecosystem respiration by treatments, year, decay classes or species types

Variables	df	N	F values	P values
Soil				
Treatment	2	9	100.37	0.001
Year	2	9	1.92	0.260
Down dead wood				
Treatment	2	45	19.24	0.001
Year	2	45	0.01	0.994
Decay class	4	45	3.58	0.015
Snag				
Treatment	2	63	34.20	0.001
Year	2	63	0.00	0.996
Decay class	6	63	8.65	0.001
Sapwood				
Treatment	2	36	24.88	0.001
Year	2	36	0.00	0.997
Species	3	36	15.00	0.001
Leaf				
Treatment	2	36	10.20	0.001
Year	2	36	0.00	0.999
Species	3	36	7.03	0.001
Ecosystem				
Treatment	2	9	291.02	0.001
Year	2	9	1.46	0.334

Table 4.3. Ecosystem respiration, component respiration (g C m^{-2} y^{-1}) and percentage (%) in the three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM) in 2003, 2004, and 2005.

	NHM			UAM			EAM		
	2003	2004	2005	2003	2004	2005	2003	2004	2005
Soil	1188.0	1185.1	1208.2	1308.5	1308.3	1311.8	1059.0	1110.1	1123.5
	72%	73%	73%	77%	77%	78%	85%	85%	85%
Down dead wood	40.4	39.0	39.7	39.8	39.4	39.3	151.3	157.9	159.8
	2%	2%	2%	2%	2%	2%	12%	12%	12%
Snag	88.6	86.5	87.4	106.3	105.2	104.6	0	0	0
	5%	5%	5%	6%	6%	6%	0%	0%	0%
Sapwood	160.6	156.7	158.4	114.7	113.9	113.9	22.6	23.6	23.8
	10%	10%	10%	7%	7%	7%	2%	2%	2%
Leaf	161.3	162.1	163.2	121.7	122.3	123	8.2	8.5	8.6
	10%	10%	10%	7%	7%	7%	1%	1%	1%
Ecosystem	1638.8	1629.4	1656.8	1691	1689.1	1692.5	1241	1300.1	1315.6
	100%	100%	100%	100%	100%	100%	100%	100%	100%

Table 4.4. Total down dead wood (m^3 ha^{-1}) for five decay class in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM).

Decay class	NHM	UAM	EAM
1	4.5	104.0	185.1
2	21.3	287.7	715.5
3	49.6	62.4	705.0
4	233.3	63.2	309.8
5	198.9	36.9	113.3
Sum	507.5	554.2	2028.7

Table 4.5. Cumulative down dead wood respiration per ground area (g C m^{-2} y^{-1}) for the five classes and their sums in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM) in 2003, 2004, and 2005.

Decay classes	NHM			UAM			EAM		
	2003	2004	2005	2003	2004	2005	2003	2004	2005
1	0.3	0.3	0.3	7.5	7.5	7.5	13.1	13.6	13.7
2	1.4	1.3	1.3	18.8	18.6	18.5	46.0	48.0	48.7
3	4.1	3.9	4.0	5.2	5.2	5.1	57.8	60.3	61.1
4	19.8	19.2	19.5	5.5	5.4	5.4	26.1	27.2	27.5
5	14.8	14.3	14.5	2.8	2.8	2.7	8.4	8.7	8.8
Sum	40.4	39.0	39.7	39.8	39.4	39.3	151.3	157.9	159.8

Table 4.6. Total snag surface area (m^2 ha^{-1}) for seven decay classes in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM).

Decay classes	NHM	UAM	EAM
1	1022.5	191.8	0
2	194.3	1038.0	0
3	129.8	182.9	0
4	442.7	478.5	0
5	118.8	9.8	0
6	121.3	285.3	0
7	31.1	12.8	0
Sum	2060.5	2199.2	0

Table 4.7. Cumulative snag respiration per ground area (g C m^{-2} y^{-1}) for the seven decay classes and their sums in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM) in 2003, 2004, and 2005.

Decay classes	NHM			UAM			EAM		
	2003	2004	2005	2003	2004	2005	2003	2004	2005
1	9.5	8.7	9.1	18.6	17.9	17.3	0	0	0
2	36.6	36.2	36.3	19.6	19.6	19.6	0	0	0
3	12.7	12.3	12.5	18.3	18.1	18.0	0	0	0
4	13.5	13.5	13.5	26.4	26.5	26.4	0	0	0
5	4.2	3.9	4.1	0.4	0.3	0.3	0	0	0
6	9.1	8.9	9.0	21.8	21.6	21.6	0	0	0
7	2.9	2.9	2.9	1.2	1.2	1.2	0	0	0
Sum	88.6	86.5	87.4	106.3	105.2	104.6	0	0	0

Table 4.8. Sapwood volume (m^3 ha^{-1}) for four species in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM)

Species	NHM	UAM	EAM
White oak	444.0	235.2	13.2
Hickory	229.8	250.0	2.1
Black oak	534.7	429.7	11.3
Short leaf pine	164.7	95.7	28.2
Sum	1373.2	1010.6	54.8

Table 4.9. Cumulative stem respiration per ground area (g C m^{-2} y^{-1}) for the four species and their sums in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM) in 2003, 2004, and 2005.

Species	NHM			UAM			EAM		
	2003	2004	2005	2003	2004	2005	2003	2004	2005
White oak	65.6	64.3	64.9	35.1	34.9	35.0	7.7	8.0	8.0
Hickory	18.1	17.7	17.9	20.0	19.8	19.8	0.7	0.7	0.7
Black oak	63.7	62.0	62.7	51.8	51.4	51.4	5.3	5.5	5.6
Short leaf pine	13.2	12.7	12.9	7.8	7.7	7.7	9.0	9.4	9.5
Sum	160.6	156.7	158.4	114.7	113.9	113.9	22.6	23.6	23.8

Table 4.10. Total leaf dry mass (g m^{-2}) for four species in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM).

Species	NHM	UAM	EAM
White oak	148.9	124.6	51.4
Hickory	29.5	32.6	4.0
Black oak	32.7	18.5	72.4
Short leaf pine	115.8	64.9	61.4
Sum	327.0	240.6	189.2

Table 4.11. Cumulative leaf respiration per ground area (g C m^{-2} y^{-1}) for the four species and their sums in three treatments (non harvest management: NHM, uneven age management: UAM, and even age management: EAM) in 2003, 2004, and 2005.

Species	NHM			UAM			EAM		
	2003	2004	2005	2003	2004	2005	2003	2004	2005
White oak	92.6	93.4	93.2	25.7	25.7	26.1	0.1	0.2	0.2
Hickory	11.6	11.6	11.7	12.2	12.2	12.3	2.5	2.6	2.6
Black oak	46.0	46.1	47.0	77.3	77.9	78.0	2.4	2.5	2.5
Short leaf pine	11.1	11.1	11.2	6.5	6.5	6.6	3.1	3.3	3.3
Sum	161.3	162.1	163.2	121.7	122.3	123.0	8.2	8.5	8.6

Figure 4.1 Soil temperature measured at 5cm by HOBO datalogger and the direct measurements while soil respiration was taking.

Figure 4.2. Soil respiration was as a function of soil temperature at 5cm in three treatment stands (non harvest management: NHM, uneven age management: UAM, and even age management: EAM). The short dished line, solid dark line, and gray solid line are represent exponential fitted lines for EAM, NHM, and UAM stands, respectively.

Figure 4.3 Down dead wood respiration per log volume for decay class 1 (a), 2 (b), 3 (c), 4 (d), and 5 (e) was functions of down dead wood temperature. The solid dark lines are exponential fitted lines for different decay classes.

Figure 4.4 Snag respiration per surface area for decay class 1 (a), 2 (b), 3 (c), 4 (d), 5 (e), 6(f), and 7(g) was as functions of snag wood temperature. The solid dark lines are exponential fitted lines for different decay classes.

Figure 4.5 Sapwood respiration per sapwood volume for white oak, black oak, hickory, and short leaf pine was a function of sapwood temperature. The short dished line, long dished line, gray solid line, and dark solid line are exponential fitted lines for black oak, hickory, short leaf pine, and white oak, respectively.

Figure 4.6. Estimated daily mean soil, stem, leaf, down dead wood, snag, and total ecosystem respiration during years 2003, 2004, and 2005 in the even age management (EAM; a), uneven age management (UAM; b), and non harvest management (NHM; c) stands.

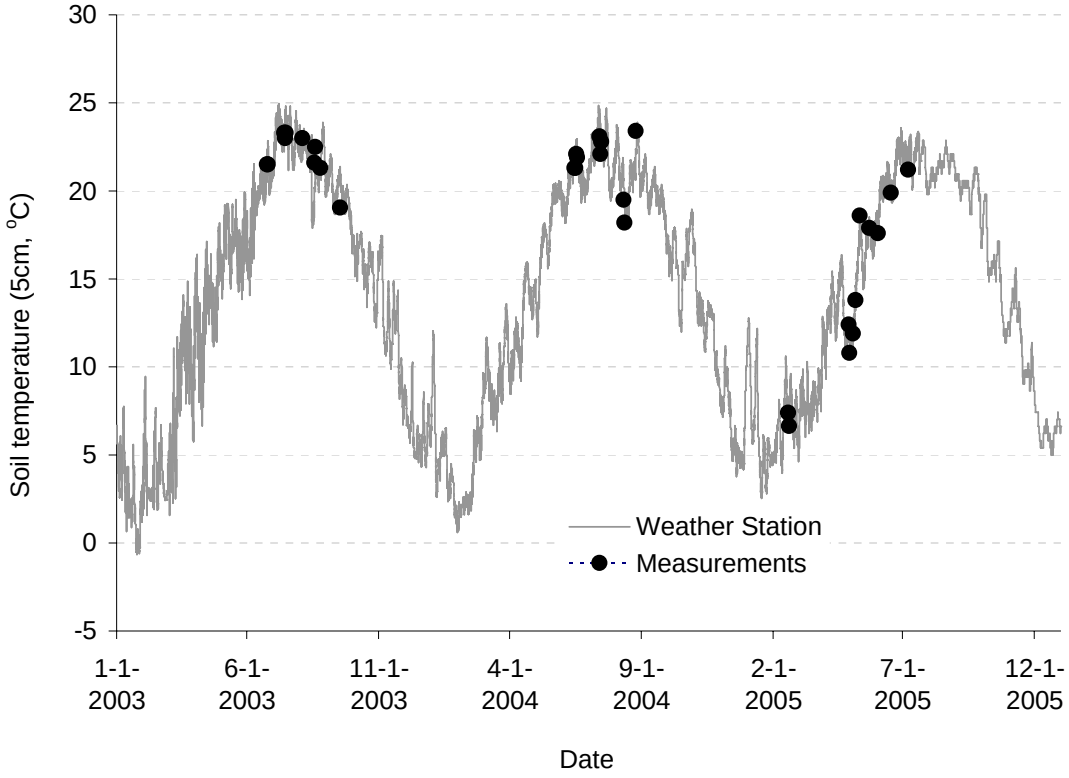

30
25
20
15
10
5
0
-5
Soil temperature (5cm, °C)
Weather Station
Measurements
1-1-2003
6-1-2003
11-1-2003
4-1-2004
9-1-2004
2-1-2005
7-1-2005
12-1-2005
Date

Figure 4.1

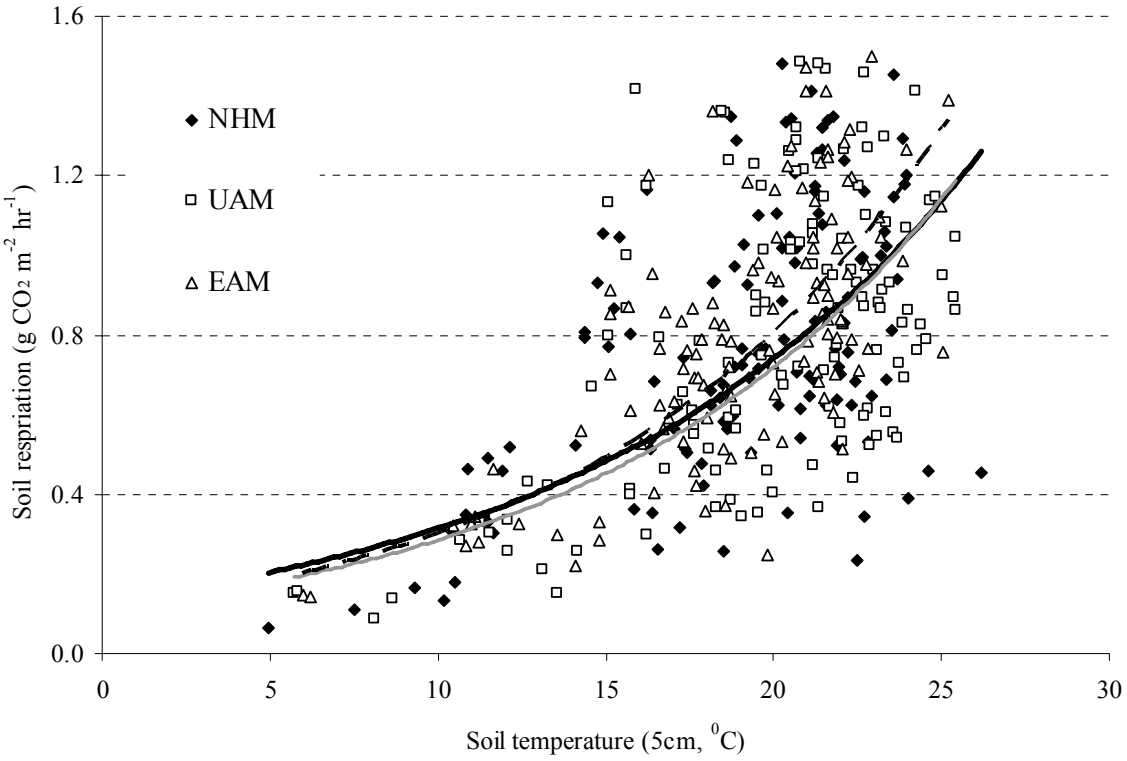

1.6
1.2
0.8
0.4
0.0
0
5
10
15
20
25
30
NHM
UAM
EAM
Soil respriation (g CO2 m-2 hr-1)
Soil temperature (5cm, 0C)

Figure 4.2

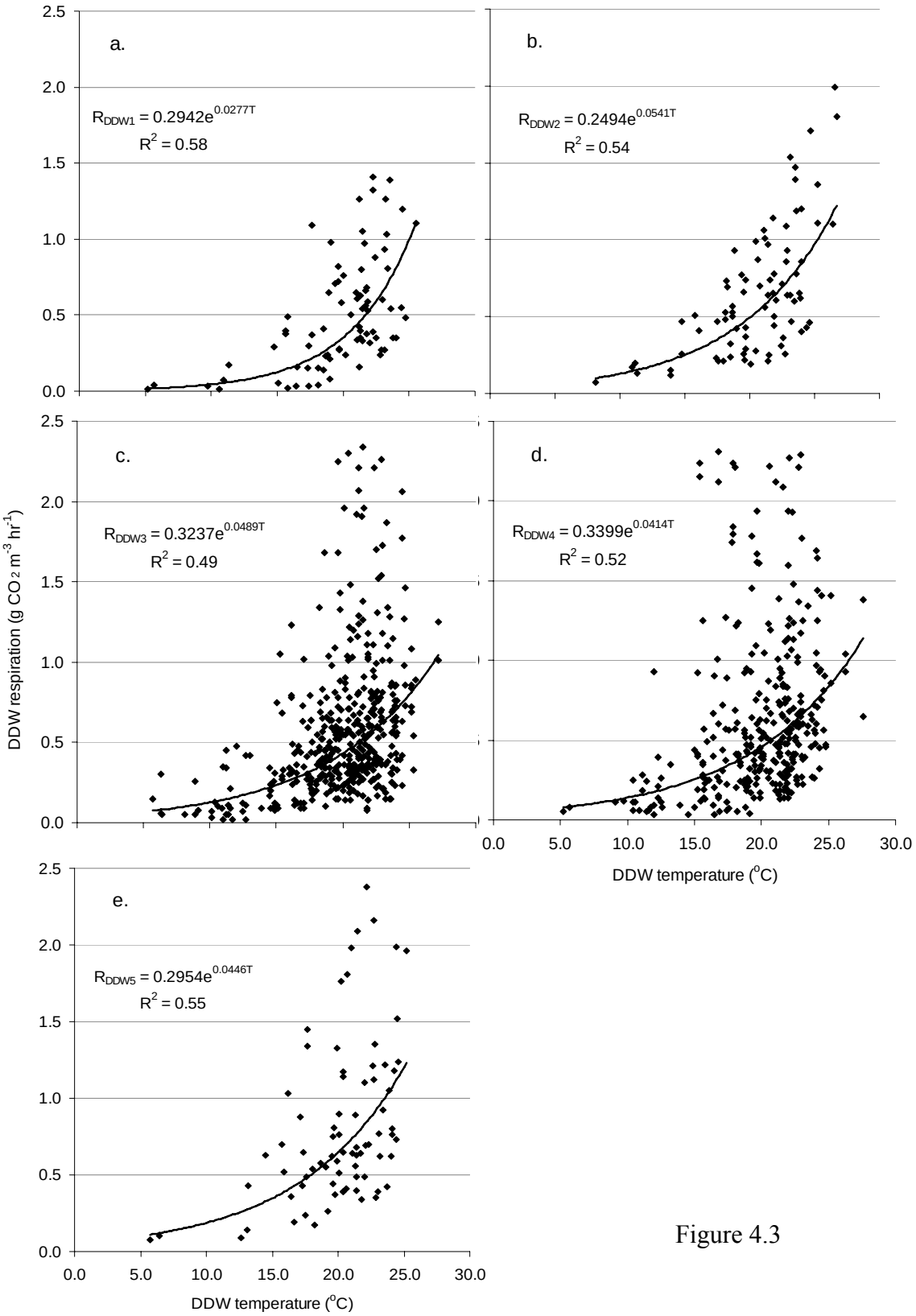

a.
$R_{DDW1} = 0.2942e^{0.0277T}$
$R^2 = 0.58$
b.
$R_{DDW2} = 0.2494e^{0.0541T}$
$R^2 = 0.54$
c.
$R_{DDW3} = 0.3237e^{0.0489T}$
$R^2 = 0.49$
d.
$R_{DDW4} = 0.3399e^{0.0414T}$
$R^2 = 0.52$
e.
$R_{DDW5} = 0.2954e^{0.0446T}$
$R^2 = 0.55$
DDW respiration (g CO_2 m^{-3} hr^{-1})
DDW temperature (^oC)
0.0
0.5
1.0
1.5
2.0
2.5
5.0
10.0
15.0
20.0
25.0
30.0

Figure 4.3

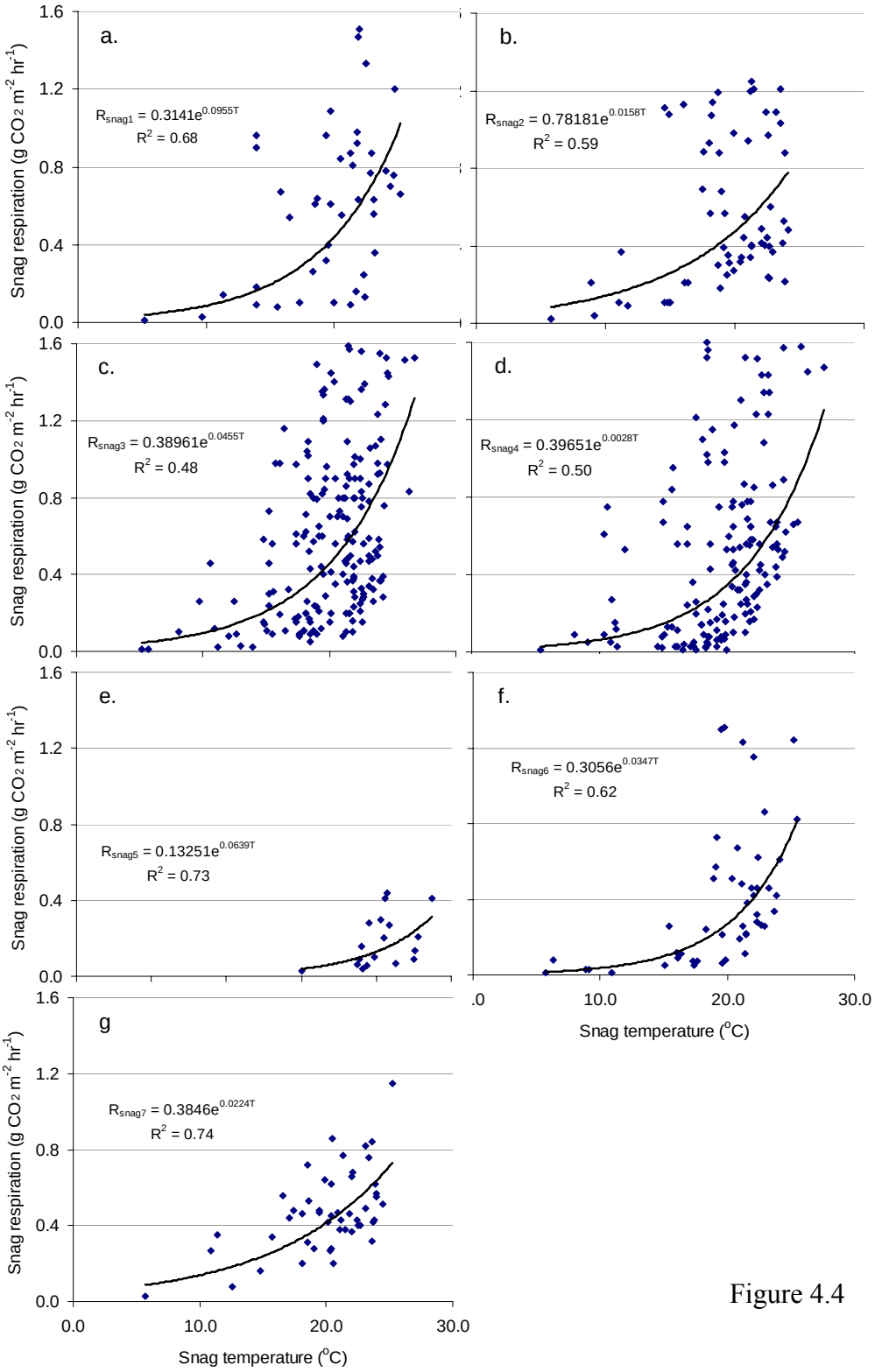

a.
$R_{snag1} = 0.3141e^{0.0955T}$
$R^2 = 0.68$
b.
$R_{snag2} = 0.78181e^{0.0158T}$
$R^2 = 0.59$
c.
$R_{snag3} = 0.38961e^{0.0455T}$
$R^2 = 0.48$
d.
$R_{snag4} = 0.39651e^{0.0028T}$
$R^2 = 0.50$
e.
$R_{snag5} = 0.13251e^{0.0639T}$
$R^2 = 0.73$
f.
$R_{snag6} = 0.3056e^{0.0347T}$
$R^2 = 0.62$
g
$R_{snag7} = 0.3846e^{0.0224T}$
$R^2 = 0.74$
Snag respiration (g CO_2 m^{-2} hr^{-1})
Snag temperature (^oC)
0.0
0.4
0.8
1.2
1.6
10.0
20.0
30.0

Figure 4.4

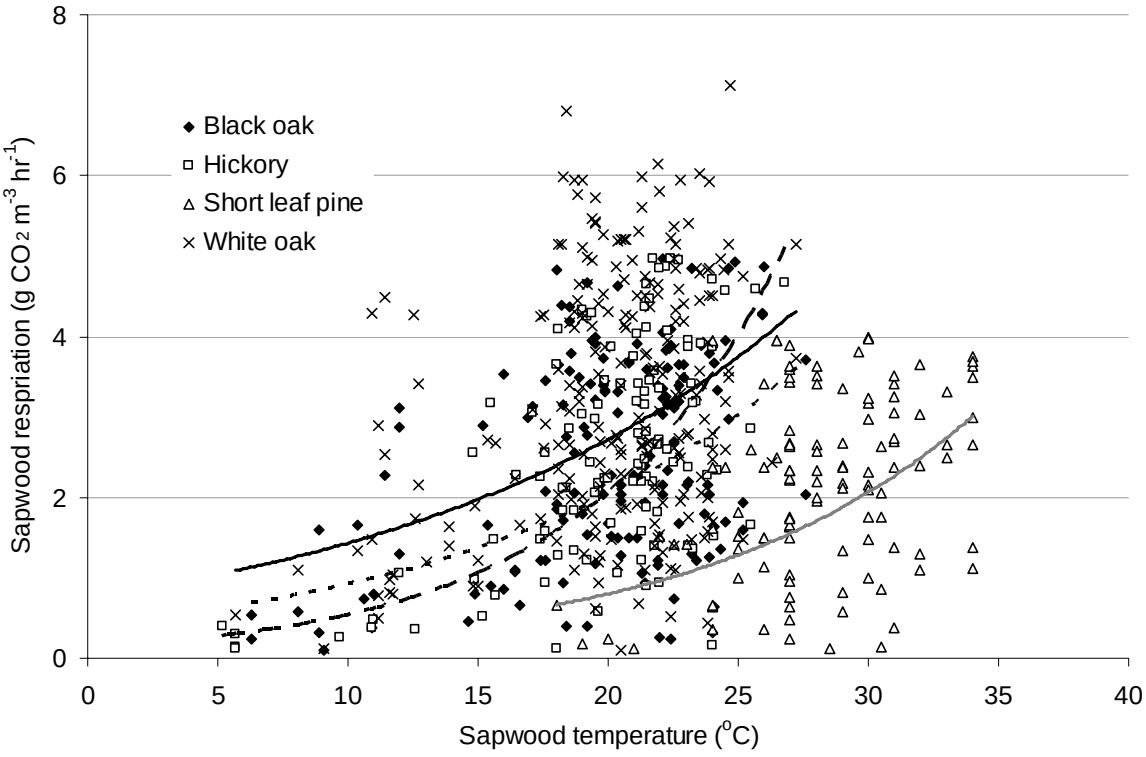

Black oak
Hickory
Short leaf pine
White oak
Sapwood respiration (g CO2 m-3 hr-1)
Sapwood temperature (°C)
0
2
4
6
8
0
5
10
15
20
25
30
35
40

Figure 4.5

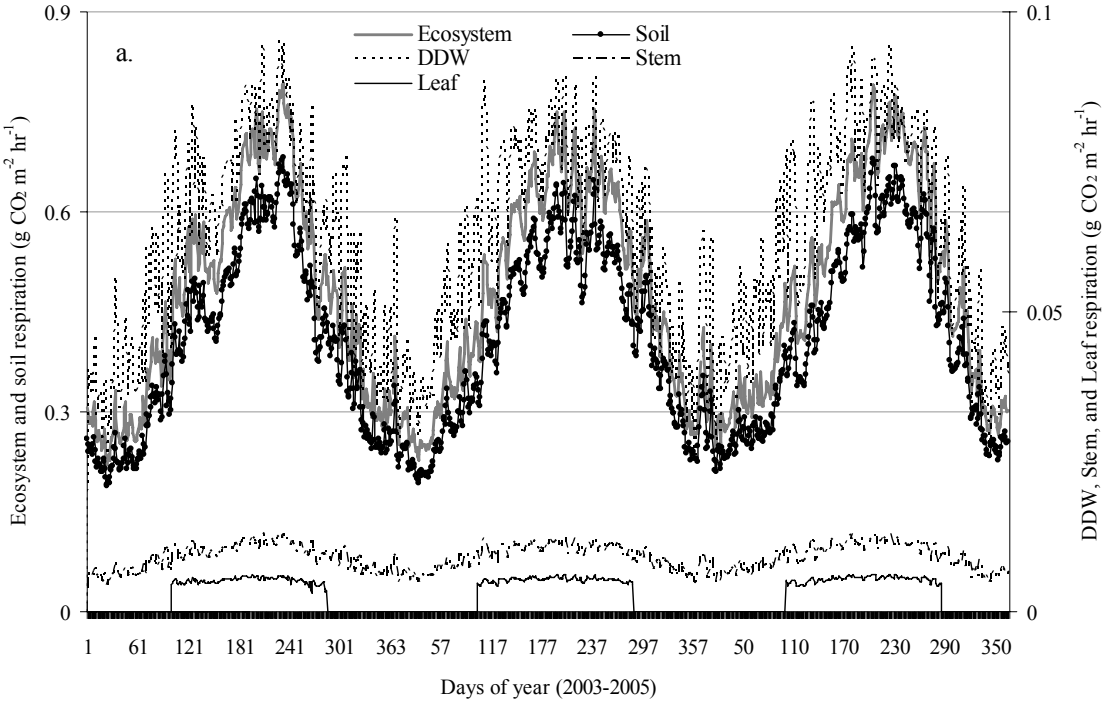
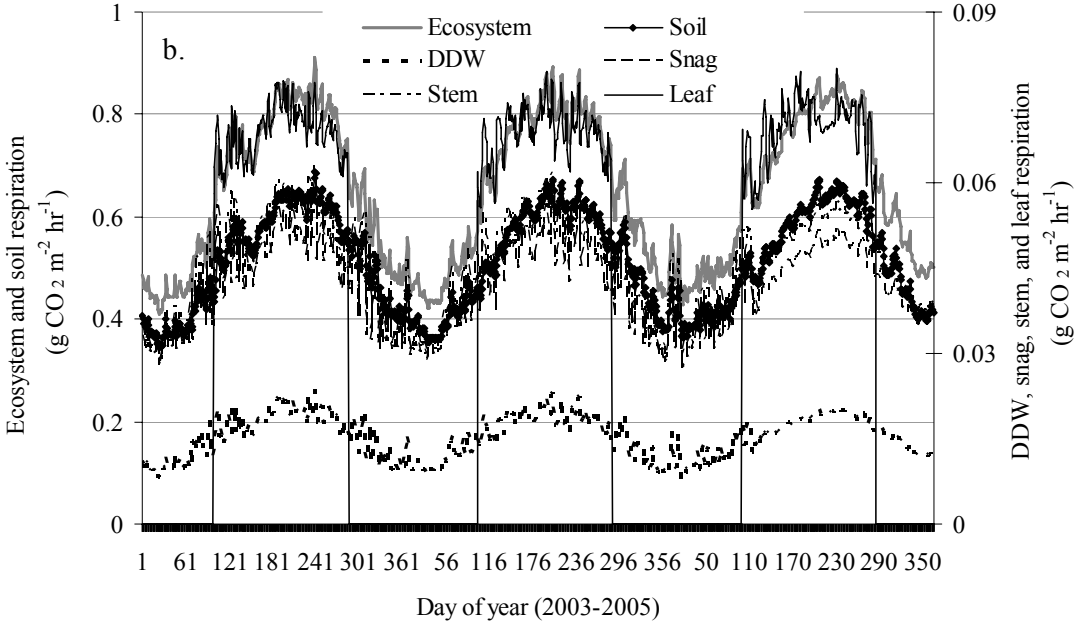
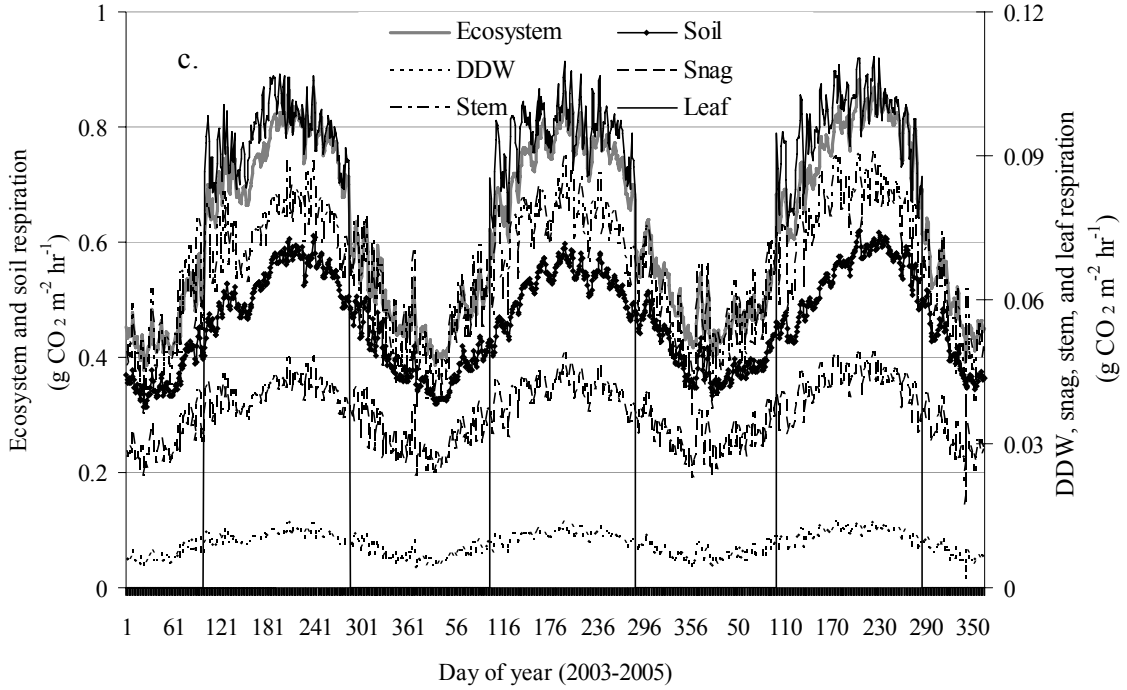

a.
Ecosystem
Soil
DDW
Stem
Leaf
Ecosystem and soil respiration (g CO2 m-2 hr-1)
DDW, Stem, and Leaf respiration (g CO2 m-2 hr-1)
0.9
0.6
0.3
0
0.1
0.05
0
1 61 121 181 241 301 363 57 117 177 237 297 357 50 110 170 230 290 350
Days of year (2003-2005)

Figure 4.6


b.
Ecosystem
Soil
DDW
Snag
Stem
Leaf
Ecosystem and soil respiration (g CO 2 m-2 hr-1)
DDW, snag, stem, and leaf respiration (g CO 2 m-2 hr-1)
0
0.2
0.4
0.6
0.8
1
0
0.03
0.06
0.09
1 61 121 181 241 301 361 56 116 176 236 296 356 50 110 170 230 290 350
Day of year (2003-2005)


c.
Ecosystem
Soil
DDW
Snag
Stem
Leaf
Ecosystem and soil respiration (g CO 2 m-2 hr-1)
DDW, snag, stem, and leaf respiration (g CO 2 m-2 hr-1)
0
0.2
0.4
0.6
0.8
1
0.03
0.06
0.09
0.12
1 61 121 181 241 301 361 56 116 176 236 296 356 50 110 170 230 290 350
Day of year (2003-2005)

Chapter 5 Conclusions

5.1 Lessons from this study

This study was designed to explore ecosystem carbon storage and fluxes in the southeastern Ozark forest landscape (MOFEP compartments) in relation to timber harvesting activities. The central hypothesis is that alternative management activities would change major forest ecosystem processes and thus define the magnitude of carbon sequestration within the ecosystem. Using an empirical approach, I estimated the short-term effects of experimental treatments (i.e., even age management, uneven age management, and non harvest management) on carbon pool sizes. Furthermore, I was able to determine the leaf litter decomposition rates and the effects of timber harvesting on these rates by using mixed leaf litter (oaks, hickories, and short leaf pine). In addition, ecosystem and its components respiratory carbon losses were quantified by using chamber based measurements in different harvest management stands. I was able to conclude that timber harvesting altered ecosystem processes by reducing plant biomass in a forest ecosystem. Three primary lessons were learned from this study.

First, major forest carbon pool sizes were directly and significantly affected by timber harvesting regimes in my studied forest ecosystem. I found that timber harvesting significantly increased the mineral soil carbon pool in the uneven age management stands

after the first 8 years of a harvesting event, whereas timber harvesting decreased above ground carbon pool sizes in the UAM and EAM stands. This suggests that alternative forest management is critical in determining forest carbon pool sizes. I also observed a positive relationship between soil nitrogen and carbon pool sizes. The negative relationships exist between canopy coverage and forest floor, and between soil temperature and live tree biomass. These further suggest that timber harvesting altered environmental conditions (i.e., soil temperature) and site factors (i.e., canopy coverage), and these altered conditions and/or factors were correlated to the carbon pool sizes.

Second, understanding the mechanisms of mixed leaf litter decomposition and its potential influence on carbon and nitrogen cycling will help in understanding humus formation and soil carbon sequestration. In this study I demonstrated that mixed oak-hickory leaf litter decay was significantly faster than either oak or oak-pine litter mixtures. I discovered that the specific leaf area rather than the leaf initial chemistry was most important in influencing the decay processes. The decay constant of mixed leaf litter at MOFEP was between 0.39 to 0.51 yr^{-1}. This infers that mixing leaf litter is an effective activity in prompting the rate of leaf litter decay. When developing forest floor management plans for soil organic matter accumulations, leaf litter mixtures should be seriously considered because of their significant role in determining litter decomposition processes in a ecosystem.

Third, the ecosystem and its component respiration were successfully measured using direct chamber measurements at MOFEP compartments. An exponential temperature responses model was successfully applied with my data to predict annual respiratory carbon losses. I found that timber harvesting significantly affected major

ecosystem component respiration. These findings suggest that ecosystem respiratory carbon losses are directly affected by biomass removal and the magnitudes of the effects could be predicted by the temperature responses' models (i.e., Q_{10} model).

Overall, the results of this study provide valuable and fundamental information on the capacity of carbon storage, litter decomposition processes, and respiratory carbon losses for assessing the effects of timber harvesting on ecosystem functions. This study also enhances our ability to model ecological processes, such as ecosystem and its component respiration, using basic temperature data. The empirical models developed in this study are valuable to understand the interactions between microclimate and ecological processes and to provide reliable predictions for forest management activities for a mixed oak forest ecosystem in the Missouri Ozarks.

5.2 Further study directions

My primary recommendation for further research is to continue studies relating ecological processes to successional stages in the Missouri Ozarks. The MOFEP clear-cut even age management strategy set the forest succession back. Following timber harvesting, the ecosystem had a substantial loss of carbon from vegetation and soil. The secondary successional pattern was that most species either recruited by stump sprouting or seedlings which colonized shortly thereafter allowing species composition to change within the stands. The pattern of the ecosystem carbon storage initially declined, because carbon inputs from plant production were too low to counteract losses by ecosystem respiration. Furthermore, intensive timber harvesting may also lead to long term decreases in soil organic matter content. On the other hand, regenerating forests may

gradually compensate the initial carbon losses by storing more carbon in plant biomass as plants grow. The capacity of regenerating forests to store carbon depends on forest age and species composition. For the MOFEP study site, only one timber harvesting event happened 8 years before this project, and I could not put this one event into a successional context. This study helped to explain the capacity of forest ecosystems to store carbon, and the magnitude of ecosystem component respiratory carbon losses. Thus, long term ecosystem process studies associated with successional stages and species composition in future research efforts.

This study demonstrated that mixed leaf litter decomposition was affected by species composition and timber harvest activities. The oak-hickory mixtures decayed faster than oak and oak-pine mixtures at MOFEP; however, discovering what mechanisms underlie the mixed litter decomposition will be important. For fully understanding the mechanisms of mixed litter decomposition and their controlling factors, both field long term comparable incubations (i.e., single vs. mixed leaves) and laboratory experiments are necessary for further elucidating the controls and environmental conditions. Meanwhile, measuring the mass and nutrient content of annual litter input, labile material, leaching losses, and soil fauna are important to decomposition processes. Thus, long term, comprehensive, and comparable leaf litter decomposition experiments will be helpful in explaining forest floor dynamics, carbon, and nutrients cycling in the forest ecosystem.

5.3 Recommendations for forest managers

This study suggests that ecosystem carbon storage was greatly changed following timber harvesting at MOFEP compartments. Specifically, coarse woody debris was significantly increased after timber harvesting. I recommend that forest managers take coarse woody debris into consideration and be included as management goals for the harvesting stands. Coarse woody debris also increased the quantity of fuel loading in those stands, which is a hazard to the forests from fire. Coarse woody debris can alter the micro habitats suitable for microorganisms' colonization, which can promote decomposition processes. Thus, coarse woody debris should be given more attention in forest management plans, especially, after intensive timber harvesting.

Leaf litter mixtures promoted decomposition processes in the MOFEP study sites. This suggests that mixed species rather than monoculture forest management were more beneficial for carbon and nitrogen cycling, especially, nutrient release from litter decomposition processes. Although multi-species composition within a management plan is often adopted in forest management for promoting biodiversity, it also should be considered for carbon and nitrogen cycling objectives, and thus fulfill multiple ecological goals at different scales within the same management activity.