A Thesis

Entitled

Partitioning Soil CO_2 Efflux through Vertical Profiles of Manipulated Forests in MOFEP

by

Rachel Henderson

Submitted as partial fulfillment of the requirements for the

Master of Science in Biology

Advisor: Dr. Jiquan Chen

Committee Member: Dr. Christine Mayer

Committee Member: Dr. Michael Weintraub

College of Graduate Studies

The University of Toledo

May 2007

An Abstract of

Partitioning Soil CO_2 Efflux through Vertical Profiles of Manipulated Forests in MOFEP

Rachel Henderson

Submitted as partial fulfillment of requirements for
The Master of Science in Biology

The University of Toledo
May 2007

Soil efflux (SEF) is an important component in the global carbon cycle. The combination of root and microbial respiration, SEF is often used as a measure of biological productivity in the soil. Although SEF has been widely studied, some areas have been neglected, including the effect of timber harvest management on SEF and SEF in different soil horizons. Timber harvesting compacts the soil, removes standing vegetation, increases debris, alters the microclimate, etc., all of which could potentially alter SEF.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term study in which the Missouri Department of Conservation (MDC) installed experiments of singletree uneven-age (UAM), clear-cut even-age (EAM), and control no-cut (NHM) timber harvests to seek ecosystem-management alternatives. To determine the effect of timber harvest on subsurface soil efflux, I dug 9 soil pits (maximum depth 120 cm), 3 in each treatment to directly measure the magnitude of changes of SEF across the soil profile. In each pit, I measured SEF (g m^{-2} hr^{-1}), soil temperature (˚C), soil moisture (%), soil carbon (%, C), nitrogen (%, N), and C/N ratio, fine and coarse root biomass (g), and fine root total C (%), N (%), and C/N ratio. I had hypothesized that SEF would decrease with increasing depth because of decreasing roots and microbes. I also hypothesized that only the ground and surface horizons would have a different treatment SEF because of microclimate and biological inputs that were different on the surface and would homogenize deeper in the soil. My field data in 2005 and 2006 led me to reject these hypotheses. Instead, I found SEF to be the highest in the deepest portion of the soil pit for EAM and UAM, double that of NHM at the same depth and surface efflux of all three treatments.

Acknowledgements

I would like to thank the many people that made this project possible. First, I would like to thank my advisor, Dr. Jiquan Chen, for his support and advice. I would also like to thank my committee members, Dr. Christine Mayer and Dr. Michael Weintraub, for their advice and constructive criticism.

Second, I would like to everyone at the Landscape Ecology and Ecosystem Science Laboratory, both past and present, who provided training in field equipment use, statistical analysis, graduate school logistics, and gave advice on presentation, especially Dr. Asko Noormets, Nan Lu, and Gwen Tenney. In particular, I would like to thank my partner in this project, Qinglin Li, without whom I would have been lost.

Next, I would like to thank the people in Missouri who assisted me throughout this project. In particular, I would like to thank the MDC researchers Randy Jensen, Kyle Steele, and Brandon Kell. These people helped in the planning, the digging of soil pits, and fixing other miscellaneous problems. I would also like to thank my field assistants: Taylor Troiani, Ashley Rhea, and Sally Betz.

Finally, I would like to thank the Missouri Department of Conservation and the University of Toledo for their financial and technical support.

Table of Contents

List of Tables

List of Figures

List of Symbols

Treatments:

NHM	No-Harvest Management
EAM	Even-Age Management
UAM	Uneven-Age Management

Other:

C	Carbon
D_X	Depth (cm)
DBH	Diameter at Breast Height
MOFEP	Missouri Ozark Forest Ecosystem Project
N	Nitrogen
SEF	Soil CO_2 Efflux

X=depth where measurement was taken

1.0 Introduction

1.1 Soil Efflux in Soil Profiles

A report of a recent NSF-sponsored workshop brought to the attention of policymakers the need for more in-depth studies of the soil, not just the rooting zone, because subsurface soil horizons are poorly understood (Brantley et al., 2006). Soil efflux (SEF) is the process of releasing carbon dioxide (CO_2) from the soil into the atmosphere and is controlled by CO_2 production, the strength of the concentration gradient between the soil and the atmosphere, wind speed, and soil properties, such as pore size and temperature (Raich and Schlesinger, 1992). Surface SEF is the combined flux from roots and microorganisms from different soil depths and is used as a measure of biological productivity in the soil. The annual global CO_2 flux from soils is estimated to be an average of 68 Pg C yr^{-1} (Raich and Schlesinger, 1992). SEF can help us understand the terrestrial C cycle and provide clues for many uncertainties in C cycle science. The overall objective of this study was to examine SEF in a soil profile for three experimental harvest treatments. The goal of this study was to determine if even-age clear-cutting (EAM) or uneven-age single-tree harvesting (UAM) would alter the SEF, especially in the sub-surface strata. Management practices that reduce the overall biological productivity of the soil, measured by SEF, may have negative effects on both the ecosystem and global C cycling.

Previous studies have estimated root respiration to account for as much as 70% of total SEF and most roots were in the first 30 cm of the soil (Pregitzer et al., 1998, Kuzyakov and Cheng, 2001, Lee et al., 2003). Root respiration in sugar maple plantations declined with depth and larger root diameters (Pregitzer et al., 1998). Since root respiration is a key component of SEF, I expected the highest SEF in the places with the largest number of fine roots. Additionally, microbial richness, diversity, and total microbial biomass decreased with soil depth (Fierer et al., 2003, LaMontagne et al., 2003). Microbial densities were almost 1-2 orders of magnitude higher at the soil surface than at 2 m depth (Fierer et al., 2003). It follows that since the surface has the most roots and microbes, the SEF closest to the surface would be the highest (Fig. 1). A study by Davidson et al. (2006) used mathematical calculations based on field data to demonstrate this principle.

Because SEF is the combination of root and microbial efflux, factors that affect roots and microbes also influence SEF. Several factors and their interactions affect SEF rates, such as soil temperature, moisture, and texture, root N concentrations, and substrate quantity and quality (Raich and Schlesinger, 1992, Grant and Rochette, 1994, Boone et al., 1998, Pregitzer et al., 1998). Soil temperature is usually the dominant driver of SEF (Raich and Schlesinger, 1992, Lloyd and Taylor, 1994, Kirschbaum, 1995). In water limited systems, soil moisture has been seen to be an important variable in explain SEF (Concilio et al., 2005). Other variables, such as soil C and N and root C, N, biomass, etc., have also been used to explain SEF (Schenk and Jackson, 2002, Hibbard et al., 2005, Davidson et al., 2006).

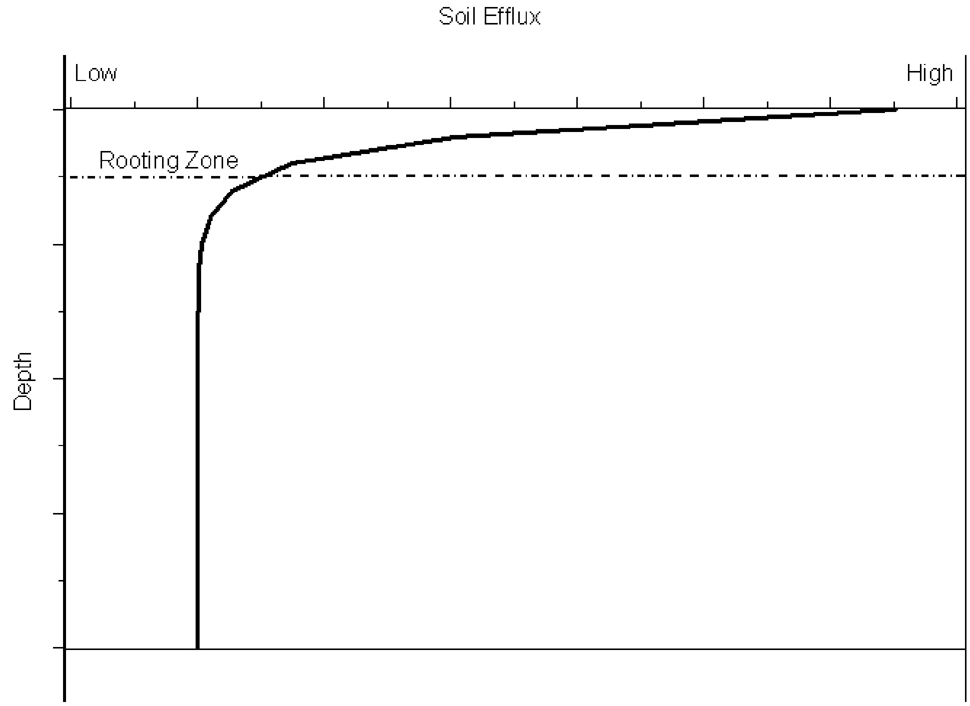

Figure 1. Theoretical soil efflux with increasing depth.

Although much research has been conducted on SEF over the past century, some areas of research have been largely neglected, such as the CO_2 efflux below the soil surface. Management effects on SEF is becoming a more popular topic, but is hardly ever combined with belowground SEF research. This study hopes to provide insight on these topics.

1.2 Management Effects

Examining soil beyond the top 30 cm is a relatively new and infrequently researched area. Even less research has been performed on management practices and their effect on deeper soil horizons. Timber harvesting compacts the soil, removes standing vegetation, increases debris, alters the microclimate, etc., all of which could potentially alter SEF. We also do not know how these disturbances alter the C dynamics below the surface soil layers.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a large-scale study that attempts to look at the effect of different timber harvest managements on multiple biotic and abiotic ecosystem characteristics and overall functional response (Fig. 2). Lessons can be learned about the application of large-scale, both spatially and temporally, experiments in natural resources management. This project provides important, long-term data for managers. The experimental treatments are clear-cut even-age management (EAM), singletree uneven-age management (UAM), and control no-harvest management (NHM).

1.3 Objectives

To better understand the effect timber harvest management has on SEF of subsurface soil horizons, I dug 9 soil pits at MOFEP. The goal was to determine if EAM or UAM would alter surface or subsurface SEF when compared to a control. The factors that ordinarily have the largest influence on SEF, soil temperature and moisture, tend to be more variable near the surface and be affected by timber harvesting. For this reason, I hypothesized that the treatments would be significantly different. When separated by depth, I expected the surface level of the soil profile to be the most different and, since the variation in the factors tends to decrease with increasing soil depth, the treatments would become more similar deeper in the soil. Management practices that reduce the overall biological productivity of the soil, measured by SEF, may have negative effects on both the ecosystem and global C cycling.

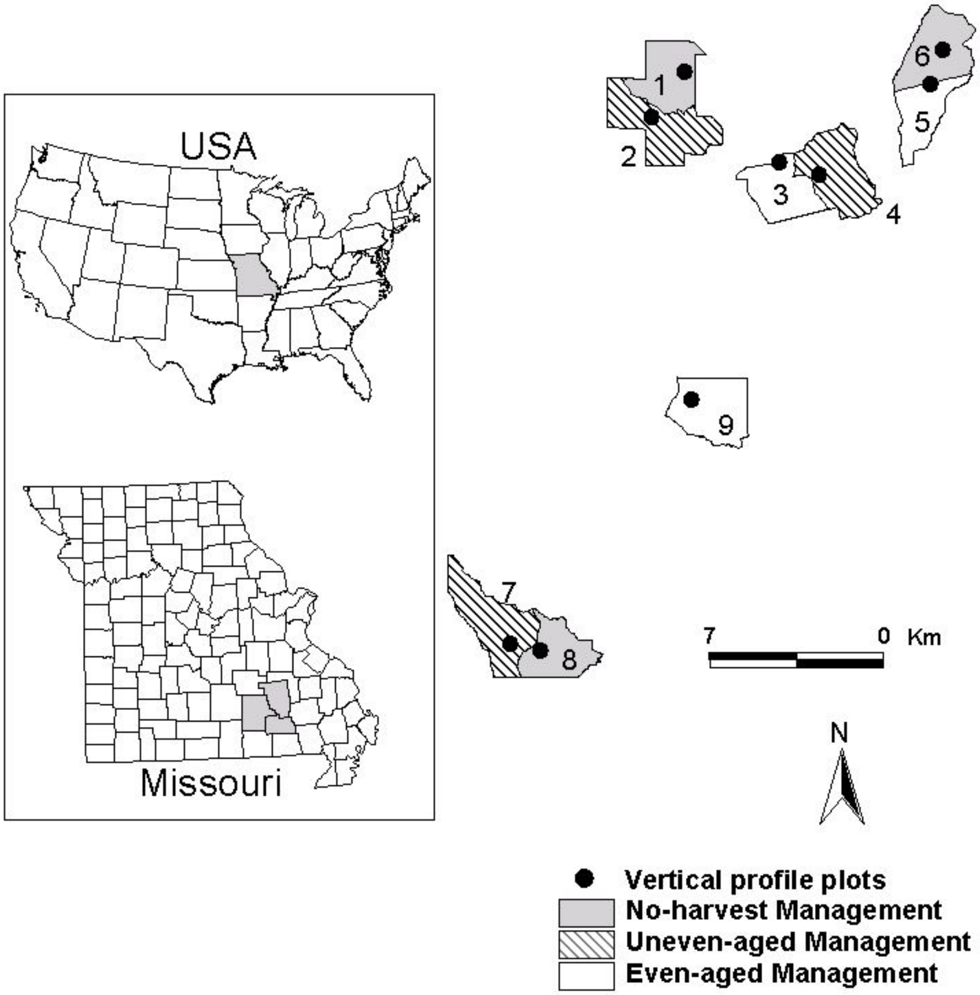

Figure 2. The location and experimental treatments for the Missouri Ozark Forest Ecosystem Project (MOFEP).

2.0 Methods

2.1 Study Area

The Missouri Ozark Forest Ecosystem Project (MOFEP) was a 100-year study located in the southeastern Missouri Ozarks (19°12’W and 37°06’N) and occupied Reynolds, Carter, and Shannon counties. Defined by the Missouri Department of Conservation (MDC) guidelines, MOFEP was a random-block design with a total of nine compartments that include three control no-harvest (NHM), even-age clear-cut harvest (EAM), and uneven-age single-age harvest (UAM) compartments each (Fig. 3a and b) (Brookshire and Dey, 2000)

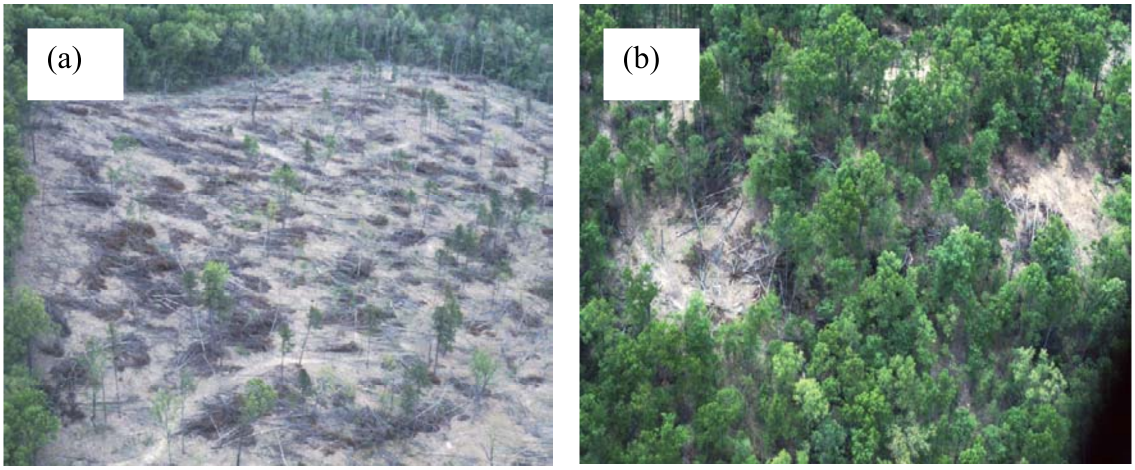

Figure 3. (a) Even-age experimental treatment (EAM) and (b) uneven-age experimental treatment (UAM) at MOFEP in the southeast Missouri Ozarks.

The treatments were initiated in 1996 and ranged from 260-527 ha. MOFEP's old-growth trees were approximately 50-70 years old and the forest was predominantly oak-hickory. In 2005-2006, EAM had over double the number of trees, vines, and shrubs than NHM and UAM, with 77.32% of this vegetation falling in the 0-5 cm diameter at breast height (DBH) class. UAM and NHM had 41.53 and 33.90% of its vegetation in this DBH class, respectively. NHM had more trees in the 5-10 cm and 10-15 cm DBH class (Table 1). Oaks (*Quercus spp.*) were the major species in all treatments. EAM had more sassafras (*Sassafras albidum*) and flowering dogwood (*Cornus florida*) than the other treatment (Table 2; Randy Jensen, *pers.comm.)*.

Table 1. Percent of trees in each diameter breast height (DBH, cm) class (2005-2006).

DBH (cm)	NHM	EAM	UAM
0-5	33.90 %	77.32%	41.53%
5-10	37.07%	13.27%	34.95%
10-15	17.32%	6.23%	17.58%
15-20	9.02%	2.04%	5.27%
20-25	2.68%	0.81%	0.66%
25-30	-	0.31%	-

Table 2. Percentage of major species in each treatment (2005-2006).

Species	NHM	EAM	UAM
*Acer rubrum (*Red Maple*)*	12.5%	13.07%	0.20%
Carya texana (Black Hickory)	6.13%	2.09%	5.33%
Cornus florida (Flowering Dogwood)	5.64%	14.77%	5.33%
Quercus alba (White Oak)	27.45%	6.98%	13.32%
Q. coccinea (Scarlet Oak)	9.31%	6.98%	13.32%
Q. veluntina (Black Oak)	20.59	8.18%	15.98%
Sassafras albidum (Sassafras)	2.69%	12.38%	2.25%

The region was almost 85% forest with breaks for roads and small towns. This study took place in 2005 and 2006. MOFEP's average annual temperature and rainfall was 13.3°C and 1120 mm, respectively (Xu et al., 1997).

2.2 Profile Characteristics

The locations of the soil pits (N=9) were chosen to minimize differences between soil types, slopes, and aspects. Three pits were dug in each treatment type. The soil pits were located in plots designated as the Clarksville soil series, classified as Mesic Typic Paleudults, on north and east facing slopes with similar aspects (N=9). They were on backslopes or shoulders and the parent material was defined as gravelly colluvium over clayey residuum from cherty dolstone. This soil series was strongly acidic, goes from silt loam to clay loam, silty clay loam, or clay down the soil profile. Rock fragments ranged from 0 to 70% down the series profile. Finally, the soil went from a dark grayish brown in the A horizon to red by the Bt horizon (Skoor, 2006). I was unable to determine bulk density. Selected physical and chemical properties are shown in Table 3 (Brookshire and Dey, 2000).

Table 3. General physical and chemical properties of the soil profiles (Brookshire and Dey, 2000). Temperature and moisture ranges were obtained from data collected between May and August 2005 and 2006. ND means no data available.

Treatment	Site	Depth (cm)	Surface Texture	Subsurface Texture	Temperature Range (ºC)	Moisture Range (%)
NHM	1	120	Cobbly silt loam	Cobbly silt loam	10.7-24.9	10.14-46.65
NHM	6	60	Very gravelly silt loam	Very cobbly silt loam	12.5-25.5	10.05-48.62
NHM	8	60	Very gravelly silt loam	Very gravelly silty clay loam	13.5-27.8	10.05-45.75
EAM	3	120	Very gravelly silt loam	Very gravelly silty clay loam	9.4-28.1	10.03-45.08
EAM	5	76	ND	ND	14.5-26.2	10.62-48.98
EAM	9	60	Extremely cobbly silt loam	Very cobbly silt loam	13.5-29	10.09-42.37
UAM	4	120	Very gravelly silt loam	Very gravelly silt loam	8-27	10.19-49.44
UAM	2	76	Very gravelly silt loam	Very gravelly silt loam	12.3-28.1	10.39-35.17
UAM	7	86	Extremely cobbly silt loam	Very cobbly silty clay loam	13.3-26.6	10.03-49.72

2.3 Instrumentation and Measurements

In May 2005, the nine soil profiles were evacuated to a maximum depth of 120 cm (depending on the soil depth). A maximum of six fine root samples were taken every 10 cm for the first 30 cm and then every 30 cm for the remaining 90 cm using a soil core (81 cm^2). Coarse roots (≥ 2 mm diameter) were removed in the same increments as the fine roots for the entire pit. The root samples were washed, oven-dried, and weighed. Soil samples were taken every 30 cm. Fine root and soil samples were oven-dried (65˚C), sieved to 2 mm, and crushed. Total carbon and nitrogen were measured with a CHN analyzer (Perkin Elmer 2400 Series II CHN/O Analyzer).

The trench walls were sealed with a plastic vapor barrier, insulated, and roofed. Two PVC collars (10 cm diameter) were inserted vertically into the pit wall every 30 cm. Two collars were placed on the ground adjacent to the soil pits. All of the soil collars were placed at least 2 cm into the soil to ensure a good seal with the ground (Fig. 4). SEF measurements were made on the PVC collars with a portable infrared gas analyzer (IRGA, EGM-4 Environmental Gas Monitor, PP Systems, UK) attached to a SEC-1 soil respiration chamber (PP Systems; Fig. 5). SEF

Figure 4. Installation of soil efflux measurements.

measurements were taken over a 100 sec period. Two time domain reflectometer (TDR) probes were inserted in the soil inside each of the collars and measured using a TDR 100 unit (Campbell Scientific Inc, Logan UT) for volumetric soil moisture content (%, Fig. 6). Soil temperature was measured with a handheld thermometer (˚C, Taylor pocket digital thermometer) simultaneously with SEF and moisture measurements.

Continuous soil temperature data were also recorded as 30 min means with hobo dataloggers (Onset Computer Corp., Bourne, MA). Data was collected once every week to 10 days between June-September 2005 and May-September 2006 and once approximately every 3 months for the remainder of the year. In 2006, 3 additional soil pits were dug, hobo dataloggers for continuous soil temperature were inserted into the soil profile, and then the soil pits were refilled to determine the temperature differences between open and closed pits.

Figure 5. Picture of the EGM-4, which is used to measure SEF.

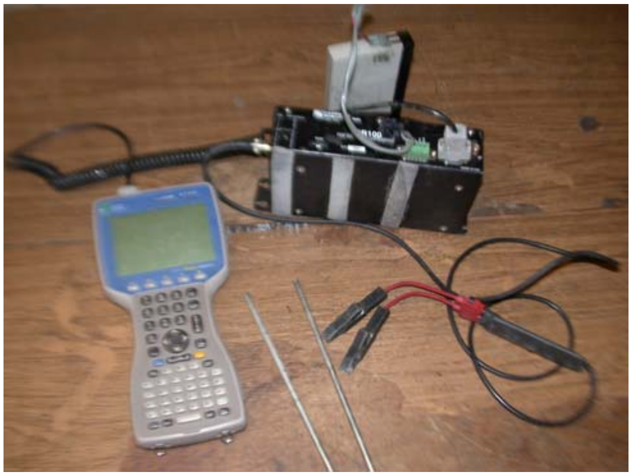

Figure 6. Picture of TDR 100, Allegro, and rods used to measure soil moisture.

2.4 Statistical Analysis

SEF lower than 0 and higher than 5 g CO_2 m^{-2} hr^{-1} were eliminated from the analysis (total: 0.5% removed). Moisture data below 10% and above 50% were also eliminated (total: 15% removed). These data were removed because of biophysical impossibilities and mechanical inaccuracies. The data on the same soil level in each soil pit were averaged before analysis. Shapiro-Wilk tests for normality showed that data were skewed and significantly non-normal. SEF, soil temperature, fine root weight, and soil C, N, and C/N were transformed using natural log to meet the assumption of normality. Coarse root biomass was transformed to meet assumptions of normality by $\log_{10}$. Soil moisture was transformed to assume the normality of residuals using an inverse function. Means and standard errors were calculated for all these variables by treatment and depth (N=3 per treatment). Repeated-measure ANOVAs, ANCOVAs, and Tukey's tests determined differences between treatment and depths for $\alpha=0.05$. I also performed correlations to determine the variables that corresponded with SEF (SAS version 9.1; SAS institute Inc, 2005). These analyses were conducted separately on the summer and winter data.

Since temperature is known to often strongly influence SEF, an exponential equation (Eq. 1) was used to describe the relationship between temperature and efflux:

$$R=R_0*e^{\beta T} \qquad \text{(Eq. 1)}$$

where R was soil efflux, T was temperature, and R_0, or base efflux, and β were fitted parameters. Q_{10} is an indicator of temperature sensitivity, defined as the increase in the rate of a chemical reaction when the temperature increases 10ºC. It is used in many ecosystem models and is often regarded as a constant (Xu and Qi, 2001). The Q_{10} values were derived by the equation (Eq. 2):

$$Q_{10}=e^{10\beta} \qquad \text{(Eq. 2)}$$

CO_2 concentration and soil diffusivity may influence measured SEF, although it does not affect the true efflux rate of roots or microbes in the soil. Flux was the difference between the CO_2 concentration in the soil and the concentration in the EGM chamber divided by the distance. If the distance between these two concentrations was greater, then the flux was smaller because of diffusivity. When the diffusivity factor was separated into two terms, then 1/D (diffusivity) was substituted by α and C2/D (the chamber concentration divided by diffusivity) was substituted by $-\beta$. These substitutions yielded Eq. 3:

$$\text{Flux}=C_1 * \alpha + \beta \qquad \text{(Eq. 3)}$$

where flux was the measured SEF, C_1 was the measured CO_2 concentration, and α and β were previously defined. The α and β values were then used to calculate the flux determined by the measured concentration. I calculated diffusivity by dividing 1 by α and the chamber concentration by dividing β by α.

3.0 Results

3.1 Variables Affecting SEF

A repeated-measures ANOVA determined significance for treatment, depth, time, and the interaction. An ANCOVA was performed with depth as a covariate. EAM was 19.91˚C at D_{105}, compared to 17.77 and 17.86 for NHM and UAM, respectively ($F_{treatment}$=4.62, P=0.0105; F_{depth}=69.60, P<0.0001; Table 4; Fig. 7a). Treatment was not significant without the depth factor ($F_{treatment}$=0.10, P=0.9070). Depth was a significant covariate (F= 23.26, P<0.0001; Table 5). There were no significant differences between treatments in the winter (Fig. 7b). Temperature correlated with SEF for all three treatments (R=0.42799, P<0.0001; R=0.26332, P=0.0002; R=0.25833, P=0.0003, for NHM, EAM, and UAM, respectively). In general, soil temperature decreased with increasing depth in the summer and increased with increasing depth in the winter. The continuous temperature difference, measured by hobo dataloggers, between the open and refilled soil pits ranged from 0.05-1.33ºC.

Soil moisture was variable throughout the summer. Overall, EAM had higher soil moisture than the other treatments ($F_{treatment}$=13.12, P<0.0001; F_{depth}=0.81, P=0.5190). Treatment was not significant without the depth variable in the model ($F_{treatment}$=0.98, P=0.3776). Treatment was significant when depth covaried with treatment (F=6.98, P<0.0001). The soil moisture in the winter was not significantly different (Fig. 8). Soil moisture correlated with SEF for EAM and UAM (R=0.21099, P=0.0086; R=0.23129, P=0.0097, respectively).

Table 4. A two-way ANOVA table for soil efflux, temperature, and moisture for the terms treatment, depth, time, and the interaction between treatment and depth.

Term	Soil Efflux		Soil Temperature		Soil Moisture	
	F-value	P-value	F-value	P-value	F-value	P-value
Treatment	9.04	0.0002	4.62	0.0105	13.12	<0.0001
Depth	15.52	<0.0001	69.60	<0.0001	0.81	0.5190
Time	5.93	<0.0001	125.94	<0.0001	12.42	<0.0001
Treatment* Depth	4.54	<0.0001	1.33	0.2280	3.62	0.0006

Table 5. ANCOVA F and P-values for soil efflux, temperature, and moisture by treatment, depth, time, and the interaction between treatment and depth

Term	Soil Efflux		Soil Temperature		Soil Moisture	
	F-value	P-value	F-value	P-value	F-value	P-value
Treatment	2.21	0.1104	1.33	0.2646	6.98	0.0011
Depth	21.73	<0.0001	23.26	<0.0001	1.23	0.2684
Time	1.49	0.1054	3.08	<0.0001	8.12	<0.0001
Treatment* Depth	3.64	0.0270	4.26	0.0146	1.71	0.1828

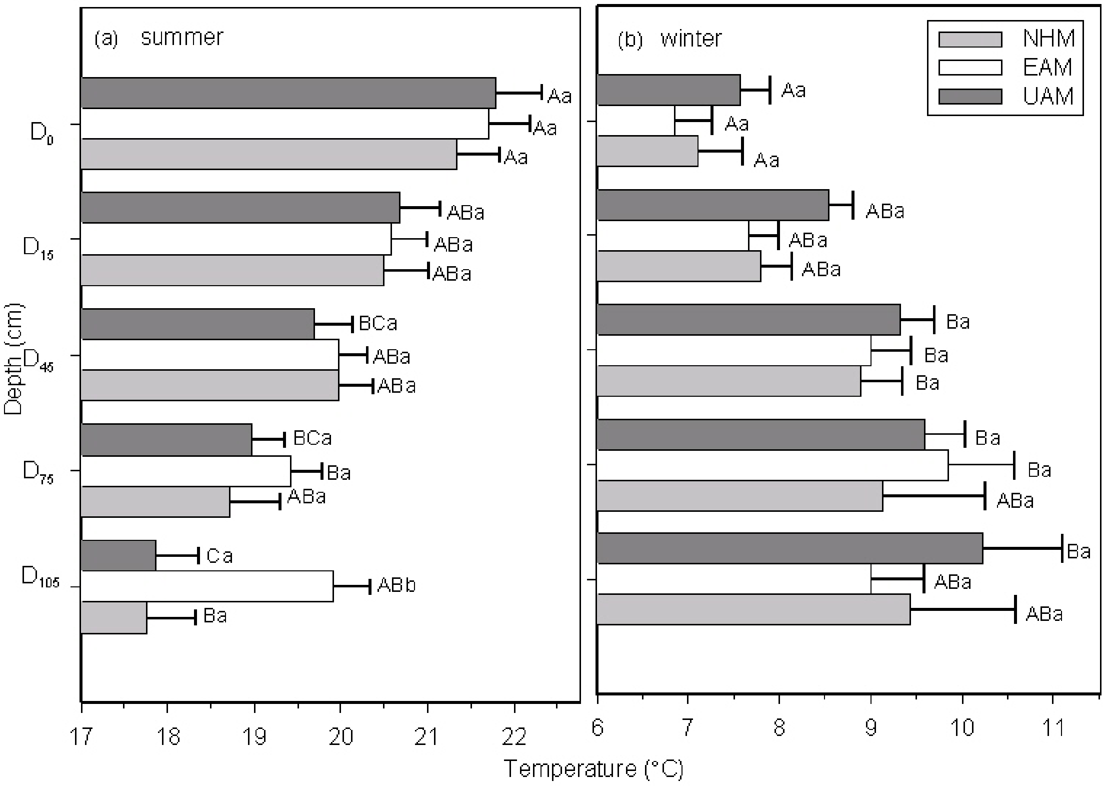

Figure 7. (a) Mean summer soil temperature for no harvest (NHM), even-age (EAM), and uneven-age (UAM) managements by depth. (b) Mean winter soil temperature for the three treatment types by depth. Upper case letters signify differences among depths, while the lower case letters represent significant differences between treatments. Statistics were performed on transformed data. Error bars=1 SE.

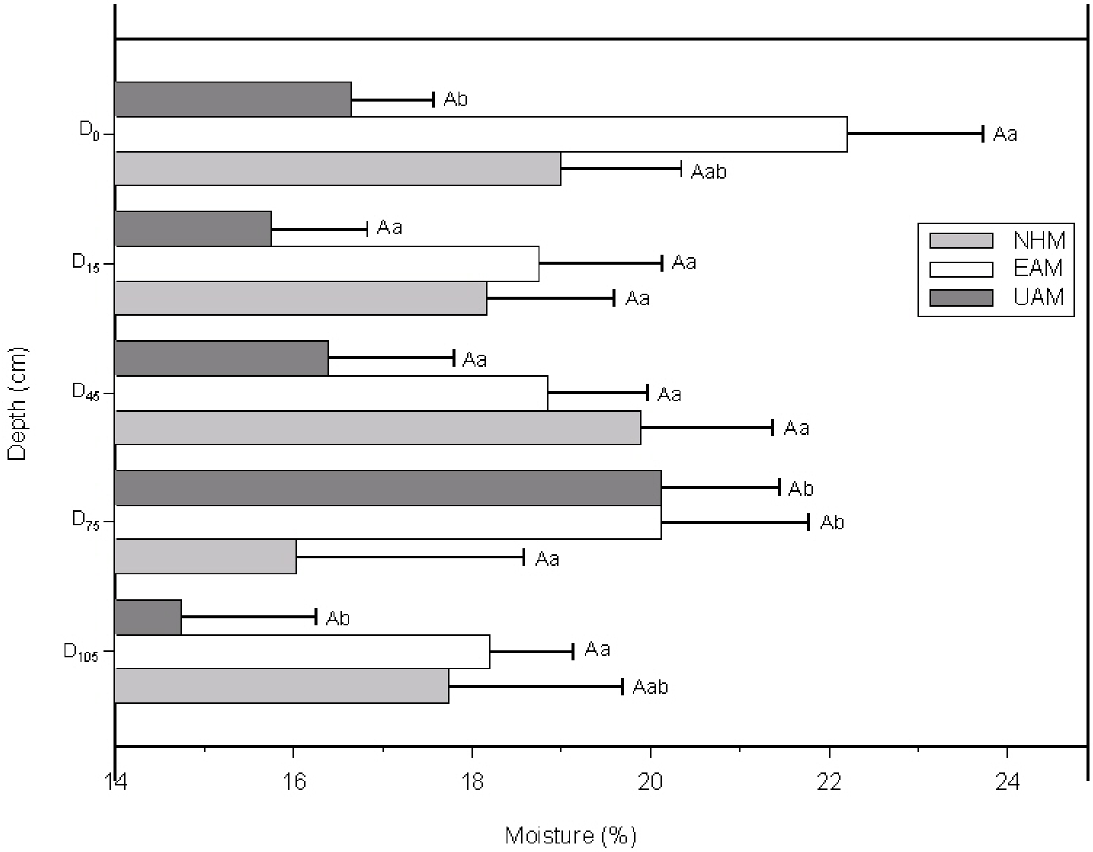

Figure 8. Mean summer soil moisture by depth for the three harvest management treatments. Abbreviations the same as in Fig. 7. Statistics were performed on transformed data. Error bars=1 SE.

Since root respiration is a major part of SEF, we can assume that a larger biomass of roots will correspond with a higher SEF, especially fine roots which tend to respire more. Fine and coarse root biomass showed no differences between treatments (Fig. 9a and b). Fine root biomass, although not significant, negatively correlated with SEF (R=-0.71412, P=0.0714). For the total roots, EAM (5973.48 g) had a lower biomass than both NHM (9681.1 g) and UAM (12,255 g, Fig. 10). Both fine and coarse root biomass decreased with soil depth.

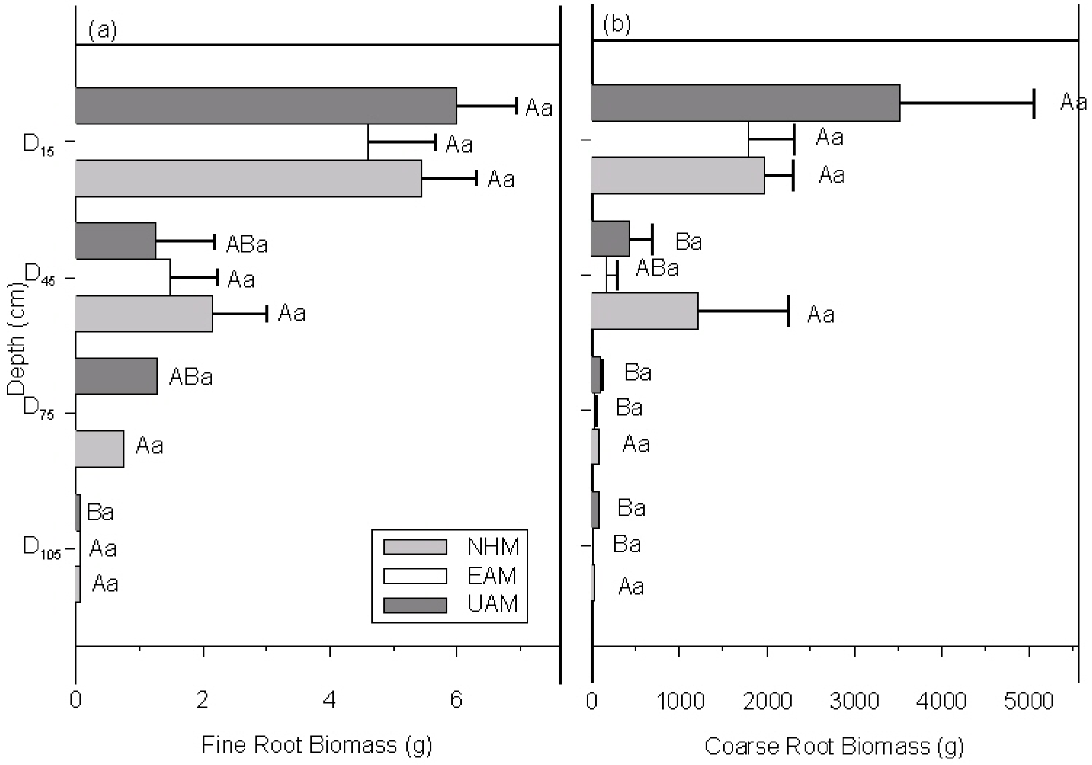

Figure 9. (a) Mean fine root biomass and (b) mean coarse root biomass of three experimental treatments at the MOFEP site. Abbreviations the same as in Fig. 7.

In NHM and UAM, root C varied between 30 and 38% throughout the profile, while EAM increased with depth and from 26 to 42%. Root N varied between 0.22 and 0.88%, usually decreasing with depth. The root C/N ratio ranged from approximately 47-180, 37-196, and 39-138 for NHM, EAM, and UAM, respectively (Table 6). There were no treatment differences for root C, N, or C/N ratio. Depth was significant for root N and C/N ratio (F=23.69, P<0.001; F=62.71, P<0.0001), but the C/N ratio was calculated for root N, so that may account for this result.

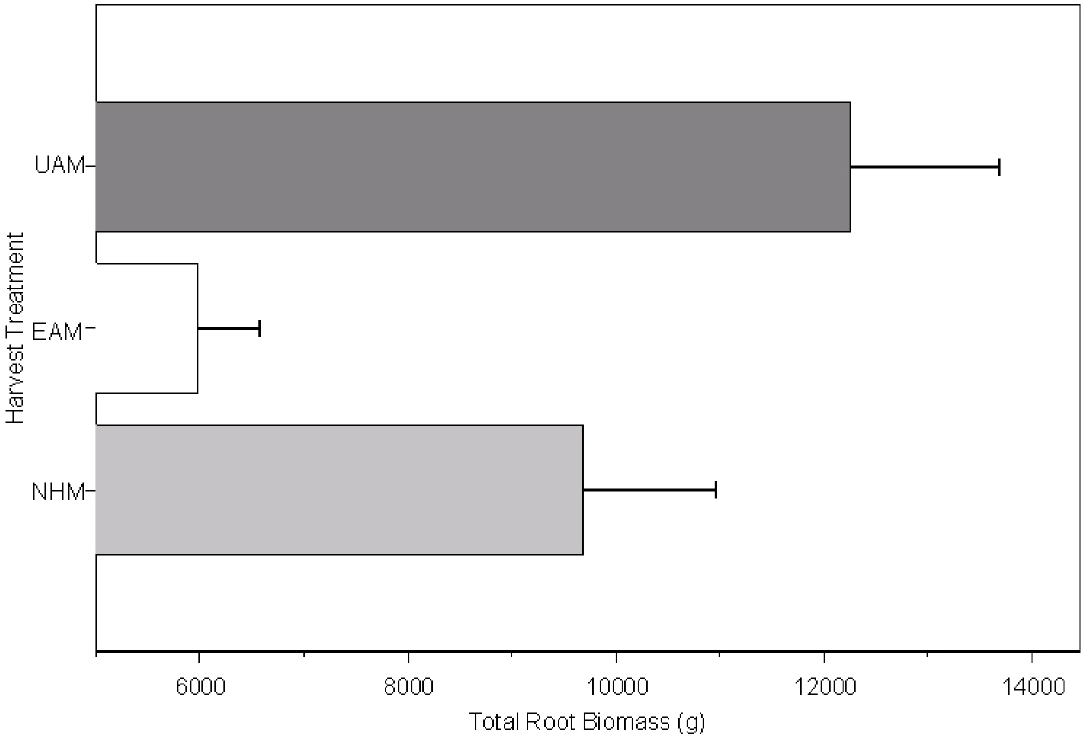

Figure 10. Total root biomass for the three experimental treatments. Error bars=1 SE.

Soil C, N, and C/N ratio tended to decrease with depth, so the nutrient richness was highest at the surface. There were no treatment differences for soil C, N, or C/N ratio. Depth, however, was a significant factor for all three variables ($F_{soil\ C}$=37.23, P<0.0001; $F_{soil\ N}$=10.42, P<0.0001; $F_{soil\ C/N}$=14.90, P<0.0001; Table 7).

Table 6. Mean root C, N, and C/N ratio values of no-harvest (NHM), even-age (EAM), and uneven-age (UAM) management by depth. Capital letters represent significant differences among treatments. Lower case letters signify differences between treatments.

Treatment	Depth	C (%)	N (%)	C/N ratio
NHM	D_{5}	31.36^{Aa}	0.73^{Aa}	47.97^{Aa}
	D_{15}	37.29^{Aa}	0.39^{Ba}	97.68^{Ba}
	D_{25}	30.46^{Aa}	0.35^{Ba}	95.54^{Ba}
	D_{45}	30.28^{Aa}	0.25^{Ba}	112.39^{Bab}
	D_{75}	31.71^{Aa}	0.44^{ABa}	86.92^{ABa}
	D_{105}	38.49^{Aa}	0.22^{Ba}	180.64^{Cab}
EAM	D_{5}	26.46^{Aa}	0.78^{Aa}	37.09^{Aa}
	D_{15}	26.72^{Aa}	0.42^{Ba}	65.50^{Bb}
	D_{25}	35.41^{Aa}	0.64^{ABb}	64.57^{ABa}
	D_{45}	33.70^{Aa}	0.51^{ABb}	82.15^{Ba}
	D_{75}			
	D_{105}	42.13^{Aa}	0.22^{Ba}	195.70^{Ca}
UAM	D_{5}	33.58^{Aa}	0.88^{Aa}	38.92^{Aa}
	D_{15}	31.60^{Aa}	0.44^{Ba}	72.65^{Bb}
	D_{25}	37.57^{Aa}	0.41^{Bab}	93.69^{Ba}
	D_{45}	34.19^{Aa}	0.29^{Ba}	138.03^{Cb}
	D_{75}	31.18^{Aa}	0.27^{Ba}	119.83^{Ca}
	D_{105}	34.66^{Aa}	0.35^{Ba}	101.93^{Bb}

Table 7. Mean soil C, N, and C/N ratio for no-harvest (NHM), even-age (EAM) and uneven-age (UAM) treatment types by depth. Capital letters represent significant differences among treatments. Lower case letters signify differences between treatments.

Treatment	Depth	C (%)	N (%)	C/N ratio
NHM	D_{15}	1.35^{Aa}	0.13^{Aa}	11.19^{Aa}
	D_{45}	0.51^{Ba}	0.09^{Aa}	7.39^{ABa}
	D_{75}	0.31^{Ba}	0.13^{Aa}	5.19^{Ba}
	D_{105}	0.41^{ABa}	0.06^{Aa}	7.40^{ABa}
EAM	D_{15}	1.23^{Aa}	0.10^{Aa}	12.12^{Aa}
	D_{45}	0.49^{Ba}	0.08^{ABa}	6.98^{Ba}
	D_{75}	0.27^{BCa}	0.42^{Ba}	6.37^{BCa}
	D_{105}	0.29^{Ca}	0.11^{ABa}	3.59^{Cb}
UAM	D_{15}	1.47^{Aa}	0.10^{Aa}	14.14^{Aa}
	D_{45}	0.48^{Ba}	0.05^{Bb}	8.92^{Ba}
	D_{75}	0.39^{Ba}	0.08^{Ba}	6.19^{Ba}
	D_{105}	0.28^{Ba}	0.06^{Ba}	4.94^{Bab}

3.2 Soil Efflux and CO_2 Concentration

The only treatment different for the summer was that NHM was almost half that of EAM and UAM for D_{105} ($F_{treatment}$=9.04, $P<0.0002$; F_{depth}=15.52, $P<0.0001$; Fig. 11a). Treatment was not significant without the depth term in the model. Depth was a significant covariate (F=21.73, $P<0.0001$). In the winter, UAM was higher than NHM at D_0 (Fig. 11b).

The measured CO_2 concentration tended to increase with soil depth. As with SEF, treatment was not significant, but depth was significant (F=47.16, P<0.0001; Fig. 12a and b). UAM for the winter was twice as high as NHM and EAM at D_0.

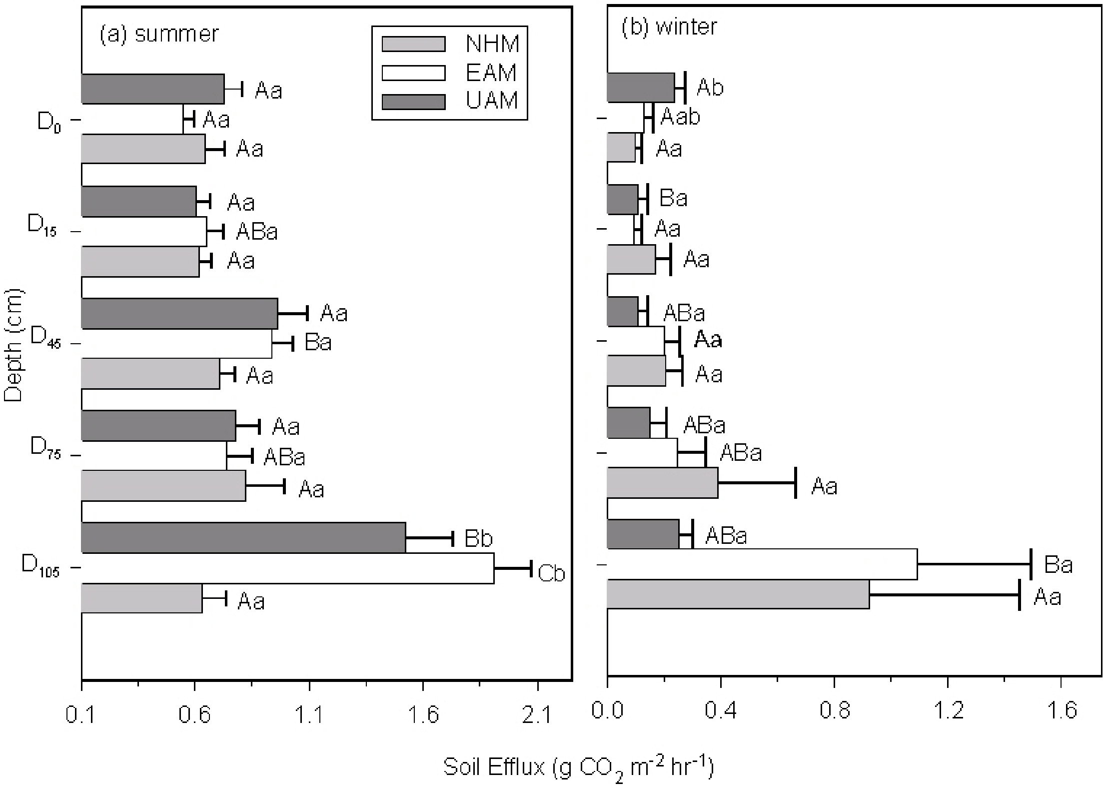

Figure 11. (a) Mean summer soil efflux for no harvest, even-age, and uneven-age management treatments by sampled depth. Abbreviations the same as in Fig. 7. (b) Mean winter soil efflux for the three treatments and five depths. Upper case letters signify differences among depths, while the lower case letters represent significant differences between treatments. Statistics were calculated on lnSEF. Error bars=1 SE.

Using the Q_{10} model, I found that Q_{10} value for each depth and treatment. The D_{105} had the lowest Q_{10} value for NHM and EAM. It was the third lowest value for

UAM. D_{75} had the highest Q_{10} for EAM and UAM. NHM had the highest Q_{10} for D_{15} (Table 8).

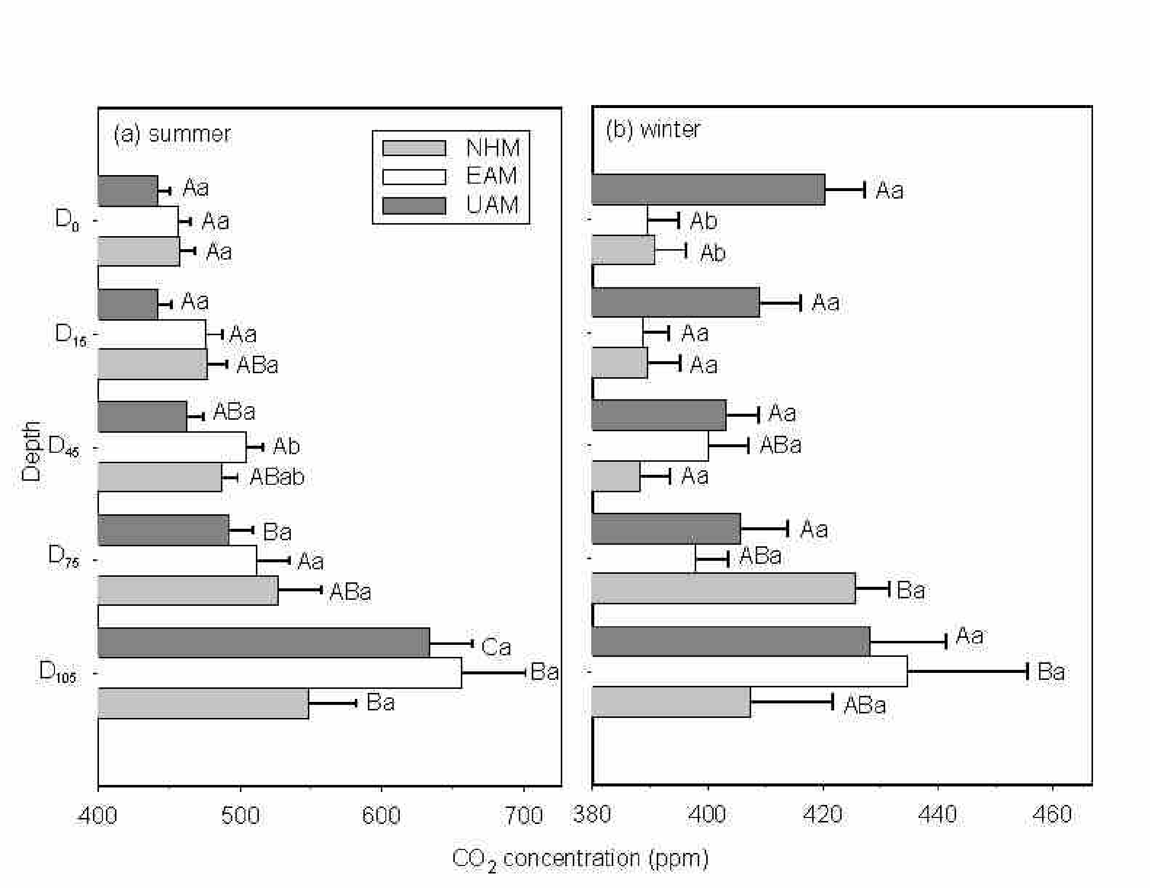

Figure 12. Measured CO_2 concentration by depth for (a) summer and (b) winter. Abbreviations are the same as in Fig. 7.

Table 8. Q_{10} values by depth and treatment.

Depth	NHM	EAM	UAM
D_0	2.6738	2.2707	1.2773
D_{15}	5.2492	1.8991	3.4507
D_{45}	3.0868	1.1618	2.1479
D_{75}	3.5220	9.7451	5.4946
D_{105}	1.1331	1.0049	3.3842

With these Q_{10} values, I was able to predict SEF based on temperature, which correlated with SEF in each treatment. The measured and predicted SEF values followed the same pattern. EAM and UAM had a higher SEF deeper in the soil profile than those of NHM (Fig. 13).

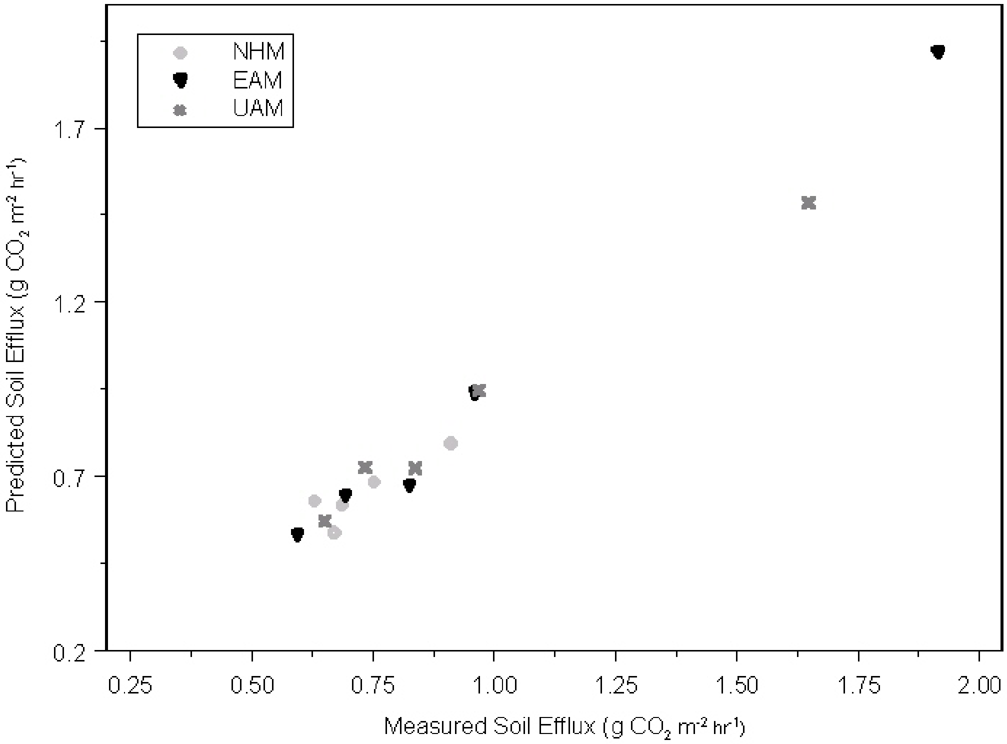

Figure 13. Soil efflux as predicted by the Q_{10} model using the measured soil temperatures and the measured values for each depth.

Using the measured flux and CO_2 concentration, I determined α and β where α was 1/diffusion and β was the concentration of the soil chamber over diffusion. These α and β values were then used to calculate the diffusivity and concentration in the chamber (C2). In both the summer diffusivity and C2, NHM tended to be higher than EAM and UAM. For diffusivity, EAM tended to be higher than UAM (Fig. 14a and b). C2 followed the opposite trend (Fig. 15a and b). In the winter for both diffusivity and C2, NHM D_{45} was much higher than any of the other treatments of depth. This extreme value was an example of problems that can develop when dividing two modeled numbers by each other. Although both numbers were good, and the modeled flux data showed that they were, but when divided they provided a bad result. This value was eliminated to see the pattern in the other treatments. The α, β, and measured concentration values were used to predict the SEF for each depth and management (Fig. 16). The measured and estimated SEF values were very similar.

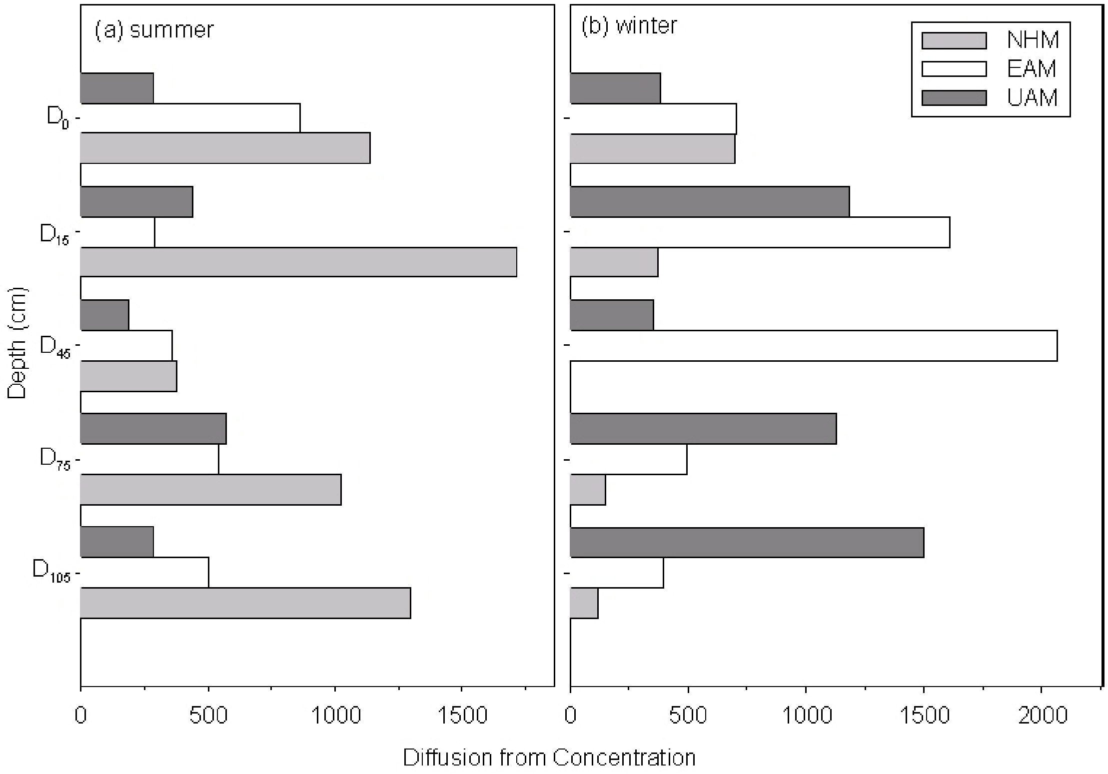

Figure 14. The diffusion in the soil pits by treatment and depth by (a) summer and (b) winter.

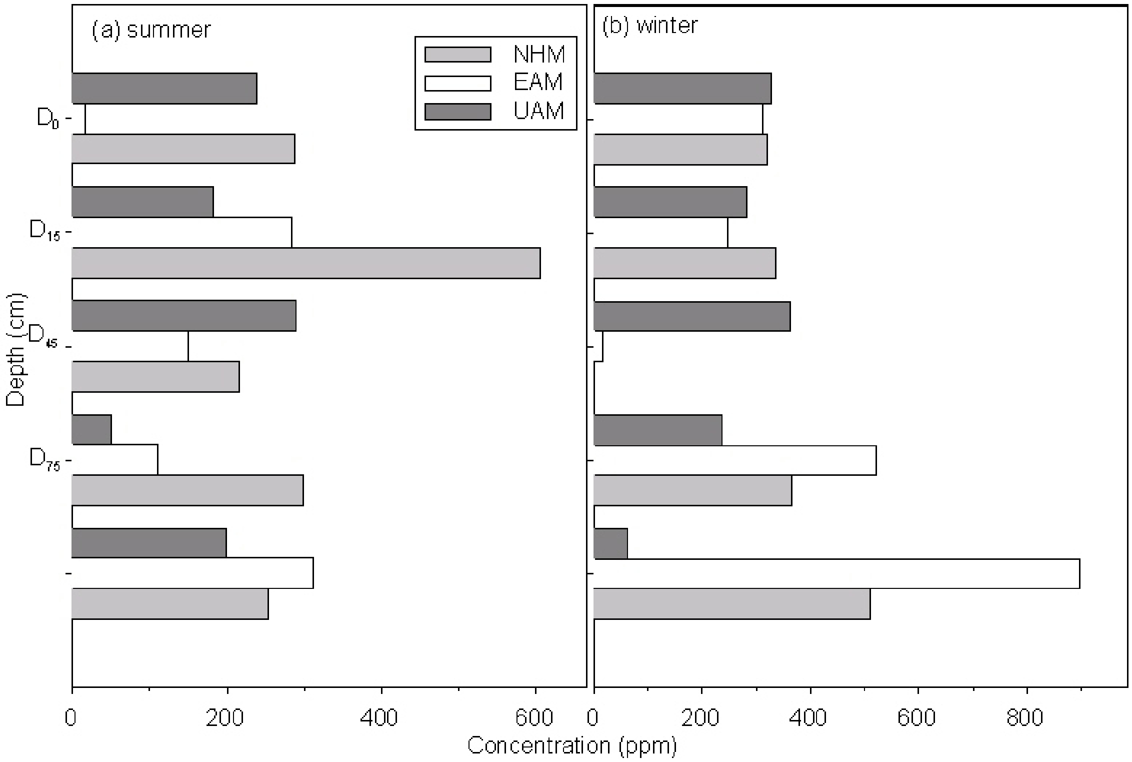

Figure 15. The concentration in the PP Systems EGM chamber in (a) summer and (b) winter by treatment and depth.

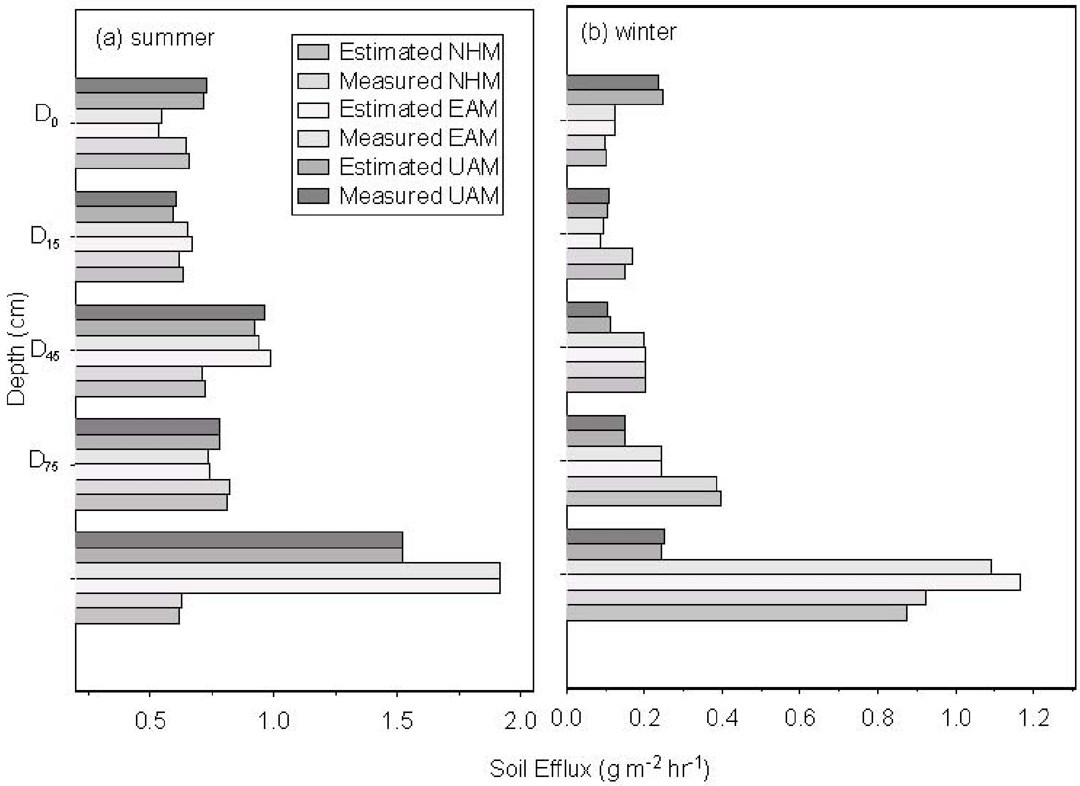

Figure 16. Measured and estimated SEF using concentration by depth and treatment. Abbreviations are the same as in Fig. 7.

4.0 Discussion

4.1 Treatment Effects

EAM and UAM SEF were double the SEF of NHM for $D_{105.}$ They were also double the surface SEF for all treatments, which is unusual because there were fewer microbes and roots deeper in the soil. This finding refuted the commonly held belief that deeper soil would have a lower efflux. On the surface, timber harvesting did not influence soil efflux 10 years after harvesting in the summer. The lack of difference between EAM, UAM, and NHM for summer SEF data for D_0 was surprising in the light of an earlier study that found UAM to be significantly different than EAM and NHM (Concilio et al., 2005). In the winter, however, UAM was significantly higher than that of NHM on the ground.

SEF is controlled by the rate of CO_2 produced by roots and microbes, the strength of the CO_2 gradient between the soil and the atmosphere, and soil properties (Raich and Schlesinger, 1992). The measured CO_2 concentration increased with depth, as expected, and followed the same patterns as SEF. Increased CO_2 concentration may have altered the concentration gradient between the soil and the atmosphere, which would have affected the diffusivity and changed SEF. The higher concentration of CO_2 in deeper soil horizons could be from high CO_2 production rates, slow CO_2 diffusion rates out of the subsurface horizons, or a combination of the two (Hamada and Tanaka, 2001, Cattanio et al., 2002, Fierer et al., 2005). Since only EAM and UAM experienced an increase in SEF and CO_2 concentration deeper in the soil, this suggested that a factor related to timber harvesting caused this change.

Temperature, usually the major predictor of SEF, was not as successful interpreting the differences seen in these data. In the summer, EAM had a higher soil temperature than NHM and UAM, although it was not always significant, possibly because clear-cut harvesting opens the canopy more and allows solar radiation reach the ground (Zheng et al., 2000). The open soil pit raised the temperature between 0.05 and 1.33ºC from the closed pit for each treatment and depth. Bergner et al. (2004) found a 0.4-0.9ºC temperature increase to raise SEF by 20%. Although the open pit clearly changed the temperature, it was an increase experienced uniformly so we are still able to examine overall trends. We did not know, however, if the deeper soil horizons would be more sensitive to changes in temperature.

Q_{10} is a measure of SEF to sensitivity temperature. Therefore, the lower the Q_{10} value, the less sensitive the SEF is to temperature changes. A study by Davidson et al. (2006) showed lower Q_{10} values in the C horizon than in the A or B horizons. Although the official soil series does not define a C horizon, some of these soil pits may have reached it. A low Q_{10} may also be because of easily metabolized C, differences in microbial communities, decreases in C quality, or the interaction between CO_2 production and nutrient availability (Fierer et al., 2003). These possibilities, however, did not explain why UAM was not similarly affected. Two studies found that Q_{10} increased with depth, although one study only went to 50 cm (Xu and Qi, 2001, Davidson et al., 2006).

Using these Q_{10} values, I was able to predict SEF and compare it to the measured SEF. The measured SEF was always higher than the predicted SEF, which may be because SEF-temperature sensitivity models tend to be underestimated in field conditions and may actually be unreliable (Gu et al., 2004). Gu et al. (2004) argued that these temperature sensitivities may be distortions caused by labile C pool dynamics, which could alter the estimates for soil organic C as a source of atmospheric CO_2 in long-term climate predictions. On the other hand, even if these values were underestimations, the Q_{10} for NHM and EAM at D_{105} was still lower than all the other levels and UAM.

Soil moisture is generally used as the other major predictor of SEF. In this case, soil moisture correlated with SEF for EAM and UAM, but not very strongly in either case. Soil moisture for EAM was generally higher at NHM and UAM, but this was not usually significant. The total root biomass of EAM was lower than NHM and UAM, although not significant, which may explain the difference in soil moisture. Previous studies had found that when moisture was limited to the extent that it influenced SEF, it became the most important variable in explaining SEF (Concilio et al., 2005). However, unlike previous studies, neither soil temperature nor moisture explained much of the variation in SEF, suggesting that neither temperature nor moisture had reached this threshold (Mariko et al., 2000, Concilio et al., 2005).

The root C values seemed low. However, these low values may be due to the fact live, dead, and woody roots were not separated before being ground and analyzed. The dead and woody root portions may be responsible for lowering these values. That said, dead roots, on average, only composed of 20% of total root biomass (data not shown). Roots seem to be the likeliest reason for the differences between NHM, EAM and UAM.

EAM and UAM both have the legacy of roots from 10 years ago that may still be decomposing and being incorporated into the soil. EAM, and to some extent UAM, has a high percentage of smaller vegetation by DBH. In fact, 10 years after harvesting, UAM looks compositionally and structurally more like NHM than EAM.

A previous C study at MOFEP found that harvesting reduced stand density by 30% in UAM and 53% in EAM, but did not alter stand species composition. Li et al. (In press) also found that harvesting reduced live tree C and increased the C in coarse woody debris and mineral soil, especially for EAM. Finally, the total C pools were 182, 170, and 130 Mg C ha^{-1} in NHM, UAM, and EAM, respectively, with the most C in live trees for NHM and UAM, but mineral soil stored the most C in EAM (Li et al., In press). Clearly, harvesting has an influence on the aboveground and surface soil, but only rudimentary studies have looked at subsurface effects.

This study has many problems, such as the rise in soil temperature, the possible changes in soil moisture, and the relatively few root and soil samples to SEF, temperature, and moisture samples, which were collected weekly. One final factor that might influence SEF was the compaction of the soil from digging. SEF values taken for another study a maximum of 100 m away found the surface SEF of the soil pits to be between 33 to 53% lower than the undisturbed soil (data not shown). T-tests determined these differences to be significant for each treatment (F_{NHM}=40.54, $P<0.0001$; F_{EAM}=4.90, $P<0.0001$; F_{UAM}=2.93, $P=0.0027$). This compaction would change the SEF values uniformly throughout the study, but alter them from what would be seen naturally.

Clearly, more data needs to be collected before the mechanism of this process can be determined. Soil analysis of the total microbes, porosity, and texture could determine differences at these particular sites that could not be anticipated from earlier studies. Further studies should also attempt to go even deeper into the soil profile to see if this trend continues, or if it was just an anomaly particular D_{105}.

4.2 Conclusions

Different manipulations of the Ozark forest had a clear effect of raising the SEF in soil deeper than a meter. The reason for this increase, however, was not as clear. This study refuted my hypotheses that SEF with decrease with depth and that the treatments would be more dissimilar at the surface. ANOVAs demonstrated that the treatment effect was strongly dependent on the soil depth. We could see that timber harvesting influenced SEF and CO_2 concentrations in soils over a meter deep. Timber harvesting compacts the soil, alters the vegetation structure and composition, creates more coarse woody debris, and generates a legacy of decaying roots. SEF values between the soil pits and undisturbed area was quite different, but the treatments were not different for the undisturbed plots, which dissuades the argument that the SEF values are from harvest compaction. NHM and UAM vegetation structure and composition were similar 10 years after harvesting, while EAM had more, smaller vegetation. Coarse woody debris had not had enough time to incorporate into the soil, which leaves decaying roots. Legacy roots from timber harvesting may be responsible for this pattern, but clearly more studies need to be done to determine if this is the case.

5.0 References

Boone, R. D., Nadelhoffer, K. J., Canary, J. D., and Kaye, J. P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature. 396, 570-572.

Brantley, S. L., White, T. S., White, A. F., Sparks, D., Richter, D., Pregitzer, K. S., Derry, L., Chorover, J., Chadwick, O., April, R., Anderson, S., and Amundson, R., 2006. Frontiers in exploration of the critical zone: Report of a workshop sponsored by the National Science Foundation (NSF). October 24-26, 2005. Newark, DE. 1-30.

Brookshire, B. L., and Dey, D. C., 2000. Establishment and data collection of vegetation-related studies on the Missouri Ozark Forest Ecosystem Project study sites. In: SR Shifley and BL Brookshire. Missouri Ozark Forest Ecosystem Project: Site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. St. Paul, MN: USDA-Forest Service. Pages 1-18.

Cattanio, J. H., Davidson, E. A., Nepstad, D. C., Verchot, L. V., and Ackerman, I. L., 2002. Unexpected results of a pilot throughfall exclusion experiment on soil emissions of CO_2, CH_4, N_2O, and NO in eastern Amazonia. Biology and Fertility of Soils. 36, 102-108.

Concilio, A., Ma, S. Y., Li, Q. L., LeMoine, J., Chen, J. Q., North, M., Moorhead, D., and Jensen, R., 2005. Soil respiration response to prescribed burning and thinning in mixed-conifer and hardwood forests. Canadian Journal of Forest Research. 35, 1581-1591.

Davidson, E. A., Savage, K. E., Trumbore, S. E., and Borken, W., 2006. Vertical partitioning of CO_2 production within a temperate forest soil. Global Change Biology. 12, 944-956.

Fierer, N., Allen, A. S., Schimel, J. P., and Holden, P. A., 2003. Controls on microbial CO_2 production: A comparison of surface and subsurface soil horizons. Global Change Biology. 9, 1322-1332.

Fierer, N., Chadwick, O. A., and Trumbore, S. E., 2005. Production of CO_2 in soil profiles of a California annual grassland. Ecosystems. 8, 412-429.

Grant, R. F., and Rochette, P., 1994. Soil microbial respiration at different water potentials and temperatures - Theory and mathematical-modeling. Soil Science Society of America Journal. 58, 1681-1690.

Gu, L. H., Post, W. M., and King, A. W., 2004. Fast labile carbon turnover obscures sensitivity of heterotrophic respiration from soil to temperature: A model analysis. Global Biogeochemical Cycles. 18.

Hamada, Y., and Tanaka, T., 2001. Dynamics of carbon dioxide in soil profiles based on long-term field observation. Hydrological Processes. 15, 1829-1845.

Hibbard, K. A., Law, B. E., Reichstein, M., and Sulzman, J., 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochemistry. 73, 29-70.

Kirschbaum, M. U. F., 1995. The Temperature-Dependence of Soil Organic-Matter Decomposition, and the Effect of Global Warming on Soil Organic-C Storage. Soil Biology & Biochemistry. 27, 753-760.

Kuzyakov, Y., and Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology & Biochemistry. 33, 1915-1925.

LaMontagne, M. G., Schimel, J. P., and Holden, P. A., 2003. Comparison of subsurface and surface soil bacterial communities in California grassland as assessed by terminal restriction fragment length polymorphisms of PCR-amplified 16S rRNA genes. Microbial Ecology. 46, 216-227.

Lee, M. S., Nakane, K., Nakatsubo, T., and Koizumi, H., 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. Plant and Soil. 255, 311-318.

Li, Q. L., Chen, J. Q., Moorhead, D. L., DeForest, D. L., Jensen, R., and Henderson, R. A., In press. Effects of timber harvest on carbon pools in Ozark forests. Canadian Journal of Forest Research.

Lloyd, J., and Taylor, J. A., 1994. On the Temperature-Dependence of Soil Respiration. Functional Ecology. 8, 315-323.

Mariko, S., Nishimura, N., Mo, W. H., Matsui, Y., Kibe, T., and Koizumi, H., 2000. Winter CO2 flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. Ecological Research. 15, 363-372.

Pregitzer, K. S., Laskowski, M. J., Burton, A. J., Lessard, V. C., and Zak, D. R., 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiology. 18, 665-670.

Raich, J. W., and Schlesinger, W. H., 1992. The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus Series B-Chemical and Physical Meteorology. 44, 81-99.

Schenk, H. J., and Jackson, R. B., 2002. The global biogeography of roots. Ecological Monographs. 72, 311-328.

Skoor, D. M., 2006. Soil survey of Reynolds County, Missouri.USDA Soil Conservation Service.

Xu, M., and Qi, Y., 2001. Spatial and seasonal variations of Q(10) determined by soil respiration measurements at a Sierra Nevadan forest. Global Biogeochemical Cycles. 15, 687-696.

Xu, M., Saunders, S. C., and Chen, J., 1997. Analysis of landscape structure in the southeastern Missouri Ozarks. In: BL Brookshire and SR Shifley. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research. St. Paul, MN: USDA-Forest Service. Pages 41-55.

Zheng, D. L., Chen, J. Q., Song, B., Xu, M., Sneed, P., and Jensen, R., 2000. Effects of silvicultural treatments on summer forest microclimate in southeastern Missouri Ozarks. Climate Research. 15, 45-59.