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Characterization of forest floor carbon dioxide efflux from three forest ecosystems in East Tennessee, USA

M. Lala S Chambers

To the Graduate Council:

I am submitting herewith a thesis written by M. Lala S Chambers entitled "Characterization of forest floor carbon dioxide efflux from three forest ecosystems in East Tennessee, USA." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Wilfred M. Post III, Major Professor

We have read this thesis and recommend its acceptance:

Paul J. Hanson, Michael D. Mullen, Stephen C. Nodvin

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

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We have read this thesis
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Associate Vice Chancellor and
Dean of the Graduate School

CHARACTERIZATION OF FOREST FLOOR CARBON DIOXIDE EFFLUX FROM THREE FOREST ECOSYSTEMS IN EAST TENNESSEE, USA

A Thesis

Presented for the

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Degree

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Abstract

One of the most serious potential consequences of human activity (emissions from fossil fuels and deforestation), brought about by increasing levels of greenhouse gas concentrations is climate change, particularly global warming. Carbon dioxide (CO_2) is a major contributor to this phenomenon and is the central driver of the global carbon cycle. The reality that climate change can affect everything from agriculture to energy systems clearly demands a comprehensive understanding of the factors and associated dynamics influencing the global carbon cycle. Climate change is expected to express itself in seasonal changes, as well. Forest soils are of special interest because they contain 40% of all below ground carbon, are thought to account for part of the global carbon budget imbalance, and may release more CO_2 due to soil warming brought about by global warming. Forest soils, clearly an important compartment of the global carbon cycle, are the subject of this research.

The principal objective of this thesis is the characterization of seasonal forest floor carbon dioxide efflux rates from three forest ecosystem sites located in East Tennessee, varying in age, climate, elevation and tree species. Soil physical, chemical, and biological properties were measured during July, September, November of 1994 and January and April of 1995 to assess the factors responsible for the seasonal differences among the three forest ecosystem sites. Even though many of these factors were not found to be statistically significant in explaining the carbon dioxide efflux rate differences, characterization of their seasonal patterns is relevant to complete the understanding of global carbon processes.

The findings are presented in parts. Except for Parts 1 and 6, each part contains all the elements of a journal article. Part 1, the introduction, provides a short synopsis of the climate change issue and a description of the problems in resolving the global carbon cycle. Part 2 characterizes the physical and chemical properties of the soils on a seasonal basis. Part 3 characterizes the seasonal patterns of microbial biomass carbon of these three forest soils. Part 4 reviews forest floor carbon dioxide efflux rates from boreal and temperate forest soils and the methods used to measure the flux. Part 5 provides the seasonal characterization of forest floor carbon dioxide efflux from the three forest ecosystems and describes the factors responsible for the differences. Part 5 also discusses the

verification and expansion of a simple, empirical nonlinear equation that estimates forest floor carbon dioxide efflux rates. Part 6 summarizes the research and conclusions of this thesis and suggests recommendations for future research.

The highest elevation site, located in a spruce-fir forest, typically produced the smallest soil CO_2 efflux. The lowest elevation site, located in an upland-oak forest, produced the largest soil CO_2 efflux during only one of the five periods measured, and the middle-elevation site, located in a conifer-hardwood forest, was responsible for the largest soil CO_2 efflux during two periods. Soil temperature and Oi water content were determined by multiple linear regression to explain 73% of the seasonal variation in forest floor CO_2 efflux rates across the three forest ecosystems. Forest floor CO_2 efflux rates exhibited an exponential relationship with soil temperature and a linear relationship with Oi water content. A simple, empirical nonlinear equation, which estimates forest floor CO_2 efflux rates primarily from a soil temperature function (Q_{10}), was tested using the soil temperature data from this study and was able to account for 59% of the seasonal variation in rates across the three ecosystem sites. When a linear term of Oi water content was added, the equation accounted for 78% of seasonal forest floor CO_2 efflux variations across the three sites, a substantial improvement.

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PART 1

INTRODUCTION

Background

Currently, climate change is one of the most critical consequences of human activity (emissions from fossil fuels, land-use change, and deforestation), induced by increasing concentrations of greenhouse gases (Boden et al., 1994), such as carbon dioxide, methane, nitrogen, and chloroflurocarbon-11, some major greenhouse gases (Houghton et al., 1996). Emissions from fossil fuels, land-use change, and deforestation has disrupted the carbon cycle balance throughout the biosphere (Schimel et al., 1995). The absorption of the earth's infrared radiation by carbon dioxide (CO_2) helps to facilitate an overall warmer atmospheric temperature (Anthes et al., 1978). The absorption properties of CO_2 along with increasing atmospheric concentrations or levels of CO_2 have led to this gas accounting for 60 to 80% of the greenhouse warming effect (Rodhe, 1990; Lashof and Ahuja, 1990), making it the most important greenhouse gas. Prior to the industrial revolution, in 1750, atmospheric CO_2 concentrations were approximately 280 ppm (Neftel, et al., 1994) with subsequent CO_2 concentrations increasing to 361 ppm in 1996 (Keeling and Whorf, 1996). This represents an increase of 29% with over half occurring since 1950 (Sundquist, 1993).

During typical transitions from glacial to interglacial periods in the past, atmospheric CO_2 concentrations have varied from approximately 200 ppm to 280 ppm (Barnola et al., 1994), respectively, with a subsequent increase in temperature of 5 to 7 °C (Folland et al., 1992). This increase in CO_2 concentration and temperature occurred over 10,000 to 20,000 years during the past glacial periods (Sundquist, 1993) and current CO_2 levels have increased by the same amount in just over 250 years. In addition, when the recent rate of CO_2 increase of 1.43 ppm yr^{-1}, averaged over the period 1981 to 1992 (Conway et al., 1994), was compared to the earlier 1958 rate of increase of about 0.6 ppm yr^{-1} at Mauna Loa, Hawaii (Schimel et al., 1995), it indicated that global CO_2 levels are increasing at an increasing rate.

Global temperatures have increased between 0.5 to 0.7 °C since 1850 (Hansen and Lebedeff, 1987; Jones, 1994) and there is substantial evidence for the association between atmospheric CO_2 concentrations and global temperature (Barnola et al., 1987; Houghton et al., 1996; Jouzel et al., 1993; Raynaud et al., 1993; Thomson, 1995). Increasing greenhouse gas concentrations over the next

several decades, are expected to result in a 1 to 4 °C increase in global mean temperature (Boer et al., 1992; Bretherton et al., 1990; Houghton et al., 1992; Lorius et al., 1990). The temperature increase is expected to alter the hydrologic cycle (Boer et al., 1992; Rind et al., 1990; Varallyay, 1990). Overall, the influence of increasing CO_2 levels and increasing temperature values on biological, chemical, and physical properties may lead to serious and extensive consequences for agriculture, water resources, aquatic and terrestrial ecosystems, and hydroelectric energy systems (Bolin et al., 1986; Pearman, 1988; U. S. Environmental Protection Agency, 1988).

With such strong support for climate change (Barnola et al., 1994; Bretherton et al., 1990; Folland et al., 1992; Jones and Bradley, 1992; Keeling and Whorf, 1996; Neftel et al., 1994; Thomson, 1995) and the potential serious consequences resulting from climate change, understanding factors controlling the global carbon (C) cycle is crucial to predicting and hopefully mitigating its future direction. Key to this are 1) the determination of the sources and sinks of C, 2) the understanding of the biological, chemical, and physical processes underlying C production, uptake, and emission, and 3) the interaction of these processes with other factors, such as increased atmospheric CO_2 levels, nitrogen deposition, precipitation deficits, and soil warming (Aber et al., 1995; Goulden et al., 1996; Hudson et al., 1994; Mooney et al., 1991).

Statement of Problem

For over twenty years, researchers have tried to balance the global CO_2 budget (Craig and Holmén, 1995; Gifford, 1994; Hudson et al., 1994; Houghton, 1996; Sarmiento et al., 1995). However, to date the accounting process has identified more sources than sinks of C (Sundquist, 1993). Although Broecker et al. (1979) first talked about the missing C or unexplained C sink, it was the more recent work of Tans et al. (1990) that has been pivotal in calling attention to this imbalance. There is disagreement as to the exact amount of the unexplained C sink. Tans et al., (1990) estimated an imbalance of 2.0 to 3.4 X 10^{15} g C yr^{-1}; Friedlingstein et al., (1995) calculated the unexplained C sink to be 0.6 to 3.0 X 10^{15} g C yr^{-1}; and a more recent analysis by Houghton (1996) indicates a missing C sink of 0.0 to 2.2 X 10^{15} g C yr^{-1}.

Although the exact quantity is disputed, there is much support for terrestrial ecosystems to be the source of the unexplained C sink (Chan et al., 1996; Dai and Fung, 1993; Schindler and Bayley, 1993; Tans et al., 1990). Northern hemisphere temperate forest ecosystems are considered to be responsible for a substantial portion of the sink (Ciais et al., 1995; Dixon et al., 1994; Goulden et al., 1996; Houghton, 1996; Kauppi et al., 1992; Schindler and Bayley, 1993; Sedjo, 1992). Marine ecosystems likely account for the remaining portion of the unexplained C sink (Ciais et al., 1995; Sarmiento and Sundquist, 1992; Schindler and Bayley, 1993).

Overall, terrestrial ecosystems contain 610 X 10^{15} g C in vegetation and 1580 X 10^{15} g C in soils and detritus while the atmosphere and ocean reservoirs hold 750 X 10^{15} g C and 39,000 X 10^{15} g C, respectively (Eswaran et al., 1993; Potter et al., 1993; Siegenthaler and Sarmiento, 1993). Even though terrestrial ecosystems have far less carbon content than do marine ecosystems, the annual C flux to the atmosphere is only slightly less than that of the ocean, 61 X 10^{15} g C versus 72 X 10^{15} g C (Smith et al., 1993).

Of the various terrestrial ecosystems, forests undoubtedly have a strong impact on the carbon cycle. Forests cover more than 4.1 X 10^{9} hectares of the Earth's land area (Dixon et al., 1994), approximately 33% of the total land area, and carry out about 66% of the global photosynthesis (Kramer 1981). Forests contain an estimated total of between 1146 X 10^{15} (Dixon et al., 1994) and 1410 X 10^{15} g C (Olson et al., 1983; Post et al., 1982), which represents 80% of all the above ground C and 40% of all below ground C (Ajtay et al., 1979; Dixon and Turner, 1991; Olson et al., 1983; Schlesinger, 1984; Waring and Schlesinger, 1985; Whittaker and Likens, 1975; Zinke et al., 1984). Forests are a major influence on climate, which is due not only to their significant role in the carbon cycle, but also because of their role in watershed processes and biogeochemical cycling of other nutrients (Waring and Schlesinger, 1985).

Globally, forest ecosystems can be C sources or sinks (Watson et al., 1996). Deforestation of tropical forests is creating a C source (Brown et al., 1993; Dixon et al., 1994) while temperate and boreal forest regrowth is thought to be responsible for the accumulation of C (Dixon et al., 1994; Houghton, 1996; Sedjo, 1993; Wofsy et al., 1993). Houghton (1996) calculated terrestrial C storage

using two current procedures and determined that reforestation accounts for only half of the observed C accumulation in northern and mid-latitude forests. The remaining forest C accumulation has been attributed to 1) CO_2 fertilization, the increase in plant biomass due to higher CO_2 levels (Friedlingstein et al., 1995; Hudson et al., 1994; Norby et al., 1992; Wullschleger et al., 1995); 2) nitrogen fertilization, the increase in plant biomass due to increased N deposition (Galloway et al., 1995; Hudson et al., 1994; Rastetter et al., 1991; Schindler and Bayley, 1993); and 3) climate variability, normal variability in temperature, precipitation and incoming radiation (Dai and Fung, 1993; Goulden et al., 1996; Grace et al., 1995). Some of the uncertainties in quantifying the carbon budget of forest ecosystems are due to 1) inconsistent approaches for estimating C fluxes in terrestrial ecosystems (Dixon et al., 1994; Houghton, 1996), 2) possible errors in land-use history reconstruction (King et al., 1995); 3) possible errors in the emission and uptake estimates of fossil fuel (King et al., 1995); and 4) lack of definitive data on ecosystem responses to elevated CO_2, increased temperature, and changes in precipitation patterns (Luxmoore et al., 1993; Rogers et al., 1994).

The global flux of CO_2 from the soil has an estimated range of 50 to 75 $X\ 10^{15}$ g C (Houghton and Woodwell, 1989; Schlesinger, 1977) and terrestrial net primary production (NPP) has an estimated range of 50 to 60 $X\ 10^{15}$ g C (Ajtay et al., 1979; Bolin, 1983; Box, 1978; Houghton and Woodwell, 1989; Olson et al., 1983). Not only is soil a critical compartment of the carbon cycle, it is also the medium in which nitrogen, sulphur, phosphorus, calcium, magnesium, potassium and other minerals are cycled and made available for uptake by plants and organisms. Soils and organic matter also act to retain nutrients for future availability (Miller and Donahue, 1990; Tate III, 1987). The soil and organic layers store water that is intercepted by leaves, branches, and litter holding it in reserve to be used by plants and organisms when needed (Waring and Schlesinger, 1985).

Forest soils hold more than half, approximately 69%, of the C residing in forests and 40% of the world's soil C, which clearly demonstrates their important role in the global carbon cycle (Dixon et al., 1994; Schlesinger, 1984; Waring and Schlesinger, 1985; Zinke et al., 1984). Forest vegetation is estimated to contain 483 $X\ 10^{15}$ g C (Olson et al., 1983) and forest soils are estimated to contain 927 $X\ 10^{15}$ g C (Post et al., 1982). The estimates by Dixon et al. (1994) are considerably lower with 359

X 10^{15} g C contained in forest vegetation and 787 X 10^{5} g C contained in forest soils. The factors described here have focused attention on forest soils as responsible for a portion of the unexplained C sink (Dixon et al., 1994; Gifford, 1994; Harrison et al., 1993; Sedjo, 1992).

Certain issues which may affect the direction and magnitude of climate change have not been resolved. Warmer atmospheric temperatures may cause warmer soils and this would lead to increased decomposition rates which could result in higher soil CO_2 emission (Luxmoore et al., 1993; Raich and Schlesinger, 1992; Schlesinger, 1995; Townsend et al., 1992). Warmer soil temperatures have also resulted in higher N mineralization due to enhanced microbial activity (Bonan and Van Cleve, 1992; Lükewille and Wright, 1997; Peterjohn et al., 1994). Tree growth and fine root growth have been found to be positively related to increasing soil temperature and N mineralization (Bonan and Van Cleve, 1992; Nadelhoffer et al., 1985; Steele et al., 1997). This increased root and microbial activity in the soil has resulted in higher CO_2 flux from the soil (Mitchell et al., 1994; Peterjohn et al., 1994). Interactions among CO_2 fertilization, decomposition, N mineralization, N deposition, and soil warming create uncertainty regarding the direction and magnitude of climate change, which must be addressed. The uncertain outcome of these interactions in terrestrial ecosystems needs to be resolved in order to refine models which can accurately predict the direction and magnitude of climate change (Craig and Holmén, 1995; Sarmiento et al., 1995).

Since soil biological, physical, and chemical dynamics are intrinsically linked to the production and transport of CO_2 within the soil (Singh and Gupta, 1977), an improved understanding of the interplay of these soil factors with soil C is needed to resolve the relationship between the C cycle and climate change (Bouwman and Leemans, 1995; Kirschbaum, 1995; Matson and Harriss, 1995). There are some other issues that are preventing a complete picture of the C cycle/climate change relationship. First, data of soil respiration in association with the soil type and quantity and quality of organic matter are scarce or insufficient (Raich and Potter, 1995). Second, the use of air temperature and precipitation as surrogates for soil temperature and moisture diminishes the accuracy of global soil CO_2 emission estimates (Kicklighter et al., 1994; Raich and Potter, 1995). Finally, better global data sets of environmental parameters and a better understanding of the effects of small scale spatial

variability on large-scale processes are needed to improve global soil CO_2 efflux estimates (Raich and Potter, 1995).

Objectives

The research reported here is intended to further the understanding of forest floor CO_2 efflux in relation to soil biological, chemical, and physical processes over space and time. Seasonal forest floor CO_2 efflux rate (FFcer) patterns of three sites located in three forest ecosystems were characterized and the factors resulting in the different FFcer patterns across the sites were assessed. The three forest ecosystems, varying in age, climate, elevation, and tree species, are located in East Tennessee, U.S.A. The following variables were determined from seasonal measurements made from July, 1994 through April, 1995: soil temperature, soil water content, microbial biomass C in the organic layers and soil, small root density, total C and N in the organic layers and soil, mass of the litter layers, litterfall, water content of the top litter layer, soil pH, exchangeable Al, Ca, K, Mg, and Na, soil texture and soil coarse fraction. The results of this research will help researchers in testing and improving model parameterizations of the forest soil C cycle. In addition, the in-depth site characterization will expand the data bases of forest soil processes as they relate to CO_2 production and flux.

This thesis is organized into five parts, with each written in the format of a journal article (i.e., each part has its own abstract, text, and list of references). The various soil biological, chemical, and physical parameters were measured during July, September, and November of 1994 and January and April of 1995. Physical and chemical properties in the organic layers and mineral soil, which can govern CO_2 production and exchange, were characterized on a seasonal basis for the three forest ecosystem sites in Part 2. In Part 3, the seasonal differences in forest floor microbial biomass carbon (MBC) across the three forest ecosystem sites are described and compared. In addition, the soil physical and chemical properties characterized for the sites in Part 2 and root biomass were analyzed to assess the factors accounting for forest floor MBC differences. Carbon dioxide efflux rates from boreal and temperate forest soils and the methods used in measuring this flux are reviewed in Part 4.

Seasonal forest floor CO_2 efflux rates (FFcer) of the different forest ecosystem types (boreal, temperate conifer, temperate mixed, temperate deciduous, and temperate broad-leaved evergreen) are presented in Part 4, with the data from this study included.

Part 5 presents the seasonal characterization of FFcer for the three forest ecosystem sites and the factors responsible for the differences among the sites. Soil biological, chemical, and physical parameters assessed in Parts 2 and 3 were analyzed to determine the factors influencing these differences. The factors responsible for FFcer differences were incorporated into a simple equation that estimates FFcer.

Part 6 is a summary of the results, influential factors, and associated conclusions of the various parts in the thesis. This part includes suggestions of ways to improve upon some aspects of the current research and recommendations for future research.

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PART 2

PHYSICAL AND CHEMICAL CHARACTERIZATION OF THREE FOREST ECOSYSTEM SOILS

Abstract

Forest soils contain 40% of all below-ground carbon, making them an important compartment of the global carbon (C) cycle. It has been suggested that forest soils may account for a portion of the global C imbalance. Soil warming has been shown to enhance carbon dioxide release and nitrogen mineralization. Because of the concern regarding enhanced C release from soil ecosystems due to feedback mechanisms, there has been an emphasis on identifying and understanding soil biological, physical, and chemical processes. In this part, soil physical and chemical properties of three forest ecosystems, varying in age, climate, elevation, and tree species located in East Tennessee, USA were characterized. The assessment of the soil physical and chemical properties was done in connection with the characterization of seasonal forest floor carbon dioxide efflux rates across the three forest ecosystem sites, the central objective of this thesis. Oi layer mass, Oe/Oa layer mass, Oi water content, soil water content, and soil temperature are the physical properties which were measured over time. Bulk density, total soil porosity, coarse fraction, and soil texture are some properties considered to remain constant over one year, and thus, were determined once only. The soil chemical properties, total (organic and inorganic) C and nitrogen (N) in the Oi layer, Oe/Oa layer, and mineral soil and soil pH, were also measured over time. Since the exchangeable bases, Ca, Mg, K, and Na, and exchangeable Al are considered to be constant over one year, they were determined only once. Seasonal measurements were made over the period of July, 1994 to April, 1995. The seasonal soil temperature and soil water content patterns were distinctly different for each site. Typically, soil temperature decreased and water content increased with the increasing elevation of the sites. The two older sites, dominated by coniferous species, tended to have similar organic layer and mineral soil C and N contents, and the younger site, dominated by deciduous species, was distinctly different from them. The same was true for soil pH. Elevation appears to have had the strongest influence on the soil physical properties at each site and tree species, precipitation amount, and parent material seemed to have governed the development of soil chemical properties at each site.

Introduction

Global warming, induced by increasing greenhouse gases (Boden et all, 1994), of which carbon dioxide (CO_2) is the most important (Lashof and Ahuja, 1990; Rodhe, 1990; Watson et al., 1996), can potentially affect everything from agricultural systems to energy systems (hydroelectric power) (Watson et al., 1996). Forest soils contain 40% of all below-ground carbon, making them an important compartment of the global C cycle (Ajtay et al., 1979; Dixon and Turner, 1991; Olson et al., 1983; Schlesinger, 1984; Whittaker and Likens, 1975; Zinke et al., 1984). Forest soils are of interest because they may account for a portion of the C imbalance (Dixon et al., 1994; Gifford, 1994; Harrison et al., 1993; Sedjo, 1992). Furthermore, concern regarding enhanced C release caused by feedback interactions between plants and microorganisms has focused attention on forest soils (Kirschbaum, 1995; Lükewille and Wright, 1997; Peterjohn et al., 1994).

The dynamics of the soil biological, physical, and chemical properties are intrinsically linked to the status of soil CO_2 production and flux (Singh and Gupta, 1977). While biological components, mainly microbial and root processes, produce CO_2, the physical attributes, such as porosity, water content, and temperature, influence its flux by controlling transport and affecting the metabolism of the biological components (Singh and Gupta, 1977). Soil texture, a physical property, influences porosity, the retention of essential nutrients, such as N, Ca, Mg, and, K and water holding capacity, another physical property (Hillel, 1982; Pritchett and Fisher, 1987). The quantity of N, C, Ca, Mg, and, K represent some soil chemical properties which affect the degree of biological activity (Paul and Clark, 1996; Singh and Gupta, 1977). The interaction of these properties over temporal and spatial scales produce an environment in which biological activity is enhanced or diminished (Curtis et al., 1994; Pritchett and Fisher, 1987). Understanding the interplay of soil biological, chemical, and physical dynamics on a local scale will contribute toward resolving the relationship between the C cycle and climate change on a global scale (Bouwman and Leemans, 1995; Curtis et al., 1994; Kirschbaum, 1995; Schlesinger, 1995).

In this part of the thesis, soil physical and chemical properties of three forest ecosystems, varying in age, climate, elevation, and tree species located in East Tennessee, USA (biological

dynamics are examined in Part 3) will be characterized. Oi layer mass, Oe/Oa layer mass, Oi water content, soil water content, and soil temperature are the physical properties which were measured over time. Bulk density, total soil porosity, coarse fraction, and soil texture are some properties considered to remain constant over four seasons, and thus, were determined once only. Total (organic and inorganic) C and N in the Oi layer, Oe/Oa layer, and mineral soil and soil pH are the chemical properties which were measured over time. Some other chemical properties, the exchangeable bases Ca, Mg, K, and Na and exchangeable Al, are considered to be constant over one year and thus, they were determined only once. Cation exchange capacity (CEC) and percent base saturation were computed from the exchangeable bases and exchangeable Al. The assessment of the soil physical and chemical properties was done in connection with the characterization of seasonal forest floor carbon dioxide efflux rates across the three forest ecosystem sites (Part 5), which was the central objective of this thesis. The soil physical and chemical properties were analyzed to determine which factors explained the seasonal differences in forest floor CO_2 efflux rates among the three sites (Part 5). Soil physical and chemical parameters were chosen on the basis of their impact on forest floor production and flux of CO_2.

Materials and Methods

SITE DESCRIPTIONS

Tree species composition, climate, and elevation were the guiding factors for choosing the three forested sites for this study. Two sites were located in the Great Smoky Mountains National Park (GSMNP), TN, one within a spruce-fir forest and the other within a conifer-hardwood forest. The third site was located in an upland-oak forest on the Walker Branch Watershed, U. S. Dept. of Energy Reservation, Oak Ridge, TN. Because the GSMNP and Walker Branch Watershed have been sites of intensive ecological research, published background information was available. Topographic and climatic data are given in table 2.1 and a relief map of the sites is provided in Appendix B. Climate data (1947 - 1950), from two sites in the GSMNP (Stephens, 1969) which most resembled the spruce

Table 2.1. Topographic and Climatic Data for the SPR, COV, and OAK sites.

Site	Map	Lat/long (7.5 min)	Elev (m)	aOrien (deg)	bPrec (cm)	bMean Max Temp (°C)	bMean Min Temp (°C)
SPR	Clingmans Dome, NC-TN	35°35′N, 83°28′W	1859	65	230	18	-5
COV	Mount Le Conte, TN-NC	35°41′N, 83°27′W	975	72	194	22	-4
OAK	Bethel Valley, TN	35°58′N, 84°17′W	335	152	137	31	-3

aThe orientation or compass direction toward which the site faces. bMean maximum and mean minimum air temperature data, for the warmest and coldest month, respectively, and precipitation data are from Stephens, 1969.

-fir forest and cove conifer-hardwood forest sites, were used to depict the weather at the sites in this study. Climate data for the site in Oak Ridge, TN was made available by the Atmospheric Turbulence and Diffusion Division, a division of the National Atmospheric and Oceanic Administration (Birdwell, 1997). The 1931 classification scheme by Thornthwaite was used to categorize the climate of each site because it provided more useful designations than did the newer scheme.

Spruce-fir forest site

The highest elevation site, 1859 m (6100 ft), was situated in a spruce-fir forest (SPR) off the Appalachian trail, southwest of Mt. Collins in the GSMNP, TN and approximately 93 km southeast from Knoxville, TN. Sloping gently toward the east, northeast (65°), this site was somewhat sheltered from harsh weather. The SPR site can be found on the Clingman's Dome, NC-TN 7.5 min. quadrangle at latitude and longitude of 35°35'N and 83°28'W. The location of this site was considered to be the least disturbed in an area where the balsam woolly adelgid has severely impacted the *Abies fraseri* population for the past fifteen years (Busing et al., 1988).

Since the Anakeesta Formation, part of the Ocoee Series, underlies most of the state line ridge (Golden, 1974), it is likely that this formation also underlies this site. Sandstone layers common to the Thunderhead Sandstone formation have been observed to be interbedded with the Anakeesta formation (King, et al., 1968). The observance of quartzite protrusions and sand in the soil, provide

evidence that these soils likely formed predominantly from sandstone and to a lesser degree from the slate, phyllite (fabric between slate and schist) or schist produced by the metamorphosed Anakeesta rock. Soils in the general area are dominated by shallow inceptisols (immature profile development) with a thick organic horizon (Busing et al., 1988). Golden (1974) determined the soil type in the spruce-yellow birch forest type, similar to this site but slightly lower in elevation, to be fairly equally divided among histosols (organic soils), Lithic Dystrochrepts, and Typic Dystrochrepts.

Within the 15 m X 20 m SPR site, *Picea rubens* species (red spruce) account for 88% (24 trees) of the total basal area (67.7 m^2 ha^{-1}), followed by *Betula alleghaniensis* (yellow birch) and *Abies fraseri* (fraser fir) which represent 7% (1 tree) and 5% (47 trees), respectively. Whittaker (1956) found the red spruce forest type to dominate in subalpine stands between 1372 m (4500 ft) and 1829 m (6000 ft) and the fraser fir forest type to dominate above 1829 m (6000 ft). The proportion of basal area represented by *Picea rubens* and the number of *Abies fraseri* at this site demonstrate this site to be within a spruce-fir forest type (Whittaker, 1956). Standing remains of dead *Abies fraseri* indicate that larger trees of this species were once present before succumbing to the balsam woolly adelgid. The range of the diameter breast height of the larger spruce trees, 42 to 67 cm, confirmed this site as an old-growth community (Blum, 1990; U.S. Dept. of Agric., Forest Service, 1997, unpublished).

Climate data collected at the 1920 m (6300 ft) station (Stephens, 1969) most closely typified the weather at this site. On average, 230 cm of precipitation fall on this site each year, with fog occurring each month of the year. The mean maximum and minimum temperatures for the hottest and coldest months, respectively, are 18 °C and -5 °C with extremes of 27 °C and -24 °C. According to Thornthwaite's (1931) climate classification scheme, this site is considered a cool, temperate rain forest.

Cove conifer-hardwood forest site

The middle-elevation site, 975 m (3200 ft), is located in a sheltered or cove conifer-hardwood forest (COV), near the Grotto Falls trail head within the GSMNP, TN and approximately 67 km southeast of Knoxville, TN. This site slopes steeply toward the east, northeast (72°) above the Roaring

Fork stream and can be found on the Mount Le Conte, TN-NC 7.5 min. quadrangle at a latitude of 35°41'N and a longitude of 83°30'W.

Given the proximity to the Roaring Fork stream, the Roaring Fork Sandstone formation very likely underlies the COV site (King et al., 1968). The Roaring Fork Sandstone formation, part of the Ocoee Series, is composed of dark fine-grained sandstone beds that alternate with mostly phyllitic silty and argillaceous rocks (King et al., 1968). In a forest type similar to this, Golden (1974) classified 68% of the soils as Typic Dystrochrepts and the remaining as Typic Haplumbrepts and Lithic Dystrochrepts.

The COV site had the largest total basal area, 72.4 m^2 ha^{-1}. *Tsuga canadensis* (eastern hemlock) dominate the 15 m X 20 m site, accounting for 53% (26 trees) of the total basal area. *Acer rubrum* L. (red maple), *Halesia carolina* (silver bell), and *Fagus grandifolia* (American beech) represent 29% (2 trees), 17% (4 trees), and 1% (2 trees) of the remaining basal area, respectively. Because of the sheltered location of this site and the proportion of the basal area (47%) in hardwood species, sites of this description are often called a cove hardwood forest type (Cain, 1943; Whittaker, 1956). A diameter breast height range of 22 to 94 cm for the larger trees confirmed the COV site as a mature to old-growth community (Godman and Lancaster, 1990; Sluder, 1990; Tubbs and Houston, 1990; U.S. Dept. of Agric., Forest Service, 1997, unpublished; Walters and Yawney, 1990).

The 1200 m (3850 ft) weather station (Stephens, 1969) most closely depicts the weather for the COV site. The site receives 194 cm of precipitation per year with minimal occurrence of fog (Stephens, 1969). The mean maximum and minimum temperatures for the hottest and coldest months, respectively, are 22 °C and -4 °C with extremes of 32 °C and -21 °C (Stephens, 1969). Based on Thornthwaite's (1931) climatic classification scheme, the COV site was considered a temperate rain forest.

Upland-oak forest site

The low-elevation site, 335 m (1100 ft), was situated within a secondary-growth, upland oak forest (OAK) on Chestnut Ridge in the Walker Branch Watershed, U. S. Dept. of Energy, Natl. Environ. Research Park, Oak Ridge, TN. This site is approximately 42 km west of Knoxville, TN and can be pinpointed on the Bethel Valley, TN 7.5 min. quadrangle at a latitude and longitude of 35°58'N and

84°17'W. It is part of the Throughfall Displacement experiment in which precipitation is being diverted to create wet, ambient, and dry plots to investigate stress on forest ecosystems due to changes in precipitation input induced by climate change (Hanson et al., 1995). The ambient plot of the Throughfall Displacement experiment represented the OAK site in this study. The site slopes steeply to the south, southeast (152°) and likely was more influenced by weather events than were the two other sites.

The Copper Ridge Dolomite formation, which underlies this site, has been described as gray, coarsely crystalline, asphaltic, and as including highly siliceous dolomite (Henderson et al., 1971). The very cherty, infertile, and highly permeable soils are mostly Typic Paleudults (old, weathered soils) and belong to the Fullerton series (Henderson et al., 1971). Far less organic matter was observed at the OAK site than at the other two sites.

The OAK site had a total basal area of 20.5 m^2 ha^{-1} and a large variety of species, which reflected the difference in successional stages between the OAK site and the other two sites. *Quercus Alba* (white oak), *Quercus Prinis* (chestnut oak), *Quercus falcata,* var. *falcata* (southern red oak), *Quercus stellata*, (post oak), and *Quercus rubra* (northern red oak) dominate the 80 m X 80 m site, accounting for 47% (66 trees) of the total basal area, in that order (Hanson et al., 1995). *Nyssa sylvatica* (Black Gum) and two maple species, *Acer rubrum* (red maple) and *Acer saccharinum* (sugar maple), represent 19% (66 trees) and 18% (40 trees), respectively. The remaining basal area of 16% (63 trees) was represented by *Liriodendron tulipfera* (yellow poplar), *Oxydendrum arboreum* (sourwood), *Carya spp.* (Hickory), *Pinus echinata* (short leaf pine), *Cornus florida* (flowering dogwood), and *Prunus serotina* (black cherry), respectively. This site was labeled an upland oak forest because of the dominance of the oak species and its location on the side of the ridge (Hanson et al., 1995).

Climate data from the Oak Ridge, TN national weather station (266 m elevation) were used to characterize weather conditions at the OAK site (Birdwell, 1997). The area receives a mean of 137 cm of precipitation, annually. Temperatures vary from a mean maximum of 31 °C during the hottest month to a mean minimum of -3 °C during the coldest month with extremes of 39 °C and -27 °C

(Birdwell, 1997). On the basis of Thornthwaite's climate classification scheme (1931), the OAK site was considered to be a temperate forest.

EXPERIMENTAL DESIGN

A completely randomized design was used in conducting this research. The study areas in the spruce-fir and old-growth cove hardwood forest ecosystems were 15 m X 20 m with five rows (transects) and four columns spaced at 5 m increments yielding 20 monitoring locations. The rows were arranged perpendicular to the slope. Sampling occurred randomly within 2 m of the monitoring locations.

Because the upland-oak forest ecosystem was part of the Throughfall Displacement Experiment (TDE), it had a different arrangement with three research plots: wet, ambient, and dry. The ambient plot was used as the study area for this research, which had dimensions of 80 m X 80 m with ten rows (transects) and ten columns spaced at 8 m increments and rows arranged perpendicular to slope. Due to border transition among the three plots of the TDE, border columns were avoided such that nine columns were sampled. Because the OAK site was much larger than were the two other sites, soil temperature, soil water content, and CO_2 efflux data were collected along an upper (row 8), a middle (row 5), and a lower row (row 2) which yielded 27 monitoring locations. This monitoring scheme captured the overall character of the site while maintaining a similar number of monitoring points to that of the SPR and COV sites. Litter and soil samples used in OAK site data analyses were collected at the right and left margins and alongside rows 8, 5, 3, and 2 of the TDE site to prevent disturbance to the TDE. The 'treatments' of this research were the three forest ecosystems themselves, that is, the influence of their differences in climate, elevation, age, and tree species.

SAMPLING

Most soil physical and chemical parameters were sampled on a seasonal basis emphasizing periods of moisture and temperature extremes, growing season, and litterfall from July, 1994 to April, 1995. Measurements were made during July (Jul.), 1994, September (Sep.), 1994, November (Nov.), 1994, January (Jan.), 1995, and April (Apr.), 1995.

During each measurement period, litter and soil core samples were collected sequentially from the soil profile at 10 of 20 monitoring locations at the SPR and COV sites. The purpose in sampling only 10 of the 20 monitoring locations was to limit disturbance to the sites and to save time. All rows were sampled each time, with even or odd columns sampled alternately during each measurement period. To keep the sampling pattern at the OAK site consistent with that at the SPR and COV sites, 10 out of 20 locations were sampled, five on each side of the TDE site and alongside rows 8 (upper slope), 7, 5, 3, and 2 (lower slope). Non-destructive soil temperature and water content measurements were made at all monitoring points. Bulk density and porosity were assessed from undisturbed soil samples collected during July, 1997.

Litter and Organic layers

Six plastic containers, with approximate collection areas of 0.21m^2, were placed throughout the SPR and COV sites to catch litterfall. Litter (leaves, stems, seeds, etc.) was collected five times over the period August, 1994 through April, 1995 from the SPR and COV sites and stored in plastic bags at 4 °C until they were dried for mass determination. Litterfall data for the OAK site was provided by Hanson et al., (1995) and represents the period from August, 1994 through August, 1995. Data from six collection baskets (area = 0.20 m^2), chosen randomly from rows 8 (upper), 5 (middle), and 3 (lower) on the ambient plot of the Throughfall Displacement Experiment site were computed for OAK litterfall.

Oi and Oe/Oa layer samples were collected during Jul., Sep., and Nov. of 1994, and Apr. of 1995. Litter was gathered by hand through a plastic cylinder (dia. of 0.189 m) which outlined the collection area (the Oe and Oa layers were combined due to time constraints). The Oi layer, the top organic layer, consists of the unaltered remains of plants and animals; the Oe layer, immediately below the Oi, consists of fragmented, partly decomposed organic matter; and the Oa layer, between the Oe and the mineral soil, consists of well-decomposed, amorphous organic matter (Pritchett and Fisher, 1987). At the time of sampling, portions of Jul., 1994 Oi layer and the Nov., 1994 and Apr., 1995 Oe/Oa layer samples were removed for organic layer microbial biomass carbon analysis (Part 3). After

the Oi layer samples were weighed for gravimetric water content determination, the remaining samples were stored in plastic bags at 4 °C until they were processed for physical and chemical analyses.

Soil samples

Mineral soil cores were collected during Jul., Sep., and Nov., 1994 and Apr., 1995 to an average depth of 21 cm using a open or closed bucket auger (dia.=0.077 m and 0.073 m, respectively) and stored in plastic bags at 4 °C for microbial biomass C analysis and physical and chemical analyses. Additional soil cores were collected to an average depth of 26 cm for root biomass determination during Jul., Sep., and Nov., 1994 and Apr., 1995, using the same bucket augers (see Appendix A for results). These sample depths were used because microbial biomass C values, organic matter content, and root distribution are highest in the top 20-30 cm of the soil (Charley and Richards, 1982; Johnson et al., 1995; Ross and Tate, 1993). After soil samples for microbial biomass C analysis had been set aside (Part 3), the samples were air dried and sieved (<2 mm) as required for the various physical and chemical analyses. Approximately 10 g of each sample was pulverized with a mortar and pestle for the total C and N analyses. The Sep. and Nov., 1994 soil cores, collected to an average depth of 26 cm, were washed through a 2 mm sieve and the fragments > 2 mm were air dried to assess coarse fraction.

Undisturbed soil samples (original volume preserved) were collected from random locations at each of the three sites during July, 1997 to assess bulk density and total porosity. Five samples were collected at the SPR and COV sites, by pressing a cylindrical metal sampler into the mineral soil to an approximate depth of 9 cm (Blake and Hartge 1986). At the OAK site, eight samples were collected to an approximate depth of 5 cm, four from each side of the Throughfall Displacement Experiment site, using a hammer-driven cylindrical metal sampler (Blake and Hartge 1986).

Soil temperature and water content

Soil temperature was measured to a depth of 15 cm to the nearest 0.1 °C during Jul., Sep., and Nov., 1994, and Jan. and Apr., 1995, using a digital thermometer (OMEGA 872A or OMEGA 450 AET type E probe, OMEGA, Stamford, CT). Volumetric soil water content was measured to a depth of 35 cm to the nearest 0.1 cm^3 cm^{-3} during Jul., Sep., and Nov., 1994, and Jan. and Apr., 1995, using

time domain reflectometery, the method developed by Topp and Davis (1985) (Trase System 6050X1, Soilmoisture Equip. Corp., Goleta, CA). The Jul., 1994 water content measurements were made to a 15 cm depth using portable steel rods. Thereafter, water content was measured to a depth of 35 cm because this depth better represented the conditions under which maximum biological activity occurs (Charley and Richards, 1982; Pritchett and Fisher, 1987). Stainless steel 35 cm rods used in measuring water content were installed after the Jul., 1994 date and left in place for the experiment's duration.

ANALYTICAL METHODS

Litterfall was weighed after being oven-dried at 70 °C and the mass per collection area per year was calculated to the nearest 1 g $m^{-2} \cdot yr^{-1}$. The Oi and Oe/Oa layer samples were oven-dried (70 °C), weighed and the mass per collection area computed to the nearest 1 g m^{-2}. The Oi material was weighed before and after oven-drying to determine the gravimetric water content to the nearest 1% (based on g g^{-1}). The dried Oi and Oe/Oa samples were ground using a Cyclone grinder or Wiley mill (20 mesh screen) and mixed by shaking prior to total C and N analyses.

Coarse fraction (fragments > 2 mm), which is the rock volume relative to the soil volume, was calculated to the nearest 0.001 cm^3 cm^{-3} with rock volume obtained by water displacement of the rocks. For each site, soil texture was determined to the nearest 1% from the particle size analysis of three samples, each of which was a combination of Jul. and Sep., 1994 samples (Gee and Bauder, 1986). Bulk density was computed to the nearest 0.1 g cm^{-3} based on the oven-dry weight of the sample per sampler volume from the undisturbed soil samples, which were weighed before and after oven-drying (105 °C) (Blake and Hartge 1986). Subsequently, total porosity was calculated to the nearest 1% from bulk density, gravimetric water content (of the undisturbed samples), and particle density, which was assumed to be 2.65 g cm^{-3} (Hillel, 1982; Miller and Donahue, 1990).

Total C and N of the Oi layer, Oe/Oa layer and the mineral soil were quantified to the nearest 0.01% (based on g g^{-1}) by the high-temperature induction furnace method (Bremner and Mulvaney, 1982; Nelson and Sommers, 1982) using a carbon/nitrogen/sulphur analyzer (LECO CNS2000, LECO, St. Joseph, MI). The C to N (C:N) ratios were calculated from these results. The April, 1995 samples

were analyzed for exchangeable bases, Ca, K, Mg, and Na (Thomas, 1982), using the inductively coupled Argon plasma-optical emission spectrometer (ICAP61, Thermo Jarrell Ash Corp., Franklin, MA) with results given to the nearest 0.001 $cmol_c\ kg^{-1}$. Analysis of the April, 1995 samples for K was done using an atomic absorption spectrophotometer with results given to the nearest 0.001 $cmol_c\ kg^{-1}$ (Perkin-Elmer atomic absorption spectrophotometer 5000, Perkin-Elmer Corp., Norwalk, CT). The April, 1995 samples were analyzed for Al by the pyrocatechol violet method (American Public Health Association et al., 1992) using the Skalar autoanalyzer, with results given to the nearest 0.001 $cmol_c\ kg^{-1}$. Soil pH (H_2O) was measured with the Corning pH Ion Analyzer 355 (McLean, 1982).

STATISTICAL ANALYSIS

Analysis of variance (SPSS Inc., Chicago, IL) was applied to assess significance among the sites for each parameter on a given sampling date at an alpha level of 0.05 ($P<0.05$). The Student-Neuman-Keul's test (SPSS Inc., Chicago, IL) was used to determine which sites were significantly different.

Results

Average annual litterfall at the SPR, COV, and OAK sites for 1994-1995 was 250, 423, and 439 $g\ m^{-2}$, respectively.

SOIL PHYSICAL PROPERTIES

Bulk density, total soil porosity, coarse fraction, and soil texture are the physical properties considered to be constant over the duration of this study and are provided in table 2.2. Bulk density was lowest at the COV site, 0.3 $g\ m^{-3}$, and highest at the OAK site, 0.9 $g\ m^{-3}$, which led to highest porosity at the COV site, 88%, and lowest porosity at the OAK site, 65%. The COV site had the lowest coarse fraction value, 0.008 $cm^3\ cm^{-3}$ and the OAK site had the highest coarse fraction value, 0.113 $cm^3\ cm^{-3}$. The bulk density and coarse fraction magnitudes paralleled each other across the sites. The SPR soil had the lowest percent clay-sized particles and was classified as a sandy clay loam texture. The COV and OAK soils were each classified as having a clay loam texture, with the OAK site having the higher percent clay-sized particles.

Table 2.2. Soil physical properties, typically constant over one year, assessed for three forest ecosystem sites from samples collected during the period of July, 1994 to April , 1995.

Site	[c]Bulk density ($g\ cm^{-3}$)	Porosity (%)	Coarse frac. ($cm^3\ cm^{-3}$)	Texture (%)			
				sand	silt	clay	class.
SPR	0.6	78	0.020	52	23	25	sandy cl. loam
COV	0.3	88	0.008	44	22	34	clay loam
OAK	0.9	65	0.113	24	37	39	clay loam

[c]Samples for bulk density and porosity determination were collected in July, 1997.

Oi layer mass measurements and associated details are provided in table 2.3. Oi layer mass ranged from 308 g m^{-2} at the SPR site in Nov., 1994 to 1300 g m^{-2} at the COV site in Sep., 1994. During all the periods measured, the SPR Oi layer mass was the lowest in Jul. and Nov., 1994 and the OAK Oi layer mass was the lowest in Sep., 1994 and Apr., 1995. The COV site consistently had the highest Oi layer mass values and was significantly different ($P<0.05$) from the SPR site for all measurement periods and from the OAK site for all periods, except July, 1994. All sites were significantly different ($P<0.005$) for Nov., 1994 and Apr., 1995.

Oe/Oa layer mass measurements and associated details are presented in table 2.4. Oe/Oa layer mass ranged from 811 g m^{-2} at the OAK site in Sep., 1994 to 13,240 g m^{-2} at the COV site in Nov., 1994.The OAK Oe/Oa layer consistently produced the lowest mass values. The COV Oe/Oa layer mass values were the highest for all dates except Jul., 1994 when it was slightly lower than the SPR Oe/Oa layer mass. For all measurement periods the SPR and COV Oe/Oa layer mass values were not significantly different, but the OAK Oe/Oa layer mass values were significantly lower than the two sites ($P<0.05$) for all dates.

Oi water content measurements and associated details are given in table 2.5. Oi water content ranged from 6 % at the OAK site in Apr., 1995 to 226 % at the SPR site in Jul., 1994 with the OAK Oi layer consistently the driest and the SPR Oi layer consistently the wettest. The SPR Oi water content was significantly different ($P<0.005$) from that of the other two sites for Jul., 1994, Nov., 1994, and

Table 2.3. Seasonal Oi layer mass measurements for the three forest ecosystem sites for the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		g m^{-2}		
SPR	746a	793a	308a	780a
COV	1042b	1300b	928b	1027b
OAK	848	708a	547c	371c

Means in columns with different lower-case letters indicate significant a difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.4. Seasonal Oe/Oa layer mass measurements for the three forest ecosystem sites for the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		g m^{-2}		
SPR	5273a	3576a	11631a	7129a
COV	5223a	4613a	13240a	7926a
OAK	3513b	811b	2906b	4756b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.5. Seasonal gravimetric Oi layer water content measurements for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	226a	188a	93a	83a
COV	141b	148a	49b	48b
OAK	112b	67b	20b	6c

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Apr., 1995. In Sep., 1994, the OAK Oi water content was significantly different ($P<0.005$) from that of the other two sites and in Apr., 1995, all three sites were significantly different ($P<0.005$).

Soil water content values and associated details are provided in table 2.6. The soil water content ranged from 16.8 % at the OAK site in Jul., 1994 to 36.3 % at the SPR site in Jan., 1995. Consistently, the OAK soil was the driest and the SPR soil was the wettest. The SPR site differed significantly ($P<0.005$) from the other two for all five measurement dates and all three sites were significantly different ($P<0.005$) in Jul., 1994, Nov., 1994, and Jan., 1995.

Soil temperature values and associated details are provided in table 2.7. Soil temperature ranged from -0.9 °C at the SPR site in Jan., 1995 to 19.6 °C at the OAK site in Jul., 1994, with the SPR soil consistently being the coolest. The OAK soil was the warmest for all dates except Jan., 1995 when the COV soil was slightly warmer than the OAK soil. Soil temperature values for all sites were significantly different ($P<0.005$) for all dates except Jan., 1995, when the SPR site was significantly lower ($P<0.005$) than the other two sites.

SOIL CHEMICAL PROPERTIES

The soil chemical properties which were considered constant for the duration of this study include exchangeable bases, Ca, Mg, K, and Na, exchangeable Al, percent base saturation, and cation exchange capacity (CEC) and are presented in table 2.8. Exchangeable Ca was lowest at the SPR site, 0.140 $cmol_c\ kg^{-1}$ and the highest at the OAK site, 0.854 $cmol_c\ kg^{-1}$. The SPR site's exchangeable Mg was the lowest, 0.148 $cmol_c\ kg^{-1}$, and the OAK site's was the highest, 0.164 $cmol_c\ kg^{-1}$. Exchangeable K increased from 0.161 $cmol_c\ kg^{-1}$ at the OAK site to 0.176 $cmol_c\ kg^{-1}$ at the SPR site. Exchangeable Na increased from 0.004 $cmol_c\ kg^{-1}$ at the COV site to 0.007 $cmol_c\ kg^{-1}$ at the SPR site. Exchangeable Al increased from 0.857 $cmol_c\ kg^{-1}$ at the OAK site to 3.759 $cmol_c\ kg^{-1}$ at the SPR site with the COV site's exchangeable Al only slightly less, 3.743 $cmol_c\ kg^{-1}$. The exchangeable bases and Al produced the lowest CEC at the OAK site, 2.0 $cmol_c\ kg^{-1}$, and the highest CEC at the COV site, 4.3 $cmol_c\ kg^{-1}$, with the SPR CEC, 4.2 $cmol_c\ kg^{-1}$, only slightly less than that of the COV site. The lowest percent base saturation occurred at the SPR site, 11.1%, and the highest occurred at the OAK site, 58.1%, with COV percent base saturation, 13.4%, somewhat higher than that of the SPR site.

Table 2.6. Seasonal volumetric soil water content measurements, sampled to a depth of 35 cm, for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Jan-95	Apr-95
		% based on $cm^3\ cm^{-3}$			
SPR	31.9a	32.7a	34.5a	36.3a	33.8a
COV	28.5b	22.4b	23.8b	29.0b	26.8b
OAK	16.8c	22.2b	17.9c	25.1c	25.8b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.7. Seasonal soil temperature measurements, sampled to a depth of 15 cm, for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Jan-95	Apr-95
		°C			
SPR	11.2a	10.9a	3.9a	-0.9a	1.9a
COV	15.7b	13.7b	10.0b	6.1b	9.4b
OAK	19.6c	17.8c	12.1c	5.4b	12.9c

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.8. Soil chemical properties, typically constant over one year, assessed for the three forest ecosystem sites from samples collected in April , 1995.

Site	Ex. Bases ($cmol_c\ kg^{-1}$)				Ex. Al ($cmol_c\ kg^{-1}$)	CEC ($cmol_c\ kg^{-1}$)	%Base sat.
	Ca	Mg	K	Na			
SPR	0.140	0.148	0.176	0.007	3.759	4.2	11.1
COV	0.258	0.151	0.167	0.004	3.743	4.3	13.4
OAK	0.854	0.164	0.161	0.006	0.857	2.0	58.1

Oi layer C values and associated details are given in table 2.9. Total Oi layer C ranged from 40.50 % at the OAK site in Jul., 1994 to 47.01% at the COV site in Nov., 1994. The OAK Oi layer C was consistently the lowest and the COV Oi layer C was the highest, except in Sep., 1994 when the SPR Oi layer C was slightly higher. The differences between the SPR and COV sites did not lead to any significant differences, however, the OAK site was significantly different ($P<0.05$) from the other two for all four periods.

Oe/Oa layer C values and associated details are provided in table 2.10. Total Oe/Oa layer C ranged from 18.38 % at the OAK site in Jul., 1994 to 39.37% at the COV site in Nov., 1994, with the OAK Oe/Oa layer consistently having the lowest C content. The highest Oe/Oa layer C content occurred at the COV in Sep. and Nov., 1994. In Jul., 1994, the SPR and COV sites equally had the highest Oe/Oa layer C content and in Apr., 1995, the SPR site had the highest value. However, the SPR and COV Oe/Oa layer C values were not significantly different for any date. The OAK Oe/Oa layer C was significantly lower ($P<0.05$) than that of the other two sites in Jul., 1994 and than that of the COV site in Nov., 1994.

Mineral soil C values and associated details are presented in table 2.11. Total mineral soil C varied from 2.31 % at the OAK site in Jul., 1994 to 8.23% at the COV site in Sep., 1994. Consistently, the OAK soil had the lowest C content and the COV soil had the highest C content. The OAK soil C was significantly lower ($P<0.005$) than that of the other two in Jul., 1994, Nov., 1994, and Apr., 1995 and lower than that of the COV site in Sep., 1994 ($P< 0.05$).

Oi layer N values and associated details are given in table 2.12. Total Oi layer N ranged from 0.70 % at the OAK site in Nov., 1994 to 1.52% at the SPR site in Sep., 1994. The Oi layer N content was consistently lowest at the OAK site. The SPR Oi layer N content was the highest except for the Jul., 1994 when the COV Oi layer N was slightly higher. The OAK Oi layer N was significantly different ($P< 0.05$) from that of the other two in Sep., 1994 and from that of the COV site in Jul., 1994. Oi layer N content for all sites was significantly different ($P<0.005$) in Nov., 1994 and Apr., 1995.

Table 2.9. Seasonal total carbon (organic plus inorganic) measurements in the Oi layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	46.10a	46.60a	46.70a	46.58a
COV	46.71a	45.49a	47.01a	46.91a
OAK	40.50b	42.84b	45.48b	44.75b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.10. Seasonal total carbon (organic plus inorganic) measurements in the Oe/Oa layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	34.92a	34.22	34.17	31.48
COV	34.92a	36.19	39.37a	30.27
OAK	18.38b	30.76	31.72b	22.37

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.11. Seasonal total carbon (organic plus inorganic) measurements in the mineral soil, sampled to an average depth of 21 cm, for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	6.08a	7.85	6.72a	5.70a
COV	7.34a	8.23a	8.08a	7.50a
OAK	2.31b	4.85b	2.37b	2.58b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05

Table 2.12. Seasonal total nitrogen (organic plus inorganic) measurements in the Oi layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	1.30	1.52a	1.15a	1.34a
COV	1.45a	1.47a	0.86b	1.16b
OAK	1.16b	1.22b	0.70c	0.71c

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Oe/Oa layer N values and associated details are provided in table 2.13. Total Oe/Oa layer N varied from 0.76 % at the OAK site in Apr., 1995 to 1.70% at the COV site in Nov., 1994, with the OAK Oe/Oa layer N content consistently being the lowest. The SPR Oe/Oa layer N content was the highest in Jul., 1994 and Apr., 1995 and the COV Oe/Oa layer N content was highest in Sep. and Nov., 1994. The OAK Oe/Oa layer N content was significantly different from that of the other two in Jul., 1994 ($P<0.005$), Nov., 1994 ($P<0.005$), and Apr., 1995 ($P<0.005$) and from that of the COV site in Sep., 1994 ($P<0.05$).

Mineral soil N values and associated details are presented in table 2.14. Total mineral soil N ranged from 0.11 % at the OAK site during Jul., 1994, Nov. of 1994, and Apr. of 1995 to 0.47% at the COV site in Apr., 1995. The OAK site consistently had the lowest soil N content and the COV site consistently had the highest soil N content. While the SPR and COV soil N values were never significantly different, the OAK soil N values were significantly the lowest ($P< 0.005$) for all measurement dates.

Oi layer C:N ratios and associated details are given in table 2.15. Oi layer C:N ratios varied from 31.12 at the COV site during Sep., 1994 to 67.55 at the OAK site in Nov., 1994. The COV Oi layer had the lowest C:N ratios in Jul. and Sep., 1994 and the SPR Oi layer had the lowest C:N ratios in Nov., 1994 and Apr., 1995. The OAK Oi layer C:N was highest for all dates except Jul., 1994 when

Table 2.13. Seasonal total nitrogen (organic plus inorganic) measurements in the Oe/Oa layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	1.65a	1.46	1.52a	1.48a
COV	1.54a	1.59a	1.70a	1.42a
OAK	0.78b	1.18b	1.04b	0.76b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.14. Seasonal total nitrogen (organic plus inorganic) measurements in the mineral soil, sampled to an average depth of 21 cm, for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	0.32a	0.38a	0.35a	0.33a
COV	0.36a	0.39a	0.37a	0.47a
OAK	0.11b	0.21b	0.11b	0.11b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.15. Seasonal carbon to nitrogen ratio in the Oi layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
SPR	36.65	31.22	41.12a	35.27a
COV	32.61	31.12	55.65b	41.07a
OAK	35.38	35.66	67.55c	63.46b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

the SPR Oi layer C:N was slightly higher. Oi layer C:N ratios were significantly different in Nov., 1994 ($P<0.005$) across all sites. In Apr., 1995, the OAK Oi layer C:N ratio was significantly lower than that of the other two ($P<0.005$).

Oe/Oa layer C:N ratios and associated details are provided in table 2.16. The Oe/Oa layer C:N ratios ranged from 21.10 at the SPR site in Jul., 1994 to 30.62 at the OAK site in Nov., 1994. The SPR Oe/Oa layer C:N ratio was the lowest in Jul. and Nov., 1994 and the COV Oe/Oa layer C:N ratio was the lowest in Sep., 1994 and Apr., 1995. The OAK Oe/Oa layer C:N was consistently the highest. In Nov., 1994 and Apr., 1995, the OAK Oe/Oa layer C:N was significantly higher ($P<0.005$) than that of the SPR and COV sites.

Mineral soil C:N ratios and associated details are given in table 2.17. Mineral soil C:N ratios ranged from 17.18 at the COV site in Apr., 1995 to 23.79 at the OAK site in Sep., 1994. The SPR site had the lowest values for all dates except Apr., 1995 when the COV site was slightly lower. The highest C:N values occurred at the OAK site for all dates except Nov., 1994 when the COV soil C:N was slightly higher. The OAK soil C:N was significantly higher ($P<0.05$) than that of the SPR site for all dates and significantly higher ($P<0.01$) than that of the COV site during Sep., 1994. The COV soil C:N ratio was significantly higher than that of the SPR site ($P<0.05$) in Nov., 1994 and not significantly different from either site during Jul., 1994 and Apr., 1995.

Soil pH values and associated details are given in table 2.18. Soil pH varied from 3.3 at the SPR site in Sep., 1994 to 4.9 at the OAK site in Sep., 1994. The SPR site had the lowest soil pH for all dates except for the Jul., 1994 date when it equalled the COV site. The OAK soil consistently had the highest pH. For all four measurement periods, the OAK soil pH values were significantly ($P<0.005$) higher than that of the SPR and COV sites and the latter two sites were not significantly different for any date.

Discussion

The assessment of the soil physical and chemical properties of the three forest ecosystems has been presented to describe of the soil attributes at these sites and to be used in assessing the

Table 2.16. Seasonal carbon to nitrogen ratio in the Oe/Oa layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
SPR	21.10	23.43	22.55a	21.22a
COV	23.05	22.75	23.08a	20.97a
OAK	23.11	26.83	30.62b	29.79b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.17. Seasonal carbon to nitrogen ratio in the mineral soil for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
SPR	18.74a	20.20a	19.06a	17.37a
COV	20.27	20.82a	21.94b	17.18
OAK	21.71b	23.79b	21.37b	21.65b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 2.18. Seasonal measurements of soil pH for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
SPR	3.9a	3.3a	3.6a	3.6a
COV	3.9a	3.6a	3.7a	3.7a
OAK	4.7b	4.9b	4.7b	4.9b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

factors significantly associated with the forest floor CO_2 efflux patterns across the three sites (Part 5). Because the emphasis was on describing soil physical and chemical properties of the three sites, variables which might have affected seasonal differences in the properties across the sites were not assessed. The explanations offered for the seasonal differences observed in soil physical and chemical properties among the three sites are based on conclusions from other studies.

SOIL PHYSICAL PROPERTIES

Soil texture refers to the distribution of sand, silt, and clay size particles of a soil and is a permanent attribute of a soil (Hillel, 1982). Soil texture influences the water retention, nutrient retention, cation exchange capacity, and porosity of the soil (Hillel, 1982; Pritchett and Fisher, 1987) and therefore, soil biological and chemical properties. The clay-sized particles are especially important because they adsorb water, exchangeable cations, and organic matter (Coleman and Crossley, Jr., 1996). Parent material and the degree of weathering (physical and chemical) determine the texture of a particular soil (McBride, 1994). The SPR site's sandy clay loam designation is likely due to the presence of quartzite material. The COV site's clay loam textural class is probably due to the presence of phyllitic silty and argillaceous rocks in the parent material. The siliceous dolomite parent material at the OAK site likely led to its clay loam textural classification. Given the texture classifications of the three sites, it is clear that clay-sized particles play an important role in the soil chemical dynamics.

Soil porosity, that volume not taken up by soil, influences soil water retention, aeration status, and the rate at which gases move into or out of the soil (Hillel, 1982) and hence, is a very important property for plants and microorganisms. Soil porosity is determined by the texture, structure, and amount of organic matter (Pritchett and Fisher, 1987). In addition, microbial degradation products help soil structure formation and the movement of fauna and roots in the soil aids the development of soil porosity (Pritchett and Fisher, 1987). It appears that the greater amounts of organic matter at the SPR and COV sites contributed to a higher soil porosity values at these sites and smaller amounts of organic matter at the OAK site influenced its lower soil porosity value.

Coniferous forests provide a continuous but smaller return rate of litter than do deciduous forests (Cole and Rapp, 1980; Landsberg and Gower, 1997; Pritchett and Fisher, 1987). Litterfall rates

increased from the coniferous-dominated SPR and COV sites, to the deciduous-dominated OAK site, which agrees with this point. However, the OAK site litterfall was only slightly greater than the COV site litterfall. It seems that the eight deciduous species, which account for 47% of the total basal area at the COV site, made a substantial contribution to the litterfall. The greater accumulation of woody biomass in the COV forest due to its age might also mean greater litterfall mass per collection area (Landsberg and Gower, 1997).

Evergreen forests typically accumulate more organic matter than do deciduous forests (Vogt et al., 1986). In addition to wide variations in accumulation values within a forest type, maximum forest floor accumulation values are related either to higher elevations or higher latitudes (Vogt et al., 1986). Coniferous forests generally produce litter having a lower N content and a higher acid content (Cole and Rapp, 1980; Pritchett and Fisher, 1987). Thus, cooler temperatures at the SPR and COV sites and the associated reduced litter quality slowed litter decomposition, contributing to greater organic matter accumulation at these sites than that of the OAK site (Coleman and Crossley, Jr., 1996; Pöhhacker and Zech, 1995; Waring and Schlesinger, 1985).

A cool climate and dominance of coniferous vegetation indicated a mor humus type at the SPR site (Waring and Schlesinger, 1985). The humus type refers to the three organic layers, collectively (Pritchett and Fisher, 1987). Mor humus has greater water-holding capacity than does mull humus (Pritchett and Fisher, 1987). In addition, cooler temperatures at the SPR site slowed soil water evapotranspiration (Kelliher and Scotter, 1992) and resulted in high soil and Oi water content values. While the SPR site consistently had higher Oe/Oa layer mass values than did the OAK site, it had the lowest Oi layer mass values on two occasions. The decline of the fraser fir trees due to the balsam wooly adelgid infestation (Busing et al., 1988) at the SPR site clearly led to diminished litterfall which probably accounts for these two occasions of lower Oi layer mass at the SPR site.

The mix of conifer and deciduous species at the COV site produce a duff mull humus type which has lower water-holding capacity than that of the mor humus (Pritchett and Fisher, 1987). Lower evapotranspiration at the COV site, in part because of the site's warmer temperatures over that of the SPR site, seems to have contributed to lower soil and Oi water content values at this site than at the

SPR site. Because deciduous litter decomposes more readily than does coniferous litter (Landsberg and Gower, 1997), the COV site likely undergoes greater decomposition than does the SPR site. However, the combination of a high litterfall rate, almost as high as that of the OAK site, and cool temperatures probably account, in part, for the COV site having the highest organic layer masses.

Deciduous forest in warm-temperate climates produce a mull humus type which has a low water-holding capacity and this describes the humus type at the OAK site (Waring and Schlesinger, 1985). The combination of the warm temperatures, readily decomposable litter, and the most distinct seasonal litter input at the OAK site led to it's generally having the least organic matter accumulation. In addition, the higher-than-normal precipitation input during the year over which the OAK site was sampled, 1994 - 1995 (Birdwell, 1997), would also have enhanced decomposition. The decline in fraser fir from the balsam wooly adelgid infestation over the past 15 years has changed the organic matter accumulation dynamics at the SPR site and probably accounts for occasions when the OAK Oi mass was higher than that of the SPR site.

Amount of precipitation, extent of tree canopy closure, degree of interception, air saturation deficit (decreases with decreasing temperature and increasing elevation), and air turbulence control how much water can potentially reach the forest floor (Kelliher and Scotter, 1992; Kimball and Lemon, 1971; Pritchett and Fisher, 1987; Waring and Schlesinger, 1985). At the forest floor, Oi water content depends on humus layer type, litter porosity and litter temperature (Pritchett and Fisher, 1987; Waring and Schlesinger, 1985). Warmer soil surface or litter temperatures, greater air-litter contact (higher porosity), higher air saturation deficits, and greater surface air turbulence enhance evaporation from Oi layer (Kimball and Lemon, 1971; Pritchett and Fisher, 1987; Waring and Schlesinger, 1985). All these factors appear responsible for differences in Oi water content values across the sites.

In addition to factors which control the amount of water reaching the forest floor, litter water content, soil texture, porosity, coarse fraction, root water uptake, and soil temperature govern soil water content (Hillel, 1982; Pritchett and Fisher, 1987). As litter water evaporates, so does the soil water but at a slower rate than that of bare soil (Balisky and Burton, 1995; Kelliher and Scotter, 1992). Soil texture, through a higher percentage of sand or of clay, can cause water loss or retention (Hillel, 1982).

The distribution of small relative to large pores (Kelliher and Scotter, 1992) and the amount of coarse fraction (Pritchett and Fisher, 1987) control the drainage rate of water through the soil. Along with litter and soil temperature's influence on evaporation, the major difference between the SPR and COV sites and the OAK site was reflected in their coarse fraction content, soil texture and porosity. Lack of statistical difference between the COV and OAK soil water contents in Sep., 1994 and Apr., 1995 might have been due to precipitation events just prior to sampling.

Although various factors influence soil temperature, values generally decreases as latitude and elevation increase (Pritchett and Fisher, 1987). In the northern hemisphere, southerly and westerly oriented slopes receive more solar radiation, resulting in warmer soil temperatures (Pritchett and Fisher, 1987). Degree of tree canopy closure and of forest floor cover also influence the amount of solar radiation reaching the soil surface (Balisky and Burton, 1995; Pritchett and Fisher, 1987). Higher amounts of organic matter covering the forest floor prevent soil temperature extremes in the winter and summer (Pritchett and fisher, 1987). Soil texture, water content, and organic matter content influence the heat capacity and thermal conductivity of the soil (Balisky and Burton, 1995; Pritchett and Fisher, 1987). While all these factors influenced temperature differences among the sites, soil temperature across the sites was clearly inversely related to elevation for all dates except for Jan., 1995. In Jan., 1995, the COV soil was slightly warmer than the OAK soil. The insulating effects of the organic layer thickness and soil water content (Pritchett and Fisher, 1987), both of which were greater at the COV site, might have prevented a lower soil temperature at the COV site. In addition conifer stands reflect less solar radiation than do deciduous stands (Landsberg and Gower, 1997). Since conifers dominate the COV site, there was less energy lost.

SOIL CHEMICAL PROPERTIES

Temperature, water content, and quality of the litter (Killham, 1994; Singh and Gupta, 1977; Vogt et al., 1986) govern microbial decomposition and thus, the amount of C and N that becomes mineralized. Litter quality not only corresponds to the C to N ratio of the substrate, but also to the lability of C and degree of acidity in the substrate (Berg, 1986; McClaugherty et al., 1985; Killham, 1994). In addition, if the N content is insufficient, the material can't be degraded (Charley and

Richards, 1982; Killham, 1994; Smith, 1993). Forest floor mass has been found to be highly positively associated with forest floor N content (Vogt et al., 1986). The cooler temperatures at the SPR and COV sites slowed the decomposition of the organic layers which resulted in greater accumulations of organic matter and therefore, C and N contents at these sites over that of the OAK site. Because the Great Smoky Mountains National Park is known to receive N from acid deposition, this might also account for higher N values at the SPR and COV sites (Johnson and Lindberg, 1992).

Deciduous species not only take up almost twice the N that coniferous species do, but they also translocate significantly more N from old to new tissue during leaf senescence (Cole and Rapp, 1980). Extent of canopy closure can influence nutrient content by controlling the amount of understory vegetation present that compete for nutrients (Cole and Rapp, 1980). Because the OAK site is a second-growth forest with more understory vegetation and because it is almost totally composed of deciduous species, there was significantly less N in the soil and in its litter, resulting in lower C and N content in the litter and soil. The differences in C and N contents between the SPR and COV sites and the OAK site appear to be due to the N strategy and canopy-closure extent at the OAK site and cooler temperatures at the SPR and COV sites, with the latter likely playing a smaller role. The decrease in C:N ratios with depth across all sites is a characteristic occurrence and results from the differences in decomposition rates between foliage and woody litter over time (Coleman and Crossley, Jr., 1996; Pritchett and Fisher, 1987).

Factors such as, vegetation type, parent material, water content, and microbial and root processes all influence soil pH (McBride, 1994; Miller and Donahue, 1990; Pritchett and Fisher, 1987). As previously mentioned, conifer leaves and litter are more acidic than those of deciduous species, which likely contributed to the lower pH values at the SPR and COV sites (Pritchett and Fisher, 1987). The weathering of parent material containing pyrite (FeS_2), can lower soil pH (McBride, 1994), however, it is not known whether or not this influenced soil pH at the sites. Nitrification by microorganisms and cation nutrient uptake by roots contribute hydrogen ions to the soil solution and this enhances soil acidity (McBride, 1994), which probably was the case at all the sites. In places receiving large amounts of precipitation such as the SPR and COV sites, cations which slow acidity

(Ca, Mg, K, Na) become leached (McBride, 1994). As this happens, hydrogen and aluminum ions adsorb to the clay/organic matter complex exchange sites and thereby greatly enhance soil acidity. Large organic matter accumulations and large amounts of precipitation also results in the leaching of organic acids, contributing to soil acidity. When carbon dioxide, produced by microorganisms and roots, reacts with water, its forms a weak acid at pH values above five and this probably influenced pH values to some degree, in the OAK soil (McBride, 1994). All these factors are likely to have contributed to the soil pH values, however, the vegetation type, organic matter accumulation, and precipitation amount at the SPR and COV sites probably resulted in the significant difference between these sites and the OAK site. Higher exchangeable Al and lower exchangeable Ca at the SPR and COV sites and the lower exchangeable Al and higher Ca at the OAK site support the soil pH patterns across the sites. Acid deposition might also have contributed to the soil pH dynamics at the SPR and COV sites (Johnson and Lindberg, 1992).

Summary and Conclusions

The characterizations of the soil physical and chemical properties, some of which varied seasonally and some of which were considered constant, for three forest ecosystem sites have been presented. All three sites had distinctly different seasonal patterns of soil temperature and soil water content values and the soil temperature values were inversely related to the elevation gradient across the sites. The large amount of precipitation and the incidence of fog typically occurring at the SPR and COV sites contributed to the Oi layer and soil water dynamics. The cooler temperatures at the SPR and COV sites also led to lower evapotranspiration rates which resulted in higher Oi layer and soil water content values at these sites over that of the OAK site.

The high- and mid-elevation sites, SPR and COV, had greater accumulations of organic matter than did the low-elevation site, OAK, which seemed to result from diminished organic matter decomposition brought about by cooler temperatures and reduced litter quality at these sites. The soil textural classifications of the sites were influenced by the parent material and degree of weathering at

each site. The amount of organic matter present at each site seemed to emerge as the most important factor influencing soil porosity differences among the sites.

The SPR and COV sites tended to have more similar patterns of organic layer and mineral soil C and N contents, as well as similar patterns of soil pH values, with the patterns at the OAK site being distinctly different. The larger C and N content of the organic layers and soil at the SPR and COV sites, was due to the greater organic matter accumulations at these sites and perhaps, N deposition. In addition, the translocation of N from old to new tissue during leaf senescence at the OAK site contributed to the differences in N between the OAK site and the SPR and COV sites. The lower soil pH values, lower base cation concentrations, and higher Al concentrations at the SPR and COV sites resulted from the acid content of the litter and the large amounts of precipitation that caused the leaching of these elements.

Elevation appears to have had the strongest influence on the development of soil physical properties at each site and the development of soil chemical properties at each site seems to have been governed by tree species, degree of precipitation, and parent material. Because soil physical and chemical properties have such a strong effect on the biochemical reactions of plants and microorganisms and the flux of gases in the soil, identifying their seasonal differences in various ecosystems will help scientists model potential feedback mechanisms in the global C cycle.

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PART 3

SEASONAL PATTERN OF MICROBIAL BIOMASS CARBON IN THREE CLIMATICALLY DIFFERENT FOREST ECOSYSTEM SOILS

Abstract

Because of the important contribution that forest soils make to the carbon cycle, understanding forest soil processes is vital to the balancing of the global carbon budget. Microorganisms and roots, the biological components of the soil, are the primary producers of soil carbon dioxide. Through detrital decomposition, microorganisms not only cycle Ca, Mg, K, P, and S but also help drive the carbon and nitrogen cycles, making them integral to plant/soil processes. Given that soil warming could lead to enhanced decomposition, understanding soil microbial dynamics is essential. This study was conducted to identify seasonal patterns of forest floor microbial biomass carbon within and among the three forest ecosystems, varying in age, climate, elevation, and tree species, located in East Tennessee, USA. Microbial biomass carbon (C) in the mineral soil was determined from samples gathered during July and November, 1994 and April, 1995. In addition, July, 1994 Oi layer samples and November, 1994 and April, 1995 Oe/Oa layer samples were assessed for site (and not seasonal) differences in microbial biomass C. Seasonal differences in soil microbial biomass C values did occur among the sites, but values were fairly constant within each site over time. Of the various soil physical, chemical, and biological parameters which can influence soil microbial biomass C, soil nitrogen and Oi layer mass were significant in explaining 63% of the seasonal variation in these values. Oi layer nitrogen accounted for 14% of the Oi layer microbial biomass C variation among sites for July, 1994 and there were no significant differences in Oe/Oa layer microbial biomass C among sites.

Introduction

Climate change, global warming brought on by increasing greenhouse gases (Boden et al., 1994), can potentially affect everything from agricultural systems to energy systems (hydroelectric power) (Watson et al., 1996). Carbon dioxide (CO_2) plays the central role in the global carbon (C) cycle, and it is considered the most important of the greenhouse gases (Lashof and Ahuja, 1990; Rodhe, 1990; Watson et al., 1996). Because forest soils contain 40% of all belowground carbon, they play an important role in the global C cycle (Ajtay et al., 1979; Dixon and Turner, 1991; Olson et al., 1983; Schlesinger, 1984; Whittaker and Likens, 1975; Zinke et al., 1984). It has been suggested that

forest soils may account for a portion of the imbalance in the global C budget (Dixon et al., 1994; Gifford, 1994; Harrison et al., 1993; Sedjo, 1992). While biological, physical, and chemical processes in the soil are all intrinsically linked to the status of soil CO_2 (Singh and Gupta, 1977), it is the uncertain response of the biological component to increasing CO_2 and increasing temperature which may have the greatest influence on the future of the global soil C balance (Bonan and Van Cleve, 1992; Curtis et al., 1994; Luxmoore et al., 1993; Norby et al., 1995; O'Neill, 1994; Ryan and Aravena, 1994). Indeed, recent studies have shown enhanced carbon dioxide efflux and nitrogen (N) mineralization on a short term basis due to artificially-induced soil warming (Kirschbaum, 1995; Chapman and Thurlow, 1996: Jenkinson et al., 1991; Lükewille and Wright, 1997; Peterjohn et al., 1994).

Most of the CO_2 produced in the soil results from the metabolism of microorganisms (MO) and roots, which, in addition to fauna, comprise the biological component of the soil (Singh and Gupta, 1977). Microorganisms which include bacteria, fungi, viruses, algae, and protozoa, are generally less than 0.16 mm in length (except fungi which can be much longer) and in forest soils, their total biomass values can range from 8 to 13 Mg ha^{-1} (Atlas and Bartha, 1993; Coleman and Crossley, Jr., 1996; Landsberg and Gower, 1997). Plants and the majority of MO living in the soil are aerobic, that is they require O_2 for their metabolism (Atlas and Bartha, 1993; Killham, 1994). Fine roots ($\leq$ 5 mm in diameter) are largely responsible for nutrient and water uptake and account for approximately 40 to 73% of the total net primary production in coniferous and deciduous forests (Coleman and Crossley, Jr., 1996; Landsberg and Gower, 1997). The microbial contribution to soil CO_2 is estimated to be anywhere from 20 to 77% with the root contribution ranging from 23 to 80% (Behera et al., 1990; Bowden et al., 1993; Cheng et al., 1993; Dörr and Münnich, 1987; Edwards and Sollins, 1973; Raich and Nadelhoffer, 1989; Tate et al., 1993).

The activities of MO and roots greatly influence that of each other (Paul and Clark, 1996). In fact, MO and roots interact synergistically in two ways. First, root exudates and root detritus attract microbial populations that can be up to 100 times higher in the rhizosphere, the thin layer of soil adhering to the roots, than in bulk soil (Atlas and Bartha, 1993; Cheng et al., 1993). Second, the mycorrhizal association in which fungi invade root systems, enhances plant nutrient and water uptake

and provides fungi with C substrate (Atlas and Bartha, 1993; Charley and Richards, 1982). Fungi dominate forest soils because they are the primary decomposers of organic matter and because they can tolerate the acid soils which are typical in forests (Killam, 1994). Through detrital decomposition, microorganisms cycle important nutrients needed by plants such as Ca, Mg, K, P, and S and they drive the soil C and N cycles (Anderson and Domsch, 1980; Díaz-Raviña et al., 1993; Laskowski et al., 1995; Smith, 1993). Microorganisms account for 1 to 3% of soil organic C and store, on average, 60%, 47%, and 28% of the N, P, and S required for plant uptake (Jenkinson and Ladd, 1981; Smith and Paul, 1990). Given the microbial role in the C cycle and their influence on plants, determination of factors that influence their processes is critical to resolving feedback mechanisms in the global C cycle (Curtis et al., 1994; Luxmoore et al., 1993; Ryan and Aravena, 1994; Schlesinger, 1995).

This part of the thesis identifies seasonal patterns of forest floor microbial biomass carbon within and among three forest ecosystems, varying in age, climate, elevation, and tree species, located in East Tennessee, USA. The microbial biomass carbon (MBC) parameter was chosen to measure because it is associated with the flow of C and other nutrients through ecosystems (Smith and Paul, 1990; Voroney et al., 1993). In addition to being a major constituent of microbial cells, carbon is required by chemoheterotrophic MO (require organic C substrate), the dominant microorganism in most ecosystems, for energy production (Atlas, 1984; Paul and Clark, 1996). To account for the seasonal differences in MBC within and among the three forest ecosystem sites, certain soil physical, chemical, and biological parameters were measured seasonally.

Materials and Methods

SITE DESCRIPTIONS (See Part 2 for specific details; Appendix B provides a relief map of the sites)

The highest-elevation site (SPR) is located within an old-growth spruce-fir forest. The middle-elevation site (COV) is located in a sheltered old-growth conifer-hardwood forest. The lowest-elevation site (OAK) is located within a secondary-growth oak forest. Climatic and topographic data are given in table 3.1.

Table 3.1. Topographic and Climatic Data for the SPR, COV, and OAK sites.

Site	Map	Lat/long (7.5 min)	Elev (m)	aOrien (deg)	bPrec (cm)	bMean Max Temp (°C)	bMean Min Temp (°C)
SPR	Clingmans Dome, NC-TN	35°35′N, 83°28′W	1859	65	230	18	-5
COV	Mount Le Conte, TN-NC	35°41′N, 83°27′W	975	72	194	22	-4
OAK	Bethel Valley, TN	35°58′N, 84°17′W	335	152	137	31	-3

aThe orientation or compass direction toward which the site faces. bMean maximum and mean minimum air temperature data, for the warmest and coldest month, respectively, and precipitation data are from Stephens, 1969.

EXPERIMENTAL DESIGN (See Part 2)

SAMPLING (See Part 2 for further details)

Measurements were made during July (Jul.), 1994, September (Sep.), 1994, November (Nov.), 1994, January (Jan.), 1995, and April (Apr.), 1995. The measurement dates were chosen on the basis of soil temperature and water content extremes, growing season, and litterfall.

Litter and Organic layers

Six plastic containers, with approximate collection areas of 0.21m², were placed throughout the SPR and COV sites to catch litterfall. Litter (leaves, stems, seeds, etc.) was collected five times over the period August, 1994 through April, 1995 from the SPR and COV sites and stored in plastic bags at 4 °C until they could be dried for mass determination. Litterfall data for the OAK site was provided by Hanson et al., (1995) and represents the period from August, 1994 through August, 1995. Data from six collection baskets (area = 0.20 m²), chosen randomly from rows 8 (upper), 5 (middle), and 3 (lower) on the ambient plot of the Throughfall Displacement Experiment site (see experimental design) were computed for OAK litterfall.

Oi and Oe/Oa layer samples were collected during Jul., Sep., and Nov. of 1994, and Apr. of 1995. Litter was gathered by hand through a plastic cylinder (dia. of 0.189 m) which outlined the collection area (the Oe and Oa layers were combined due to time constraints). The Oi layer, the top

organic layer, consists of the unaltered remains of plants and animals; the Oe layer, immediately below the Oi, consists of fragmented, partly decomposed organic matter; and the Oa layer, between the Oe and the mineral soil, consists of well-decomposed, amorphous organic matter (Pritchett and Fisher, 1987). Originally, only the Oi layer was to be assessed for organic layer microbial biomass C, but because the sample quantity was inadequate (for all analyses), the Oe/Oa layer, which was abundant, was assessed for MBC analysis. Portions of Jul., 1994 Oi layer and the Nov., 1994 and Apr., 1995 Oe/Oa layer samples were removed for microbial biomass carbon analysis and ground using a Waring blender prior to analysis to increase surface area. After the Oi layer samples were weighed for gravimetric water content determination, the remaining samples were stored in plastic bags at 4 °C until they were processed for physical and chemical analyses.

Soil samples

Mineral soil cores were collected during Jul., Sep., and Nov., 1994 and Apr., 1995 to an average depth of 21 cm using a open or closed bucket auger (dia.=0.077 m and 0.073 m, respectively) and stored in plastic bags at 4 °C for microbial biomass C analysis and physical and chemical analyses. These sample depths were used because microbial biomass C values, organic matter content, and root distribution are highest in the top 20-30 cm of the soil (Charley and Richards, 1982; Johnson et al., 1995; Ross and Tate, 1993). Samples subject to microbial biomass analysis were mixed by shaking the bags, sieved (2-mm mesh), and stored at 4 °C in plastic bags until they were extracted for organic C (Harden et al., 1993; Ross, 1991). Time constraints limited soil microbial biomass C analysis to the Jul. and Nov., 1994 and Apr., 1995 sampling periods.

After soil samples for microbial biomass C analysis had been set aside, the samples were air dried and sieved (<2 mm) as required for the various physical and chemical analyses. Approximately 10 g of each sample was pulverized with a mortar and pestle for the total C and N analyses. Additional soil cores were collected to an average depth of 26 cm during Jul., Sep., and Nov., 1994 and Apr., 1995 for root biomass determination using the same bucket augers. The Sep. and Nov., 1994 soil cores, collected to an average depth of 26 cm, were washed through a 2 mm sieve and the fragments > 2 mm were air dried to assess coarse fraction.

Undisturbed soil samples (original volume preserved) were collected from random locations at each of the three sites during July, 1997 to assess bulk density and total porosity. Five samples were collected at the SPR and COV sites, by pressing a cylindrical metal sampler into the mineral soil to an approximate depth of 9 cm (Blake and Hartge 1986). At the OAK site, eight samples were collected to an approximate depth of 5 cm, four from each side of the Throughfall Displacement Experiment site, using a hammer-driven cylindrical metal sampler (Blake and Hartge 1986).

Soil temperature and water content

Soil temperature was measured to a depth of 15 cm to the nearest 0.1 °C during Jul., Sep., and Nov., 1994, and Jan. and Apr., 1995, using a digital thermometer (OMEGA 872A or OMEGA 450 AET type E probe, OMEGA, Stamford, CT). Volumetric soil water content was measured to a depth of 35 cm to the nearest 0.1 $cm^3\ cm^{-3}$ during Jul., Sep., and Nov., 1994, and Jan. and Apr., 1995, using time domain reflectometery, the method developed by Topp and Davis (1985) (Trase System 6050X1, Soilmoisture Equip. Corp., Goleta, CA). The Jul., 1994 water content measurements were made to a 15 cm depth using portable steel rods. Thereafter, water content was measured to a depth of 35 cm because this depth better represented the conditions under which maximum biological activity occurs (Charley and Richards, 1982; Pritchett and Fisher, 1987). Stainless steel 35 cm rods used in measuring water content were installed after the Jul., 1994 date and left in place for the experiment's duration.

ANALYTICAL METHODS

Soil, Oi, and Oe/Oa layer MBC were estimated to the nearest 1 μg MBC g^{-1} of soil or organic layer sample. The chloroform fumigation extraction method was used to extract microbial C from the samples, with results expressed on an oven-dry weight basis for soil (105 °C) and on an oven-dry weight basis for Oi and Oe/Oa layers (70 °C) (Voroney et al., 1993). Extracted microbial biomass C (MBC) solutions were left frozen until they were analyzed with the Dohrmann DC-80 Carbon analyzer which uses low temperature persulfate digestion to determine organic carbon content. An efficiency rate of 0.25, the efficiency with which the microbial C is extracted from the sample solution, was used to calculate MBC (Voroney et al. 1993). Live roots $\leq$ 5mm in diameter (Fogel, 1985; Nadelhoffer and

Raich, 1992) were removed by hand from the soil samples and after being oven-dried at approximately 100 °C, root biomass was calculated to the nearest 0.01 Mg ha^{-1} soil (Hanson et al., 1993).

Litterfall was weighed after being oven-dried at 70 °C and the mass per collection area per year was calculated to the nearest 1 g $m^{-2} \cdot yr^{-1}$. The Oi and Oe/Oa layer samples were oven-dried (70 °C), weighed and the mass per collection area computed to the nearest 1 g m^{-2}. The Oi material was weighed before and after oven-drying to determine the gravimetric water content to the nearest 1% (based on g g^{-1}). The dried Oi and Oe/Oa samples were ground using a Cyclone grinder or Wiley mill (20 mesh screen) and mixed by shaking prior to total C and N analyses.

Coarse fraction (fragments > 2 mm), which is the rock volume relative to the soil volume, was calculated to the nearest 0.001 cm^3 cm^{-3} with rock volume obtained by water displacement of the rocks. For each site, soil texture was determined to the nearest 1% from the particle size analysis of three samples, each of which was a combination of Jul. and Sep., 1994 samples (Gee and Bauder, 1986). Bulk density was computed to the nearest 0.1 g cm^{-3} based on the oven-dry weight of the sample per sampler volume from the undisturbed soil samples, which were weighed before and after oven-drying (105 °C) (Blake and Hartge 1986). Subsequently, total porosity was calculated to the nearest 1% from bulk density, gravimetric water content (of the undisturbed samples), and particle density, which was assumed to be 2.65 g cm^{-3} (Hillel, 1982; Miller and Donahue, 1990).

Total C and N of the Oi and Oe/Oa layers and the mineral soil were quantified to the nearest 0.01% (based on g g^{-1}) by the high-temperature induction furnace method (Bremner and Mulvaney, 1982; Nelson and Sommers, 1982) using a carbon/nitrogen/sulphur analyzer (LECO CNS2000, LECO, St. Joseph, MI). The C to N (C:N) ratios were calculated from these results. The April, 1995 samples were analyzed for exchangeable bases, Ca, K, Mg, and Na (Thomas, 1982), using the inductively coupled Argon plasma-optical emission spectrometer (ICAP61, Thermo Jarrell Ash Corp., Franklin, MA) with results given to the nearest 0.001 $cmol_c$ kg^{-1}. Analysis of the April, 1995 samples for K was done using an atomic absorption spectrophotometer with results given to the nearest 0.001 $cmol_c$ kg^{-1} (Perkin-Elmer atomic absorption spectrophotometer 5000, Perkin-Elmer Corp., Norwalk, CT). The April, 1995 samples were analyzed for Al by the pyrocatechol violet method (American Public Health

Association et al., 1992) using the Skalar autoanalyzer, with results given to the nearest 0.001 $cmol_c$ kg^{-1}. Soil pH (H_2O) was measured with the Corning pH Ion Analyzer 355 (McLean, 1982).

STATISTICAL ANALYSIS

Analysis of variance was applied to assess the significant differences in soil microbial biomass C (MBC) and other parameters among the sites for a given sampling date at an alpha level of 0.05 ($P<0.05$). Multiple regression analysis was used to determine which factors were significant in explaining seasonal differences in MBC within and among the sites. After some consideration, it was decided that the Oi layer MBC (Jul., 1994) and the Oe/Oa layer MBC (Nov., 1994 and Apr., 1995) were not equivalent and thus, they could not be analyzed for seasonal differences. However, they were analyzed for site differences for their respective collection dates. The Student-Neuman-Keul's test was used to determine which sites were significantly different. Software from SPSS Inc., Chicago, IL, was used in all data analyses.

Results

Some soil physical and chemical properties, considered to remain constant over one year are presented in tables 3.2 and 3.3 (soil physical and chemical properties are discussed in depth in Part 2). For 1994-1995, the mean litterfall at the SPR, COV, and OAK sites was 250, 423, and 440 g m^{-2}, respectively. The presentation of results focuses on soil MBC since this parameter was measured seasonally. (Data not provided here can be found in Parts 2, 5, and Appendix A).

Seasonal soil MBC measurements for each site are provided in table 3.4. SPR soil MBC varied from 1268 µg g^{-1} in Nov., 1994 to 1430 µg g^{-1} in Apr., 1995 with no significant seasonal differences within the site ($P=0.667$). Soil MBC at the COV site ranged from 1424 µg g^{-1} in Nov., 1994 to 1958 µg g^{-1} in Jul., 1994 with no significant differences among dates ($P=0.267$). OAK site soil MBC varied from 469 µg g^{-1} in Apr., 1995 to 719 µg g^{-1} in Jul., 1994 with no significant differences among dates ($P=0.168$).

Table 3.2. Soil physical properties, typically constant over one year, assessed for three forest ecosystem sites from samples collected during the period July, 1994 to April , 1995.

Site	[c]Bulk density ($g\ cm^{-3}$)	Porosity (%)	Coarse frac. ($cm^3\ cm^{-3}$)	Texture (%)			
				sand	silt	clay	class.
SPR	0.6	78	0.020	52	23	25	sandy cl. loam
COV	0.3	88	0.008	44	22	34	clay loam
OAK	0.9	65	0.113	24	37	39	clay loam

[c]Samples for bulk density and porosity determination were collected in July, 1997.

Table 3.3. Soil chemical properties, typically constant over one year, assessed for the three forest ecosystem sites from samples collected in April , 1995.

Site	Ex. Bases ($cmol_c\ kg^{-1}$)				Ex. Al ($cmol_c\ kg^{-1}$)	CEC ($cmol_c\ kg^{-1}$)	%Base sat.
	Ca	Mg	K	Na			
SPR	0.140	0.148	0.176	0.007	3.759	4.2	11.1
COV	0.258	0.151	0.167	0.004	3.743	4.3	13.4
OAK	0.854	0.164	0.161	0.006	0.857	2.0	58.1

Table 3.4. Seasonal microbial biomass carbon measurements in the mineral soil of three forest ecosystem sites, sampled to an average depth of 21 cm, during the period July, 1994 to April, 1995.

Site	Jul-94	Nov-94	Apr-95
		$\mu g\ g^{-1}$ sample	
SPR	1411a	1268a	1430a
COV	1958a	1424a	1609a
OAK	719b	567b	469b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

The seasonal patterns of the soil MBC measurements for all sites are illustrated in figure 3.1. Across all the sites, soil MBC ranged from 469 μg g^{-1} at the OAK site in Apr., 1995 to 1958 μg g^{-1} at the COV site in Jul., 1994 (table 3.4). Distinct seasonal patterns in soil MBC emerged with the OAK site consistently having the lowest values and COV site consistently having the highest values. The soil MBC at the OAK site was significantly different ($P<0.005$) from that at the SPR and COV sites for all dates. The SPR and COV soil MBC patterns were similar with no significant differences during any of the dates.

When soil MBC was regressed against all the factors, soil N ($P<0.005$) and Oi layer mass ($P<0.005$) accounted for 53% (unadjusted) and 11% (unadjusted), respectively, of the seasonal variation across the SPR, COV, and OAK sites (figures 3.2 and 3.3). Together, soil N and Oi layer mass accounted for 63% (adjusted R^2, $P<0.005$) of the soil MBC variation across the three sites. Soil MBC exhibited a linear relationship with soil N (figure 3.2) and with Oi layer mass (figure 3.3), respectively. The estimated regression equation (standard error in parentheses) was soil MBC = -4.7(±116) + 2559(±285) × soil N + 0.68(±0.14) × Oi layer mass. Soil N and Oi layer mass data are given in tables 3.5 and 3.6, respectively. Basically, the seasonal soil MBC pattern closely paralleled the seasonal soil N pattern at each site, with the OAK site consistently having the lowest values and the COV site consistently having the highest values. However, the seasonal patterns of soil MBC and Oi layer mass for each site exhibited more divergence.

All Oi layer and Oe/Oa layer MBC data are provided in table 3.7. The Jul., 1994 Oi layer MBC varied from 18,431 μg g^{-1} at the SPR site to 26,728 μg g^{-1} at the COV site with the COV Oi layer MBC significantly different ($P<0.05$) from that of the other two sites. Of the variables assessed, only Oi layer N ($P<0.05$) weakly accounted for 14% of the Oi layer MBC variation among the sites (figure 3.4). The Oi layer N data are provided in table 3.8. The estimated regression equation (standard error in parentheses) was Oi MBC = 2096(±8807) + 14,988(±6561) × Oi layer N. There were no significant differences among sites for Oe/Oa layer microbial biomass C values during either Nov., 1994 ($P=0.48$) or Apr., 1995 ($P=0.36$). The Nov., 1994 Oe/Oa layer MBC values ranged from 9825 μg g^{-1} at the COV

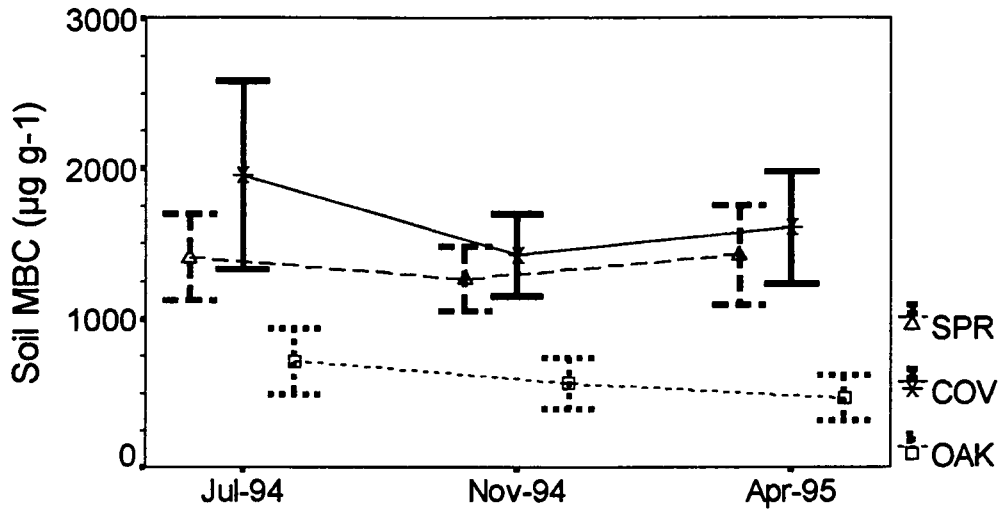

Figure 3.1. SPR, COV, and OAK soil microbial biomass carbon (mean±2SE) measured during three seasons.

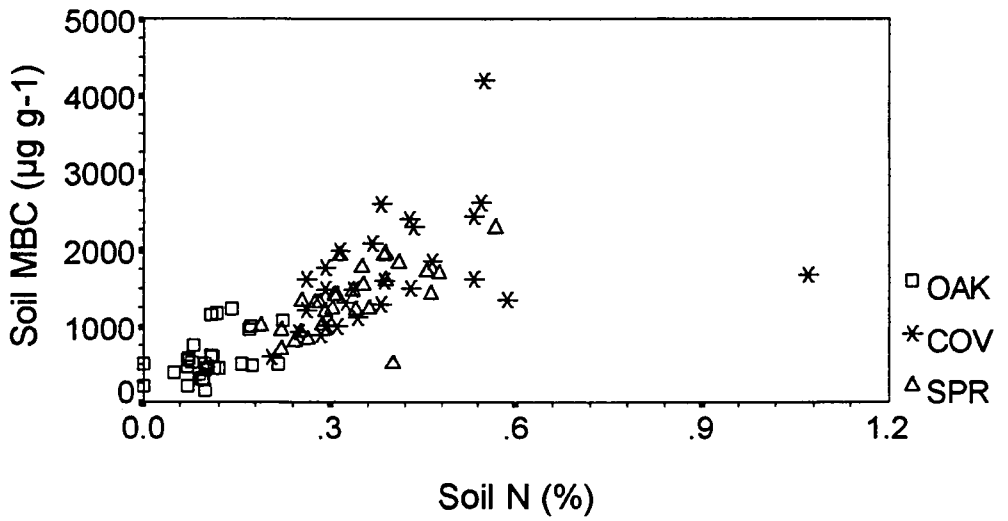

Figure 3.2. Significant influence of soil nitrogen (unadjusted R^2=0.53, P<0.005) on seasonal soil microbial biomass carbon differences across three forest ecosystem sites for July, 1994, November, 1994, and April, 1995.

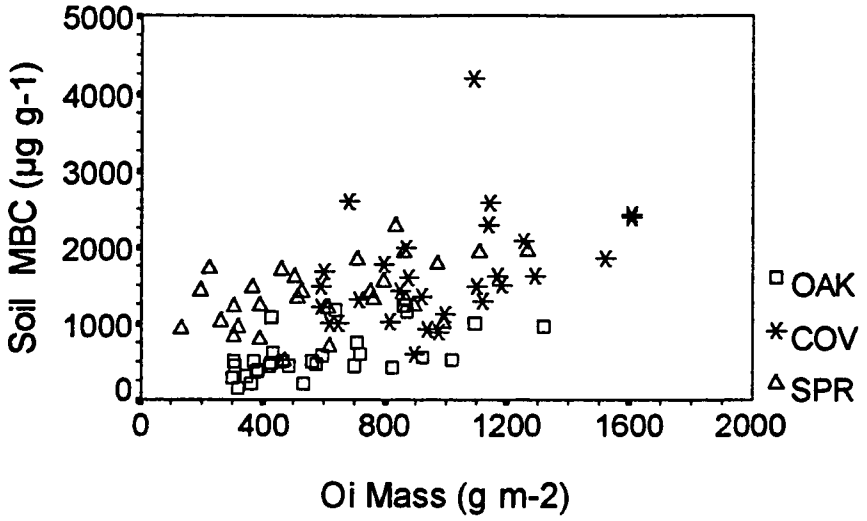

Figure 3.3. Significant influence of Oi layer mass (unadjusted R^2=0.11, P<0.005) on seasonal soil microbial biomass carbon differences across three forest ecosystem sites for July, 1994, November, 1994, and April, 1995.

Table 3.5. Seasonal total nitrogen (organic plus inorganic) measurements in the mineral soil, sampled to a depth of 25 cm, for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	0.32a	0.38a	0.35a	0.33a
COV	0.36a	0.39a	0.37a	0.47a
OAK	0.11b	0.21b	0.11b	0.11b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 3.6. Seasonal Oi layer mass measurements for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		$g\ m^{-2}$		
SPR	746a	793a	308a	780a
COV	1042b	1300b	928b	1027b
OAK	848	708a	547c	371c

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 3.7. Microbial biomass carbon measurements in the organic layers at three forest ecosystem sites assessed from samples collected in July, 1994, November, 1994, and April, 1995.

Site	Oi layer	Oe/Oa layer	Oe/Oa layer
	Jul-94	Nov-94	Apr-95
	$\mu g\ g^{-1}$ sample		
SPR	18431a	11374	8267
COV	26728b	9825	6859
OAK	19490a	11622	7312

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

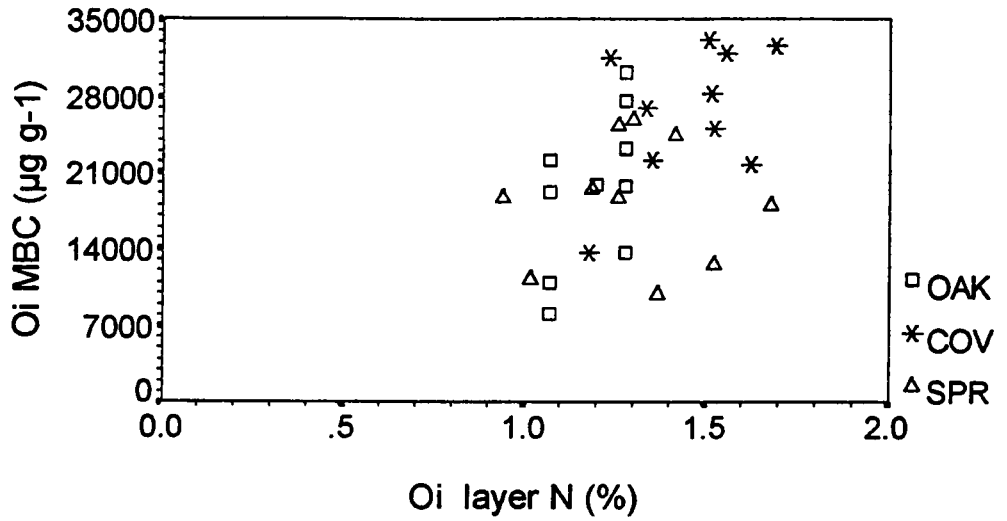

Figure 3.4. Influence of Oi layer nitrogen (adjusted R^2=0.14, P<0.05) on Oi microbial biomass carbon differences across three forest ecosystem sites for July, 1994.

Table 3.8. Seasonal total nitrogen (organic plus inorganic) measurements in the Oi layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	1.30	1.52a	1.15a	1.34a
COV	1.45a	1.47a	0.86b	1.16b
OAK	1.16b	1.22b	0.70c	0.71c

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

site to 11,622 μg g^{-1} at the OAK site and the Apr., 1995 Oe/Oa layer MBC values ranged from 6859 μg g^{-1} at the COV site to 8267 μg g^{-1} at the SPR site (table 3.7). Although soil temperature and Oi layer C were not significantly related to soil or organic layer MBC, because these properties typically have a strong influence on biological processes, the data have been provided in tables 3.9 and 3.10, respectively.

Discussion

Soil microbial biomass C (MBC) values of the SPR, COV, and OAK sites compared well with those of the 38 German forest soils studied by Joergensen et al. (1995). The Organic layer microbial biomass C values of the three sites were comparable to those of an old-growth beech forest in New Zealand (Ross and Tate, 1993).

Chemoheterotrophic microorganisms (MO) dominate soil environments, requiring substrate carbon for energy and for cell biomass synthesis (Paul and Clark, 1996; Singh and Gupta, 1977; Smith and Paul, 1990). Large amounts of C are needed since the break down and utilization of nutrients requires much energy (Davidson, 1995; Smith, 1993; Smith and Paul, 1990). However, unless the substrate contains enough N, essential for cell peptide and protein synthesis, the MO can not decompose the substrate (Charley and Richards, 1982; Killham, 1994; Melillo et al., 1984). In this study, the need for substrate N significantly influenced seasonal differences in soil microbial biomass C across sites and influenced site differences in Oi layer microbial biomass C. Although substrate C was not a statistically significant factor, perhaps the need for large quantities of C (table 3.9) led to the secondary significant influence of the Oi layer mass on seasonal soil microbial biomass C differences across sites.

Maximum forest floor organic matter accumulations are related to either higher elevations or higher latitudes which is due to cooler temperatures (Vogt et al., 1986). In addition, evergreen or coniferous forests normally accumulate more organic matter than do deciduous forests (Vogt et al., 1986). The COV site, which was the mid-elevation site always had the greatest Oi layer mass.

Table 3.9. Seasonal soil temperature measurements, sampled to a depth of 15 cm, for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Jan-95	Apr-95
		°C			
SPR	11.2a	10.9a	3.9a	-0.9a	1.9a
COV	15.7b	13.7b	10.0b	6.1b	9.4b
OAK	19.6c	17.8c	12.1c	5.4b	12.9c

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Table 3.10. Seasonal total carbon (organic plus inorganic) measurements in the Oi layer for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		% based on g g^{-1}		
SPR	46.10a	46.60a	46.70a	46.58a
COV	46.71a	45.49a	47.01a	46.91a
OAK	40.50b	42.84b	45.48b	44.75b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

However, the OAK site, at the lowest elevation, had a greater Oi layer mass than did the high-elevation SPR site two out of four dates. The reasons for this might be the seasonal litter input at the OAK site and the impact to the fraser fir stand by the balsam woolly adelgid (Busing et al., 1988) at the SPR site. Although temperature undoubtedly contributed to the organic matter accumulations at the SPR and COV sites, it was not a significant influence on microbial biomass C variations.

Coniferous and deciduous forests have particular attributes that might have contributed to the importance of nitrogen and Oi layer mass on the MBC variations. Coniferous forests produce litter having a lower N content and a higher acid content than do deciduous forests and they also shed litter at a slower and smaller rate (Cole and Rapp, 1980; Pritchett and Fisher, 1987). However, the SPR and COV sites always had higher N contents in the organic layers and mineral soil, which was possibly due to the influence of temperature on organic matter decomposition (Paul and Clark, 1996). The low N content in the organic layers and mineral soil at the OAK site was conceivably due to the translocation of substantial amounts of N from old to new tissue during leaf senescence (Cole and Rapp, 1980).

The different coniferous/deciduous species composition at each site may have affected the influence of Oi layer mass on MBC variations. Large amounts of precipitation generally lead to the leaching of the organic layers, resulting in the translocation of nutrients to the mineral soil (Guggenberger and Zech, 1994). Since the SPR and COV sites have moist environments throughout the year, this could have added to the importance of the Oi layer mass.

The great difference in soil MBC values between the SPR and COV sites and the OAK site might be the result of different nutritional strategies of the microorganisms present (Paul and Clark, 1996). The OAK soil MBC was always significantly lower than that of the other two sites. Nutritionally, microorganisms can be put into two groups, oligotrophs and copiotrophs. Oligotrophic organisms can grow in nutrient-low environments and tend to be more stable and permanent members of the microbial community (Atlas and Bartha, 1993; Paul and Clark, 1996). On the other hand, copiotrophic organisms grow very rapidly on fresh or nutrient-rich substrate and decline rapidly once the substrate is depleted (Atlas and Bartha, 1993; Paul and Clark, 1996). If the seasonal input of litter at the OAK

site stimulated more of the copiotrophic-type MO, this could possibly explain some of the span in soil MBC values between the OAK site and the other two sites. In addition, soil fauna, through their comminution of fresh litter (reduction into smaller pieces) can enhance microbial proliferation or diminish their numbers through grazing on them (Coleman and Crossley, Jr., 1996; Edwards et al., 1970; Maraun and Scheu, 1995). The OAK site might have had a greater presence of soil fauna which would also have resulted in smaller numbers.

Summary and Conclusions

This study has identified seasonal patterns of soil microbial biomass C across three forest ecosystem sites distinct in age, climate, elevation, and tree species. Only site (and not seasonal) differences in Oi and Oe/Oa layer microbial biomass C could be determined since neither was measured during all three dates. Definite seasonal differences in soil microbial biomass C values did emerge among the sites with the COV site consistently having the largest values and the OAK site consistently having the smallest values. However, within each site, soil microbial biomass C values were fairly constant from season to season. Soil N and Oi layer mass were significant in explaining 63% of the seasonal differences in soil microbial biomass C across the sites. The largest Oi layer microbial biomass C mean occurred at the COV site and the smallest mean occurred at the SPR site. Oi layer N significantly accounted for only 14% of the differences in Oi layer microbial biomass C among sites.

Some other factors might have added to the understanding of microbial dynamics across these three sites. Knowing the type of microorganisms present in forest ecosystems along with their nutrient strategy could provide some insight into feedback mechanisms involved in climate change. Assessing the soil faunal populations in the three ecosystems might have contributed to the explanation for the difference in microbial biomass C values. Because microbial biomass C can and does vary seasonally and among forest floor layers, not only should soil microbial biomass C be determined over more seasons, but Oi layer and Oe/Oa layer microbial biomass C should be as well. Measuring microbial

dehydrogenase enzyme activity over seasons and sites might have been a better indicator of when they are actually decomposing substrate and thus respiring CO_2.

This study has provided a characterization of microbial behavior in relation to their cycling of C across different forest ecosystems and over time, and includes the factors influencing differences in the behavior. In addition, the study has provided some understanding as to why the governing factors exert influence over microbial biomass C differences. Information from this and other studies, will contribute toward resolving the uncertainties in the feedback mechanisms of the global C cycle.

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PART 4

RATES AND MEASUREMENT METHODS OF CARBON DIOXIDE EFFLUX FROM BOREAL AND TEMPERATE FOREST SOILS

Abstract

Seasonal boreal and temperate forest floor carbon dioxide (CO_2) efflux rates, from studies conducted since 1978, are presented along with a description and discussion of methods used in the collection and detection of CO_2 efflux. Enclosure and micrometeorological techniques are the principal methods used to collect or capture forest floor CO_2 efflux. Because the enclosure (chamber) technique captures CO_2 efflux from a small area ($<1^2$ m^2), it is more suitable for studying small-scale ecosystem processes. Whereas, since micrometeorological techniques capture the efflux from a larger area ($>10^2$ m^2), they are more suitable for studying large-scale ecosystem processes. Alkali absorption, infrared radiation absorption, and gas chromatography are the primary methods used to detect CO_2 concentration fluxes with the latter two methods considered to be more accurate. The boreal forest soils produced the mean minimum winter CO_2 efflux rate of 0.3 µmol m^{-2} s^{-1} and the temperate deciduous forest soils produced the mean maximum summer CO_2 efflux rate of 2.8 µmol m^{-2} s^{-1}. The temperate coniferous forests exhibited the smallest range in seasonal forest floor CO_2 efflux rates, 1.0 to 2.0 µmol m^{-2} s^{-1} and the boreal forests exhibited the largest range, 0.3 to 2.6 µmol m^{-2} s^{-1}. The smallest absolute CO_2 efflux rate, 0.1 µmol m^{-2} s^{-1}, occurred during the spring in a temperate mixed coniferous/deciduous forest and the largest absolute CO_2 efflux rate, 5.4 µmol m^{-2} s^{-1}, occurred during the summer in a temperate deciduous forest. Most of the studies ascribed seasonal variations in forest floor CO_2 efflux rates to soil temperature and soil water content. When possible soil temperature values for the different studies were included since it often has the strongest influence on CO_2 flux. When soil temperature was regressed against forest floor CO_2 efflux rates for all study sites, it accounted for 23% of the linear association and 22% of the nonlinear association with the latter producing higher R-squared values for most of the individual forest types. Several factors may have biased the forest floor CO_2 efflux rates, such as the use of contrasting methods to collect and detect CO_2, contrasting numbers of measurements made per measurement interval, contrasting measurement intervals per year, different deployment times, and some made daytime measurements while others made diurnal measurements.

Introduction

Global warming, precipitated by increasing levels of greenhouse gas concentrations, is one of the most serious consequences of human activity (emissions from fossil fuels and deforestation) (Boden et al., 1994; Houghton et al., 1996; Pearman, 1988; Thomson, 1995; U. S. Environmental Protection Agency, 1988). The reality that climate change can affect everything from agriculture to energy systems clearly demands a comprehensive understanding of the factors and their dynamics contributing to this process. Carbon dioxide (CO_2) which plays a major role in the global carbon (C) cycle, has been found to be responsible for 60 to 80% of the greenhouse warming effect, making it the most important of the greenhouse gases (Rodhe, 1990; Lashof and Ahuja, 1990; Watson et al., 1996). Modelling the magnitude and direction of the global C cycle can not be achieved without direct measurements which verify the factors and the processes controlling global C dynamics.

Soils are the second largest C reservoir (Schimel et al., 1995) and forest soils contain 40% of all belowground C, making them an important compartment of the global C cycle (Ajtay et al., 1979; Dixon and Turner, 1991; Olson et al., 1983; Schlesinger, 1984; Whittaker and Likens, 1975; Zinke et al., 1984). Forest soils are also thought to account for part of the global C budget imbalance (Dixon et al., 1994; Gifford, 1994; Harrison et al., 1993; Sedjo, 1992). Given the important influence of forests soils on the global C cycle and that climate-induced temperature increases are predicted to affect seasonal soil CO_2 efflux patterns, a review of seasonal forest soil CO_2 efflux rates will greatly enhance the understanding of global C dynamics (Raich and Schlesinger, 1992). Boreal and temperate forest soils were of particular interest because of the forest types examined in this thesis (Part 5). In addition to the extensive survey of soil and organic layer CO_2 efflux data by Singh and Gupta in 1977, more recently, Raich and Schlesinger (1992) and Raich and Potter (1995) reviewed global soil CO_2 flux and Kicklighter et al. (1994) evaluated temperate forest soil CO_2 flux. This overview presents CO_2 efflux rates from boreal and temperate forest soils reported in studies done since 1978, with the emphasis on seasonal patterns. Factors influencing CO_2 production and flux and methods for collecting and detecting CO_2 flux are also described and discussed.

Production of CO_2

SOURCES OF CO_2

Carbon dioxide production in the mineral soil and the organic layers is a product of both biological activity and chemical reactions (Singh and Gupta, 1977). While the biological production of CO_2 which is due to metabolism, involves soil fauna, the major producers are microorganisms (MO) and roots (Cheng et al., 1993; Ross and Tate, 1993; Singh and Gupta, 1977; Tate et al., 1993). Microorganisms which include bacteria, fungi, viruses, algae, and protozoa, are generally less than 0.16 mm in length and in forest soils, their total biomass values range from 8 to 13 Mg ha^{-1} (Atlas and Bartha, 1993; Coleman and Crossley, Jr., 1996; Landsberg and Gower, 1997). Plants and the majority of MO living in the soil are aerobic, that is they require O_2 for their metabolism (Atlas and Bartha, 1993; Killham, 1994). The fine roots ($\leq$ 5 mm in diameter) are largely responsible for nutrient and water uptake and account for approximately 40 to 73% of the total net primary production in coniferous and deciduous forests (Coleman and Crossley, Jr., 1996; Landsberg and Gower, 1997). Chemical CO_2 production, involving reactions among water, organic acids, and carbonate compounds, is a minor component compared to the biological production of CO_2 (Kicklighter et al., 1994; McBride, 1994; Šimůnek and Suarez, 1993).

The microbial contribution to soil CO_2 is estimated to be anywhere from 20 to 77% with the root contribution ranging from 23 to 80% (Behera et al., 1990; Bowden et al., 1993; Cheng et al., 1993; Dörr and Münnich, 1987; Edwards and Sollins, 1973; Raich and Nadelhoffer, 1989; Tate et al., 1993). Of the total forest floor CO_2 production, above ground litter decomposition can contribute up to 48% (Edwards and Sollins, 1973; Ross and Tate, 1993; Bowden et al., 1993). Because MO and roots interact synergistically by way of the rhizosphere and mycorrhizal associations, it has been very difficult to determine precisely how much CO_2 each source produces (Bowden et al., 1993; Cheng et al., 1993; Killham, 1994). In the rhizosphere, the soil area immediately affected by the root system, roots secrete sugars, amino acids, proteins, and other small molecular weight compounds, resulting in microbial

populations up to 100 times greater than that in remaining bulk soil (Atlas and Bartha, 1993; Paul and Clark, 1996). On the other hand, MO mineralize organic matter, cycling C, N, P, and S, nutrients needed by plants (Smith and Paul, 1990). In the mycorrhizal association, the root system's ability to take up water and nutrients is enhanced and the fungi receive photosynthate, or C substrate, via the roots (Atlas and Bartha, 1993; Killham, 1994).

INFLUENCES ON CO_2 PRODUCTION AND FLUX

Flow of CO_2 within and from the soil occurs either by convection (mass flow) or molecular diffusion (Hillel, 1982; Matson and Harriss, 1995). Because CO_2 concentrations in the soil can be ten and sometimes one-hundred times greater than that in the atmosphere, a gradient develops, such that CO_2 almost always flows from the soil to the atmosphere (Hillel, 1982).

Soil temperature and water content have long been demonstrated to have the greatest influence over the production and flux of CO_2 (Anderson, 1973; Dörr and Münnich, 1987; Edwards, 1975; Garrett and Cox, 1973; Hanson et al., 1993; Lundegårdh, 1927; Reiners, 1968; Šimůnek and Suarez, 1993; Singh and Gupta, 1977). By influencing the rate at which biochemical activity proceeds, temperature directly impacts microbial and root CO_2 production (Paul and Clark, 1996; Pritchett and Fisher, 1987). Because the density of a gas depends on its temperature in part, the movement of CO_2 from the soil can be augmented by a soil/atmosphere temperature difference (Hillel, 1982).

Soil water content modifies the pathway by which CO_2 can move out of and O_2 can move into the soil and thus, influences soil aeration (Hillel, 1982). Soil water influences plant roots and MO through its effect on the solubilization of nutrients, by providing the medium by which they take in nutrients, and it is an essential component of their metabolism (Paul and Clark, 1996; Pritchett and Fisher, 1987; Smith and Paul, 1990). Water content in the organic layers can be as influential as temperature on CO_2 production, especially in the Oi layer (De Santo et al., 1993; O'Connell, 1990; Ross and Tate, 1993; Singh and Gupta, 1977).

Roots and MO are affected by soil aeration because they require at least 10% of the pore space to be air-filled (Hillel, 1982). Since the proportion of sand, silt, and clay affect not only water

retention but also aggregate formation, soil texture influences the air capacity or porosity of the soil (Hillel, 1982; Paul and Clark, 1996). In addition, soil texture influences plants and MO by controlling nutrient retention (Coleman and Crossley, Jr., 1996). While the organic matter/clay complex can protect soil organic matter from microbial decomposition, the clay content can influence the amount of nutrients retained, such as, Ca, Mg, K, and NH^+ (Parton et al., 1994; Pastor and Post, 1986; Paul and Clark, 1996).

Soil chemical properties mainly affect CO_2 by their effect on roots and MO (Pritchett and Fisher, 1987; Smith and Paul, 1990). Parent material and soil pH control the availability of nutrients and nutrient availability governs the growth of both MO and roots (Paul and Clark, 1996; Pritchett and Fisher, 1987). Nitrogen and lignin content of litter influence CO_2 production by controlling litter decomposition rates (Berg, 1986; Beyer et al., 1991; McClaugherty et al., 1985). Microorganisms not only govern nutrient availability (N, P, Mg, K, and S) to plants through either the mineralization or immobilization of organic matter, but upon their death, they become a rich source of these nutrients (Díaz-Raviña et al., 1993; Smith and Paul, 1990). Very low or very high soil pH conditions can result in either toxic levels of particular nutrients or nutrient deficiencies for plants and MO (Atlas and Bartha, 1993; Kramer and Kozlowski, 1979; Pritchett and Fisher, 1987).

Processes occurring above the forest floor surface can modify the rate at which CO_2 flows from the soil to the atmosphere (Kimball, 1983). The primary mechanism for gas exchange above and within plant canopies is turbulence, the mixing of the air, and is defined as irregular fluctuations in atmospheric fluid motions (Arya, 1988; Kimball, 1983). These irregular fluctuations in atmospheric fluid motions are caused by solar heating of the earth's surface, frictional drag due to the earth's surface (in this case, the top surface of forests), and the earth's topography (Stull, 1988). The turbulence associated with forest canopies is dominated by coherent structures, which consist of strong downward gusts (sweeps) and weaker upward moving air (ejections) (Shaw, 1985; Gao et al., 1989). The geometric structure, openness, and species type (conifer or deciduous) influence the extent of the turbulent mixing within the forest canopy (Jarvis et al., 1976; Rauner, 1976).

Determination of CO_2 Flux Rate

Forest floor CO_2 efflux is defined as the combined flux of CO_2 produced within the mineral soil and within the organic layers to the atmosphere (Hanson et al., 1993). Carbon dioxide flux from the ground (under forests, crops, etc.) has been of interest for a long time with some of the earliest measurements made by Stoklasa and Ernest around 1905 (Singh and Gupta, 1977). The measurement of forest floor CO_2 efflux rate (FFcer) involves the collection (i.e., capture of CO_2), sampling, detection (identification) and the analysis of CO_2,, all of which culminate in a concentration per unit area per unit time (Dabberdt et al., 1993; Denmead and Raupach, 1993; Edwards, 1982; Hutchinson and Livingston, 1993; Matson and Harriss, 1995). The specific details involved in the analysis of CO_2 will not be discussed (see Matson and Harris, 1995). While sampling will not be discussed in detail, it will be included with detection.

COLLECTION

Direct collection of CO_2 flux, the first-hand capture of the flux, can be done either in the laboratory or in the field at the actual site of production (Singh and Gupta, 1977). For laboratory collection of CO_2 flux, an undisturbed soil sample is collected from the field, stored in an sealed container, and transported, usually in a cooled container to maintain sample integrity, to the laboratory (Paul and Clark, 1996; Singh and Gupta, 1977). In the laboratory, the soil sample evolves CO_2 over time within a sealed storage container (Singh and Gupta, 1977). In field measurements (at the site or *in situ*), the CO_2 efflux is captured as it evolves from the forest floor surface (Singh and Gupta, 1977). Currently, enclosure and micrometeorological techniques are the main approaches used to measure atmosphere-surface CO_2 exchange (Hutchinson and Livingston, 1993; Matson and Harriss, 1995). The objective of the research, the medium being measured, the size of the area to be represented, and the funding and resources available control the method chosen to collect CO_2 (Matson and Harriss, 1995; Norman et al., 1992). These two techniques will be described along with the advantages and disadvantages of each.

Enclosure techniques

Enclosures, or chambers, essentially isolate the surface over which they are placed, preventing the direct exchange of CO_2 with the atmosphere, such that the gas which evolves over time into the head space (volume of the chamber above the soil) can be analyzed as a concentration change (Denmead and Raupach, 1993; Livingston and Hutchinson, 1995; Singh and Gupta, 1977). The enclosure is an open-ended box or cylinder, which covers an area ranging from 1.75×10^{-2} m^2 to 1 m^2 (Livingston and Hutchinson, 1995). Chambers have typically been classified as either dynamic/open systems or static/closed systems (Denmead and Raupach, 1993; Livingston and Hutchinson, 1995). In dynamic/open systems, the gases evolving from the soil into the chamber are removed by the constant flow of external air through the head space and in static/closed systems, the gases evolved from the soil accumulate in the head space (Denmead and Raupach, 1993; Hutchinson and Livingston, 1993). Recently, Livingston and Hutchinson (1995) described the dynamic/open systems as steady-state systems and the static/closed systems as a non-steady-state systems. In steady-state systems, steady-state conditions of the gas concentration gradient are maintained within the enclosure, whereas, in non-steady-state systems, the trace gas concentration gradient diminishes as the concentration increases within the enclosure (Livingston and Hutchinson, 1995). Different design and deployment considerations are clearly implicit for each system (Livingston and Hutchinson, 1995).

Enclosure techniques are low in cost, easy to use, effective in capturing inter- and intrasite spatial variability of soil CO_2 efflux rates, and can provide temporal and spatial replicate measurements when required (Dugas, 1993; Hutchinson and Livingston, 1993; Livingston and Hutchinson, 1995). In addition, enclosure techniques are effective in isolating specific emission processes and identifying the source of variability within ecosystems (Livingston and Hutchinson, 1995). Essentially, these techniques are most useful when understanding the relationship between ecosystem properties, processes and fluxes is the goal (Dabberdt et al., 1993; Denmead and Raupach, 1993; Hutchinson and Livingston, 1993; Livingston and Hutchinson, 1995).

With respect to disadvantages, enclosure techniques don't represent gas exchange over large areas, for example, 10^2 -10^3 m^2, as well as do micrometeorological techniques (Denmead and Raupach, 1993, Hutchinson and Livingston, 1993; Matson and Harriss, 1995). For large scale flux estimates, such as landscape and regional scales, enclosure measurements must be extrapolated over space and time, which introduces error into the estimates due to ecosystem heterogeneity (Matson and Harriss, 1995; Schimel and Potter, 1995). The presence of the chamber and the operator (if needed) automatically alter the microclimate and the physical and biological conditions of the site being investigated (Denmead and Raupach, 1993; Hutchinson and Livingston, 1993; Matson and Harriss, 1995). Depending on the deployment of the system, steady-state- or non-steady-state, the ratio of chamber to ambient air pressure can be distorted (Hutchinson and Livingston, 1993; Livingston and Hutchinson, 1995). A deployment time of 30 minutes has been determined to produce substantial error in fluxes measured by static or non-steady-state systems (Healy et al., 1996). The enclosure material composition greatly affects the temperature difference within the chamber relative to that outside the chamber, which would influence the flux (Hutchinson and Livingston, 1993).

Micrometeorological techniques

Micrometeorological (micromet.) techniques utilize the turbulence-driven exchange at the Earth's surface-atmosphere interface to integrate the flux of gases over horizontal scales ranging from meters to kilometers (Arya, 1988; Denmead and Raupach, 1993; Lenschow, 1995). These techniques don't actually collect or capture CO_2. Depending on the technique, the sensors detect CO_2 in the air flowing across them (Auble and Meyers, 1992). The conservation equation is basic to micromet. measurement and interpretation of gas exchange (Baldocchi et al., 1988). The equation expresses that at a fixed point in space the time rate of change for the mean mixing ratio (i.e., the concentration) of a chemical constituent is balanced by

- mean horizontal and vertical advection,
- the mean horizontal and vertical divergence or convergence of the turbulent flux,

- molecular diffusion, and
- any source or sink.

Turbulence transport coefficients change drastically from within plant canopies, ranging from 10,000 to 100 $cm^2 s^{-1}$, to the soil surface, ranging from 0.1 to 0.01 $cm^2 s^{-1}$ (Livingston and Hutchinson, 1995). The lower limit of the turbulence transport coefficient at the soil surface is the molecular diffusion coefficient (Kimball, 1983), effective within a few millimeters of the soil surface (Livingston and Hutchinson, 1995).

The various micromet. techniques include eddy covariance, eddy accumulation, gradient, Lagrangian, convective boundary layer budget, and surface energy budget (Dabberdt et al., 1993; Denmead and Raupach, 1993; Matson and Harriss, 1995). However, only the methods used most commonly, eddy covariance, eddy accumulation, gradient, and surface energy budget, will be discussed (Dabberdt et al., 1993; Lenschow, 1995).

Eddy covariance is considered the most direct and favored approach because it requires no assumptions about eddy diffusivities, stability corrections or the shape of the wind profile (Dabberdt et al., 1993; Denmead and Raupach, 1993; Lenschow, 1995). With this method, an average of the instantaneous product of the vertical velocity (w) and constituent density (species mass per volume) yields the flux rate (Dabberdt et al., 1993). Eddy covariance can be difficult to execute, because it requires fast response instrumentation for the trace species of interest, and if the instrumentation is not available, it is impossible to execute (Dabberdt et al., 1993; Lenschow, 1995).

With the eddy accumulation technique, air from updrafts and downdrafts are sampled in separate reservoirs at a rate proportional to the vertical velocity, after which slow-response, high-resolution sensors measure the mean gas concentrations for each reservoir (Denmead and Raupach, 1993). This method is direct and does not rely on empirically determined relationships (Lenschow, 1995). Based on work by Hicks and McMillen (1984), Dabberdt et al. (1993) synthesized some drawbacks of this method which are 1) this method requires very accurate mean concentration

measurements, 2) it is difficult to control the flow rate for the required speed, accuracy, and dynamic range, and 3) mean vertical velocity offsets must be removed in real time.

The gradient technique estimates the flux rate from the difference in concentration, calculated from the integral of the flux-gradient similarity relationship, between two or more levels (Lenschow, 1995). The flux-gradient theory assumes that turbulent transfer is analogous to molecular diffusion, and that the turbulent flux is proportional to the product of the mean vertical mixing ratio gradient and an eddy diffusivity (Baldocchi et al., 1988). While this method requires no fast-response measurements, it is inadequate for flux determination within plant canopies because counter-gradient transport occurs (Baldocchi et al., 1988). In addition, CO_2 concentration gradients within and above the plant canopy can be too weak to quantify accurately (Rosenberg et al., 1983).

Using the surface energy budget method to estimate the flux of CO_2 involves the Bowen ratio, the ratio of sensible to latent heat fluxes, combined with the terms of the surface energy budget (Baldocchi et al., 1988; Dabberdt et al., 1993; Lenschow, 1995). This method estimates the flux from the relationship of net solar radiation at the forest floor surface and soil heat flux to the differences in gas species, air temperature, and specific humidity between two heights (Lenschow, 1995). The influence of specific heat of air, moist air density, and latent heat of H_2O vaporization on the flux is also taken into account (Lenschow, 1995). This method does not require eddy flux measurements and stability corrections (Dabberdt et al., 1993). However, this method is based on the assumption that the transfer characteristics and the distribution of surface sources and sinks for temperature, humidity, and the gas species are identical and it requires the measurement of net radiation and soil heat flux (Dabberdt et al., 1993).

The main advantages that micromet. techniques have over enclosure techniques is that they don't disturb the environment or site being investigated, they readily allow continuous measurements, and can provide spatially integrated flux measurements over large areas (Baldocchi et al., 1988; Denmead and Raupach, 1993; Lenschow, 1995). However, these techniques require sophisticated instrumentation (sensors), an electrical power source, elaborate data processing, are costly, and they

are not considered effective below a certain spatial scale (10^2 m^2) (Hutchinson and Livingston, 1993). Because micromet. techniques depend on the transport of turbulence, which diminishes drastically at the soil surface, these methods may not be capable of accurately capturing CO_2 efflux at the forest floor surface (Kimball, 1983; Lenschow, 1995). In addition, some of these methods depend on certain assumptions being met and some rely on empirically determined relationships (Lenschow, 1995) which might restrict the use of these methods to particular environments, seasons, and/or periods in a day. For example if stationarity in the wind field can not be assumed, which means that the statistical characteristics of the wind flow are not changing with time, micromet. techniques can not be used (Baldocchi and Meyers, 1991; Matson and Harriss, 1995).

DETECTION

Once a sample is collected, the gas of interest, CO_2 in this case, is detected or identified. Basically, there are three methods used to detect CO_2, chemical, spectroscopic, and chromatographic (Crill et al., 1995). Collection and detection do not always take place in the same setting, however, collection and sampling generally occur in the same setting. The spectroscopic method is the only one in which collection, detection, and analysis occur at one time (Crill et al., 1995). When using the chromatographic method to identify CO_2, the actual detection takes place in the laboratory (Crill et al., 1995). Enclosure techniques are used in conjunction with all three detection methods, and while micromet. techniques are typically combined with spectroscopic methods (Baldocchi and Meyers, 1991; Hanson et al., 1993), they can be used with chromatographic methods.

Chemical

Chemical methods, which were among the first methods employed to measure CO_2 (Stoklasa and Ernest, 1905), utilize the acid-base chemical behavior of the gas to sample and detect CO_2 (Crill et al., 1995), and these methods are generally used with enclosure techniques. Essentially, a basic or alkali absorption compound (e.g. NaOH/lime, NaOH, KOH, ascarite) is placed under an enclosure to trap the CO_2, which is absorbed as CO_3^{2-} and then analyzed as a solution or solid form (Edwards, 1982). In absorbing solutions, after $BaCl_2$ is added to stabilize CO_3^{2-}, the remaining unneutralized NaOH or KOH is titrated with HCL and subtracted from the initial quantity to determine the CO_2

concentration (Anderson, 1973). The solid absorbant is dried and weighed before and after use and the CO_2 concentration is determined from the weight difference with a correction for chemically lost water (Edwards, 1982). These methods are simple, inexpensive, and easy to implement, however, either very small or very large CO_2 concentration gradients at the soil/atmosphere interface can bias results (Crill et al., 1995). Specifically, when flux rates are low, the absorbant absorbs CO_2 too quickly, resulting in overestimated rates and when flux rates are high, the absorbant can not absorb CO_2 rapidly enough, resulting in underestimated rates (Jensen et al., 1996).

Spectroscopic

Spectroscopic (optical) techniques physically detect a compound as the result of the interaction of matter and electromagnetic radiation (E) (Loudon, 1988). The process relies on the Beer-Lambert law, $A = lc\epsilon$, which states that the absorbance (A, the optical density) is proportional to the path length (l) of E times the concentration (c) of the absorbing compound times the molar absorptivity (ϵ, the proportionality constant) (Loudon, 1988). Infrared radiation (IR), one form of electromagnetic radiation, has proven to be highly useful in the detection and quantification of atmospheric trace gases, especially CO_2, because gases absorb radiation at a characteristic diagnostic wavelength (Crill et al., 1995). In particular, non-dispersive IR approaches quantify CO_2 by the selective filter absorption of IR passing through an unknown CO_2 concentration in a sample cell which is then compared to the IR passing through a known CO_2 concentration, typically zero, in a reference cell (Crill et al., 1995; LI-COR, 1987). Because these systems can be packaged to be portable and to rely on solar-powered energy, they can monitor gas flux continuously, and on site in remote areas (Auble and Meyers, 1992; Kolb et al., 1995). While this is the only technique capable of unambiguous quantification of trace gas species, interference from other atmospheric species and change in the sample gas's pressure can introduce error into the analytical results (Kolb et al., 1995).

Chromatographic

Of the chromatographic methods, gas chromatography is used most often to detect trace gases (Crill et al., 1995). This method works by partitioning the trace species between a stationary and a mobile phase, using a carrier gas, as they pass through a separation column (Crill et al., 1995). As

the gases pass out of the column, each causes a change to the electrical signal in the detector, expressed as a peak above a baseline and it is the area under the peak which translates into a concentration (Crill et al., 1995). Generally, the time required for a gas to move through the column detects or identifies the gas of interest, however in the case of CO_2, the other atmospheric gases pass through the column early as one large peak (Crill et al., 1995). This method of detection is used typically with enclosure techniques. The definite identification of CO_2 requires assessment of the sample by either thermal conductivity or flame ionization (Crill et al., 1995). While only a small sample is required for this process, the sample must be preserved from the field to the laboratory, much skill is required to deliver small samples to the gas chromatograph, and for absolute verification, this method must be combined with mass spectroscopy (Crill et al., 1995).

Forest Floor CO_2 Efflux

Boreal and temperate forest ecosystem types comprise the majority of forest types worldwide with tropical evergreen and tropical deciduous forest ecosystem types remaining (Landsberg and Gower, 1997). This review summarizes carbon dioxide efflux data from boreal and temperate forest ecosystems reported in thirty-three studies. The data were averaged over the months of a season when possible, with rates presented to the nearest 0.1 in units of $\mu mol\ m^{-2}\ s^{-1}$.

FOREST CLASSIFICATIONS

The forest ecosystem is a biotic community in which trees, as the dominant feature, profoundly influence the community through their interaction with the physical, chemical, and other biological components of the environment, as well as being influenced by those interactions (Pritchett and Fisher, 1987). Since the influence of climatic factors on CO_2 flux is of interest, a classification scheme of forest types that associates the forest type with its climatic zone was used. The following description of forest types are based on classifications developed by Landsberg and Gower (1997) and Pritchett and Fisher (1987). However, Melillo et al. (1993) actually originated the classification scheme which Landsberg and Gower (1997) describe. In addition to associating forests with the major climatic zones, this

classification scheme evaluates forests by their physiognomy, the outward expression of their genetic composition (Landsberg and Gower, 1997).

Boreal forests (taiga), consisting primarily of conifers, inhabit the harsh environment of the high latitudes in the northern hemisphere (Landsberg and Gower, 1997; Pritchett and Fisher, 1987). The tree species of the boreal forests, *Abies, Betula, Larix, Picea, Populus, and Salix*, are well adapted to the annual precipitation of < 45 cm, cold winters, short growing seasons, and wet, highly leached soils (Landsberg and Gower, 1997; Pritchett and Fisher, 1987). The regions occupied by these forests experience 50 or less frost-free days in the summer (Landsberg and Gower, 1997).

Temperate forest types are divided into coniferous, mixed coniferous/deciduous, deciduous, and broad-leaved evergreen forests (Landsberg and Gower, 1997). Relative to boreal forests, temperate forest types are found in a variety of climates which are warmer climates (temperatures ranging from -15 to 35°C), receive more precipitation (> 45 cm), have higher evapotranspiration rates, and are on more fertile soils (Jarvis and Leverenz, 1983; Landsberg and Gower, 1997; Pritchett and Fisher, 1987). The temperate forests on the most fertile land are disappearing to agricultural and other human uses (Landsberg and Gower, 1997). Temperate coniferous forests occur in the greatest variety of climates, from mountains to coastal plains, and generally grow on xeric and/or infertile soil (Landsberg and Gower, 1997; Pritchett and Fisher, 1987). The mixed coniferous/deciduous forests can be found in transition zones between pure conifer stands in high latitudes and/or high elevations and the pure deciduous stands south of high latitudes and at lower elevations (Pritchett and Fisher, 1987). Except for southern Argentina and southern Chile, deciduous forests are found primarily in the northern hemisphere between 30° to 50° N latitude which experience warm, humid summers and cool to cold winters with precipitation fairly evenly distributed throughout the year (Landsberg and Gower, 1997; Pritchett and Fisher, 1987). Broad-leaved evergreen forests occur with fairly equal incidence in the northern and southern hemispheres in areas having Mediterranean-type climates typified by winter rain and summer drought or in areas having humid, frost-free climates (Landsberg and Gower, 1997; Pritchett and Fisher, 1987).

CO_2 EFFLUX RATES

The majority of the studies reported forest floor CO_2 efflux data for spring and summer seasons. Seasonal forest floor CO_2 efflux rates (FFcer) along with related soil temperature data, or in some cases air temperature, and measurement technique for boreal and temperate forest types are presented in tables 4.1 through 4.5. The tables also include descriptive information about the sites, such as tree species, latitude and longitude, elevation, and climatic data. Because seasonal FFcer values that include all seasons were scarce, the seasonal FFcer results from this thesis (Part 5) were included in these tables. SPSS Inc. software (Chicago, IL) was used to compute seasonal FFcer means for each forest type and to test the linear and nonlinear association between seasonal FFcer and soil temperature.

Mean FFcer in boreal forests, representing 13% of all the entries, ranged from 0.3 μmol m^{-2} s^{-1} in the winter to 2.6 μmol m^{-2} s^{-1} in the summer, which was the second highest of all the types (figure 4.1). The boreal forest types had the smallest mean minimum FFcer of the forest ecosystem types. In addition, the boreal group had the largest range of the FFcer values. However, the smallest absolute FFcer, 0.1 μmol m^{-2} s^{-1}, occurred in spring in a temperate mixed coniferous/deciduous forest type (table 4.3). Given that only two of the boreal forest studies included winter and fall FFcer data, this is not likely a good representation of the FFcer patterns for winter and fall means.

The temperate coniferous sites comprised the greatest proportion of data with 39% of the entries. The mean FFcer of the temperate coniferous forests ranged from 1.0 μmol m^{-2} s^{-1} in the winter to 2.0 μmol m^{-2} s^{-1} in the summer, which represented the smallest range of FFcer values for the forest types (figure 4.1). The temperate mixed coniferous/deciduous forests mean FFcer ranged from 0.4 μmol m^{-2} s^{-1} in the winter to 2.2 μmol m^{-2} s^{-1} in the summer and accounted for 13% of the data entries (figure 4.1). Constituting 26% of the total entries, the temperate deciduous mean FFcer means ranged from 0.8 μmol m^{-2} s^{-1} in the winter to 2.8 μmol m^{-2} s^{-1} in the summer, which was the highest mean maximum FFcer of the types (figure 4.1). The largest absolute FFcer was 5.4 μmol m^{-2} s^{-1} and also occurred in a temperate deciduous forest type during the summer (table 4.4). The

Table 4.1. Seasonal forest floor CO_2 efflux rates and soil temperature (or air temperature indicated by e) values for some Boreal forest sites.

Species	Location	Eleva. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m^{-2} s^{-1} °C				Author(s)
						Win	Spg	Sum	Fall	
Pinus spp.	Can., 53°54'N, 104°41'W	579	40	0.1, yrly.	eddy flux/aIR	---	0.2	0.4	---	Baldocchi et al., 1997
						---	---	---	---	
Picea /Pinus spp.	Scot.	90	---	---	benclo./IR	0.5	1.1	3.3	0.7	Chapman & Thurlow, 1996
						2.9	9.8	9.4	2.0	
Picea spp.	AK, USA, 64°45'N, 148°15'W	200	28	-4, yrly.	enclo./calkali	---	2.4	2.9	---	Gorden et al., 1987
						---	8.0	6.7	---	
Pinus spp.	Fin.,62°47'N, 30°58'E	144			enclo./IR	0.1	0.3	1.0	0.5	Pajari, 1995
						1.1	7.3	12.4	4.4	
Picea spp.	AK, USA, 64°48'N, 147°51'W	229	29	-4, yrly.	enclo./alkali	---	2.1	3.1	---	Schlentner & Van Cleve, 1985
						---	3.9	6.3	---	
Betula spp.	"	"	"	"	"	---	1.8	3.6	---	"
						---	5.7	7.3	---	
Populus spp.	"	"	"	"	"	---	1.8	3.2	---	"
						---	7.3	8.7	---	
Picea spp.	"	470	"	"	"	---	2.0	2.6	---	"
						---	11.8	7.0	---	

aIR: infrared gas analysis. benclo: enclosure. calkali absorption.

Table 4.2. Seasonal forest floor CO_2 efflux rates and soil temperature (or air temperature indicated by e) values for some Temperate Conifer forest sites.

Species	Location	Elev. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m^{-2} s^{-1} / °C				Author(s)
						Win	Spg	Sum	Fall	
Pinus spp.	Austl., 38°00'S, 143°30'E	520	79	18, max.	enclo./alkali	2.3	4.6	2.2	2.6	Carlyle & Ba Than, 1988
						6.7	15.5	18.9	9.8	
Picea/Abies spp.	TN, USA, 35°35'N, 83°28'W	1859	230	18, max.	enclo./IR	0.3	0.5	3.4	1.0	Chambers, 1998 (Part 5)
						-0.9	1.9	11.2	3.9	
Pinus spp.	FL, USA, 28°32'N, 81°22'W	—	—	—	enclo./IR	1.7	4.0	4.1	2.7	Ewel et al., 1987
						—	—	—	—	
Pinus spp. (1991)	WI, USA, 46°10'N, 89°40'W	500	—	20, max.	enclo./alkali	—	1.7	2.2	—	Haynes & Gower, 1995
						—	—	—	—	
Pinus spp. (1992)	"	"	—	"	"	—	1.2	2.3	—	"
						—	—	—	—	
Pinus spp. (1993)	"	"	—	"	"	—	1.5	2.3	—	"
						—	—	—	—	
Cedrus spp.	India, 29°07' to 29°26N, 79°15' to 79°38'E	2300	249	27, max.	enclo./alkali	0.4	0.9	1.8	—	Joshi et al., 1991
						9.1	19.8	17.9	—	
Pinus spp.	"	1850	"	"	"	0.2	0.6	1.2	—	"
						10.8	23	19.6	—	
Tsuga /Pseudo. /Thuja spp.	WA, USA, 47°50'N, 124°00'W	—	350	16, max.	enclo./alkali	1.2	1.4	1.7	1.4	Marra & Edmonds, 1994
						8.5	12.3	15.3	10.2	
Cryptomeria spp.	Japan, 34°25'N, 132°30'E	450	166	13, yrly.	enclo./alkali	0.6	1.2	2.8	0.9	Nakane, 1995
						2.5	15.6	20.6	9.0	

Table 4.2 (continued)

Species	Location	Elev. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m⁻² s⁻¹ °C Win	Spg	Sum	Fall	Author(s)
Picea/Abies spp.(Sa,1991)	WY, USA, 41°20'N, 106°20'W	3182	---	---	gas collec./ dGC	--- ---	0.5 0.5	--- ---	--- ---	Sommerfeld et al., 1993
" (Sa,1992)	"	"	---	---	"	--- ---	0.4 0.5	--- ---	--- ---	"
Picea/Abies spp. (Sb,1991)	"	"	---	---	"	--- ---	0.7 0.5	--- ---	--- ---	"
" (Sb,1992)	"	"	---	---	"	--- ---	0.5 0.5	--- ---	--- ---	"
Alnus spp.	WA, USA, 47°36'N, 122°20'W	210	185	8, yrly.	enclo./alkali	1.0 5.2	1.8 9.2	1.7 13.2	1.6 9.1	Vogt et al., 1980
Pseudotsuga spp.	"	"	"	"	"	1.2 4.6	1.0 9.9	1.5 14.1	1.1 8.4	"
Tsuga spp.	"	"	"	"	"	0.8 3.9	1.9 8.4	2.1 13.6	1.3 7.8	"
Abies spp.	"	1150	230	6, yrly.	"	0.7 0.5	1.7 4.2	2.4 11.1	1.6 4.2	"

Table 4.2 (continued)

Species	Location	Elev. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m⁻² s⁻¹ °C				Author(s)
						Win	Spg	Sum	Fall	
Pinus spp. (1920 stand)	Can., 45°25'N, 75°43'W	—	—	—	enclo./alkali	— —	1.0 18.0	1.3 22.3	1.1 7.0	Weber, 1985
" (1962 stand)	"	—	—	—	"	— —	1.0 18.0	1.2 22.3	1.0 7.0	"
" (1963 stand)	"	—	—	—	"	— —	1.1 18.0	1.3 22.3	1.1 7.0	"
" (1964 stand)	"	—	—	—	"	— —	1.0 18.0	1.2 22.3	1.0 7.0	"
" (1977 stand)	"	—	—	—	"	— —	1.1 18.0	1.2 22.3	1.0 7.0	"

dGC: gas chromatography

Table 4.3. Seasonal forest floor CO_2 efflux rates and soil temperature (or air temperature indicated by e) values for some Temperate Mixed coniferous/deciduous forest sites.

Species	Location	Eleva. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m^{-2} s^{-1} / °C				Author(s)
						Win	Spg	Sum	Fall	
Nothofagus /Quercus spp.	F.R.G., 54°04'N, 10°00'E	---	39	10, yrly.	enclo./alkali	---	1.2	1.6	1.6	Beyer, 1991
						---	6.6	13.0	---	
Picea spp.	"	---	67	10, yrly.	"	---	0.6	1.0	0.8	"
						---	9.1	13.8	---	
Tsuga/Acer /Halesia/Fagus spp.	TN, USA, 35°41'N, 83°27'W	975	194	22, max.	enclo./IR	0.5	1.2	3.7	1.1	Chambers, 1998 (Part 5)
						6.1	9.4	15.7	10.0	
Tsuga/Pinus /Prunus /Quercus spp.	NH, USA, 43°08'N, 71°57'W	---	110	8, yrly.	enclo./GC	0.2	1.6	3.9	1.4	Crill, 1991
						e-0.2	12.7	19.5	6.2	
Nothofagus /Picea spp.	F.R.G., 49°24'N, 8°43'E	---	---	---	enclo./alkali	0.4	1.2	1.9	1.1	Dörr & Münnich, 1987
						3.5	8.3	12.8	7.2	
Fagus/Betula /Acer/Picea spp.	ME, USA, 44°52'N, 68°06'W	---	106	20, max.	enclo./alkali	0.7	1.4	1.6	1.4	Fernandez et al., 1993
						1.0	6.0	15.2	10.0	
Acer/Fraxinus /Ulmus/Fagus /Pinus spp.	Can. 45°22'N, 75°43'W	79	---	---	enclo./GC	---	1.7	3.0	1.5	Lessard et al., 1994
						---	10.5	15.0	9.0	
Fagus/Betula /Acer/Tsuga /Picea spp.	NY, USA, 42°52'N, 71°58'W	650	123	5, yrly.	enclo./GC	---	0.1	1.11	---	Yavitt et al., 1995
						---	---	---	---	

eAir temperature was measured instead of soil temperature.

Table 4.4. Seasonal forest floor CO_2 efflux rates and soil temperature (or air temperature indicated by e) values for some Temperate Deciduous forest sites.

Species	Location	Eleva. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m^{-2} s^{-1} / °C				Author(s)
						Win	Spg	Sum	Fall	
Quercus/Acer /Betula spp.	MA, USA, 42°29'N, 72°11'W	331	---	---	enclo./alkali	--- ---	--- ---	2.0 ---	--- ---	Bowden et al., 1993
Quercus/Nyssa /Acer spp.	TN, USA, 35°58'N, 84°17'W	335	137	31, max.	enclo./IR	0.4 5.4	1.1 12.9	4.5 19.6	1.1 12.1	Chambers, 1998 (Part 5)
Populus spp.	Can., 51°02'N, 115°04'W	---	65	14, max.	enclo./IR	0.6 0.7	--- ---	--- ---	--- ---	Coxson & Parkinson, 1987
Quercus spp.	TN, USA, 35°58'N, 84°17'W	350	139	14, yrly.	enclo./alkali	0.8 e3.8	1.8 19.0	1.8 22.7	1.9 7.3	Edwards et al., 1989
Quercus/Carya spp.	MO, USA, 38°45'N, 92°12'W	245	96	13, yrly.	enclo./IR	0.6 e---	2.0 ---	5.4 22.1	2.5 14.7	Garrett et al., 1978
Quercus/Liro-dendron/Acer spp.(NE slope)	TN, USA, 35°58'N, 84°17'W	350	139	14, yrly.	enclo./IR	1.0 7.1	3.2 16.8	3.7 21.4	1.7 12.3	Hanson et al., 1993
Lirodendron /Fagus/Acer spp.(valley)	"	"	"	"	"	1.1 7.3	3.0 16.5	4.0 20.2	1.5 12.3	"
Quercus/Acer spp.(SW slope)	"	"	"	"	"	1.0 6.8	3.3 17.2	3.5 21.2	1.6 12.7	"
Quercus/Acer /Pinus spp.(ridge)	"	"	"	"	"	1.2 7.3	3.6 17.2	3.9 21.3	1.8 13.0	"
Populus/Acer /Quercus spp. (GRTR)	MI, USA, 45°33'N, 84°42'W	---	---	---	enclo./alkali	--- ---	1.3 ---	1.5 ---	--- ---	Jurik et al., 1991

Table 4.4 (continued)

Species	Location	Eleva. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m⁻² s⁻¹				Author(s)
						°C				
						Win	Spg	Sum	Fall	
Populus/Acer /Quercus spp. (UPGR)	MI, USA, 45°33'N, 84°42'W	---	---	---	enclo./alkali	--- ---	1.4 ---	1.7 ---	--- ---	Jurik et al., 1991
Quercus spp. (Camp Br.)	TN, USA, 35°38'N, 85°18'W	---	145	---	enclo./alkali	1.1 e2.9	2.1 14.3	2.3 19.0	1.4 5.3	Larkin & Kelly, 1987
Quercus spp. (Cross Cr.)	"	---	155	---	"	1.1 e6.1	2.2 15.0	2.1 20.4	1.5 7.8	"
Betula/Acer /Quercus spp.	MA, USA, 42°30'N, 72°10'W	---	108	20, max.	enclo./GC	--- ---	--- ---	1.0 18.3	0.3 6.6	Peterjohn et al., 1994
Acer/Quercus /Tilia spp.	MI, USA, 44°48'N, 85°48'W	450	81	7, yrly.	enclo./alkali	--- ---	1.9 ---	2.5 ---	1.5 ---	Toland & Zak, 1994

eAir temperature was measured instead of soil temperature.

Table 4.5. Seasonal forest floor CO_2 efflux rates and soil temperature (or air temperature indicated by e) values for some Temperate Broad-leaved Evergreen forest sites.

Species	Location	Eleva. (m)	Precip. (cm)	Temp. (°C)	Method	µmol m^{-2} s^{-1}				Author(s)
						°C				
						Win	Spg	Sum	Fall	
Quercus spp.	India, 29°07' to 29°26'N, 79°15' to 79°38'E	2360	249	27, max.	enclo./alkali	0.5	1.1	2.3	—	Joshi et al., 1991
						5.5	18.0	16.4	—	
Quercus spp.	"	2275	"	"	"	0.4	1.0	2.3	—	"
						8.3	19.5	17.2	—	
Quercus spp. (Prades, upper)	Spain, 41°13'N, 0°55'E	975	55	—	enclo./IR	0.6	0.6	1.4	0.6	Piñol et al., 1995
						—	—	—	—	
Quercus spp. (Prades, lower)	"	700	"	—	"	0.3	0.4	0.6	0.5	"
						—	—	—	—	
Quercus spp. (Montseny)	Spain, 41°46'N, 2°21'E	670	90	—	"	0.1	0.7	0.9	0.2	"
						—	—	—	—	
Nothofagus spp.	N.Z. 42°13'S, 172°15'E	400	200	15, max.	enclo./alkali	1.1	—	2.2	—	Tate et al., 1993
						6.2	—	13.6	—	

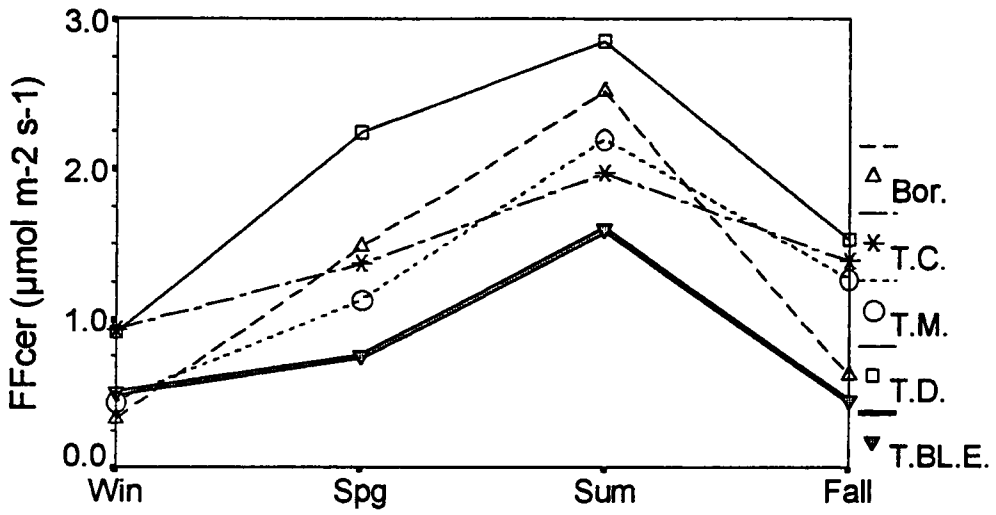

Figure 4.1. Seasonal forest floor CO_2 efflux rates for some boreal (Bor.), temperate coniferous (T.C.), temperate mixed coniferous/deciduous (T.M.), temperate deciduous (T.D.), and temperate broad-leaved evergreen (T.BL.E.) forest ecosystem sites.

temperate broad-leaved evergreen mean FFcer ranged from 0.5 µmol m^{-2} s^{-1} in the winter to 1.6 µmol m^{-2} s^{-1} in the summer (figure 4.1) and represented the smallest proportion of the data, 10%.

FACTORS CONTROLLING CO_2 EFFLUX RATES

Seasonal FFcer variations were attributed primarily to soil temperature and soil water content, which are the most important factors influencing biological activity (Singh and Gupta, 1977). However, it is the interaction of these two factors which influences FFcer variation over time, because when soil water is not limiting, temperature controls FFcer variations and when soil water is limiting, it controls FFcer variations (Carlyle and Ba Than, 1988; Vogt et al., 1980). Soil water content is controlled by precipitation amount, evapotranspiration potential, and soil texture or clay content (Dörr and Münnich, 1987; Hillel, 1982). Since precipitation and evapotranspiration potential vary seasonally, they indirectly affect seasonal FFcer. Seasonal variations in 1) substrate quality (carbon substrate type) and quantity, obviously more prevalent in deciduous forests than in coniferous forests, 2) nutrient availability (e.g., N, Ca, Mg, K, P), 3) root activity, and 4) soil microbial populations contribute to seasonal differences

in FFcer, as well (Bray and Gorham, 1964; Crill, 1991; Nakane, 1995; Vogt et al., 1980; Weber 1985). The climatic factors, air temperature and precipitation, are generally used to model seasonal global soil CO_2 efflux variations, due to their availability (Kicklighter et al., 1994; Raich and Potter, 1995; Raich and Schlesinger, 1992).

Soil temperature was included in tables 4.1 through 4.5 because it has such a major effect on the physiological reaction rates of microbes and plants (Landsberg and Gower, 1997; Paul and Clark, 1996). In addition, the linear and nonlinear relationships of seasonal FFcer values to soil temperature across all forest types were evaluated (figure 4.2). Seasonal FFcer values and soil temperature have exhibited strong linear and nonlinear relationships in other studies (Hanson et al., 1993; Part 5; Schlentener and Van Cleve, 1985). In this case, soil temperature ($P<0.005$) was linearly, significantly correlated to seasonal FFcer with an R^2 of only 0.23. When a nonlinear equation, $FFcer = Rb \times (Q^{(soil\ temp./10)})$, with soil temperature expressed as a Q_{10} function was used to estimate seasonal FFcer values, it produced an R^2 of 0.22. The Rb is the base respiration when soil temperature is 0 °C and Q is the influence of a 10 °C increase on biological activity, with initial parameters of 0.84 and 2.3, respectively (Hanson et al., 1993; Paul and Clark, 1996). The nonlinear relationship produced higher R-squared values for most of the forest types when they were individually analyzed and certain types had higher R-squared values in both the linear and nonlinear analyses (tables 4.6 and 4.7).

Some possible reasons for this low correlation include the fact that 1) soil temperature was measured at differing soil depths among the studies and sometimes air temperature was used instead, 2) winter and fall FFcer and soil temperature were often not measured, 3) soil water might have been a more important factor in the temperate coniferous sites which occurred over such a broad range of climates, and 4) the alkali absorption overestimates at a low CO_2 flux and overestimates at a high CO_2 flux from the soil surface.

The employment of contrasting methods of collection and detection along with the differences in the number of measurements made per sampling interval and the variations in the measurement intervals across the studies (tables 4.1 - 4.5) suggest that this FFcer survey is an approximate

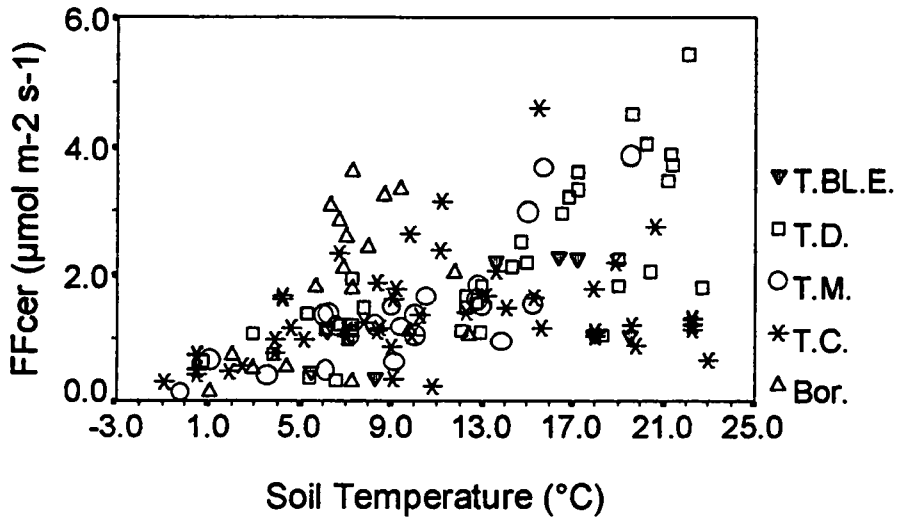

Figure 4.2. Seasonal variations in forest floor CO_2 efflux rates for all forest types, boreal (Bor), temperate coniferous (T.C.), temperate mixed coniferous/deciduous (T.M.), temperate deciduous (T.D.), and temperate broad-leaved evergreen (T.BL.E) exhibited a significant linear (R^2=0.23) and nonlinear (R^2=0.22) relationship with soil temperature ($P<0.005$).

Table 4.6. Linear regression Coefficients of forest floor CO_2 efflux rates estimated from soil temperature measurements for Boreal, Temperate Conifer, Temperate Mixed Coniferous /Deciduous, Temperate Deciduous, and Temperate Broad-leaved Evergreen forest sites and for all sites together.

Parameter	Boreal	Tem. Con.	Tem. Mix.	Tem. Dec.	Tem. Broad-leaved Ever.	All
Slope (±SE)	0.16 (0.08)	0.03 (0.01)	0.15 (0.03)	0.15 (0.02)	0.08 (0.05)	0.08 (0.01)
Intercept (±SE)	0.76 (0.64)	0.96 (0.18)	-0.01 (0.27)	0.10 (0.31)	0.37 (0.68)	0.74 (0.15)
Sig. T	0.08	0.02	0.000	0.000	0.17	0.000
Adj. R^2	0.12	0.07	0.61	0.58	0.17	0.23

Table 4.7. Nonlinear regression coefficients of forest floor CO_2 efflux rates estimated from soil temperature measurements for Boreal, Temperate Conifer, Temperate Mixed Coniferous /Deciduous, Temperate Deciduous, and Temperate Broad-leaved Evergreen forest types and for all sites together.

Parameter	Boreal	Tem. Con.	Tem. Mix.	Tem. Dec.	Tem. Broad-leaved Ever.	All
fRb	1.21	1.05	0.43	0.67	0.70	0.97
fQ	1.8	1.2	3.1	2.2	1.6	1.5
Adj. R^2	0.12	0.07	0.72	0.60	0.24	0.22

fThe initial values for Rb and Q come from Hanson et al. (1993).

comparison of seasonal FFcer values. In practically all of the studies, the enclosure technique was used solely to capture CO_2 flux, however, each of the three methods of detection was utilized. Basic or alkali absorption was used 61% of the time to sample and detect CO_2, followed by infrared gas analysis and gas chromatography which were used 25% and 14% of the time, respectively. The problem that the alkali absorption technique has in estimating FFcer at low and high CO_2 flux from the soil introduced error into the data (Jensen et al., 1996). Another source of discrepancy was that the length of time for enclosure deployment varied among the studies (Healy et al., 1996). Some measurements were made during the day and night while others were made during the daytime only which can result in different rates (Jensen et al., 1996). The number of measurements made within a measurement interval differed and the number of measurement intervals per year differed among the studies, creating divergence in the comparison. Lastly, it should also be noted that since almost all the FFcer data were in graph form, some error was introduced due to the interpretation of the values from the graphs.

Summary and Conclusions

This survey has presented seasonal boreal and temperate forest floor CO_2 efflux rates including soil temperature, from studies conducted since 1978. The various studies employed different methods for collection, detection, and data and sample processing. In all except one of the studies,

FFcer were collected using the enclosure method, which captures the flux over small, defined areas (<1 m^2) and in the one exception, the micromet. method was used, which integrates the flux over large areas (>10^2 m^2). The understanding and estimation of small or large scale processes controls the choice of collection method. Alkali absorption, infrared radiation absorption, and gas chromatography are the primary methods used to detect CO_2 concentrations with the latter two methods considered more accurate.

The boreal forests exhibited the smallest mean FFcer, 0.3 μmol m^{-2} s^{-1}, and the temperate deciduous forests had the largest mean FFcer, 2.8 μmol m^{-2} s^{-1}. The temperate coniferous forests exhibited the smallest range in seasonal FFcer, 1.0 to 2.0 μmol m^{-2} s^{-1} and the boreal forests exhibited the largest range, 0.3 to 2.6 μmol m^{-2} s^{-1}. The smallest, 0.1 μmol m^{-2} s^{-1}, and largest, 5.4 μmol m^{-2} s^{-1}, absolute FFcer values occurred in the spring in a temperate mixed coniferous/deciduous forest and in the summer in a temperate deciduous forest, respectively.

Soil temperature and soil water content were named within most of the studies as the major factors influencing seasonal FFcer variations. When the soil temperature data were regressed against the FFcer values, it could only account for 23% of the linear association and 22% of the nonlinear association. However the nonlinear association produced larger R-squared values for most of the forest types when they were analyzed individually. Some possible reasons for the weak association were the differing sampling depths across the studies; lack of winter and fall data; the broad range of climates over which the temperate coniferous sites occurred; and the error in the alkali absorption method that results when sampling CO_2 efflux at low and high CO_2 flux from the soil surface.

This review contributes to the global picture of seasonal carbon dynamics, however, some steps could be taken in the future to improve this picture. Not only were winter and fall FFcer data lacking, but the number of studies representing boreal and temperate broad-leaved evergreen forest types were scarce. In addition, seasonal soil temperature and soil water content values along with other parameters significantly related to FFcer need to be reported in all cases.

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PART 5

SEASONAL FOREST FLOOR CARBON DIOXIDE EFFLUX PATTERNS AMONG THREE FOREST ECOSYSTEM SITES, ASSOCIATED INFLUENTIAL FACTORS, AND A SIMPLE MODEL

Abstract

Forest soils contain 40% of all below ground carbon, are thought to account for part of the global carbon budget imbalance, and may release more carbon dioxide (CO_2) due to soil warming brought about by global warming. Clearly, forest soils play an important role in the global carbon cycle. To accurately model the role of forest soils in the global carbon cycle, the understanding of seasonal and spatial soil carbon flux dynamics is necessary on a local as well as regional basis. A study was conducted to characterize seasonal forest floor CO_2 efflux patterns among three forest ecosystems located in East Tennessee, USA, varying in age, climate, elevation, and tree species. To evaluate sources of significant influence, soil physical, chemical, and biological parameters were measured along with forest floor CO_2 efflux rates during different seasons. The forest floor CO_2 efflux patterns for the three sites did not vary consistently over time and soil temperature and Oi water content were determined by multiple linear regression to explain 73% of the seasonal variation in the rates. Forest floor CO_2 efflux rates exhibited an exponential relationship with soil temperature and a linear relationship with Oi water content. The nonlinear relationship between the CO_2 efflux rates and soil temperature led to the use of a nonlinear equation to describe the seasonal CO_2 efflux rate patterns. A simple, empirical nonlinear equation, which estimates forest floor CO_2 efflux rates primarily from a soil temperature function (Q_{10}), was first tested using the soil temperature data from this study. It was able to account for 59% of the seasonal variation in rates across the three ecosystem sites. When a linear Oi water content term was added, the equation accounted for 78% of seasonal forest floor CO_2 efflux variations across the three diverse sites, a substantial improvement.

Introduction

In terrestrial ecosystems, autotrophs (which synthesize their own carbon substrate) convert the atmospheric carbon dioxide (CO_2) into organic carbon (C) forms such as cellulose, hemicellulose, and lignin which become cycled in the lithosphere (Killham, 1994). As autotrophs utilize the C they have synthesized and as heterotrophs (require external organic C source) feed on organic matter, they respire CO_2, as a function of their metabolism, returning it to the atmosphere. A similar process occurs

in aquatic ecosystems where the CO_2, respired by the organisms, dissolves into the inorganic C forms, H_2CO_3, HCO_3^-, and CO_3^-, in surface waters and equilibrates with atmospheric CO_2 (Atlas and Bartha, 1993). Beginning with the industrial age in the late 1700's, the burning of fossil C has and is currently contributing additional CO_2 to the atmosphere, leading to an imbalance in the global C budget (Houghton et al., 1996; Neftel et al., 1994). Carbon dioxide concentrations have increased by 81 ppm since 1750, with 29% of the increase occurring since 1950 (Keeling and Whorf, 1996; Sundquist, 1993). Increasing levels of atmospheric CO_2 are considered to be responsible for the global temperature increase of 0.6(±0.1) °C which has occurred since 1850 (Hansen and Lebedeff, 1987; Houghton et al., 1996; Jones, 1994). Because climate change may have serious consequences, affecting everything from agricultural to energy systems (i.e., hydroelectric power), being able to predict the direction of the global C cycle is essential to ameliorating some of these consequences.

Forests perform 66% of the global photosynthesis (Kramer, 1981) and contain approximately 80% of all above ground C and 40% of all below ground C, making them a major compartment of the global C cycle (Ajtay et al., 1979; Dixon and Turner, 1991; Olson et al., 1983; Schlesinger, 1984; Whittaker and Likens, 1975; Zinke et al., 1984). Within forest ecosystems, soils are of particular interest because they hold 70% of the total C, are thought to account for part of the C imbalance, and may release more CO_2 due to soil warming (Dixon et al., 1994; Gifford, 1994; Houghton, 1996; Peterjohn et al., 1994; Waring and Schlesinger, 1985). Soil warming, brought about by global warming, is expected to enhance biological activity and thereby, increase soil CO_2 efflux rates (Watson et al., 1996).

The status of soil CO_2 is intrinsically linked to soil biological, chemical, and physical properties with most of the CO_2 produced as a result of the metabolism of the biological component, the roots, microorganisms (MO), and to a lesser extent, soil fauna (Singh and Gupta, 1977). While the ecosystem type can influence the total amount of soil CO_2 produced (Paul and Clark, 1996), microbes typically contribute anywhere from 20 to 77% and roots contribute anywhere from 23 to 80% (Behera et al., 1990; Bowden et al., 1993; Cheng et al., 1993; Dörr and Münnich, 1987; Edwards and Sollins, 1973; Raich and Nadelhoffer, 1989; Tate et al., 1993). Because forest floor CO_2 flux rates vary with

season and space, it is important to measure the biological, chemical, and physical properties on a seasonal and spatial basis, as well (Davidson, 1995; Matson and Harriss, 1995; Raich and Potter, 1995).

By understanding the dynamic relationship of forest floor CO_2 flux to soil biological, chemical, and physical properties, forest floor CO_2 efflux patterns from ecosystems similar to these can be integrated into the global carbon cycle models. Models are developed to estimate parameters because it is impossible to sample all areas of the Earth (Ågren et al., 1991; Dämmgen et al., 1996). Models which describe a system or event based on its physiological processes are mechanistic or process-based models and those which describe the system or event based on observed, statistically significant relationships are empirical models (Landsberg and Gower, 1997). Mechanistic models are flexible in that they can be used under different conditions and can simulate not only steady-state conditions but also conditions impacted by change (Landsberg and Gower, 1997). While empirical models are site specific and can only reflect current steady-state conditions, they can provide practical and immediate use in cases such as predicting forest stand yield estimates (Landsberg and Gower, 1997). In addition, mechanistic models often include empirical relationships (Landsberg and Gower, 1997).

This study was conducted to characterize seasonal forest floor CO_2 efflux patterns and to determine significant differences among three forest ecosystem sites which were located in East Tennessee, USA and which varied in age, climate, elevation, and tree species. The null hypothesis proposed is that there will be no significant differences in forest floor CO_2 efflux among the three ecosystem sites over time. Soil physical, chemical, and biological parameters were measured during the different seasons to determine which parameters explained seasonal forest floor CO_2 efflux rate differences among the three forest ecosystem sites. The results of this analysis are used to test and expand a simple, empirical nonlinear equation developed by Hanson et al. (1993) which estimates forest floor CO_2 efflux rates (FFcer represents forest floor CO_2 efflux rate or rates).

Materials and Methods

SITE DESCRIPTIONS (See Part 2 for specific details; Appendix B provides a relief map of the sites)

The highest-elevation site (SPR) is located within an old-growth spruce-fir forest. The middle-elevation site (COV) is located in a sheltered old-growth conifer-hardwood forest. The lowest-elevation site (OAK) is located within a secondary-growth oak forest. Climatic and topographic data are given in table 5.1.

EXPERIMENTAL DESIGN (See Part 2)

SAMPLING (See Part 2 for further details)

Measurements were made during July (Jul.), 1994, September (Sep.), 1994, November (Nov.), 1994, January (Jan.), 1995, and April (Apr.), 1995. The measurement dates were chosen on the basis of soil temperature and water content extremes, growing season, and litterfall.

Forest floor CO_2 efflux rate

Forest floor CO_2 efflux rates were measured to the nearest 0.1 μmol m^{-2} s^{-1} using a modified Li-Cor 6200 (LI-COR, Lincoln, NE), which is a closed gas-exchange system (nonsteady-state) that detects CO_2 by infrared gas analysis. Forest floor CO_2 efflux rates were measured Jul., Sep., and Nov., 1994 and Jan. and Apr., 1995. An open-ended aluminum cylinder fitted with the Li-Cor sensor housing and a gas inlet and outlet ports was used to sample FFcer (Hanson et al., 1993). The cylinder measured 8.8 cm high and 27.5 cm in diameter with a chamber volume of 5265 cm^3 and covered an approximate area of 596 cm^2. To obtain a good seal without forcing CO_2 from the soil, the chamber was placed on a foam template which outlined the measurement surface and which changed the area measurement of CO_2 to 455 cm^2 (P. J. Hanson, personal communication, 1994). In Jan., 1995, due to the amount of snow at the SPR site, flanges (wings) were attached to each side of the cylinder to prevent its sinking into the snow and forcing CO_2 from the surface.

When the system displayed CO_2 concentrations that were near ambient about one meter above the forest floor (e.g., 350 to 400 ppm), the chamber was placed on approximately level ground considered to be undisturbed (i.e., had not been walked on), and three subsamples were recorded

Table 5.1. Topographic and Climatic Data for the SPR, COV, and OAK sites.

Site	Map	Lat/long (7.5 min)	Elev (m)	[a]Orien (deg)	[b]Prec (cm)	[b]Mean Max Temp (°C)	[b]Mean Min Temp (°C)
SPR	Clingmans Dome, NC-TN	35°35′N, 83°28′W	1859	65	230	18	-5
COV	Mount Le Conte, TN-NC	35°41′N, 83°27′W	975	72	194	22	-4
OAK	Bethel Valley, TN	35°58′N, 84°17′W	335	152	137	31	-3

[a]The orientation or compass direction toward which the site faces. [b]Mean maximum and mean minimum air temperature data, for the warmest and coldest month, respectively, and precipitation data are from Stephens, 1969.

over 60 seconds at 20 second intervals. When CO_2 subsample rates $\geq$ 1.0 µmol m^{-2} s^{-1} were not within 0.5 µmol m^{-2} s^{-1} of each other or those $\leq$ 1.0 µmol m^{-2} s^{-1} were not within 0.1 µmol m^{-2} s^{-1}, the subsamples could not be considered statistically similar and thus, the area had to be resampled. The subsamples were averaged and recorded as one FFcer observation. Carbon Dioxide sampling at the SPR and COV sites took place from 1000 to 1500 LST (local standard time) and at the OAK site from 0900 to 1600 LST.

Litter and Organic layers

Six plastic containers, with approximate collection areas of 0.21m^2, were placed throughout the SPR and COV sites to catch litterfall. Litter (leaves, stems, seeds, etc.) was collected five times over the period August, 1994 through April, 1995 from the SPR and COV sites and stored in plastic bags at 4 °C until they could be dried for mass determination. Litterfall data for the OAK site was provided by Hanson et al., (1995) and represents the period from August, 1994 through August, 1995. Data from six collection baskets (area = 0.20 m^2), chosen randomly from rows 8 (upper), 5 (middle), and 3 (lower) on the ambient plot of the Throughfall Displacement Experiment site (see experimental design) were computed for the OAK litterfall.

Oi and Oe/Oa layer samples were collected during Jul., Sep., and Nov. of 1994 and Apr. of 1995. Litter was gathered by hand through a plastic cylinder (dia. of 0.189 m) which outlined the collection area (the Oe and Oa layers were combined due to time constraints). The Oi layer, the top

organic layer, consists of the unaltered remains of plants and animals; the Oe layer, immediately below the Oi, consists of fragmented, partly decomposed organic matter; and the Oa layer, between the Oe and the mineral soil, consists of well-decomposed, amorphous organic matter (Pritchett and Fisher, 1987). At the time of sampling, portions of Jul., 1994 Oi layer and the Nov., 1994 and Apr., 1995 Oe/Oa layer samples were removed for microbial biomass carbon analysis (Part 3). After the Oi layer samples were weighed for gravimetric water content determination, the remaining samples were stored in plastic bags at 4 °C until they were processed for physical and chemical analyses.

Soil samples

Mineral soil cores were collected during Jul., Sep., and Nov., 1994 and Apr., 1995 to an average depth of 21 cm using a open or closed bucket auger (dia.=0.077 m and 0.073 m, respectively) and stored in plastic bags at 4 °C for microbial biomass C analysis and physical and chemical analyses. Additional soil cores were collected to an average depth of 26 cm for root biomass determination during the same dates and using the same bucket augers. This sample depth was used because microbial biomass C values, organic matter content, and root distribution are highest in the top 20-30 cm of the soil (Charley and Richards, 1982; Johnson et al., 1995; Ross and Tate, 1993). After soil samples for microbial biomass C analysis were set aside (Part 3), the samples were air dried and sieved (<2 mm) as required for the various physical and chemical analyses. Approximately 10 g of each sample was pulverized with a mortar and pestle for the total C and N analyses. The Sep. and Nov., 1994 soil cores, collected to an average depth of 26 cm, were washed through a 2 mm sieve and the fragments > 2 mm were air dried to assess coarse fraction.

Undisturbed soil samples (original volume preserved) were collected from random locations at each of the three sites during July, 1997 to assess bulk density and total porosity. Five samples were collected at the SPR and COV sites, by pressing a cylindrical metal sampler into the mineral soil to an approximate depth of 9 cm (Blake and Hartge 1986). At the OAK site, eight samples were collected to an approximate depth of 5 cm, four from each side of the Throughfall Displacement Experiment site, using a hammer-driven cylindrical metal sampler (Blake and Hartge 1986).

Soil temperature and soil water content

Soil temperature was measured to a depth of 15 cm to the nearest 0.1 °C during Jul., Sep., and Nov., 1994, and Jan. and Apr., 1995, using a digital thermometer (OMEGA 872A or OMEGA 450 AET type E probe, OMEGA, Stamford, CT). Volumetric soil water content was measured to a depth of 35 cm to the nearest 0.1 cm^3 cm^{-3} during Jul., Sep., and Nov., 1994, and Jan. and Apr., 1995, using time domain reflectometery, the method of Topp and Davis (1985) (Trase System 6050X1, Soilmoisture Equip. Corp., Goleta, CA). The Jul., 1994 water content measurements were made to a 15 cm depth using portable steel rods. Thereafter, water content was measured to a depth of 35 cm because this depth better represented the conditions under which maximum biological activity occurs (Charley and Richards, 1982; Pritchett and Fisher, 1987). Stainless steel rods used in measuring water content were installed after the Jul., 1994 date and left in place for the experiment's duration.

ANALYTICAL METHODS

Microbial biomass C (MBC) of the mineral soil was estimated to the nearest 1 µg MBC g^{-1} of soil using the chloroform fumigation extraction method with results expressed on an oven-dry weight basis (Voroney et al., 1993; see Part 3 for specific details). Root biomass was calculated to the nearest 0.01 Mg ha^{-1} soil from live roots ≤ 5mm in diameter (Fogel, 1985; Nadelhoffer and Raich, 1992) removed from soil samples by hand and oven-dried at approximately 100 °C (Hanson et al., 1993).

Litterfall was weighed after being oven-dried at 70 °C and the mass per collection area per year was calculated to the nearest 1 g $m^{-2} \cdot yr^{-1}$. The Oi and Oe/Oa layer samples were oven-dried (70 °C), weighed and the mass per collection area computed to the nearest 1 g m^{-2}. The Oi material was weighed before and after oven-drying to determine the gravimetric water content to the nearest 1% (based on g g^{-1}). The dried Oi and Oe/Oa samples were ground using a Cyclone grinder or Wiley mill (20 mesh screen) and mixed by shaking prior to total C and N analyses.

Coarse fraction (fragments > 2 mm), which is the rock volume relative to the soil volume, was calculated to the nearest 0.001 cm^3 cm^{-3} with rock volume obtained by water displacement of the rocks. For each site, soil texture was determined to the nearest 1% from the particle size analysis of three samples, each of which was a combination of Jul. and Sep., 1994 samples (Gee and Bauder,

1986). Bulk density was computed to the nearest 0.1 g cm^{-3} based on the oven-dry weight of the sample per sampler volume from the undisturbed soil samples, which were weighed before and after oven-drying (105 °C) (Blake and Hartge 1986). Subsequently, total porosity was calculated to the nearest 1% from bulk density, gravimetric water content (of the undisturbed samples), and particle density, which was assumed to be 2.65 g cm^{-3} (Hillel, 1982; Miller and Donahue, 1990).

Total C and N of the Oi layer, Oe/Oa layer, and the mineral soil were quantified to the nearest 0.01% (based on g g^{-1}) by the high-temperature induction furnace method (Bremner and Mulvaney, 1982; Nelson and Sommers, 1982) using a carbon/nitrogen/sulphur analyzer (LECO CNS2000, LECO, St. Joseph, MI). The C to N (C:N) ratios were calculated from these results. The April, 1995 samples were analyzed for exchangeable bases, Ca, K, Mg, and Na (Thomas, 1982), using the inductively coupled Argon plasma-optical emission spectrometer (ICAP61, Thermo Jarrell Ash Corp., Franklin, MA) with results given to the nearest 0.001 $cmol_c$ kg^{-1}. Analysis of the April, 1995 samples for K was done using an atomic absorption spectrophotometer with results given to the nearest 0.001 $cmol_c$ kg^{-1} (Perkin-Elmer atomic absorption spectrophotometer 5000, Perkin-Elmer Corp., Norwalk, CT). The April, 1995 samples were analyzed for Al by the pyrocatechol violet method (American Public Health Association et al., 1992) using the Skalar autoanalyzer, with results given to the nearest 0.001 $cmol_c$ kg^{-1}. Soil pH (H_2O) was measured with the Corning pH Ion Analyzer 355 (McLean, 1982).

STATISTICAL ANALYSIS

Analysis of variance was applied to assess significant differences for FFcer among the sites at an alpha of 0.05 ($P<0.05$) for each date. The Student-Neuman-Keul's test was used to determine which sites were significantly different. Differences in FFcer were evaluated for each site, individually and for all sites combined, with the focus on the latter. Stepwise multiple regression analysis was used to determine which of the soil biological, chemical, and physical parameters were most influential on FFcer variation among the sites. The variables significant in explaining FFcer variation were evaluated for significant differences at an alpha of 0.05 ($P<0.05$) by date using analysis of variance. Nonlinear regression analysis was used to analyze the exponential relationship between FFcer and the

associated significant parameters. Software from SPSS Inc., Chicago, IL, was used in all data analyses.

Results

All seasonal soil physical, chemical, and biological parameters were analyzed, but not all the data are included in this part (see Parts 2, 3, and appendix A for these data). Data of some soil physical and chemical properties, considered to remain constant (over one year) are presented in tables 5.2 and 5.3. Mean annual litterfall, during 1994-1995, at the SPR, COV, and OAK sites was 250, 423, and 440 g m^{-2}, respectively.

Forest Floor CO_2 efflux rates (FFcer) ranged from 0.3 µmol m^{-2} s^{-1} at the SPR site in Jan., 1995 to 4.5 µmol m^{-2} s^{-1} at the OAK site in Jul., 1994 (figure 5.1a). The SPR site, located at the highest elevation (i.e., coolest temperatures), typically had the lowest FFcer, except during Sep., 1994 when it was not significantly different from the OAK site FFcer (figure 5.1a). The OAK site, located at the lowest elevation (i.e., warmest temperatures), had a significantly higher FFcer ($P<0.005$) than that of the other two sites during only Jul., 1994. The COV site, located at an elevation between the other sites, had significantly the highest FFcer ($P<0.005$) in Sep., 1994 and Jan., 1995 (figure 5.1a). During Nov., 1994, FFcer among the sites did not differ significantly and in Apr., 1995, the SPR site FFcer was significantly ($P<0.005$) lower than that of the other two sites (figure 5.1a).

It is clear from figure 5.1a that the FFcer patterns among the three sites did not vary consistently over time. The SPR and COV sites had the most similar FFcer patterns with the COV FFcer consistently larger than that of the SPR site. The SPR and COV sites produced the greatest change in FFcer from Sep., 1994 to Nov., 1994, when FFcer decreased by 1.6 µmol m^{-2} s^{-1} and 2.5 µmol m^{-2} s^{-1}, respectively (figure 5.1a). The largest change in OAK FFcer occurred from Jul., 1994 to Sep., 1994 when FFcer decreased by 2.1 µmol m^{-2} s^{-1} (figure 5.1a). Individually, each site demonstrated a strong seasonal FFcer pattern (figure 5.1a; table 5.4).

Table 5.2. Soil physical properties, typically constant over one year, assessed for three forest ecosystem sites from samples collected during July, September, and November of 1994.

Site	*Bulk density ($g\ cm^{-3}$)	Porosity (%)	Coarse frac. ($cm^3\ cm^{-3}$)	Texture (%)			
				sand	silt	clay	class.
SPR	0.6	78	0.020	52	23	25	sandy cl. loam
COV	0.3	88	0.008	44	22	34	clay loam
OAK	0.9	65	0.113	24	37	39	clay loam

*Samples for bulk density and porosity determination were collected in July, 1997.

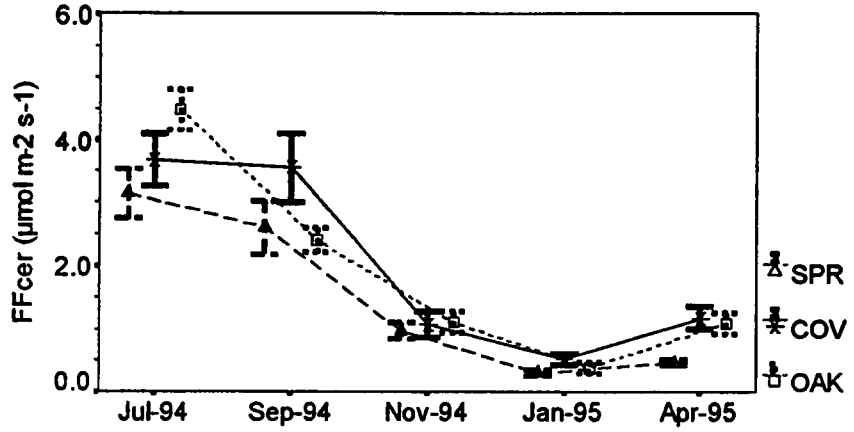
Table 5.3. Soil chemical properties, typically constant over one year, assessed for three forest ecosystem sites from samples collected in April , 1995.

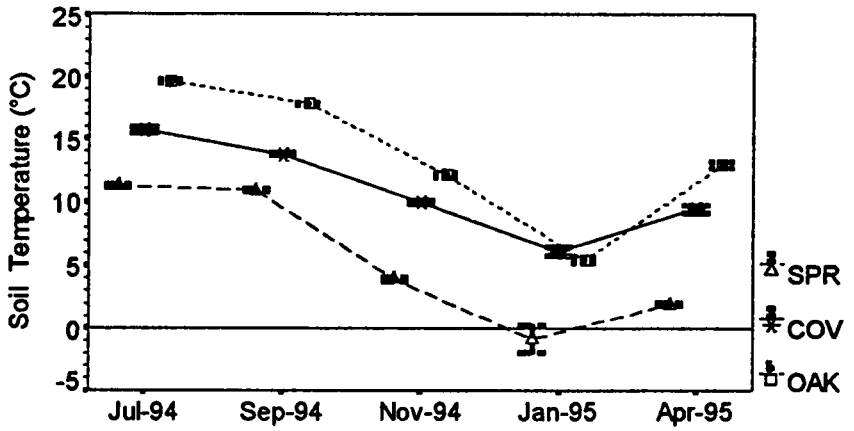
Site	Ex. Bases ($cmol_c\ kg^{-1}$)				Ex. Al ($cmol_c\ kg^{-1}$)	CEC ($cmol_c\ kg^{-1}$)	%Base sat.
	Ca	Mg	K	Na			
SPR	0.140	0.148	0.176	0.007	3.759	4.2	11.1
COV	0.258	0.151	0.167	0.004	3.743	4.3	13.4
OAK	0.854	0.164	0.161	0.006	0.857	2.0	58.1

Table 5.4. Seasonal forest floor CO_2 efflux rates within sites for the period July, 1994 to April, 1995.

Date	SPR	COV	OAK
		µmol $m^{-2}\ s^{-1}$	
Jul-94	3.14a	3.68a	4.50a
Sep-94	2.60bb	3.56aa	2.40bb
Nov-94	0.97ccc	1.08bbb	1.11ccc
Jan-95	0.31ddd	0.53cccc	0.39dddd
Apr-95	0.47eee	1.18ddbd	1.10eece

Means for each site with different letters indicate a significant difference among those dates as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.





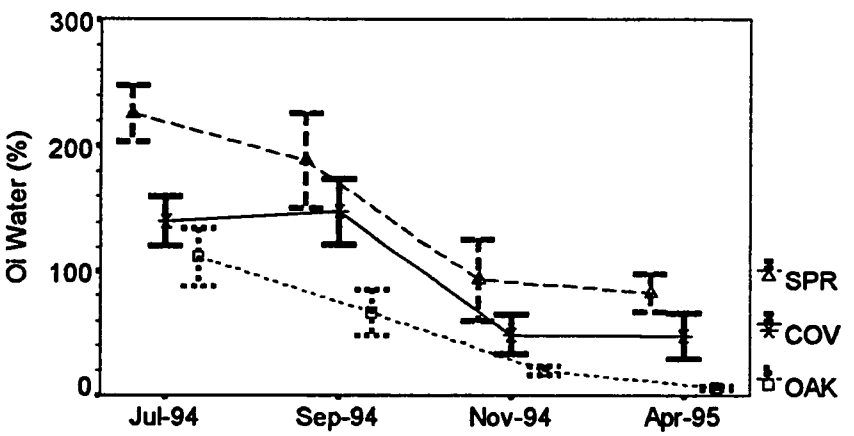


Figure 5.1. SPR, COV, and OAK seasonal a) forest floor CO_2 efflux rates, b) soil temperature, and c) Oi water content (Jan., 1995 Oi water content was not assessed). (Values are mean±2SE).

When FFcer was linearly regressed against all the parameters, soil temperature ($P<0.005$) and Oi water content ($P<0.005$) were significantly, positively correlated ($R^2=0.73$) with seasonal fluctuations in FFcer. Soil temperature and Oi water content each accounted for 41% and 34% (unadjusted partial R^2 percent) of FFcer variation. The estimated linear regression equation (standard error in parentheses) was FFcer = -1.28(±0.18) + 0.19(±0.01) × soil temperature + 0.01(±0.001) × Oi water content.

Soil temperature differed significantly for all dates except Jan., 1995 when only the SPR soil temperature was significantly ($P<0.005$) lower than that of the COV and OAK sites (figure 5.1b). In this case, the SPR and OAK sites had more similar seasonal patterns of soil temperature (figure 5.1b). The COV site soil temperature pattern fluctuated more moderately over time than did that of the other two sites (figure 5.1b). Oi water content was significantly ($P<0.005$) different across all sites during only Apr., 1995 (figure 5.1c). During Jul. and Nov., 1994, the SPR site had significantly ($P<0.005$) the highest Oi water content and during Sep., 1994, the OAK site had significantly ($P<0.005$) the lowest Oi water content (figure 5.1c). The SPR and OAK sites also appear to have more similar seasonal patterns of Oi water content. While the SPR and OAK Oi water contents decreased from Jul. to Sep. of 1994, the COV Oi water content increased which coincided with this site having significantly the highest FFcer ($P<0.005$).

Forest floor CO_2 efflux rates demonstrated an exponential relationship with soil temperature values across all sites and dates (figure 5.2a). However, the sharp exponential increase in FFcer for each site occurred at different soil temperatures. The minimum FFcer at the SPR site, 0.2 μmol m^{-2} s^{-1}, occurred at a minimum soil temperature of 1.0 °C and the minimum FFcer at the COV, 0.2 μmol m^{-2} s^{-1}, and OAK, 0.1 μmol m^{-2} s^{-1}, sites corresponded to a similar minimum soil temperature of about 5 °C (figure 5.2a). The SPR, COV, and OAK maximum FFcer of 5.1, 6.3, and 5.8 μmol m^{-2} s^{-1}, respectively, corresponded to maximum soil temperatures of 11 °C, 14 °C, and 19 °C (figure 5.2a). (The values given here are absolute and not mean values).

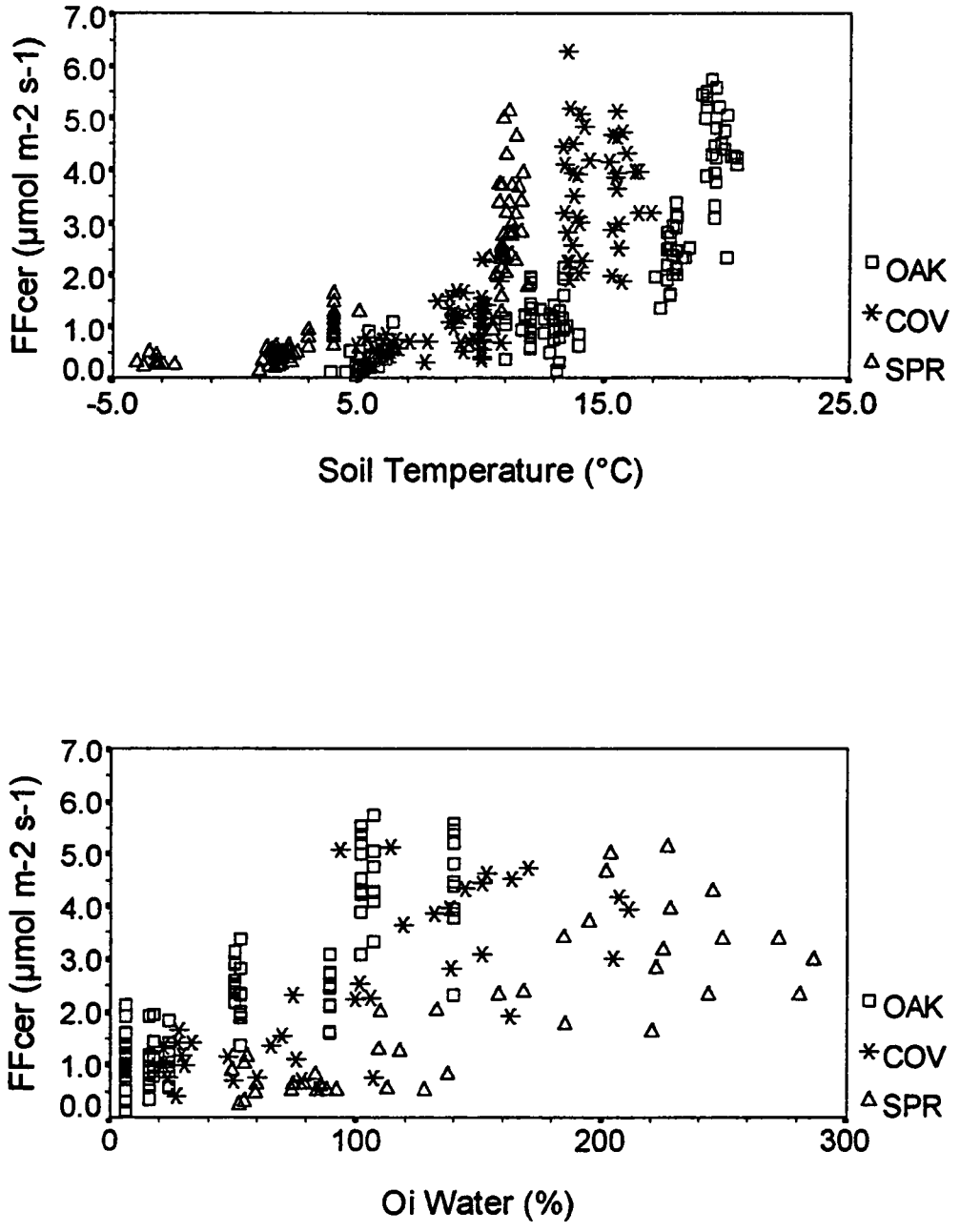


Figure 5.2. SPR, COV, and OAK seasonal forest floor CO_2 efflux rates in relation to seasonal a) soil temperature and b) Oi water content.

Oi water content and FFcer basically exhibited a linear relationship across all sites and dates (figure 5.2b). The SPR, COV, and OAK minimum Oi water contents, 53, 23, and 6 %, coincided with minimum FFcer of 0.2, 0.7, and 0.8 μmol m^{-2} s^{-1} for these sites, respectively (figure 5.2b). (The minimum FFcer provided here are different from those related to the minimum soil temperature values because Oi water content was not assessed for Jan., 1995). Maximum FFcer of, 5.1, 6.3, and 5.8 μmol m^{-2} s^{-1}, at the SPR, COV, and OAK sites corresponded to maximum Oi water contents of 227, 114, and 107 %, respectively. (The values given here are absolute and not mean values).

Discussion

FACTORS INFLUENCING FFcer

Soil physical, chemical, and biological properties affect the biological production of CO_2 and the flux of CO_2. Soil temperature and water content are physical properties that have been demonstrated to have the greatest influence on both CO_2 production and flux (Anderson, 1973; Dörr and Münnich, 1987; Edwards, 1975; Garrett and Cox, 1973; Hanson et al., 1993; Lundegårdh, 1927; Reiners, 1968; Šimůnek and Suarez, 1993; Singh and Gupta, 1977). By influencing the rate at which biochemical activity proceeds, temperature governs CO_2 production (Paul and Clark, 1996; Pritchett and Fisher, 1987). A soil/atmosphere temperature gradient is one of the factors that can induce the convective movement of CO_2 from the soil to the atmosphere (Hillel, 1982). Soil water content modifies the pathway by which CO_2 can move out of and O_2 can move into the soil, thereby influencing soil aeration (Hillel, 1982). In addition to influencing CO_2 flux, water effects the concentration of nutrients available to plant roots and MO, and it is required for their metabolism (Paul and Clark, 1996; Pritchett and Fisher, 1987; Smith and Paul, 1990). Litter water content has been shown to be as important as temperature for litter decomposition (De Santo et al., 1993; O'Connell, 1990; Singh and Gupta, 1977).

In this study, soil temperature and Oi water content proved to be the most important influences over seasonal FFcer variation across the three diverse forest ecosystems. The influence of soil temperature on FFcer reflected, in part, the contribution of soil microorganisms and roots to FFcer and

the significance of Oi water content appeared to reflect the contribution of microbial decomposition in the Oi layer to FFcer.

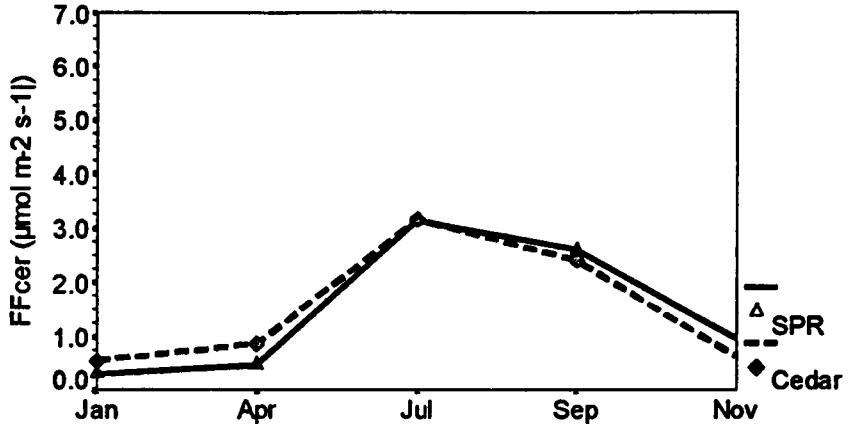
COMPARING FFcer

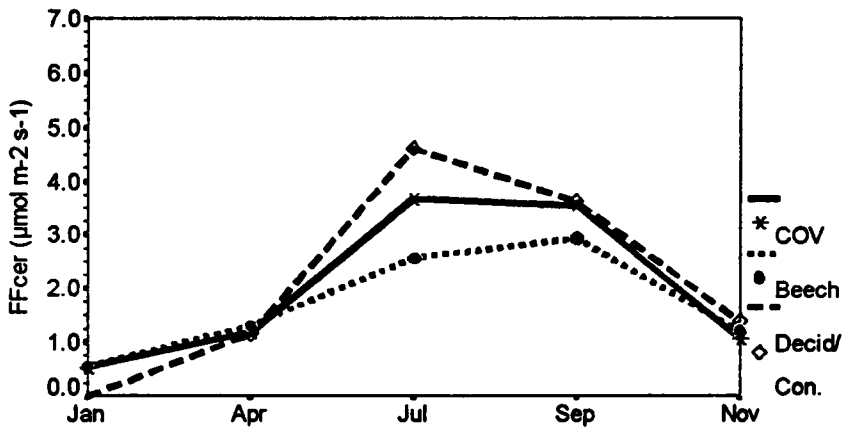
The SPR seasonal mean FFcer (figure 5.3a) were quite comparable, both in pattern and actual values, to the seasonal FFcer of a cedar plantation in Japan which ranged from 0.55 to 3.16 μmol m^{-2} s^{-1} (Nakane, 1995). The COV seasonal mean FFcer (figure 5.3b) compared well to a beech stand in England, ranging from 0.54 to 2.94 μmol m^{-2} s^{-1} (Anderson, 1973) and an old-growth deciduous/conifer forest in New Hampshire, ranging from 0.00 to 4.61 μmol m^{-2} s^{-1} (Crill, 1991), with the exception of the summer season. From late spring and throughout the summer, the FFcer of the COV site, the beech stand, and the old-growth deciduous/conifer stand diverged, with the COV FFcer being in the middle. With the exception of late summer and fall, the OAK seasonal mean FFcer (figure 5.3c) were fairly comparable with FFcer of the old-growth deciduous/conifer forest in New Hampshire (Crill, 1991) and with FFcer measured in the same forest twenty years earlier, which ranged from 0.65 to 6.72 μmol m^{-2} s^{-1} (Edwards, 1975). The FFcer of the OAK site, the old-growth deciduous/conifer stand, and those measured twenty years previously at the OAK site diverged during the late summer and fall, with the greatest variance occurring in Sep. and with the OAK FFcer between that of the other two sets of measurements.

MODELLING FFcer

In predicting global C flux estimates, it is necessary to be able to estimate C fluxes in the different compartments, especially from that of forest soils (Kicklighter et al., 1994; Raich and Potter, 1995). The significance of soil temperature and Oi water content in this study and the exponential relationship of FFcer to soil temperature led to the testing and expansion of the empirical, nonlinear equation developed by Hanson et al. (1993),

$$FFcer=(Rb \times Q^{(Ts/10)}) \times (1-Cf/100). \quad (1)$$





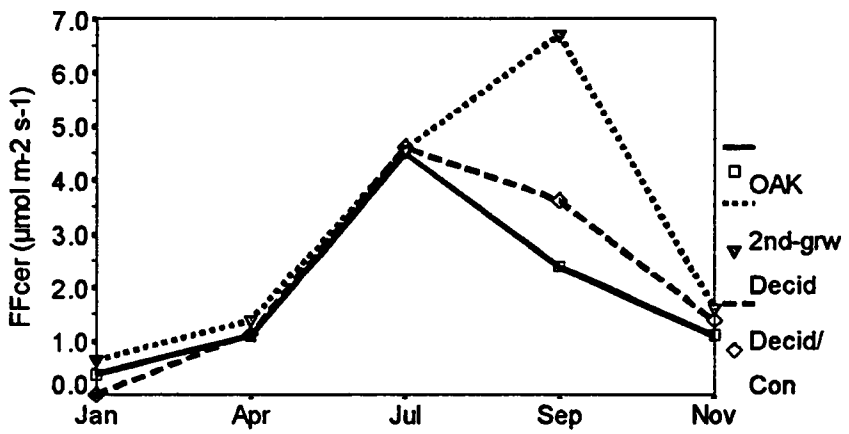


Figure 5.3. Seasonal forest floor CO_2 efflux rate comparisons: a) SPR site to a cedar plantation, b) COV site to a beech stand and an old-growth decid/conifer stand, and c) OAK site to measurements made 20 yrs previously in the same forest and to an old-growth decid/conifer stand.

In this equation, *FFcer* is the forest floor CO_2 efflux rate (μmol m^{-2} s^{-1}), *Q* is the effect of a 10 °C temperature increase on biological activity and thus FFcer, *Ts* is soil temperature (°C), *Rb* is the CO_2 efflux when *Ts* is zero and moisture is not limiting, and *Cf* is the percent soil coarse fraction (the percent vol. of fragments > 2 mm relative to the vol. of the soil sample).

When the soil temperature and coarse fraction data from this study were used in Hanson et al.'s (1993) equation to estimate FFcer for all three ecosystem sites, it accounted for 59% of the seasonal FFcer variation. However, when equation (1) was used to estimate the FFcer for each site, individually, it produced better estimates of FFcer for the SPR and OAK sites than for the COV site (table 5.5). When Oi water content was added to the equation, the equation's ability to estimate FFcer was improved substantially, accounting for 78% of the variability in seasonal FFcer (figures 5.4a and 5.4b; table 5.5). The equation took the form,

$$FFcer=(Rb + h \times (OiH_2O/OiH_2O_{max}) \times (Q^{(Ts/10)}) \times (1-Cf_f). \quad (2)$$

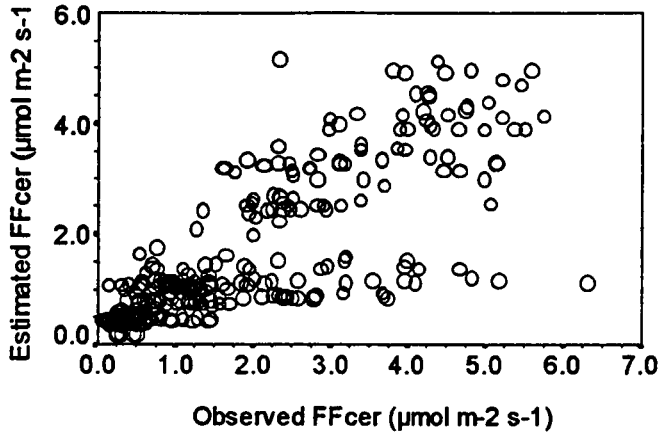
In equation (2), OiH_2O is the percent Oi water content, OiH_2O_{max} is the (absolute) maximum percent Oi water content, *h* is a coefficient which changes with Oi water content variations, and Cf_f is simply the soil coarse fraction on a vol/vol basis (vol. of fragments ≥ 2 mm relative to the vol. of the soil sample). Essentially, *h* transforms the units of Oi water content so that it can be regressed against FFcer. Oi water content appears to represent the effect of water content on CO_2 production and possibly flux. The initial parameter values for Rb, h, and Q, were 0.50, 1.0, and 2.4, respectively (table 5.5), and were based on information in Hanson et al. (1993) and Raich and Schlesinger (1992). The Rb, h, and Q parameter values produced by nonlinear regression, using equation (2), were 0.32, 1.1, and 2.6 respectively (table 5.5).

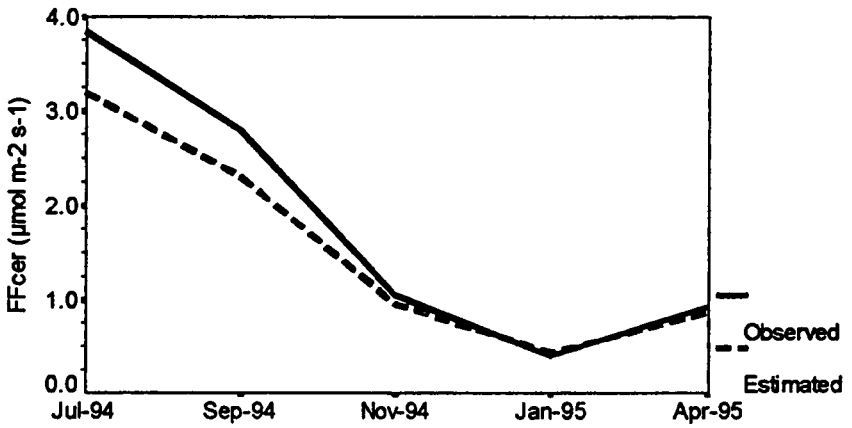
Equation (2) underestimated the actual FFcer values from Jul., 1994 to Sep., 1994 with the greatest difference in Jul., 1994 (figure 5.4b). The same phenomenon was observed by Hanson et al. (1993) when the observed FFcer were compared to the values estimated by equation (1) and by Schlentner and Van Cleve (1985) when they compared observed FFcer to FFcer estimated from an

Table 5.5. Estimated Regression Coefficients for the SPR, COV, and OAK sites, individually and for all sites combined based on Equation (1) and (2).

Site	Rb	Q	h	Corrected R^2
Equation (1)				
Initial	0.84	2.3	na	na
SPR	0.40±0.07	6.0±0.94	na	0.79
COV	0.24±0.06	6.0±0.97	na	0.67
OAK	0.10±0.02	7.2±0.82	na	0.83
ALL	0.50±0.05	3.13±0.19	na	0.59
Equation (2)				
Initial	0.50	2.4	1.0	na
SPR	0.31±0.13	3.5±1.18	0.67±0.41	0.77
COV	0.18±0.07	5.4±1.66	0.25±0.18	0.77
OAK	0.21±0.07	3.8±0.98	0.37±0.28	0.81
ALL	0.32±0.04	2.6±0.14	1.1±0.11	0.78

na: not applicable.





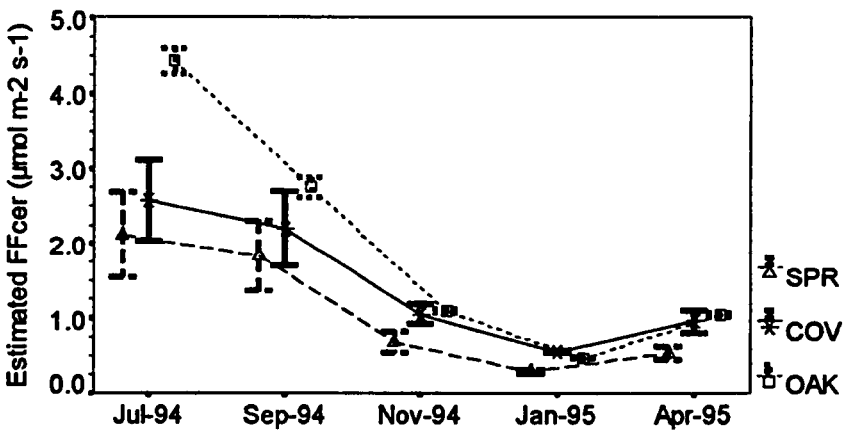


Figure 5.4. Seasonal forest floor CO_2 efflux rates: a) estimated versus observed, b) observed and estimated for all sites combined, c) estimated seasonal patterns for each site. (Estimated rates based on equation 2 which includes soil temperature and Oi water content functions).

equation they developed. This phenomenon seems to parallel the period during which plants and trees experience the greatest growth in North America, particularly deciduous plants. To resolve this difference, Hanson et al (1993) incorporated root activity data from other studies into equation (1), and achieved much better estimates of FFcer. Although root activity was not determined for this study, an attempt was made to capture the enhanced influence of roots on FFcer during the growing season by measuring root biomass (Mg ha^{-1}). However, in this experiment, root biomass was not significantly correlated to FFcer (P=0.10), possibly due to error in processing samples or an inadequate number of samples.

TESTING THE MODEL

To assess the predictive capabilities of equation (2), it was used to estimate the FFcer of three different forest ecosystem sites in interior Alaska (Schlentner and Van Cleve 1985), based on the soil temperature and litter water data from the three sites (figure 5.5). The three forest ecosystems, an aspen, a birch, and a white spruce stand, were each approximately 70 years old. The sites experienced an annual mean air temperature of -3.5 °C, a minimum of -9.2 °C and a maximum of 2.2 °C. The area receives an average of 28.6 cm precipitation, yearly. Schlentner and Van Cleve (1985) developed the BRESP (Best-fit RESPiration) equation to estimate soil respiration based on a temperature function (Daniel and Wood, 1980) and a moisture function (Bunnell et al., 1977). They estimated FFcer for each stand from BRESP based on soil temperature and organic layer water content, which were measured to a depth of 15 cm at all three sites.

The FFcer estimated by the BRESP equation for the Aspen, Birch, and White Spruce stands yielded R-squared values of 0.58, 0.49, and 0.55, respectively. When equation (2) was used to estimate FFcer for the same three stands, it yielded R-squared values of 0.51, 0.53, and 0.50 for the Aspen, Birch, and White Spruce stands, respectively. Equation (2) did basically as well as the BRESP equation in estimating FFcer for the three stands and provided more consistent estimates across the stands than did the BRESP equation. Equation (2) also did well reflecting the general pattern across the three stands, consistently underestimating FFcer values by an average of

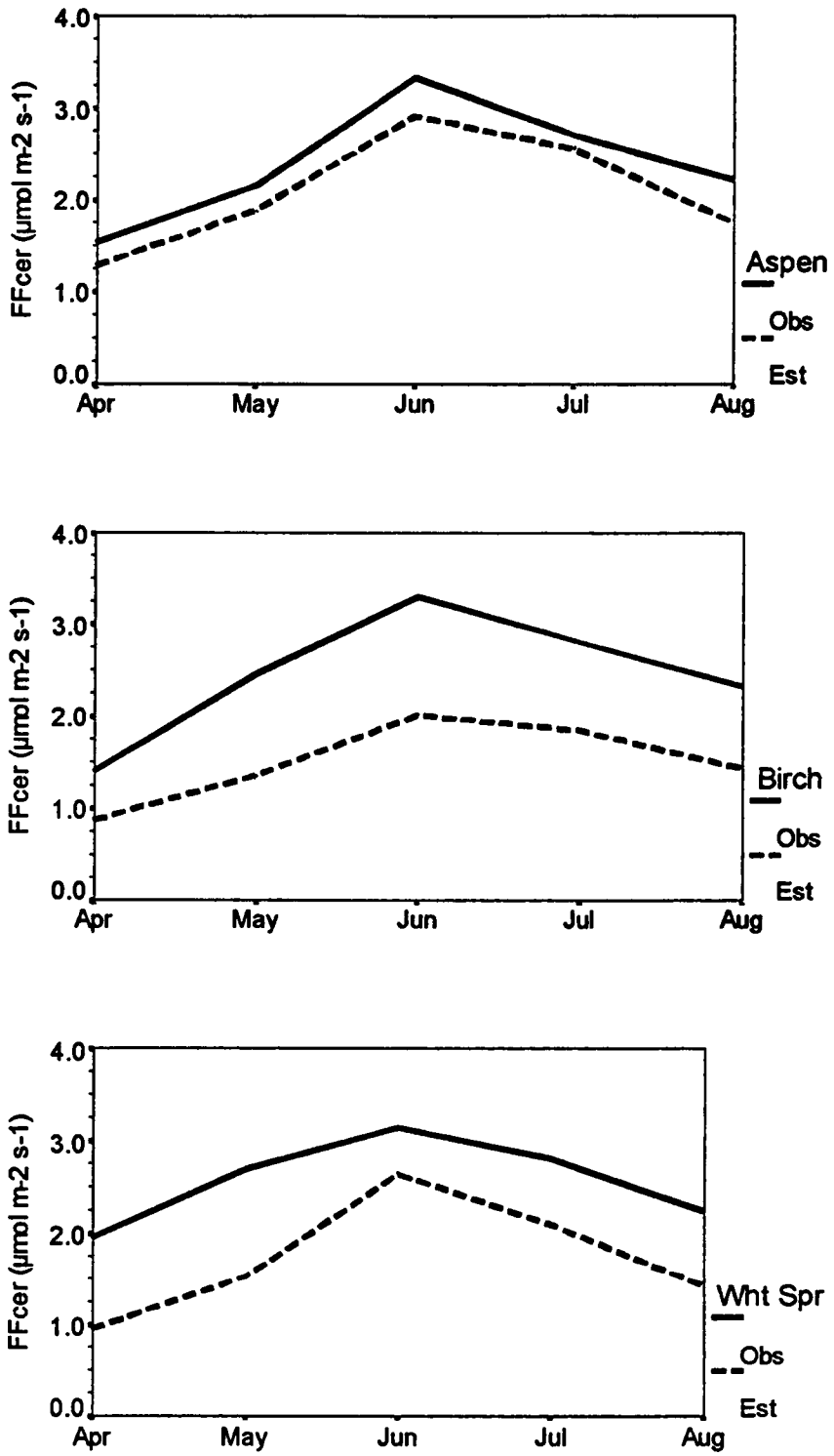


Figure 5.5. Combined 1980 and 1981 observed and estimated (from equation 2) forest floor CO_2 efflux rates for a) Aspen, b) Birch, and c) White Spruce stands in interior Alaska (Schlentner and Van Cleve, 1985).

0.70 μmol m^{-2} s^{-1} (figure 5.5). Failure to account for increased biological activity during the growing season likely explains part of the underestimation of FFcer by equation (2) for the three stands. In addition, the relationship of FFcer to water content for the three forest stands may not be linear as it is represented in equation (2).

Summary and Conclusions

This research centered on the seasonal characterization of FFcer across three distinct forest ecosystem sites, which varied in age, climate, elevation, and tree species. Clearly, the FFcer patterns for the three sites did not vary consistently over time. Only the COV FFcer was consistently larger than the SPR FFcer over time. The OAK FFcer was significantly the largest during Jul., 1994 only and the COV FFcer was significantly the largest during Sep., 1994 and Jan., 1995. Forest Floor CO_2 efflux rates ranged from 0.3 μmol m^{-2} s^{-1} at the SPR site in Jan., 1995 to 4.5 μmol m^{-2} s^{-1} at the OAK site in Jul., 1994.

While various soil physical, chemical, and biological properties influence CO_2 production and flux, FFcer was significantly correlated (linearly) to only soil temperature and Oi water which accounted for 73% of the seasonal FFcer variation across the three sites. Forest floor CO_2 efflux rates demonstrated an exponential relationship to soil temperature and a linear relationship to Oi water content. The significance of soil temperature appears to reflect the contribution to FFcer by roots and soil microorganisms. The importance of Oi water content seems to reflect the contribution to FFcer by microbial Oi layer decomposition.

A simple, empirical nonlinear equation by Hanson et al. (1993) which estimates FFcer primarily from a soil temperature function (Q_{10}), was tested using the soil temperature data from the three sites of this study. This equation accounted for 59% of the variation in seasonal FFcer across the sites. When this equation was expanded to include the linear Oi water content function produced from this study, the new equation explained 78% of the seasonal FFcer variation across the three forest ecosystem sites. Clearly, the addition of Oi water content strengthened the equation's ability to

estimate FFcer. Although the three sites were quite diverse, the same Q_{10} value was sufficient for all three ecosystem sites.

While the second equation, based on soil temperature and Oi water content, accounted for a substantial portion of the seasonal FFcer variation, it did underestimate FFcer during the summer. Based on the findings of Hanson et al. (1993), including some indicator of the increased below-ground biological activity (root and microbial) during the growing season would likely further improve the equation's predictive capability. The findings of this study and those of Hanson et al. (1993) imply that a factor representing the increased biological activity Only when the dynamic details of each compartment of the global C cycle are understood can scientists resolve the uncertainties in the global C budget. By increasing the understanding of the relationship between FFcer and the factors which influence variation in its production and flux on a seasonal basis, this study has helped scientists to more realistically represent the dynamics of forest floor carbon flux in carbon models.

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PART 6

SUMMARY AND CONCLUSIONS

Climate change caused by increasing temperatures induced by greenhouse gases, primarily carbon dioxide (CO_2), can potentially affect everything from the agricultural industry to energy systems. In order to understand and predict this process and mitigate its consequences, much effort has been employed to assess the various carbon (C) compartments and understand the interaction of these compartments with the various factors in their environment. Because forest soils contain 40% of all below ground C, understanding and documenting C dynamics in relation to forest soil processes is important to balancing the global C budget.

This research focused on characterizing the seasonal patterns of forest floor carbon dioxide efflux rates (FFcer) of three forest ecosystem sites, varying in age, climate, elevation, and tree species located in East Tennessee, USA. Because FFcer is intrinsically linked to soil physical, chemical, and biological properties, they were measured on a seasonal basis to evaluate the factors responsible for the seasonal differences in FFcer patterns among the sites.

The depiction of the soil physical and chemical properties of the three sites revealed the importance of elevation. While all three sites were basically located at the same latitude (35°), each was at a different elevation that coincided with the distinctly different soil temperature and water content patterns at each site. Cooler temperatures and the abundance of precipitation likely influenced the dominance of coniferous tree species at the higher-elevation SPR and COV sites. The OAK site, at the lowest elevation, had temperatures which were warmest and had the greatest seasonal variation, and the least precipitation which seems to have been responsible for the dominance of the deciduous tree species. Elevation seems to have had the strongest influence on the soil physical properties at each site. The development of the soil chemical properties at each site appears to have been governed by tree species, amount of precipitation, and parent material.

Microorganisms drive the soil C and N cycle and for that reason understanding their dynamics within forest ecosystems is essential for a complete picture of the global C cycle. The characterization of seasonal patterns of soil microbial biomass C (MBC) and site variations in organic layer microbial biomass C provided some insight regarding their behavior in forest ecosystems. Distinct patterns in soil microbial biomass C emerged with the COV site consistently having the highest values and the

OAK site consistently having the lowest soil MBC values across all dates. Mean soil microbial biomass C values ranged from 468.63 to 1957.98 μgMBC g^{-1}soil. Soil N and Oi layer mass accounted for 63% of the seasonal differences in soil microbial biomass C, with the COV site always having the highest soil N and the OAK site always having the lowest soil N. Differences among sites only occurred with respect to Oi layer MBC and Oi layer N accounted for only 14% of these differences.

The forest floor CO_2 efflux rates did not vary consistently among the three sites over time. Seasonal mean forest floor CO_2 efflux rates ranged from 0.3 μmol m^{-2} s^{-1} during Jan., 1995 at the SPR site, the highest-elevation site, to 4.5 μmol m^{-2} s^{-1} during Jul. 1994 at the OAK site, the lowest-elevation site. Undoubtedly, all physical, chemical, and biological soil properties influenced CO_2 production and flux to some extent. However, when the FFcer were linearly regressed against all the parameters, soil temperature and Oi water content alone significantly accounted for 73% of the seasonal FFcer variations among the three sites

The SPR site experienced the lowest soil temperatures of the sites and usually produced the lowest FFcer values. However, the OAK site, the lowest elevation site, typically experienced the warmest soil temperatures, but produced the highest significant FFcer value only one time out of the five seasonal measurements. While the COV site, the middle-elevation site, generally had soil temperatures between that of the two other sites, it produced the highest significant FFcer values during the two of the five seasonal measurements. The COV site exhibited the most moderate seasonal variation in soil temperature and had neither the highest nor the lowest Oi water content, which seem to have influenced the site's FFcer. The significant influence of soil temperature reflects the contribution to FFcer by the soil microorganisms and roots. The significant effect of Oi water content seems to reflects the contribution of microbial Oi decomposition.

Forest floor CO_2 efflux rates demonstrated an exponential relationship to soil temperature and a linear relationship to Oi water content. Understanding the relationship between C fluxes and the factors influencing the fluxes on a local scale is essential for their estimation on a regional and global scale. Thus, soil temperature data for the three forest sites were used to test a simple, empirical nonlinear equation which estimates FFcer based on a Q_{10} soil temperature function. The equation

accounted for 59% of the seasonal variations in FFcer. When the nonlinear equation was expanded to include a linear Oi water content function, it could account for 78% of the seasonal FFcer variation among the three sites, a substantial improvement over that of the original equation. In addition, a base respiration (Rb) of 0.32, and a Q_{10} of 2.6 served all three sites for the nonlinear estimation of FFcer.

The following ideas and suggestions developed as the desire for more or different information arose during this study. To provide a more complete characterization of seasonal microbial biomass C, measurements during the winter season and more measurements during the other seasons should be made. In addition, the influence of Oi water content to FFcer variation suggest that measuring MBC in the Oi as well as the Oe/Oa would provide important information regarding their behavior in the organic layers. Using an enzyme assay, such as a dehydrogenase, could probably render a more definite indication of when the microorganisms are active (i.e., producing CO_2), and might result in a stronger statistical relationship between microbial processes and FFcer than did the microbial biomass C values in this study. While root biomass did not have a significant influence on FFcer variations in this study, other studies have found root activity to be significantly associated to FFcer variations. The assessment of more soil samples for root biomass might have improved the statistical relationship between roots and FFcer variation. Possibly, the use of root growth chambers or enzyme assays would have been a better indicator of root activity. Finally, more frequent FFcer measurements over each season and periodically over 24-hour periods during each season would undoubtedly have produced a more accurate seasonal characterization.

These findings have contributed to the understanding and knowledge of forest soil physical, chemical, and biological processes and expanded the global data base of environmental parameters affecting carbon flux. Furthermore, the simple, empirical nonlinear equation tested and expanded with the results in this study contributes greatly to the efforts to model the global C cycle. In addition, this study has increased the knowledge of soil physical, chemical, and biological processes in the Great Smoky Mountains National Park, an international biosphere reserve, and provided a comparative understanding of these processes at the forest ecosystem level.

APPENDICES

Appendix A. Other Soil Biological Properties

A.1. Seasonal forest floor CO_2 efflux rate measurements for the three forest ecosystem sites during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Jan-95	Apr-95
		$\mu mol\ m^{-2}\ s^{-1}$			
SPR	3.1a	2.6a	1.0	0.3a	0.5a
COV	3.7a	3.6b	1.1	0.5b	1.2b
OAK	4.5b	2.4a	1.1	0.4a	1.1b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

A.2. Seasonal root biomass measurements for the three forest ecosystem sites, sampled to an average depth of 26 cm, during the period July, 1994 to April, 1995.

Site	Jul-94	Sep-94	Nov-94	Apr-95
		$Mg\ ha^{-1}$		
SPR	1.11a	0.07a	0.41	0.60a
COV	2.35b	0.42b	0.73	1.36b
OAK	0.74a	0.94c	0.35	1.38b

Means in columns with different lower-case letters indicate a significant difference as determined by the Student-Neuman-Keul's test at an alpha level of 0.05.

Appendix B. Map of Sites

Cumberland Plateau
Oak Ridge
OAK
Knoxville
Gatlinburg
COV
SPR
Great Smoky Mountains
Chattanooga
50 km

VITA

M. Lala S. Chambers was born on September 17, 1950 in Knoxville, Tennessee and attended local schools, graduating from South High School in June, 1969. Because of interests in everything from psychology to meteorology, she worked in various jobs for the experience and economic support while attending school. She attended Freed-Hardeman College in West Tennessee, David Lipscomb College in Nashville, Tennessee, and the University of Tennessee in Knoxville from which she earned a Bachelor of Arts degree in August, 1980 in Geography with a minor in Psychology.

After receiving her bachelor's degree, she obtained a job with Lockheed Corporation, in Oak Ridge, Tennessee. Government cuts eliminated this position. Because family responsibilities required that she stay in the Knoxville area, she worked outside her field in various occupations until she obtained a position as research assistant with NOAA's Atmospheric Turbulence and Diffusion Division in Oak Ridge. While working with this laboratory, she developed an interest in the climate change issue and carbon dioxide dynamics, which prompted her to take classes in mathematics, physics, chemistry, and ecology at Roan State Community College, Oak Ridge, Tennessee. Continued interest in climate change and carbon dioxide dynamics lead her to pursue a degree in the Ecology Program at the University of Tennessee, Knoxville, Tennessee. She received a Master of Science degree in Ecology and Evolutionary Biology in May, 1998.

While working on her own project, she also participated in the Walker Branch Throughfall Displacement Experiment, a large-scale manipulative field experiment conducted to identify important forest ecosystem responses that may result from future precipitation changes brought about by climate change. In addition, she conducted a small experiment to compare the two different systems used to measure forest floor carbon dioxide efflux rates. She is a member of The Honor Society of Phi Kappa Phi, the Association of Women in Science, and the Ecological Society of America.