

Forest management and soil respiration: Implications for carbon sequestration

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Abstract: It is recognized that human activities, such as fossil fuel burning, land-use change, and forest harvesting at a large scale, have resulted in the increase of greenhouse gases in the atmosphere since the onset of the industrial revolution. The increasing amounts of greenhouse gases, particularly CO₂ in the atmosphere, is believed to have induced climate change and global warming. With the ability to remove CO₂ from the atmosphere through photosynthesis, forests play a critical role in the carbon cycle and carbon sequestration at both global and local scales. It is necessary to understand the relationship between forest soil carbon dynamics and carbon sequestration capacity, and the impact of forest management practices on soil CO₂ efflux for sustainable carbon management in forest ecosystems. This paper reviews a number of current issues related to (1) carbon allocation, (2) soil respiration, and (3) carbon sequestration in the forest ecosystems through forest management strategies. The contribution made by forests and forest management in sequestering carbon to reduce the CO₂ concentration level in the atmosphere is now well recognized. The overall carbon cycle, carbon allocation of the above- and belowground compartments of the forests, soil carbon storage and soil respiration in forest ecosystems and impacts of forest management practices on soil respiration are described. The potential influences of forest soils on the buildup of atmospheric carbon are reviewed.

Key words: greenhouse gas, CO₂ concentration, review, carbon sequestration, forest ecosystem.

Résumé : On reconnaît que les activités humaines, comme le brûlage d'huiles fossiles, les modifications de l'utilisation du territoire et la récolte des forêts sur de grandes échelles ont conduit à une augmentation de l'effet serre dans l'atmosphère, depuis le début de la révolution industrielle. On croit que l'augmentation des gaz à effet serre dans l'atmosphère, particulièrement le CO₂, a induit le changement climatique et le réchauffement global. Avec leur capacité à éliminer le CO₂ de l'atmosphère par la photosynthèse, les forêts jouent un rôle critique dans le cycle du carbone et la séquestration du carbone, à la fois à l'échelle globale et à l'échelle locale. On doit comprendre les relations qui existent entre la dynamique du carbone des sols forestiers et leur capacité de séquestration, ainsi que l'impact des pratiques d'aménagement sur l'efflux de CO₂, dans la perspective de l'aménagement durable des écosystèmes forestiers. Les auteurs présentent une synthèse des problématiques actuelles reliées à (1) l'allocation du carbone (2) la respiration du sol et (3) la séquestration du carbone dans les écosystèmes forestiers par des stratégies d'aménagement forestier. On reconnaît maintenant très bien le rôle des forêts et de l'aménagement forestier dans la séquestration du carbone pour réduire la teneur en CO₂ de l'atmosphère. Les auteurs décrivent le cycle global du carbone, l'allocation du carbone aux compartiments épigés et hypogés des forêts, l'accumulation du carbone dans le sol et la respiration des sols des écosystèmes forestiers, ainsi que les impacts des pratiques d'aménagement forestier sur la respiration des sols. On passe en revue les influences potentielles des sols forestiers sur l'accumulation du carbone atmosphérique.

Mots-clés : gaz à effet serre, teneur en CO₂, revue, séquestration du carbone, écosystème forestier.

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Introduction

The increase of greenhouse gas (GHG) (primarily carbon dioxide (CO₂)) concentrations in the atmosphere has become one of the top public concerns in recent years (Tans et al. 1990; Houghton et al. 1990; Dixon et al. 1994; Gifford 1994; Woodwell and McKenzie 1995; Pollack et al. 1998;

Shaver et al. 2000). Rising atmospheric CO₂ concentration is a major driver for global warming and climate change (Eamus and Jarvis 1989; Prentice et al. 2001; Malhi et al. 1999). Carbon dioxide is the primary anthropogenic greenhouse gas (IPCC 1990; Kerr 1995; Hasselmann 1997; Grace 2004; IPCC 2005) and cumulatively responsible for approximately 55% of greenhouse-gas-related climate forcing, popularly known as "the greenhouse effect" (Houghton et al. 1990).

Human activities, such as fossil fuel burning, land-use change, and deforestation, are altering the transfer rate of CO₂ among the main global C reservoirs. Such activities are responsible for the buildup of CO₂ in the atmosphere (Houghton et al. 1990; Bueno and Helene 1991; Brown et al. 1993; Dixon et al. 1994; IPCC 1990; Kerr 1995; Hasselmann 1997; Pendall et al. 2004; Demirbas 2007). The estimated total carbon (C) emission to the atmosphere amounts

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to 7.1 Gt C year⁻¹, including 5.5 Gt C year⁻¹ from fossil fuel burning and about 1.6 Gt C year⁻¹ from deforestation and other sources associated with land-use change (Detwiler and Hall 1988; Cannell 1995).

Forests play an important role in the C cycle and C sequestration at both local and global scales (Dixon et al. 1994; Brown et al. 1996; King 2005). The recognition that CO₂ is increasing in the atmosphere (IPCC 2001, 2003, 2005) has led to the explicit economic valuation of C sequestration as an important forest ecosystem function (NRC 2000). Trees remove CO₂ from the atmosphere through photosynthesis and store C in different tree components and in the soil (Landsberg and Gower 1997; Malhi et al. 1999; Hiroshima 2004). Whether a forest acts as a C sink or source depends on the difference between photosynthetic uptake and respiratory release of CO₂ (Landsberg and Gower 1997; Malhi et al. 1999), and disturbance (IPCC 2006, 2007).

Soil is a major source of atmospheric CO₂ (Elberling 2007) and an integral part of the global C cycle (Schlesinger and Andrews 2000). Soil CO₂ flux (FCO₂) is one of the largest CO₂ fluxes from land to the atmosphere (Raich and Schlesinger 1992; Schimel et al. 1994; Taneva et al. 2006), second only to photosynthesis in influencing forest C budgets (Gower et al. 1996; Goulden et al. 1996; Schlesinger and Andrews 2000), the primary contributors being autotrophic respiration by living roots and heterotrophic respiration by soil microbes (Elberling 2007). On a smaller scale, soil FCO₂ dynamics may determine whether a specific land-use or management practice causes a system to be a C source or a sink (Maier and Kress 2000; Maier et al. 2004). The fluctuation of soil FCO₂ can result in significant changes in global C cycling (Kirschbaum 1995; Giardina and Ryan 2000). This flux is also an indicator of the overall biological activity of the soil (Rochette et al. 1997). Assessing forest floor FCO₂ in conjunction with soil nutrient pools can provide further insight into management impacts on critical soil processes (Butnor et al. 2006).

Manipulation of soils to increase their C storage capacity has been proposed as a method for slowing the accumulation of atmospheric CO₂ (IPCC 2000). Much discussion focuses on the feasibility of this approach (Raich and Nadelhoffer 1989; Anderson 1991; Dixon and Turner 1991; Jenkinson et al. 1991; Johnson and Kern 1991; Schlesinger 1990; Winjum et al. 1992; Smith et al. 1997). Norby et al. (1995) and Thomas et al. (1996) have suggested that forest ecosystems may sequester more C into soils as atmospheric levels of CO₂ continue to rise. However, other studies have indicated that increase in atmospheric CO₂ concentration will cause an increase in belowground C allocation and as well as in root density, and thus might be accompanied by increased CO₂ loss from the soil (Luo et al. 1996; Hungate et al. 1997). Thus monitoring soil FCO₂ in conjunction with related soil parameters is important for investigating how microbial and root activities may respond to climate change (Raich and Schlesinger 1992), and provides important insights into potential means to enhance C sequestration.

Soil temperature and moisture are two important factors influencing soil FCO₂ (Edwards 1975; Singh and Gupta 1977; Schlesler 1982; Schlentner and Van Cleve 1985; Jenkinson et al. 1991; Raich and Schlesinger 1992; Hanson et al. 1993; Huc et al. 1994; Peterjohn et al. 1994; Luo et al.

1996; Trumbore et al. 1996; Keith et al. 1997; Singh and Gupta 1977; Billings et al. 1998; Andr n et al. 1999; Rustad et al. 2000; Euskirchen et al. 2003; Ma et al. 2004; Sulzman et al. 2005; Tang et al. 2005). Soil FCO₂ increases with increasing temperature, and this relationship is usually described using an exponential (Arrhenius) equation (Lloyd and Taylor 1994). There is an increasing consensus that global climate change is occurring (Harris et al. 2006), which is expected to result in increased FCO₂ due to increased soil temperatures. A climate warming of 1 °C would be associated with C release of 11–30 Pg C annually to the atmosphere (Schimel et al. 1994). The possibility of a reduction in global soil C under climate warming has been raised by a number of authors (Jenkinson et al. 1991; Schimel et al. 1994; Kirschbaum 1995). A climate-induced decrease in soil C could result in a positive feedback of CO₂ release to the atmosphere. The relationship between soil FCO₂ and soil moisture can be described as an upwardly convex curve (Peng and Thomas 2006). The FCO₂ is normally low under dry conditions due to low root and microbial activities, and generally increases with soil water content (W_g), but can show decreases under waterlogged conditions (Londo et al. 1999).

Interest in the ability of forest soils to sequester atmospheric CO₂ has recently increased because of the threat of projected climate change (Lal 2005). Understanding the mechanisms and factors affecting soil FCO₂ in forest soils is important to identifying and enhancing natural C sinks for mitigating climate change. Among published studies of management impacts on soil C dynamics, little is known about the impacts of global warming and forest management on plant–soil–microbe interactions (Sadowsky and Schortemeyer 1997; Toal et al. 2000). The rhizosphere represents the most chemically and biologically active microsite in soil (Cheng 1999; Klironomos 2002; Seguin et al. 2004; Xu and Chen 2006), and the importance of belowground processes and their interactions with above-ground processes, has been highlighted in a recent issue of *Science*: “Soils — The Final Frontier” (Wardle et al. 2004; Xu and Chen 2006). Temporal trends of soil FCO₂ are important for understanding and predicting atmospheric CO₂ concentrations and the global C cycle (Oechel et al. 1993; Brooks et al. 1997; Fahnstock et al. 1998). An improved understanding of forest management effects on important soil C dynamics in forest ecosystems is therefore urgently needed (Xu and Chen 2006). Knowledge gaps on the biological and chemical processes in forest ecosystems hamper efforts to accurately predict effects of forest management on soil C dynamics (Lee and Shibu 2003). Understanding the mechanisms of controlling belowground C processes is useful in predicting future changes in soil C stores in response to climate and land-use change (Pendall et al. 2004). The current interest in characterizing, predicting and managing soil C dynamics has focused on making accurate estimates of C inputs to soil (Bolinder et al. 2007).

The carbon issue

The global carbon cycle

Carbon is a key element of all life on earth and has a complicated biogeochemical cycle. Carbon dioxide is a trace

gas in the earth's atmosphere that has a substantial effect on earth's heat balance by absorbing infrared radiation (IPCC 1990, 2001). This gas, like water vapor (H_2O), CH_4 , and N_2O , has a strong greenhouse effect and is of great importance to global climate change (IPCC 1990; 2001). In the last 150 years, human activities have fundamentally altered many of the earth's biogeochemical cycles. The global C cycle consists of the geochemical reservoirs that store C on the earth and the pathways that transport C between them. Without human activities, C is transferred at a natural rate in the form of CO_2 among the atmosphere, the oceans, the terrestrial biosphere, and the lithosphere (Heimann 1993; Cannell 1995).

The atmosphere contains about 750 Gt C. Approximately 120 Gt C is fixed each year by land vegetation (13%) as gross primary production, and about 60 Gt C year^{-1} is returned to the atmosphere by autotrophic respiration (Cannell 1995; Jobbagy and Jackson 2000; IPCC 2006, 2007). The other 60 Gt C (the net primary production) passes to the soil and detritus pools, which, in a steady state, release 60 Gt C year^{-1} back to the atmosphere. However, the land seems to be a net sink, sequestering an amount that is less than 2% (about 1.7 Gt C year^{-1}) of the 100 Gt C that it exchanges with the atmosphere annually (Cannell 1995; Jobbagy and Jackson 2000; IPCC 2006). The oceans contain a massive reservoir of C, 1020 Gt C in surface waters and 38 100 Gt C in deeper waters. They exchange about 90 Gt C each year (12%) and sequester about 2 Gt C (0.4 Gt C is added to the surface waters and 1.6 Gt C added to deeper waters) each year, mostly as dissolved inorganic C (Cannell 1995).

Increase of atmospheric CO_2 concentration

Human alteration of the earth system is substantial and growing, and the carbon cycle is undergoing considerable shifts due to anthropogenic stresses. The industrial revolution (Dixon et al. 1994) as a result of human activities changed the transfer rates of CO_2 (Houghton et al. 1990; Hasselmann 1997; Pendall et al. 2004; Demirbas 2007). Mean global concentration of atmospheric CO_2 has increased significantly since pre-industrial time, from about 280 ppm circa 1750 to about 350 ppm in 1980s (Barnola et al. 1987; Lashof and Tirpak 1990), and to 364 ppm by 1997 (Malhi et al. 1999), and to nearly 380 ppm in 2005, 40% above the pre-industrial levels of our current warm period (IPCC 2007). Atmospheric CO_2 concentration has increased globally by nearly 30% and temperature by approximately 0.6 °C, and these trends are projected to accelerate (e.g., IPCC 2001; Karl and Trenberth 2003; Murphy et al. 2004; Stainforth et al. 2005), particularly with more extreme climatic conditions (Cook et al. 2004; Meehl and Tebaldi 2004; Stott et al. 2004). Fossil fuel and cement emissions rose from 5.4 ± 0.3 Pg C year^{-1} in the 1980s to 6.4 ± 0.4 Pg C year^{-1} (cement production accounts for only 2% of this total) in the 1990s (Malhi et al. 2002; Marland et al. 2006). They have continued to increase between the 1990s and 2000 to 2005, climbing to 7.2 ± 0.3 Gt C year^{-1} . These numbers are estimated based upon international energy statistics for the 1980 to 2003 period (Marland et al. 2006) with extrapolated trends for 2004 to 2005 (IPCC 2007). Moreover, this increase is expected to continue and

the CO_2 concentration is predicted to reach between 500 and 800 ppm by the year 2050 (Idso 1989; IPCC 2007). The rate of increase in atmospheric CO_2 concentration during the past century is an order of magnitude greater than the world experienced over the last 20 000 years (Prentice et al. 2001). The IPCC (2001) projects that every 3 Pg of C emission will result in 1 ppm increase in atmospheric CO_2 concentration and a 0.01 °C in the global mean temperatures. By 2100 a global temperature increase of up to 5.5 °C would be expected (Malhi et al. 2002) based on a hierarchy of models, ranging from atmosphere–ocean general circulation models (AOGCMs) and earth system models of intermediate complexity (EMICs) to simple climate models (SCMs) (IPCC 2007).

The role of forest ecosystems in carbon cycle

Forest ecosystems are the largest terrestrial ecosystem (4.1 billion ha) (Brown et al. 2002; Dixon et al. 1994) and are critical in reducing the rate of CO_2 build-up in the atmosphere that is responsible for climate change (Streck and Scholz 2006). Forests account for 80%–90% of the total global C reservoir in living biomass (Dixon et al. 1994), cover 30%–40% of the vegetated area of the earth (Waring and Running 1998), and exchange C with the atmosphere through photosynthesis and respiration (Landsberg and Gower 1997; Malhi et al. 1999; Hiroshima 2004) thus playing an important role in the global C cycle. The controlling regional and global C pools and fluxes have been studied in detail (Brown and Lugo 1984; Grieron et al. 1992; Dixon et al. 1994; Vogt et al. 1986, 1998; Cairns et al. 1997). Forest ecosystems accumulate C through the photosynthetic assimilation of atmospheric CO_2 and the subsequent storage in the form of biomass (trunks, branches, foliage, roots, etc.) (Brown et al. 1996; Malhi et al. 2002; Houghton 2005), necromass (including litter, woody debris, soil organic matter) and forest products (Malhi et al. 2002), and organic C in the soil (Houghton 2005).

Carbon balance in a forest ecosystem

The C balance of a forest ecosystem (net ecosystem production (NEP)) is the net result of C acquisition through photosynthesis and C losses through autotrophic and heterotrophic respiration (Landsberg and Gower 1997; Malhi et al. 1999). In other words, whether a forest ecosystem is a C sink or source depends on the balance of photosynthetic uptake and respiratory release of CO_2 (Landsberg and Gower 1997; Malhi et al. 1999; Janisch and Harmon 2002). Total C assimilation of a forest by photosynthesis, ignoring photorespiration, is termed the gross primary production (GPP). The difference between GPP and autotrophic respiration is defined as net primary production (NPP).

The NEP is an important indicator for estimating C sink or source in terrestrial ecosystems and is influenced by land-use and management through a variety of anthropogenic actions such as deforestation, afforestation, fertilization, irrigation, harvest, and species choice (IPCC 2005). Disturbances (e.g., harvesting, conversion to non-forest uses, wildfires, etc.), can convert a forest from a sink to a source for atmospheric C when NEP and net biome produc-

tion (NBP) become negative (Janisch and Harmon 2002). On the other hand, an area can become a C sink if the forest is allowed to regenerate after a disturbance when NEP and NBP become positive (Brown et al. 1996). In recent years (1980–1996), Canada's forests have been estimated to be moderate sinks of 5–25 Pg C year⁻¹, as a result of a balance between the negative effects of increased disturbance (e.g., fire and deforestation) and positive effects of nondisturbance factors (e.g., forestation and forest conservation) (Chen et al. 2000).

At a global scale 44% of the world's forest are exploited for timber production (Misson et al. 2005), although only 10% of the world's forests are considered actively managed for goods and services (Winjum et al. 1992). Temperate and boreal forests are C sinks largely because both natural and human disturbances are managed or controlled (Dixon et al. 1994; Pacala et al. 2001; Albani et al. 2006). Previous studies estimated that the world forest is currently a C source, mainly because of the deforestation and forest degradation in the tropics (Brown et al. 1996; Houghton 1996). However, carbon stocks of tropical forests are also highly uncertain (Eva et al. 2003; Fearnside and Laurance 2003; Houghton 2005), so the range of possible emissions of carbon from tropical deforestation and degradation is much broader than commonly thought (Houghton 2005).

In recent years, a number of research reviews have identified the need for additional detailed study of C flux in managed forests (e.g., Chen et al. 2004) because of their widespread distribution in terrestrial ecosystems. There is a consensus that afforestation and reforestation should be a useful means by which C could be stored in the various components of a forested ecosystem (Brown et al. 1996; Richter et al. 1999; King 2005). The long-term net carbon flux between terrestrial ecosystems and the atmosphere has been dominated by changes in the area of forests and changes in forest biomass per hectare resulting from management and regrowth (Houghton 2005).

C allocation in forest soils

The belowground compartments are an important determinant of the capacity of forests to store carbon (Nakane et al. 1996; Valentini et al. 2000; Lee et al. 2005). Globally, soil contains about 1580 Gt C, two times as much C as is stored in the atmosphere (790–930 Gt C) and three times as much C as in terrestrial vegetation (610 Gt C) (Dixon et al. 1994; Sedjo 1992; Schlesinger 1997; IPCC 2007), accounting for 75% of the total terrestrial C in the world (Dixon et al. 1994; Henderson 1995; Schlesinger and Andrews 2000).

Soil C is the largest active terrestrial C pool, and contributes an annual CO₂ flux to the atmosphere 10–11 times greater than that from fossil fuel combustion (Schlesinger 1997; Marland et al. 2001), so small changes in soil system may cause huge impacts on the global C cycle. Understanding the processes of controlling soil CO₂ efflux (FCO₂) is thus critical for understanding and predicting atmospheric CO₂ concentrations and the global carbon (C) cycle (Oechel et al. 1993; Brooks et al. 1997; Fahnestock et al. 1998).

Soil CO₂ efflux

The evolution of CO₂ from the soils is the second largest

flux in the C budget of forest ecosystems (Gower et al. 1996) and is therefore one of the key components in the C cycle at regional and global scales (Raich and Schlesinger 1992; Gower et al. 1996). It amounts to 60%–90% of total ecosystem respiration (Goulden et al. 1996; Schlesinger and Andrews 2000; Davidson et al. 2006) and is a major portion of the global C cycle (Raich and Schlesinger 1992; Schlesinger 1997; Marland et al. 2001). Therefore, even a small impact on soil, the soil FCO₂ could have profound effects on changes in atmospheric CO₂ concentration (Andrews et al. 1999).

Soil FCO₂ is defined as the total CO₂ efflux from the soil–litter surface and is comprised of root respiration (RR) (or autotrophic respiration) and microbial respiration (or heterotrophic respiration), including microbial decomposition of soil organic matter (SOM) derived from dead roots, root exudates and mycorrhizal hyphae (lumped here as “root litter C decomposition”), and microbial decomposition of aboveground litterfall and woody litter (Edwards et al. 1970; Ewel et al. 1987; Coleman and Crossley 1996; Lavigne et al. 1997; Vose et al. 1997; Hanson et al. 2000; Davidson et al. 2000, 2006; Butnor et al. 2003; Bond-Lamberty et al. 2004). In summary, soil FCO₂ is the process of CO₂ release by soil microorganisms and plant roots (Davidson et al. 2006), because there are so many sources contributing to soil FCO₂, it is a sensitive indicator of metabolic activity of the soil and the rate of conversion of SOM to CO₂ (Rochette et al. 1997). Ecosystems with high levels of primary and secondary productivity can be expected to have high soil FCO₂ rates (Knapp et al. 1998).

Root respiration (RR) is the respiration by roots to obtain energy for maintenance of metabolism and concentration gradients in cells (maintenance respiration), growth, and active uptake of nutrients (George et al. 2003), which represents a significant CO₂ efflux by autotrophic organisms in soil (Paul and Clark 1996). Root production and respiration can consume large portions of NPP in forest ecosystems (Grier et al. 1981; Keyes and Grier 1981; Vogt et al. 1986; Bowden et al. 1993; Hendrick and Pregitzer 1993; Schimel et al. 1994). Interest in RR is increasing, as many quantitative estimates have suggested that it represents a large component of the annual carbon balance of forest ecosystems (Lee et al. 2005). Any factor that alters the amount or physiological activity of tree roots will also likely have a large impact on soil FCO₂ (Boone et al. 1998; Pregitzer et al. 1998; Hanson et al. 2000).

Microbial respiration (MR) is the respiration by heterotrophic microorganisms decomposing organic substances (Horwath et al. 1994). Microbial respiration clearly belongs to respiration by heterotrophs. We do not consider here the contribution of soil macro- and mesofauna involved in predator–prey interactions with rhizosphere microorganisms, since their direct contribution to the FCO₂ is negligible (Paul and Clark 1996; Kuzyakov and Larionova 2005).

Partitioning the components of soil CO₂ efflux

Many previous studies have estimated the contribution of RR to total soil respiration (SR) in forest soils (Coleman 1973; Edwards 1991; Bowden et al. 1993; Nakane et al. 1996; Thierron and Laudelout 1996; Hanson et al. 2000; Ohashi et al. 1999; Lee and Shibu 2003), though outstanding

methodological issues remain. The contribution of RR to total SR varies widely, ranging from 27% to 71% (Lee et al. 2005), or 10% to 90% (Hanson et al. 2000). Root respiration commonly accounts for approximately 50%–70% of total soil FCO₂ in temperate forest ecosystems (Nakane et al. 1996; Pregitzer et al. 1998; Ohashi et al. 1999; Högborg et al. 2001; Lee et al. 2005). Partitioning SR is difficult and various methods have been applied to this problem over many decades as reviewed by Hanson et al. (2000), and recent studies reflect a continuing evolution of methodologies (Andrews et al. 1999; Bond-Lamberty et al. 2004; Jiang et al. 2005; Chen et al. 2006; Schuur and Trumbore 2006; Trumbore et al. 2006). Trenching is a widely used approach that has been used to isolate blocks of soil without living roots within forest stands (Ewel et al. 1987; Bowden et al. 1993). However, the impact of soil disturbance and enhanced decomposition from freshly killed roots may increase FCO₂ compared with control plots (Schuur and Trumbore 2006). Disturbance effects are also a concern with methods that directly measure respiration from excavated roots (Palta and Nobel 1989; Qi et al. 1994; Burton et al. 1996) and other components of soil (Kelting et al. 1998).

Direct methods for determination of RR, subdivided into component integration, root exclusion and isotope techniques, are reviewed by Hanson et al. (2000). A major problem with direct measurement methods to distinguish RR and MR is that RR is only measured *in vitro*, and removal and separation of soil components reflects significant soil disturbance particularly of the root–soil interface, altering the soil atmosphere, and separating roots from most of their associated microbial community (Trumbore et al. 2006). The indirect determination of root respiration by regression analysis is non-invasive, and can give a good match to direct measurements in well-characterized systems (Rodeghiero and Cescatti 2006). Regression and statistical methods also provide a significant step forward in the development of this analysis by accounting for spatial heterogeneity and temporal variations in FCO₂ (Hanson et al. 2000).

Factors influencing soil CO₂ efflux

Soil FCO₂ can be affected by many biotic and abiotic factors at different spatial and temporal scales; however, at short time scales variation in soil FCO₂ is mainly driven by soil temperature and moisture (Edwards 1975; Singh and Gupta 1977; Schleser 1982; Schlentner and Van Cleve 1985; Jenkinson et al. 1991; Raich and Schlesinger 1992; Hanson et al. 1993; Huc et al. 1994; Peterjohn et al. 1993; Luo et al. 1996; Trumbore et al. 1996; Keith et al. 1997; Billings et al. 1998; Rustad et al. 2000; Euskirchen et al. 2003; Ma et al. 2004; Tang et al. 2005). The critical factors controlling soil FCO₂ in forest ecosystems are fine root production (Chen et al. 2003, 2004), microbial activity (Chen et al. 2006; Mariani et al. 2006), SOM (Ewel et al. 1987), soil pH (Raich and Schlesinger 1992; Tang et al. 2005), soil type, nutrient availability, phenology, and vegetative cover type (Singh and Gupta 1977). Many other additional factors, such as aboveground productivity (Craine et al. 1998), substrate supply (Gardenas 2000; Janssens et al. 2001; Luo et al. 2001), and fire (Knapp et al. 1998) can regulate respiration as well. It is highly likely that forest management practices have significant effects to involve those of the control

factors, therefore significantly affect soil FCO₂ (Toland and Zak 1994).

Forest root systems

Roots are a key component of the belowground system, and they are a main source of SOM and influence soil microbial activity and decomposition processes (Cheng 1999; Janssens et al. 2002). On a mass basis, coarse roots contribute more to total ecosystem biomass than fine roots, and when establishing C budgets and C allocation at an ecosystem level, coarse root biomass and production data should be collected (Vogt et al. 1998). However, coarse roots account for only a small portion of annual root production (Grier et al. 1981). In contrast, fine roots have a high turnover rate despite the fact that they account for only a small fraction of total root biomass (Chen et al. 2004). Due to their high metabolic activity, fine root production and turnover plays a critical role in forest C dynamics.

Fine roots are an important structural and functional component of forested ecosystems (Grier et al. 1981), representing an important C input to the soil and can equal or exceed aboveground detritus production in some systems (Grier et al. 1981; Fogel 1983; Vogt 1991). A large proportion of forest production is allocated to fine roots, resulting in a large C flux into the belowground system (Kurz et al. 1996). For example, increased fine root biomass was accompanied by an increase in soil FCO₂ of 27%–30% in young stands of trembling aspen and paper birch (King et al. 2001). The definition of fine roots has varied among different studies. For instance, Chen et al. (2004) defined all roots <5 mm to be fine roots. However, most other studies have considered the diameter of fine roots to be less than 2 mm (Vogt and Persson 1991; Hendrick and Pregitzer 1992, 1993) or (less commonly) 1 mm (Fahey and Hughes 1994; Burton et al. 1997; Zogg et al. 1996).

Fine root turnover is defined as the ratio of the total amount of fine roots produced in 1 year over the mean living biomass of roots (Aber et al. 1985) or annual fine root production divided by total root biomass (Gill and Jackson 2000). Fine root turnover is a critical component of ecosystem C balance and nutrient cycling, representing a large and dynamic portion of belowground biomass and nutrient capital in forest ecosystems, and accounting for a significant fraction of NPP (Persson 1978; Vogt et al. 1986; Vogt 1991). Carbon input from fine roots to soil can equal or exceed aboveground detritus production (Grier et al. 1981), making it one of the main pathways to soil C cycle (Vogt 1991). Janssens et al. (2002) estimated that fine root turnover released C with 400 g C m⁻² year⁻¹ (0.9 m depth) in a 70-year-old Scots pine (*Pinus sylvestris* L.) forest in the Belgian Campine region. The turnover rate was 0.8 year⁻¹ for roots < 1 mm and 0.3 year⁻¹ for roots 1–2 mm, and the total C cost involved in fine root turnover was estimated between 170 and 240 g C m⁻² year⁻¹ (Janssens et al. 2002).

Fine root production and turnover is thus a very important determinant of soil FCO₂ and the global C cycle. Although researchers have studied for fine root production and turnover in some detail, the influence of forest management (e.g., fertilization, thinning, harvesting, soil amendments etc.) and carbon sequestration on fine root production and

turnover associated with either MR or soil FCO₂ has received relatively little attention.

Forest management and carbon sequestration

As atmospheric CO₂ concentrations continue to rise, it is important to identify and encourage management strategies that promote terrestrial C sequestration (Concilio et al. 2005). Global environmental change may lead to higher NPP; however, the C stock of an entire forest ecosystem may actually decrease (Pussinen et al. 2002). This is mainly due to warmer temperatures that greatly stimulate the decomposition of SOM (Raich and Schlesinger 1992; Kirschbaum 1995; Lloyd and Taylor 1994), and also result in increased nutrient availability (Melillo et al. 1993). Forest productivity will be greatly altered due to these changes, and may have a strong influence on the optimal rotation length and economic profitability of forestry as well, which in turn have considerable repercussions to forest C sequestration (Pussinen et al. 2002). Forest management can make substantial contributions to attempts to reduce the amount of CO₂ in the atmosphere via the accumulation and storage of C in biomass, soil and wood products (Eriksson 2006), and potentially through reduced C release from soil (Brown et al. 1996; Jandl et al. 2007).

Forest management influences C sequestration and C stocks in forest biomass, soil, and wood products (Houghton 1996; Kaipainen et al. 2004). In the framework of the Kyoto Protocol, countries can decide to credit managed forests as C sink or source according to Article 3.4 (UNFCCC 1997). Thus, forest management practices can be an effective means for reducing net emissions and mitigating CO₂ concentration in the atmosphere, and have been given greater prominence with the adoption of the Kyoto Protocol (UNFCCC 1997). Currently there is a strong demand for an optimum strategy to maximize the carbon sequestration of forests, to describe the role of management practices, and to quantify the duration of carbon sinks (Schmid et al. 2006).

In general, forest management practices to conserve and sequester C can be grouped into four major categories: (i) maintaining existing C pools (e.g., slowing deforestation and forest degradation), (ii) expanding existing C sinks and pools (e.g., increasing C density by modifying forest structure, growth, and belowground processes), (iii) creating new C sinks and pools by expanding tree and forest cover (afforestation), and (iv) substituting renewable wood-based fuel for fossil fuels (Dixon et al. 1994). Forestry activities that can alter C stocks include: forest soil fertilization, other soil amendments (such as liming), harvesting, pest management, forest fuel and fire management, forest thinning, harvest quantity and timing, low-impact harvesting, reductions in forest degradation, and forest regeneration (Brian et al. 2000). Forest management has been demonstrated to decrease the time required for stands to shift from a C source to a C sink (Maier and Kress 2000; Lai et al. 2002; Maier et al. 2004; Sampson et al. 2006). Additionally, forest practices affect soil FCO₂ and MR by influencing NPP and SR process (Tyree et al. 2006). The largest impact on NEP comes from increased productivity; however, an additional benefit of forest management may be a reduction in C evolution

from forest soils (Tyree et al. 2006). Widely used forest management options that presently offer high economic returns are thinning and the addition of nitrogen fertilizers (Bengtson 1979; O'Hara 2002). The specific implementation of these practices, however, varies greatly within and among both private and public forest lands (Thomas et al. 1999). A detailed understanding of the effects of silvicultural thinning and fertilization on soil FCO₂ is thus essential to manage forests effectively for sustained production of wood products and enhance C enhancing sequestration.

Soil FCO₂ can be varied with forest productivity in different ecosystems (Knapp et al. 1998) and silvicultural treatments. Forest management activities have different effects on soil FCO₂ and C sequestration (Johnson 1992; Post and Kwon 2000; Johnson and Curtis 2001). The influences of forest management practices, such as thinning, harvesting, and fertilization on soil C dynamics are explained by specific site and soil conditions (Jandl et al. 2007). However, little is known about the effects of forest management on C sequestration from the perspective of soil processes. There is an increasing need to understand the mechanisms by which forest management affects soil processes, to scrutinize forest management strategies with respect to their influences on soil C pools, and to recommend management activities that can lead to long-term C sequestration in forest soils (Jandl et al. 2007).

Effects of forest harvesting and thinning on soil carbon and soil CO₂ efflux

Forest harvesting commonly results in significant changes in aboveground C stocks and fluxes in forest ecosystems (Law et al. 2006; Wang et al. 2003), but its effects on soil C is less well understood (Sun et al. 2004). Individual studies comparing soil CO₂ efflux in cut block effects on soil FCO₂ in mature forest have found conflicting results. It has been suggested that tree harvesting reduces soil FCO₂ (Edwards and Ross-Todd 1983; Weber 1990; Chang and Trofy-mow 1996; Striegl and Wickland 1998), but others demonstrate an increase in soil FCO₂ (Ewel et al. 1987; Lytle and Cronan 1998), and some studies have indicated that forest harvesting may have no effect on soil FCO₂ (Fernandez et al. 1993; Toland and Zak 1994; Johnson and Curtis 2001). The important factors contributing to this variation are likely due to differences in the length of time following harvest, and variation in composition of tree species and stand ages among studies. Rannik et al. (2002) found that a 5 year-old clearcut site was a substantial C source, while a 38-year-old Scots pine forest was a net C sink of CO₂. Selective harvests that increased soil FCO₂ by 43% and 14% in a mixed-conifer forest and a hardwood forest were also reported (Concilio et al. 2005).

Forest harvesting is expected to cause changes in root density and production, insolation, litter-fall input, and soil microbial activity, and hence should result in predictable changes in soil FCO₂ (Peng and Thomas 2006). Yanai et al. (2003) demonstrated that the short- and long-term effects of harvesting on soil C can be quite complex either decreasing C by enhancing soil FCO₂ or increasing C by enhancing inputs of detritus. Several studies showed an initial decrease in soil FCO₂ immediately after clear-cutting, followed by an increase to soil FCO₂ values similar to those in mature

stands (Weber 1990; Striegl and Wickland 2001). However, the time that it took for soil FCO₂ to return to the pre-harvest level varied with studies: two years for aspen stands (Weber 1990) and eight years for jack pine forest (Striegl and Wickland 2001). In British Columbia, it is assumed that cut blocks remain a CO₂ source for at least 10 years after harvest (Kurz and Apps 1994). Butnor et al. (2006) found that whole-tree and forest floor removal from a 10-year-old loblolly pine (*Pinus taeda* L.) plantation had no effect on forest floor FCO₂ for 10 years after harvest in eastern North Carolina. Among published studies of harvesting impacts on soil FCO₂, almost all studies deal with the effects of soil FCO₂ in response to clear-cutting. Only a few studies have examined selection harvesting or thinning effects (e.g., Laporte et al. 2003; Ohashi et al. 1999; Son et al. 2004; Tang et al. 2005), on soil FCO₂, and very little information is available on the spatial and temporal patterns of soil FCO₂ in response to harvesting.

Among silvicultural practices, thinning is one of the most common treatments applied by foresters to produce wood for commercial purposes, while decreasing competition between the remaining trees (Misson et al. 2005). Forest thinning, defined as the partial removal of trees from an even-aged plantation, is an important silvicultural practice (Tang et al. 2005). Thinning decreases stand density and leaf area, increases light and nutrient availability, and changes soil temperature, soil water, belowground root density and the microbial community, and can improve the remaining tree productivity, reduce the wildfire risk and maintain a healthy forest (Tang et al. 2005). The impact of thinning on tree growth has been widely studied (e.g., Assmann 1970; Breda et al. 1995; Misson et al. 2003), a few studies provide results on the effects of different thinning strategies on above-ground NPP (Coops 1999; Mitchell et al. 1996; Mund et al. 2002), or C accumulation in the forest floor (Vesterdal et al. 1995), or soil (Sievänen et al. 2002).

Several studies have examined thinning impacts on soil FCO₂ in conifer stands (e.g., Ohashi et al. 1999; Ma et al. 2004; Son et al. 2004; Tang et al. 2005; Concilio et al. 2005, 2006; Misson et al. 2005), but these studies have not directly examined the time-course of the response. Among these studies, soil FCO₂ responses to thinning vary considerably. For instance, in some studies thinning increased soil FCO₂ (Ohashi et al. 1999; Concilio et al. 2005, 2006). Soil FCO₂ in thinned Japanese cedar forest was 2.57–3.06 Kg C m⁻² year⁻¹ while it was 1.83–2.17 Kg C m⁻² year⁻¹ in unthinned stands (Ohashi et al. 1999). However, no difference in FCO₂ between thinned and unthinned was found by Ma et al. (2004), and thinning decreased soil FCO₂ by 13% in a study by Tang et al. (2005).

Comparisons of soil FCO₂ responses between thinning and control areas may provide insights into the relative role of RR (Brumme 1995; Hanson et al. 2000). It is likely that thinning can both enhance and inhibit root and microbial respiration, and may directly reduce living root biomass (and root respiration) by removing trees and other vegetation. However, thinning also reduces competition for soil moisture and nutrients, which may stimulate growth in the surviving trees resulting in increased living root activity (Ma et al. 2004). Although total RR may decrease after thin-

ning, the rate of RR from the remaining trees may increase as a result of increases in photosynthetic rate and growth of new roots and reduced competition (Tang et al. 2005).

Forest fertilization and soil CO₂ efflux

Fertilization has been widely used as an effective practice to enhance forest productivity, improve health of trees, accelerate nutrient availability, and regulate nutrient balance in forest soils (Allen et al. 1990; Fisher and Binkley 2000; Fox 2000), and has been suggested as a method to enhance the total amount of C stored both above and belowground (Valentini et al. 2000). It is recognized that fertilization can affect the ability of forest ecosystems to sequester C (e.g., Keith et al. 1997; Maier and Kress 2000; Samuelson et al. 2004; Olsson et al. 2005). Because fertilization directly alters biological and chemical processes in soils, root production and SOM turnover rates, it therefore also affects soil processes such as respiration, microbial activity, and soil pH (Lee and Shibu 2003).

A critical ecological question in forest management is whether fertilization, which generally increases yield, results in enhanced C sequestration over short rotations (Sampson et al. 2006). Improved soil nutrient availability leads to increases in leaf area index (LAI) and yield; therefore, on nutrient-poor sites optimum fertilization treatments can increase annual stem volume increment by 10 m³ ha⁻¹ (Albaugh et al. 1998) or more (Jokela and Martin 2000; Borders et al. 2004).

Forest fertilization studies examining belowground C dynamics (soil FCO₂, RR, and MR) have yielded conflicting results. For example, application of N fertilization can result in an increase in soil FCO₂ (Fisk and Fahey 2001; Pries and Folster 2001), a decrease in soil FCO₂ (Haynes and Gower 1995; Maier and Kress 2000; Butnor et al. 2003; Lee and Shibu 2003; Bowden et al. 2004; Olsson et al. 2005), or unchanged soil FCO₂ (Smolander et al. 1994; Vose et al. 1997; Fernandes et al. 2002). Nitrogen fertilization in mature forests generally reduces root and mycorrhizal growth or respiration, or both (Haynes and Gower 1995). It is likely the effects of improved soil fertility on FCO₂ and fine root production are dependent on the stage of development of the forest system (Johnsen et al. 2001). As trees mature, fertilization favours carbon allocation above-ground at the expense of fine root production and the ratio of fine root-to-above-ground biomass decreases (Haynes and Gower 1995). Therefore, more data and comprehensive research on soil FCO₂ from various forest ecosystems are required for assessing and predicting soil FCO₂ and its responses to the management practises, including the application of fertilizers.

Although it has been demonstrated that soil mineral nutrient additions generally decrease MR in the short term (Kowalenko et al. 1978; Söderström et al. 1983; Smolander et al. 1994; Lovell and Hatch 1997; Thirukkumaran and Parkinson 2000), and cause reductions in RR (Haynes and Gower 1995; Butnor et al. 2003), several studies have reported no fertilization effect on soil FCO₂ (Castro et al. 1994; Vose et al. 1995; Maier and Kress 2000). In addition, RR frequently increases in response to fertilization (Zogg et al. 1996; Griffin et al. 1997; Lu et al. 1998), and increases in belowground biomass associated with fertilization (Al-

baugh et al. 1998; Johnsen et al. 2001) have been demonstrated. Increased belowground C allocation under nutrient stress and (or) water stress has been commonly reported, especially in seedlings (Cromer and Jarvis 1990; Lee and Shibu 2003). The heterogeneity of results among the studies is likely attributable to varying experimental designs, forest types, fertilizer quantity and dosages, and forest ages. In general, fertilization will increase belowground biomass production for young trees and seedlings. As trees mature, fertilization favours C allocation above ground, and the ratio of fine root to aboveground biomass declines (Haynes and Gower 1995). Differences in tree age are thus likely critical in understanding variability among studies. The responses of tree to fertilization in terms of productivity also likely vary among species.

Many studies have been conducted to seek the effects of nitrogen (N) additions on soil FCO₂, fine root production and MR. However, very few studies address the influence of non-nitrogen additions on soil FCO₂ in forest ecosystems. Recently, human activities have caused substantial alternation of the global N cycle through the industrial development, agriculture practises and land-use changes, and result in high accumulation of N in some regions (Galloway et al. 1995; Vitousek et al. 1997). Thus, the response of ecosystem processes in systems that are approaching N saturation is an increasingly important issue. In particular, the influence of phosphorus (P) and Potassium (K) additions to N saturated soil on belowground C dynamics including soil FCO₂, fine root production, and microbial respiration are still unclear.

Soil acidification and liming effects on soil processes

Soil acidification and degradation problems may arise from the air emissions originating from industrial facilities such as thermal power plants, petroleum refineries, and petrochemical industries and have become a serious environmental concern (Unlu et al. 1999). Increased soil acidity is generally linked with a decrease of SOM decomposition (Alexander 1980; Jenkinson 1981), although the extent of the decrease varies with the nature of the organic materials (Abrahamsen et al. 1977; Baath et al. 1980). Forest productivity is thought to have declined in response to acid precipitation over extensive areas of Europe and eastern North America (Chen et al. 2000). Many researchers have concentrated on the effects of atmospheric acidic deposition inputs on soils and their roles in forest decline (Schulze 1989), which has been a significant economic and environmental problem in Europe (Carreira et al. 2000). Forest damage is frequently associated with acute nutritional imbalances (Tomlinson 1990), often caused by base cations (Mg and K) leaching from the soil (Ulrich et al. 1980; Van Breemen et al. 1983) and induced cation deficiencies (van Dijk and Roelofs 1988; Kazda 1990). The induction of P deficiency has also been proposed as a possible effect of acidic deposition (Foy et al. 1978), resulting in N saturation caused by acidic deposition from air (Binkley et al. 1989; Carreira et al. 2000; Chen et al. 2000). A limited number of reports have indicated that pollutant inputs are inducing P deficiency in forest trees, at least in some sensitive areas both in North America (Paré and Bernier 1989; Gradowski and Thomas 2006) and in Europe (Mohren et al. 1986; van Dijk and Roelofs 1988; Houdijk and Roelofs 1993). Phosphorus defi-

ciency is known to be a key limiting factor in forest production across Europe (Harrison 1989). However, little research has been carried out on changes in soil P cycling induced by acidic precipitation inputs and resulting effects of the imbalance between N and P nutrition on tree growth (Carreira et al. 2000).

Liming is a common soil amendment used in forest management to improve quality of acid soils by increasing soil pH (Schierl and Kreutzer 1991; Mohamed 1993; Driscoll et al. 1996; Smallidge and Leopold 1997; Saarsalmi and Malkonen 2001; Nohrstedt 2002; Timmer et al. 2003), soil cation exchange capacity (Houle et al. 2002), and nutrient availability (Fuentes et al. 2006). Liming has been used to counteract acidification and re-supply the soil with magnesium and calcium (Ca) (Phillips et al. 1988; Rehfuss et al. 1991; Kreutzer 1995; Ingerslev 1997; Timmer et al. 2003). Liming increases soil pH and thereby affects the activity and composition of microbial populations (Tate 2000), enhancing nitrification and subsequent nitrate leaching (Belkacem and Nys 1995; De Boer et al. 1993; Smolander et al. 1994). Liming can also enhance the deprotonation of organic substances and, as a result, the bonding between organic compounds and soil particles decreases, and make organic substances more available for microbial consumption (Curtin et al. 1998). Increased bioavailability of carbon under increasing pH has been considered a destabilization process where SOM becomes less resistant to degradation and more accessible to microorganisms and soil enzymes (Sollins et al. 1996); increased rates of infiltration and induced nitrate leaching may also be important (Smolander et al. 1994; Belkacem and Nys 1995). Liming also has a strong effect on the structure and function of soil biota (Kreutzer 1995; Wallander et al. 1997; Zelles et al. 1990). Liming results in increased microbial biomass and N immobilization (Adams and Cornforth 1973; Popovic et al. 1988; Fuentes et al. 2006) as well as N mineralization by the release of labile organic matter in the form of dissolved organic compounds (Curtin et al. 1998). For improving nutrient availability in soil, slow-release minerals such as apatite and biotite, are promising alternatives to liming and to traditional fast-release P, K, and Mg salts (Aarnio et al. 1995; Hartmann et al. 1999; Mälkönen et al. 1999, 2000; Martikainen et al. 1989).

Liming has been found by many workers to increase soil FCO₂ by indirectly improving soil nutrient availability, especially in the short term (Halstead et al. 1963; Saloniemi 1972; Nommik 1978). Liming has been shown to reduce volume growth in some conifer stands (Derome and Pätilä 1989), but to improve foliar nutrient status, crown vigor, and growth (Moore et al. 2000; Timmer et al. 2003) in other species, including sugar maple (Timmer et al. 2003; Gradowski 2006). In spite of its widespread application, particularly as a means of ameliorating acidic deposition, liming effects on forest C sequestration and soil FCO₂ have received little attention.

Effects of litterfall removal on soil CO₂ efflux

Litterfall and decomposition represent the major pathway for the transfer of nutrients between plants and the soil (Swift et al. 1979; Vitousek and Sanford 1986), and it is widely believed that the release of nutrients from decaying

plant matter is critical for the maintenance of ecosystem production (Jordan 1985; Cuevas and Medina 1986). The litter layer helps to maintain favourable conditions for decomposition by regulating the microclimate (e.g., Anderson and Swift 1983; Vasconcelos and Laurance 2005; Sayer 2006) and creating habitats for arthropods (David et al. 1991; Arpin et al. 1995). Litter removal and litter addition treatments in temperate forests not only caused substantial changes to the microclimate on the forest floor, but also affected the number of decomposer organisms, such as arthropods (David et al. 1991; Ponge et al. 1993; Arpin et al. 1995) and fungi (Tyler 1991; Cullings et al. 2003). Furthermore, changes in litterfall modify the amounts of available nutrients in the soil (Sayer 2006), which may also affect decomposition rates (Ostertag and Hobbie 1999; Hobbie and Vitousek 2000; Rothstein et al. 2004).

There are limited studies on the effects of litter removal or the combined impacts of thinning and litter removal on plant respiration and C allocation (e.g., Lavigne 1988a, 1988b, 1991). Previous studies have only concentrated on soil FCO₂ in response to thinning treatments in the absence of soil amendments or manipulations. However, thinning is commonly conducted in conjunction with soil amendments, and thinning operations and tree removal generally result in large disturbances to the litter layer.

Conclusions

Evidence has mounted that the global climate has been changing since the beginning of the industrial revolution (IPCC 1996). As the atmospheric CO₂ concentration continues to increase, forest management strategies should be developed to mitigate effects of rising greenhouse gas concentration and to alter the distribution of CO₂ at the atmosphere interface by using forest ecosystems to “pump” CO₂ out of the atmosphere and into storage in forests (Lee and Shibu 2003) via the increase in photosynthesis rate and the decrease in soil FCO₂ emission to the atmosphere. Studies on soil C have received much recent attention because a small impact on the soil may significantly affect the global C cycle and climate system. Soil FCO₂ may accelerate global warming by acting as a positive feedback in the global C cycle (Jenkinson et al. 1991; Kirschbaum 1995; Trumbore et al. 1996; Cox et al. 2000). Forest soil FCO₂ is the major avenue for C loss from the terrestrial pool and is considered the main determinant of C balance in forests in the northern hemisphere (Valentini et al. 2000). Moreover, forest ecosystems are subjected to natural and human disturbance or are manipulated and eventually harvested to gain timber and non-timber values (Oliver 1980). Therefore, studies examining patterns and mechanisms of soil FCO₂ in response to management practises considered possible means of enhancing forest C sequestration are necessary and important. Such studies are critical to accurately predict effects of forest management on the C cycle and to develop appropriate forest management strategies aimed at reducing atmospheric CO₂ concentrations.

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