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PLANT-SOIL INTERACTIONS DOMINATE SOIL MICROBIAL RESPIRATION AND SOIL ORGANIC CARBON SEQUESTRATION IN A SUBTROPICAL MOIST EVERGREEN BROADLEAVED FOREST IN CHINA

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DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Agriculture, Food and Environment
at the University of Kentucky

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2020

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ABSTRACT OF DISSERTATION

PLANT-SOIL INTERACTIONS DOMINATE SOIL MICROBIAL RESPIRATION AND SOIL ORGANIC CARBON SEQUESTRATION IN A SUBTROPICAL MOIST EVERGREEN BROADLEVED FOREST IN CHINA

Tropical forest soils contain one-third of global soil carbon (C). The warm and moist climate in tropical forests leads to rapid soil organic carbon (SOC) decomposition, with the highest soil microbial respiration rates in the world, so even a slight change in soil C and microbial respiration could affect atmospheric carbon dioxide concentration. However, there remains a lack of understanding of the mechanisms driving microbial respiration in tropical forests, due to different climate and biophysical drivers compared to temperate or boreal forests. Furthermore, forest conversions (from natural forests to plantations) are most widespread in tropical regions, leading to a loss of SOC during harvesting and reforestation processes. However, the magnitude and direction of SOC changes vary greatly. These uncertainties result in great variability in, and disagreement among, models predicting the response of SOC to future climate in tropical forests.

To quantify the contribution of recent photosynthesis and SOC decomposition to soil microbial respiration, I separated microbial respiration from total soil respiration using the trenching method with 150 μm pore size of nylon mesh sheets in a subtropical moist evergreen broadleaved (SMEB) forests. In addition, I excavated five 50 cm × 50 cm mineral soil columns from the forest and incubated them in the open. Measures of soil microbial respiration, soil temperature and moisture, and photosynthetically active radiation (PAR) were automated, recorded simultaneously every 30 minutes. Results demonstrated that current photosynthates contributed 88 % of C sources to soil microbial respiration, and soil temperature was not the controlling factor for Rm on the diel scale; rather, soil microbial respiration was strongly controlled by PAR. These results suggest the need for a new conceptual model of C cycling in SMEB forests, in contrast to most microbial respiration models based on temperature-dependent SOC decomposition in temperate forests.

The intensification of human activities in forest management have led to large SOC losses during the establishment of tree plantations from former natural forests. I quantified three major SOC loss pathways in the establishment of a Chinese fir plantation, demonstrating that converting of natural forest to Chinese fir plantation resulted in 28 % loss of SOC present prior to conversion 11 % through volatilization by slash burning, 10 % via soil erosion, and 7 % via increasing SOC mineralization. Forest conversion also altered the available C sources for soil microbes from newly formed carbohydrates in the natural forest to SOC in the plantation. Finally, I found SOC did not recover after 40 years. My results highlight that slash burning during forest conversion leads to a dramatic, and lasting, decline in SOC in SMEB forests during the establishment of tree plantations converted from former natural forest.

Although we have a good understanding of the mass loss rate and nutrient release of plant residues during decomposition, the role of incorporation of plant residues into SOC is still poorly understood and often neglects the influence of live roots on SOC sequestration. In this study, I examined changes in bulk and rhizosphere SOC across three developmental stages of Chinese fir plantation (6, 18, and 42 years old) with age-associated differences in net primary productivity (NPP). My results indicated that SOC concentration in bulk soils did not vary significantly with forest age, but SOC concentration in rhizosphere soils was higher in 6 yrs and 42 yrs stands, both of which had lower NPP. Both labile and recalcitrant C pools in rhizosphere soils were smallest in the 18 yrs stand, which had the highest NPP. Variation in rhizosphere SOC was correlated with soil phosphorus and microbial biomass carbon: nitrogen ratio (MBC:MBN), which drove labile and recalcitrant SOC dynamics in different ways depending on forest age. My results demonstrated that variability in forest productivity and nutrient demand with time are key factors controlling rhizosphere SOC sequestration and nutrient cycling.

Altogether, this work provides insights into the magnitude and pathways of SOC losses due to conversion of natural forest to tree plantation in SMEB forests, and its feedback to tree plantation development in a rotation. This study also highlights the dominance of photosynthates on soil microbial activity and SOC sequestration. The findings from these studies will improve our understanding of C cycling in tropical forests and reduce the uncertainty in modeling future C dynamics in tropical forests.

KEYWORDS: Subtropical forest, forest conversion, soil organic carbon, photosynthates, soil microbial respiration, rhizosphere.

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10/23/2020

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To my family

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The sharp rise in atmospheric carbon dioxide (CO_2) concentration over the last 150 years is causally linked to increasing temperature and accelerating global change. Soil respiration from terrestrial ecosystems is the second largest CO_2 flux to the atmosphere; even a slight change in the rate of soil respiration could considerably alter the concentration of atmospheric CO_2 (Schlesinger & Andrews, 2000; Bond-Lamberty & Thomson, 2010). Thus, it is essential to improve understanding of the factors controlling soil respiration (Bauer *et al.*, 2008). Soil respiration research has primarily focused on temperate and boreal forests, ecosystems in which soil microbial activity is largely controlled by temperature. The highest rates of soil respiration occur in tropical forests (Whitaker *et al.*, 2014; Bond-Lamberty *et al.*, 2018), yet we still have limited information on the factors that control it.

In contrast to temperate and boreal forests, tropical forests generally experience warm temperatures throughout the year, and a lack of temperature limitation on plant and soil microbial activities (Vitousek, 1982; Townsend *et al.*, 1992; Cusack *et al.*, 2010). Compared to the relatively deep organic horizons found in temperate and boreal forests, tropical forests are characterized by highly weathered soils with low soil organic carbon (SOC) and low substrate availability for soil microbial activity (Trumbore, 1993). Furthermore, high plant productivity and belowground carbon allocation, coupled with a longer growing season in tropical compared to temperate and boreal forests, provides two to four times greater input of fresh plant-derived C to support soil microbial activities (Raich & Schlesinger, 1992; Giardina & Ryan, 2000). In tropical forests, soil microorganisms are highly dependent on current plant-derived C, leading to tight

interactions between plants and soil microbes (Trumbore, 1997; Carbone & Trumbore, 2007; Giardina *et al.*, 2014). Despite these differences in the factors controlling soil microbial respiration, most models that predict soil microbial respiration focus on the response of SOC to temperature (Holland *et al.*, 2000; Dungait *et al.*, 2012). When applied to tropical forests, these models result in nearly three times the predictive uncertainty as that for temperate and boreal forests (Cavaleri *et al.*, 2015).

Tropical forests account for 55% of world forest C stocks, 32% of which is stored in the soil (van Straaten *et al.*, 2015; Don *et al.*, 2011). Due to the high, and increasing, demand for timber, bioenergy, and food, a large area of natural forests in the tropics has been converted into tree plantation, grassland, and farmland (Powers *et al.*, 2011). Deforestation in the tropics has contributed one-third of the past SOC losses over the last 150 years, the second largest C source to the atmosphere after fossil fuel emissions (Lugo *et al.*, 1986). Research from Africa, South America and Southeast Asia, from sites where natural forests have been converted to cropland, pasture, and tree cash crop plantations, suggests that the magnitude of SOC changes after tropical forest conversions is controlled by multiple factors, including precipitation, vegetation type, clay mineralogy, and time since conversion (Don *et al.*, 2011; Powers *et al.*, 2011; van Straaten *et al.*, 2015). Still lacking is research on SOC changes when natural forest is converted to tree plantation, which is the primary forest conversion practice in subtropical China (Sheng *et al.*, 2010; Chen *et al.*, 2016; Yang *et al.*, 2019). Furthermore, there are few studies in the tropics that have examined the dominant pathways of SOC losses after forest conversion (Yang *et al.*, 2005; Guillaume *et al.*, 2015). When the magnitude of SOC losses has been examined, the research has been conducted using 'space-for-time' substitution, a robust methodology for comparing the differences in SOC after forest conversion (Yang *et al.*,

2009; Don *et al.*, 2011; Guillaume *et al.*, 2018). However, few studies have elucidated the primary pathways of SOC losses that occur with forest conversions, resulting in high uncertainties in SOC losses after tropical forest conversions.

The establishment of fast-growing tree plantations throughout the world is championed as an efficient way to mitigate climate warming by increasing C sequestration in biomass and soil relative to that in natural forests (IPCC, 2007). Research has calculated that tree plantations could absorb two-thirds of CO_2 emissions from human activities, due to the high rate of biomass C accumulation during forest growth (Bastin *et al.*, 2019). China manages the largest area of tree plantations in the world, 69.33 million ha, and almost 65% of the area is currently made up of young and middle-aged plantations (Tang *et al.*, 2018). The magnitude of C accumulation in tree biomass during the growth of tree plantations in China is fairly well known (Chen *et al.*, 2013; Yang *et al.*, 2016). However, there is a paucity of information regarding the responses of SOC sequestration to the development of tree plantations, approximately 42 % of which are located in the subtropical region of China. As the primary C sources to soil, above- and below-ground plant inputs are largely controlled by tree plantation age, and they have differences in SOC sequestration efficiency between bulk and rhizosphere soils (Sokol *et al.*, 2019). In turn, the quantity and quality of plant C inputs stimulate microbial activity to decompose soil organic matter, providing nutrients for tree growth. However, the dynamic competition for nutrients between plants and soil microorganisms, which varies with NPP and forest age, affects microbial carbon use efficiency, thereby influencing SOC storage and composition (Raich & Schlesinger, 1992; Schlesinger & Andrews, 2000). These effects are especially pronounced in the rhizosphere, which is the primary zone for C and nutrient exchange (Phillips *et al.*, 2012). A better understanding of

rhizosphere SOC changes under stands with different rates of NPP, and the interactions between C inputs and SOC in the rhizosphere, will improve our ability to model C and nutrient dynamics in these plantation forests.

The subtropical moist evergreen broadleaved (SMEB) forest in eastern China is among the most biodiverse and productive of forest ecosystems globally (Song, 1988; Yang *et al.*, 2006; Yu *et al.*, 2014). This forest type is characterized as either temperate broadleaved rain forest or temperate broadleaved evergreen forest, and dominant tree species include *Castanopsis carlesii, Castanopsis eyrei, Cyclobalanopsis chungii and Schima superba* (Song, 1988; Wang *et al.*, 2007). It occurs between 21°−35° N and 99°−123° E, covering nearly 25 % of the land area of China. Due to the uplift of the Tibetan Plateau and prevalence of the East Asian monsoon, the climate and landscape in this region of China differs significantly from other regions in the same latitude, many of which are dominated by dry and hot desert. The mean annual temperature and annual precipitation in this region of China are 15−20 °C and 900−2000 mm, respectively. The SMEB in China differs from the Mediterranean and subtropical forests in the Southern hemisphere, which also occur at approximately the same latitudes. These differences in SMEB in China lead to higher forest net ecosystem productivity (NEP) and rate of soil microbial respiration than other tropical and temperate forests in Asia or other forest ecosystems at the same latitude (Sheng *et al.*, 2010; Yu *et al.*, 2014). The monsoon climate also leads to specific processes that affect soil microbial respiration (Ding *et al.*, 2018). Despite the uniqueness of these factors for soil microbial respiration and the large land area affected, there are only limited data on soil microbial respiration in this forest type.

Chinese fir (*Cunninghamia lanceolata*), an evergreen conifer that is native to East Asia, is insect and decay resistant and has been widely used in furniture and construction. In Southern China, Chinese fir is a crucial timber resource and plays an important role in the economy. The cultivated history of Chinese fir, which is widely planted in south China, Laos, Vietnam, and southern Japan, extends more than a thousand years since the first record of these plantations in a poem from the Tang Dynasty (Yang, 1998). Chinese fir plantations currently account for 19% of the total forest plantation area and 25 % of the timber volume in China (SFA, 2016). Chinese fir plantations are planted as monocultures converted from natural forests. Forest conversion typically involves intense human disturbances including clearcut harvest, slash burning, and site preparation. The large amount of harvest residues remaining on the soil surface is allowed to dry for several months and then burned, preparing the site for planting tree seedlings. This process of drying and burning results in considerable SOC loss through volatilization (Yang *et al.*, 2005). Because most forests across the south and east of China occupy mountainous and hilly areas that receive high amounts and intensity of precipitation, massive soil and water erosion can occur in the first few years following establishment of tree plantations (Ma *et al.*, 2000; Yang *et al.*, 2005; de Blécourt *et al.*, 2013). The low canopy cover also leads to higher soil temperature than is found under mature tree canopies. In combination with high nutrient availability after harvest residue burning, these factors lead to high soil microbial respiration and accelerated SOC decomposition after forest conversion. Few studies have quantified the primary sources and mechanisms of SOC losses after the conversion of natural forest to Chinese fir plantation in Southern China.

While tree plantations have been shown to be effective at removing atmospheric CO_2 (Bastin *et al.*, 2019), most studies have focused on biomass C accumulation (Pan *et al.*, 2011). There is considerable uncertainty regarding SOC sequestration with tree plantation growth, especially in China, where 65% of tree plantation area is made up of young and middle-aged forests (Tang *et al.*, 2018). Litterfall and fine root production, which differ among tree plantation ages, are two major pathways for C input into soil (Raich & Tufekciogul, 2000; Cotrufo *et al.*, 2013; Castellano *et al.*, 2015). However, research has shown that litterfall and fine roots differ in efficiency for forming SOC (Sulman *et al.*, 2014; Cotrufo *et al.*, 2015; Sokol & Bradford, 2019). Furthermore, differences in forest productivity among forest ages could alter soil microbial activities and biogeochemical processes. All of these possible alterations in controls of the C inputs and outputs from these systems complicate our understanding of SOC sequestration across different aged forest stands.

To close the gaps in our understanding of the controls on soil microbial respiration of SMEB forests, the pathways of SOC losses and changes in SOC dynamics during the development of Chinese fir plantations must be elucidated. This dissertation addresses three main knowledge gaps: (1) The temporal dynamics of soil microbial respiration, and the main drivers of soil microbial respiration and its C sources in SMEB forest in eastern China (Chapter Two); (2) The main pathways of SOC loss during the establishment of tree plantation and recovery of SOC during a typical Chinese fir plantation rotation (Chapter Three); and (3) The response of bulk and rhizosphere SOC to changing above- and below-ground C inputs under Chinese fir plantations of differing age and NPP. These research gaps were studied in a secondary naturally-regenerated SMEB forest and three different aged Chinese fir plantations (young, middle-aged, and mature) located near the

Research Station of Subtropical Forest Responses to Changing Environments near Sanming City, Fujian Province in southeast China. This research station is located in the central subtropical zone in China, which has the zonal vegetation typical of the subtropical forest in China and is also an important region for Chinese fir plantations, and a center for the ecological study of forest ecosystem function and its response to the future predicted changes in temperature and precipitation in future. These forests provide an opportunity to explore the characteristics and controls of soil microbial respiration in SMEB forests and to evaluate the effects of development of Chinese fir plantations on soil organic carbon pools.

CHAPTER TWO: WAVELET ANALYSIS REVEALS CURRENT PHOTOSYNTHATES ARE THE PRIMARY CARBON SOURCE FOR SOIL MICROBIAL RESPIRATION IN SUBTROPICAL MOIST BROADLEAVED EVERGREEN FOREST

ABSTRACT

Studies of soil microbial respiration are expanding globally, yet few have identified the temporal dynamics of carbon sources for soil microorganisms, especially in the tropics and subtropics. To address this gap, soil microbial respiration was measured continuously (hourly) in a subtropical moist evergreen broadleaved forest and from excavated soil cores incubated in a nearby open canopy site. I applied wavelet analysis to these continuous measures to identify the temporal dynamics of available carbon sources that fuel soil microbial respiration, and to examine the temporal correlations and time lags between soil microbial respiration and photosynthetically active radiation (PAR), soil temperature, and soil water content. The varying magnitude of soil microbial respiration at multiple periods in the continuous time series revealed the temporal variation of carbon sources supporting soil microorganism metabolism. PAR was the primary factor driving variation in soil microbial respiration at diel scales, and soil water content influenced the transfer rate of photosynthates to the soil. Current photosynthates were the primary C source fueling soil microbial metabolism, contributing 98% to soil microbial respiration in the growing season and 68 % in the winter months. The low temperature sensitivity (Q_{10} = 1.4) of soil organic carbon decomposition and the relationship between soil

microbial respiration and PAR supported the finding that soil microbial respiration rate is highly dependent on substrate C availability from current photosynthates and PAR, rather than on temperature. My results challenge empirical models based on the tenet that soil temperature regulates soil microbial respiration, and highlight the tight linkage between plant physiology and soil microbial activity in a subtropical forest.

INTRODUCTION

Tropical and subtropical forests play a vital role in terrestrial carbon (C) cycles, containing 55 % of the terrestrial C stock and contributing 70 % of the C sink of global forests (Pan *et al*., 2011). At the same time, the warm and moist climate in tropical and subtropical forests induces rapid C turnover, with the highest soil microbial respiration (Rm) rates in the world (Bond-Lamberty *et al*., 2004; Chen *et al*., 2014). As the largest CO_2 source from terrestrial ecosystems contributing to the atmosphere, even a small change in Rm may cause significant changes in net ecosystem C gain, or the difference between net primary production (NPP) and Rm (Tian *et al*., 1998). However, the factors that control Rm in tropical and subtropical forests are not well known, with only 14% of global soil respiration data coming from these forests, and a particular lack of data from tropical and subtropical forests in Asia (Bond-Lamberty *et al*., 2018). With higher belowground C allocation and higher C turnover rates in tropical and subtropical forests compared to temperate and boreal forests, these regions should be of high priority for examining variability in Rm and potential response to climate change (Cavaleri *et al*., 2015; Prestele *et al*., 2016).

Temperature has been documented as the primary environmental factor controlling soil microbial respiration in many earth system models (Ryan & Law, 2005; Davidson & Janssens, 2006). According to several model predictions, SOC will decline with global warming due to increases in SOC decomposition driven by increasing temperature (Davidson *et al*., 2000; Schlesinger *et al*., 2016). However, these predictions conflict with many field warming experiments and syntheses of global datasets, in which the changes of dead organic materials and SOC with respect to increases in temperature were much less than the response of Rm to increases in temperature (Giardina *et al*., 2014; Carey *et al*., 2016; Crowther *et al*., 2016; Bond-Lamberty *et al*., 2018). For example, based on a synthesis of a global soil respiration dataset, it has been shown that although Rm has increased by 1.2 % with warming of 0.7 °C in the last 25 years there was little change in SOC (Bond-Lamberty *et al*., 2018). These studies demonstrated that other important available C sources for soil microbial metabolism exist, and temperature is not the sole controlling factor for Rm.

Studies have confirmed that plant productivity plays a key role in regulating soil respiration through transporting current photosynthates from the canopy to the soil to support root and microbial respiration (Janssens *et al*., 2001; Ryan & Law, 2005; Litton *et al*., 2011; Giardina *et al*., 2014). For example, a study using tree girdling to prevent belowground photosynthate allocation showed that soil respiration declined by 37% within 5 days of girdling treatment in a boreal forest (Hogberg *et al*., 2001). Unlike SOC, most of which is physically and chemically protected by soil minerals, rendering it

resistant to microbial attack and therefore characterized by slow turnover rates at millennia timescales (Townsend *et al*., 1992; Davidson *et al*., 2000; Trumbore, 2000; Giardina *et al*., 2014), current photosynthates can be easily used by soil microorganisms. It has been shown that a large fraction of low molecular weight carbohydrates, approximately 45% of belowground C allocation, entered soil through root exudates and was decomposed by soil microbes (Högberg *et al*., 2002; Kuzyakov, 2002). Despite these important findings, the importance of fresh plant-derived C for soil microbes is often neglected in studies of soil microbial respiration, partly because it is difficult to separate root respiration from soil microbial respiration in conventional soil CO_2 efflux measurements in the field.

The allocation and transport of photosynthates which is important for soil microbial metabolism are sensitive to soil temperature, soil moisture, and plant productivity. For example, diel variations in Rm and photosynthesis are highly correlated with soil water content, which affects the transport rate of photosynthates from canopy to soil (Tang *et al*., 2005; Högberg & Read, 2006; Kuzyakov & Gavrichkova, 2010). The time lag between photosynthesis and soil respiration has been shown to vary, with a lag between peaks for both fluxes of 12 hours in September compared to 6 hours in June in the Sierra Nevada Mountains with Mediterranean climate (Tang *et al*., 2005). Studies in humid tropical forests have shown that warm temperature with little seasonal variability reduces temperature stress on soil microbes; instead, the high amount and greater frequency of precipitation brings plenty of dissolved organic carbon into the soil through canopy and

litter layer leaching, stimulating Rm (Cleveland *et al*., 2010). Heavy rain can also increase soil water content and decrease O_2 concentration, changing soil redox conditions and releasing mineral-protected organic C into the soil solution (Silver, 1998). In addition, soil rewetting following drought may start plant and soil microbial activities and stimulate soil respiration rate by up to 10 times (Jarvis *et al*., 2007; Moyano *et al*., 2013). However, most of our understanding of the relationship between environmental factors and Rm comes from measurements on weekly or monthly time scales, limiting our understanding of impacts to short-term microbial processes (Kuzyakov & Gavrichkova, 2010; Vargas *et al*., 2010; Drake *et al*., 2016). This lack of knowledge regarding the relative and temporal contributions of photosynthates for soil microbes limits the ability to predict shifts in Rm with changing climate. High temporal resolution of Rm can help uncover the nuances of environmental controls over Rm and improve monthly and yearly CO_2 flux estimation (Vargas *et al*., 2011).

The trenching method is widely applied to separate contributions of root respiration and soil microbial respiration from field measurements of soil CO_2 efflux, with materials such as a plastic sheet, fiberglass sheet, and cloth commonly used to prevent root invasion into measurement sites (Rey *et al*., 2002; Wang & Yang, 2007; Yang *et al*., 2007; Drake *et al*., 2012). However, these materials limit dissolved organic matter movement and change the soil environment inside the plot. Recently, nylon mesh sheets have been shown to effectively separate root and fungal mycelium respiration, with minimal

influences on soil environment, C flow, and nutrient exchange between plants and microbes (Moyano *et al*., 2008).

In addition to experimental trenching, wavelet analysis has been demonstrated as an effective tool to resolve the role of variable C sources for soil respiration through the transformation of time series measurements of respiration rate into varied frequency sub-signals to identify multiple C sources involved in Rm (Torrence & Compo, 1998; Vargas *et al*., 2010). In physics, the phase of a periodic function of some real variable is an angle representing the number of periods spanned by that variable. Using wavelet coherence analysis, the phase relationship (i.e., the differences in the frequency distribution) between two time series can be used to establish possible cause-effect relationships between Rm and environmental variables (Vargas *et al*., 2010; Jia *et al*., 2018). Thus, in this study I used wavelet analysis to identify different substrate C sources for soil respiration.

The subtropical moist evergreen broadleaved (SMEB) forests of China are among the most biodiverse and productive forests globally and occupy 25 % of the land surface of China (Yu *et al*., 2014). In this region, the East Asian summer monsoon brings much of the rainfall to southeastern China. The East Asian summer monsoon typically starts at the beginning of April, going through June in southern China, then moves north and then back to southern China in September, leaving a period of drought in mid-summer. The East Asian summer monsoon ends at the beginning of November; the East Asian winter monsoon lasts from December to February, during which this region is cold and dry

(Ding *et al*., 2018). The movement and transition of the monsoon leads to distinct seasonal weather patterns, providing an opportunity to study the relationship between above and belowground processes, and the contribution of different C sources to Rm in association with changes in environmental conditions.

The main purposes of this study were to examine the importance of photosynthesis on soil microbial respiration, and to explore the temporal synchrony between soil microbial respiration and photosynthetically active radiation (PAR) on multiple time scales in a SMEB forest in southern China. The temporal variation of soil microbial respiration was surveyed using automatic continuous measurement systems, and wavelet analysis was applied, to explore the temporal correlation between Rm and PAR, soil temperature, and soil water content. This approach aims to improve our understanding of the effect of environmental drivers (soil temperature, soil water content, and PAR) in regulating soil microbial respiration rate. I hypothesized that the monsoon transitions lead to changes in soil water content and plant phenology, which in turn influence allocation and transport of photosynthates, and therefore C sources for soil microorganisms and thus microbial respiration. I further hypothesized that photosynthesis influences soil microbial respiration at multiple time scales independent of soil temperature, because consistently warm temperature is not a limiting factor for Rm in subtropical forests. Instead, soil water content will affect the relative contribution and time lag of photosynthates to soil microbial respiration, and as such plays a vital role in plant-microbial interactions.

MATERIAL AND METHODS

Site description

The experiment was conducted in a SMEB forest, located within a state-owned forest farm (26° 19’ N，117° 36’ E) in Chenda County, Sanming City, Fujian Province in southeastern China. The mean annual temperature is 20.1 °C, with a mean annual rainfall of 1670 mm from 1959 to 2016 measured by the Sanming City meteorological station.

Soils at the site are Ultisols according to the USDA soil taxonomy (Soil Survey Staff, 1999), developed from biotite granite, and are characterized by low SOC content, low pH and cation exchange capacity, and abundant Fe and Al oxides (Fan *et al*., 2019). The soil is highly developed, and the profile exceeds 1 m in thickness in most areas. The dominant tree species of the SMEB forest are *Castanopsis carlesii, Schima superba,* and *Cinnamomum camphora*. Most of the litterfall inputs occur in April following the arrival of the summer monsoon, with the growth of new leaf buds and fine root growth. The fine root necromass increases during the summer drought period (Yang *et al*., 2004a,b).

Soil microbial respiration measurements

Three 20 m X 20 m plots randomly distributed in the study forest were used to conduct the experiment. Within each plot, three randomly selected 1 m × 1 m subplots were trenched in April 2010, for a total of 9 trenched subplots, and the trenches were backfilled with soil from the same layer. I placed nylon mesh sheets with 150 μm pore size 1 m into the soil to exclude fine root entry while allowing for lateral water movement and ingrowth of mycorrhizal fungi, which have been shown to contribute more than 2/3 of

fresh root C transport into forest soils (Zhang *et al*., 2019). Based on previous research, most of the remaining root residue will be decomposed within nine months in subtropical forests (Sheng *et al*., 2010). After the trenching was completed, the subplots were kept free of ingrowth of new seedlings and understory vegetation. One polyvinyl chloride (PVC) collar (20 cm inside diameter×8 cm height) was inserted into the soil to 4 cm depth in each trenched subplot, and Rm was measured from March 28th, 2012 until December 2014.

Following the installation of the collar, I used a Li-8100-103 portable CO_2 infrared gas analyzer (Li-Cor Inc, Lincoln, NE, USA) to measure *in situ* Rm rate (Rm-f). Soil temperature was measured by a portable thermometer (Model SK-250WP, Sato Keiryoki MFG. CO., LTD. Tokyo, Japan) and soil volumetric water content was measured using soil moisture meter (Model TDR-300, Spectrum Technologies, Aurora, IL, USA) at a depth of 8 cm soil, while taking measurements of Rm-f. The rates of Rm-f were monitored from 9:00 am to 12:00 pm based on previously established information that this period encompasses the average rate of daytime respiration (Sheng *et al*., 2010). After 16 months, a collar with the average Rm rate of each 20 m x 20 m plot was chosen for high frequency measurements by automated measurement using Li-8100-104 automated long-term chamber. Soil temperature (Tf) and soil water content (Wf) were monitored using the temperature thermistor and moisture probe from 8100-401 chamber control kit (Li-Cor Inc, Lincoln, NE, USA). In these three sub-plots, Rm-f, Tf, and Wf were measured every 30 minutes from August 1st, 2013 until December 31st, 2014.

Meanwhile, photosynthetically active radiation (PAR), air temperature, and rainfall were monitored within 50 m distance at a weather station outside the forest. Rm and all the environmental variables were monitored with the same frequency simultaneously. The high frequency measurements allowed us to conduct wavelet analysis (see below).

To evaluate the magnitude of SOC decomposition rate and its response to soil temperature in the absence of new C inputs. Five soil cores (length × wide × depth: 0.5m × 0.5m × 0.6 m) were excavated from the forest and incubated them in the open in a location 1 km from the forest in January 2015. The respiration rate (Rm-o), soil temperature (To) and soil volumetric water content (Wo) were monitored simultaneously from Jan 2015 through December 2016, as described above. However, to minimize the influence of disturbance to the soil structure and decomposition of litter and root residues likely stimulated by core excavation, only data collected from January 2016 to December 2016 were used in this study.

We used an exponential equation ($R=a\times e^{(b\times T)}$) to explore the function between the rate of SOC decomposition (Rm-o) with soil temperature (To) in the excavated soil cores incubated in the open. To quantify temperature-dependent SOC decomposition in the forest (Rm-fsoc), we assumed the thermodynamics of SOC did not differ between excavated soil cores incubated in the open and in situ forest soils. The fixed constants of the exponential equation developed using the open core data were used to calculate Rm-fsoc using soil temperatures measured in the forest. The difference between total Rm in

the forest (Rm-f) and Rm-fsoc was defined as the contribution of current photosynthesis to Rm (Rm-fp).

Wavelet analysis

Wavelet analysis has emerged as a useful tool for analyzing temporal variation over different frequencies in non-stationary time series with wide applications in geophysics, hydrology, and soil respiration research (Torrence & Compo, 1998; Lafrenière & Sharp, 2003; Vargas *et al*., 2010). Wavelet transform is an analytical approach that enables the distillation of data-dense time series measurements into patterns that reflect frequencies of change in measured variables through time. Detailed explanations of the wavelet analysis and the exact procedures can be found in Torrence & Compo (1998), Lafrenière and Sharp (2003), Grinsted *et al*. (2004), and Vargas *et al*. (2010). In brief, continuous wavelet transform was applied to analyze the non-stationary power at different frequencies of Rm and biophysical factors time series, by transforming an original measurement consisting of different wavelet functions into a series of wavelet functions. These wavelet functions are derived from the Morlet mother wavelet function. The mother wavelet was translated and scaled along the time series to obtain a series of sine wavelets. These wavelets can be localized in both time and frequency space. The extraction of frequencies over localized time series using wavelet functions reflects the changes in the non-stationary signal on a certain frequency, such as 24 hr, over the time series. The detailed features of the results can be displayed in a three-dimensional expression of time series by time (x; date of measurement), period (y; signal frequency),

and wavelet power (z; magnitude of variance at many different frequencies), defined as the wavelet power spectrum.

The local wavelet power spectrum refers to the magnitude of the variance in the time series at a specific wavelet period and location in time. The global wavelet power spectrum is the time-averaged variance at a given period, and it provides a graph of power versus periods, or frequencies, which can be used to quantify the power, or strength, of a time series (Torrence and Compo, 1998). The wavelet coherence analysis was used to identify temporal covariance between Rm and biophysical factors in both time and period/frequency, and quantifies the phase differences, or time lags, between time series of Rm and biophysical factors. Phase difference is the difference, in degrees of angle or in time, between two waves (or time series) that have the same frequency referenced to the same point in time. If two time series oscillate synchronously, with a phase difference, at a given period, or frequency, it would suggest a possible cause-effect relationship between Rm and a particular biophysical factor. The potential phase difference between two time series (such as Rm-f and Wf) ranges from 0 - 180°. A phase difference of 0°, for example, would mean the time series of Rm and soil water content have no phase difference, or no time lag, and are considered to be in phase; a 180° phase difference means the two times series are completely out of phase with each other. In our analysis, at a period of 24 hours, a 90° phase difference between soil respiration and a biophysical factor would indicate that the time series of the two variables were synchronized with a 6-hour time lag (90°/360°□24 hr = 6 hr). I also analyzed wavelet coherence, based on

wavelet transform, to examine intermittent cross-correlations between two time series at multiple time scales (Grinsted *et al*., 2004).

The statistical significance (5 % significance level) of the wavelet power spectrum was tested against a null hypothesis, which assumes that the signal is generated by a stable process of a given background power spectrum. I used red noise (i.e., the noise produced by Brownian motion, also called Brownian noise) as the background spectrum in this study, because the red noise is widely used in geophysical time series. The variance of the red noise increases with the increasing period (or decreasing frequency). The comparisons between wavelet spectrum and background spectrum were tested within the cone of influence (COI). The COI is the zone where edge effects associated with zero-padding ends are present. Zero padding is needed to avoid false periodic events (Cazelles *et al*., 2008). Outside of the COI the data are unreliable and are excluded from interpretation. Data analyses were computed using MATLAB_R2012b (The MathWorks Inc). The wavelet analysis package can be downloaded from http://paos.colorado.edu/research/wavelets/ (Torrence & Compo, 1998; Grinsted *et al*., 2004).

Partial dependence plot

The partial dependence plot (PDP) is a machine-learning model that estimates the potential relationship between two features, to show the functional relationships between one or two input variables. The PDP relies on a "black-box model" in which the marginal effect of a single factor is tested when the other factors are non-limiting, and generates a

function that depends exclusively on the explanatory factor of interest (Greenwell, 2017). In this study, I used one-way PDP to obtain the effect of biophysical factors on soil microbial respiration (Rm-f). First, the black-box model was obtained by using the tree-based machine learning BRT algorithm (Elith *et al*., 2008). Secondly, the PAR or Wf data sets were submitted to the PDP function to obtain the average prediction of Rm-f using the black-box model. Finally, the relationships between predicted Rm-f and PAR and Wf were plotted graphically. These analyzes were run using the DALEX package in R studio (Biecek, 2018).

RESULTS

Seasonal variation in soil microbial respiration and biophysical factors

Soil temperature and soil water content measured in the forest (Tf and Wf, respectively) and in the soil incubated in the open (To and Wo, respectively) showed different diel and seasonal patterns (Figure 2.1). The Tf had relatively low diel variation throughout the year compared to To (Figure 2.1). Average monthly Tf varied from 5.0 °C in February to 27.7 °C in August, and remained nearly constant at 22.3 °C from April to July, and was less than 10°C from December to February (Figure 2.1). Soil temperature in the open (To) had much higher diel and seasonal variation throughout the year compared to Tf, ranging from 0.7 °C in February to 45.6 °C in July (Figure 2.1). Soil water content in the open (Wo) also showed greater variability than Wf (Figure 2.1), although soil water content in both treatments responded rapidly to rainfall events. The annual rainfall was 1789 mm, with rain starting at the beginning of March when air and soil temperatures

were low and ending in November. Most rainfall occurred from April to July during the East Asian summer monsoon (Figure 2.1). At the middle of the otherwise dry summer, typhoon Traimi brought 13 % (234 mm) of annual rainfall at the end of August 2014. The second rain stage, from November 11 to December 17, contributed 183 mm rainfall (~10 %) (Figure 2.1).

Both the diurnal and seasonal variation of soil microbial respiration differed substantially between the forest (Rm-f) and the excavated soil cores in the open (Rm-o). The annual average of Rm-f, 2.66 μ mol m^{-2} s^{-1}, was higher than the Rm-o, 0.37 μ mol m^{-2} s^{-1} (Figure 2.1). Rm-o had very low diel and seasonal variation, with highest rates in July and lowest rates in winter (Figure 2.1), aligned with seasonal variation in soil temperature (Figure 2.1). By contrast, Rm-f showed significant diurnal variation during the two rainy periods, one from April to July, and one in November, with less-pronounced diurnal dynamics at other times (Figure 2.1).

The Q_{10} of Rm-o was 1.4 when To was lower than 25 °C, but Rm-o declined when soil temperature exceeded 25 °C. Based on fitting of the exponential constants developed from the trenched plots, soil microbial respiration from SOC decomposition in the forest (Rm-fsoc) was 0.31 μ mol m^{-2} s^{-1} and only contributed 12% of Rm-f. The contributions of current photosynthates (Rm-f - Rm-fsoc) to Rm-f were most pronounced from April to November, during which Rm-fsoc was only 2 % of Rm-f, whereas Rm-fsoc was 32 % of Rm-f during the winter.

Wavelet power spectrum of soil microbial respiration

The global wavelet power spectrum showed distinctive differences in 24h period between the forest soil and the soil in the open. Based on the global wavelet analysis, the 24h period was the only prominent frequency for both Rm-f and Rm-fp (i.e., the difference between Rm-f and Rm-fsoc, or the contribution of current photosynthesis to Rm) across the yearly time series, indicating strong diurnal signatures of soil microbial respiration during the year (Figure 2.2). In contrast, the magnitude of the global wavelet power spectrum was low and not significant around the 24h period in the Rm-o time series, indicating no significant variance at the diel period for excavated soil cores incubating in the open (Figure 2.2).

Results of the local wavelet power spectrum, like the global wavelet power spectrum, revealed differences in the 24h period between the forest soil and soil in the open, but unlike the global wavelet power spectrum, the local wavelet power spectrum can provide short-term patterns. The local wavelet power spectrum showed that the statistically significant power of Rm-f was concentrated at the 24h period from April to July (days 90 to 220), and was strongest in April (days 90-106) and July (days 185-220) as shown with black contours outlining dark red areas in Figure 2.3. Rm-f also had significant power at the 12h period in April (days 93-108) and July (days 183-214), when Rm-f was at its highest of the year (Figure 2.3). During the second rainy season stage in October and November, there was weak but significant power of Rm-f around the 24h period (days 286-303; Figure 2.3, shown with green color). In contrast, the power of Rm-

o at the 24h period was weak and scattered throughout the year (Figure 2.4, orange color areas).

Temporal correlation between soil microbial respiration and biophysical factors

Based on the analysis of wavelet coherence, which was used to identify the temporal relationships between Rm-f and biophysical factors, Rm-f was tightly correlated with PAR and soil temperature at the 24h period throughout most of the year, and Rm-f also had a significant correlation with PAR at the 12h period from April to July (Figure 2.5). The diel variations in Rm-f were mostly out of phase with variations in PAR. The phase differences between Rm-f and PAR increased from April and July to December and February at the 24 h period, during which Rm-f lagged PAR by 2.0 to 6.5 hours. The diel variations in Rm-f were also mostly out of phase with variation in Tf, with Rm-f leading Tf by 1.8 hours most of the time.

In contrast to the diel variation, both Rm-f and Rm-o had strong and statistically significant coherence with Tf at longer periods, around 256 h, with no phase difference when Tf was lower than 23 °C (for Rm-f) and when To was below 25 °C (for Rm-o) (Figure 2.6). The coherence between Rm-f and Wf was statistically significant at time periods longer than 24h during the rainy seasons (around 128 – 512 h periods between days 90-130, and at the 256 h period between days 310-330). There was scattered distribution of coherence between Rm-f and Wf around the 24 h period in October and December when rains relieved the drought.

The PDP predicted that Rm-f increases with increasing PAR, reaching a peak Rm of 2.7 μmol m^{-2} s^{-1} at 790 μ mol (photon) m^{-2} s^{-1}, then decreased with increasing PAR (Figure 2.7a). In contrast to the relationship with PAR, the predicted Rm-f decreased with increasing soil water content when water content was very low, below 18 %, but increased with increasing soil water content when it was above 18 % (Figure 2.7b). The prediction of Rm-f by air temperature and soil temperature revealed a temperature threshold for Rm-f at 34 °C and 23 °C, respectively, above which Rm-f declined (Figure 2.7c & d).

DISCUSSION

The large and significant differences in soil microbial respiration rate between the forest (Rm-f) and in the open (Rm-o) (Figure 2.1) indicated that current photosynthates are likely an important source of the C available for soil microbial activity and respiration in the subtropical forest. Based on the differences between Rm-f and Rm-fsoc, which was derived from the temperature-dependence of SOC decomposition of soil incubated in the open, current photosynthates contributed to more than 88 % of annual soil microbial respiration, which accounted for almost 98 % and 68 % of soil microbial respiration during the growing and winter seasons, respectively. This contribution was higher than those reported for temperate and boreal forests (50 %) but similar to that of tropical forests (90 %) (Trumbore, 1993; Giardina *et al*., 2014). The transfer of photosynthates belowground is the primary source of low molecular weight compounds in dissolved organic matter and root exudates, which can be directly assimilated by the soil microbes

(Högberg & Högberg, 2002; Van Hees *et al*., 2005; Drake *et al*., 2016; Kuzyakov *et al*., 2019). In contrast, the complex chemical fractions of SOC, such as lignin, do not provide enough energy to support soil microbial enzyme formation, and the mineral protected C can be unavailable for microbial attack, especially organic matter bound by Fe and Al oxides in highly weathered tropical and subtropical soils (Giardina & Ryan, 2000; Six *et al*., 2002; Fissore *et al*., 2013). Previous studies using isotopic techniques have demonstrated that most of the belowground C fluxes were respired by soil microbes and were not used to form root biomass (Matamala, 2003; Körner *et al*., 2005; Högberg & Read, 2006), supporting the role of current photosynthates on regulating soil microbial activity and respiration.

The role of current photosynthates in regulating soil microbial respiration is also supported by the results of wavelet spectrum analysis. The strong power of the global wavelet of Rm-f at the 24h period throughout the year (Figure 2.2) suggests that soil microbial respiration likely originated from carbohydrates from current photosynthesis, which can be directly assimilated by microbes. The strong and consistent temporal correlation between local wavelet spectrum of Rm-f and PAR at the 24 h period between April and July, when the Rm-f rate was the highest in the year (Figure 2.3), points to the role of substrate availability from current photosynthesis in regulating the temporal dynamics and magnitude of soil microbial respiration. The weak and non-significant power at the 24 h period in the Rm-o time series (Figure 2.4) provided further indication that, without a tree canopy and therefore no addition of current photosynthates as a C

source, the temporal dynamics of Rm-o were strongly tempered. The lagging behind of Rm-f relative to PAR at the 24 h period (Figure 2.5) showed that PAR leads to the dynamics of Rm-f. On the other hand the lagging behind of Tf relative to Rm-f by two hours at the diurnal scale (Figure 2.5) indicates that soil temperature was not the key factor controlling soil microbial respiration at the diurnal period, as has also been suggested previously (Tang *et al*., 2005; Jia *et al*., 2018). This is supported by the observed insensitivity of soil microbial respiration to soil temperature ($Q_{10} < 1.4$) and the precedence of shifts in Rm before temperature shift in the forest (Giardina & Ryan, 2000; Davidson *et al*., 2006).

Through high frequency monitoring of Rm and environmental conditions, we provide the first empirical evidence illustrating that current photosynthate contributes most to soil microbial respiration in these subtropical humid forests and challenges many models, such as CENTURY, BPES, and bio-BGC models, in which soil microbial respiration derives primarily from SOC pool mineralization driven by temperature functions (Ryan & Law, 2005; Davidson & Janssens, 2006). The similar responses of photosynthesis and soil microbial respiration to PAR (Figure 2.7a) strongly point to the dependence of soil microbial respiration on carbohydrates from photosynthesis, as has been suggested by several studies (Van Hees *et al*., 2005; Kuzyakov & Gavrichkova, 2010). It has been shown that photosynthesis rate increases with increasing air temperature with a temperature threshold near 33 °C in tropical forests (Wood *et al*., 2012), above which photosynthesis is limited so that the transport of carbohydrates from

the canopy to the soil stops, resulting in a reduced supply of substrate C sources for soil microbes. In our study, based on the PDP modeling, the predicted Rm-f response to increasing air temperature also shows a threshold temperature around 33 °C, above which Rm-f no longer increases with increasing temperature.

In the studied forest and perhaps many SMEB forests, variation in rainfall likely has substantial effects on soil respiration while temperature effects are limited. The warm but not extremely high temperature during much of the year in SMEB forests results in little temperature stress on plant growth and soil microbial activity. Rainfall variation, on the other hand, may affect plant phenology and the quantity and quality of C inputs into soil, resulting in variation of soil microbial respiration (Cleveland *et al*., 2010; Yu *et al*., 2014; Han *et al*., 2014). The Rm-f rate was highest in the rainy season from April to July, and Rm-f rates in April and July were higher than in May and June (Figure 2.1). The higher Rm-f was likely due to increased temporal availability of substrate supply from photosynthates at 12 h and 24 h periods (Figure 2.5), which was influenced by the rainfall pattern. There were 35 rainy days in May and June, compared to 20 days in April and July, which likely led to lower photosynthetic activity in May and June because rainy days, in general, have lower PAR. As a result, the magnitude of carbohydrates from photosynthesis allocated for soil microbial respiration was likely lower in April and July relative to May and June. Furthermore, total belowground C allocation may decline in May and June due to higher nutrient availability associated with the higher amount of precipitation (624 mm) than in April and July (413 mm). High precipitation may have

resulted in higher throughfall and stem flow that brought high amount of nutrients from the canopy and litter layer via leaching (Vitousek, 1984; Jiang *et al*., 2019).

Unlike the dominance of current photosynthates on the regulation of soil microbial respiration during the rainy periods, there was no evidence of current photosynthate driven Rm-f during the dry periods based on results of local wavelet power spectrum. The local wavelet power spectrum of Rm-f revealed strong power at long periods (> 256 h) in the summer drought season from August to October (Figure 2.3). The phase differences between Rm-f and PAR, Tf, and Wf in the drought season, from August to October, showed that Rm-f preceded both PAR and soil temperature around 512 h period, and lagged behind Wf around the 1024 h period in the dry summer (Figure 2.5). The phase differences and the lack of wavelet spectrum at 24 h period in the dry season indicated that current photosynthates are unlikely to be the substrate C source for soil microorganisms during this period. In a study of the effects of precipitation variability and fire on soil CO_2 efflux, it was shown that longer periods (> 24 h) of the wavelet power spectrum are likely associated with C sources other than current photosynthates (Vargas *et al*., 2012). However, Rm-f in the drought season was still high and equal to Rm-f in May, indicating the stimulation of original SOC under low soil water content. This finding is supported by a warming experiment near our site where soil warming resulted in low soil water content and increased soil respiration (Lin *et al*., 2018). The decline in soil water content stimulated CO_2 production from deep soils due to improved O_2 availability (Silver *et al*., 1999).

My high frequency monitoring also showed rapid increases of soil microbial respiration in response to rewetting of dried soil by pulse rains during the drought season (Figure 2.1). The pulse rains may disturb soil aggregates and increase substrate C availability from previously protected C, and stimulate microbial population growth and activity during the otherwise dry period. The sudden increase of soil microbial respiration associated with pulse rains, known as the Birch effect, has been frequently reported in regions with rain pulses in the dry season (Jarvis *et al*., 2007; Matteucci *et al*., 2015). Although the rain pulses stimulate soil microbial respiration, it has been shown that water from rain pulses in the dry season is weakly available to plants, and so has limited effects on plant phenology (Unger *et al*., 2010). This may help to explain the lack of diel dynamics of canopy photosynthesis that led to the diminishment of variation of Rm-f at the 24 h period in the dry season in this study.

Soil water availability is essential for plant photosynthesis and biogeochemical cycling in soils. The PDP predictive curve indicated that soil microbial respiration was negatively related to soil water content when soil water content was less than 18 % (Figure 2.7b), possibly due to increased CO_2 production from deep soil to surface associated with improved aeration. The 18 % soil water content is close to the wilting point in this soil (15 %) (Yang, unpublished data). Plant growth and photosynthesis are limited below the wilting point so that there was a dramatic reduction of photosynthates inputs into soil (Wood *et al*., 2012). However, CO_2 production in deep soil, where the water content was high, was likely enhanced by improved O_2 diffusion and the lower

surface soil water content improved the diffusion of CO_2 from deep soil to surface soil (Silver *et al*., 1999). When the soil water content was higher than 18 %, the relief of water limitation likely improved stomatal conductance and photosynthetic rate. This enhances carbohydrate synthesis and the subsequent transport of photosynthates belowground, which in turn stimulates soil microbial respiration as observed in this study (Figure 2.7b). The result suggests that the main location and source of Rm differed between the rainy period and the dry period.

CONCLUSIONS

This study demonstrates that current photosynthates are the primary C sources for soil microbial respiration in the SMEB forest, contributing 98 % of C sources for microbial respiration in the growing season and 68 % in winter. This is the first *in situ* study to demonstrate the importance of new photosynthates on soil microbial respiration and top-down regulation of soil microbial metabolism in tropical forests. The opposite time lags of soil microbial respiration with PAR and soil temperature on a diel scale indicated that soil microbial respiration dynamics responded to PAR but always preceded shifts in soil temperature. This finding strongly suggests that soil microbial respiration is not controlled by soil temperature in SMEB forests; instead, the diel dynamics of soil microbial respiration were strongly controlled by PAR. My results challenge the assumption of most empirical models that soil temperature regulates soil microbial respiration, and illustrates a scenario in which plant physiology plays a key role in

regulating soil microbial activity, a scenario which may be not uncommon in subtropical moist evergreen broadleaved forests.

TABLES AND FIGURES

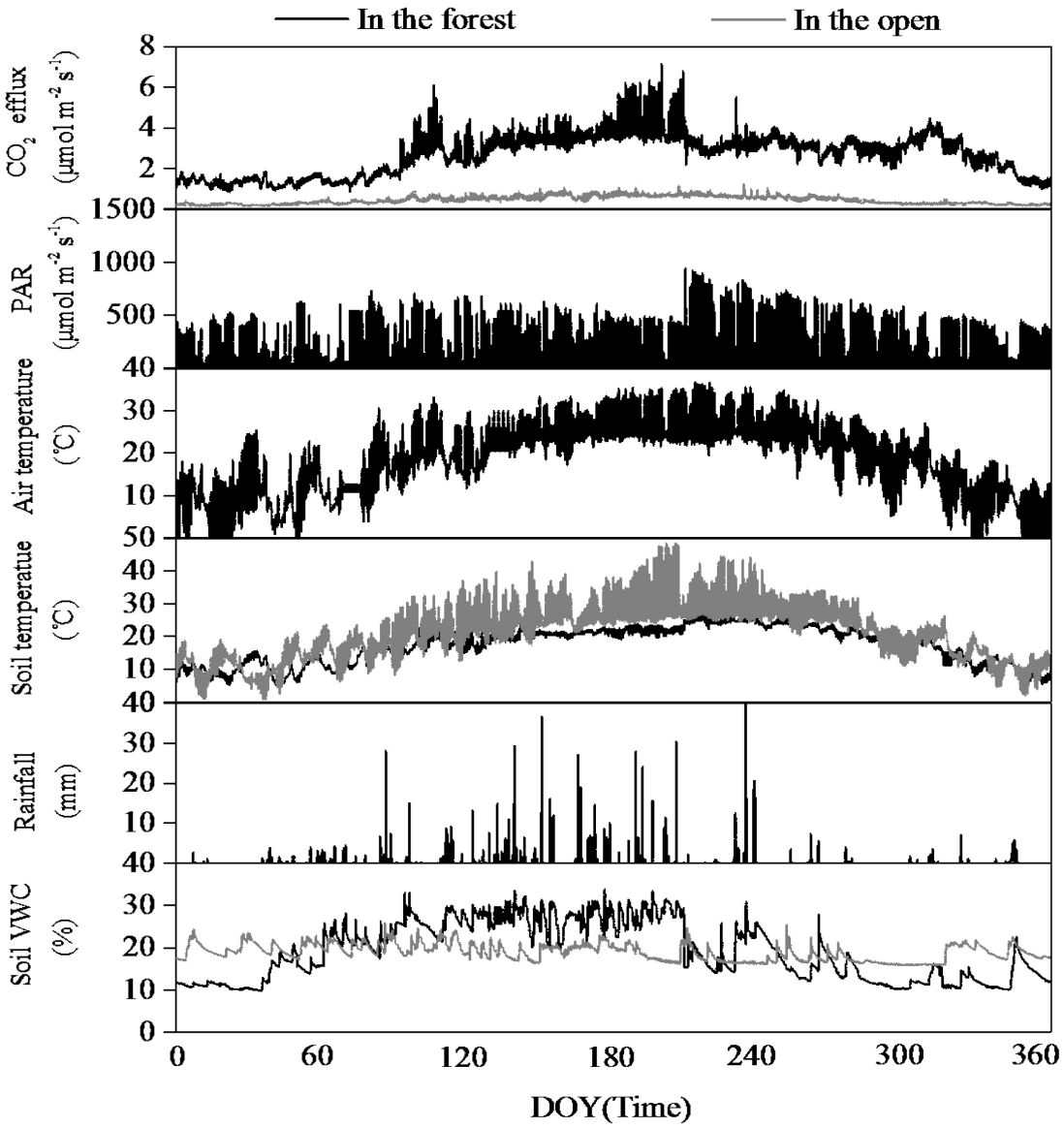

Figure 2.1 Diel and seasonal trends of soil microbial respiration rate, soil temperature and soil volumetric water content at 10cm soil depth in the forest soil and excavated soil cores

incubated in open canopy. Diel and seasonal trends of precipitation, air temperature, and photosynthetically active radiation (PAR) measured during the studies. DOY, day of the year after January 1.

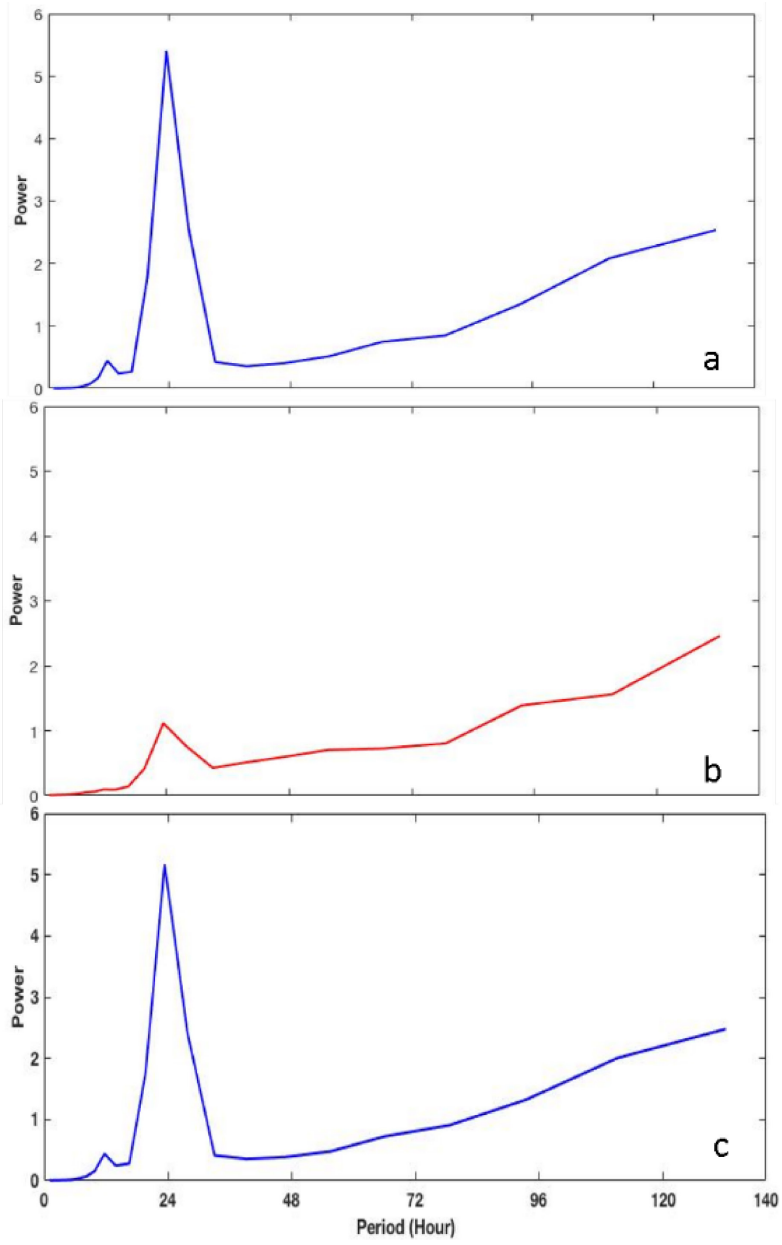

Figure 2.2 Global wavelet power spectrum of (a) soil microbial respiration in forest soil (Rm-f), and (b) soil microbial respiration at open canopy (Rm-o), and (c) soil microbial

respiration from current photosynthates (Rm-p), which was calculated by the difference between Rm-f and the rate of SOC decomposition (Rm-fsoc) in forest soil

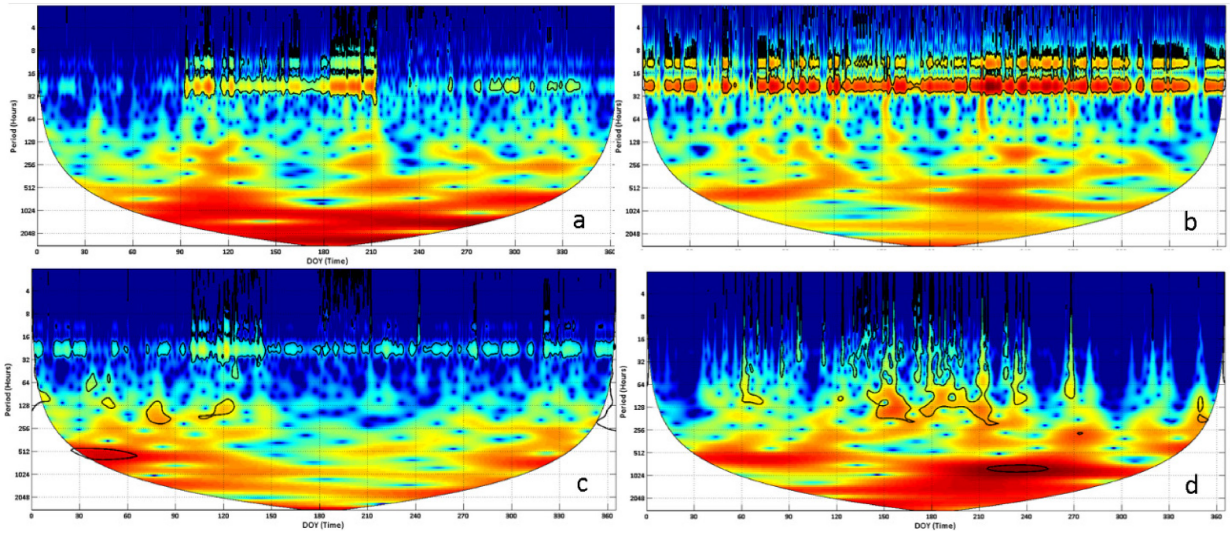

Figure 2.3 The local wavelet power spectrum, which shows the magnitude of the variance in the time series at a specific wavelet period and location in time, for soil microbial respiration and environmental factors in the forest: (a) Rm-f; (b) PAR; (c) Tf; (d) Wf. The color codes for power values are from dark blue (low values) to dark red (high values). The black contour lines depict the areas where the power is significant. The thick black line indicates the cone of influence that delimits the region not influenced by edge effects. DOY, day of the year after January 1.

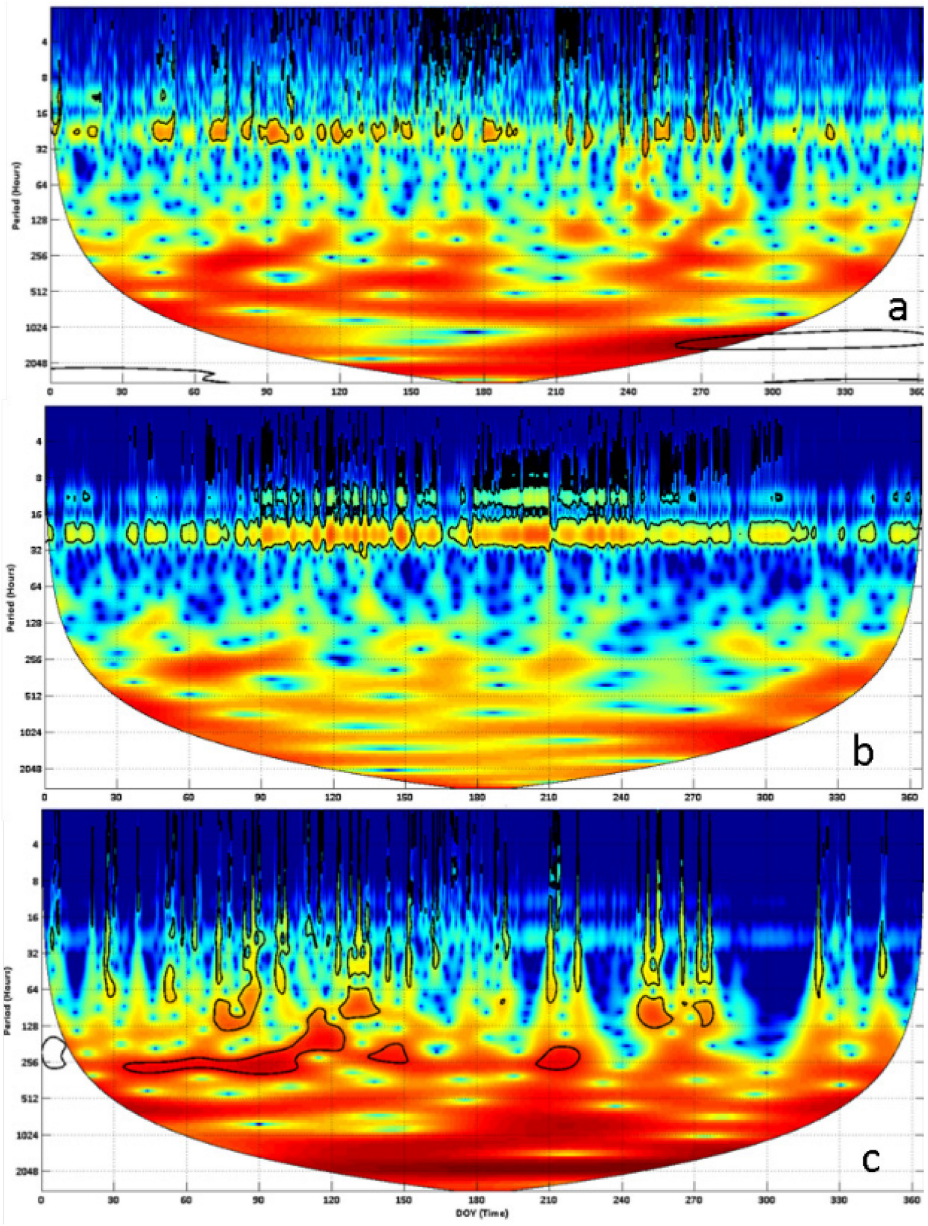

Figure 2.4 The local wavelet spectrum for soil microbial respiration and biophysical factors measured beneath the open canopy: (a) Rm-o; (b) To; (c) Wo. The color codes for power values are from dark blue (low values) to dark red (high values). The black contour lines depict the areas where the power is considered significant, and thick black line indicates the cone of influence that delimits the region not influenced by edge effects. DOY, day of the year after January 1.

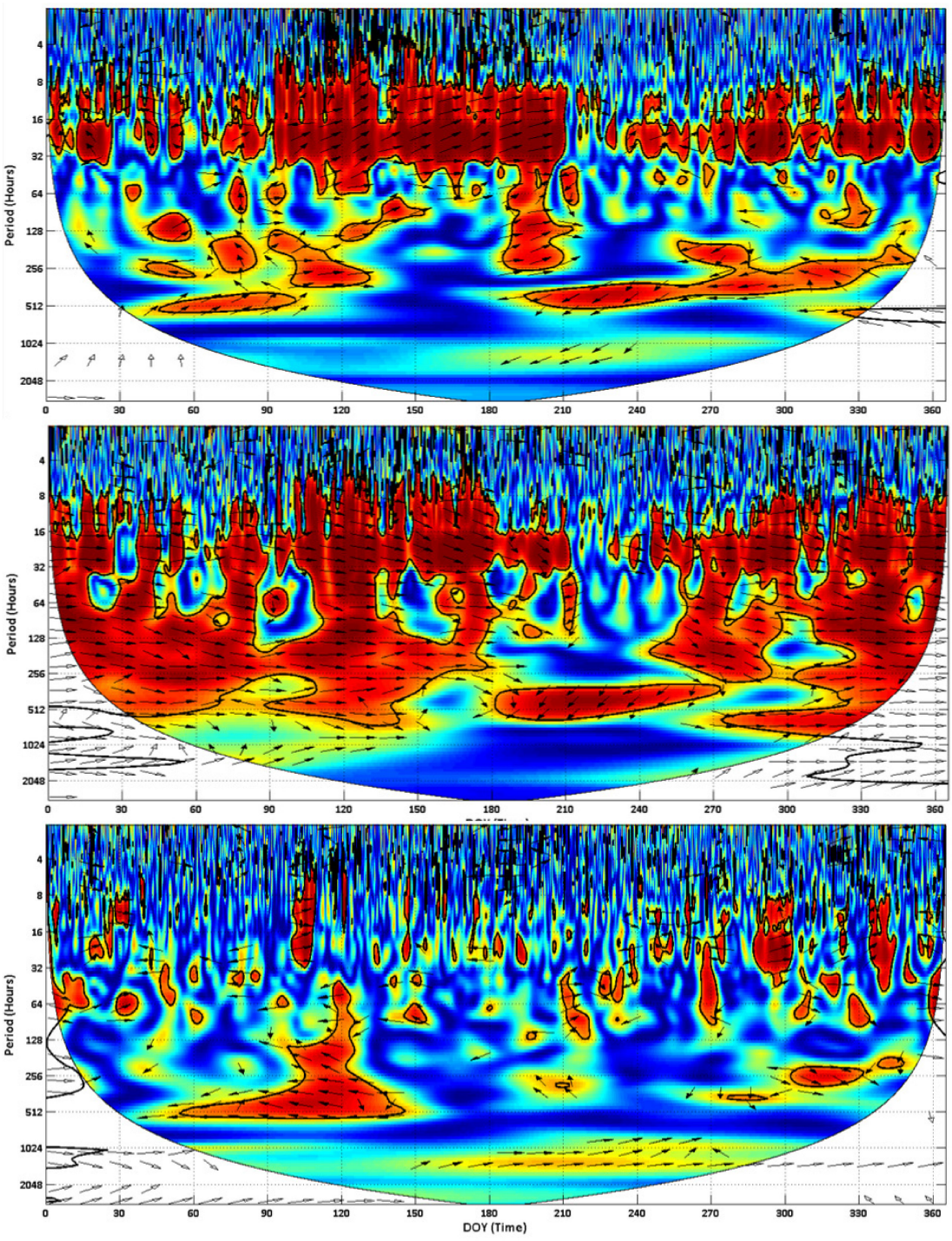

Figure 2.5 Wavelet coherence analysis and phase difference between soil microbial respiration and (Upper) PAR, (Middle) soil temperature, and (Below) soil water content in the forest. The phase difference is shown by arrows: in-phase pointing to the right (no

lags between time series), out of phase pointing in other direction (representing lags between time series). The color codes for power values of coherence are from dark blue (low values) to dark red (high values). Black contour lines represent the 5 % significance level, and thick black line indicates the cone of influence that delimits the region not influenced by edge effects. DOY, day of the year after January 1.

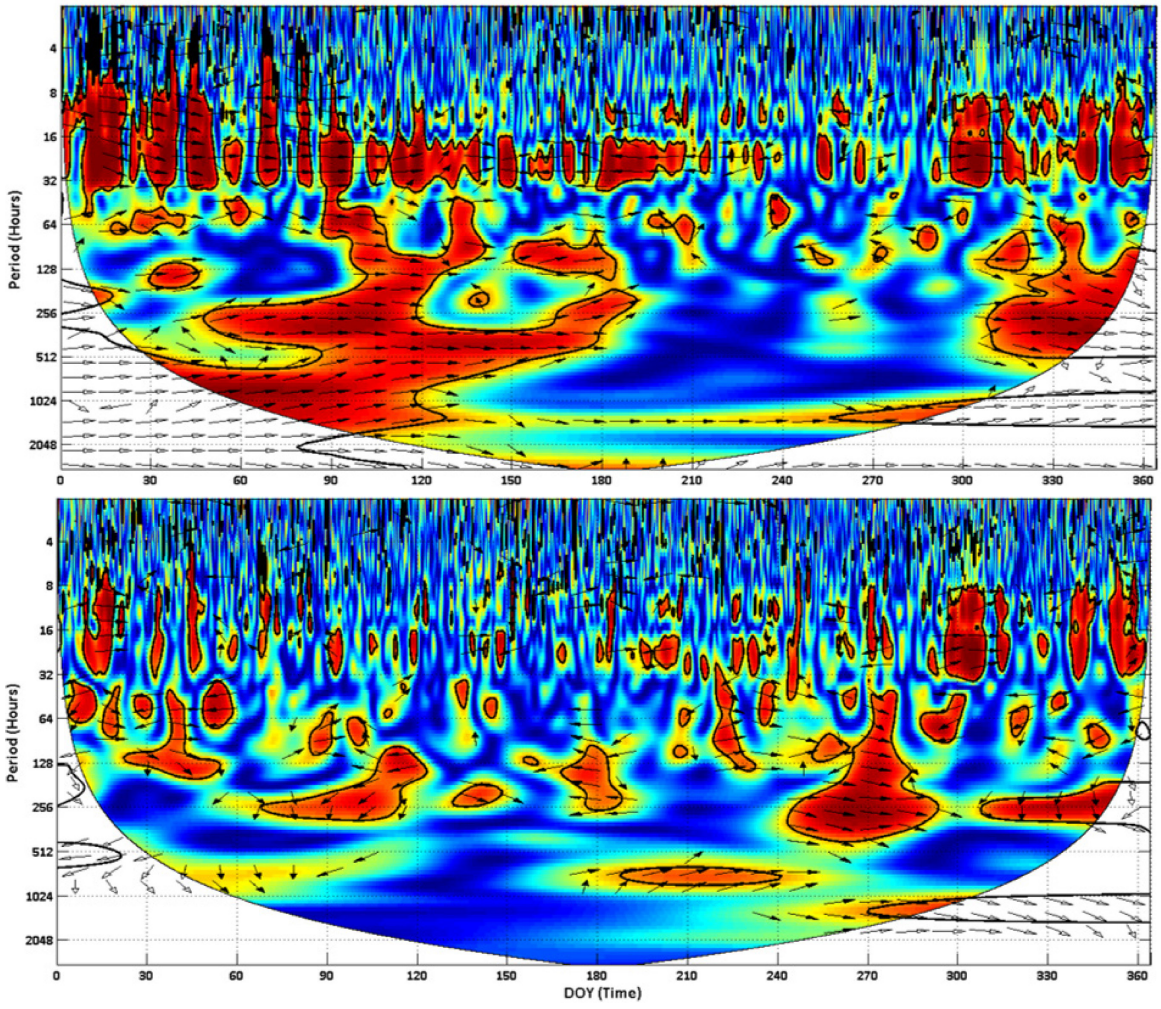

Figure 2.6 Wavelet coherence analysis and phase difference between soil microbial respiration and (Upper) soil temperature, and (Below) soil water content in the open. The phase difference is shown by arrows: in-phase pointing right (no lags between time series),

out of phase pointing in other direction (representing lags between time series). The color codes for power values of coherence are from dark blue (low values) to dark red (high values). Black contour lines represent the 5 % significance level, and thick black line indicates the cone of influence that delimits the region not influenced by edge effects. DOY, day of the year after January 1

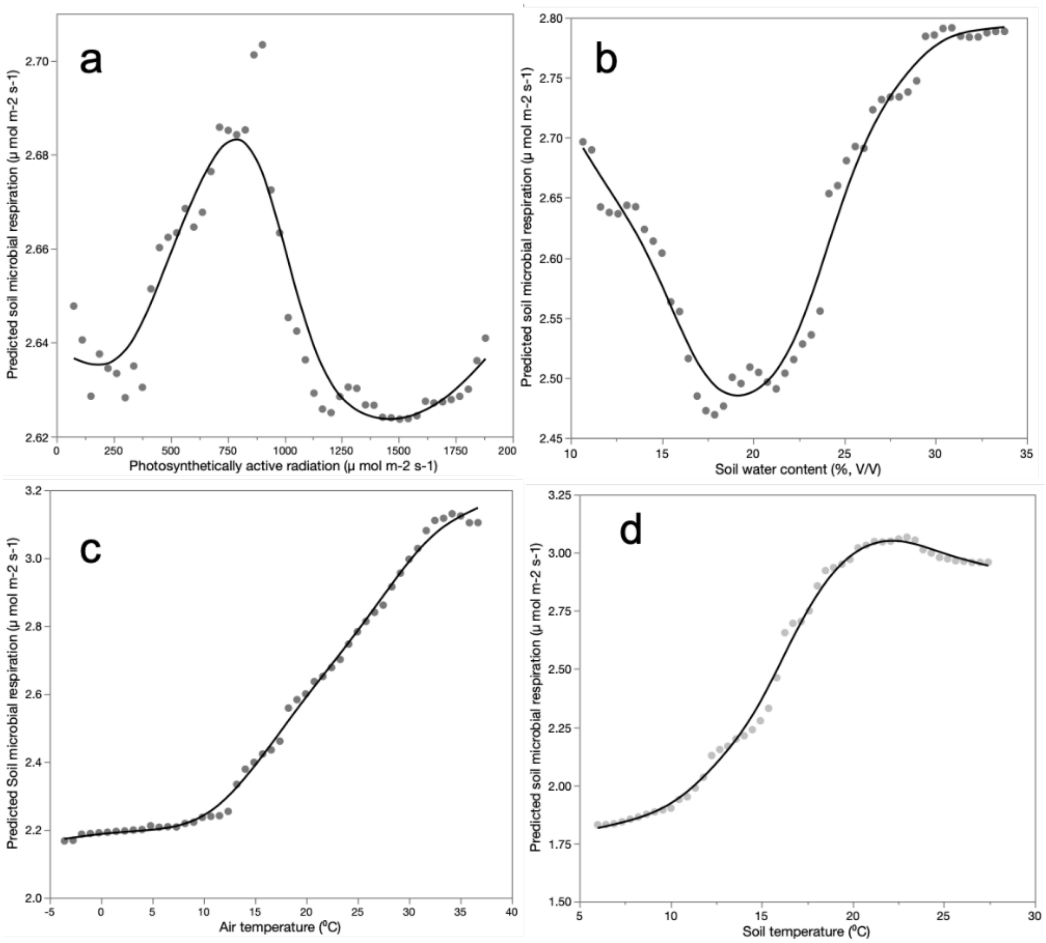

Figure 2.7 Partial dependence plot (PDP) for the soil microbial respiration prediction model and (a) photosynthetically active radiation (PAR), (b) soil water content, and (c) Air temperature, and (d) Soil temperature.

CHAPTER THREE: LOSS OF SOIL ORGANIC CARBON FOLLOWING NATURAL FOREST CONVERSION TO CHINESE FIR PLANTATION

ABSTRACT

China manages the largest area of forest plantations on the globe, with most of them converted from natural forests. Establishment and management of forest plantations often involves severe human disturbances such as slash burning and intense site preparation which could lead to rapid and substantial soil organic carbon (SOC) losses and affect long-term SOC recovery. In this study I examined SOC dynamics and soil microbial respiration following the conversion of natural secondary forest to a Chinese fir plantation with slash burning in southern China. SOC decreased by 28 % in the first year after forest conversion, with more than 40% of the decrease due to volatilization from slash burning. Slash burning also increased soil microbial respiration in the first five months following forest conversion. SOC of the Chinese fir plantation did not recover to the pre-burning level in 40-years, indicating that the loss of SOC is a long-term phenomenon in forest conversion. I found that soil microbial respiration was largely controlled by photosynthesis in the natural secondary forest; however, in the young Chinese fir plantation both newly formed photosynthates and SOC were important C sources for soil microorganisms. The intensive burning of harvest residue not only induced direct SOC losses through volatilization, but may also have accelerated the decomposition of SOC in the first few years after forest conversion. I conclude that slash burning is the primary, initial pathway by which SOC is lost in these subtropical forest plantations, and that the

recovery of SOC in this subtropical forest system will likely be a slow process, requiring centuries or more. Replacing natural forest with Chinese fir plantations using slash burning is likely to substantially deplete C stored in the soil for many years and may negatively affect long-term SOC sequestration potential.

INTRODUCTION

China manages 69.33 million ha of tree plantations, accounting for 26.2 % of the world's tree plantations as of 2013, with plantation area in China increasing by approximately 5 million ha $year^{-1}$ between 2004 and 2013 (SFA, 2016). Most forest plantations in China are monocultures converted from former natural forests, with approximately 42 % of the forest plantations located in the sub-tropical region of China (FAO, 2010). The rapid increase of forest plantations is essential to meet the increasing timber demand in China; however, it also raises some environmental concerns, such as impacts on biodiversity conservation, soil fertility, and soil organic carbon (SOC) loss (Yang *et al.*, 2009; Xu, 2011; Hua *et al.*, 2016).

In the subtropics, intensive burning and site preparation are traditional plantation establishment practices and can cause large SOC losses in a short period (Yang *et al.*, 2005; Huang *et al.*, 2013; Guo *et al.*, 2016). Although it is widely recognized that forest conversion can alter SOC storage, the magnitude and direction of SOC change after conversion of natural forest to tree plantation is still uncertain. For example, through a global meta-analysis, Guo and Gifford (2002) reported that when natural forests were converted to conifer plantations SOC decreased by 13 % but there was no significant

change when converted to broadleaf plantations (Guo & Gifford, 2002). Differences in SOC changes associated with the conversion of natural forests to forest plantations have been explained by differences in precipitation, clay mineralogy, and tree species among sites (Don *et al.*, 2011; Powers *et al.*, 2011; van Straaten *et al.*, 2015). Interestingly, although anthropogenic disturbances associated with forest conversion, including harvest regime, residue burning, site preparation, and weeding, are known to have major effects on SOC (Yang *et al.*, 2009; Nave *et al.*, 2011; Guillaume *et al.*, 2015), they have not been invoked to explain cross-site differences in SOC change following forest conversions.

Both Guo and Gifford (2002) and Powers *et al*. (2011) highlighted the lack of studies of forest conversion effects on SOC in tropical regions. Although several studies have examined SOC alteration following forest conversion in Africa, South America, and East Asia recently, they focused on the conversion of natural forests to cash tree plantations, such as rubber, oil palm, and cacao agroforestry plantations, not forest plantations (Chiti *et al.*, 2014; Guillaume *et al.*, 2015; van Straaten *et al.*, 2015). However, the most important driver of forest conversions in the subtropical region of China is the need for forest products and results in tree plantations being planted on former natural forest, with Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) being the single most important plantation species accounting for 63 % of the total forest plantation area of China (SFA 2007). Given the fact that China manages the largest acreage of forest plantations in the world and most of the forest plantations were converted from natural

forests, the lack of studies from this region represents an important knowledge gap in our understanding of the effects of forest conversion on SOC.

In subtropical China, forest conversion typically starts with clear-cutting natural forest followed by slash burning site preparation, and causes large SOC losses through volatilization, water run-off and soil erosion, and increased SOC decomposition after forest conversion (Ma *et al.*, 2000; Andreu *et al.*, 2001; Yang *et al.*, 2005). The large amounts of residues post-harvest, such as small branches and leaves, are left on the site and burned before seedlings are planted which can lead to intensive fires causing SOC volatilization losses as high as 17-27 % in the surface mineral soil (Yang *et al.*, 2005). Furthermore, deforestation followed by burning leaves the post-fire soil unprotected such that soils may experience heavy soil erosion in the following spring and summer rainy season (March to July), during which more than 60 % of the annual rain in southeastern China falls (Yang *et al*. 1998). Slash burning may also kill microorganisms in the surface soil, unlocking carbohydrates which may then stimulate the growth of soil microorganisms later (Knicker, 2007). Few studies have elucidated the relative contributions of these processes on SOC losses following forest conversion in the southeastern region of China.

Soil organic C accumulates through litter and root turnover, and adsorption of dissolved organic carbon on minerals. However, many studies in tropical and sub-tropical regions have found that SOC content decreased in the first few years after forest conversion and then reached a relatively stable but lower level than before the conversion,

never fully recovering to pre-disturbance levels (Chen *et al.*, 2013; de Blécourt *et al.*, 2013; Guillaume *et al.*, 2015). For example, using a 2 to 88-year-old Chinese fir plantation chronosequence in southern China, Chen *et al*. (2013) showed that compared to an adjacent natural forest, SOC content was nearly 30 % lower in a 7-year-old plantation and remained at the low level throughout the chronosequence. Despite the accumulating evidence of reductions in SOC content following forest conversion coupled with a lack of recovery in tropical and subtropical forests, explanations for the underlying mechanisms accounting for these observations remain unclear.

Soil microbes use and respire C from aboveground litter, belowground root exudates and detritus, and soil organic matter (Ryan & Law, 2005). The relative contribution of each component to substrate C for soil microbial activity may affect long-term SOC storage (Binkley & Resh, 1999; Schlesinger & Lichter, 2001; Giardina *et al.*, 2014). If much of the microbial respiration stems from C in litter, root exudates and detritus, one might expect that eventually this flux of C will return to pre-harvest values or even increase as forest plantation regrowth gradually returns these inputs to pre-disturbance levels. In contrast, if much of the heterotrophic C demand is met by soil organic matter, there could be persistent negative effects as SOC storage can take long time periods to recover from disturbance.

In this study, I tried to better understand the processes contributing to the lack of short-term recovery of SOC following conversion of natural forests to Chinese fir plantations in the subtropical region of southeastern China by addressing three questions.

First, what are the magnitude and direction of SOC changes through time? Second, what are the relative contributions of burning and soil microbial respiration to initial SOC losses? Finally, how do the C sources for soil microbial respiration vary through time? A thorough examination of these questions is critical to improve our comprehension of the mechanisms by which conversion of natural forests to forest plantations alters soil C storage. Given the large area that Chinese fir plantations occupy on a global scale, the answers to these questions have implications for the global C budget.

MATERIAL AND METHODS

Study Site

The study site was located at Sanming City, Fujian Province, China. The landscape is characterized by low mountains and hills with an average elevation of 300 m and slope steepness of 25°- 45°. The soil was classified as sandy clay Ferric Acrisol according to the FAO/UNESCO soil classification system (FAO, 2017) and was developed from biotite granite. Subtropical evergreen broadleaved forests are the dominant natural vegetation of this area. The region has a typical maritime subtropical monsoon climate, with annual mean temperature of 20.1 °C and mean annual rainfall of 1670 mm measured between 1959 and 2006, with approximately 80 % of rainfall occurring between March and August (Yang *et al.*, 2018).

The experiment was conducted at a state-owned forest farm in Chenda, Sanming City. Prior to 1958, the area was covered by natural broadleaf forests dominated by *Castanopsis carlesii*. However, with increasing timber demand for use in construction,

the natural forests were gradually logged and have been replaced by plantations (mainly Chinese fir) or allowed to naturally-regenerate into secondary forests (NRS).

Experiment design

In 2011, an area of 1.1 ha within the NRS was selected to study the effects of forest management treatments on SOC dynamics. The 1.1 ha area was divided into nine plots each with an area of 0.12 ha, evenly distributed in the upper, middle, and toe-slope positions. Within these nine plots, three treatments, assisted natural regeneration, Chinese fir plantation, and *Castanopsis carlesii* plantation, were each replicated three times and assigned using a randomized block design blocked by the slope positions. Because the main objective of this study was to explore how the conversion of a natural secondary forest to a Chinese fir plantation affects SOC, I only examined SOC changes associated with the conversion of secondary natural forest to Chinese fir plantation. Thus, this study incorporates only the three plots in Chinese fir plantation treatments and are referred to as young Chinese fir (YCF). The adjacent uncut and naturally regenerated secondary forest (NRS) was treated as the control, and three plots were also arrayed across the same three slope positions. To compare SOC dynamics in young vs. mature Chinese fir plantations, a mature Chinese fir (MCF) plantation, with similar slope positions and aspect 800 m away was identified, and three similar sized plots were established in upper, middle, and toe-slope positions. Because plots in different slope positions are likely to differ in many important factors affecting plant growth and soil properties (e.g., soil moisture, exposure to wind and light), this design minimized the confounding of slope position with

treatments (see below) on my measurements. The two mature forests (NRS and MCF) were both converted from a natural *C. carlesii* forest in 1976 (i.e., both were 36 years old in 2012). Details of the experimental design are described in Yang *et al*. (2018). For this study, I compared SOC among YCF, MCF, and NRS (n=3 in each slope position) to quantify changes due to conversion to Chinese fir plantation and over time. The effects of slash burning on SOC and soil microbial respiration were determined by comparing pre- and post-burning data collected from YCF and comparing post-burn SOC in YCF to MCF and NRS on the YCF immediate post-burn date only (n=3 in each slope position). I assumed there would be no difference in SOC across a one-day time period in the unburned forest treatments (NRS and MCF; see burn details below).

To create the young Chinese-fir plantation plots used in this study, a naturally-regenerated mature secondary forest was clear cut in December 2011 and harvested. Following common management practices in southern China as described by Yang *et al*. (2005), residues (fine branches < 2 mm, twigs <2 mm, and leaves) were evenly spread over the land and tree stumps were left in the field (untreated). After a three-month exposure and drying period, the residues were burned on March 27th, 2012 before spring rains. Fire temperature reached as high as 330 °C in surface soil during prescribed burning in my study. Following burning, the area was planted with Chinese-fir seedlings at a density of 2,860 seedlings per hectare on March 29th, 2012. Following the common practices for establishing Chinese-fir plantations in China, weeds were cut with a wood chopper by hand twice a year, in June-July and again in October-November, in the first

three to five years depending on levels of canopy closure (i.e., when canopy was closed, weeding stopped).

Because burning has the greatest impact on surface soil (Yang *et al*. 1998), the top 0-5 cm surface soil was sampled in each plot to determine the effects of slash burning on SOC concentration. To study the immediate influence of burning on SOC loss, five samples of upper mineral soil were collected from each plot of the YCF using a soil corer (5 cm inside diameter) on March 27th 2012 immediately before the burning and on March 28th 2012 immediately after the burning. To evaluate SOC changes following plantation establishment, I re-sampled surface soil on March 27th, 2013 and March 27th 2017. I also sampled surface soil in MCF and NRS on March 27th, 2012 and 2013, and again five years later on March 29th, 2017. All soil samples were air dried, sieved, and the < 2 mm fraction analyzed for SOC using a Vario MAX CN analyzer (Elementar, German). Because the soil in my study site is very acidic with pH of approximately 4.0, it is assumed that there was no inorganic C present in the soil. Soil bulk density of 0-5 cm soil was measured with a knife ring (diameter 5 cm) in pre-fire, post-fire, and 1-year later, respectively. Rock and gravel (> 2 mm diameter) were sieved from each soil sample. The amount of SOC per unit area was calculated by multiplying SOC concentration by soil bulk density (pre-fire:1.2 g cm^{-3}, and post-fire: 1.0 g cm^{-3}) and soil depth (5 cm).

To evaluate the loss of SOC through mineralization (i.e., soil microbial respiration, Rm) I trenched three randomly selected 1 m × 1m subplots in each plot of the YCF and NRS treatments in April 2010. Roots were excluded by trenching 150 μm fiber net sheets

1 m into the soil to prevent root entry, but which allowed for lateral water movement and mycorrhizal fungi ingrowth. The trenches were back filled with the same soil. The subplots were left undisturbed until March 2012 when prescribed burning was conducted. I assumed that by then the contribution of the remaining roots to total respiration should be minimal. After the trenching was completed, the subplots were kept free of ingrowth of new seedlings and understory vegetation. One polyvinyl chloride (PVC) collar (20 cm inside diameter × 8 cm height) was inserted into the soil to 4 cm depth in each trenched subplot for sampling of Rm, starting on March 28th, 2012. To evaluate the response of Rm to burning, I began my measurements of Rm, from the first day after burning. The rate of Rm (together with soil water content and temperature) was manually measured at each collar from 9:00 am to 12:00 pm using a Li-8100-103 portable CO_2 infrared gas analyzer (LiCor Inc, Lincoln, NE, USA). This timeframe was previously established as the average rate of daytime respiration (Sheng *et al.*, 2010). I initially measured Rm on a daily basis and when the temporal fluctuation became much smaller four months later, Rm was measured biweekly. I assumed that the rate of soil microbial respiration measured biweekly represented the average rate of the two weeks, and the annual flux was the sum of C emitted during all sampling periods.

To detect different C sources used for Rm, I added a high frequency measurement on one collar in the middle slope trenched subplots of the YCF and NRS treatments by automated measurements using Li-8100-104 long-term chamber on a 30-minute basis starting from the 16th month post-burn and lasting for one year (from August 1st, 2013 to

July 31st, 2014). The collar that had the Rm closest to the mean of all collars per treatment in the first 16 months was chosen for the high frequency measurements. The high frequency measurements were used to conduct wavelet analysis (Vargas *et al.*, 2010).

Data analysis

I used a paired t-test to examine the difference of SOC immediately before and after the burning in YCF. For the post-burning measurements, I used a general linear model with repeated measurements to examine the differences of SOC among YCF, MCF and NRS and among different sampling times in 2012, 2013, and 2017, the within group factor. The difference in soil microbial respiration (Rm) flux from manual measurements between the NRS forest (control) and YCF plantation in the first year (i.e., measurements taken at one point in time) was examined using a t-test. For the SOC across forest treatments and the Rm analyses, slope position was included in the initial models, as I anticipated slope may affect my results. However, neither slope nor its interaction with forest treatment were found to be significant; therefore, only forest treatment and time effects are presented. The statistical analyses were conducted using JMP Pro 14 (SAS Institute Inc., USA). Assumptions of normality and homogeneity of variances were checked, and dependent variables were natural log transformed where necessary. All effects were considered significant at the $P < 0.05$ level.

Wavelet analysis has been widely applied in the geosciences for time series data, and has been introduced into soil respiration research in a mixed conifer-oak forest in California and a grassland in New Mexico, USA (Vargas *et al.*, 2010, 2012). The global

wavelet power spectrum, defined as the average variance contained in all wavelet coefficients of the same frequency, provides quantification of the main periodic components of a time series (Torrence and Compo 1998) and can be used to quantify the spectral characteristics of nonstationary time series. The high frequency component of the spectrum (i.e., high turnover rate) may be associated with respiration from immediately available C substrate (Mahecha *et al.*, 2010; Vargas *et al.*, 2012). I used Morlet wavelet as mother wavelet described by Torrence and Compo (1998) to calculate the global wavelet power spectrum of high temporal resolution measurements of Rm (Torrence & Compo, 1998). A mother wavelet is a transformation function that forms the basis for various transformation processes. It could be considered as a windowed function that moves along the time-series signal from time t = 0 to time t =T. The portion of the signal in that window is multiplied by the mother wavelet and then integrated over all times to get the wavelet coefficients. The global wavelet power spectrum was computed using MATLAB_R2018a. Details of the wavelet analysis and the exact procedures are referred to Torrence & Compo (1998) and Vargas *et al*. (2010).

RESULTS

Magnitude and pathways of SOC losses in the early stage of forest conversion

There was no significant difference ($F = 0.045$, $df = 1$, $P = 0.842$) in SOC between the naturally-regenerated secondary forest (NRS) (29.86±1.38 g kg^{-1}, mean ± standard error) and the young Chinese-fir plantation (YCF) forest prior to burning (29.61±1.42 g kg^{-1}). Immediately following the slash burning in the YCF, SOC concentration in the 0-5

cm soil declined significantly by 5.06 g kg^{-1}, or 15.2%, from 29.61 g kg^{-1} to 24.55 g kg^{-1} ($t = 5.774$, $df = 2$, $P = 0.029$), representing a loss of 3.04 t C ha^{-1}. The post-burning SOC concentration was not different between soils of the YCF and mature Chinese-fir plantation (MCF) but both were significantly lower than that of NRS and remained that way for the duration of the study (Figure 3.1). There was no significant difference in SOC among the three post-burn sampling years for any forest type (Figure 3.1). Although SOC appeared lower one year after burning compared to immediately after the burning in YCF (Figure 1A), the difference was not statistically significant ($P = 0.162$).

Slash burning stimulated soil microbial respiration (Rm) in YCF compared to that measured in NRS in the first year post-burn (Figure 3.2A). C efflux through Rm was 2.00 t C ha^{-1} or 39 % higher in the YCF (6.41 t C ha^{-1}) than the NRS (4.41 t C ha^{-1}) from April 2012 to August 2012 (Figure 3.2B). The difference between forest types became non-significant five months post-burning. Although the difference between treatments became significant again between December 2012 and April 2013, soil microbial respiration in both forests was considerably lower during this period than in the first five months following the burning, and there was no difference between the two forests when integrated over these months.

Global wavelet analysis of soil microbial respiration

From high temporal resolution measurements of soil microbial respiration between August 2013 to July 2014, average annual soil microbial respiration in NRS (10.06 t C ha^{-1} y^{-1}) was 65 % higher than YCF (6.51 t C ha^{-1} y^{-1}). The differences in Rm between the

two forests were most pronounced in the main rainfall and growing seasons between March and July (Figure 3.3A). This corresponded to the period when temperature and soil water content were high (Figure 3.3B &C). Differences in soil microbial respiration between the two forests were much reduced in the dry period from August 2013 to October 2013 and dry and cold period from December 2013 to February 2014 in the next year. (Figure 3.3).

The global wavelet spectrum derived from the high frequency measurements of soil microbial respiration indicated that soil microbial respiration in both YCF and NRS had a 24 hour periodicity (Figure 3.4a & d); however the power, which reflects the number of times that the periodicity occurred, was nearly 4x greater for NRS than YCF (Figure 3.4a & d). In addition to the 24-hour periodicity, YCF had another peak of periodicity at nearly 72 hours during the rainy season (Figure 3.4b), which was not evident in the NRS (Figure 3.4e). In contrast, both forests had similar, limited periodicity during the dry and cold season (Figure 3.4c and 4f).

DISCUSSION

SOC losses in relation to human disturbance associated with plantation establishment

Despite the rapid expansion of forest plantations on former natural forest sites in the tropics and subtropics, the effects of forest conversion on SOC have not been well quantified. In the meta-analysis of the effect of land-use change on tropical soil C stocks by Powers *et al*. (2011), only 7 % of the observations involved natural forests replaced with forest plantations. In my study a total of 28 % of the SOC was lost in the first year

following forest conversion, 11% (3.04 t C ha^{-1}) through fire-associated volatilization (i.e., the difference immediately before and after slash burning), 7 % (2.0 t C ha^{-1}) through stimulated microbial respiration during the first 5 months post-burn, and 10% (2.6 t C ha^{-1}) via erosion (from Yang *et al*. 2018), respectively. The 28 % loss of SOC following forest conversion in my study is in alignment with the 19.8 %-38.0 % losses reported in several studies in subtropical Australia and China (Chen *et al.*, 2004; Yang *et al.*, 2009), but are considerably greater than the -20% to +10% change reported for the conversion of tropical forests to forest plantations by Powers *et al*. (2011). Such differences highlight the need for a more comprehensive survey and mechanistic understanding of the effects of forest conversion on C sequestration because the effect varies considerably between regions, which could affect the contribution of forest conversions to plantation to the calculation of the global C budget.

The large loss of SOC immediately following forest conversion and the lack of difference in SOC content between young (1-5 yrs old) and mature (35-40 yrs old) Chinese-fir stands (Figure 3.1) suggest that SOC does not recover to pre-burn NRS levels for more than three decades. The finding of high SOC loss immediately following forest conversion is similar to that of other studies in the tropics and subtropics (Yang *et al*., 2004; Solomon *et al*., 2007; Chen *et al*., 2013; de Blécourt *et al*., 2013). For example, following the conversion of forests to rubber plantation, 24 % of SOC was lost in the first three years, but only an additional 3 % of SOC was lost in the next 7 years (Yang *et al*., 2004). Many studies have reported that the reduction of SOC associated with the

conversion of tropical forests to cash tree plantations is related to management practices such as fruit harvest and litterfall exclusion (Chiti *et al*., 2014; Guillaume *et al*., 2015). The results from my cross-year measurements in the young and mature Chinese fir plantations provide the first evidence indicating that slash burning, a common practice in forest conversion, has an immediate, and pervasive effect on SOC loss that cannot be erased thirty years after forest conversion.

The loss of SOC by slash burning depends on the intensity of fire, which is influenced by surface fuel abundance and quality, fuel moisture, and rate of spread (Yang *et al.*, 2005; Wang *et al.*, 2016). In most of subtropical China, harvest residues are left on the soil surface under the sun for several months. In my study site, the amount of residues was 15.3 t C ha^{-1} (Yang unpublished data) which was comparable to the fine wood fuel amount reported in wildfire (Raymond & Peterson, 2005). At my site, most of the harvest residues are fine woody debris and leaves that burn easily (Yang *et al.*, 2005) and can reach temperatures (330 °C) higher than that required for SOC volatilization (220 °C - 315 °C, Knicker 2007; Yang *et al*., 2005).

In addition to the fire-induced volatilization of SOC, the increased soil microbial respiration measured in the first 5 months after slash burning may have contributed 26 % of total loss of SOC. Temperature is a possible driver of the increases of Rm in the slash burning site as soil temperature was higher due to low plant coverage and low shade following the burning (Figure 3.3). However, if temperature is key, I would expect to see increases in Rm between August and October, not the decreases I observed (Figure 3.2).

It is also possible that burning and subsequent liming (also common in this region) altered soil pH and the availability of nutrients (Knicker, 2007), or that microbes were responding to carbohydrates released from cell lysis caused by burning (Certini, 2005; Dooley & Treseder, 2011) or to reductions in plant-microbe competition for nutrients. Furthermore, the addition of ash and carbohydrates following slash burning may stimulate soil microorganism activity, and increase SOC decomposition through priming effects, especially in deep soils (Fontaine *et al.*, 2007). Ash-induced increases of Rm may be further maximized by the absence of plant competition for soil water and nutrients in the first five months of Chinese fir plantation.

In this study, I found that SOC content in Chinese fir plantations did not recover to the level in the adjacent natural forest even > 30 years after the forest conversion. Despite continuous input of both above- and below-ground C to the soil over the > 30 years study period, SOC levels in the Chinese fir plantation did not change with time, suggesting that little of the new plantation-derived added C was retained in the soil. This result is similar to that observed in a FACE experiment in the Duke forest where high CO_2 concentrations increased foliage production and the litter layer, but had no effect on SOC in mineral soil (Powers & Schlesinger, 2002). Similarly, a study in a *Eucalyptus* woodland in Australia reported no effects of CO_2 enrichment on SOC, and soil microbial biomass and activity, although it increased canopy photosynthesis and soil respiration (Drake *et al.*, 2016). That study suggested that the increases of soil respiration came from photosynthate that was transported belowground (Drake *et al.*, 2016). Studies of

belowground C cycling in some tropical forests have also suggested that most of the belowground C allocation was returned to the atmosphere by soil microorganisms, despite the overall increase of gross primary productivity with warming (Giardina *et al.*, 2014). Regardless of the exact causes, the lack of changes in SOC in the afforested site with time indicates that the initial loss of SOC following forest conversion cannot be remediated in several decades, which has major implications for soil C dynamics following forest conversion.

Forest conversion changes C sources for soil microorganisms

The short (24-hour) periodicity of Rm in the global wavelet spectrum is often attributed to rapid turnover of carbohydrate from photosynthesis (Mahecha *et al.*, 2010; Vargas *et al.*, 2012). This implies that newly formed carbohydrate from photosynthesis was an important source of C for microbial respiration in both YCF and NRS stands and suggests that plant activity plays an important role in soil microbial respiration, particularly in the NRS, where the 24-hour periodicity was 4x stronger than in YCF. This finding is consistent with others who have shown that spatial and temporal variation of soil CO_2 is influenced by newly formed photosynthate (Steinmann *et al.*, 2004; Tang *et al.*, 2005). Using a dual isotope (^{13}C and ^{14}C) pulse label technique, Carbone & Trumbore (2007) found that more than half of new photosynthetic C was respired in 24 hours in Owens Valley, US (Carbone & Trumbore, 2007). I was able to detect the difference in power of 24-hour periodicity between NRS and YCF during the rainy season, which contributed most of the annual difference in Rm between the two treatments because there

was no difference in the power of 24-hour periodicity in the dry season. In addition, most of the differences in soil microbial respiration observed in the second year following the burning between these two forests also occurred in rainy season, which supports that carbohydrates from photosynthesis were an important determinant of soil microbial respiration. Thus, I was able to detect the possibility of using carbohydrates formed within 24 hours as the main C sources for soil microbes in subtropical forest based on high frequency measurements of soil microbial respiration.

The lower 24-hour periodicity in YCF, coupled with another 72-hour periodicity appearing during the rainy season that was not measured in the NRS treatment indicated less reliance on active photosynthate and a greater importance of other C sources for soil microorganisms in YCF. While my plots were trenched and lined in an effort to separate root and microbial sources of respiration (Rey *et al.*, 2002; Wang & Yang, 2007; Drake *et al.*, 2012), which presumably should have reduced the photosynthate signal in my dataset as my liners did not allow re-growth of roots into the plots, my liners do not exclude fungi nor do they prevent the transport of root exudates and litter breakdown products into the plots via soil water movement. Root-associated mycorrizhae, which have access to photosynthate, could be contributing to the strong diurnal signal observed in my data, or newly formed photosynthetic C (e.g., root exudates) may have been moving into the plots with soil water. Both possible sources are likely greater under the older, more established NRS than the YCF, and thereby might have contributed to the stronger diurnal signal seen in NRS.

The 72-hour periodicity observed in the YCF, but not the NRS, during the rainy season indicates that microbes in the YCF were utilizing different C sources to support their activity. Longer periodicity has been suggested to reflect the use of low turnover rate C sources (Vargas *et al.*, 2012). In other words, while NRS mostly used newly derived photosynthates for Rm, soil microorganisms in YCF used both newly formed photosynthates (24-hour periodicity) and SOC for respiration (72-hour periodicity). There are at least three possible causes driving my conclusion for the use of older C sources by soil microbes in YCF. First, the transport of photosynthates into soil through root exudates or mycorrhizal symbionts from plants outside the trenched plots was likely reduced by intensive slash burning. Burning has been shown to negatively affect mycorrhizae, destroying propagules when soil temperature exceeds 94 °C (Neary *et al.*, 1999; Xiang *et al.*, 2015). In addition, the younger trees in YCF likely had less belowground C allocation and, therefore, less newly formed photosynthates were available for transport into the plots and used by soil microbes, causing microbes to potentially seek out other sources of carbohydrates (Ekblad & Högberg, 2001; Högberg & Högberg, 2002; Giardina *et al.*, 2014). Second, slash burning and other site preparations (e.g., hole digging) have been shown to disrupt stability of soil aggregates, which may mobilize protected C thereby making it more available for soil microbes in forests experiencing those disturbances (Mataix-Solera *et al.*, 2011; Mastrolonardo *et al.*, 2015). Third, weeding, a common management practice in young forest plantations, killed much

of the understory vegetation, further cutting off transport of photosynthates into soil and requiring microbes to utilize other C sources (Tang *et al.*, 2005; Högberg & Read, 2006).

CONCLUSIONS

My study showed that slash burning, commonly practiced in the conversion of subtropical natural forests to Chinese fir plantations, induced a total of 28 % SOC loss in the first year and did not recover to the levels measured pre-burning decades later. I also found that slash burning applied during forest conversion in a subtropical forest changed substrate available C sources for soil microbes, which accelerated SOC mineralization in young Chinese fir plantation. My results highlight that the establishment of tree plantations in subtropics can dramatically reduce SOC by slash burning with long-lasting effects on SOC recovery.

TABLES AND FIGURES

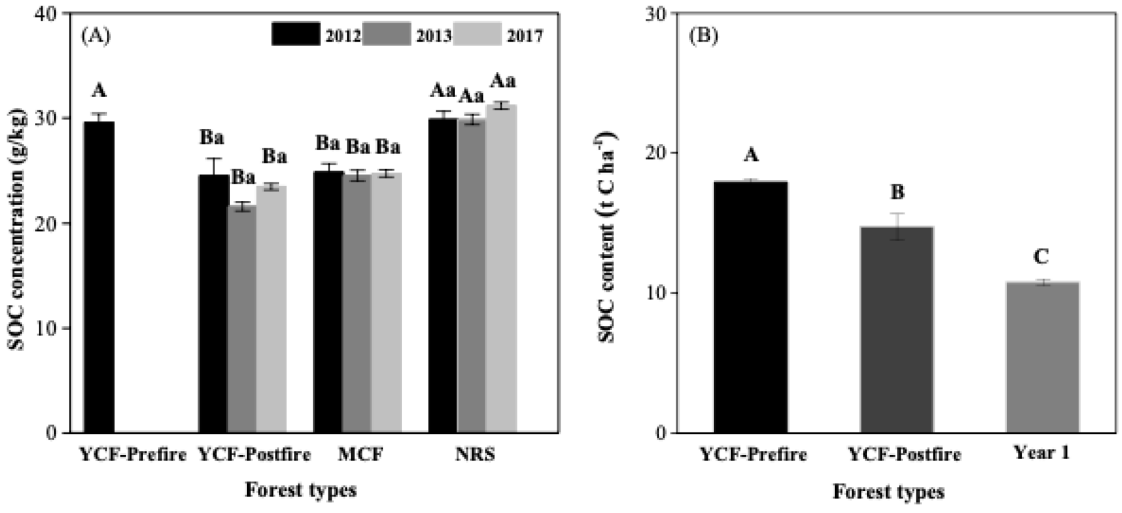

Figure 3.1 (A) Soil organic carbon (SOC) concentration of young Chinese fir plantation (YCF), mature Chinese fir plantation (MCF) and naturally regenerated secondary forest (NRS) measured in three years. Note that the measurements in 2012 were taken after the burning in the YCF, when both the MCF and NRS were 35 years old. (B) soil organic carbon content changed before and after prescribed burning, and 1 year later on young Chinese fir plantation. Error bars reflect ±1 SE (n=3). The capital letters indicate significant differences in SOC among forests within the same years.

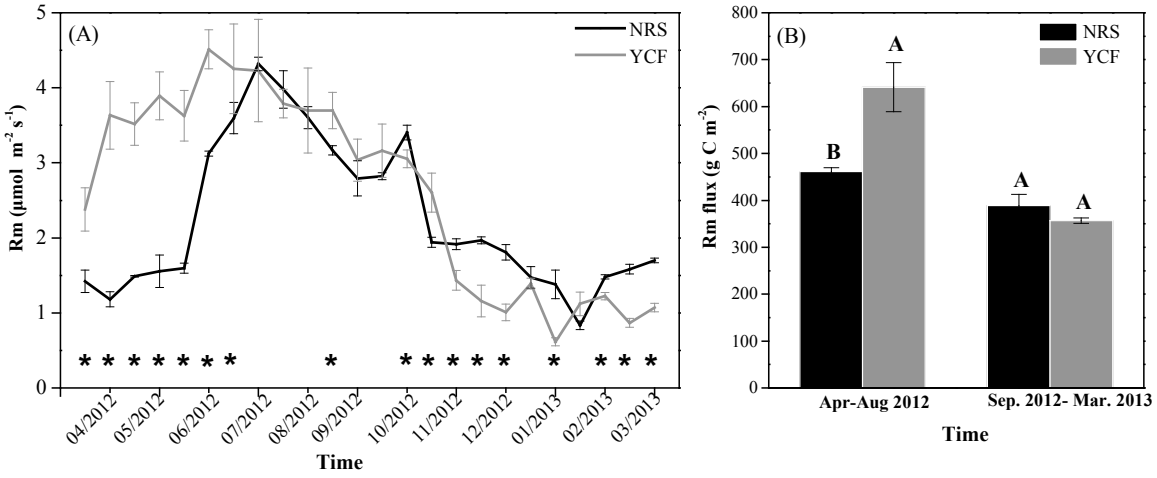

Figure 3.2 Soil microbial respiration rate and CO_2 fluxes between mature naturally regenerated secondary forest (NRS) and young Chinese-fir plantation (YCF) in the first year following burning. Error bars reflect ±1SE (n=3). The star symbols indicate significant differences in soil microbial respiration between the two treatments (2A). Capital letters indicate soil microbial respiration differences between forest types during two different time periods following burning (2B).

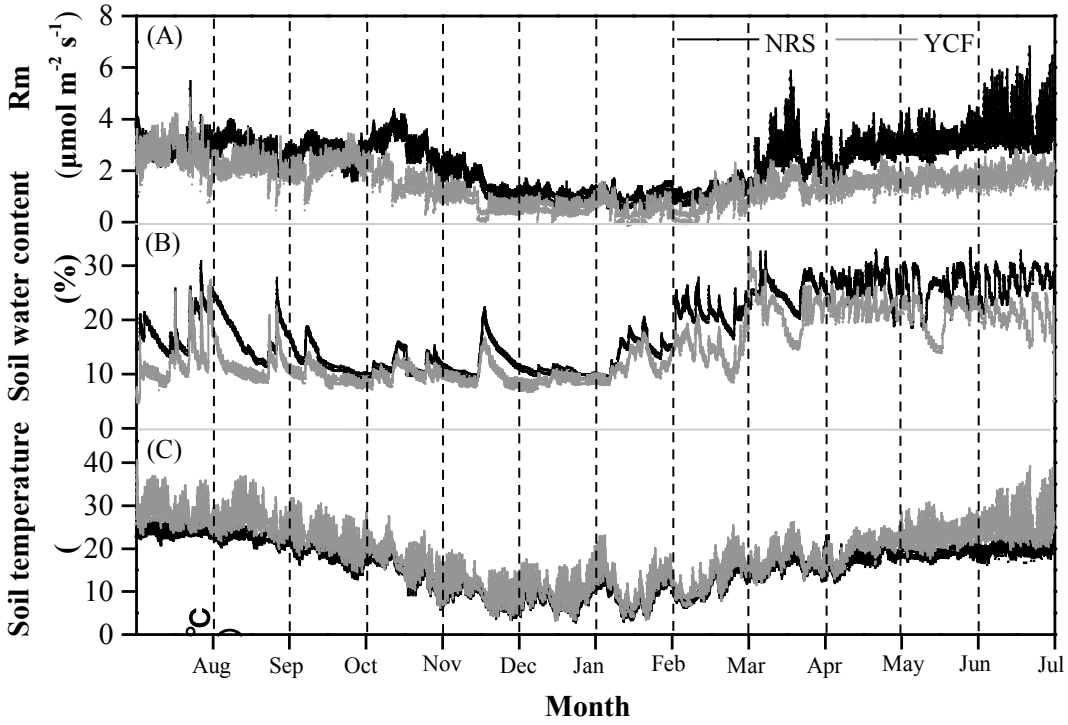

Figure 3.3 High temporal resolution of soil microbial respiration (Rm), soil temperature, and soil water content between natural regenerated forest (NRS) and young Chinese fir plantation (YCF) from August 2013 to July 2014.

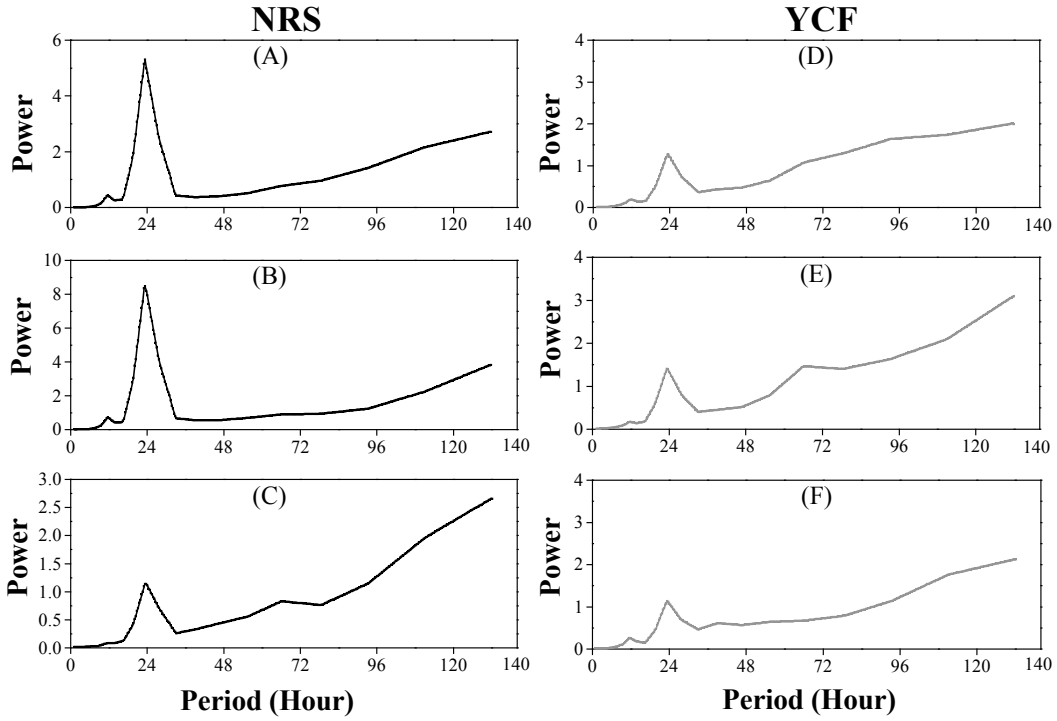

Figure 3.4 Global wavelet power spectrum of soil microbial respiration signals in a mature natural regenerated secondary forest (a-c) and young Chinese-fir plantation (d-f) from August 2013 to July 2014, by year (a, d), monsoon rainy season (March-July) (b, e), and monsoon dry season (August – next February) (c, f). Note that the y-axis scales differ across panels, to better illustrate peaks.

CHAPTER FOUR: VARIATION IN FOREST PRODUCTIVITY INFLUENCES RHIZOSPHERE SOIL ORGANIC CARBON IN A CHINESE FIR PLANTATION IN SOUTHEASTERN CHINA

ABSTRACT

Tree plantations worldwide are a critically important terrestrial carbon (C) sink. Previous studies on the capacity of tree plantations to sequester atmospheric CO_2 have mostly focused on aboveground biomass accumulation; the importance of soil organic carbon (SOC) to C sequestration remains relatively poorly understood. Living root C inputs influence SOC via plant-microbe interactions in the rhizosphere and play an essential role in nutrient cycling. Here, I examine changes in bulk and rhizosphere SOC and other soil nutrients across three developmental stages of Chinese fir plantation (6, 18, and 42 years old) in subtropical China and relate observed trends to differences in net primary productivity (NPP). SOC was separated into labile and recalcitrant C components using the acid-hydrolysis method. I also measured total and available nitrogen (N) and phosphorus (P), soil microbial biomass C and N, and C, N, and P-related enzymes. Soil organic C concentration in bulk soils did not vary significantly with NPP, but SOC concentration in rhizosphere soils was higher in young (6 yrs) and mature (42 yrs) stands, both of which had lower NPP compared to middle-aged stands (18 yrs). Labile and recalcitrant C pools in rhizosphere soils were lowest in the highest NPP stand (18 yrs). The decoupling of NPP from rhizosphere SOC concentrations may be driven by N and P tree growth requirements, belowground C allocation, and resultant microbial activity in this highly weathered subtropical soil. Positive correlations between labile C pools and MBC/MBN in the rhizosphere soil of the young stands suggests a tight linkage between

belowground C allocation and SOC dynamics. In mature stands, recalcitrant C pools in rhizosphere soil were positively correlated with total P, suggesting the importance of soil P in determining soil microbial characteristics, such as low microbial C/N and high enzyme activities, that stimulated the transformation of root-derived C to microbial residue and stable SOC formation. The relationships between forest NPP and rhizosphere SOC pools suggest top down regulation of SOC sequestration in a subtropical plantation forest mediated through tree demands for N and P. Accurate predictions of SOC sequestration dynamics in Chinese fir plantations require an improved understanding of rhizosphere processes during plantation development.

INTRODUCTION

Soil organic carbon (SOC) is the largest terrestrial carbon (C) pool, accounting for twice the C stocks of the atmosphere and terrestrial vegetation combined (Dixon *et al*., 1994; Jobbagy & Jackson, 2000). Continued SOC storage in forest ecosystems plays a vital role in mitigating climate change and is also essential for promoting soil structure, soil fertility, and plant productivity. Globally, the growth of tree plantations has been identified as the most effective method to mitigate climate change, with the potential to absorb two-thirds of C emissions by human activity since the industrial revolution (Bastin *et al*., 2019). Although the factors that control C sequestration in tree plantation biomass are relatively well understood, there is considerable uncertainty regarding SOC accumulation.

Plant C inputs from above- and belowground, which are controlled by plant productivity, are the primary sources for SOC sequestration (Cotrufo *et al*., 2013; Castellano *et al*., 2015). Although we have a good understanding of the mass loss rate

and nutrient release of plant residues during decomposition, the role of incorporation of plant residues into SOC pools is still poorly understood and often neglects the influence of recent photosynthate from live root exudates on SOC sequestration (Sulman *et al*., 2014; Sokol & Bradford, 2019). Root exudates contain higher concentrations of labile C than plant residues, including low molecular weight carboxylic acids, amino acids, and carbohydrates. These compounds can stimulate the formation of stable SOC pools because they promote high microbial use efficiency and high microbial residue production (Cotrufo *et al*., 2019; Sokol & Bradford, 2019). In fact, a new model suggests that bulk and rhizosphere soils have different mechanisms of SOC formation (Sokol & Bradford, 2019). Bulk SOC is thought to accrue through the direct sorption of plant residues to mineral surfaces, due to low soil microbial density and activity limiting microbial decomposition of plant material. Conversely, the enrichment of microbes in rhizosphere soils drives the high biogeochemical activity often observed there (Phillips *et al*., 2013; Finzi *et al*., 2015; Sulman *et al*., 2017; Sokol *et al*., 2019), and benefits the sequestration of stabilized microbial residues and mineral-protected SOC in this zone (Cotrufo *et al*., 2013; Castellano *et al*., 2015; Lavallee *et al*., 2019). Thus, there is a growing awareness of the need for adding the processes occurring in rhizosphere soil into global terrestrial C cycle models (Sulman *et al*., 2014; Terrer *et al*., 2018). This may be especially important in tropical and subtropical forests, which have higher plant productivity and a more extended growing season than other forests, but a relatively low quantity and quality of bulk SOC (Giardina & Ryan, 2000; Crowther *et al*., 2019). Soil microbial activity is highly reliant on living root inputs in these systems, with the rhizosphere having been found to contribute nearly 90 % of total soil respiration in tropical ecosystems, and may therefore be particularly important in determining relative

contributions to labile and recalcitrant soil C pools (Trumbore, 2000; Giardina *et al*., 2014).

Studies in tropical and subtropical forests have found that, despite observing changes in above- and belowground C inputs across both a plantation chronosequence and a warming experiment, bulk SOC was not affected (Chen *et al*., 2013; de Blécourt *et al*., 2013; Giardina *et al*., 2014; Li *et al*., 2018). These findings were similar to the results of a FACE experiment in the Duke forest, where elevated CO_2 led to increased plant biomass C accumulation but not bulk SOC (Schlesinger & Lichter, 2001; Drake *et al*., 2016; Kuzyakov *et al*., 2019). Because increased plant residues both above- and belowground did not appear to lead to an increase in SOC, it was hypothesized that increases in root exudates, rhizodeposits, and/or increased investment to symbiont mycorrhizal hyphal production stimulated SOC decomposition (the so-called priming effect) (Phillips *et al*., 2012; Sulman *et al*., 2014), to meet the nutrient demand of increased plant productivity and soil microorganisms under elevated CO_2. Most studies examining the effects of belowground C on nutrient availability have focused on temperate forests with abundant ectomycorrhizal fungi species (ECM) (Chapman *et al*., 2006), where N availability is often a limiting factor for tree growth. In contrast, highly weathered tropical and subtropical forest soils typically have relatively high abundances of inorganic N but are strongly limited by P availability (Vitousek, 1984; McGroddy *et al*., 2008). Phosphorus is an essential element for plant growth and soil microbial activity, and P limitation is one of the most critical factors influencing plant growth and soil microbial activity in tropical and subtropical forests, where P is present in low concentrations and is relatively immobile (McGroddy *et al*., 2004; Cleveland & Townsend, 2006; Li *et al*., 2006). Thus, P availability may be of primary importance in governing plant productivity, belowground

allocation, and SOC sequestration in forests of the tropics and subtropics. Increases in tree growth or areal plantation expansion in these areas, occurring in response to climate change or economic and policy changes, may exacerbate P limitation.

China has the largest area of tree plantations in the world, and nearly 35% of these forests are less than 20 years old (Tang *et al*., 2018). Most tree plantations in China are monocultures and located in the subtropics; within that region, Chinese fir (*Cunninghamia lanceolata*) is the primary species. Previous studies have reported no SOC accumulation in mineral bulk soil across a Chinese fir plantation chronosequence spanning 88 years, despite increases in litter and fine root inputs stemming from increasing above- and belowground productivity with time (Chen *et al*., 2013). These studies also found that bulk soil respiration did not change among different plantation ages, but rhizosphere soil respiration was dynamic with time (Chen *et al*., 2016). Fine root biomass had positive linear relationships with microbial metabolic quotients (qCO_2), suggesting a strong influence of labile C inputs, mediated by forest productivity, on soil microbial activity and efficiency (Chen *et al*., 2013, 2016). To date, changes in rhizosphere SOC with time have not been quantified. In this study, across three different aged Chinese fir plantations [six years old (young), 18 years old (middle-aged), and 42 years old (mature)] that also differed in net primary productivity (NPP), I examined the mechanisms by which plant-microbe-soil interactions influence SOC concentration in highly weathered subtropical forest soil. I hypothesized that rhizosphere SOC concentration would differ with NPP, due to differences in fine root inputs, microbial activity, and related nutrient cycles.

MATERIAL AND METHODS

Site description

I conducted this study at a state-owned forest farm (26° 19'N，117° 36'E) in Chenda, Sanming City, Fujian Province, China. Based on the records of the local meteorological office and forestry department, the mean annual temperature is 20.1 °C with a mean annual rainfall of 1670 mm from 1959 to 2016, with most of the precipitation (80 %) occurring between March and August. The natural vegetation is subtropical moist evergreen broadleaved (SMEB) forest, and dominant tree species include *Castanopsis carlesii, Schima superba*, and *Cinnamomum camphora*. Soil at this site is sandy clay Ferric Acrisol according to the FAO/UNESCO soil classification system (FAO, 2010), developed from biotite granite. The soil profile exceeds 1 m in thickness in most areas. Chinese fir is the dominant species in tree plantations in this region, typically planted as a monoculture. The stands of Chinese fir used in this study were selected because they were converted from the naturally-regenerated secondary forest using standard practices for Chinese fir plantation management in southern China, consisting of clear-cutting, slash burning, digging to plant seedlings, and a scheduled weeding before the canopy closes, approximately three to five years after Chinese fir seedlings were planted. An additional thinning, conducted at 10-15 years old, is used to remove suppressed trees.

I used a 'space-for-time' substitution experiment design, with young, middle-aged, and mature Chinese fir plantations that were 6, 18, and 42 years old in 2018, respectively. Within each of the three stands, I established three experimental plots, each 20m × 20m. In all nine plots, the diameter at breast height (DBH) and tree height were measured each December since 2012 when the young plantation was established, and the components of tree biomass (stem, branch, and coarse root) were calculated by allometric equations that were established in a previous Chinese fir chronosequence study (Chen *et al*. 2013). Litterfall was collected in six litter traps (50 cm × 50 cm) per plot every two weeks, and

fine root production was monitored using six minirhizotrons per plot to capture changes in fine root length to a depth of 60 cm; minirhizotron images were collected at monthly intervals and processed using BTC ICAP imaging software to record root diameter, new root production, length of live roots and root mortality (I-CAP version 4.01, Bartz Technology Corp. CA).

Soil sampling protocol

Soil samples were collected in June of 2018 from each of the three 20 m × 20 m replicate plots for each stand (n = 9 plots). I chose June for soil sampling because it is the peak of the growing season and coincides with the highest rates of aboveground biomass accumulation and fine root turnover for Chinese fir (Chen *et al*. 2016). Using the tree census data collected in each plot, we selected five trees with average tree height and DBH for the plot. Five to seven soil and root samples were collected under each tree. At each sampling point, I removed the organic layer and carefully followed the direction of root growth to find fine roots (< 2 mm diameter) still attached to the tree, as this is likely the most active area for root uptake (Yang *et al*., 2004). In this location, I collected surface soil (0-20 cm depth) using a 10cm diameter corer, because most Chinese fir fine roots are in the top 20 cm soil layer (Chen *et al*., 2013).

Soil samples were processed within 24 h of collection, separating the soil samples into rhizosphere and bulk soil fractions. Soils from all five tree replicates were composited for each replicate plot into a sorting basin where large aggregates were gently broken by hand. I carefully collected fine roots and the adhering rhizosphere soil from the basin, shaking gently to remove loose soil. Soil adhering to fine roots after gentle shaking was defined as rhizosphere soil; the adhering soil was gently scraped and picked off of fine roots using tweezers. The soil not adhering to fine roots was defined as bulk soil.

After separation, the bulk soil fraction was sieved through a 2 mm mesh. Soil pH value in H2O (Soil: water ratio 1:2.5) was determined using pH meter (PHS-3B). In brief, 4 g air-dry soil was added to each tube with 10 mL water for three replications. The solution was shaken for 10 minutes (250 rpm), then allowed to stand for 30 minutes. Soil moisture was expressed on a gravimetric basis; 10 g of moist soil (< 2 mm) was weighed and dried at 105 °C for 12 hours.

Soil organic carbon fractions

I used the acid hydrolysis method to separate SOC into different C fractions (Rovira & Vallejo, 2002). In brief, to obtain labile C pool I (LPI-C), about 0.5 g of air-dried soil was passed through a 2 mm sieve and then hydrolyzed with 20 mL of 5 N H_2SO_4 for 30 min at 105 °C in a Teflon tube. The hydrolysate was centrifuged for 10 min at 4000 rpm, and the solution was collected. Twenty mL of deionized water was added to the residue and centrifuged. Both hydrolysates were mixed and passed through a 0.45 μm glass fabric filter for C concentration measurement by TOC analyzer (Shimadzu, Japan).

To separate labile C pool II (LPII-C), the remaining residue of the first step was hydrolyzed with 2 mL of 26 N H_2SO_4 for 12 hours at room temperature on a continuous shaking bed. Then, the solution was diluted with deionized water to 2 N, and samples were hydrolyzed for another 3 hours at 105 °C. The hydrolysate was centrifuged for 10 mins at 4000 rpm, then filtered through 0.45 μm glass fabric filter, and C concentration measurement by TOC analyzer (Shimadzu, Japan).

The remaining residue was washed with deionized water three times, then transferred to a pre-weighed plate, and dried at 60 °C for 24 hours. This fraction was regarded as the recalcitrant C pool (RP-C), and carbon and nitrogen concentrations of RP-C were determined using C/N analyzer (ElementarVario, MAX, Germany).

Total SOC and N were also determined using the C/N analyzer (ElementarVario, MAX, Germany). Soil samples were analyzed for total P by $HClO_4$-H_2SO_4 digestion and extractable P by Mehlich-3 (Kuo, 1996; Mehlich, 1994). The P concentrations in all extracts were measured using a continuous flow analyzer (SKALAR san++, The Netherlands).

Dissolved organic carbon/nitrogen (DOC/DON), microbial biomass carbon/nitrogen (MBC/MBN), and ammonium (NH_4^+) and nitrate (NO_3^-)

Dissolved organic C and DON were extracted by deionized water. Briefly, 20 mL deionized water was added to 5 g of fresh soil to make a solution. The solution was shaken for 30 min at 250 rpm, then centrifuged for 10 min at 4000rpm. The supernatant was collected and passed through a 0.45 μm glass fabric filter. The C and N concentrations in solution were measured using a TOC analyzer (Shimadzu, Japan) and a continuous flow analyzer (SKALAR san++, The Netherlands). The pentose and hexose concentrations of DOC were measured following the procedure in Carter and Gregorich (2006). In brief, for hexose analysis, 1 mL of DOC sample was added to a 10 mL glass test tube with 2 mL of anthrone-sulfuric acid reagent. The mixture was vortexed and left at room temperature for 15 minutes. The absorbance was read at 625 nm in a spectrophotometer. For pentose measurements, 1 mL DOC solution was added to 1 mL iron chloride reagent and 1 mL of orcinol reagent in a glass test tube, kept in a water bath at 95 °C for 20 minutes, and then incubated in ice water for 5 minutes. After that, 2 mL of 95 % ethanol was added to the mixture and vortexed. The absorbance was read at 660 nm by a spectrophotometer. Pentoses are primarily composed of plant-derived carbohydrates, whereas, hexoses are mainly of microbial origin. Thus, the hexose/pentose ratio is

considered a useful index illustrating the relative contribution microbially-derived carbohydrates in dissolved organic matter.

Soil ammonium (NH_4^+) and nitrate (NO_3^-) were extracted using 2N KCl. The procedure was the same as the process of DOC extraction. NH_4^+ and NO_3^- were measured using a continuous flow analyzer (SKALAR san++, The Netherlands).

MBC and MBN were determined using the chloroform (CH_3Cl_3) fumigation and potassium sulfate (K_2SO_4) extraction techniques (Brookes *et al*., 1985). Briefly, 5 g fresh soil was weighed and placed in a dark vacuum container with $CHCl_3$ fumigation for 24 hours, paired with unfumigated controls. The unfumigated controls were extracted with 20 mL 0.5N K_2SO_4 immediately when fumigation started. All soil solutions were centrifuged for 10 min at 4000 rpm, and the supernatant was collected and filtered by a 0.45 μm glass fabric filter. The C and N of the solution was measured using a TOC analyzer (Shimadzu, Japan) and a continuous flow analyzer (SKALAR san++, The Netherlands). MBC and MBN were calculated by the difference between the fumigated and unfumigated samples, using the conversion factor for C of 0.45 (Back *et al*., 1997) and for N of 0.54 (Brookes *et al*., 1985). Data were expressed as μg C/N g^{-1} oven-dry soil (Drake *et al*. 2016).

Soil enzyme assays analysis

I analyzed six enzymes that are relevant to C, N, and P release from the labile and recalcitrant components of soil organic matter. Beta-glucosidase (βG) and cellobiohydrolase (CBH) are C-degrading enzymes that release glucose from cellulose and degrading cellulose, respectively. β-1,4-N-acetylglucosaminidase (NAG) is a hydrolytic enzyme and releases N-bearing polymers from cell walls of soil organisms, which is associated with the decomposition of chitin. Acid phosphatase (AP) is relevant

to the release of inorganic P from organic P. Both phenoloxidase (PHO) and peroxidase (PEO) oxidize recalcitrant C pools, such as lignin and humic compounds. Enzyme assays were based on the processes used in Saiya-Cork *et al*. (2002). The subsamples of rhizosphere and bulk soil for enzyme assays were kept at -20 °C and enzyme assays were performed within 48 hours after soil sampling. The substrates for enzyme assays are shown in Table 4.1.

In brief, 1g of soil was weighed into 125 mL 50 mM (pH= 5.0) acetate buffer and homogenized for 10 minutes using a magnetic stirrer. 200 µL aliquots were dispensed into 96-well microplates; each soil had 16 replicates for each enzyme assay. For the four hydrolase analyses, 50 µL of 200 µM of each enzyme substrate solution was added to each sample well, and acetate solution as the blank. In total, there were eight replicate wells for each negative control (50 µL substrate solution (10 µM 4-methylumbelliferone or 7-amino-4-methyl coumarin) + 200 µL sample suspension), quench standard (50 µL standard + 200 µL sample suspension) and blank (50 µL acetate buffer + 200 µL sample suspension). All the microplates were incubated in the dark at 20 °C for 4 hours. Then 10 µL aliquots of 1.0 N NaOH was added to each well to stop the reaction. Hydrolase activities were measured by a microplate fluorescence photometer with 365nm excitation and 450 nm emission filter. After correction with the negative control and quenching standard, the enzyme activity was quantified by the units of nmol h^{-1} g^{-1}. For the PHO and PEO assays, DOPA was used for the substrate. 50 µL 25 mM DOPA was added to each well, and an additional 10 µL H_2O_2 was added to each well for PEO analysis. Overall, there were 16 replicate wells for each soil solution (50 µL DOPA + 200 µL sample suspension), 8 replicates for negative control (50 µL DOPA + 200 µL acetate buffer) and eight replicates for blank (50 µL acetate buffer + 200 µL sample suspension). We

incubated all the microplates in the dark at 20 °C for 18 hours, using the same method to stop the reaction as above. A microplate fluorescence photometer with 450nm excitation was used to measure the oxidase activities.

Statistics

I used two-way ANOVA to test for the effects of forest age (three levels: 6-, 18- and 42-years old) and soil source (two levels: rhizosphere and bulk soil) on the SOC concentration, SOC fractions, total and available N and P, and soil microbial biomass and enzymes. The least significant difference (LSD) test was used when the ANOVA revealed significant differences in forest age and soil sources, with significant differences determined as $P < 0.05$. All analyses were conducted using JMP Pro 14.0 (SAS Institute Inc., USA).

To test possible abiotic and biotic predictors of SOC concentration and fraction, redundancy analysis (RDA) was conducted to evaluate the influence of soil abiotic and biotic factors on SOC concentration variation with CANOCO 5.0 for windows in bulk and rhizosphere soils separately.

RESULTS

NPP dynamics, and SOC and nutrient concentrations in bulk and rhizosphere soils

Net primary productivity (NPP) in the middle-aged (18 yrs) Chinese fir plantation was 1.61 and 1.74 times higher than young (6 yrs) and mature (42 yrs) plantations, respectively (Table 4.2). Although there was no statistically significant difference in NPP between young and mature plantation stands, they had contrasting allocation of NPP; mature plantations had higher litter C inputs, but lower root turnover and biomass production (stem, branch, and coarse root), compared to the young forest.

Soil organic C concentrations differed with stand age in rhizosphere soils ($p < 0.001$), but not in bulk soils ($p=0.143$; Table 4.3). The middle-aged plantation (18yrs) had the lowest SOC concentration in rhizosphere soil, but had the highest NPP among the three plantations. Relative to the middle-aged plantation, rhizosphere SOC concentrations in young and mature plantations were higher by 30 % ($p < 0.001$) and 36% ($p < 0.001$), respectively.

Soil total nitrogen (TN) and total phosphorus (TP) differed in both rhizosphere and bulk soils among stand ages (Table 4.3). The mature plantation, with the lowest biomass production and fine root turnover (Table 4.2), had the highest TN and TP compared to young and middle-aged plantations in rhizosphere and bulk soils. Ammonium (NH_4^+), the primary form of inorganic N in our study, was highest in bulk soil and lowest in rhizosphere soil in the middle-aged plantation compared to the other plantation ages. I found no significant differences in available P among the three plantation ages in rhizosphere soil. However, rhizosphere soils had higher available P than bulk soils. For bulk soil, middle-aged forests had more available P than young forests.

SOC fractions in bulk and rhizosphere soils

Although forest age did not affect overall SOC concentration in bulk soils, the mature plantation had a higher concentration of LPI-C and LPII-C than the middle-aged plantation (Figure 4.1). The LPI-C and LPII-C in bulk soil of the mature plantation were 6.79 g kg^{-1} and 2.66 g kg^{-1}, respectively, higher than middle-aged by 14 % ($p = 0.017$) and 37% ($p = 0.016$). However, RP-C in bulk soils did not vary with forest age ($p=0.081$).

In rhizosphere soils, the young plantation had higher LPI-C than the middle-aged plantation by 63 % ($p < 0.001$) and the mature plantation by 28% ($p = 0.007$) (Figure 4.1). However, the mature plantation had the highest LPII-C ($p = 0.015$) and RP-C ($p < 0.001$)

in rhizosphere soils. The middle-aged plantation had the lowest labile and recalcitrant C among all three plantations.

LPI-C and RP-C were the main components of SOC in bulk and rhizosphere soils (Figure 4.2). Forest age did not influence the contribution of SOC fractions to SOC in bulk soil in Chinese fir plantations. However, in rhizosphere soil, the contribution of LPI-C to SOC was lower with advancing age, decreasing from 47 % to 38 %. In contrast, the percentage of RP-C to SOC increased with increasing forest age, from 38 % to 52 %, in rhizosphere soil ($P = 0.0146$). These results indicate that not only was rhizosphere SOC concentration higher in mature plantation than young and middle-aged, but the SOC also was more stable. However for N, the proportions of RP-N to TN were 26 % in both bulk and rhizosphere soils, and no significant differences were found among stand ages.

Rhizosphere soils had higher concentrations of DOC and DON than bulk soils in all forest ages, especially in the young plantation, where DOC and DON in rhizosphere soil were three times and 92 % higher, respectively, than in bulk soil (Figure 4.3). The DOC/DON ratio in bulk soils did not differ among the three Chinese fir plantations. In contrast, in rhizosphere soil the DOC/DON ratio was higher in the young plantation compared to the middle-aged and mature plantations.

Forest age did not influence hexose and pentose concentrations in bulk soils, whereas rhizosphere soils in the young plantation had higher hexose and pentose concentrations than middle-aged and mature plantations (Figure 4.4). Because most hexoses in soil are microbially-derived carbohydrates, contrasting with pentoses which are plant-derived carbohydrates in DOC, hexose/pentose (H/P) ratio higher than two indicates most C in DOC is microbially-derived C. The rhizosphere in mature plantation

had the lowest H/P ratio, but all the H/P ratios in this study were 2.60 – 3.87, indicating most was microbially-derived.

Soil microbial biomass and enzymes

Forest age had few influences on MBC, MBN, and MBC/MBN ratio in bulk soils (Figure 4.5). Although no significant differences in MBC in rhizosphere soils were found among forest stands, MBN in the young plantation was lower than middle-aged and mature plantation by 116 % and 107 %, respectively. However, the young plantation had a higher MBC/MBN ratio in rhizosphere soils than middle-aged and mature plantations.

The mature plantation had higher β-1,4-glucosidase (βG) and cellobiohydrolase (CBH) in bulk and rhizosphere soils than the young and middle-aged forests (Figure 4.6). There were no differences among stands in peroxidase (PEO) and phenol oxidase (PHO) in bulk or rhizosphere soils, except the young plantation had lower PEO in bulk soils and higher PHO in rhizosphere soils. However, N-releasing and P-releasing hydrolases were influenced by forest age in both bulk and rhizosphere soils. The middle-aged plantation with the highest NPP had lower β-1,4-N-acetylglucosaminidase (NAG) and acid phosphatase (AP) than the young and mature stands.

Relationships between SOC fractions and abiotic and biotic variables

Redundancy analysis (RDA) results indicated that the soil abiotic and biotic factors explained approximately 96.8 % and 99.5 % of the variance in SOC in bulk and rhizosphere soils among different aged Chinese fir plantations, respectively (Figure 4.7). Of all the quantified parameters, total phosphorus (TP) and MBC:MBN ratio were the two primary factors explaining SOC dynamics in rhizosphere forest soils (72.7 % and 20.4 % of the variance, respectively), and TP and MBN explained 69.2 % and 9.9 % of the variance in bulk soils (Table 4.4). Soils from different-aged plantations separated

more clearly in the rhizosphere vs. bulk soil RDA. In rhizosphere soils, MBC:MBN and PHO were positively correlated with SOC in young stands, specifically with LPI-C. Rhizosphere RP-C, which was correlated with TP and TN, drove SOC trends in mature stands. The dynamics of rhizosphere SOC in middle-aged stands were correlated with NPP. Relationships across different aged stands were less obvious in bulk soils.

DISCUSSION

I found that the labile carbon pool I (LPI-C) and the recalcitrant carbon pool (RP-C) were the primary SOC pools in both bulk and rhizosphere soils in this study, contributing 33-47 % and 38-52 % of SOC, respectively. The labile C pool II (LPII-C) only made up 11-15% of the SOC. Studies have shown that both LPI-C and RP-C are a mixture of plant and microbially-derived C pools; LPI-C is comprised of non-cellulosic polysaccharides, and RP-C is composed of plant-derived lignin and microbial residues that associate with mineral particles, whereas LPII-C consists of cellulose primarily (Oades *et al*., 1970; Rovira & Vallejo, 2002). I also found the hexose/pentose ratio in DOC was > 2.6 in bulk and rhizosphere soils in all three plantations, which suggests that microbially-derived C constituted the majority of SOC in our sites (Kalbitz & Kaiser, 2008). Other studies have shown that plant-derived C only accounted for 10 % of RP-C by NMR analysis (Rovira & Vallejo, 2002). Our results support recent research showing that microbially-derived C is the primary component for SOC (Cotrufo *et al*., 2013; Castellano *et al*., 2015; Lavallee *et al*., 2019) and microbial residue C contributed up to 60 % of bulk SOC in subtropical forests (Shao *et al*., 2017; Huang *et al*., 2019; Liang *et al*., 2019).

Forest age, and thereby NPP, did not influence bulk SOC concentration, but rhizosphere SOC concentration and composition differed with forest age (Table 4.5). The low NPP in young and mature plantations had higher rhizosphere SOC concentration than

middle-aged plantation with high NPP, illustrating that plant C inputs are important in driving rhizosphere SOC sequestration (Lavallee *et al*., 2019; Sokol & Bradford, 2019). Variation in rhizosphere SOC across forest ages was mostly explained by total phosphorus (TP) and MBC:MBN ratio, suggesting that changes in P and microbial activities with time were controlling the quantity and composition of rhizosphere SOC. Phosphorus is the primary limitation to forest productivity and microbial activity in tropical and subtropical forests on highly weathered soils (Giardina *et al*., 2003; Cleveland *et al*., 2011). It has been shown that the concentration of microbial residue C was positively related to soil P in subtropical forest when natural forest was converted to tree plantations (Yang *et al*., 2019a), and microbial residue C is the main agent to form microaggregation or to absorb on the surface of mineral particles to promote stable SOC formation (Cotrufo *et al*., 2013). I found that the variation of RP-C was positively correlated with TP in rhizosphere soils in mature stands (Figure 4.7). With this finding, I posit that low plant P demand in mature plantations, resulting from low overall NPP, improved soil microbial acquisition of P, which stimulated soil microbial biomass and C hydrolase production, and thereby enhanced the transfer of labile rhizosphere C to microbial residue C and stable SOC formation (García-Oliva *et al*., 2003; Schwendenmann *et al*., 2003; McGroddy *et al*., 2008).

Although mature and young plantations did not differ statistically in total NPP, the young plantation had higher LPI-C and lower RP-C than mature plantation (Table 4.5), indicating a different strategy of SOC sequestration in the young plantation. The low LAI in the young stands likely resulted in the transport of fewer carbohydrates from photosynthesis to rhizosphere than in mature stands with higher LAI, which led to low substrate C availability for microbes. The limited canopy cover in young stands also led

to higher soil temperature than other stands, stimulating SOC mineralization in young stands (Chen *et al*., 2016). The low substrate C availability in young plantation than middle-aged and mature plantation led to different microbial community composition with high MBC:MBN. It has been indicated that microbial biomass with high MBC:MBN has low turnover rate. As the most active labile C pools in soil, soil microbial biomass is the primary source of LPI-C pools. Thus, the low turnover rate of soil microbial biomass by high MBC:MBN related with high LPI-C in rhizosphere soils of the young plantation. The low C use efficiency in SOC mineralization limited microbial residue production in young stands. Coupled with the mass of SOC lost by the intensive soil and water erosion during plantation establishment (Yang *et al*., 2019b), these processes together may have induced low recalcitrant C recovery in the young plantation.

Up to 40 % of newly assimilated carbohydrates from photosynthesis are allocated to root exudates, upon which rhizosphere microorganisms rely as their primary available C source (Brüggemann *et al*., 2011). This flow of carbohydrate triggers soil microbial biosynthesis and N immobilization (Phillips *et al*., 2011; Huang *et al*., 2019; Liang *et al*., 2019), which may limit N availability for plant growth. However, plants can produce microbial inhibitors in their root exudates to suppress microbial N immobilization in soils dominated by NH_4^+ (Subbarao *et al*., 2007, 2015), thereby increasing plant N acquisition (Townsend *et al*., 1992; Templer *et al*., 2008). My results showed a decline of total N and P, soil microbial biomass C and enzyme activities in rhizosphere soil in middle-aged plantations with the highest NPP, and thus most likely the highest nutrient demand. High tree nutrient demand may constrain microbial residue C formation and contribute to the low rhizosphere SOC concentrations observed in these middle-aged stands, especially the LPI-C and RP-C pools, as both are mainly microbially-derived.

Fresh root C input into rhizosphere soils stimulates soil microbial activity and biomass to produce extracellular enzymes that release N and P from soil organic matter, making it available for plant uptake. This is known as the rhizosphere priming effect (Kuzyakov, 2010; Huo *et al*., 2017). Though the rhizosphere priming effect has been highlighted during interactions between root activity and soil organic matter (Kuzyakov & Xu, 2013; Spohn & Kuzyakov, 2013), there is limited research evaluating how rhizosphere priming is altered by stand development with time and related changes in plant productivity. In a temperate forest dominated by ectomycorrhizal tree species under elevated CO_2, increased photosynthate C input belowground stimulated extracellular enzyme activities to access the labile and recalcitrant SOC pools to meet the enhanced N demand by the trees driven by increased NPP (Drake *et al*., 2011; Phillips *et al*., 2012; Brzostek *et al*., 2013). However, my findings showed that variation in rhizosphere SOC was not closely related to enzyme activities. I found no significant differences in MBC, recalcitrant N, or PEO in the rhizosphere soils among plantations, and low NAG, PHO, and AP in middle-aged plantation, despite having higher NPP than the other stands (Table 4.5). These differences compared to temperate forest systems may be related to differences in mycorrhizal fungal types and soil clay minerals. Chinese fir associates with arbuscular mycorrhizal fungi species that have limited enzymatic capability to obtain enough N and P by decomposing SOM (Zak *et al*., 2000; Hodge *et al*., 2001; Lin *et al*., 2019). In addition, amorphous clays which dominate in highly weathered tropical and subtropical soils (e.g.,Oxisols and Ultisols), such as Fe and Al oxides and hydroxides, bind organic matter strongly and inhibit microbial access (Vitousek & Matson, 1988; Torn *et al*., 1997). Together, these factors may lead to different C, N, and P dynamics than is observed in temperate forests.

CONCLUSIONS

In this study, I demonstrated that NPP and tree nutrient demand strongly influence rhizosphere SOC dynamics in Chinese fir plantations in subtropical China. Variation in rhizosphere SOC was correlated with soil P and MBC:MBN, which drove labile and recalcitrant SOC dynamics in different ways depending on forest age. Lower competition for nutrients in mature stands due to lower NPP increased soil P and recalcitrant SOC sequestration in rhizosphere soils. In contrast, high NPP in middle-aged stands, and hence high tree demand for nutrients, reduced labile C and microbial activity and inhibited recalcitrant SOC sequestration in the rhizosphere. Results emphasized that plant productivity across different growing stages and varying rhizosphere soil microbial activities contribute to the regulation the quantity and quality of rhizosphere SOC in a subtropical forest plantation. There is growing evidence that models of C and N dynamics should incorporate the linkages between newly assimilated belowground C input and SOC sequestration in the rhizosphere. My results demonstrated that variability in forest productivity and nutrient demand with time is an important factor controlling rhizosphere SOC sequestration and composition.

TABLES AND FIGURES

Table 4.1 Extracellular enzymes assayed (abbreviation in parentheses), enzyme commission number (EC), corresponding substrate in this study.

Enzyme	EC	Substrate
β-1,4-glucosidase (βG)	3.2.1.21	4-MUB-β-D-glucoside
Cellobiohydrolase (CBH)	3.2.1.91	4-MUB-β-D-cellobioside
β-1,4-N-acetylglucosaminidase (NAG)	3.1.6.1	4-MUB-N-acetyl-β-D-glucosaminide
Acid phosphatase (AP)	3.1.3.2	4-MUB-phosphate
Phenol Oxidase (PHO)	1.10.3.2	L-DOPA
Peroxidase (PEO)	1.11.1.7	L-DOPA

(DOPA=L-3,4-dihydroxyphenylalanine; 4-MUB=4-methylumbelliferyl)

Table 4.2 Stem density, basal area, leaf area index, and allocation of NPP in three Chinese fir plantations in Sanming City, Fujian Province, China ranging in age from 6 to 42 years since plantation planting.

Stand age in 2018	Stem density (stems ha-1)	Basal area (m^2 ha^{-1})	Leaf area index (m^2 m^{-2})	Net primary productivity (t C ha^{-1} y^{-1}, NPP)			
				Biomass production	Litterfall production	Fine root production	Total production
6	2124(76)A	7.59(0.41)C	2.13(0.11)B	3.51(0.23)B	1.34(0.12)B	1.69(0.15)A	6.54(0.49)B
18	1594(58)B	37.84(1.85)B	5.76(0.26)A	4.45(0.21)A	3.98(0.18)A	2.12(0.23)A	10.50(0.61)A
42	1461(54)B	48.45(2.31)A	4.98(0.23)A	1.17(0.07)C	3.42(0.16)A	1.43(0.06)B	6.02(0.28)B

Note: Capital letters indicated significant differences among plantation ages at $P < 0.05$. The values are means (standard error).

Table 4.3 Rhizosphere and bulk SOC and nutrients across different aged Chinese fir plantations

	Bulk soil			Rhizosphere soil			P-values		
	6 yrs	18 yrs	42 yrs	6 yrs	18 yrs	42 yrs	Forest ages	Soil sources	Interaction
Soil moisture (%)	23.2(2.3) AB	26.4(0.2)A	21.2(2.4)B	24.0(5.2) A	26.9(1.7)A	23.8(1.0) A	0.0472	0.3054	0.7560
pH	4.44(0.08)	4.44(0.06)	4.48(0.05)	4.47(0.06)	4.38(0.03)	4.37(0.06)	0.1866	0.9105	0.7914
SOC (g kg^{-1})	17.62(0.95)b	15.49(1.03)	18.35(0.68)b	20.90(0.48)Ba	14.61(0.07)C	22.99(0.29)Aa	<0.0001	0.0012	0.0042
TN（g kg^{-1}）	1.14(0.08) AB	1.02(0.05)B	1.29(0.05)A	1.14(0.03)AB	0.99(0.04)B	1.36(0.07)A	0.0004	0.6842	0.6852
NH_4^+（mg kg^{-1}）	4.81(0.11) B	6.81(0.24)Aa	4.53(0.15)Bb	4.68(0.27)B	4.64(0.09)Bb	5.70(0.21)Aa	0.0009	0.0338	0.0001
NO_3^-（mg kg^{-1}）	1.27(0.15) A	0.61(0.08)B	0.43(0.03)Bb	1.36(0.16)A	0.69(0.07)B	1.44(0.09)Aa	0.0002	0.0008	0.0014
TP（mg kg^{-1}）	64.73(2.44)Aa	44.04(4.96)B	72.97(3.02)A	52.28(2.29)Bb	42.50(2.75)B	83.24(3.01)A	<0.001	0.6440	0.0135
Available P（mg kg^{-1}）	1.35(0.16) Bb	1.92(0.14)A	1.57(0.03)ABb	2.28(0.24)a	2.34(0.12)	2.43(0.22)a	0.2125	0.0002	0.2911

Note: Upper case letters indicate significant differences among plantation ages in either rhizosphere or bulk soils. Lower case letters indicate significant differences between rhizosphere and bulk soils within the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$. The values are means (standard error).

Table 4.4 Correlations between soil abiotic and biotic factors and RDA ordination of SOC pools in bulk and rhizosphere soils. Significant parameters are bolded.

Bulk soil (BS)				Rhizosphere soil (RS)			
Factors	Explains (%)	Pseudo-F	*P* values	Factors	Explains (%)	Pseudo-F	*P* values
TP	69.2	15.7	0.004	TP	72.7	18.7	0.002
MBN	9.9	4.9	0.04	MBC/MBN	20.4	17.6	0.002
DON	3	1.6	0.188	PHO	0.9	8.8	0.044
Soil moisture	2.3	1.4	0.292	βG	3.4	4.7	0.054
Biomass production	1.6	1	0.432	Biomass production	1.2	2.1	0.154
AP	2.9	7.8	0.104	Litterfall	1.2	3.3	0.114
CBH	0.4	0.09	0.990	AP	0.2	8.9	0.288

Table 4.5 Variations of SOC, nutrients, and enzyme activities in rhizosphere soil among three plantations showing young plantations as the baseline, marked as "◯". Values higher than the young forest were marked " ↑ ", those lower than the young forest were marked " ↓ ". The " ↓ ↓ " indicates the values were lower than both of the other two forests. And "◯" means no difference from the young plantation.

Variables	Young	Middle-age	Mature
NPP	◯	↑	◯
SOC concentration	◯	↓	↑
Total P	◯	↓	↑
Available P	◯	◯	◯
Total N	◯	↓	↑
NH_4^+	◯	◯	↑
NO_3^-	◯	↓	◯
Labile C pool - I	◯	↓↓	↓
Labile C pool - II	◯	↓	◯
Recalcitrant C pool	◯	↓	↑
Beta-glucosidase	◯	◯	↑
Cellobiohydrolase	◯	↓	↑
Peroxidase	◯	◯	◯
β-1,4-N-acetylglucosaminidase	◯	↓↓	↓
Acid phosphatase	◯	↓	◯
Phenoloxidase	◯	↓	↓
MBC	◯	◯	◯
MBN	◯	↑	↑
MBC/MBN	◯	↓	↓

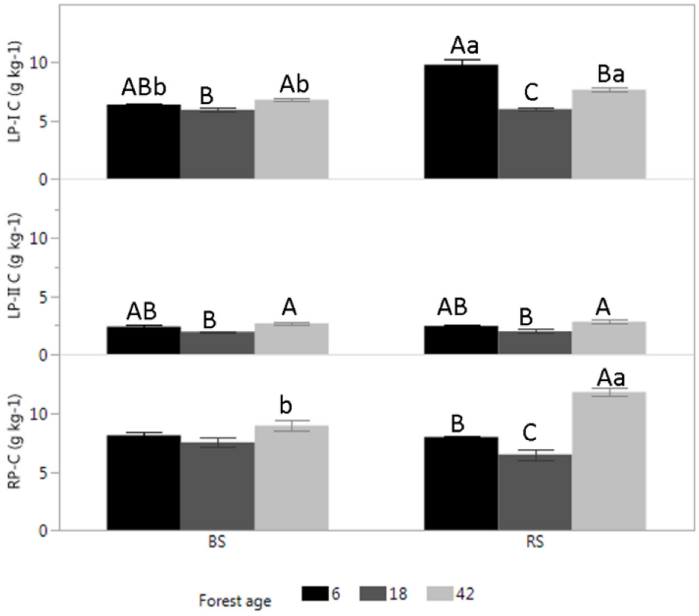

Figure 4.1 SOC fractions in bulk and rhizosphere soils (BS vs. RS, respectively) of different Chinese fir plantation ages. Upper case letters indicate significant differences among plantation ages in rhizosphere and bulk soils, respectively. Lower case letters indicate significant differences between RS and BS in the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$, and error bars are standard error.

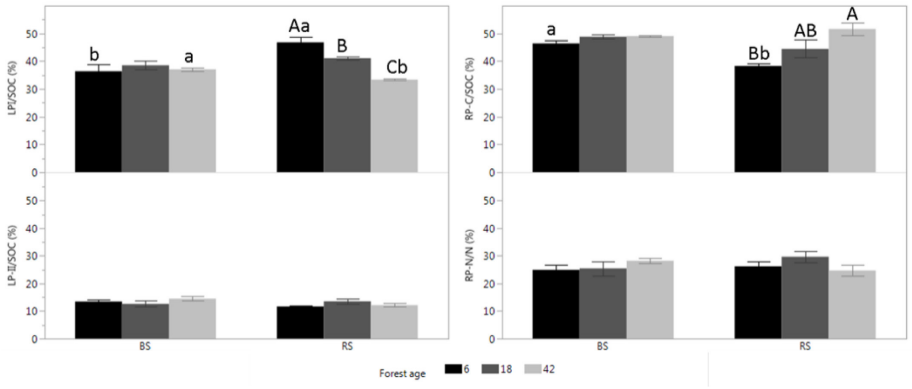

Figure 4.2 The ratio of LPI-C, LPII-C and recalcitrant C to SOC, and recalcitrant N to total N ratio among soils of different Chinese fir plantation ages. RS: Rhizosphere soil; BS: Bulk soil. Upper case letters indicate significant differences among plantation ages in rhizosphere and bulk soils. Lower case letters indicate significant differences between RS and BS in the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$, and error bars are standard error.

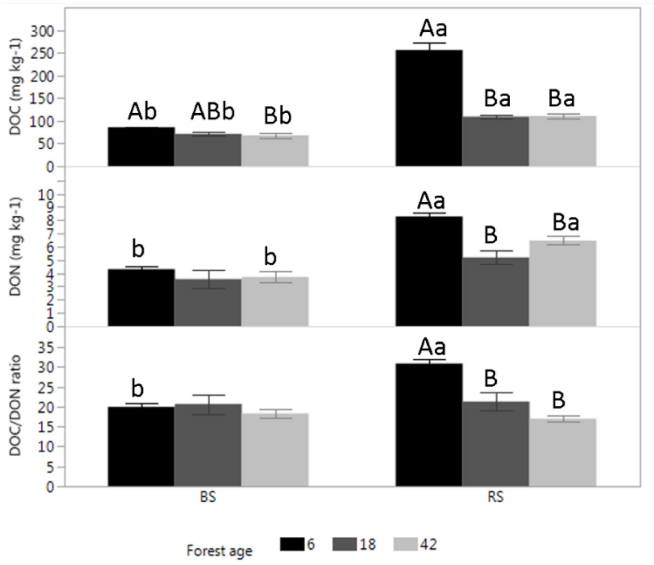

Figure 4.3 Dissolved organic C and N and dissolved organic C:N ratio in BS and RS among different Chinese fir plantation ages. Upper case letters indicate significant differences among plantation ages in RS and BS. Lower case letters indicate significant differences between RS and BS in the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$, and error bars are standard error.

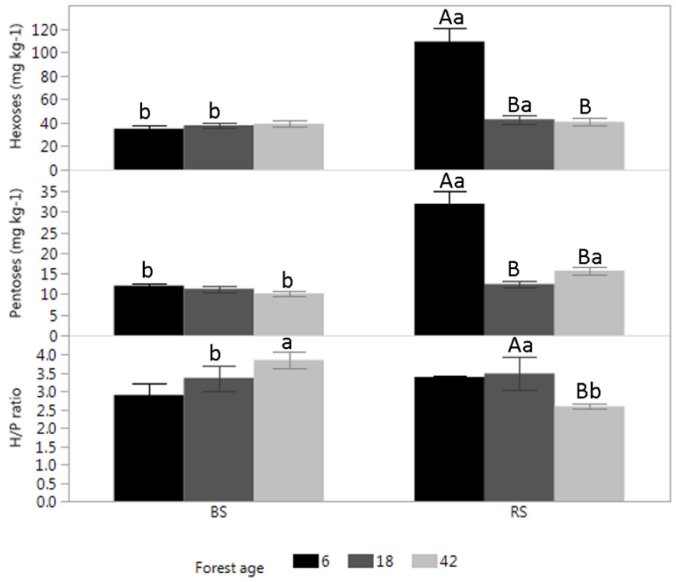

Figure 4.4 Hexose and pentose concentrations in DOC among soils of different Chinese fir plantation ages. Upper case letters indicate significant differences among plantation ages in RS and BS. Lower case letters indicate significant differences between RS and BS in the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$, and error bars are standard error.

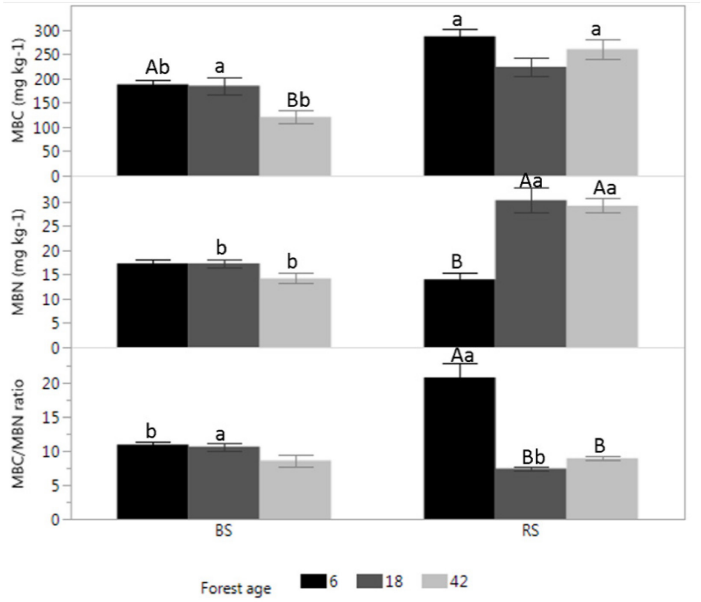

Figure 4.5 Microbial biomass carbon (MBC) and nitrogen (MBN), and MBC/MBN ratio in BS and RS among soils of different Chinese fir plantation ages. Upper case letters indicate significant differences among plantation ages in RS and BS. Lower case letters indicate significant differences between RS and BS in the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$, and error bars are standard error.

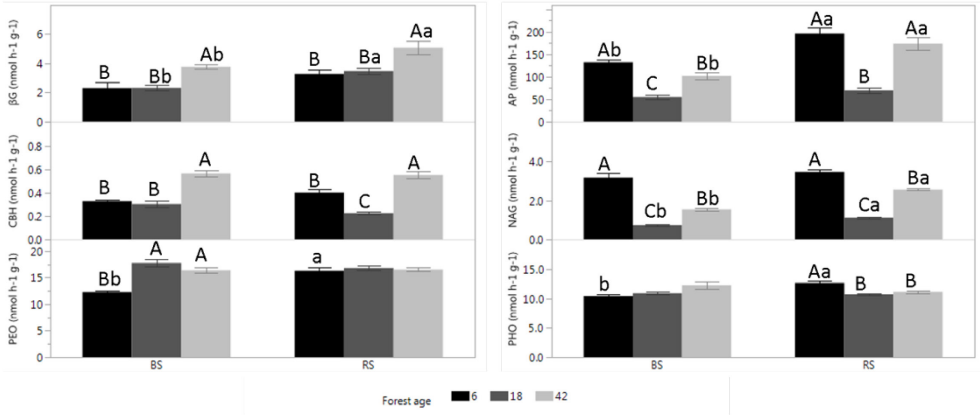

Figure 4.6 Soil enzymes in BS and RS among soils of different Chinese fir plantation ages. Upper case letters indicate significant differences among plantation ages in RS and BS. Lower case letters indicate significant differences between RS and BS in the same plantation age. Missing letters indicate no significant differences among forest ages or soil sources. The significant differences were tested at $P < 0.05$, and error bars are standard error.

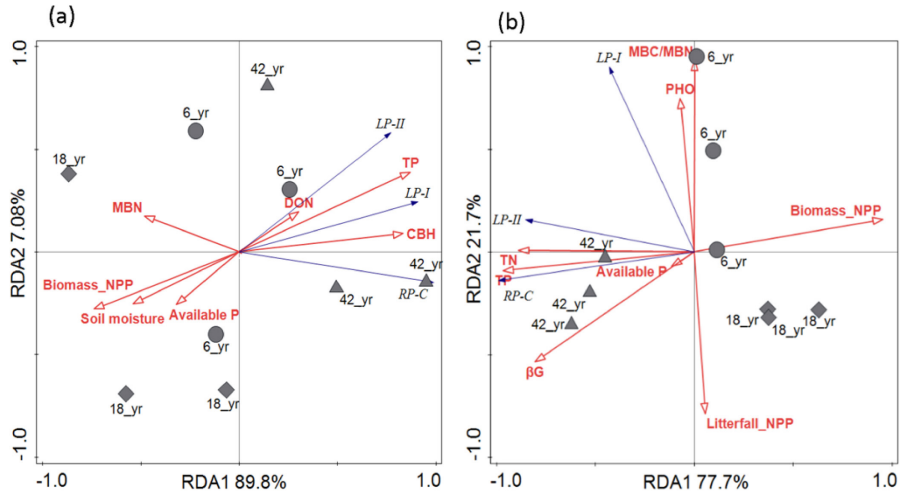

Figure 4.7 Redundancy analysis illustrating the linkages between SOC pools and soil abiotic and biotic factors in the bulk (a) and rhizosphere soils (b).

CHAPTER FIVE: CONCLUSIONS AND FUTURE DIRECTIONS

Soil organic carbon (SOC) is the largest terrestrial C pool and soil respiration is the largest CO_2 flux from soil to atmosphere, releasing about 60 Pg y^{-1}. Thus, even a slight change in the rate of soil respiration could considerably alter the concentration of atmospheric CO_2. Although many studies have examined soil respiration in relation to biophysical factors, few such measurements are from tropical and subtropical forests. The tropical and subtropical regions have very diverse climate conditions containing 66 of the world's 116 life zone such that the relationships between soil respiration and environmental factors are likely also diverse and cannot be generalized from the limited studies. Subtropical moist evergreen broadleaved (SMEB) forests of China are among the most biodiverse and productive forests globally covering 25 % of the land surface of China. However, our limited understanding of soil microbial respiration in relation to biophysical factors in SMEB hinders our predictions of how climate change affects C cycling both in the region and at the global scale.

The temperature responses of SOC decomposition have been used in earth system models (ESMs), leading to greater variability of soil microbial respiration predictions in the tropics than in any other region. Through field measurements of soil microbial respiration, I found that current photosynthates, but not SOC, are the primary C sources for soil microbial respiration. I also found that photosynthetically active radiation (PAR) controlled the diurnal variation of soil microbial respiration in the SMEB forests. Although the role of recent photosynthates in regulating soil microbial respiration has been suggested previously, through high frequency measurements (every 30 minutes), I found unambiguous evidence showing that plant productivity regulates soil microbial respiration through transporting current photosynthates from the canopy to the soil to

support microbial respiration. Furthermore, I also observed that available C sources and soil microbial respiration rates were affected by precipitation and soil moisture. Future work to develop accurate ESMs should take into account the supply of available C from belowground allocation to improve confidence in future climate predictions.

Soil microbial activity is highly dependent on C inputs, which is ultimately linked to primary productivity, but many models use temperature to predict SOC sequestration. Long-term SOC sequestration is strongly linked to forest productivity, which regulates C inputs from the aboveground litter to bulk soils and belowground root inputs in rhizosphere soils. These two different pathways of C inputs lead to differences in the efficiency of SOC sequestration. I found that the plant-microbe-soil continuum dominated rhizosphere SOC sequestration, and variation in rhizosphere SOC was correlated with soil phosphorus and the ratio of microbial biomass carbon and nitrogen, which drove SOC dynamics in different ways depending on forest age and productivity. I suspect that recent photosynthates could also play an important role in regulating soil microbial processes in other regions and recommend a thorough examination of its role at the global scale as it could improve our predictions of climate effects on global C cycling.

Conversion of natural forests to tree plantation, agricultural lands, and grasslands result in large SOC losses in the tropics. However, the magnitude and direction of SOC losses remains highly uncertain due to the paucity of direct measurements of the responses of SOC losses to anthropogenic activities during forest conversions. I found that slash burning immediately following the conversion of natural forest to forest plantations in SMEB forests is a major cause for the loss of a large quantity of SOC. My study casts doubt of the report of the Intergovernmental Panel on Climate Change (IPCC) Guidelines for Greenhouse Gas Inventory, in which SOC does not change, with a default

value of 1, when natural forest is converted to forest plantations. Moreover, I found that the losses of SOC did not re-accumulate to pre-conversion levels within the timeline of a forest rotation, showing the need for a new approach to management of forest plantations in tropical and subtropical forests. Thus, I propose that the IPCC should revise the default value in the future reports through a more comprehensive survey of changes in SOC during forest conversions.

Altogether, the findings from this dissertation had one broad objective: to investigate the factors that drive C cycles and SOC dynamics in an effort to reduce their uncertainty in current ESMs and guide effective C sequestration through forest management. I found current photosynthates are the main C sources to soil microbial respiration in SMEB forests, and the variation of soil microbial respiration is controlled by PAR on diurnal scales. Current photosynthates also dominated variation in rhizosphere SOC, and factors related to SOC dynamics varied with forest age and productivity. The dramatic reduction in SOC by slash burning during the establishment phase did not re-accumulate to pre-conversion levels, indicating the anthropogenic activities accelerated the loss of SOC to the atmosphere by forest conversions in SMEB forests. The allocation and transport of photosynthates, which drive soil microbial respiration and SOC sequestration, are sensitive to warming, increased atmospheric CO_2 concentration, and precipitation changes under global changes. However, current ESMs are highly dependent on the direct measurement of the responses of soil microbial respiration to biophysical factors, to infer long-term SOC sequestration. Perhaps the greatest future research needs are for more recognition of the influence of plant physiology on the soil C dynamics, documented through direct measurements made in diverse forest settings, and especially in the highly diverse tropics. Such studies could address key questions, such as: What are

the responses of belowground C allocation to changes in environmental factors? How does microbial C use efficiency respond to different sources of new C inputs (e.g., root exudates and litter leachate)? What are the key needs for constraining uncertainty in models and to improve model performance? And perhaps most importantly, how can research like that conducted for this dissertation guide future forest management to enhance C sequestration in forest plantations? Answers to these questions will improve our ability to stabilize atmospheric CO_2 concentration under changing climate.

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