

Department of Forestry and Resource Conservation College of Bioresources and Agriculture National Taiwan University Master Thesis

臺灣溪頭孟宗竹林土壤呼吸之時間變異及影響因子 Temporal variation in soil CO₂ efflux and the controlling factors in a moso bamboo forest, central Taiwan

謝宜芳

Hsieh, I-Fang

指導教授: 久米朋宣 博士

Advisor: Kume, Tomonori, Ph.D.

中華民國 102 年 8 月

August 2013

國立臺灣大學(碩)博士學位論文 口試委員會審定書

台灣溪頭孟宗竹林土壤呼吸之時間變異及影響因子 Temporal variation in soil CO₂ efflux and the controlling factors in a Moso bamboo forest, central Taiwan.

本論文係謝宜芳君(學號 R00625027)在國立臺灣大學森林環境 暨資源學系、所完成之碩(博)士學位論文,於民國 102 年 6 月 18 日承下列考試委員審查通過及口試及格,特此證明

口試委員:

ADT (簽名)

(指導教授)



系主任、所長

Acknowledgement



感謝久米老師,在研究上給予許多建議以及鼓勵!

感謝台大,提供良好的學習環境以及豐富的資源。

感謝鄭智馨老師以及土壤研究室的成員們,提供我在分析上需要的儀器以及知 識,也感謝洪志祐學長提供論文資料。

感謝梁偉立老師以及水文研究室的成員,每週的 meeting 讓我維持研究的感覺。 感謝王立志老師,提供相關的論文資訊以及巧遇時的關心。

感謝溪頭的洪志遠學長,余瑞朱學姊,以及幫我們解決供電問題的黃大哥等等, 也感謝王亞男處長,讓我們在溪頭的研究能夠順利進行。

感謝柯柯,在資料分析上幫了非常大的忙。

感謝親愛的家人,在我學習路上給予的一切支持,讓我在生活上無後顧之憂。 感謝雅涵、謝欣、鴻彬讀書會的時光總是非常快樂,感謝你們補充(並加強?)我 那消失殆盡的文學素養。

感謝曾經,以及不斷給予我精神支持的所有朋友,大龜、Emily、姊妹、貴婦、 Simon, thank you all, for keeping me motivated !

感謝研究室的所有夥伴, Sophie、學姊、美里、孟穎、子芸, 感謝你們協助我完成 24 小時監測以及分享資料, 和你們相聚的每一刻都是美好的回憶!

最後,感謝老天爺,賞賜給我們下不停的的西北雨、美麗的山景以及豔陽、雙子 座流星雨以及林間閃爍的滿滿螢光,讓我們在平安完成實驗的同時也能享受大自 然的美妙。

感謝!

摘要

土壤呼吸在陸域碳循環中扮演相當重要的角色,在評估森林固碳效益時為不 可或缺之一環。土壤呼吸之特性依生態系統而異,植被以及土地利用型態的改 變,必然會改變土壤呼吸之特性,進而影響區域之中的二氧化 CO2釋出量。在 台灣,孟宗竹林引進自中國大陸,主要分布於台灣中部地區,其快速生長的特性 使得許多竹林在廢耕之後快速擴張,侵略並取代週遭植被。為了瞭解竹林擴張可 能導致的碳循環改變,首先必須釐清孟宗竹林土壤呼吸的特性。本研究主要探究 孟宗竹林土壤 CO2 通量之時間變異以及受環境因子的影響。自 2012 年 4 月起, 於溪頭實驗林中選定孟宗竹純林,以動態密閉氣室法,進行每月一至二次,為期 一年之土壤二氧化碳通量監測,並以數據配合前人提出之模式建立實驗式。結果 指出,土壤呼吸速率具有不定趨勢之日變化現象,在總呼吸速率較高的測量日期 之中,日變化中之最高速率可超出最低速率之兩倍;土壤呼吸速率亦具有明顯之 季節變異,呼吸速率於生長季(4月)及夏季(6-9月)達最高,冬季月份最低,範圍 由 1.54 至 7.98 μ mol m⁻²s⁻¹。土壤溫度對於土壤呼吸速率季節變化之影響力大於 土壤含水率,温度對呼吸速率具有非線性相關,評估結果以 Q10 公式對於解釋土 壤溫度對土壤呼吸速率影響表現最佳。Q10指數為5.14,亦即土壤溫度上升10℃, 呼吸速率將增加5.14倍。以Q10公式預測本樣區土壤呼吸年量為1304.85 gCm⁻²yr⁻¹,高於鄰近之柳杉林。本研究結果可用以評估植被改變對於土壤呼吸以 及碳循環的影響,並在以減緩溫室氣體排放為導向的林相經營策略上具有重要參 考價值。

關鍵字:土壤呼吸、孟宗竹、時間變化、環境因子、Q10指數

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Abstract

Understanding soil respiration (R_S) in moso bamboo stands is crucial for accessing potential impact of bamboo invasion on terrestrial carbon cycle in Asian regions. This study aimed to evaluate the seasonal and diurnal variations of R_S in a moso bamboo (Phyllostachys pubescens) forest in central Taiwan with their abiotic drivers and to estimates annual Rs based on their temporal change characteristics. We selected a 401 m² plot in a conservatively managed moso bamboo stand in National Taiwan University Forest, central Taiwan. The 20 measuring locations were set in a 401 m² plot. R_S rates were measured from April 2012 to April 2013 by using a closed dynamic chamber system. Once a month, we observed the R_S averaged over the 20 locations and the diurnal variation at 2 locations with soil temperature (T_S) and soil volumetric water contents (SWC) measurements. To characterize seasonal variations in Rs, using models proposed by previous studies, this study examined the model performs in describing R_S with T_S and/or SWC.

 R_S showed distinctive diurnal variations in some measurement campaigns. In the measurement campaign on June, we found the maximum R_S rate exceed twice the minimum rate (from 3.43 to 9.91 µmol m⁻²s⁻¹). One year observation showed R_S averaged over 20 locations ranged from 1.54 to 7.98 µmol m⁻²s⁻¹ with the highest R_S in the summer season. Seasonal variations of R_S were considerably corresponded to

T_s. The relationship between R_s and T_s could be described the most significantly with the exponential Q₁₀ function. In the equation, the Q₁₀ value of 5.07 estimated in this study was considerably higher than those of adjacent Japanese cedar plantations under the same weather condition and the average from worldwide literatures (= 2 to 3). Estimated annual R_s rate using the function and continuously measured Ts was 1304.85 gCm⁻²yr⁻¹, which was higher than that of the Japanese cedar plantations (661 to 729 gCm⁻²yr⁻¹). Our results provided crucial information of the major CO₂ source in moso bamboo forest in Sitou, Taiwan.

Keywords: soil respiration, moso bamboo, biotic factors, temporal variation, Q10 value

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Chapter 1 Introduction



Knowledge of global carbon cycle has received considerable attention in terms of CO_2 a greenhouse gas, which can have the similar increasing trend as global temperature rising. Therefore the rising concentration of CO_2 is considered as a cause to global warming and further in relation to climatic changes. Numerous consequences resulting from global-warming have been proposed, showing directly or indirectly anthropogenic activities have been affecting our environments. In searching solution for mitigating CO_2 concentration, scientists have been making efforts in clarifying and quantifying different paths of carbon cycle.

Among those carbon pathways, the one in fixing CO_2 into terrestrial ecosystems is the photosynthesis process which naturally occurrs by all kinds of plants. Plants uptake CO_2 and convert it into organic carbon through photosynthesis. The assimilated carbons are then either allocated to grow plant tissues (i.e., leaf, shoot, or root growth) or broken down into CO_2 for energy supply. It is reported that 35% to 80% of total assimilated carbon is sent below-ground for root growth, micorrhizae, and root exudates (Kuzyakov, 2006). Those below-ground plant tissues will afterwards form organic carbon and either stored or decomposed in soil, the major carbon pool in terrestrial ecosystem. Soil plays a pivotal role in global carbon cycle by holding approximately 1,500 Pg (10¹⁵ g) C, nearly twice the amount held in the atmosphere and three times the amount in terrestrial vegetation. In an aspect of terrestrial ecosystems, carbon input is mainly by vegetation uptake and allocation. On the other side, the output process is through respiratory process, from above-ground parts of vegetation or from soil surface. In fact, many studies have pointed out that soil respiration generally accounts for 20 to 95% of total ecosystem respiration (Law et al., 1999), making soil respiration the major pathway of carbon loss from terrestrial ecosystem.

Soil respiration (or soil CO₂ efflux, abbreviated as R_S) indicates CO₂ flux from the soil-litter surface and is the sum of complex respiration sources, including root respiration, soil organic matter decomposition, microbial activity, roots exudes, and soil animal activities which can be broadly categorized into autotrophic (R_A) and heterotrophic (R_H) sources (Boone et al. 1998, Widén and Majdi 2001). The interactions between sources, their responses to environmental variables, and the contribution ration of each source to the total soil CO₂ efflux determine the characteristic of R_S in forests. That is, R_S characteristics are highly site dependent. Reported estimates of the contribution of root respiration to the total soil CO₂ efflux in forests ranged from 10 to 90% with the average of 40% to 60% (Hanson et al. 2000). In an aspect of temporal variation, both heterotrophic and autotrophic respirations are reported to perform high but different correlation with abiotic factors such as soil moisture and soil temperature. For example, root respiration was found to perform stronger sensitivities to soil temperature dynamics than microbial decomposition in temperate coniferous forest (Buchmann, 2000); cool and wet soil are more sensitive to temperature changes (Lloyd and Taylor, 1994; Davidson et al., 1998); and in regions with regularly occurred draught (i.e., Mediterranean regions), soil respiration rate tend to have higher dependency on precipitation pulses (Inglima, 2009). The temporal dynamics are studied under intact or dynamic environment of certain vegetation types and thus inevitable biotic factors.

Vegetation types determined the site qualities such as soil organic carbon (SOC) content, soil acidity, soil microbial community, stand structure, litter or root exudate supplement, and the ration of R_S sources composition (Hanson et al., 2000; Kuzyakov et al., 2006). Therefore, changing vegetation type will alter soil condition in the region and further affect the soil respiration characteristics.

Moso bamboo (*Phyllostachys pubescens*, sometimes described as *Phyllostachys edulis* is characterized as a temperate monopodial species in Phyllostachys genera. It is native to China, where it occurs broadly (30,000 km² or 70% of total bamboo cover), accounts up to 20% of total bamboo cover around the globe (Jiang, 2008). It is widely cultivated for both poles and edible shoots throughout South-Eastern and Eastern Asian countries. It has been noticed that the moso bamboo forests have been expanding in some regions with their highly developed rhizome systems. In southwestern Tokyo, the

area of moso bamboo coverage increased 2.7 and 3.4 times from 1961 to 1974 and 1987 respectively (Okutomi et al., 1996). On the other hand, in Kyoto, moso bamboo coverage increased from 24km² to 174 km² from 1953 to 1985. The increase of bamboo vegetated area was originally covered with secondary broadleaf forest (Okutomi et al., 2008). In Taiwan, aerial photographs showed that expansion of moso bamboo forest had been also occurring in regions with artificial moso bamboo stands (Chiou et al., 2009). As R_S can change with vegetation types, it is possible that the invasion or expansion of moso bamboo will alter regional carbon cycle through the changes in Rs. Under the global trend of carbon-fixing oriented land-use management, it is necessary to take into consider the function of moso bamboo on regulating carbon and the impact of bamboo expansion on original carbon cycle. However, our understanding of Rs has been still limited in moso bamboo forests, because only very few studies have been conducted in China and no study was conducted in Taiwan. To complete this consideration, information in characterizing R_S in moso bamboo forest is certainly needed.

For the purpose of filling the gap of knowledge in moso bamboo forest carbon cycling and further linking regional carbon budgets in response to temperature rising under global warming scenario, the objectives of this study are (1) to clarify the diurnal and seasonal variations in R_s ; (2) to detect the environmental variables regulating seasonal variations in R_s ; (3) to provide annual R_s amount; furthermore, (4) to characterize R_S in Moso bamboo forest by comparing with those of adjacent Japanese cedar forests under the same climate condition and also other forest types from worldwide literatures.

Chapter 2 Literature review



2.1 Soil respiration

Respiration is defined as a biochemical process that catabolizes organic materials to generate energy and produce water and CO₂ in a cell. All living organisms, including soil microbes, fauna, and plant parts such as plant roots and rhizomes, share similar respiratory processes for energy supply. Soil is defined as a mixture of living organisms including roots, soil microbes, soil fauna, and soil organic matters (Killham, 1994; Luo et al., 2006) and abiotic materials such as dead organic matter, air temperature, soil water content, and weathered rock, supporting plant growth (Buscot, 2005). Soil respiration, in this case, is considered as CO₂ emission during energy generation by soil living organic components. Soil respiration is also called belowground respiration, contrasting to above ground respiration which indicates CO₂ produced by plant parts above soil surface. The belowground respiration processes is complex and hence it is difficult to quantify them directly (Hanson et al., 2000). Belowground respiratory processes consist of soil CO₂ effluxes from different soil profiles and generate pressure gradients of CO₂ concentration in the soils. The pressure gradient between soil profile and atmosphere triggers CO₂ upward and finally release CO₂ from soil surface. In this case, the CO₂ efflux from soil surface is considered as soil respiration (belowground

respiration).



2.2 Soil respiration in carbon cycle

To evaluate ecosystem carbon budgets, generally consider the balance between photosynthetic uptake and carbon loss from respiration, according to the formula: NEP=GPP-Ra-Rs.

Where NEP, GPP, Ra, and Rs represent net ecosystem production, gross primary production, above ground respiration, and soil respiration, respectively. NEP indicates in physiological aspect, plants absorb CO₂ through photosynthesis and convert it into organic carbon. Those assimilated carbons are either allocated to grow plant tissues (i.e., leaf, shoot, or root growth) or broken down into CO₂ for energy supply. The term "allocation", described by Litton et al., (2007), has been used to describe different subjects such as living biomass, carbon flux from some particular plant tissue, or carbon flux from a fraction of photo-assimilated carbon. In this study, the term carbon allocation indicates carbon distribution from photosynthesis production (i.e., carbon flux).

Carbon allocated belowground for root growth, micorrhizae, root exudates, account for 35% to 80% of total amount of photo-assimilated carbon (Kuzyakov, 2006). Among those belowground processes, the growth of fine roots is one of the most important processes. Noted that fine roots are non-woody roots that in charge of water and nutrition uptake. They accounts a small part in total ecosystem living biomass but with a relatively fast turnover rate of fine roots, comparing to woody plant tissue that determines fine roots the main belowground organic carbon input (or belowground detritus production) pathway in the scale of carbon cycle (Kuzyakov, 2006). Except the growth of fine roots, the other important pathway to belowground input is plant litter-fall, which accounted for 10% of total carbon allocation (Kuzyakov, 2006). However, our understanding for the allocation ratio of total assimilated carbon has been not enough.

The carbon allocation can change with not only tree species but also environmental conditions (Nadelhoffer and Raich, 1989). For instance, it was found that increasing in soil nutrient availability and soil water content will lead to decrease of carbon amount allocated belowground (Running and Gower., 1991). Despite that, a range of estimated amount of 35% to 80% plant-assimilated carbon is sent belowground for root growth, micorrhizae, root exudates (Kuzyakov, 2006), and 10% contributes annually to aboveground litter. Those carbons allocated to the growth of leaves, stems, and roots fixed in plants until the tissue reach the end of its life span. Leaves and fine roots have life spans last from months to a few years while wood (stems, bulks or course roots) can live for decades. Those organic residuals from dead plants mix with other non-living organic factors form soil organic matter (SOM). SOM is known to have a relatively long turnover rate that enables carbon to store in soils for decades or hundreds of years (reviewed by Kuzyakov, 2006) to those from other sources. The turnover rate of different sources, as previously mentioned, is pointed out an important factor for evaluating carbon cycle in different temporal scales (Kuzyakov, 2006). Qualities (i.e., lignin content) of plant tissues will determine its turnover rate and influence the time it remains in soil. Therefore, inspecting soil respiration in partitioned components has become important in studying soil respiration temporal dynamics.

2.3 Sources of soil respiration

 R_S is a combination of several respiratory processes that we can broadly categorize into two components: respiration by heterotrophs (R_H) and respiration by autotrophs (R_A). As shows, R_H is the sum of CO₂ efflux from root exudates, microbial decomposition of soil organic matter (SOM), and activity of mycorrhizal hyphae; R_A means roots derived respiration; respiration from mycorrhizal hyphae and root-associated microbes are classified as R_A while they are R_H in some studies. Both components R_A and R_H are known to contribute to total R_S with a ratio of 10% to 95% (Hanson et al., 2000), varying among ecosystems and seasons. For example the R_A components contribute 23% to total R_S in a boreal coniferous forest (Bomd-Lamberty et al., 2004) while it is 70% to total R_S in a tropical deciduous forest (Epron et al., 2004). In addition, all contributors have different turnover rates, which influence the flux contribution of each component in different time scales. Composition rates of those sources, soil organic carbon content, and types of heterotroph and autotroph components determine the characteristics of soil respiration, and the CO_2 fluxes rates originated from different sources responds differently to environmental conditions (i.e., soil temperature and soil water content). Therefore, it is important for us to partition and discuss these CO_2 sources separately, for better understanding the mechanisms of changing R_s efflux (Ryan and Law, 2005).

2.4 Environmental influences on soil respiration

Soil respiration involves an array of chemical, physical, and biological processes that direct or indirectly respond to external influences. Soil respiration is sensitive to many environmental influences such as soil temperature (Lloyd and Taylor, 1994; Boone et al., 1998), soil water content (Moore and Knowles, 1989), substrate quality (Raich and Tufekcioglu, 2000), and photosynthesis active radiation (PAR) (Högberg et al., 2001; Kuzyakov and Cheng, 2002). Plenty of studies have dedicated to understanding the mechanisms of these variables effect on Rs in different spatial or temporal scale, in order to estimate or predict the dynamic of carbon cycle under global warming scenario.

2.4.1 Soil temperature



Soil temperature is the most significant driver having impact on almost all aspects of soil respiration processes. The soil temperature impacts on root respiration (result from root growth) and microbial activity differently. Note that both components contribute to a large part in total R_s . Buchmann (2000) found root exert stronger sensitivities to T_s dynamics than microbial decomposition in temporal forest. Exponential dependence of R_s upon T_s is found in many studies, described models according to site conditions of each study.

Most models are basically modified from a theoretical model which was previously developed by van't Hoff (1884):

$$R = \alpha e^{\beta T}$$

R indicates respiration, α indicates the respiration rate at 0°C, β is a coefficient of temperature response, and T indicates temperature. Many other equations are modified from this exponential equation applied with empirical data. 14 years later, van's Hoff (1898) provided another function which becomes the most widely used Q₁₀ function : Q₁₀ = (R_{T0+10})/R_{T0}

Where R_{T0} and R_{T0+10} are respiration rates at reference soil temperature T_0 and T_0+10° C, respectively. Q_{10} is an indicator for respiration temperature sensitivity by representing the relative increase of CO₂ flux as temperature increases by 10°C. Q_{10} value provides an information of times of soil respiration rate increase with the soil temperature increased by 10° C.Cited Q₁₀ from literature is averagely 2.4 (ranged from 1.3 to 3.3) (Raich and Schlesinger 1992). In Raich and Schlesinger's (1992) study, Q₁₀ is pointed out to vary with temperature and biomes. It is reported that the increase of Ts from a relative low temperature will positively alter Q₁₀ value (Lloyd and Taylor, 1994). In other words, biomes such as temperate or boreal forests are likely to perform stronger positive feedback between the increasing T_S and soil respiration rate..

Changes in T_S can explain R_S variation in different time scale, diurnal to annual, and also varies spatially. On a global scale, annual T_S can be a powerful indicator of annual mean R_S rate among biomes (Raich and Schlesinger, 1992). Linear models using mean annual T_S and precipitation to predict R_S have been provided to estimate monthly mean R_S by Fung et al. (1987), though the models with only T_S as variant shows high representative. Some studies have pointed out the uncertainties covered by Q_{10} . For example, Davidson et al (2006) proposed that Q_{10} estimated in growing season tend to be affected by seasonality of plant phenology of increased root growth.

2.4.2 Soil water content

Soil water content (SWC) is another influencing factor that has been studied for a long time. It theoretically affects soil respiration by two mechanisms: soil physical property (i.e., soil type and soil porosity) and physiologically. Laboratory studies showed that high soil water content could impede gas diffusion in soil by directly influences soil aeration (Romell, 1922). Soil porosity directly determines gas movement within soil. Soil water content levels too high or too low will limit substrate or O_2 diffusion meanwhile influence CO_2 diffusion (Liu et al., 2002).

Soil respiration rate maximizes at optimum water content and declines both with the increasing and decreasing soil water content. The theoretical optimum water content, which differed among soil conditions, is suggested to near water capacity when macropore spaces are filled with air and microspore spaces are water-filled. In fact, studies have shown that in some water-limited ecosystems, soil CO2 release increased temporarily after precipitation events (Almagro et al., 2009). Inspecting precipitation in a physical aspect, however, is not likely to explain the pulse release of CO_2 from soil surface. During or after rainfall, the infiltrated water moving downward in soil, forming a wetting front which is estimated to accounts for only 7 to 9% of the normal aeration and the entrapped air mostly not forced out and remains (Romell, 1922). The rewetting of dry soil results from rainfall that immediately activates microbe activities (Gliński, W. Stepniewski, 1985) and further increase the CO₂ released from decomposition of SOM by up to 200% (Fiereer and Schimel, 2003).

Predictability of models varies with studying ecosystems and is highly site-dependent. Therefore, no general consistent dependence pattern of soil respiration to soil water content has been found. Models have been constructed to predict R_s from SWC, however, most studies suggest that SWC coherent with T_s on influencing R_s .

2.5 Moso bamboo (*Phyllostachys pubescens*)

"Bamboo" is the common term of a taxonomic group of the largest woody grass family *Poaceae*. Bamboos encompass 1,439 species (which Asia accounts for about 1,000 about) within 116 genera (Grass Phylogeny Working Group (GPWG), 2001). Different species can vary with their adaptation of climate conditions. It is reported that most bamboos distributed in the tropical region and adapt to typical monsoon climate (Fu, 1998). In fact, bamboos origin from across a range of climate zones from tropical to temperate and distributes worldwide across latitudes from 46'N to 47'S and can disperse to 4,300 m above sea level (IFAR/INBAR, 1991; Isagi et al., 1997). The moso bamboo species is habituated in temperate regions. The general climate regulations are 15 to 20°C of mean annual temperature and 1000-1500 mm of least mean annual precipitation (Scurlock et al., 2000).

Bamboos are known to have very long flowering periods of 30 to 130 years (Lin, 1996). They regenerate mainly by asexual reproduction that budding from the internodes of the underground rhizome systems which generally occupy the top 30-50 cm of soil and may spread for tens of meters. Through the characteristic of sprouting from rhizome, all bamboo culms in a stand are connected together underground (Isagi,

1994). Morphologically, all rhizome systems are categorized into monopodial or sympodial types (Fu and Banic, 1995; Valade and Dahlan, 1991). Rhizome systems are found to determine the adaptations of a bamboo species to climatic conditions. In the study by Kleinhenz and Midmore (2001), bamboo species with monopodial rhizomes are likely to adapt for temperate climates, while those with sympodial types of bamboo are likely to adapt for tropical climates.

Bamboo are generally considered as crop for food and material productions, therefore many studies on bamboo morphology, physiology, productivity and potential applications. *Phyllostachys pubescens* (moso bamboo, sometimes described as *Phyllostachys edulis*), the researching subject of this study, is characterized as a temperate monopodial species in Phyllostachys genera. It is native to China, where it occurs broadly (30,000 km² or 70% of total bamboo cover), accounts up to 20% of total bamboo cover around the globe (Jiang, 2008). It is widely cultivated for both poles and edible shoots throughout South-East Asia. The climate requirement for growth of moso bamboo is precipitation of 1200-1800 mm, mean annual temperature of 13-20° C without freezing (Qiu et al., 1992). The sprouting season last from March to May, sprouts emerge from rhizome internodes and generally elongate to full height in 30 to 33 days.

Moso bamboo was introduced to Japan in 1746 (Suzuki, 1978) on the purpose of

economical utility, and has well adapted and naturalized since then. It has been reported that the naturalization of bamboo was resulting from the vigorous rhizome system with fast sprouting and the mechanism of undemanding to light conditions either to regeneration or elongation of culms (Isagi et al., 1997; Okutomi et al., 1996). Under this growing condition, the abandoned moso bamboo stand has been invading and substituting the surrounding vegetation (mainly consist of secondary broad-leafed forest). The expansion of bamboo stands has provided regional ecological problems of invasion and substitution to original vegetation. Studies of the expansion area of moso bamboo have occurred in several regions. Cases of expansion have been studied in Japan since 1950s. The study conducted in Kyoto, central Japan pointed out that the moso bamboo covered area increased from 24km^2 to 174 km^2 in 1953 - 1985 (Ogura, 1981). Another study in southwestern Tokyo (Okutomi et al., 1996) found that that bamboo coverage in 1974 and 1987 has increased by 2.7 and 3.4 times compared with that in 1961, respectively. Despite the fact that many studies, most from Japan, emphasize the ecological threats of alternating local plant communities and caused by moso bamboo expansion (Isagi, 1994; Isagi et al, 1997).

3. Methods



3.1 Site description

This study was conducted in a conventionally managed pure moso bamboo forest in National Taiwan University experimental forest, Sitou, central Taiwan (23° 40' N, 120°47′ E, elevation 1120 m) under the influence of a montane subtropical humid climate (Fig. 1). The monthly average temperature and precipitation data shown in figure 2 were acquired by averaging monthly average data of years from 1941 to 2008. The average annual temperature was 16.6° C with the lowest temperature of 7.7 °C occurred in January and the highest of 24.2°C in July(Fig. 2). Average annual precipitation was 2,614 mm, mostly concentrated between May to September with annually occurred typhoon events in the time period from July to October. The site has soils with a loam to sandy-loam texture. Average soil acidity was pH 4.1. The moso bamboo stand under study (target area) is an area of 401 m^2 . The plant community was consisted of pure moso bamboo (Phyllostachys pubescens) stand in the height up to 12 m with average DBH of 8.9 cm. This bamboo stand was conventionally managed (stand density was 5000 live stems/ha). It has been fertilized once with nitrate fertilizer in March of 2012 before measurement.

3.2 Measuring total soil CO₂ efflux (R_S) in field

We established a 10 x 20 m plot within the $400m^2$ moso bamboo stand. The plot was divided into fifty 2 x 2 m grids. In 2012 April, twenty measurement locations were randomly selected from these 50 grids. In each selected grid, a polyvinyl chloride (PVC) collar (10 cm inside diameter, 5 cm tall) was inserted to a depth of 2– 3 cm in the soil for measuring total soil respiration. All collars were left under undisturbed conditions throughout the study and all aboveground parts of living plant or moss in the collar were removed with minimal soil disturbance.

Soil CO₂ efflux was measured with an EGM-4 portable CO₂ infrared gas analyzer (IRGA; PP Systems, Amesbury, MA) equipped with a 10 cm inside diameter, closed dynamic chamber (SRC-1 closed type chamber; PP Systems, Amesbury, MA). Every measurement at a collar was repeated three times and the average of the three measurements was used in this study. Within each measuring campaign, we observed R_s of the 20 locations generally within the time period from 8:00 to 13:00.

We selected location No. 5 and No. 9 for observing diurnal variations, which were measured within 24 to 28 hours in every measuring campaign, generally starting from 9:00 and ending around 12:00 the next day. The measuring interval was every 2 to 3 hours.

3.3 Measurements for environmental factors



3.3.1 Soil temperature (T_s)

 T_S data was measured concurrently with R_S in 20 locationswith a simple portable thermometer (E-3630, Every Day, Taiwan). Every measurement was taken by inserting the thermometer into soil of 10 cm deep and remained 5 minute for temperature synchronizing. The measured T_S is averaged from T_S within from soil surface to the soil depth of 10 cm. Continuous T_S measurement of different soil depths was set in two locations within the plot, which commenced in 12 May of 2012. The two sets of thermistas (Model 111N, Campbell Inc, UT) were buried in depths of 10, 20 and 50 cm, and the measurements were performed every 30 minutes and stored in a data logger (CR1000, Campbell Inc., UT).

3.3.2 Soil volumetric water content (SWC)

Soil SWC data of the 20 locations was measured every time when measuring R_s , by using a simple portable thermometer (Delta-T Devices, Cambridge, EG). Within every measurement, moisture meter was inserted into soil depth of 7 cm. The measurements of SWC were repeated three times at each measurement location and the three measurements were averaged. As well, SWC was measured continuously using a dielectric aquameter senser (EC-5, Decagon Device Inc., WA). The 2 set of 3 sensors were buried in the depth of 10, 20, and 50 cm in the plot and the SWC measurements were performed every 30 minutes.

3.3.3 Mass and carbon content of litter-fall

Above ground litter consist of bamboo leafs, twigs, and sheaths. We collected aboveground litters for a year from April 12, 2012, to April 25, 2013 with five 1 m² area litter-traps which distributed throughout the study plot. Litters were collected once a month, and were oven-dried at 70°C to a constant mass and weighted. Oven-dried litter were powdered and analyzed for carbon content with element analyzer (Perkin Elmer 2400, Waltham, MA, USA). All litter C content was obtained by multiplying average litter C content percentage (45%) to oven-dried litter mass. We separated litters into three categories: leaf, branch, and sheath.

3.3.4 Soil carbon content

We estimated soil carbon content in the top 30 cm layer. Soil samples were collected and mixed from surface to the depth of 30 cm in 6 different locations within study area in March 12, 2012 and February 13, 2013. Soil samples were air-dried and sieved with a 2 mm mesh. Powdered samples were then analyzed for the carbon content with an element analyzer (Perkin Elmer 2400, Waltham, MA, USA).

3.4 Estimating annual soil CO₂ efflux



As to find the influences of environmental variables to seasonal changes in R_S , we use T_S and/or SWC as parameters and correlates R_S to both factors with empirical models introduced by previous studies (Table 1). Considering different possibilities of R_S to be influenced by single or multiple factors, the R_S dependence was tested with T_S or SWC as single influence, as well as the function combining T_S and SWC. Non-linear regression was fitted with function *optim*ize using software R (version i386 2.15.2). Based on this analysis, the most appropriate models for interpolation of R_S and hence annual R_S estimates were determined in this study.

Table 1 Empiric temperature.	al equations used to describe the relationships	between soil respiration a	nd
Parameter	Equation	Reference	Number
$T_s = Soil$ temperature C of	$R_{s} = ae^{-\mathrm{Ea}/\mathrm{R}T}$	Arrhenius (1889)	Eq. 1
(T=kelvin) Temperautre; R=8.314 JK ⁻¹ mol ⁻¹)	$R_{s} = R_{0} Q_{10}^{(\frac{T_{s} - T_{0}}{10})}$	van't Hoff (1898)	Eq. 2
$\theta = \%$ volumetric water content	$R_s = a(\theta - 0.1)(0.7 - \theta)^b$	Mielnick and Dugas (2000)	Eq. 3
	$R_s = \exp(a - b\theta)$	modified version of Janssens et al. (2001)	Eq. 4
	$R_s = \frac{a\theta}{\theta + b}$	Subke et al. (2003)	Eq. 5
$T_S = Soil$ temperature C of $0 - 10$ cm depth $\theta = \%$ volumetric water content	$R_{s} = ae^{(-Ea/RT)}(\theta - 0.1)(0.7 - \theta)^{b}$	Eq(1) * Eq(3)	Eq. 6
Ea = activate energy	$R_s = a e^{(-Ea/RT)*(b-c\theta)}$	Eq(1) * Eq(4)	Eq. 7
	$R_{s} = ae^{(-Ea/RT)} * \left(\frac{\theta}{\theta + c}\right)$	Eq(1) * Eq(5)	Eq. 8
	$R_{s} = R_{0}Q_{10}^{\left(\frac{T_{s}-T_{0}}{10}\right)} \times (\theta - 0.1)(0.7 - \theta)^{c}$	Eq(2) * Eq(3)	Eq. 9
	$R_{s} = R_{0}Q_{10}^{\left(\frac{T_{s}-T_{0}}{10}\right)} \times \exp(c - d\theta)$	Eq(2) * Eq(4)	Eq. 10
	$R_{s} = R_{0}Q_{10}^{(\frac{T_{s}-T_{0}}{10})} \times \left(\frac{\theta}{\theta+c}\right)$	Eq(2) * Eq(5)	Eg. 11

Note: a, b, c, d, R_0 , and Q_{10} are empirical coefficients to be estimated by maximum likelihood analysis. Ea is the activate energy fitted with data of this study, 99 KJ mol⁻¹.

Eq(2) * Eq(5)

Eq. 11

3.5 Calibration of soil temperature data



In this study, portable- and fixed-type thermometers were used to measure soil temperature in different depths and frequencies. Differences among the two kinds of temperature measurements were found as shown in Figure 3. Thus, calibration between surface T_S and continuous T_S from different depths is necessary for interpolation of R_S data using the models mentioned above. Note that the T_S data used for model fitting were obtained with portable thermometer. For avoiding potential error result from T_S differences, we computed linear regressions between the surface T_S averaged over 20 points and daily mean T_S from fix-typed sensors in same day at the three depths, respectively.

Table 2 Linear regression (y=ax+b) between the surface soil temperature averaged over 20 locations (x) and the soil temperature (y) measured at the depth of 10cm (T_{s-10}) , 20cm (T_{s-20}) , and 50 cm (T_{s-50}) , respectively.

x	а	b	r^2
T _{S-10}	1.075	-0.6743	0.91593
T _{S-20}	1.189	-2.665	0.94657
T _{S-50}	1.384	-6.122	0.96525

The derived results were shown in Table 3. Surface T_S and T_{S-50} has the highest correlation with the function (r²=0.965, p<0.001) :

 $T_{S-surface} = 1.384*T_{S-50} - 6.122.$ (Eq.12)

3.6 Total belowground carbon flux (TBCF)



As to understand the soil carbon dynamics, we aim to characterize the Rs in this site. With the field data, we calculated total belowground carbon flux (TBCF) with an approach suggested by Raich and Nadelhoffer (1989):

$TBCF = R_s - Above ground litter C content$

Previous literature has suggested negligible soil carbon dynamics and soil carbon stock in situ is under steady state in a long time period such as a year (Davidson et al., 2002; Raich and Nadelhoffer, 1989). Validity of this function in tropical rainforests has also been examined (Giardina and Ryan, 2002; Malhi et al., 2009) though in this study, we could not examine the validity of this assumption with the data in situ. We therefore, highlight the requirement of further study in soil carbon dynamics in situ.

Chapter 4 Results and Discussion



4.1 Diurnal variation of R_S and daily mean R_S

We measured R_S in all 20 locations once or twice a month, in the time between 8:00 to 14:00 for seasonal variation. During the same time within every measuring campaign, we also measured R_S in 2 of the 20 locations for 24 to 28 hours with the interval of 2 to 3 hours.

In all measuring campaigns, R_s rates tend to peak in the time period between afternoon to evening (18:00) and the lowest R_s rates generally appear in morning before 9:00. We found significant diurnal R_s variations in some measuring campaigns, including April 28 to 29, June 8 to 9, and June 26 to 27 (Fig.4 a, c, and d), in which the highest R_s rate exceed twice the lowest rate. Meanwhile, less significant diurnal variations in R_s were found in some measurement campaigns between October and March. The seasonal variation of the amplitude in the diurnal R_s variations (i.e., the difference between daily maximum and daily minimum) is shown in Figure 5. We can see stronger fluctuations in some measuring campaign where higher daily mean R_s rate were also observed (Fig. 5 and 6).

The phenomenon of diurnal R_S variations perform more significant in particular months within a year has been pointed out in previous literature (Liu *et al.*, 2006;

Savage et al., 2009). General mechanisms of diurnal R_S dynamics in this study were not analyzed and have not clarified in related studies. However, assumptions have been made that some temperature-independent drivers can have stronger influence on R_S than temperature, by affecting dynamics of R_A. Vargas et al., (2011) pointed out that diurnal canopy photosynthesis (flux rate inferred from eddy covariance technique) and R_s dynamics are very consistent and that canopy photosynthetic rate reacts faster than R_s, in four different forest types under different climate. Also, Savage et al.(2009) found the diurnal pattern of photosynthetically active radiation (PAR), air temperature and $R_{\rm S}$ diurnal are highly similar. As for soil temperature dynamics, weaker correlations comparing to factors previously mentioned is reported (Savage et al., 2009; Vargas et al., 2011). This finding, in addition to evidence provided by previous studies that canopy photosynthesis have direct influence on R_S rate, had gave a plausible mechanism of daily photosynthesis influencing diurnal R_s rate dynamics (Högberg et al., 2001; Kuzyakov and Cheng, 2001). These assumptions were examined with high resolution of R_S rate and related flux data within the condition in a particular time period of a year which is often called the growing season. That is, the possible mechanism of diurnal R_s variation may only applicable in the particular time period of a year. The exact growing season in our study site is not clear, as the temperature and moisture in Sitou region in the studying period did not reach to the values that will cause limitation to plant growth.

In addition, little knowledge to moso bamboo phenology has limited the speculation on growing season in this study. Besides, our field data is invalid for examine these hypothesis. Therefore, we suggest further examinations for clearer understanding of the growing season in Sitou region and phenology of moso bamboo, in finding the mechanism of diurnal R_s variation in Sitou moso bamboo forest.

Diurnal variations in R_S can be a source of errors for daily or annual R_S estimates if they were not accounted appropriately. Previous study has suggested that the R_S data taken between 0900 and 1100 provided the low sampling error of 0.9 to 1.5%, comparing with those of the entire daytime measurements (Xu and Qi, 2001). In our study, all 20 points data of single measurement were acquired between times of 0800 to 1400. The result of single measurement and daily averaged data were shown in Figure 6. The R_S values between single measurements and daily averages were slightly different, but the trend of R_S dynamics over study period was similar between both measurement frequencies. Then we calculated percentage of difference between the R_S single measurement and daily mean values averaged over 24 hours at the two measurement locations. The percentage differences between the daily mean R_S and the R_S at single measurement at each location were calculated with formula:
Percentage of Difference = $(R_s - mean R_s)/R_s * 100\%$



Here, R_s , represents R_s acquired in single measurement and *mean* R_s represent daily average of the diurnal measurements of R_s .

Result of the seasonal variations in the percentage of difference (*PD*) is shown in Figure 7. The *PD* ranged between -20% and 10% and between -30 and 60% at the location of No5 and No9, respectively. The *PD* in the No9 showed larger *PD* in the winter season (Nov–Mar) with the low values of R_s and the indistinctive diurnal variations in Rs (Fig. 4 and7). While *PDs* were mostly less than 10% through the year. Further, mean *PDs* in the whole study period in both locations were -4.14%. That is, diurnal variation of R_s in our study site has contributed 4.14% difference to the R_s measured in 0800 to 1400. This may suggests high temporal representativeness of the single measurements performed in the period from 8:00 to 14:00 in our study site.

4.2 Seasonal pattern of R_S, environmental factors and litter C content

Seasonal fluctuations of R_S were measured from April 2012 to April 2013. A relatively high R_S was observed in June 9, 2012 (Fig. 8). High R_S were observed in

April, June, and August. The seasonal variations in R_s are likely to have a similar trend with T_s . Mean annual R_s was $3.24 \pm 2.21 \ \mu$ mol C m⁻²s⁻¹, ranging from 1.54 to 7.98 μ mol C m⁻²s⁻¹. Soil temperature was 18.75° C, ranging from 12.5 to 22.3 °C. SWC ranged from 0.2 to 0.54 which were higher in spring and summer than in fall and winter, which corresponded to precipitation pattern (Figure 8d).

Figure 8a shows monthly collected aboveground litter C content. From 2012 April 28 to 2013 April 27, the total aboveground litter C was 209.54 g C m⁻²yr⁻¹ with sheath of 12.32 g C m⁻²yr⁻¹ and branch of 7.57 g C m⁻²yr⁻¹, mainly consisted of leaf (= 189.65 g C m⁻²yr⁻¹). Bamboo leaves were collected throughout the year, accounts for 85% of total aboveground litter. Relatively higher amounts of leaves was collected in April and July, which were the beginning of the growing seasonand a typhoon event period, respectively; Bamboo sheaths were collected in late April to June which is two months after newly formed bamboo shoots reached to full length; Branches were collected in the time of late June to middle September.

4.3 Controlling factors of R_S seasonal variation – soil temperature (T_S) and soil volumetric water content (SWC)

Soil temperature and soil moisture are among the most important abiotic factors controlling the soil CO₂ flux (Raich and Schlesinger, 1992; Raich and Potter, 1995; Davidson et al., 1998). The influences of T_S and SWC are highly site-specific. Correlations between soil temperature and R_S are generally described with positive exponential functions. For example the Arrhenius type equation (Lloyd and Taylor, 1994) or Q_{10} function proposed by van't Hoff (1898). Soil moisture positively affects R_S in ecosystems with low soil moisture or previously experienced drought stress (Balogh et al., 2011; Inglima et al., 2009). Except that, many studies suggested fragment relationships of SWC negatively influence R_S and coherent with T_S (Davidson et al., 1998; Xu and Baldocchi, 2004; Flanagan and Johnson, 2005).



 Table 3 Results of model fitting using all data points as independent observations

 models are listed in Table 1.

Equation	RMSE value	R-squared	AIC	ΔAIC
1	1.791403	0.3769724	1304.741	143.014
2	1.739651	0.3799566	1163.902	2.175
3	2.002657	0.1901011	1246.687	84.96
4	2.022624	0.162351	1252.52	90.793
5	1.998375	0.1815543	1245.428	83.701
6	2.116606469	0.0953732	1303.964	142.237
7	2.046125447	0.1427011	1253.251	91.524
8	2.028636623	0.1787107	1250.583	88.856
9	1.786312	0.3698851	1181.466	19.739
10	1.73412	0.3838007	1166.03	4.303
11	1.727341	0.3887685	1161.727	0

Figure 9 and 10 represent relationships between T_S , SWC and R_S . The R_S increased exponentially increasing with T_S (Fig. 9). The larger R_S were found around the SWC of 0.4–0.5 (m³/m³) and smaller R_S were found in the SWC of <0.3 and >0.6 (Fig. 10).

In order to understand the R_S seasonal variation mechanisms, 11 empirical models provided by previous studies have been fitted and evaluated with field data of this study (Table 1). Model 1 and 2 include T_S as single parameter while model 3 to 5 include only SWC, and model 6 to 11 include both T_S and SWC as parameters. The performances of models categorized with parameters are listed in Table 3.

Table 3 shows evaluations of all models fitted with field data of our study. T_s as single parameter can explain 38% of seasonal R_s variation (p<0.001, Fig. 7). The

correlation between T_S and R_S is described well by model 2. SWC as single parameter can explain at most 18% of total R_S seasonal change; and T_S and SWC both as parameters can explain 39%. That is, T_S performs as a dominant driver in regulating seasonal R_S change than SWC.

As well, model 11 have the lowest RMSE and AIC values (Table 3), showing its performance is better than other models. Meanwhile, the subtle difference in AIC and RMSE values of Model 2 and 11 indicate that these four equations performs almost equally well and better than other equations (Table 3). In choosing model for estimating annual R_s , due to the fact that the continuous measurement of SWC data is incomplete, we choose model 2 which performs almost as well as model 11, for year R_s estimation. Annual R_s was calculated by integrating modified T_s data from continuous measured daily T_s . Note that the calibration of T_s was described in section 3.5

Evaluating model performances, our study showed that T_S have a stronger positive correlation with R_S than SWC. Exponential function best correlates R_S to T_S and performs almost equally well as the function including both T_S and SWC as parameters, indicating T_S is the major environmental driver rather than SWC. In this study, the active energy (Ea) in Arrhenius equation was fitted to be 99 KJ mol⁻¹ (r^2 =0.38) which is much larger than previous literature suggested around 50 KJ mol⁻¹(Lloyd and Taylor, 1994). Based on the condition of Arrhenius equation only taken temperature as influence, we assume that the high Ea fitted in this study result from the vegetation system differences.

Our finding is similar to the study by Buchmann (2000) that T_S controls regional R_S in an exponential function, in a Norway spruce forest. The study by Liu et al (2011) also showed similar result that either T_S or SWC positively correlate to R_S in two moso bamboo stands and a subtropical broad-leaved forest. In Taiwan, the R_S rates have positive correlation with T_S and negative exponential correlation to SWC in three Japanese cedar (*Cryptomeria japonica*) forests under the same climate condition of this study (Hung, 2011). Also, in a subtropical mountain cloud forest in Taiwan, SWC and T_S both affect R_S in which high SWC and confounding low T_S result in very low R_S (Chang et al., 2008). Therefore, controlling factors on R_S and their effects on Rs can be highly site dependent.

Direct influence of T_S on R_S is difficult to obtain in field studies. Incubation studies have found positive correlations between T_S and soil diffusivity (Nobel, 2005) and between T_S and microbial respiration (Flanagan and Veum, 1974) at given SWC. SWC fluctuation in our study is between 20% and 60%, not lower than 0.2 (m³m⁻³) which is a suggested threshold of prohibiting microbial activities and not high above 0.7 (m³m⁻³) to limit soil aeration (Papendick and Campbell, 1981). In other words, SWC in our study does not reach to both limitation conditions and thus contrasting the influence of T_S .

Model 2 directly provides extra information of T_S sensitivity of R_S, also known as Q_{10} value. Q_{10} value in this study is 5.07. That means R_s rate in site will increase to 5.07. times by 10 degrees of T_S increase, with the reference temperature of 12.5 °C (ie, minimum temperature at this site). Comparing to the Q₁₀ values with Japanese cedar, which is 1.18 to 2.05 (Hung, 2012), the Q_{10} value of our study was much higher. In other words, R_S in moso bamboo forest is more sensitive to temperature change than in Japanese cedar forests under the same climate condition. This difference can be partly explained with the differences of soil water content between this study and Hung's. The soil moisture was averagely higher in the Japanese cedar forests than the moso bamboo forest of this study which may cause inhibition on T_S directly influence R_S and thus a lower Q10 value. We also supposed the phenology of fine root, such as growth rate and turnover rate of these two different vegetation types may respond differently to meteorological dynamics and further result in different Q₁₀ values.

Liu et al (2011) found Q_{10} values were 1.92 in a subtropical broadleaf forest, 3.24 in a conventionally managed moso bamboo forest, and 2.46 for intensively managed bamboo forest in Southern China, indicating Q_{10} in the bamboo forests were larger than surrounding vegetation, which agreed with the results in this study. However, Q_{10} value in moso bamboo forest in this study is much higher than the values reported in Liu's study. We assume that the different Q_{10} of this study and Liu's can be partly explained with the soil organic carbon (SOC) content based on the data we have. The SOC of our study was 6.58(1.98) while in the study of Liu et al (2011) was 2.22(0.04). The influence of SOC on R_s is by supplying substrate to decomposition whereas influence basal soil respiration and hence Rs (Franzluebbers et al., 2001). However, mechanisms of causing temperature sensitivity difference in same vegetation type but different environment is lack of study. We suggest further experiment filling this gap is needed.

On a global scale, Raich and Schlesinger (1992) had suggested a median Q_{10} value of 2.4 (ranging from 1.3-3.3) in R_s from studies including most types of vegetation. Studies by Davidson et al (1998) and Janssens et al (2003) suggested that Q_{10} value ranged from 2.0 to 6.3 for European and North American forests. Q_{10} values vary with biome types and climate condition. The Q_{10} value differences among ecosystems can also result from the site-specific reference temperature difference. Lloyd and Taylor (1994) suggested that Q_{10} value decrease with reference temperature increase in a general scale. However, we found this theory invalid in this study as the relationship between Q_{10} value and reference is insignificant and even positively relates to reference temperature (Table 4). To examine this, we had arranged all data into 6 groups by the dates of measuring campaign. Table 4 listed the Q_{10} values fitted with different T_0 which is the lowest temperature in each group.



Table 4 Q_{10} values fitted with T_0 of different group of data.

Data	Date	Q10	T ₀		
group				11	
Α	4/13/2012	23.86	17.9	49	
	4/14/2012				
	4/28/2012				
В	5/12/2012	23.85	18.8	56	
	6/8/2012				
	6/9/2012				
С	6/28/2012	47.67	21.1	49	
	7/25/2012				
D	8/6/2012	3.23	18.3	40	
	10/20/2012				
	11/16/2012				
E	12/14/2012	0.97	12.5	60	
	1/24/2013				
	2/22/2013				
F	3/16/2013	7.86	14.1	40	
	4/26/2013				

For revealing the implications behind Q_{10} value in this study, we suggest experiments of R_S partitioning into root respiration, and base soil respiration and incubation experiments is needed.

4.4 Annual soil respiration

We integrated calibrated T_S data into model 2 with fitted parameters and summing up (Fig. 11). Based on the Ts data and the Model 2, the annual R_S rate was estimated as 1304 g C m⁻²yr⁻¹. The mean annual Rs, calculated by averaging over the 12 measurement campaigns (=3.24 μ mol m⁻²s⁻¹) and directly scaling up to the unit of g C m⁻²yr⁻¹, was 1226.12 g C m⁻² yr⁻¹, which is close to the value of annual R_s estimation by integrating T_s into function.

We compared our results with a study by Hung (2012) which reported soil respirations in three Japanese cedar (Cryptomeria japonica) plantations in Sitou experimental forest. The Rs in bamboo forest was considerably larger than that of Japanese cedar plantations (Fig. 12). Although they were under the same meteorological condition, the results indicated that the R_S characteristics were very different between these two vegetation types and that in moso bamboo forest. Soil in the bamboo forest probably played a stronger source of CO₂ than that of nearby Japanese cedar forests. On a global scale, soil respiration varies greatly with vegetation types, climate, soil, and biological phenology. Moisture and annual mean temperature are positively correlated to the mean annual R_S of ecosystem (Raich and Potter, 1995). Among classifications of vegetation type, the annual R_S estimated in this study falls in the group of "Tropical moist forest" (Raich and Schlesinger, 1992; Subke et al., 2003) while climate condition in Sitou is subtropical moist forest.

4.5 Soil carbon balance

Annual R_s in this study was estimated as 1304 gCm⁻²yr⁻¹. The annual litter-fall C was estimated as 209.54 g C m⁻²yr⁻¹ and hence TBCF was estimated as 1095.31 g C

m⁻²yr⁻¹. A general trend of annual aboveground litter-fall C mass and annual R_S was found linearly correlated, as shown in Figure 13 (Raich and Nadelhoffer, 1989: Davidson et al., 2002). TBCF of our study exceed those of the adjacent Japanese cedar plantations and the range of regression lines predicted from Rs and litter-fall C rate based on the world-wide literatures (Davidson et al., 2002). Some studies plotted in Figure 11 also exceed the regression lines, which were derived from Brazilian evergreen tropical rainforests with higher ration of root biomass for surviving in temporary drought (Nepstad et al., 1994). In our study, the relatively high TBCF has emphasized the belowground process in carbon cycle whereas given an aspect of implying mechanism of R_S seasonal dynamics, which could link to plant phenology. In addition, moso bamboo species is mainly reproduced by rhizome systems extension and shooting, which intensive expansion of bamboos to surroundings have been reported. Therefore, the larger TBCF in moso bamboo than that of other forests might be a plausible explanation to the intensive expansion of moso bamboo and the great R_S seasonal fluctuations. As a global relationship demonstrated that TBCF is the single largest carbon flux in forest ecosystems aside from canopy assimilation, our result emphasized the importance of belowground processes on carbon budgets in the moso bamboo forest.

Chapter 5 Conclusion



Our study showed temporal variations in soil respiration (R_s) in the moso bamboo forest at the diurnal and the seasonal scale based on the 12-month observations. In this study, we found considerable diurnal variations in R_S in some measurements campaigns, which generated averagely 4.14% error compared to the data acquired in the period between 9:00 and 13:00. The R_S seasonal pattern showed maximum fluxes in April and summer and the minimum in winter. This seasonal variation could be explained using exponential Q_{10} function. The derived Q_{10} value was higher than that of the general average from forests worldwide, indicating the moso bamboo forest has a stronger positive feedback to global warming. In addition, Q₁₀ values fitted in this study are positively correlates to reference temperature, which opposite to the theory suggest by previous study. Soil moisture also positively correlated to R_S, although the model performance including solely the effect of soil moisture was not as significant as that of soil temperature. Estimated annual R_S of this study using the Q₁₀ function was almost twice as large as the annual R_S observed in surrounding C. japonica forests and the amount in the bamboo forest was similar to that observed in tropical moist forests. The large total below ground carbon allocation (TBCA) estimated from the difference between Rs and litter C content in this site have indicated the importance of

belowground processes in carbon budget in the moso bamboo forest. Thus, our study showed that the inflated soil CO_2 efflux and higher sensitivity to temperature increase could support significant moso bamboo expansion into *C. japonica*.

Further studies including partition into R_S sources (i.e. root and microbial processes) and understanding for the effects of T_S , SWC, and plant phenology on each Rs source are needed to clarify our further understanding of soil respiration in moso bamboo forests.

References



Arrhenius, S. (1889) Uber die Reaktionsgeschwindigkeit bei der Inversion von

Rohrzucker durch Sauren. Zeitschrift fur Physik Chemique, 4, 226-248.

Almagro, M., J. López, J. I. Querejeta and M. Martínez-Mena (2009). "Temperature dependence of soil CO₂ efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem." Soil Biology and Biochemistry 41(3): 594-605.

- Balogh, J., K. Pintér, S. Fóti, D. Cserhalmi, M. Papp and Z. Nagy (2011). "Dependence of soil respiration on soil moisture, clay content, soil organic matter, and CO₂ uptake in dry grasslands." Soil Biology and Biochemistry 43(5): 1006-1013.
- Bond-Lamberty, B., C. Wang and S. T. Gower (2004). "Contribution of root respiration to soil surface CO₂ flux in a boreal black spruce chronosequence." Tree Physiology 24(12): 1387-1395.
- Boone, R. D., K. J. Nadelhoffer and J. D. K. Canary, J P (1998). "Roots exert a strong influence on the temperature sensitivity of soil respiraiton." Nature 396.
- Buchmann, N. (2000). "Biotic and abiotic factors controlling soil respiration rates in Picea abies stands." Soil Biology & Biochemistry 32: 1625-1635.
- Buscot F. (2005) What are soils? In Microorganisms in soils: Roles in genesis and functions. (F.

Buscot, and A. Varma, eds.), pp. 3-17, Soil Biology Series, Vol. 3, Springer-Verlag,

Heidelberg, Germany.

- Chang, S.-C., K.-H. Tseng, Y.-J. Hsia, C.-P. Wang and J.-T. Wu (2008). "Soil respiration in a subtropical montane cloud forest in Taiwan." Agricultural and Forest Meteorology 148(5): 788-798.
- Chiou, C.-R., Chen, T.-H., Lin, Y.-J., Yang, Y.-J., Lin, S.-D., (2009) Distribution and change analysis of bamboo forest in northern Taiwan. Quarterly Journal of Chinese Forestry. 42: 1:89-105.
- **Davidson, E. A., E. Belk and R. D. Boone (1998).** "Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest." Global Change Biology 4(2): 217-227.
- Davidson, E. A., Savage, K., Bolstad, P., Clark, P. A., Curtis, P. S., Ellsworth, D. S., Hanson,
- P. J., Law, B. E., Luo, Y., Pregitzer, K. S., Randolph, J. C., and Zak, D. (2002).

"Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil

respiration measurements." Agricultural and Forest Meteorology 113,, 39-51

Davidson, E. A., I. A. Janssens and Y. Luo (2006). "On the variability of respiration in terrestrial ecosystems: moving beyond Q₁₀." Global Change Biology 12(2): 154-164.

Epron, D., Y. Nouvellon, O. Roupsard, W. Mouvondy, A. Mabiala, L. Sant-Andre, R.

Joffre, C. Jourdan, J. M. Bonnefond, P. Berbigier and O. Hamel (2004). "Spaital and

temporal variations of soil respiration in a Eucalyptus plantation in Congo." Forest

Ecology and Management 202: 149-160.

- Fiereer, N. and Schimel, J. P. (2003). "A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. "Soil Science Society of America Journal 67, 798-805
- Flanagan, L. B. and B. G. Johnson (2005). "Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland." Agricultural and Forest Meteorology 130(3-4): 237-253.
- Flanagan, P. W., and Veum, A. K. (1974). "Relationships between respiration, weight loss, temperature and moisture in organic residues on tundra." In Soil organisms and decomposition in tundra (A. J. Holding, O. W. Heal, S. F. MacClean, Jr., and P. W.

Flanagan, eds.), pp. 249-277, IBP Tundra Biome Steering Committee, Stockholm, Sweden.

Franzluebbers, A. J., Haney, R. L., Honeycutt, C. W., Arshad, M. A., Schomberg, H. H.,

- and Hons, F. M. (2001). "Climatic influences on active fractions of soil organic matter." Soil Biology and Biochemistry 33(7-8), 1103-1111.
- Fu, M. (1998) "Criteria for selection of superior bamboo varieties, propagation, and plantation establishment", Research Institute of Subtropical Forestry CAF, Fuyang, Zhejiang, China, pp. 1-2.
- Fu, Maoyi & Banik, R. L. (1995). Bamboo production systems and their

management. Propagation and Management, 18.

- Fung, I.Y., Tucker, C.J. & Prentice, K.C. (1987) Application of advanced very-high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO₂- Journal of Geophysical Research, 92, 2999-3015.
- Giardina, C. P., Ryan, M. G. (2002) Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. Ecosystems. Vol.5 pp. 487-499.
- Gliński, J., Stępniewski, W. (1985) Measuring soil aeration. In Soil Aeration and its Role for Plants, eds., J. Gliński and W. Stępniewski, pp. 181–187. CRC Press, Boca Raton, FL.

Grass Phylogeny Working Group, Barker, N. P., Clark, L. G., Davis, J. I., Duvall,

- M. R., Guala, G. F., Hsiao, C., Kellogg, E. A., Linder, H. P. (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). Annals of the Missouri Botanical Garden. 88: 373-457.
- Hanson, P. J., N. T. Edwards, C. T. Garten and J. A. Andrews (2000). "Separating root and soil microbial contributions to soil respiration: A review of methods and observations." Biogeochemistry 48: 115-146.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Loefvenius, M., and Read, D. J. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411,789-792

- Hung, C.-Y. (2012). Assessment of ecosystem carbon stock and net ecosystem productivity of old-aged Japanese cedar plantations in Sitou. In School of Forestry and Resource Conservation. National Taiwan University, Taipei.
- IFAR/INBAR (1991). Research Needs for Bamboo and Rattan to the Year 2000. Tropical Tree Crops Program, International Fund for Agricultural Research/ International Network for Bamboo and Rattan, Singapore.
- Inglima, I., G. Alberti, T. Bertolini, F. P. Vaccari, B. Gioli, F. Miglietta, M. F. Cotrufo and A.
- **Peressotti (2009).** "Precipitation pulses enhance respiration of Mediterranean ecosystems: The balance between organic and inorganic components of increased soil CO₂ efflux." Global Change Biology 15(5): 1289-1301.
- **Isagi, Y. (1994).** "Carbon stock and cycling in a bamboo Phyllostachys bambusoides stand." Ecological Research 9: 47-55.
- **Isagi, Y., T. Kawahara, K. Kamo and H. Ito (1997).** "Net production and carbon cycling in a bamboo Phyllostachys pubesces stand." Plant Ecology 130(1): 41-52.

Janssens, I. A., Dore, S., Epron, D., Lankreijer, H., Buchmann, N., Longdoz, B., Brossaud,

J., and Montagnani, L. (2003) Climatic influences on seasonal and spatial differences in soil CO₂ efflux. In Ecological studies 163: Canopy fluxes of energy, water and carbon dioxide of European forests (R. Valentini, ed.), pp. 235-256, Springer-Verlag, Berlin and Heidelberg, Germany.

Jiang Z-Hui. (2008) Bamboo and rattan in the world. China Forestry Publishing House.

Chiou C-R., Chen, T-H., Lin, Y-J., Lin, S-D. (2009) Distribution and Change Analysis of

Bamboo Forest in Northern Taiwan. Quarterly Journal of Chinese Forestry Vol. 42.

Killham, K. (1994). "Soil Ecology." Cambridge University Press, Cambridge, UK.

Kleinhenz, V., & Midmore, D. J. (2001). Aspects of bamboo agronomy. Advances in agronomy, vol.74, 99-153.

- **Kuzyakov, Y. (2006).** "Sources of CO₂ efflux from soil and review of partitioning methods." Soil Biology and Biochemistry 38(3): 425-448.
- **Kuzyakov, Y. and W. Cheng (2002).** "Review: Factors affecting rhizosphere priming effects." Journal of Plant Nutrition and Soil Science 165(4): 382-396.
- Law, B. E., M. G. Ryan and P. M. Anthoni (1999). "Seasonal and annual respiration of a ponderosa pine ecosystem." Global Change Biology 5(2): 169-182.

Lin, W-J., Chang, T-J. (1996) Study of Taiwanese Bamboo. Journal of Forest Science Vol. 69.

- Litton, C. M., J. W. Raich and M. G. Ryan (2007). "Carbon allocation in forest ecosystems." Global Change Biology 13(10): 2089-2109.
- Liu, J., P. Jiang, H. Wang, G. Zhou, J. Wu, F. Yang and X. Qian (2011). "Seasonal soil CO₂ efflux dynamics after land use change from a natural forest to Moso bamboo plantations in subtropical China." Forest Ecology and Management 262(6): 1131-1137.

- Liu, X., Wan, S., Su, B., Hui, D., and Luo, Y. (2002). "Response of soil CO₂ efflux to water manipulation in a tallgrass prairie ecosystem." Plant and Soil 240, 213-223
- Lloyd, J. and J. A. Taylor (1994). "On the temprature dependence of soil rsepriaiton."

Functional Ecology 8: 315-323.

- Luo, Y., D. Hui and D. Zhang (2006). "Elevated carbon dioxide stimulates net accumulations of carbon and nitrogen in terrestiral ecosystems: Results of meta-analysis." Ecology 87(1): 53-63.
- Malhi, Y. (2009) The carbon balance of tropical forest regions, 1990-2005. Sustainability. Vol. 2, pp. 237-244.
- Moore, T. R. and R. Knowles (1989). "The influence of water-table levels on methane and carbon dioxide emissions from peatland soils." Canadian Journal of Soil Science 69(1): 33-38.
- Nepstad, D. C., De Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros,
- G. H., Da Silva, E. D., Stone, T. A., Trumbore, S. E., and Vieira, S. (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372, 666-669.
- Nobel, P. S. (2005). "Physiochemical and environmental plant physiology." Elsevier Academic Press, Amsterdam, the Netherlands.
- Ogura, J. (1981). "The transition of bamboo groves in Kyoto." Proceed. Of 17th IUFRO World

Congress 5:3A: 98-103

- **Okutomi, K., S. Shinoda and H. Fukuda (1996).** "Causal analysis of the invasion of broad-leaved forestby bamboo in Japan." Journal of Vegetation Science 7: 723-728.
- Papendick, R. I., and Campbell, G. S. (1981). "Theory and measurement of water potential". In Water potential relations in soil microbiology (J. F. Parr, W. R. Gardner, and L. F. Elliott, eds.), pp. 1-22, Soil Science Society of America, Special Publication No. 9, Madison, WI.

Qiu, G.-X., Shen, Y.-K., Li, D.-Y., Wang, Z.-W., Huang, Q.-M., Yang, D.-D., and

- Gao, A.-X. (1992). "Bamboo in sub-tropical eastern China". In "Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics" (S. P. Long, M. B. Jones and M. J. Roberts, Eds.), pp. 159-188. Chapman and Hall, London, U. K.
- Raich, J. W. and K. J. Nadelhoffer (1989). "Belowground carbon allocation in forest ecosystems: global trends." Ecology.
- Raich, J. W., and Potter, C. S. (1995) Global patterns of carbon dioxide emissions from soils. Global Biogeochemical Cycles 9, 23-36.
- Raich, J. W. and W. H. Schlesinger (1992). "The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate." Tellus, Series B 44 B(2): 81-99.
- Raich, J. W. and A. Tufekcioglu (2000). "Vegetation and soil respiration: Correlations and controls." Biogeochemistry 48: 71-90.

Romell, L. G. (1922) Luftväxlingen i marken som ekologisk faktor. Medd. Statens

Skogsfarsoksanstalt 19:2

Running, S. W., and S. T. Gower (1991). "Forest-BGC: a general model of forest ecosystem processes for regional application. II. Dynamic carbon allocation and nitrogen budgets."

Tree Physiology 9:147–160

- Ryan, M. G. and B. E. Law (2005). "Interpreting, measuring, and modeling soil respiration." Biogeochemistry 73(1): 3-27.
- Savage, K., Davidson, E. A., Richardson, A. D., Hollinger, D. Y. (2009) Three scales of temporal resolution from automated soil respiration measurements. Agricultural and Forest Meteorology. 149: 11, 2012-2021.
- Scurlock, J. M. O., Dayton, D. C., & Hames, B. (2000). "Bamboo: an overlooked biomass resource?" Biomass and bioenergy, 19 (4), 229-244
- Subke, J.-A., M. Reichstein and J. D. Tenhunen (2003). "Explaining temporal variation in soil CO₂ efflux in a mature spruce forest in Southern Germany." Soil Biology and Biochemistry 35(11): 1467-1483.

Suzuki, S. (1978). "Index to Japanese Bambusaceae." Gakken, Tokyo.

- Valade, I., & Dahlan, Z. (1991) "Approaching the underground development of a bamboo with leptomorph rhizomes: Phyllostachys viridis (Young) McClure." J. Amer. Bamboo Soc, 8, 23-42.
- vant's Hoff, J. H. (1884). "Studies of chemical dynamics." Frederik Muller and Co.,

Amsterdam, the Netharlands.

Vargas, R., Baldocchi, D. D., Bahn, M., Hanson, P. J., Hosman, K. P., Kulmala, L.

Pumpanen, J., Yang, B. (2011) On the multi-temporal correlation between photosynthesis and soil CO 2 efflux: Reconciling lags and observations. New Phytologist, 191(4), 1006-1017.

Widén, B. and H. Majdi (2001). "Soil CO₂ efflux and root respiration at three sites in a mixed pine and spruce forest: Seasonal and diurnal variation." Canadian Journal of Forest Research 31(5): 786-796.

- Xu, L., Baldocchi, D. D., and Tang, J. (2004). "How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature." Global Biogeochemical Cycles 18, GB4002, doi: 10.1029/2004GB002281.
- Xu, M., and Qi, Y. (2001). "Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California." Global Change Biology 7, 667-677.
- Zhu, B. and Cheng, W. (2011). "Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decompisition." Global Change Biology 17: 2172-2183.

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- Figure 9 Relationship between soil respiration rates and surface soil





Figure 1 Site location of Sitou, central Taiwan.



Figure 2 General climate condition in Xitou. Monthly average temperature and precipitation data were averaged over years from 1941 to 2008.



Figure 3 Soil temperature measured in soil surface and 3 different depths



Figure 4 Diurnal variations in soil respiration of collar 5 and 9.



Figure 5 Ranges variation of diurnal R_s rate dynamics of collar 5 and 9. The dynamic ranges are indicated by the maximum and minimum R_s rates in observed in every measuring campaign.



Figure 6 Seasonal R_S variation of collar 5 and 9. Values were calculated with two different approaches: averaging the value of diurnal measurements and single measurement in the measuring campaign.



Figure 7 Percentage of differences between R_S of single measurement and of diurnal average in the studying period.



Figure 8 Observed (a) soil respiration rates (Rs) and monthly accumulated litter C content, (b) soil surface temperature and (c) soil volumetric water content in *P. pubescens* stand (d) daily accumulated precipitation from 13 April 2012 to 27 April 2013.



Figure 9 Relationship between soil respiration rates and surface soil temperature. Red line indicates model 2: $R_s = 1.19 * 5.07^{\left(\frac{T_s - 12.5}{10}\right)}$; and green line indicate model 11: $R_s = 0.26 * e^{\left(\frac{T_s - 12.5}{10}\right)} \times \left(\frac{\theta}{\theta + 0.07}\right)$.

e)



Soil volumetric (m³m⁻³),

Figure 10 Relationship between soil respiration rates and surface soil volumetric water content. Blue line indicate fitted model 3:

$$R_{s} = 20.45 * (\theta - 0.1)(0.7 - \theta)^{0.37} \text{ and green line indicates model 11:}$$
$$R_{s} = 0.26 * e^{\left(\frac{T_{s} - 12.5}{10}\right)} \times \left(\frac{\theta}{\theta + 0.07}\right).$$



Figure 11 Modeled soil respiration (R_s) from 12 May 2012 to 12 May 2013. Filled circles show calibrated soil respiration T_s (calculated from T_s measured in 50 cm depth) and hollow circles show estimated R_s .


Figure 12 Estimated annual R_S of this study plotted with annual R_S converted by Hung (2012) in three Japanese cedar *(Cryptomeria japonica)* forests in Sitou experimental forest. Vertical bars represent standard deviation (n=115, 121, 112 and 293 for CJ73, CJ50, CJ20 and this study, respectively).





Annual soil respiration=130 +2.92*annual litter-fall; and the 95% confidence interval of Davidson et al. (2002)'s regression line: Annual soil respiration = 287+2.80*annual litter-fall.