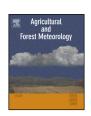
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Seasonal and inter-annual variations in net ecosystem exchange of two old-growth forests in southern China



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ABSTRACT

Old-growth forests can accumulate carbon. However, what controls the rate of net carbon accumulation in those old-growth forests is still poorly understood. Using eddy flux measurements from two old-growth evergreen broadleaf forests (subtropical forest and tropical forest) in southern China, we compared the seasonal and inter-annual variations in the carbon fluxes of those two forests and quantified the major drivers for these temporal variations. The measured flux data showed that the annual net carbon uptake of the subtropical forest was generally much larger than that for the tropical forest. The mean net ecosystem exchange (NEE) over 6 years was $-397 \pm 94 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}\,\mathrm{yr}^{-1}$ for the subtropical forest and -166 ± 49 g C m⁻² yr⁻¹ for the tropical forest with different seasonal variations. The subtropical forest was a carbon sink for most months in a year, while the tropical forest was a carbon source in wet seasons (positive NEE) and a carbon sink in dry seasons (negative NEE). Both forests were stronger carbon sink in dry years, because of much larger reduction in ER than in wet years. At the seasonal scale, GPP in wet seasons was 37.1% higher than that for dry seasons in the subtropical forest, and was only 12.4% higher in the tropical forest. The amplitude of seasonal GPP variation in the tropical forest was much weaker than in the subtropical forest, but the amplitude of the seasonal variation in ER was much larger than in the subtropical forest. The seasonal variation in NEE was largely driven by the variation in monthly ER of the tropical forest, and by both seasonal variations in monthly GPP and ER of the subtropical forest. At inter-annual scale, annual NEE varied tightly with annual rainfall from year to year. Therefore annual rainfall was suggested a fundamental driver of annual carbon sequestration in the subtropical and tropical forests in southern China.

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1. Introduction

Net ecosystem exchange (NEE) is a small difference between two large fluxes, gross primary production (GPP) and ecosystem respiration (ER), and the magnitude of net carbon uptake (= –NEE) is usually less than 20% of GPP or ER (Law et al., 2002). Therefore a small variation in GPP or ER can switch an ecosystem between being a source and being a sink. Both GPP and ER are affected by many abiotic and biotic factors, which can vary differently at different time scales (Richardson et al., 2007). At diurnal time scale, variations in GPP and ER are predominantly influenced by incoming

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photosynthetically active radiation (PAR), vapour pressure deficit (VPD) and air temperature. At seasonal time scale, GPP and ER can also be affected by soil water and temperature, canopy leaf area index (LAI) and litterfall (Stoy et al., 2005; Zhang et al., 2010). At inter-annual time scale, land use history and disturbance, and climate variation can significantly affect GPP and ER, thereby the carbon balance of an ecosystem (Albani et al., 2006). Spectral analysis shows that variations of GPP and NEE are quite similar at weekly and shorter time scales, and becomes quite different at the biweekly and longer time scales across different plant functional types (Stoy et al., 2009; Wang et al., 2011). As a result, variation in NEE is strongly influenced by both GPP and ER due to their direct responses of ecosystems to environmental variables at short-time scale (<weekly). At inter-annual time scale, the dynamics of ecosystems (i.e., phenology, growth pattern or recruitment) and their responses to environmental variables with a frequency longer than one year, such as seasonal rainfall anomaly, extreme summer heat

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and variation of the depth of groundwater table can all significantly affect NEE (Ciais et al., 2005; Dunn et al., 2007). Because our understanding of these dynamics within the ecosystem is much poorer than the direct responses of GPP and ER to environmental drivers at diurnal or seasonal time scales, and the inter-annual variation of NEE often is much more difficult to be accurately simulated than its diurnal or seasonal variations (Siqueira et al., 2006; Wang et al., 2011).

Previous study of two forest types in interior Alaska showed that the inter-annual variation in NEE of deciduous broadleaf forest was more sensitive to temperature variation than evergreen conifer forest (Welp et al., 2007). Yuan et al. (2009) found that the inter-annual variation in NEE is closely related to ER for deciduous broadleaf forests and to GPP for evergreen needleleaf forests globally. However, most previous studies on the seasonal and interannual variations in GPP, RE and NEE were on boreal and temperate forests (Barr et al., 2007; Krishnan et al., 2008; Stoy et al., 2009). In the subtropical and tropical regions, the forests had often been considered to have little seasonality in NEE because of abundant rainfall and consistently warm temperature (Holdridge, 1947; Richard, 1996). However eddy covariance measurements have showed that the seasonal variation in NEE was largely driven by ER in an Amazonian tropical forest (Saleska et al., 2003) and an Asia tropical rain forest (Zhang et al., 2010). These two studies revealed that the dry season is an important period for carbon sequestration in tropical forest ecosystems, while a north Australian tropical savanna showed an essential carbon 'neutral' in the dry season being resulted from lower GPP due to water limitation (Eamus et al., 2001; Hutley et al., 2005). To date, no studies have been made on the inter-annual variation of NEE in subtropical or tropical forests that accounts for more than 40% of the global GPP (Beer et al., 2010) and always net carbon uptake over the last two decades (Zhou et al., 2006; Pan et al., 2011; Tan et al., 2011).

Two old-growth forests, the subtropical evergreen broadleaf forest (age >400 years) and tropical seasonal rain forest (age >180 years), have been perfectly preserved in the Dinghushan Biosphere Reserve and Menglun Nature Reserve, respectively. Previous studies showed that these two old-growth forests are significant carbon sinks (Zhou et al., 2006; Tan et al., 2011). However, the major drivers of seasonal and inter-annual variations of these carbon sinks have yet to be quantified. The objectives of this study therefore are to (1) compare the seasonal and inter-annual variations of GPP, RE and NEE at two old-growth evergreen broadleaf forests in southern China; (2) identify the major biotic and abiotic drivers of the seasonal and inter-annual variations of GPP, RE and NEE of these two forests. We hypothesized that there were no pronounced differences of temporal variations in net carbon uptake between the tropical and subtropical forests because of the similar climate condition and no significant water stress in most years experienced by both forests in southern China. We also tested the hypothesis that GPP do not vary markedly neither between wet season and dry season, nor from year to year in old-growth forests based on previous studies in tropical forests (Saleska et al., 2003; Hutyra et al., 2007; Kosugi et al., 2008). This may be possible because of the full canopy cover throughout the year in tropical and subtropical forests.

2. Materials and methods

2.1. Site descriptions

The subtropical forest site $(23^{\circ}10'16'' \text{ N}, 112^{\circ}31'48'' \text{ E})$ is located in the Dinghushan Biosphere Reserve in central Guangdong Province, southern China. The total area of the reserve is 11.56 km^2 , and most area is coved with rolling hills and low mountains, with an altitude above the sea level ranging from 100 to 700 m. The region

is characterized by a typical subtropical monsoon humid climate, with a mean annual temperature of 20.5 °C. The highest and lowest monthly mean temperatures are 28.0 °C in July and 12.0 °C in January, respectively. The average annual rainfall is 1700 mm, of which more than 80% falls during wet seasons (April–September). The predominant soil type is lateritic red earth. Soil pH ranges from 4.5 to 6.0 with a rich humus layer at ground. The forest is more than 400 years old (Zhou et al., 2006), and is dominated by Castanopsis chinensis, Schima superba, Cryptocarya chinensis, Cryptocarya concinna, and Machilus chinensis. The canopy height is about 22 m and the mean LAI is about 4.9 in dry seasons and 5.6 in wet seasons. The flora includes 260 families, 864 genera, and 1740 species of wild plants (Yan et al., 2006).

The tropical forest site (21°55′39″ N, 101°15′55″ E) is located in the Menglun Nature Reserve in Xishuangbanna, Southern China. The climate is strongly seasonal with two air masses alternating between wet and dry seasons within a year (Zhang, 1966). During wet seasons (April-September), the tropical southern monsoon from the Indian Ocean delivers most of the annual rainfall, whereas the dry and cold air of the southern edges of the subtropical jet streams dominates the climate during dry seasons (October–March). The mean annual air temperature is 21.7 °C, with a maximum monthly temperature of 25.7 °C in June and a minimum of 15.9 °C in January. The mean annual rainfall is 1487 mm, about 87% of which falls during wet seasons. The soil is lateritic derived from siliceous rocks, such as granite and gneiss, with a pH from 4.5 to 5.5. The forest canopy is uneven and complex, and can be divided into three layers (A, B and C). Dominating tree species in layer A are Pometia tomentosa, Terminalia myriocarpa, Gironniera subaequalis and Garuga floribunda, which have the canopy with 40 m in height on average. Dominating tree species in layer B (16–30 m) are Barringtonia fusicarpa, Gironniera subaequalis, Mitrephora maingayi. Dominating tree species in layer C (lower than 16 m) include Garcinia cowa, Knema erratica, Ardisia sinoaustralis (Cao et al., 1996). LAI varies from 4.0 to 6.0 within a year (Zhang et al., 2010).

2.2. Measurements

As part of the ChinaFLUX network, a 38 m-tall flux tower (DHS tower) and a 70 m-tall flux tower (XSBN tower) were established in the subtropical forest site and the tropical forest site, respectively. An eddy covariance system (EC) with 3D sonic anemometer (CSAT3; Campbell Scientific Inc., Lincoln, NE, USA) and an infrared openpath gas analyzer (Li-7500; Li-Cor Inc.), were mounted at 27.0 m on the DHS tower and 48.8 m on the XSBN tower, respectively. Seven levels of air temperature, relative humidity (HMP45C; Campbell Scientific Inc., Lincoln, NE, USA), photosynthetically active radiation (LQS70-10; Apogee) and wind speed (A100R; Vector) sensors were mounted along each tower to obtain canopy profiles. Solar radiation and net radiation was measured with radiometers (CM11, CNR1; Kipp & Zonnen). Precipitation was recorded by a rain gauge (52,203; R.M. Young) at the top of both the DHS tower and XSBN tower. In each forest stand, soil temperature and moisture were measured with thermocouple (105T; Campbell Scientific Inc., Lincoln, NE, USA) and time-delay reflectometer (CS616; Campbell Scientific Inc., Lincoln, NE, USA), respectively. Routine meteorological data were recorded at 30 min intervals by data loggers (CR10X & CR23X; Campbell Scientific Inc., Lincoln, NE, USA), and the measured windspeed in each of three directions, concentrations of CO₂ and water vapour were recorded at a frequency of 10 Hz using a data logger (CR5000; Campbell Scientific Inc., Lincoln, NE, USA).

The forests are quite uniform within 5 km surrounding the flux towers at both sites, and footprints as estimated by Mi et al. (2006) varies from 130 m to 3 km, depending on the atmospheric stability. Therefore the fetch meets the requirement for eddy flux measurements at both sites. Spectral analysis showed that the contribution

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