



CO₂ uptake of a mature *Acacia mangium* plantation estimated from sap flow measurements and stable carbon isotope discrimination

H. Wang^{1,2}, P. Zhao², L. L. Zou², H. R. McCarthy³, X. P. Zeng², G. Y. Ni², and X. Q. Rao²

¹Institute of Forestry and Pomology, Beijing Academy of Agriculture and Forestry Sciences, Beijing 100093, PR China

²Key laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, PR China

³Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA

Correspondence to: P. Zhao (zhaoping@scib.ac.cn)

Received: 25 April 2013 – Published in Biogeosciences Discuss.: 10 July 2013

Revised: 16 January 2014 – Accepted: 28 January 2014 – Published: 12 March 2014

Abstract. A simple, nondestructive method for the estimation of canopy CO₂ uptake is important for understanding the CO₂ exchange between forest and atmosphere. Canopy CO₂ uptake (F_{CO_2}) of a subtropical mature *A. mangium* plantation was estimated by combining sap flow measurements and stable carbon isotope discrimination (Δ) in Southern China from 2004 to 2007. The mechanistic relationship linking F_{CO_2} , Δ in leaf sap, and sap flow-based canopy stomatal conductance (G_s) was applied in our study. No significant seasonal variations were observed in Δ or in the ratio of the intercellular and ambient CO₂ concentrations (C_i/C_a), although diurnal C_i/C_a varied between sunlit and shaded leaves. A sensitivity analysis showed that estimates of F_{CO_2} were more sensitive to dynamics in G_s than in C_a and Δ . By using seasonally and canopy averaged C_i/C_a values, we obtained an acceptable estimate of F_{CO_2} compared to other estimates. F_{CO_2} exhibited similar diurnal variation to that of G_s . Large seasonal variation in F_{CO_2} was attributed to the responsiveness of G_s to vapor pressure deficit, photosynthetically active radiation, and soil moisture deficit. Our estimate of F_{CO_2} for a mature *A. mangium* plantation ($2.13 \pm 0.40 \text{ g C m}^{-2} \text{ d}^{-1}$) approached the lower range of values for subtropical mixed forests, probably due to lower mean canopy stomatal conductance, higher C_i/C_a , and greater tree height than other measured forests. Our estimate was also lower than values determined by satellite-based modeling or carbon allocation studies, suggesting the necessity of stand level flux data for verification. Qualitatively, the sap flux/stable isotope results compared well with gas exchange results. Differences in results between the two

approaches likely reflected variability due to leaf position and age, which should be reduced for the combined sap flux and isotope technique, as it uses canopy average values of G_s and C_i/C_a .

1 Introduction

The continued increase in atmospheric carbon dioxide levels due to anthropogenic emissions has led to significant climate changes (Schneider, 1989; Pachauri and Reisinger, 2007). Rising atmospheric CO₂ is due to the imbalance between the rates that sources emit CO₂ into the atmosphere and the rates that sinks remove CO₂ from the atmosphere (Baldocchi et al., 1996). In this context, forests act as vital CO₂ sinks by storing carbon in woody biomass (Nowak et al., 2002). It has been reported that forests at northern mid-latitude sites are large CO₂ sinks (Ciais et al., 1995). A recent study suggests that old-growth forests continue to accumulate carbon (Luyssaert et al., 2008). In China, since the mid-1970s, planted forests (afforestation and reforestation) have sequestered 0.45 petagram of carbon, while natural forests have lost an additional 0.14 petagram of carbon (Fang and Chen, 2001). The biomass increments vary with stand age and many other factors, primarily resource availability (Oren et al., 2001; Peng, 2003). However, estimation of canopy scale photosynthesis has not been common. Such uncertainties hinder our ability to estimate forest CO₂ sequestration for global carbon budgets, as well as to increase CO₂ sequestration through forest management.

The tree canopy scale is an important intermediate scale between the leaf and the ecosystem. Although established photosynthesis monitoring techniques are available for both leaf and ecosystem scales (Farquhar et al., 1980; Baldocchi et al., 1996), there are currently few accepted estimation methods for photosynthesis at the tree canopy scale. This limits our understanding of canopy photosynthesis compared with canopy water fluxes, which can be determined through sap flow techniques. Notably, comparisons between water and photosynthesis fluxes must account for the fact that water fluxes are generally much larger than CO₂ fluxes. A number of methods have been designed to address the dilemma, including (1) directly adopting branch bag techniques, or combining water use efficiency obtained with branch bag techniques with whole-tree transpiration (Rayment and Jarvis, 1999; Morén et al., 2001), (2) coupling sap flow-based canopy stomatal conductance and photosynthesis (Catovsky et al., 2002), and (3) using a canopy conductance constrained carbon assimilation scheme, which couples actual or potential canopy conductance with vertical gradients of light distribution, leaf-level conductance, maximum Rubisco capacity and maximum electron transport (Schäfer et al., 2003; Kim et al., 2008). However, application of these methods still requires extensive leaf gas exchange measurements, which are time-consuming and difficult, because access to tall canopies is required. Recently, a novel approach combining sap flow measurement and stable carbon isotope techniques (the SF/SI approach) was proposed to estimate forest CO₂ uptake (Zhao et al., 2005a; Hu et al., 2010). Firstly, it is ideal for plot-scale studies, since measurements are taken at the whole tree scale, rather than scaled up or down from the leaf or the ecosystem level (Zhao et al., 2005a). Secondly, it is suitable for field studies of forests in mountainous areas, especially for upper-canopy species such as the pure *A. mangium* stand in our study. This overcomes the restrictions of the eddy covariance method (EC) associated with surface heterogeneity and complex terrain (Moncrieff et al., 1996). Lastly, it has huge potential given the large number of sites with continuous sap flow measurement and the relatively easy sampling for carbon isotope analysis.

Previous application of the SF/SI approach has accounted for both within-canopy and seasonal variability to estimate correctly CO₂ uptake in needle leaf trees in a subalpine forest (Hu et al., 2010). Hu et al. (2010) tested for differences in the carbon isotope ratio of needle sugars and water-use efficiency between sun and shade needles, throughout the growing season, and found observed the highest values of whole-tree CO₂ assimilation rates following snowmelt or summer rain events, and during weather with lower temperatures. In our study, we accounted for sub-daily and inter-annual variability, as well as within-canopy and seasonal variability for a broadleaf species in a subtropical climate. The instantaneous forest CO₂ uptake rate can be estimated based on the relationship between canopy stomatal conductance (G_s) and ¹³C discrimination (Δ) in leaf sap. Our SF/SI approach is unique

in its continuity, representativeness, accuracy and ease of use: G_s is derived from continuous measurement of sap flow (Zhao et al., 2005a); the relationship of net photosynthetic rate/canopy stomatal conductance (A_{net}/G_s) derived from Δ is very stable and representative on both temporal and spatial scales (Dawson et al., 2002); and sap flow measurement is nondestructive, easy, and relatively low cost (Granier, 1987; Zhao et al., 2005b). Given these features, we demonstrate in this paper that with appropriate sampling, CO₂ uptake obtained from the SF/SI approach is representative at the tree canopy scale, and is comparable with results from other methods, including the gas exchange method, carbon allocation studies, and modeling approaches. Hereby, the stem sap flux, carbon isotopic compositions of leaf sap, and environmental parameters in a subtropical *A. mangium* plantation in Southern China were measured from 2004 to 2007. Our aims were: (1) to provide an alternative sap flow-based method for estimating instantaneous CO₂ uptake at the canopy scale and verify it by comparing it with values obtained from other methods, (2) to investigate the diurnal, seasonal, annual and inter-annual changes of CO₂ uptake of the plantation and (3) to examine how CO₂ uptake of the plantation is regulated by stomatal conductance and environmental conditions. We expected that F_{CO_2} of a subtropical mature *A. mangium* plantation could be estimated by the SF/SI approach, by accounting for variability of sunlit vs. shaded leaves. Given that this forest is likely to be water limited, we also expected that F_{CO_2} would be higher in the wet season than in the dry season, and be highest in the mid-morning. Because CO₂ is assimilated through the stomatal pores, we expected that F_{CO_2} would be more sensitive to changes in G_s than in C_a and Δ .

2 Materials and methods

2.1 Site description and environmental conditions

This study was conducted at the Heshan Hilly Land Interdisciplinary Experimental Station of the Chinese Academy of Sciences (112°54' E, 22°41' N) in Guangdong Province, China over the 2004–2007 period. The study site is dominated by a subtropical monsoonal climate, with the wet season occurring from April to September and the dry season from October to March. Mean annual temperature is 21.7 °C and average precipitation is 1400 mm, of which 78 % occurs in the wet season.

The study stand was situated at 60–70 m altitude, on a 20° slope with a south–east aspect. The soil is an oxisol developed from sandstone with surface soil to a depth of 10 cm and subsoil for a further 50 cm (Ma et al., 2008a). *Acacia mangium* was the only overstorey species planted at a spacing of 3 m × 4 m in 1984, and reached maturity after ~20 years of growth. The understorey vegetation was very sparse and its contribution to stand CO₂ uptake was considered to be negligible for the purposes of this study. *A. mangium* is a

fast-growing legume species that has nitrogen fixing nodules on its shallow roots (Cole et al., 1996). It was introduced to China from Southeast Asia in the late 1970s and has been widely used for restoration of vegetation in tropical and subtropical China (Yang et al., 2009). A study plot with an area of 640.5 m² (36.6 m × 17.5 m) was set up within the stand. The plot comprised 47 trees (734 trees per hectare) with a basal area of 26.6 m⁻² ha⁻¹. These trees included both trees originally planted in 1984 and naturally regenerated trees. Tree height ranged from 2.4 m to 22.8 m with an average of 15.7 m. Stem diameter at breast height (DBH) was between 3.8 cm and 37.5 cm with an average of 20.1 cm.

Air temperature (T_a , °C), air relative humidity (RH, %), and photosynthetically active radiation (PAR, μmol m⁻² s⁻¹), were monitored at a weather station located 150 m away from the study site. T_a and RH were measured using an HMP35E sensor (HMP35E; Vaisala, Finland). PAR was measured with a LI-190SA quantum sensor (Li-Cor, Lincoln, US). Since the root system of *A. mangium* was mainly distributed in the upper 30 cm of the soil, volumetric soil water content (SWC, m³ m⁻³) was measured using three soil moisture probes (ML2x, Delta-T Device, UK) inserted into the upper soil (20 cm–30 cm) amongst the selected trees. The environmental data were sampled and recorded as 10 min means by a data logger synchronized to the logger for sap flow measurements. Vapor pressure deficit (D) was calculated from T_a and RH as follows:

$$D = a \times \exp\left[\frac{bT_a}{(T_a + c)}\right] \times (1 - \text{RH}), \quad (1)$$

where a , b , and c are fixed parameters, which are 0.611 kPa, 17.502, and 240.97°C (Campbell and Norman, 1998).

SWC data were converted to soil moisture deficit (SMD, dimensionless), defined as

$$\text{SMD} = \frac{\text{SWC}_{\max} - \text{SWC}}{\text{SWC}_{\max} - \text{SWC}_{\min}}, \quad (2)$$

where SWC_{\max} and SWC_{\min} are the maximum and minimum values of SWC during the study period. SWC_{\max} (0.49) occurred on 18 July 2005, while SWC_{\min} (0.11) occurred on 26 December 2005.

2.2 Projected crown area, leaf area index and sapwood area

Sapwood area (A_s), projected crown area (A_c), and leaf area index (LAI) are key parameters for calculating stand transpiration and canopy stomatal conductance. A_c of each tree in the plot was calculated as the area of an ellipse based on measurements of the widest and narrowest canopy widths. The projected crown area (A_c) of each tree in the plot was estimated to range from 0.8 m² to 53.0 m², with an average of 13.8 m². LAI was measured at 20 random locations within the stand using a plant canopy analyzer (CID-110,

CID COR., USA) at dawn, dusk or under cloudy conditions every month. A_s of each tree in the plot was calculated based on strong allometric relationships between DBH and A_s ($A_s = 0.1930(\text{DBH})^{1.944}$). This relationship, established from measurements on 23 surrounding trees, has been reported in previous studies (Zhao et al., 2005b; Wang et al., 2012).

2.3 Sap flow measurement

Sap flux density (J_s , g H₂O cm⁻² s⁻¹) was measured with self-made Granier-type sensors (Granier, 1987; Zhao et al., 2005b). Fourteen trees, representative of the DBH distribution in the plot, were selected for sap flow measurement, with tree height ranging from 12 m to 22.8 m, DBH between 13.4 and 37.5 cm and A_c ranging from 4.6 m² to 47.7 m² (see Supplement A for details). 1, 4, 5, 2, 2 trees at the < 15 cm, 15–20 cm, 20–25 cm, 25–30 cm, and > 30 cm DBH classes were selected for J_s measurement, respectively. For tree nos. 1–4, sensors were installed on the eastern, southern, western, and northern sides of the trunk, while for tree nos. 5–14, sensors were installed only on the northern side. The sensors and adjacent portions of stem were wrapped with plastic insulation to protect the probes from mechanical damage, and the entire assembly was enclosed in an outer layer of aluminum film in order to minimize spurious temperature gradients caused by radiant heating of the stem, as well as to protect against water running down the trunk (Zhao et al. 2005b). To ensure good measurements, new sets of sensors were installed 2–5 cm from the original holes at both the beginning and end of the dry season (Ma et al., 2008a). Sensors consisted of two 20 mm-long probes inserted into the xylem at breast height, with one placed 10 cm above the other. Each probe contained a copper-constantan thermocouple, and the upper probe was continuously heated with heating wire supplied with constant power. The temperature difference between the two probes was taken every 30 s and recorded as 10 min means by a data logger (Delta-T Devices Ltd., Cambridge, UK). We selected the highest temperature difference between heated and unheated probes during times of zero flux (ΔT_m) as the baseline for each day using the Baseline program developed by Yavor Parashkevov from Duke University (Granier, 1987; Phillips et al., 1997). Deviation from this baseline was used to estimate J_s (Granier, 1987). It was found that the nighttime sap flow of the same *Acacia mangium* plantation was mainly used to refill water in the trunk, rather than nighttime transpiration (Wang et al., 2012). Hereby, using the maximum temperature difference for each night did not lead to underestimation of sap flow.

2.4 Stand transpiration and canopy stomatal conductance

Whole-tree transpiration (E_t , g s⁻¹) was calculated as

$$E_t = J_s \times A_s. \quad (3)$$

A. mangium is a diffuse-porous species for which the radial variation in J_s is considered to be small (Phillips et al., 1996; Ma et al., 2008a), and sapwood depth of sample trees measured with cores was close to 2 cm. Therefore, radial variation in J_s was considered to be negligible in this study. Furthermore, the variation in J_s at different aspects was random for the studied trees (Ma et al., 2007). Hence, J_s at the north aspect was assumed to be representative of J_s of individual trees. For tree nos. 1–4, J_s was calculated as the mean of the values from four aspects, while for tree nos. 5–14, J_s was the value measured from the northern side.

The 47 trees within the stand were classified into 5 groups by DBH categories (Zhao et al., 2006) (see Supplement B for details). The average sap flux density of class i (J_{si}) was calculated as:

$$J_{si} = \sum (J_{sj} \times A_{sj}) / \sum A_{sj}, \quad (4)$$

where J_{sj} is the sap flux density of sample tree j , and A_{sj} is the sapwood area of sample tree j .

Sap flow measurements on 14 sample trees were extrapolated to stand level as in Zhao et al. (2005a):

$$E_s = \sum (J_{si} \times A_{si}), \quad (5)$$

where E_s is the stand transpiration of *A. mangium* (g s^{-1}), and A_{si} is the sum of total sapwood area in class i .

E_s was converted to stand transpiration per unit of leaf area (E_L , mm s^{-1}) as in Zhao et al. (2005a):

$$E_L = \frac{E_s}{\text{LAI} \times A_G}, \quad (6)$$

where LAI is the leaf area index ($1.95 \text{ m}^2 \text{ m}^{-2}$) and A_G is the total stand area (640.5 m^2).

For our stand, a strong coupling of canopy surface to the atmosphere can be assumed. This assumption requires three conditions to be met. Firstly, the *A. mangium* plantation had a low LAI, and thus an open, well-ventilated, aerodynamically rough canopy. Secondly, the wind speed (w) had an effect on canopy stomatal conductance (G_s) of the *A. mangium* plantation. G_s significantly decreased with w in July and December from 2005 to 2007 ($p < 0.05$; $R^2 = 0.106$; $G_s = -7.3437w + 62.548$). However, most of the time, the daily average w above the plantation was greater than or close to 2 m s^{-1} from 2005 to 2007. Thus, the boundary layer conductance was much higher than canopy stomatal conductance (Larcher, 1983). Finally, the decoupling coefficient for our stand was less than 0.2 in 2005 (Ma, 2008). Furthermore, since the alteration of the transpiration signal due to depletion and replenishment of stem-stored water was relatively small (Wang et al., 2012), the average sap flux in the sapwood multiplied by sapwood area: leaf area is equal to transpiration (E_L). Therefore, the mean canopy stomatal conductance (G_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of the study stand was calculated based

on a simplification of the Penman–Monteith equation (Köstner et al., 1992)

$$G_s = \frac{E_L \times \rho \times G_V \times (T_a + 273)}{D}, \quad (7)$$

where ρ is the density of water (998 kg m^{-3}), G_V is the universal gas constant adjusted for water vapor ($0.462 \text{ m}^3 \text{ kPa K}^{-1} \text{ kg}^{-1}$), T_a is the air temperature ($^{\circ}\text{C}$), and D is vapor pressure deficit (kPa). We used all data except for those that were excluded based on the following criteria: (1) data during and 2 h after rainfall were excluded to avoid the discrepancy between evaporation and tree transpiration (Granier et al., 2000); (2) when global radiation, vapor pressure deficit, or stand transpiration were too low ($< 5\%$ of the maximum value), because of the large relative uncertainties in computing G_s under these conditions (Granier et al., 2000); (3) when $D < 0.6 \text{ kPa}$ for G_s estimation, to keep errors in G_s estimates to less than 10% (Ewers and Oren, 2000).

Relationships between the ratio of canopy stomatal conductance to the maximum value ($G_s/G_{s\text{max}}$) and photosynthetically active radiation (PAR), vapor pressure deficit (D), and soil moisture deficit (SMD) were determined by boundary-line analysis and non-linear least squares, using the maximum of average G_s of 14 trees for different PAR (step width: $50 \mu\text{mol m}^{-2} \text{ s}^{-1}$), D (step width: 0.2 kPa), and SMD classes (step width: 0.1). The estimated boundary line was used to compare the responses among seasons or years (Webb, 1972; Rico et al., 1996).

The response of $G_s/G_{s\text{max}}$ to PAR was represented by the Michaelis–Menten quadratic hyperbolic function (Thornley and Johnson, 1990)

$$G_s/G_{s\text{max}} = \frac{\text{PAR}}{\text{PAR} + a}, \quad (8)$$

where a is a fitted parameter, representing the value of global radiation that reduces canopy conductance to one half of its maximum value.

G_s was related to D within seasons and among years in order to estimate the sensitivity of stomata to D . The response function was described as (Oren et al., 1999)

$$G_s = -m \ln(D) + b, \quad (9)$$

where the parameter $-m$, the slope of the regression, quantifies stomatal sensitivity to D , and the parameter b , the intercept, is a reference G_s when $D = 1 \text{ kPa}$ ($\ln D = 0$). $-m$ and b were estimated using least squares regression with Sigma Plot 10.0 (Systat Software Inc., San Jose, California).

The quadratic response function between $G_s/G_{s\text{max}}$ and SMD was described as follows:

$$G_s/G_{s\text{max}} = y_0 + k_1 \times \text{SMD} + k_2 \times \text{SMD}^2, \quad (10)$$

where the parameters y_0 , k_1 and k_2 were estimated using least squares regression with Sigma Plot 10.0 (Systat Software Inc., San Jose, California).

2.5 Carbon isotope measurements on leaf sap and air samples

10 mature leaves in different positions on branches in the middle canopy were collected every 1 h and repeated twice from 06:00 to 17:00 on eight representative sunny days: 6 and 17 December 2006 (winter, dry season), 9 and 10 May 2007 (spring, wet season), 26 July 2007, 1 August 2007 (summer, wet season), and 6 and 7 November 2007 (autumn, dry season). The leaf sap, composed of xylem sap, phloem sap or cell contents, was forced out through the petiole using a portable pressure chamber (PMS Instruments, Corvallis, Oregon, USA). According to the diurnal pattern leaf water potential of *Acacia mangium*, the pressure exerted varied between 1.5 bar in the morning and 15 bar at noon. After the leaf sap appeared at the petiole, 25 µl leaf sap was pipetted into a 5 ml vial, then immediately frozen and stored in the freezer at 5°C. Samples were heated in a quartz ampoule at 600°C, cooled down and vacuumized for 3 hr. After that, they were heated in a muffle furnace at 860°C for 2 hr and converted to purified CO₂. The carbon isotope ratio of these samples was determined on a gas chromatograph–isotope ratio mass spectrometer (Finnigan MAT 252, Finnigan, Bremen, Germany). Carbon isotopic compositions of soluble sugar, water-soluble organic matter in leaves and phloem sap have all been used as indicators of recent canopy photosynthate (Gessler et al., 2004; Hu et al., 2010; Rascher et al., 2010). In our study, we used carbon isotopic compositions of leaf sap as an indicator of recent photosynthate, which was needed to match with the high-resolution sap flow data.

Five air sampling points were situated at 10 m to 15 m above the ground in the canopy of the *A. mangium* plantation. Air samples were collected twice per hour during the periods when leaf sap was collected. The air samples were collected with an electromagnetic pump and a plastic tube. The samples were then injected into pre-evacuated 500 ml gas sampling bags. At the same time, atmospheric CO₂ concentration was recorded by an infrared gas analyzer (IRGA) (LI-6262, Li-Cor Inc., Lincoln, NE, USA). The CO₂ isotope ratio of air samples with cryogenic preconcentration was also determined on Finnigan MAT 252. Carbon isotopic compositions are specified as δ¹³C values (Keeling, 1958)

$$\delta^{13}\text{C} = (R_p/R_s - 1) \times 1000, \quad (11)$$

where R_p is the abundance ratio of ¹³C/¹²C of the examined sample and R_s refers to the internationally recognized standard abundance ratio of ¹³C/¹²C (PDB).

2.6 Canopy CO₂ uptake rate estimation

Canopy CO₂ uptake of *A. mangium*, estimated by combining sap flow and ¹³C techniques, as proposed by Zhao et al. (2005a), was calculated as follows. The CO₂ uptake rate (F_{CO_2} , µmol CO₂ m⁻² s⁻¹) was then given (Farquhar et al.,

1982) by

$$F_{\text{CO}_2} = g_{\text{CO}_2} \times C_a \times (1 - C_i/C_a), \quad (12)$$

where g_{CO_2} is the stomatal conductance for CO₂.

In order to account for the influence of the ¹³C/¹²C ratio in the air, isotope discrimination (Δ) was used to express the discrimination of plants against ¹³C (Farquhar et al., 1982)

$$\Delta = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_p}{1 + \delta^{13}\text{C}_p}, \quad (13)$$

where δ¹³C_a and δ¹³C_p stand for carbon isotope compositions in air and leaf sap.

Δ is frequently used to derive intercellular CO₂ concentration (C_i) according to the linear relationship (Farquhar et al., 1982)

$$\Delta = a + (b - a) \times (C_i/C_a), \quad (14)$$

where a stands for the fractionation that occurs as CO₂ diffuses through stomates (4.4‰), b for fractionation during carboxylation (27.5‰), C_i for intercellular CO₂ concentration, and C_a for ambient CO₂ concentration.

Combining Eqs. (12) and (14), we then had

$$F_{\text{CO}_2} = g_{\text{CO}_2} \times C_a \times \left(1 - \frac{\Delta - 4.4}{23.1}\right). \quad (15)$$

Stomatal conductance to water vapor ($g_{\text{H}_2\text{O}}$) was converted to conductance for CO₂ by dividing the stomatal conductance by 1.6, giving

$$F_{\text{CO}_2} = \frac{g_{\text{H}_2\text{O}}}{1.6} \times C_a \times \left(1 - \frac{\Delta - 4.4}{23.1}\right). \quad (16)$$

Equation (16) depicts a relationship linking F_{CO_2} , $g_{\text{H}_2\text{O}}$, C_a , and Δ at the leaf level. Subsequently this relationship was scaled up to canopy level by incorporating G_s calculated with Eq. (7) using the sap flow-based stand transpiration.

G_s is expressed as a product of LAI and $g_{\text{H}_2\text{O}}$:

$$G_s = \text{LAI} \times g_{\text{H}_2\text{O}}. \quad (17)$$

Thus, combining Eqs. (7), (14) and (17) led to a mean F_{CO_2} of our *A. mangium* stand

$$\bar{F}_{\text{CO}_2} = \frac{E_L \times \rho \times G_v \times (T_a + 273)}{1.6 \times \text{LAI} \times D} \times C_a \times \left(1 - \frac{\Delta - 4.4}{23.1}\right), \quad (18)$$

where Δ is seasonally integrated ¹³C discrimination taken over four representative days in the wet and dry seasons, separately. Notably, accounting for nocturnal sap flux caused by the recharge of water to trunks and branches, as well as nocturnal transpiration, is a vital step for accurately estimating canopy transpiration, and thereby canopy CO₂ uptake. Allocation of nighttime sap flow to the refilling of depleted water storage has been found in the same *A. mangium* trees

(Wang et al., 2012). In view of the obvious nocturnal water recharge, we used the 24 h diurnal sap flux to accurately estimate canopy CO₂ uptake. Furthermore, the daily canopy CO₂ uptake for our mature *A. mangium* plantation was obtained based on the sap flow measurement-derived canopy stomatal conductance and seasonally integrated ¹³C discrimination. The annual canopy CO₂ uptake for our mature *A. mangium* plantation was obtained by summarizing monthly canopy CO₂ uptake during the whole year. Daily and annual mean standard errors were also estimated. Subsequently, these values were compared with estimates from other methods, including the gas exchange method, carbon allocation studies, and modeling approaches.

2.7 Leaf gas exchange measurements

Leaf photosynthetic rate (P_n) and stomatal conductance (g_s) of 10 sun-exposed leaves and 10 shaded leaves from *A. mangium* trees at the study plot were measured with a portable gas exchange system (Li-Cor 6400, Li-Cor Inc., Lincoln, NE, USA). A frame platform was erected on the upper slope of the study plot so that the leaves within the canopy on the lower slope could be accessed. The measurements were taken on the same trees every hour from 06:00 to 19:00 (GMT + 08:00) on 6 and 17 December 2006 (winter, dry season), 9 and 10 May 2007 (spring, wet season), 26 July 2007, 1 August 2007 (summer, wet season), and 6 and 7 November 2007 (autumn, dry season).

2.8 Statistics and sensitivity analysis

Statistical analyses were performed in SPSS 16.0 (SPSS Inc., Chicago, USA) and Sigmaplot 10.0 (Systat Software Inc., San Jose, CA). Two-way ANOVA (repeated measures) (GLM procedure) was applied for parameters (C_a , C_i , C_i/C_a , $\delta^{13}C_a$, $\delta^{13}C_p$, Δ) to evaluate the main effects of season (wet season and dry season), time (from 06:00 to 19:00) and their interaction over time. Partial correlation analysis was used to determine the correlations between Δ and PAR, D , C_a , and G_s . Linear regression analyses between g_s and G_s , and between P_n and F_{CO_2} , were performed. The regression lines for sunlit and shade leaves and for the dry and wet seasons were compared by analysis of covariance. Non-linear regressions were performed on the correlation between G_s and D among seasons and years.

In order to quantify error propagation when modeling F_{CO_2} based on measurements of G_s , C_a and Δ , we applied a Monte Carlo method (Hollinger and Richardson, 2005; Hu et al., 2010) (Matlab R2008B, The Mathworks). This approach accounted for all known parameter uncertainties in calculating F_{CO_2} , including C_a and Δ (differences influenced by seasons), and G_s (differences influenced by tree size and seasonality in leaf area). For each selected day (8 d between December 2006 and November 2007), we modeled F_{CO_2} in an iterative manner (10 000 times) and ran-

domly sampled from a range of uniformly distributed G_s , C_a and Δ values to calculate F_{CO_2} . Hence, we were able to estimate F_{CO_2} without the constraint of limited sampling frequency and could determine the sensitivity of the estimated F_{CO_2} to G_s , C_a and Δ . The range of the G_s (between 4.25 and 64.52 mmol m⁻² s⁻¹), C_a (between 381.51 and 416.58 μmol mol⁻¹) and Δ (between 20.47 and 23.89 ‰) values used for constructing the pool of simulations was determined a priori. Because F_{CO_2} was modeled using both measurements of G_s , C_a and Δ , we used random values drawn from the same pool of F_{CO_2} values used in the Monte Carlo analysis, and examined the sensitivity of F_{CO_2} to G_s , C_a and Δ as independent variables. We plotted the linear regression relationship plus 95 % confidence intervals from this analysis for the data reported in Fig. 7.

3 Results

3.1 Microclimate, leaf area index, and stand transpiration

Seasonal and inter-annual variability in vapor pressure deficit (D), photosynthetically active radiation (PAR), precipitation (P), soil water content (SWC), leaf area index (LAI), and stand transpiration (E_L) from 2004 to 2007 are shown in Fig. 1. E_L has clear seasonality, corresponding to D , PAR, and P seasonality, in contrast to the relatively small seasonal variation in LAI ($p = 0.151$). The means of annual averages of D , SWC, and LAI were 0.46 kPa, 0.26 m³ m⁻³, and 1.95 m² m⁻², respectively. The means of annual totals of PAR, P , and E_L were 5752 mol m⁻², 1391 mm, and 220 mm, respectively. The inter-annual variability of D , PAR, SWC, and LAI was relatively small, with coefficients of variation (CV) of 8.6 %, 3.0 %, 7.1 %, and 4.2 %. However, large inter-annual variability of P and E_L (CV 40.7 % and 26.7 %) was observed.

3.2 Diurnal and seasonal variability of physiological parameters and carbon isotope data

The diurnal ambient CO₂ concentration (C_a), intercellular CO₂ concentration (C_i), the ratio of the intercellular and ambient CO₂ concentrations (C_i/C_a), and carbon isotope compositions in leaf sap ($\delta^{13}C_p$) were higher in the morning and at dusk, but lower at noon (Fig. 2a, b, c, d, f), while isotope compositions in the canopy air ($\delta^{13}C_a$) and the photosynthetic ¹³C discrimination (Δ) were lower in the early morning, gradually increased, and then slightly decreased from noon to dusk (Fig. 2e, g). The diurnal C_a , $\delta^{13}C_p$, $\delta^{13}C_a$, and Δ in the wet season fluctuated, while they were relatively flat in the dry season. The diurnal canopy stomatal conductance (G_s) increased rapidly just after sunrise, reached a maximum in the early or late morning, then decreased progressively, eventually declining to near-zero values around sunset (Fig. 2h). G_s exhibited a narrow peak with a maximum

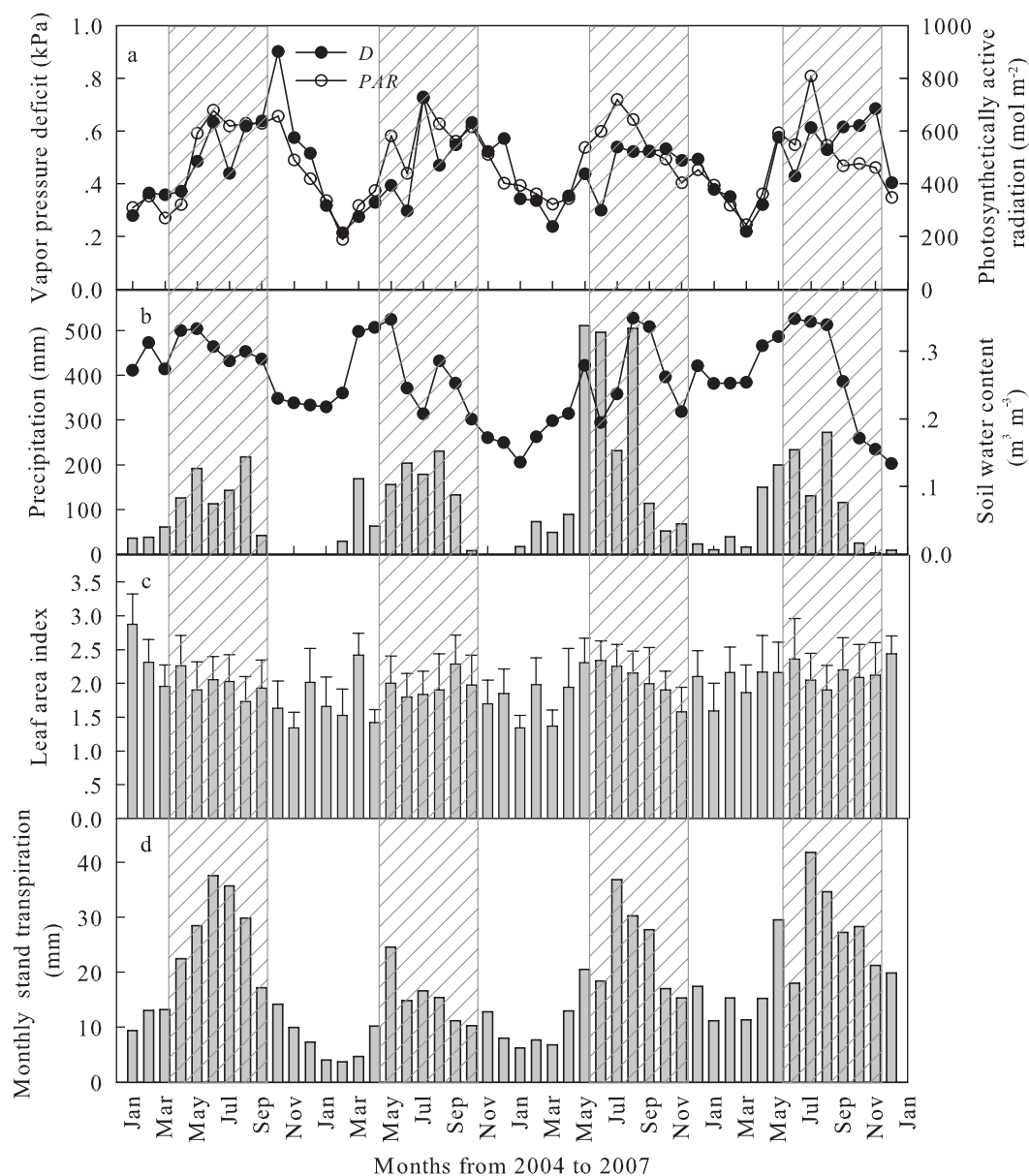


Fig. 1. (a) Monthly mean vapor pressure deficit (D) and photosynthetically active radiation (PAR) at the experimental site; (b) precipitation (P) and monthly mean soil water content (SWC) at the experimental site; (c) monthly mean leaf area index (LAI) and (d) stand transpiration (E_L) of *A. mangium*. Error bars indicate standard deviation ($n = 20$). Boxes filled with the coarse pattern in gray color indicate the wet seasons.

around $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ in the wet season, with a wider peak with a maximum around $50 \text{ mmol m}^{-2} \text{ s}^{-1}$ in the dry season. The opening of stomata, as well as the time of maximum value (around 08:00), occurred earlier in the wet season than in the dry season (around 11:00).

Diurnal C_a , C_i , C_i/C_a , $\delta^{13}C_p$, $\delta^{13}C_a$, and Δ fluctuations were observed (Table 1). CVs of diurnal C_a , C_i , C_i/C_a , $\delta^{13}C_p$, $\delta^{13}C_a$, and Δ were below 5.5%, 11.6%, 10.1%, 6.4%, 12.7%, and 11.2%, respectively. Because of the lack of strong variability in diurnal Δ values, the average Δ

value was used in subsequent calculations of F_{CO_2} for the whole season. Furthermore, values of diurnal C_i/C_a for sunlit leaves ranged between 0.55 and 0.94, while those of shaded leaves ranged between 0.68 and 0.95. The mean daily C_i/C_a value of 0.76 for sunlit leaves was significantly lower than that of 0.83 for shaded leaves ($p = 0.001$). At the seasonal scale, CVs of seasonal C_a , C_i , C_i/C_a , $\delta^{13}C_p$, $\delta^{13}C_a$, and Δ were below 5.1%, 5.0%, 3.3%, 5.1%, 14.4%, and 9.8% (Table 1). Furthermore, there were no significant differences in C_a , C_i , C_i/C_a , $\delta^{13}C_p$, $\delta^{13}C_a$, and Δ between

the wet season and dry season ($p = 0.212$, $p = 0.644$, $p = 0.446$, $p = 0.420$, $p = 0.090$, $p = 0.988$), and this did not change through time (see Supplement C for details).

Hourly Δ was negatively correlated with C_a ($r = -0.549$, $p < 0.001$) in the wet season, negatively correlated with PAR ($r = -0.425$, $p = 0.002$) and positively correlated with G_s ($r = 0.464$, $p < 0.001$) in the dry season, and positively correlated with D ($r = 0.250$, $p = 0.009$) over the entire year (Table 2). Boundary-line response curves using 10-minute values of G_s and PAR, D , and SMD were created to determine the G_s response patterns in both the wet and dry seasons (Fig. 3). G_s in relation to PAR is shown in Fig. 3a–h. G_s increased with PAR, and appeared to be light-saturated at 400 and 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season and dry season, respectively. However, all the regressions between G_s and PAR were non-significant. G_s in relation to D was shown in Fig. 3i–p. G_s decreased exponentially from D values of 0.6 and 0.8 kPa in the wet season and dry season, respectively. Nearly all the regressions between G_s and D were significant ($p < 0.0001$), with R^2 ranging from 0.60 to 0.99. Stomatal sensitivity (m) was greater in the wet season than that in the dry season (Table 3). m increased linearly with reference canopy stomatal conductance (G_{sref}) (slope = 0.70, $R^2 = 0.96$, $n = 8$). G_s in relation to SMD was shown in Fig. 3q–t. G_s decreased as SMD increased in July in 2005 and 2006. However, no significant relationships between G_s and SMD were observed across entire years (except for Tree No. 3 in 2005, $p = 0.097$, and Tree No. 4 in 2005, $p = 0.064$).

3.3 Canopy CO₂ uptake rate of mature *A. mangium* plantation

At the leaf level scale, diurnal leaf stomatal conductance (g_s) and net photosynthesis (P_n of *A. mangium*) obtained through gas exchange measurements reached their peak around 09:00 in the wet season, and around 11:00 in the dry season (Fig. 4). The diurnal means of g_s in all leaves, sunlit leaves, and shaded leaves were 136.40, 129.42, and 144.34 $\text{mmol m}^{-2} \text{s}^{-1}$ in the wet season, and 58.65, 56.74, and 60.42 $\text{mmol m}^{-2} \text{s}^{-1}$ in the dry season, respectively. The diurnal means of P_n in all leaves, sunlit leaves, and shaded leaves were 3.42, 3.93, and 2.84 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season, and 1.85, 2.17, and 1.34 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season, respectively. Notably, CVs were high (ranging mostly from 40 % to 60 %) for g_s and P_n . At the canopy level scale, diurnal canopy CO₂ uptake rate (F_{CO_2}) peaked around 09:00, with a maximum of 7.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season (Fig. 5a). Diurnal F_{CO_2} was more symmetrical and smoother, reaching a maximum of 3.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ around 11:00 in the dry season (Fig. 5a). The diurnal means of G_s and F_{CO_2} in all leaves were 56.70 $\text{mmol m}^{-2} \text{s}^{-1}$ and 2.78 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season, and 28.81 $\text{mmol m}^{-2} \text{s}^{-1}$ and 1.32 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season. Furthermore, as shown in Fig. 6, values of both g_s and P_n were higher than those of G_s and of F_{CO_2} ,

with regression coefficients of determination (R^2) of 0.58 and 0.19 in the wet season, 0.70 and 0.65 in the dry season, and 0.44 and 0.35 in all seasons, respectively. An analysis of covariance confirmed that neither the slopes nor the intercepts of nearly all the regression lines for sunlit and shade leaves, for wet and dry seasons, were significant (Table 4, $p > 0.05$).

Based on daily F_{CO_2} , monthly, seasonal, and inter-annual F_{CO_2} were calculated. Maximum monthly F_{CO_2} occurred in July (155 gC m^{-2}), May (98 gC m^{-2}), July (129 gC m^{-2}), and August (117 gC m^{-2}) in 2004, 2005, 2006 and 2007, respectively (Fig. 5b). F_{CO_2} of the *A. mangium* stand in the wet season (522 gC m^{-2}) was considerably higher than that in the dry season (255 gC m^{-2}) (Fig. 5c). Annual F_{CO_2} was 820, 564, 895 and 828 gC m^{-2} in 2004, 2005, 2006 and 2007, respectively. F_{CO_2} in the wet season contributed 72, 71, 66, and 61 % of the total annual CO₂ uptake (Fig. 5d). Across years 2004, 2005, 2006 and 2007, the daily and annual means of canopy CO₂ uptake for mature *A. mangium* plantation were $2.13 \pm 0.40 \text{ gC m}^{-2} \text{ d}^{-1}$ and $776.89 \pm 145.76 \text{ gC m}^{-2}$, respectively.

3.4 Canopy CO₂ uptake rate sensitivity analysis

We examined the sensitivity of F_{CO_2} to changes in G_s , C_a and Δ between December 2006 and November 2007 (Fig. 7). The positive correlation between G_s and F_{CO_2} was significant, and the R^2 value was high ($R^2 = 0.8263$; $p < 0.0001$). Although there were significant correlations between C_a and F_{CO_2} ($p = 0.0001$) and Δ and F_{CO_2} ($p < 0.0001$), the R^2 values were very low ($R^2 = 0.0016$ and $R^2 = 0.1348$, respectively).

4 Discussion

4.1 The theoretical basis for estimating canopy CO₂ uptake

To our knowledge, all methods for direct measurement of canopy CO₂ uptake rely on scaling. Morén et al. (2001) combined water use efficiency (WUE) on the based branch gas-exchange measurements and canopy transpiration (E) as a scalar to get canopy carbon assimilation of a boreal forest, and found that canopy WUE showed a strong dependency on vapour pressure deficit (D). Catovsky et al. (2002) combined whole-tree sap flow measurements with micrometeorological monitoring and leaf-level gas exchange to determine whole-tree carbon gain, and showed that estimates of canopy photosynthesis were most sensitive to measurements of D and the relationship between photosynthesis and conductance. However, Catovsky's and Morén's methods required a lot of measurements of gas exchange on leaves or branches. More recently, to solve the difficulties mentioned above, Zhao et al. (2005a) made use of the sap flow technique for scaling and isotope technique for plant water use, and then proposed a

Table 1. The diurnal ranges, seasonal means, and coefficients of variation (CV) in ambient CO₂ concentration (C_a), intercellular CO₂ concentration (C_i), the ratio of the intercellular and ambient CO₂ concentrations (C_i/C_a), and carbon isotope compositions in leaf sap ($\delta^{13}C_p$), isotope compositions in the canopy air ($\delta^{13}C_a$) and the photosynthetic ¹³C discrimination (Δ).

	Diurnal scale		Seasonal scale	
	Range	CV	Mean (wet season vs. dry season)	Max. CV
$C_a(\mu\text{mol mol}^{-1})$	381.51–416.58	0.02–0.05	399.06 vs. 386.85	0.05
$C_i(\mu\text{mol mol}^{-1})$	279.35–356.30	0.02–0.12	308.30 vs. 311.74	0.05
C_i/C_a	0.72–0.90	0.04–0.10	0.81 vs. 0.78	0.03
$\delta^{13}C_p(\text{‰})$	−31.96–−29.91	0.03–0.06	−31.42 vs. −30.75	0.05
$\delta^{13}C_a(\text{‰})$	−10.59–−8.82	0.04–0.13	−9.62 vs. −8.92	0.14
$\Delta(\text{‰})$	20.47–23.89	0.05–0.11	22.51 vs. 22.52	0.10

Table 2. Partial correlations between hourly Δ and photosynthetically active radiation (PAR), vapor pressure deficit (D), ambient CO₂ concentration (C_a), and canopy stomatal conductance (G_s).

Periods	Variables	Control variables	df	Δ
				Partial correlation
One year	PAR	D, C_a, G_s	107	−0.052
	D	PAR, C_a, G_s	107	0.250 ^a
	C_a	PAR, D, G_s	107	0.016
	G_s	PAR, D, C_a	107	0.127
Wet season	PAR	D, C_a, G_s	51	0.030
	D	PAR, C_a, G_s	51	0.058
	C_a	PAR, D, G_s	51	−0.549 ^a
	G_s	PAR, D, C_a	51	−0.198
Dry season	PAR	D, C_a, G_s	51	−0.425 ^a
	D	PAR, C_a, G_s	51	0.136
	C_a	PAR, D, G_s	51	0.156
	G_s	PAR, D, C_a	51	0.464 ^a

^a Indicates significant partial correlation at 0.01 level.

Table 3. Stomatal sensitivity to vapor pressure deficit (D) estimated as the slope of the relationship between canopy stomatal conductance and $\ln(D)$ (Oren et al., 1999), applied to those data in which G_s decreased exponentially with D .

Periods	Sensitivity (m)	$G_{\text{ref}}(b)$	m/b	Relative sensitivity	D threshold
Jul 2004	−114.56	162.03	−0.71	−0.40	0.60
Jul 2005	−48.27	75.25	−0.64	−0.35	0.60
Jul 2006	−71.67	113.48	−0.63	−0.26	0.60
Jul 2007	−86.52	146.65	−0.59	−0.30	0.60
Dec 2004	−16.11	34.33	−0.47	−0.40	0.60
Dec 2005	−13.36	36.70	−0.36	−0.31	0.80
Dec 2006	−56.15	79.48	−0.71	−0.69	0.60
Dec 2007	−69.50	120.20	−0.58	−0.53	0.80

Relative sensitivity was estimated using relative G_s values of each species instead of absolute values. D threshold is the value of the leaf to air vapor pressure difference from which G_s begins to decrease in an exponential form. Reference canopy stomatal conductance (G_{ref}) is G_s at $D = 1$ kPa.

new approach combining the sap flow measurements and stable ¹³C techniques to estimate forest C assimilation. Herein, the relationship between Δ and C_i/C_a laid out by Farquhar et al. (1982) is integrated with the relationship between F_{CO_2} and stomatal conductance for CO₂, so that a new relationship linking Δ , F_{CO_2} and G_s was obtained. Consistent with our study, Hu et al. (2010) used observed transpiration rates and needle sugar carbon isotope ratios to estimate whole-tree carbon assimilation rates, and then combined with species distribution and tree size to estimate gross primary productivity (GPP) using an ecosystem process model.

4.2 Temporal patterns of canopy CO₂ uptake and its dependence on environment and stomata

Canopy CO₂ uptake rate (F_{CO_2}) varied diurnally (Fig. 5). The sharp peak in photosynthesis in early morning periods during the wet season may be due to higher G_s and C_a , as well as lower Δ during this period. During the wet season G_s peaked around 08:00 and then rapidly dropped for the rest of the day (Fig. 2h). This diurnal pattern was similar to that of canopy conductance on well-watered 9-year-old *Sultana* grapevines (Lu et al., 2003), native forest composed of *Lomatia hirsuta*, *Schinus patagonicus*, *Nothofagus antarctica* and *Diostea juncea* (Fernandez et al., 2009), and pristine *Nothofagus* forest (Köstner et al., 1992). During the dry season, lower values of G_s and less acute peaks were due to a water supply from the soil that was inadequate to meet the evaporative demand.

Strong seasonality in F_{CO_2} of *A. mangium* was observed (Fig. 5). Based on this, we related F_{CO_2} to the seasonally changing environmental variables. Higher F_{CO_2} in the wet season coincided with the season of rapid growth, ample supply of water, and strong solar radiation, the typical environment of subtropical ecosystems (Figs. 1, 5). Notably, in the dry season, water supply did not match evaporative demand at the study site (P and SWC were relatively low, while PAR and T_a were still high). These conditions may induce water stress in *A. mangium*, which caused a significant reduction in stomatal conductance. Furthermore, lower annual F_{CO_2} in 2005 may be due to the frequent rainfall that occurred in

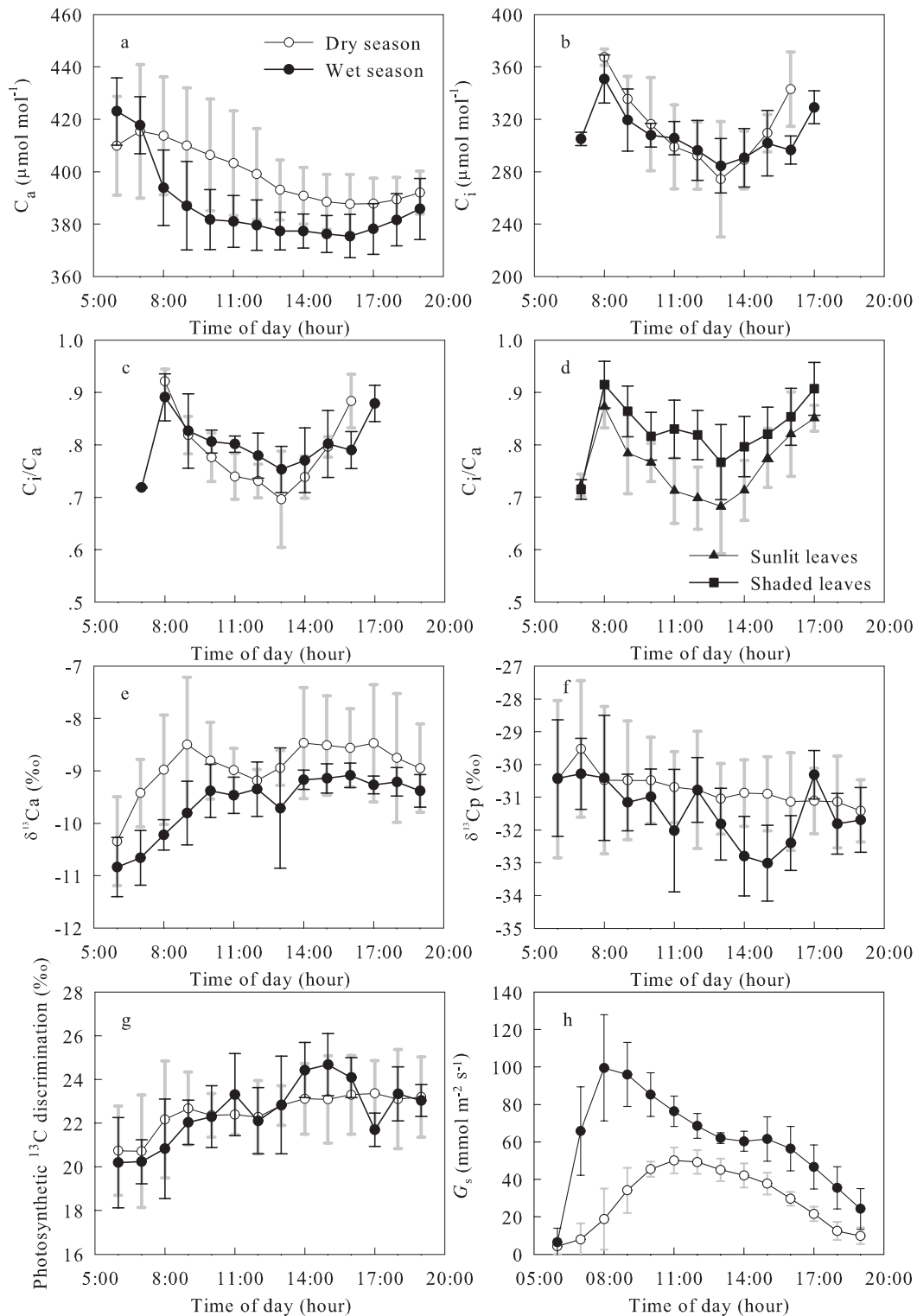


Fig. 2. Diurnal variations of (a) ambient CO₂ concentration (C_a), (b) intercellular CO₂ concentration (C_i), (c) the ratio of the intercellular and ambient CO₂ concentrations (C_i/C_a), (d) C_i/C_a in the sunlit and shaded leaves in all seasons, (e) carbon isotope compositions in canopy atmosphere ($\delta^{13}C_a$), (f) carbon isotope compositions in leaf sap ($\delta^{13}C_p$), and (g) photosynthetic ¹³C discrimination (Δ) and (h) canopy stomatal conductance (G_s) in both the wet season (9 and 10 May, 26 July, 1 August) and the dry season (6 and 7 November, 6 and 17 December). Error bars indicate standard deviation ($n = 8$). C_i/C_a was obtained by leaf gas exchange measurements. Other data were obtained by combining sap flow measurement and stable carbon isotope techniques (SF/SI approach).

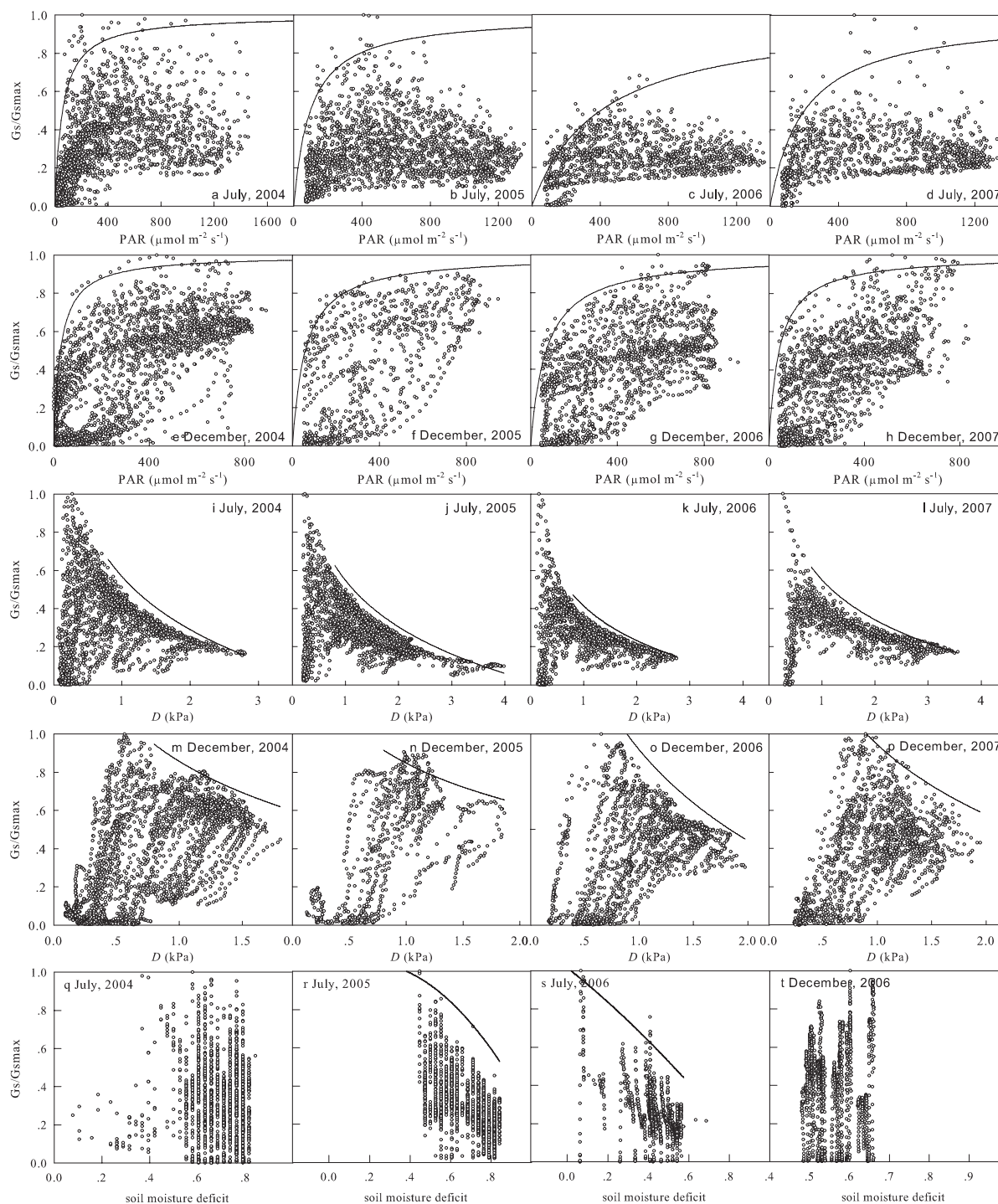


Fig. 3. Scatter plots and response functions of the ratio of canopy stomatal conductance to the maximum (G_s/G_{smax}) to changes in photosynthetically active radiation (PAR) (a–h), vapor pressure deficit (D) (i–p), and soil moisture deficit (SMD) (q–t) in both wet seasons and dry seasons from 2004–2007. Data were obtained through sap flow measurements.

June and July. Higher monthly F_{CO_2} in May 2005 may be attributed to the after-effect of soil water stress on stand transpiration, thereby F_{CO_2} .

Canopy stomatal conductance is a critical factor regulating the F_{CO_2} of *A. mangium*. It was reported that similar canopy conductance estimates for this *A. mangium* plantation were obtained from both the Penman–Monteith formula and the

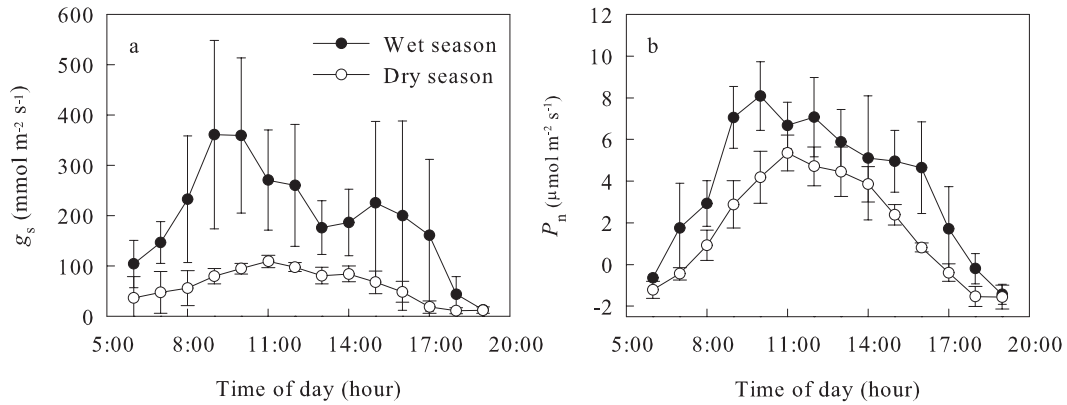


Fig. 4. Diurnal patterns of leaf stomatal conductance (g_s) and net photosynthesis (P_n) of *A. mangium* in both the wet season (9 and 10 May, 26 July, 1 August) and the dry season (6 and 7 November, 6 and 17 December). Error bars indicate standard deviation ($n = 4$). July and December are representative of wet and dry conditions, respectively. Data were obtained by leaf gas exchange measurements.

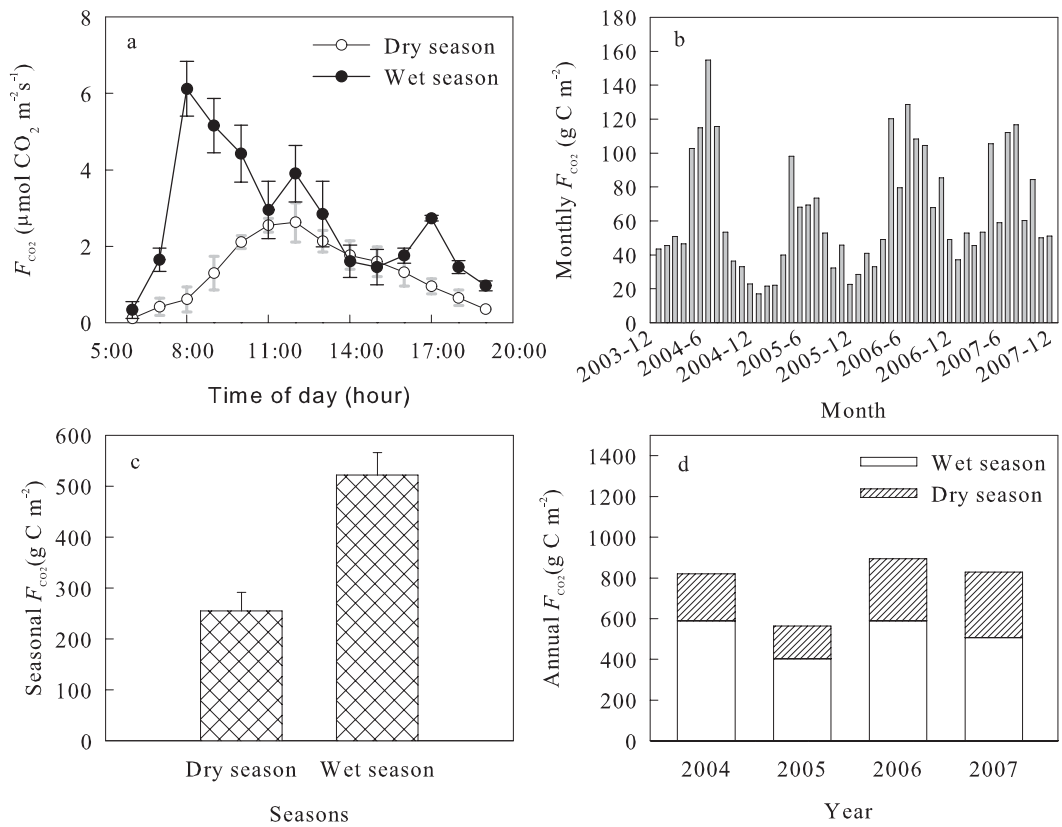


Fig. 5. Diurnal, monthly, seasonal, and annual trends of canopy CO₂ uptake rate (F_{CO_2}) of *A. mangium* plantation from 2004 to 2007. Error bars indicate standard error. Data were obtained by the SF/SI approach.

simplified equation by Köstner et al. (1992) (Ma, 2008). The diurnal pattern of F_{CO_2} was similar to that of G_s (Figs. 2, 5). G_s was mainly influenced by D and PAR (Fig. 3). When D was lower than 0.6 kPa, PAR was the main driver of G_s , because it induced stomatal opening. When D approached 0.6 kPa and beyond, D became the dominant factor. The in-

crease in D led to a decrease in G_s despite the increase in PAR, because the hydraulic system needed to be protected from cavitation. High D led to varying degrees of decline in G_s (Table 3), and thus the corresponding reduction in F_{CO_2} . The slope of this linear function between stomatal sensitivity (m) and reference canopy stomatal conductance (G_{sref}) was

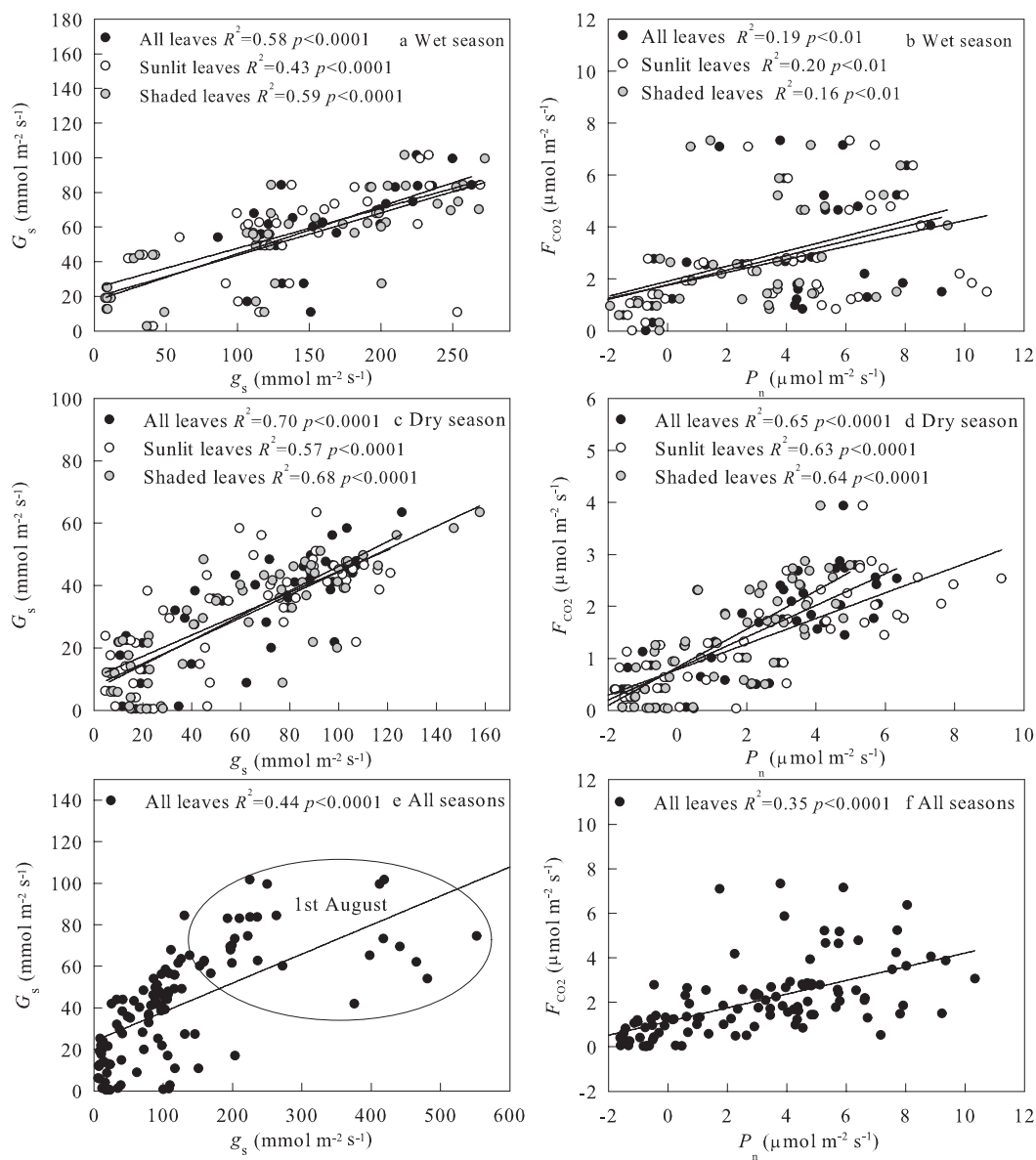


Fig. 6. Scatter plots of leaf stomatal conductance (g_s) vs. canopy stomatal conductance (G_s), and leaf net photosynthesis (P_n) vs. canopy CO₂ uptake (F_{CO_2}) in (a, b) the wet season (9 and 10 May, 26 July), (c, d) the dry season (6 and 7 November, 6 and 17 December), and (e, f) all seasons (9 and 10 May, 26 July, 1 August, 6 and 7 November, 6 and 17 December). The data in the ellipse in (e) occurred on 1 August (see text for further explanation). All regressions were highly significant ($p < 0.01$). Data were obtained by the SF/SI approach and leaf gas exchange measurements.

consistent with the shallower slope of approximately 0.60 observed for the mesic species in Oren et al. (1999).

4.3 Comparison with estimates from gas exchange measurements

With regard to the patterns, the diurnal dynamics of gas exchange results agreed well with that of the sap flux/stable isotope method (SF/SI) (Figs. 2h, 4, 5). Better agreement between F_{CO_2} and P_n in the dry season was likely due to

the fact that the lower leaf area index in the dry season (1.91 ± 0.38 in the dry season vs. 2.04 ± 0.22 in the wet season) would tend to minimize the effects of leaf shading, which can diminish conductance in lower-canopy leaves. However, F_{CO_2} from SF/SI was 27.0% lower than P_n from gas exchange measurements (Fig. 6). The diurnal C_i/C_a from gas exchange measurements and stable isotope values ranged from 0.63 to 0.94 and from 0.57 to 0.95, respectively. The seasonal C_i/C_a from gas exchange measurements and stable isotope values in the wet season (0.80, 0.78), dry

Table 4. The regression lines in Fig. 6 and covariance analysis.

Season	Leaf type	Equation	R^2	p	P_{slope}	$P_{\text{intercept}}$
Wet season	Sunlit leaves	$G_s = 24.72 + 0.23 g_s$	0.43	< 0.0001	0.251	0.605
Wet season	Shade leaves	$G_s = 19.20 + 0.24 g_s$	0.59	< 0.0001		
Wet season	Sunlit leaves	$F_{\text{CO}_2} = 1.75 + 0.25 P_n$	0.20	0.0037	0.674	0.449
Wet season	Shade leaves	$F_{\text{CO}_2} = 1.91 + 0.29 P_n$	0.16	0.0098		
Dry season	Sunlit leaves	$G_s = 10.51 + 0.34 g_s$	0.57	< 0.0001	0.514	0.698
Dry season	Shade leaves	$G_s = 7.66 + 0.37 g_s$	0.68	< 0.0001		
Dry season	Sunlit leaves	$F_{\text{CO}_2} = 0.78 + 0.25 P_n$	0.63	< 0.0001	0.009	0.038
Dry season	Shade leaves	$F_{\text{CO}_2} = 0.83 + 0.37 P_n$	0.64	< 0.0001		
Wet season	All leaves	$G_s = 17.27 + 0.27 g_s$	0.58	< 0.0001	0.060	0.120
Dry season	All leaves	$G_s = 6.65 + 0.40 g_s$	0.70	< 0.0001		
Wet season	All leaves	$F_{\text{CO}_2} = 1.77 + 0.28 P_n$	0.19	0.0048	0.578	0.001
Dry season	All leaves	$F_{\text{CO}_2} = 0.80 + 0.30 P_n$	0.65	< 0.0001		

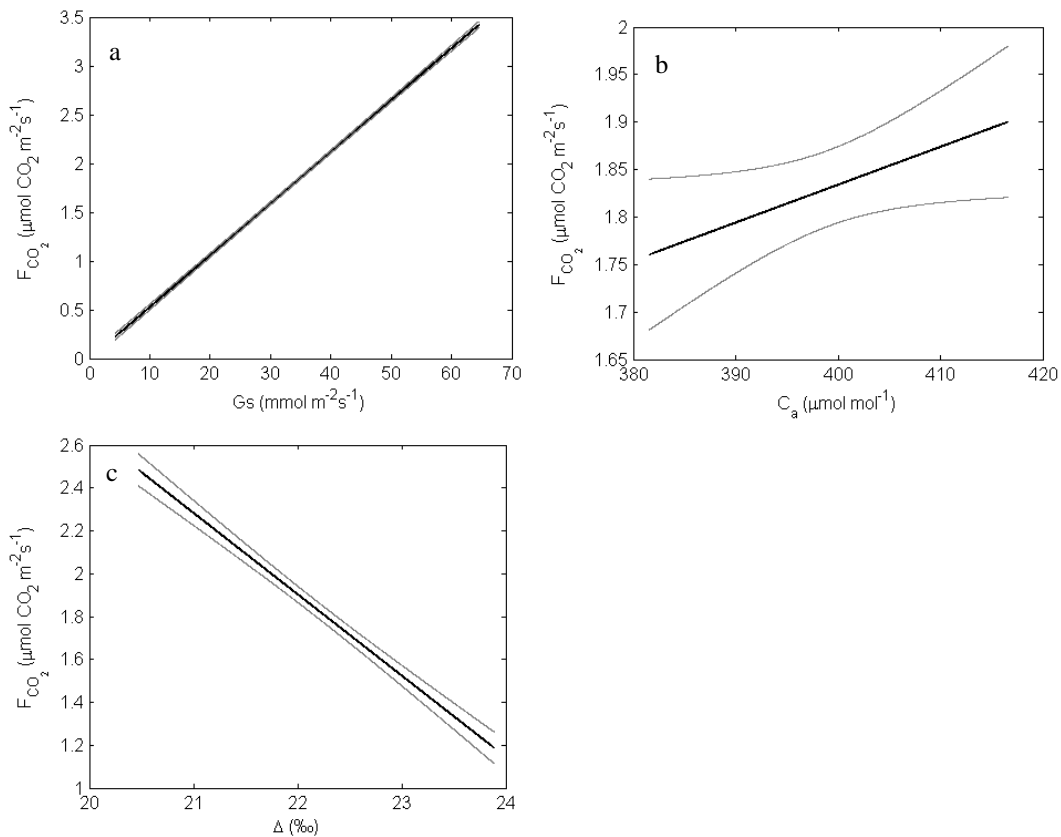


Fig. 7. Canopy CO₂ uptake rate (F_{CO_2}) sensitivity analysis. The bold black lines are the regression relationships and the thin gray lines are the 95 % confidence intervals for the data. (a) Relationship between canopy stomatal conductance (G_s) and F_{CO_2} ($F_{\text{CO}_2} = 0.0531 G_s - 0.002$, $R^2 = 0.8263$, $p < 0.0001$). (b) Relationship between ambient CO₂ concentrations (C_a) and F_{CO_2} ($F_{\text{CO}_2} = 0.004 C_a + 0.239$, $R^2 = 0.0016$, $p = 0.0001$). (c) Relationship between photosynthetic ¹³C discrimination (Δ) and F_{CO_2} ($F_{\text{CO}_2} = -0.3794\Delta + 10.2506$, $R^2 = 0.1348$, $p < 0.0001$). Data were obtained by the SF/SI approach.

season (0.78, 0.78), and whole year (0.79, 0.78) also matched well. Thus, the differences in F_{CO_2} and P_n resulted mainly from differences in stomatal conductance. G_s from the SF/SI approach was 67.3 % lower than g_s from gas exchange measurements, though the diurnal dynamics were similar. Furthermore, the differences may also be attributed to high variation in gas exchange results, which were variable by leaf position and age, and thus any one measurement was not representative of the entire canopy; variability of the average response was high. Given that F_{CO_2} was calculated based on Δ and C_i/C_a averaged across a variety of age and light classes, this source of variation was reduced for the results from the SF/SI approach. The analysis of the differences between the gas exchange and results from the SF/SI approach highlighted the advantages of the latter method.

4.4 Comparison with estimates from other approaches for estimating F_{CO_2}

For comparison, the gross primary production (GPP) of forests in different climate zones, using several different methods, was summarized in Table 5. GPP in tropical forests ($8.35 \pm 0.23 \text{ gC m}^{-2} \text{ d}^{-1}$) was significantly higher than that in subtropical forests ($5.38 \pm 0.46 \text{ gC m}^{-2} \text{ d}^{-1}$, $p < 0.001$) and temperate forests ($2.85 \pm 0.45 \text{ gC m}^{-2} \text{ d}^{-1}$, $p < 0.001$). Most of the differences in the gross primary production (GPP) of forests in various climate zones were related to climate. Our estimate of canopy CO₂ uptake for a mature *A. mangium* plantation ($2.13 \pm 0.40 \text{ gC m}^{-2} \text{ d}^{-1}$, Fig. 5) approached the lower range of values for subtropical mixed forests (Gebremichael and Barros, 2006; Gu et al., 2006). Our lower estimates of GPP may be due to the lower mean canopy stomatal conductance (0.135 cm s^{-1} vs. 0.726 cm s^{-1} , 0.25 cm s^{-1}), higher C_i/C_a (0.76 to 0.84), greater tree height (17.8 m vs. 10.8 m, 2 m), and lower LAI ($1.95 \text{ m}^2 \text{ m}^{-2}$ vs. $3.20 \text{ m}^2 \text{ m}^{-2}$, $3.77 \text{ m}^2 \text{ m}^{-2}$), compared to other subtropical mixed forests (Ma, 2008; Gebremichael and Barros, 2006; Gu et al., 2006). The canopy stomatal conductance of individual trees decreases with tree height (Schäfer et al., 2000), while the lower LAI might lead to higher conductance and more control by stomatal conductance, since there is less shading (Granier et al., 2000). The C_i/C_a ratio, which is maintained at a constant or near-constant value in many plant species, represents a balance between the rates of inward CO₂ diffusion (controlled by stomatal conductance) and CO₂ assimilation (controlled by photosynthetic light/dark reactions) (Ehleringer and Cerling, 1995). In our study, the C_i/C_a ratio varied from 0.76 to 0.84, which was higher than the ranges found in cottonwoods in a riparian woodland (0.75–0.78) (Letts et al., 2008), in 13-year-old loblolly pine (*Pinus taeda*) trees (0.45–0.80) (Maier et al., 2002), and in nine well-watered conifer species (0.57–0.68) (Brodribb, 1996). Relatively high C_i/C_a ratios have also been found in tropical rain forest species (Lloyd and Farquhar, 1994; Ishida et al., 1996), a Canarian laurel forest tree

species (*Laurus azorica*) (González-Rodríguez et al., 2001). There are three possible reasons for the inference that the C_i/C_a ratio may result in a decrease in photosynthetic rate of our study species. Firstly, high C_i/C_a values may suggest a relatively small stomatal limitation to net photosynthetic rate and non-conservative water use (González-Rodríguez et al., 2001; Ishida et al., 1996). Consistent with this inference, Cienciala et al. (2000) also observed no apparent limitation to water flux in *A. mangium*. It is likely that high transpiration rates may cause a localized leaf water deficit, which depletes photosynthetic capacity (Sharkey, 1984). Secondly, non-stomatal limitations may also be responsible for the decline in assimilation rates (Lauer and Boyer, 1992). Thirdly, the reduction in photosynthesis associated with leaf senescence should result in high C_i/C_a values (Ponton et al., 2006).

Notably, our estimate of canopy CO₂ uptake for the 20-year-old *A. mangium* stand was much lower than that for 4 to 6-year-old *A. mangium* ($8.77 \text{ gC m}^{-2} \text{ d}^{-1}$) in São Paulo, Brazil (Nouvellon et al., 2012). Our lower estimates of GPP may be partly explained by an age-related decline in photosynthesis (20-year-old vs. 4 to 6-year-old). It may also be the result of lower photosynthetically active radiation absorbed by the canopy, due to lower stand density ($734 \text{ trees ha}^{-1}$ vs. $1111 \text{ trees ha}^{-1}$), and lower LAI ($1.95 \text{ m}^2 \text{ m}^{-2}$ vs. $3.479 \text{ m}^2 \text{ m}^{-2}$) (Ma, 2008a; Nouvellon et al., 2012). Furthermore, we compared methods for quantifying GPP constrained by water use measurements. Our estimates were comparable with those of spruce ($2.66 \text{ gC m}^{-2} \text{ d}^{-1}$) and mixed forest ($0.94 \text{ gC m}^{-2} \text{ d}^{-1}$), also using the sap flow-based approach (Köstner et al., 2008; Hu et al., 2010), but lower than values determined by satellite-based modeling or carbon allocation studies (Table 5). These differences suggest the necessity of measuring species-specific fluxes in assessing CO₂ uptake.

4.5 Sensitivity analysis

Through our sensitivity analysis using a Monte Carlo approach, we were able to simulate many more combinations of G_s , C_a and Δ than obtained from our limited 8 d samplings. We found that the dynamics in the estimates of F_{CO_2} were mainly driven by dynamics in G_s , compared with C_a and Δ (Fig. 7). Hu et al. (2010) also demonstrated that the calculation of canopy photosynthesis was much more sensitive to transpiration rate than to $\delta^{13}\text{C}$ values. In our study, covariance between G_s and F_{CO_2} occurs because CO₂ is assimilated through the stomatal pores. Variation in Δ between seasons was non-significant ($p = 0.988$), compared with variation in G_s . This may be due to the fact that Δ , the proportioning coefficient between G_s and F_{CO_2} as shown in Eq. (15), is constrained as the ratio of two co-varying variables. It may also be due to the evidence that stomata functions in a way to optimize G_s and F_{CO_2} in relation to environmental changes (Wong et al., 1979). C_i/C_a is also a very useful parameter for

Table 5. Published estimates of gross primary production (GPP, gCm⁻² day⁻¹), species, site information and methodology, in different climate zones.

Climate	Site (<i>P</i> mm/ <i>T_a</i> °C) ¹	Dominate Species (Age)	Latitude/Longitude	Method	GPP	References
Tropical	Santarém, Brazil (1920/25.8)	Evergreen Forest	2°51' S/54°58' W	Satellite-based Model	7.97	Xiao et al. (2005)
	Manaus, Brazil (2200/-)	Tropical Rain Forest	2°35' S/60°06' W	Component Carbon Analyses	8.33	Malhi et al. (1998)
	São Paulo, Brazil (1280/21.3)	<i>Acacia mangium</i> (4–6)	23°02' S/48°38' W	Component Carbon Analyses	8.77	Nouvellon et al. (2012)
Subtropical	JiangXi, China	Mixed Forest ²	26°44' N/115°04' E	CEVSA Model ³	4.68	Gu et al. (2006)
		Mixed Forest ²	26°44' N/115°04' E	Flux Measurements	4.41	Gu et al. (2006)
		<i>Pinus elliottii</i>	26°44' N/115°04' E	Biome-BGC Model	5.32	Ma et al. (2008b)
	Marsyandi, Nepal	Mixed Forest	28°21' N/84°15' E	MODIS_DAO	6.36	Gebremichael and Barros (2006)
				MODIS_Tower	3.59	Gebremichael and Barros (2006)
Temperate	New South Wales, Australia	<i>Pinus radiata</i> Plantations	35°21' S/148°56' E	Component Carbon Analyses	6.78	Waring et al. (1998)
	North Carolina, USA (1140/15.5)	<i>Pinus taeda</i> ⁴	35°58' N/79°05' W	4C-A Model ⁵	6.54	Schäfer et al. (2003)
	South Island, New Zealand	<i>Nothofagus truncata</i>	41°31' S/172°45' E	Component Carbon Analyses	2.84	Waring et al. (1998)
	EUROFLUX Network	Various Species ⁶	41°–64° N/0°–24° E	Component Carbon Analyses	3.78	Janssens et al. (2001)
	Massachusetts, USA	Deciduous Forest ⁷	42°32' N/72°11' W	Component Carbon Analyses	3.50	Waring et al. (1998)
	The Oregon Transect	Coniferous, Deciduous ⁸	44°–45° N/121°–123° W	Component Carbon Analyses	3.80	Williams et al. (1997)
	Colorado, USA (800/1.5)	Mixed Forest ⁹ (100)	–/–	SIPNET Model	2.25	Hu et al. (2010)
		Mixed Forest ⁵ (100)	–/–	SF/SI ¹⁰	0.94	Hu et al. (2010)

¹ *P* denotes annual rainfall amount; *T_a* denotes average annual temperature.

² The dominant species are *Pinus elliottii*, *Pinus massoniana*, *Cunninghamia lanceolata*, and *Schima superba*.

³ CEVSA is the abbreviation for Carbon Exchange in the Vegetation-Soil-Atmosphere Model.

⁴ The even-aged *P. taeda* L. forest was planted in a clear-cut opening in 1983, with additional tree species representing seed sources of pine and broadleaf species from the surrounding area.

⁵ 4C-A is the abbreviation for canopy conductance-constrained carbon assimilation.

⁶ Sites of the European EUROFLUX network encompass a large range of tree species, such as *Fagus sylvatica*, *Quercus ilex*, *Quercus robur*, *Picea abies*, etc.

⁷ The dominant species are *Quercus rubra* and *Acer rubrum*.

⁸ Dominant species at six coniferous forest and one deciduous forest sites are 1, *Picea sitchensis*, *Tsuga heterophylla*; 2, *Alnus rubra*; 3, *Pseudotsuga menziesii*;

4, *Tsuga heterophylla*, *Pseudotsuga menziesii*; 5, *Tsuga mertensiana*, *Abies lasiocarpa*, *Picea engelmannii*; 6, *Pinus ponderosa*; 7, *Juniperus occidentalis*.

⁹ The dominant species are lodgepole pine, subalpine fir, and Engelmann spruce.

¹⁰ SF/SI is the abbreviation for sap flow measurement and stable carbon isotope techniques.

modeling F_{CO_2} . Seasonally constant C_i/C_a values have been reported from a wide range of field experiments (Norman, 1982; Ellsworth, 1999; Letts et al., 2008). A constant C_i/C_a , which is most parsimonious in terms of number of input parameters, yields results that are comparable or better than more elaborate models for predicting assimilation (Katul et al., 2000). In our study, no significant seasonal variation was observed in C_i/C_a (Fig. 2, $p > 0.05$), although variation in diurnal C_i/C_a between the sunlit leaves and shaded leaves was found. Therefore, we argue that an acceptable estimate of F_{CO_2} of a subtropical mature *A. mangium* plantation was obtained by using seasonally integrated/constant C_i/C_a values.

The relatively high sensitivity of the model to G_s and low sensitivity to C_a and Δ also indicate that one source of potential error that may be significant in the model is the uncertainty in estimating G_s . Error in G_s can occur in measurements of sap flow and tree size. We accounted for errors in G_s using the Monte Carlo approach, where we generated 99 % intervals for our modeled F_{CO_2} values. No values fell outside our 99 % confidence intervals, suggesting that most errors of G_s are accounted for in our modeled F_{CO_2} rates.

5 Conclusions

Our study demonstrated that combining sap flow measurements and stable isotope discrimination provides a simple and accurate way of estimating canopy-scale photosynthesis. The temporal changes in canopy CO₂ uptake (F_{CO_2}) of *A. mangium* plantation were attributed to the responsiveness of G_s to environmental factors. Large diurnal, seasonal, and inter-annual variability in F_{CO_2} with low variability of diurnal and seasonal C_a and Δ suggested that canopy photosynthetic patterns mimicked those of water flux to a large degree. Compared to published estimates of gross primary production for subtropical mixed forest, our lower estimate of F_{CO_2} for mature *A. mangium* plantation was likely related to the lower mean canopy stomatal conductance, higher C_i/C_a , greater tree height, and age of the stand. Compared with results from satellite-based modeling or carbon allocation studies, our estimate may suggest the necessity of considering species-specific fluxes in CO₂ assessments.

Supplementary material related to this article is available online at <http://www.biogeosciences.net/11/1393/2014/bg-11-1393-2014-supplement.pdf>.

Acknowledgements. This research was supported by the National Natural Science Foundation of China (grant nos. 41030638, 30428022, 31170673, and 41275169), Provincial Nature Science Foundation of Guangdong (grant no. S2012020010933). We acknowledge all the members of the Heshan National Field Research Station of Forest Ecosystem for their assistance in the field, and Pingheng Li at the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, for error analysis.

Edited by: M. Williams

References

- Baldocchi, D., Valentini, R., Running, S., Oechel, W., and Dahlman, R.: Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems, *Global Change Biol.*, 2, 159–168, doi:10.1111/j.1365-2486.1996.tb00069.x, 1996.
- Brodribb, T.: Dynamics of changing intercellular CO₂ concentration (ci) during drought and determination of minimum functional ci. *Plant Physiol.*, 111, 179–185, doi:10.1104/pp.111.1.179, 1996.
- Campbell, G. S. and Norman, J. M.: *An Introduction to Environmental Biophysics*. Springer-Verlag, New York, 36–51, 1998.
- Catovsky, S., Holbrook, N. M., and Bazzaz, F.A.: Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species, *Can. J. Forest Res.*, 32, 295–309, doi:10.1139/x01-199, 2002.
- Ciais, P., Tans, P. P., Trolier, M., White, J. W. C., and Francey, R. J.: A large northern hemisphere terrestrial CO₂ sink indicated by the ¹³C/¹²C ratio of atmospheric CO₂, *Science*, 269, 1098–1102, doi:10.1126/science.269.5227.1098, 1995.
- Cienciala, E., Kučera, J., and Malmer, A.: Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo, *J. Hydrol.*, 236, 109–120, doi:10.1016/S0022-1694(00)00291-2, 2000.
- Cole, T.G., Yost, R. S., Kablan, R., and Olsen, T.: Growth potential of twelve *Acacia* species on acid soils in Hawaii, *For. Ecol. Manag.*, 80, 175–186, doi:10.1016/0378-1127(95)03610-5, 1996.
- Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., and Tu, K. P.: Stable isotope in Plant Ecology, *Annu. Rev. Ecol. S.*, 33, 507–559, doi:10.1146/annurev.ecolsys.33.020602.095451, 2002.
- Ehleringer, J. R., and Cerling, T. E.: Atmospheric CO₂ and the ratio of intercellular to ambient CO₂ concentrations in plants, *Tree Physiol.*, 15, 105–111, doi:10.1093/treephys/15.2.105, 1995.
- Ewers, B. E. and Oren, R.: Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements, *Tree Physiol.*, 20, 579–589, doi:10.1093/treephys/20.9.579, 2000.
- Fang, J. Y., Chen, A. P., Peng, C. H., Zhao, S. Q., and Ci, L. J.: Changes in Forest Biomass Carbon Storage in China Between 1949 and 1998, *Science*, 292, 2320–2322, doi:10.1126/science.1058629, 2001.
- Farquhar, G. D., Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species, *Planta*, 149, 78–90, doi:10.1007/bf00386231, 1980.
- Farquhar, G. D., O’Leary, M., and Berry, J.: On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves, *Funct. Plant Biol.*, 9, 121–137, doi:10.1071/PP9820121, 1982.
- Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T.: Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 40, 503–537, doi:10.1146/annurev.pp.40.060189.002443, 1989.
- Fernandez, M. E., Gyenge, J., and Schlichter, T.: Water flux and canopy conductance of natural versus planted forests in Patagonia, South America, *Trees-Struct. Funct.*, 23, 415–427, doi:10.1007/s00468-008-0291-y, 2009.
- Gebremichael, M. and Barros, A. P.: Evaluation of MODIS Gross Primary Productivity (GPP) in tropical monsoon regions, *Remote Sens. Environ.*, 100, 150–166, doi:10.1016/j.rse.2005.10.009, 2006.
- Gessler, A., Rennenberg, H., and Keitel, C.: Stable isotope composition of organic compounds transported in the phloem of European beech – evaluation of different methods of phloem sap collection and assessment of gradients in carbon isotope composition during leaf-to-stem transport. *Plant Biol.*, 6, 721–729, doi:10.1055/s-2004-830350, 2004.
- González-Rodríguez, A. M., Morales D., and Jiménez M. S.: Gas exchange characteristics of a Canarian laurel forest tree species (*Laurus azorica*) in relation to environmental conditions and leaf canopy position. *Tree Physiol.*, 21, 1039–1045, doi:10.1093/treephys/21.14.1039, 2001.
- Granier, A.: Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements, *Tree Physiol.*, 3, 309–320, doi:10.1093/treephys/3.4.309, 1987.
- Granier, A., Loustau, D., and Bréda, N.: A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index, *Ann. For. Sci.*, 57, 755–765, doi:10.1051/forest:2000158, 2000.
- Gu, F., Cao, M., Wen, X., Liu, Y., and Tao, B.: A comparison between simulated and measured CO₂ and water flux in a subtropical coniferous forest, *Sci. China Ser. D*, 49, 241–251, doi:10.1007/s11430-006-8241-2, 2006.
- Hollinger, D. Y. and Richardson, A. D.: Uncertainty in eddy covariance measurements and its application to physiological models, *Tree Physiol.*, 25, 873–885, doi:10.1093/treephys/25.7.873, 2005.
- Hu, J., Moore, D. J. P., Riveros-Iregui, D. A., Burns, S. P., and Monson, R. K.: Modeling whole-tree carbon assimilation rate using observed transpiration rates and needle sugar carbon isotope ratios, *New Phytol.*, 185, 1000–1015, doi:10.1111/j.1469-8137.2009.03154.x, 2010.
- Ishida, A., Toma, T., Matsumoto, Y., Yap, S. K., and Maruyama, Y.: Diurnal changes in leaf gas exchange characteristics in the uppermost canopy of a rain forest tree, *Dryobalanops aromatica* Gaertn. F., *Tree Physiol.*, 16, 779–785, doi:10.1093/treephys/16.9.779, 1996.
- Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman,

- A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Global Change Biol.*, 7, 269–278, doi:10.1046/j.1365-2486.2001.00412.x, 2001.
- Katul, G. G., Ellsworth, D. S., and Lai, C. T.: Modelling assimilation and intercellular CO₂ from measured conductance: a synthesis of approaches. *Plant Cell Environ.*, 23, 1313–1328, doi:10.1046/j.1365-3040.2000.00641.x, 2000.
- Keeling, C. D.: The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas, *Geochim. Cosmochim. Ac.*, 13, 322–334, doi:10.1016/0016-7037(58)90033-4, 1958.
- Kim, H., Oren, R., and Hinckley, T. M.: Actual and potential transpiration and carbon assimilation in an irrigated poplar plantation, *Tree Physiol.*, 28, 559–577, doi:10.1093/treephys/28.4.559, 2008.
- Köstner, B. M. M., Schulze, E. D., Kelliher, F. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., McSeveny, T. M., Meserth, R., and Weir, P. L.: Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements, *Oecologia*, 91, 350–359, doi:10.1007/BF00317623, 1992.
- Köstner, B., Matyssek, R., Heilmeyer, H., Clausnitzer, F., Nunn, A. J., and Wieser, G.: Sap flow measurements as a basis for assessing trace-gas exchange of trees, *Flora*, 203, 14–33, doi:10.1016/j.flora.2007.09.001, 2008.
- Larcher, W.: *Physiological Plant Ecology*, Springer-Verlag, Berlin, 1983.
- Letts, M. G., Phelan, C. A., Johnson, D. R. E., and Rood, S. B.: Seasonal photosynthetic gas exchange and leaf reflectance characteristics of male and female cottonwoods in a riparian woodland, *Tree Physiol.*, 28, 1037–1048, doi:10.1093/treephys/28.7.1037, 2008.
- Lloyd, J. and Farquhar, G.: ¹³C discrimination during CO₂ assimilation by the terrestrial biosphere, *Oecologia*, 99, 201–215, doi:10.1007/bf00627732, 1994.
- Lu, P., Yunusa, I. A. M., Walker, R. R., and Müller, W. J.: Regulation of canopy conductance and transpiration and their modelling in irrigated grapevines, *Funct. Plant Biol.*, 30, 689–698, doi:10.1093/treephys/20.10.683, 2003.
- Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmoller, D., Law, B. E., Ciais, P., and Grace, J.: Old-growth forests as global carbon sinks, *Nature*, 455, 213–215, doi:10.1038, 2008.
- Ma, L., Rao, X. Q., Zhao, P., Lu, P., Cai, X. A., and Zeng X. P.: Diurnal and seasonal changes in whole-tree transpiration of *Acacia mangium*, *J. Beijing Forest. Univ.*, 29, 67–73, 2007. (In Chinese with English abstract)
- Ma, L.: Transpiration of *Acacia mangium* and its coupling to environmental factors at different temporal and spatial scales, Graduate School of the Chinese Academy of Sciences, Beijing, China, 2008. (In Chinese with English abstract)
- Ma, L., Lu, P., Zhao, P., Rao, X. Q., Cai, X. A., and Zeng, X. P.: Diurnal, daily, seasonal and annual patterns of sap-flux-scaled transpiration from an *Acacia mangium* plantation in South China, *Ann. For. Sci.*, 65, 402p1–402p9, doi:10.1051/forest:2008013, 2008a.
- Ma, Z., Liu, Q., Wang, H., Li, X., Zeng, H., and Xu, W.: Observation and modeling of NPP for *Pinus elliottii* plantation in subtropical China, *Sci. China Ser. D*, 51, 955–965, doi:10.1007/s11430-008-0075-7, 2008b.
- Maier, C. A., Johnsen, K. H., Butnor, J., Kress, L. W., and Anderson, P. H.: Branch growth and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees in response to elevated carbon dioxide concentration and fertilization, *Tree Physiol.*, 22, 1093–1106, doi:10.1093/treephys/22.15-16.1093, 2002.
- Malhi, Y., Nobre, A. D., Grace, J., Kruijt, B., Pereira, M. G. P., Culf, A., and Scott, S.: Carbon dioxide transfer over a Central Amazonian rain forest, *J. Geophys. Res.*, 103, 31593–31612, doi:10.1029/98jd02647, 1998.
- Moncrieff, J. B., Malhi, Y., Leuning, R.: The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water, *Global Change Biol.*, 2, 231–240, doi:10.1111/j.1365-2486.1996.tb00075.x, 1996.
- Morén, A. S., Lindroth, A., and Grelle, A.: Water-use efficiency as a means of modelling net assimilation in boreal forests, *Trees-Struct. Funct.*, 15, 67–74, doi:10.1007/s004680000078, 2001.
- Norman, J. M.: *Simulation of Microclimates*, In *Biometeorology and Integrated Pest Management*, Academic Press, New York, 1982.
- Nouvellon, Y., Laclau, J., Epron, D., Le Maire, G., Bonnefond, J., Gonçalves, J. L. M., and Bouillet, J.: Production and carbon allocation in monocultures and mixed-species plantations of *Eucalyptus grandis* and *Acacia mangium* in Brazil, *Tree Physiol.*, 32, 680–695, doi:10.1093/treephys/tps041, 2012.
- Nowak, D. J., Stevens, J. C., Sisinni, S. M., and Luley, C. J.: Effects of urban tree management and species selection on atmospheric carbon dioxide, *J. Arboriculture*, 28, 113–122, 2002.
- Oren, R., Sperry, J. S., Katul, G. G., Pataki, D. E., Ewers, B. E., Phillips, N., and Schäfer, K. V. R.: Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit, *Plant Cell Env.*, 22, 1515–1526, doi:10.1046/j.1365-3040.1999.00513.x, 1999.
- Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schäfer, K. V. R., McCarthy, H., Hendrey, G., McNulty, S. G., and Katul, G. G.: Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere, *Nature*, 411, 469–472, doi:10.1038/35078064, 2001.
- Pachauri, R. and Reisinger, A.: *IPCC fourth assessment report*, IPCC, Geneva, 2007.
- Peng, S. L.: *Study and Application of Restoration Ecology in Tropical and Subtropical China*, Science Press, Beijing, 2003.
- Phillips, N., Oren, R., and Zimmermann, R.: Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species, *Plant Cell Env.*, 19, 983–990, doi:10.1111/j.1365-3040.1996.tb00463.x, 1996.
- Phillips, N., Nagchaudhuri, A., Oren, R., and Katul, G.: Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow, *Trees-Struct. Funct.*, 11, 412–419, doi:10.1007/s004680050102, 1997.
- Ponton, S., Flanagan, L. B., Alstad, K. P., Johnson, B. G., Morgenstern, K. A. I., Kljun, N., Black, T. A., and Barr, A. G.: Comparison of ecosystem water-use efficiency among Douglas-fir forest, aspen forest and grassland using eddy covariance and carbon isotope techniques, *Glob. Change Biol.*, 12, 294–310, doi:10.1111/j.1365-2486.2005.01103.x, 2006.
- Rascher, K. G., Máguas, C., and Werner, C.: On the use of phloem sap $\delta^{13}\text{C}$ as an indicator of canopy carbon discrimination, *Tree Physiol.*, 30, 1499–1514, doi:10.1093/treephys/tpq092, 2010.

- Rayment, M. and Jarvis, P.: Seasonal gas exchange of black spruce using an automatic branch bag system, *Can. J. Forest Res.*, 29, 1528–1538, doi:10.1139/x99-130, 1999.
- Rico, M., Gallego, H. A., Moreno, G., and Santa Regina, I.: Stomatal response of *Quercus pyrenaica* Willd to environmental factors in two sites differing in their annual rainfall (Sierra de Gata, Spain), *Ann. For. Sci.*, 53, 221–234, doi:10.1051/forest:19960205, 1996.
- Schäfer, K. V. R., Oren, R., and Tenhunen, J. D.: The effect of tree height on crown level stomatal conductance, *Plant Cell Env.*, 23, 365–375, doi:10.1046/j.1365-3040.2000.00553.x, 2000.
- Schäfer, K. V. R., Oren, R., Ellsworth, D. S., Lai, C., Herrick, J. D., Finzi, A. C., Richter, D. D., and Katul, G. G.: Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem, *Glob. Change Biol.*, 9, 1378–1400, doi:10.1046/j.1365-2486.2003.00662.x, 2003.
- Schneider, S. H.: The changing climate, *Sci. Am.*, 261, 70–79, 1989.
- Sharkey, T.: Transpiration-induced changes in the photosynthetic capacity of leaves, *Planta*, 160, 143–150, doi:10.1007/bf00392862, 1984.
- Thornley, J. H. M. and Johnson, I. R.: *Plant and Crop Modelling*, Clarendon Press, Oxford, 1990.
- Wang, H., Zhao, P., Hölscher, D., Wang, Q., Lu, P., Cai, X. A., and Zeng, X. P.: Nighttime sap flow of *Acacia mangium* and its implications for nighttime transpiration and stem water storage, *J. Plant Ecol.*, 5, 294–304, doi:10.1093/jpe/rtr025, 2012.
- Waring, R. H., Landsberg, J. J., and Williams, M.: Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.*, 18, 129–134, doi:10.1093/treephys/18.2.129, 1998.
- Webb, R. A.: Use of the boundary line in the analysis of biological data, *J. Hort. Sci.*, 47, 309–319, 1972.
- Williams, M., Rastetter, E. B., Fernandes, D. N., Goulden, M. L., Shaver, G. R., and Johnson, L. C.: Prediction gross primary productivity in terrestrial ecosystems, *Ecol. Appl.*, 7, 882–894, doi:10.1890/1051-0761(1997)007[0882:pgppit]2.0.co;2, 1997.
- Wong, S. C., Cowan, I. R., and Farquhar, G. D.: Stomatal conductance correlates with photosynthetic capacity. *Nature*, 282, 424–426, doi:10.1038/282424a0, 1979.
- Xiao, X., Zhang, Q., Saleska, S., Hutya, L., De Camargo, P., Wofsy, S., Frolking, S., Boles, S., Keller, M., and Moore III, B.: Satellite-based modeling of gross primary production in a seasonally moist tropical evergreen forest, *Remote Sens. Environ.*, 94, 105–122, doi:10.1016/j.rse.2004.08.015, 2005.
- Yang, L., Liu, N., Ren, H., and Wang, J.: Facilitation by two exotic *Acacia*: *Acacia auriculiformis* and *Acacia mangium* as nurse plants in South China, *Forest Ecol. Manag.*, 257, 1786–1793, doi:10.1016/j.foreco.2009.01.033, 2009.
- Zhao, P., Lu, P., Ma, L., Sun, G. C., Rao, X. Q., Cai, X. A., and Zeng, X. P.: Combining sap flow measurement-based canopy stomatal conductance and ¹³C discrimination to estimate forest carbon assimilation, *Chinese Sci. Bul.*, 50, 2021–2027, 2005a.
- Zhao, P., Rao, X. Q., Ma, L., Cai, X. A., and Zeng, X. P.: Application of Granier's sap flow system in water use of *Acacia mangium* forest, *Journal of Tropical and Subtropical Botany* 13, 457–468, 2005b. (In Chinese with English abstract)
- Zhao, P., Rao, X. Q., Ma, L., Cai, X. A., and Zeng, X. P.: Sap flow-scaled transpiration and canopy stomatal conductance in an *Acacia mangium* forest, *Journal of Plant Ecology* 30, 655–665, 2006. (In Chinese with English abstract)