Photosynthesis-transpiration coupling model at canopy scale in terrestrial ecosystem

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Abstract At the hypothesis of big leaf, an ecosystem photosynthesis-transpiration coupling cycle model was established by the scaled SMPT-SB model from single leaf to canopy, and model parameterization methods were discussed. Through simulating the canopy light distribution, canopy internal conductance to CO_2 can be scaled from single leaf to canopy by integrating to canopy using the relationship between single internal conductance and photosynthetic photon flux density. Using the data observed by eddy covariance method from the Changbai Mountains site of ChinaFLUX, the application of the model at the canopy scale was examined. Under no water stress, the simulated net ecosystem photosynthesis rate fitted with the observed data very well, the slope and R^2 of the line regression equation of the observed and simulated values were 0.7977 and 0.8892, respectively (n = 752), and average absolute error was 3.78 μmol CO_2 m^{-2} s^{-1}; the slope, R^2 and average absolute error of transpiration rate were 0.7314, 0.4355 and 1.60 mmol H_2O m^{-2} s^{-1}, respectively (n = 752). The relationship between canopy photosynthesis, transpiration and external environmental conditions was discussed by treating the canopy as a whole and neglecting the comprehensive feedback mechanism within canopy, and it was noted that the precipitation course affected the transpiration rate simulation badly. Compared to the models based on eco-physiological processes, the SMPT-SB model was simple and easy to be used. And it can be used as a basic carbon and water coupling model of soil-plant-atmosphere continuum.

Keywords: photosynthesis rate, transpiration rate, SMPT-SB model, internal conductance, canopy scale.

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Based on field observation, the scientists set up a series of carbon and water coupling cycle models from their professional angles. These models were more based on the factorial responding model of photosynthesis and environmental variables proposed by Jarvis[1], photosynthesis model proposed by Farquhar et al.[2] and relationship model between photosynthesis and stomatal conductance proposed by Ball et al.[3] and had been widely adopted by modelers at the scale of individual leaves[4—8], at the scale of canopy[9], at the scale of landscape[10], at the scale of region[11] and in some global climate models[12—17]. These models mentioned above were very useful for understanding both photosynthesis and transpiration processes synthetically, but they were too complicated to be used easily and a lot of accessorial experiments were necessary for confirming the model parameters before. To make the modeling practical and simple, Yu et al. proposed a Synthetic Model of Photosynthesis-Transpiration based on Stomatal Behavior (SMPT-SB) for estimating photosynthesis and transpiration from an angle different from the traditional approach[18]. The SMPT-SB model was explored by introducing the internal conductance g_{ic}, of CO_2 assimilation, and proved in point at individual leaves[18,19]. It required few parameters and can be used easily, but its application has not been discussed at the scale of canopy. The setup of ChinaFLUX (Chinese Terrestrial Ecosystem Flux Observational Research Network) and data accumulation of eddy covariance[20] provide reliable parameterization and model validation data for scaling SMPT-SB model from individual leaves to canopy.

In this study, the objectives are: (1) to improve the SMPT-SB model proposed by Yu et al.[18] from individual leaves to canopy scale using the data observed by eddy covariance method in the Changbai Mountains forest ecosystem; (2) to identify the model parameters and examine its simulating ability for ecosystem canopy photosynthesis and transpiration rates; and (3) to discuss the feasibility of using the model at the canopy scale. This research can not only provide model reference for simulating CO_2 and H_2O fluxes in other ecosystems, but also offer necessary reference for constructing the soil-vegetation-atmosphere continuum (SPAC) models.

1 Model descriptions

The main idea of scaling SMPT-SB model from individual leaves to canopy was to regard the canopy as a big leaf, namely the "big leaf" hypothesis. In general, the "big leaf" hypothesis was tenable when leaf area index was bigger than 3. In this case, the ecosystem water loss primarily from transpiration and evaporation was so small that it could be ignored. So, in this paper, the canopy transpiration rate was equal to ecosystem evapotranspiration rate approximatively, and had the same concept with eddy covariance data observed in the field. Ecosystem canopy photosynthesis rate was total ecosystem photosynthesis rate, defined as ecosystem assimilation CO_2 capacity per second per square meter, and was equal to sum of CO_2 flux observed by eddy covariance and total ecosystem respiration rate.

The processes of CO_2 and H_2O fluxes at the canopy scale were controlled by several factors of atmosphere, plant, and soil. They were aerodynamic, boundary layer, canopy stomatal and internal resistance. At the single leaf scale, photosynthesis and transpiration were controlled by the stomata behavior. Fig. 1 shows the schematic of CO_2 and H_2O exchange at canopy scale.

Based on the analogy of Ohm's law in electrics, the canopy transpiration rate, E_c (mol H_2O m^{-2} s^{-1}) was basically described as

$$E_c = \frac{W_i - W_r}{r_a + r_{bw} + r_{sw}}, \tag{1}$$

where W_i (mol mol^{-1}), W_a (mol mol^{-1}) and W_r (mol mol^{-1}) were mole fraction of water vapor in the stomata space, in the air and in the air at reference height, respectively; r_a aerodynamic resistance (m^2 s mol^{-1}), r_{sw} resistance (m^2 s mol^{-1}) of stomata to H_2O diffusion, r_{bw} resistance (m^2 s mol^{-1}) of boundary layer to H_2O diffusion, respectively.

The canopy photosynthesis rate, A_c (μmol CO_2 m^{-2} s^{-1}) was generally described as

$$A_c = \frac{C_r - C_i}{r_a + r_{bc} + r_{sc}}, \tag{2}$$

where C_i (μmol mol^{-1}), C_a (μmol mol^{-1}) and C_r (μmol mol^{-1}) were intercellular CO_2 concentration, ambient CO_2 concentration within canopy and at reference height, respectively; r_{sc} resistance (m^2 s mol^{-1}) of stomata to CO_2 diffusion, r_{bc} resistance (m^2 s mol^{-1}) of boundary layer to CO_2 diffusion, respectively.

By ignoring the interaction between water molecules leaving and entering the stomata, the canopy photosynthesis could be rewritten as

$$A_c = \frac{C_r - \Gamma_*}{r_a + r_{bc} + r_{sc} + r_{ic}}, \tag{3}$$

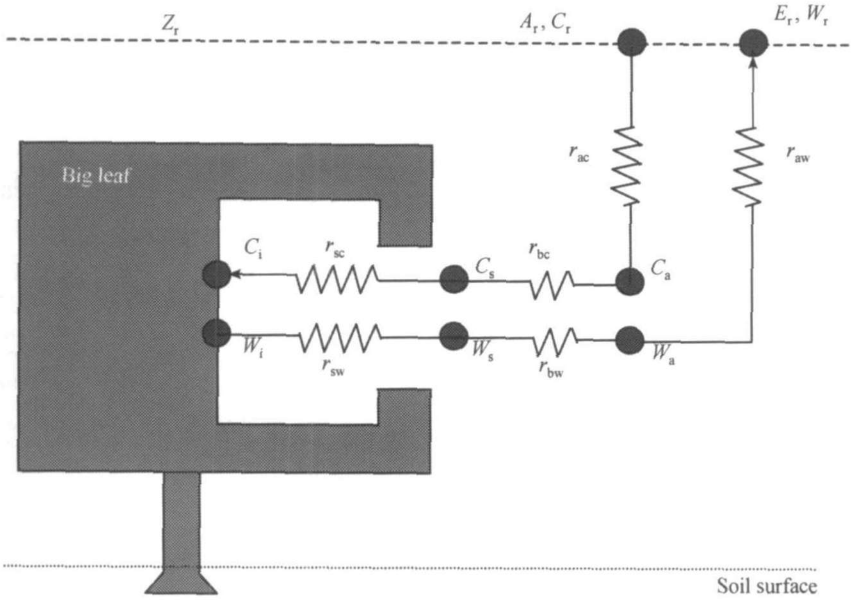

Fig. 1. Schematic of CO_2 and H_2O exchange process at canopy level.

where Γ_* was CO_2 compensation point without dark respiration (μmol mol^{-1}), and r_{ic} was canopy internal resistance (m^2 s mol^{-1}).

Affected by environmental conditions (extrinsic) and stomatal physiological factors (intrinsic), stomatal conductance was the important factor to control the CO_2 fixation and water loss. It was called the single leaf stomatal conductance, $g_{s,leaf}$ at individual leaf scale, but at the scale of canopy we called it as canopy stomatal conductance, g_{sw}, or canopy conductance, g_c for short. A series of empirical models were established between single leaf stomatal conductance and environmental factors based on gas exchange experiment at the scale of individual leaves, for example, the model proposed by Ball et al.[3]

$$g_{s,leaf} = a_1 A_{leaf} Rh_{s,leaf} / C_{s,leaf}\,, \qquad (4)$$

where A_{leaf}, $Rh_{s,leaf}$, $C_{s,leaf}$ were photosynthesis rate, leaf surface relative humidity and CO_2 concentration, respectively; a_1 was constant. Leuning further suggested that eq. (4) might still be useful if $Rh_{s,leaf}$ was replaced by a more general humidity function $f(D_s)$, and to avoid the circumstances of stomatal conductance being negative when ambient CO_2 concentration was lower than compensation point, so Ball model could be revised as[4,5]

$$g_{s,leaf} = g_0 + a_1 A_{leaf} Rh_{s,leaf}/(C_{s,leaf} - \Gamma)\,, \qquad (5)$$

where g_0 was residual stomatal conductance (as $A_m \to 0$ when $Q_p \to 0$, Q_p was photosynthetic photon flux density); Γ was the CO_2 compensation point with dark respiration. Canopy conductance was often estimated by applying detailed mechanistic models of photosynthesis-stomatal response developed for individual, then scaling leaf responses to the canopy leave using models of light penetration and leaf adaptation as functions of position within canopy[14]. While this bottom-up scaling approach had been proven effective in reproducing observed photosynthesis fluxes, it involved the specification of many species-dependent parameters and required a computationally expensive iterative solution that can become numerically unstable under certain conditions[21]. An alternative was to model the canopy response to its environment in bulk, neglecting the behavior of individual leaves. McNaughton and Jarvis demonstrated that neglected feedback develop within the canopy system that can cause the canopy to have a more stable behavior in the face of environmental fluctuations than would an isolated leaf [22]. Therefore, detailed models of stomatal response often might not provide additional accuracy in estimating stand-level fluxes. Furthermore, simple scaling techniques might neglect important feedback and system effects. At the big leaf hypothesis, assumed that the response of stomatal conductance on photosynthesis at the scale of canopy had the same mechanism as individual leaves, the canopy stomatal conductance behavior model can be described as[23]

$$g_{sw} = g_0 + a_1 A_c f(D_s) / (C_r - \Gamma). \qquad (6)$$

Assumed $g_{sw}=1.56g_{sc}$ and $g_{bw}=1.37g_{bc}$, incorporating eq. (6) into eq. (3), the model of photosynthesis-transpiration for estimating canopy photosynthesis rate was given as

$$A_c = \frac{(C_r - \Gamma_*) - 1.56(C_r - \Gamma)/\left[a_1 f(D_s)\right]}{r_a + 1.37 r_{bw} + r_{ic}}. \qquad (7)$$

Difference between CO_2 compensation point without dark respiration, Γ_*, and Γ, and between $(C_a - \Gamma_*)$ and $(C_a - \Gamma)$ were not large in field experimental conditions[18]. In this case, it might be judged that the estimation error of the photosynthesis arising from the difference between Γ_* and Γ should not be large. So eq. (7) could be rewritten as

$$A_c = \frac{(C_r - \Gamma_*)\left[1 - 1.56/(a_1 f(D_s))\right]}{r_a + 1.37 r_{bw} + r_{ic}}. \qquad (8)$$

Incorporating eq. (6) into eq. (1), the model of photosynthesis-transpiration for estimating canopy transpiration rate was given as

$$E_c = \frac{(W_i - W_r)}{r_a + r_{bw} + 1/\left[g_0 + a_1 A_c f(D_s)/(C_r - \Gamma_*)\right]}. \qquad (9)$$

2 Site descriptions and observation methods

2.1 Site descriptions

The site is situated in the northern slope of the Changbai Mountains of China with latitude 42°24′09″N, longitude 128°05′45″E and elevation 738 m. The Changbai Mountains belong to the temperate continental climate influenced by monsoon with mean annual temperature −7.3—4.9℃, annual frost-free period 109—141 d, annual sunshine duration 2271—2503 h. The rain was mainly in summer with mean annual total precipitation 600—900 mm. The *Pinus-koraiensis*-dominanted *Pinus koraiensis* broad-leaved mixed forest is the zonal vegetation distributed from 500—1100 m altitude. The observation field is flat with upland dark brown forest soil, and the forest is about 180 years old with mean canopy height 26 m, the mainly preponderant species are *Pinus koraiensis*, *Tilia amurensis*, *Quercus mongolica*, *Fraxinus mandshurica*, *Acer mono*, etc.

2.2 Observation methods

The data were from the Changbai Mountains site of ChinaFLUX. In the field, the observation tower is 62 m high with 7-level routine meteorological measurement system, including wind speed (A100R, Vector Instruments, Denbighshire, UK), air temperature and relative humidity (HMP45C, Vaisala, Helsinki, Finland) fixed on the tower at 2.5, 8, 22, 26, 32, 50 and 60 m, respectively; the photosynthetic active radiation sensor (LI190SB, LiCor., USA) above the canopy at 32 m; 5 photosynthetic active radiation sensors (LQS70-10, APOGEE) under the canopy at 2 m; in soil, 3 layers soil humidity sensor (CS616-L, Campbell, USA) imbedded at 5, 20, 50 cm, respectively; 2 soil heat flux sensors (HFP01, HUKSEFLUX, Netherlands) at 5 cm; 5 layers soil temperature sensor(105T, Campbell, USA) at 2, 10, 20, 50, 100 cm; and the rain measurement instrument fixed on the top of tower(52203,RM YOUNG). The raw data sampling frequency mentioned above was 0.5 Hz, the data were collected by datalogger (CR23X and CR10X, Campbell Scientific, USA), all data were calculated by 30 min mean value for storage except for 30 min total precipitation amount. 7-level CO_2 profiling system had the same height with 7-level routine meteorological measurement system, gas sample was sent to analyzer (Li-820, LiCor., USA) by sampling tube, raw sampling frequency was 0.5 Hz, the data were collected by datalogger (CR10X, Campbell Scientific, USA) and stored by 30 min mean value. The open-path eddy covariance system consists of three-dimension anemometer (CAST3, Campbell, USA) and open-path CO_2/H_2O analyzer (Li-7500, LiCor Inc., USA) with the raw sampling frequency 10 Hz at 40 m. In growing season, the leaf area index was measured using canopy analyzer (LiCor Inc., USA) every 5 to 10 days.

In this paper, the data for parameterization and model verification were in summer, 2003. In this period, the mean air temperature is 19.2℃; total precipitation amount is 313.8 mm, accounting for 63.3% of yearly total precipitation amount. The seasonal change of daily precipitation amount and daily mean temperature in summer, 2003 are shown in fig. 2, compared to the same historical term average value, the climate belongs to warmer and droughtier in the Changbai Mountains in 2003. The data were divided into two groups at random, one for parameterization, and another for model verification.

2.3 Data processing

Eddy covariance is a method for calculating flux by measuring scalar fluctuation. For fewer hypotheses, it was regarded as the most accurate method for measuring the CO_2, water vapor and heat fluxes between land surface and atmosphere. Neglecting the canopy storage, the fluxes measured by eddy covariance are net ecosystem exchanges. To ensure the fluxes observed by eddy covariance can reflect the ecosystem .information, the data used for parameterization and model verification were selected strictly because the open-path eddy covariance was affected more by weather conditions, especially rain. The criterion is: (1) photosynthetic active radiation, PAR>10 μmol mol^{-1}; (2) data excluded in 2 h before and after rain; and (3) no abnormal values.

At the same time, 3-dimension coordination rotation and WPL revision were performed. Coordination rotation had little affect on daily total fluxes, but had a little effect on daily variations of fluxes; and WPL revision had little effect on CO_2 flux, but had a little affect on water vapor flux.

When considering the canopy storage, net ecosystem exchange can be modified as

$$F_i = \overline{w_r' \rho_{ir}'} + \int_0^{Z_r} \frac{\partial \bar{\rho}_i}{\partial t} dz, \qquad (10)$$

where F_i (i=c denotes CO_2, i=w denotes water vapor) is net ecosystem exchange of CO_2 or water vapor between land surface and atmosphere; w_r' and ρ_{ir}' are vertical wind speed and CO_2 or water vapor concentration fluctuation; $\partial \bar{\rho}_i / \partial t$ is the change of CO_2 or water vapor concentration with time under the reference height, Z_r.

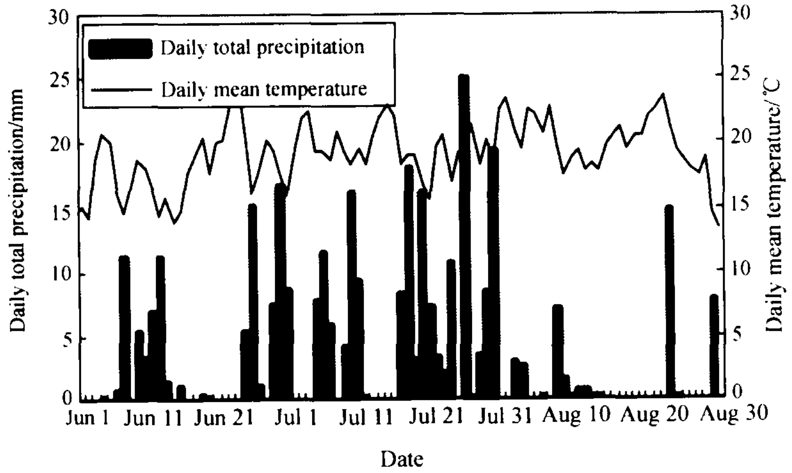

Fig. 2. Seasonal variations of daily total precipitation and mean temperature in summer, 2003 in the Changbai Mountains.

3 Model parameterizations

Before model parameterizations, total ecosystem respiration must be ensured, thus ecosystem photosynthesis rate can be obtained. In eqs. (8) and (9), the parameters needed to be confirmed are r_{ic}, r_a, r_{bw}, $f(D_s)$, a_1 and g_0.

3.1 Establishment of total ecosystem respiration model

By night, there is no solar radiation, CO_2 flux measured by eddy covariance, F_c is equal to total ecosystem respiration, R_{eco}. Under no water stress, the total ecosystem respiration varies with the temperature as follows[4]:

$$R_{eco} = ae^{(bT_a)}. \tag{11}$$

The relationship between total ecosystem and air temperature, T_a is shown in fig. 3. The model is described as

$$R_{eco} = 0.0254e^{(0.1701T_a)}. \tag{12}$$

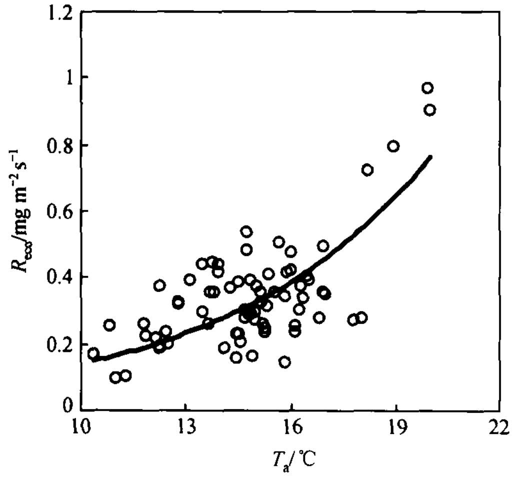

Fig. 3. Dependence of total ecosystem respiration on air temperature.

So, canopy photosynthesis and transpiration rate can be described as

$$A_c = F_c + R_{eco}, \tag{13}$$

$$E_c = F_w. \tag{14}$$

3.2 Model parameterizations

(i) Internal conductance, g_{ic}. Eq. (2) can be rewritten as

$$A_c = (C_i - \Gamma_*) / r_{ic} = g_{ic} (C_i - \Gamma_*). \tag{15}$$

In many researches, the ratio of intercellular CO_2 concentration C_i to ambient CO_2 concentration is close to a constant in specific-type vegetation, called the conservation of C_i/C_a. The ratios are 0.65—0.8 and about 0.4 for C_3 and C_4 type vegetation, respectively. In the Changbai Mountains, the mainly preponderant species are all C_3 type vegetation, so the relationship between C_i and C_a was adopted as[25]

$$C_i = 0.7C_a. \tag{16}$$

Γ_* depends on leaf temperature. For forest, an empirical second-order polynomial for C_3 plants[26] was used in this study to describe the dependence of the Γ_* on the leaf temperature, T_c (℃), namely

$$\Gamma_* = 42.7 + 1.68(T_c - 25) + 0.012(T_c - 25)^2. \tag{17}$$

Thus canopy internal conductance can be rewritten as

$$g_{ic} = A_c/(C_i - \Gamma_*). \tag{18}$$

At the scale of individual leaves, Yu et al. found that single leaf internal conductance depended on photosynthetic photon flux density, Q_p (μmol m^{-2} s^{-1}) strongly[18]. So, at the scale of canopy, canopy internal conductance can be described as

$$g_{ic} = \int_{Q_b}^{Q_t} \left(a + bQ_p\right) dQ_p = \left(aQ_p + \frac{1}{2} bQ_p^2\right)\Bigg|_{Q_b}^{Q_t}. \tag{19}$$

According to Beer-Lambert law, photosynthetic photon flux density under canopy, Q_b (μmol m^{-2} s^{-1}) can be described as[27]

$$Q_b = Q_t e^{-\varepsilon L}, \tag{20}$$

where Q_t (μmol m^{-2}s^{-1}) is photosynthetic photon flux density above canopy; ε is extinction coefficient, ($\varepsilon = 0.55$); L is leaf area index (LAI).

So, eq. (19) can be rewritten as

$$g_{ic} = aQ_t\left(1 - e^{-\varepsilon L}\right) + \frac{1}{2} bQ_t^2\left(1 - e^{-2\varepsilon L}\right). \tag{21}$$

In summer, the LAI varied from 4.62 to 5.71 in the Changbai Mountains, so the change of LAI had little effect on canopy internal conductance; the main factor was the photosynthetic photon flux density. Dependence of canopy internal conductance on photosynthetic photon flux density above canopy is shown in fig. 4, the relationship between internal conductance and photosynthetic photon flux density was second-order polynomial approximately, and had the same form with eq. (21), distinguished itself by the line relationship at the scale of individual leaves.

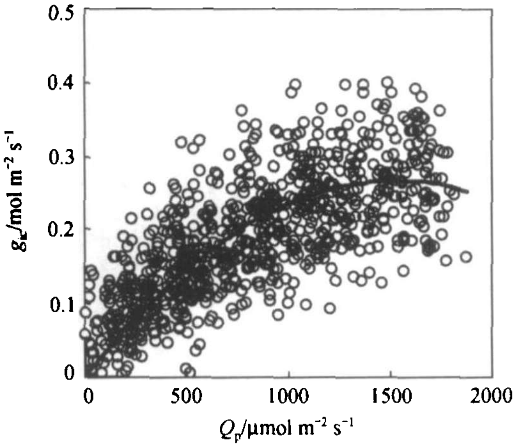

Fig. 4. Dependence of canopy internal conductance on photosynthetic photon flux density.

Combining the form of eq. (21), the general canopy internal conductance can be described as

$$g_{ic} = 3.70\times10^{-4} Q_p\left(1-e^{-\varepsilon L}\right) - 1.14\times10^{-7} Q_p^2\left(1-e^{-2\varepsilon L}\right)$$

$$(R^2=0.53,\ n=835). \qquad (22)$$

(ii) Aerodynamic resistance, r_a. Aerodynamic resistance varies with canopy character and airflow above and under canopy. In the circulation of closed canopy and neutral atmosphere, the aerodynamic resistance can be rewritten as[28]

$$r_a = 2.24\times10^{-2}\frac{1}{k^2 u_r}\left[\ln\left(\frac{Z_r-d}{Z_0}\right)\right]^2, \qquad (23)$$

where u_r is wind speed at reference height Z_r; k is Von Karmen constant and k = 0.4; d and Z_0 are zero surface displace and surface roughness, respectively, for forest, d=0.78h, Z_0=0.075h, h is canopy height.

When considering the atmosphere stability, r_a can be modified as[29]

$$r_a = 2.24\times10^{-2}\frac{1}{k^2 u_r}\left[\ln\frac{Z_r-d}{Z_0}+\Phi_m\right]^2, \qquad (24)$$

$$\Phi_m = \begin{cases} (1-5R_i)^{-1} & \text{stable,} \\ 1 & \text{neutral,} \\ (1-16R_i)^{-1/4} & \text{unstable,} \end{cases} \qquad (25)$$

where R_i is bulk Richardson number.

(iii) Boundary layer resistance, r_{bw}. For two sides of leaf distributing the stomata, the boundary layer resistance has the formula[29]

$$r_{bw} = 2.24\times10^{-2}\frac{100\alpha}{2L}\frac{(W/u_h)^{1/2}}{1-e^{(-\alpha/2)}}, \qquad (26)$$

where α is wind attenuation coefficient within canopy (α = 3); W is leaf width (m), in this paper, W = 5 cm; u_h is wind speed at the height of h (m s^{-1}); 2.24×10^{-2} is a coefficient that converts the unit of r_a and r_{bw} from s m^{-1} to m^2 s mol^{-1}.

(iv) Response function of stomata to water vapor.

At the scale of canopy, the canopy conductance, g_c can be regarded as the canopy stomatal conductance, g_{sw}. By the equation of Penman-Monteith, the canopy conductance can be described as

$$1/g_{sw}=1/g_c=\frac{\Delta(R_n-G)r_a+\rho \mathrm{VPD}_r}{\gamma\lambda E_c}-r_a, \qquad (27)$$

where Δ is slope of the saturated vapor pressure vs. temperature curve; ρ is air density; VPD$_r$ is water vapor deficit at reference height; λ is latent heat of vaporization; γ is psychrometric constant; R_n is net radiation flux density and G is soil heat flux density. At the canopy scale, when the response function of canopy stomatal conductance to water vapor was relative humidity, the line trend of Ball model is most obvious (shown in fig. 5). So, the function of $f(D_s)$ had the fol-

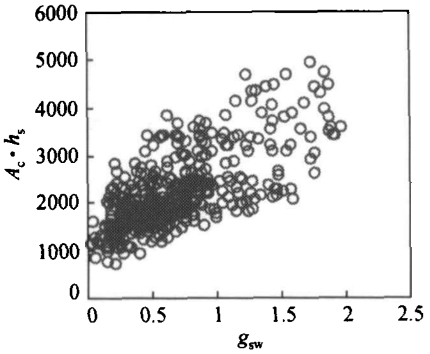

Fig. 5. Representation of Ball model at canopy scale. The abscissa is canopy stomatal conductance, g_{sw} (mol m^{-2} s^{-1}) and the ordinate is the product of canopy photosynthesis rate, A_c (μmol m^{-2} s^{-1}) and relative humidity, h_s (%).

lowing form:

$$f_1(D_s) = h_s, \quad (28)$$

where h_s is relative humidity at canopy surface (%).

Incorporating eqs. (22), (24), (26) and (27) to eqs. (8) and (9), only a_1 and g_0 were unknown. Thus two equations with two unknown, the solutions of a_1 and g_0 can be got. a_1=0.0898 and g_0=0.3263, with the 95% reliable range being [0.0383, 0.141] and [0.0951, 0.5574], respectively.

4 Model verification and discussion

4.1 Model verification

Substituting the contemporaneous meteorological data that had not joined model establishment into eqs. (8) and (9), simulated values of canopy photosynthesis and transpiration rate can be got (shown in fig. 6). In fig. 6(a), simulated canopy photosynthesis rate, A_c, simu was fit very well with the observed data using eddy covariance method, the slope and R^2 of linear regression were 0.7977 and 0.8892 (n=752), respectively, the mean absolute error was 3.78 μmol CO$_2$ m^{-2} s^{-1}. Compared to photosynthesis model, the simulated precision of transpiration model is decreased, the slope, R^2 and mean absolute error of simulated canopy transpiration rate, E_c, simu and E_c linear regression were 0.7314, 0.4355 and 1.60 mmol H$_2$O m^{-2} s^{-1} (n=752), respectively. The simulated and observed values of canopy photosynthesis and transpiration rate had the same daily variations (shown in fig. 7).

4.2 Discussion

In 2003, the Changbai Mountains had warmer and droughtier climate, but there was no water stress phenomenon. In summer, there were four periods of low soil water content (using 5 cm soil water content, S_w<0.22V V^{-1} as distinguish guideline), as shown in the shadow of fig. 8. The canopy photosynthesis rate explained by the model decreased from 88.92% to 84.42% (shown in fig. 9), but the degree was not obvious. That was because : (1) leaf area index was larger than 4.5 in the whole summer (shown in fig. 8), the big leaf hypothesis is reliable; (2) the Changbai Mountains is one of the regions with most plenty of precipitation to the north of the Yangtze River in China, in 2003, although there was less precipitation

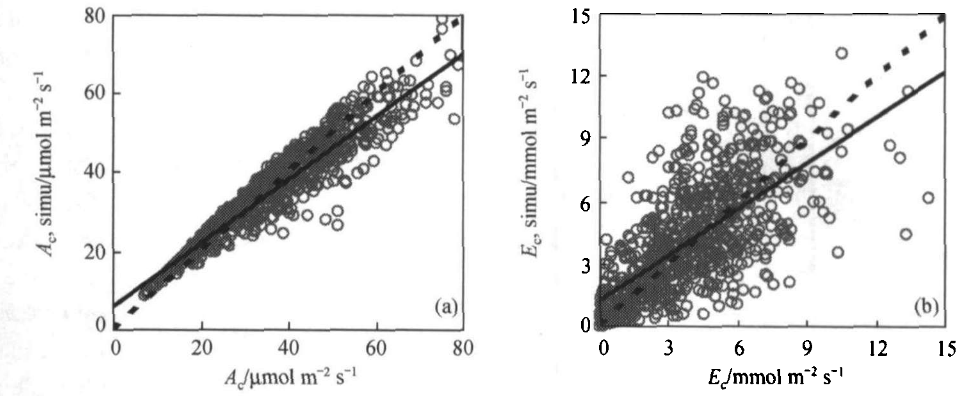

Fig. 6. Compare of simulated and observed value of canopy photosynthesis and transpiration rate. (a) Photosynthesis rate; (b) transpiration rate; ○, data point; broken and real lines are 1 : 1 and linear regression line.

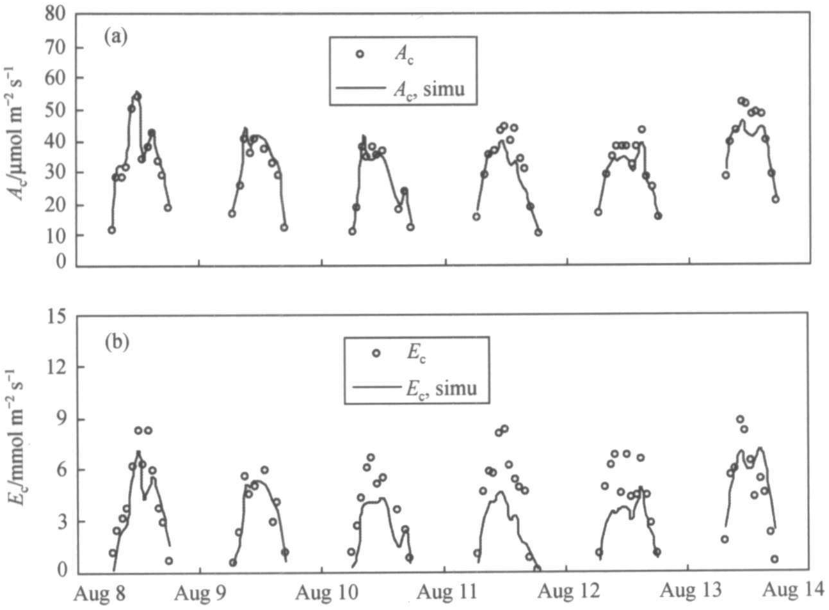

Fig. 7. Daily variations of canopy photosynthesis and transpiration rate. (a) Photosynthesis rate; (b) transpiration rate; ○, observed values; real line, simulated curve.

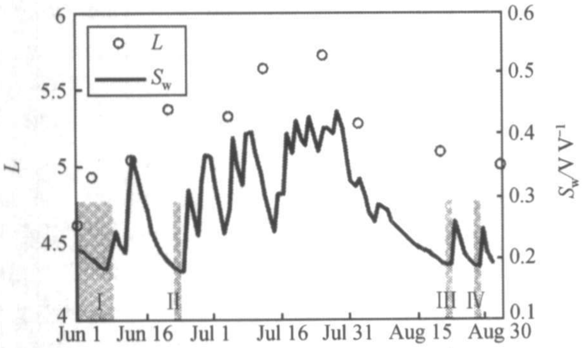

Fig. 8. Seasonal variations of leaf area index, L and 5 cm soil water content, S_w.

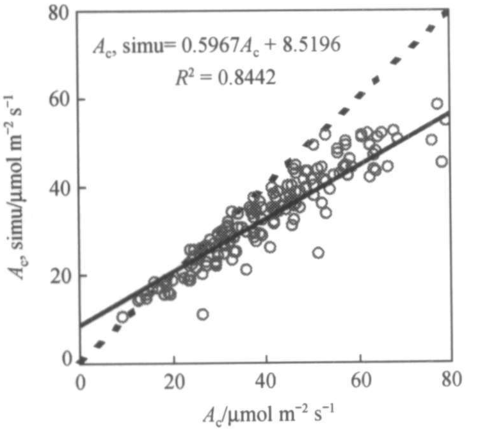

Fig. 9. Compare of simulated and observed value of canopy photosynthesis rate at low soil water content (S_w < 0.22V V^{-1}). ○, Data point; broken line, 1 : 1 line; real line, linear regression line.

and higher temperature, the change of soil water content was not obvious in the deep layer (30 cm), in the whole growing season, the 30 cm soil water content was higher than 0.25V V^{-1} all the time. Because of a lot of water repertory in deep soil, soil water can be transferred from deep to shallow layers in the drought period, which can satisfy the tree's demand for water. So, in summer at the Changbai Mountains, water was not a limited factor for canopy photosynthesis.

In this study, soil and canopy evaporation were neglected at the big leaf hypothesis, but this part of water vapor flux was included in the flux measured by eddy covariance in fact. Some researches showed that the ratio of canopy transpiration to total ecosystem evapotranspiration had a strong relationship with leaf area index[30]. At the Changbai Mountains, canopy transpiration accounted for over 60% of total ecosystem evapotranspiration[31], but the evaporation from soil and canopy were not less yet. Furthermore, the Changbai Mountains is located in the northeast of China, facing the North Pacific on its east and backing on far-flung Northeast Plain of China, because of which, the Changbai Mountains has plenty of precipitation in summer, especially terrain rain affected by special terrain. After rain, it was clear very soon and the water intercepted by leaves was vaporized quickly, so the water vapor flux observed by eddy covariance was higher than canopy transpiration at that time. Generally, water vapor flux was low correspondingly before rain because of low soil water content, little evaporation from soil, high fraction of cloud, weak solar radiation, low temperature and weak photosynthesis and transpiration. But before rain, the wind speed was low correspondingly because airflow was lifted by terrain. Wind speed distribution deviated from the logarithmic profile, especially in the presence of high vegetation, there was breeze above the tree and the wind speed was near to zero within canopy, so the simulated precision of aerodynamic resistance was decreased severely. This can cause the simulated capability of transpiration to decrease. In the circulation of no rain for a long time, the simulated canopy transpiration rate may be higher than the observed value affected by the simulated value lower than the observed value. Except for conditions mentioned above, the simulated ability should be better. From fig. 10, the guess was proven to be right. The canopy transpiration rate explained by the model increased from 43.55% (shown in fig. 9(b)) to 55.57% (shown in fig. 9(d)). The data points were still scattered, this is because all precipitation course information was included in the transpiration model, especially before and after rain. In general, poorly simulated ability of canopy transpiration was due to no consideration of evaporation from soil and canopy and the different ratios of canopy transpiration to total ecosystem evapotranspiration in different rain courses in the

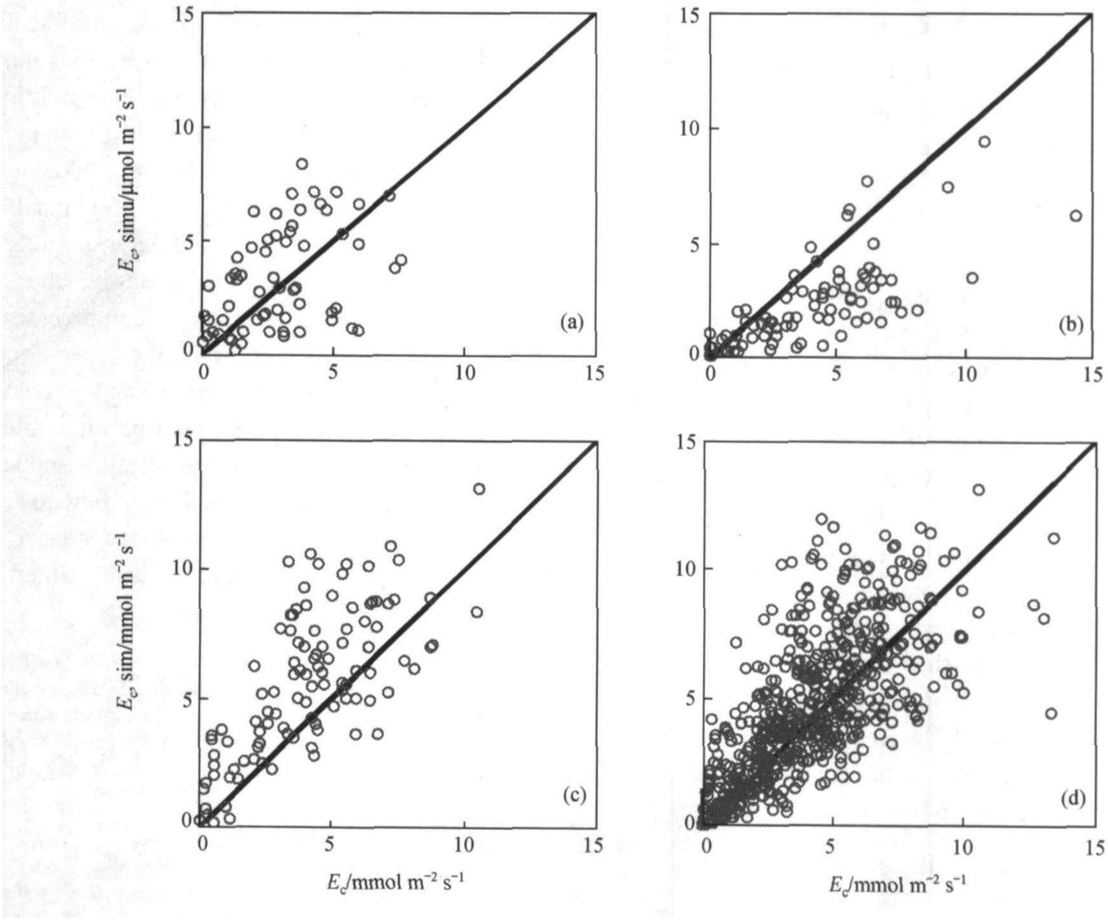

Fig. 10. Comparison of simulated and observed canopy transpiration rates in different rain courses. E_c and E_c, simu were observed and simulated canopy transpirations, respectively; (a), (b), (c), (d) were before rain, after rain, no rain for a long time and normal weather condition, respectively. Before rain was limited within 5 h before rain; after rain was limited within 5 h after rain; no rain for a long time was on 12—21 August; normal weather condition meant the other time except for (a), (b), (c). ○, Data point; real line, 1 : 1 line.

Table 1 Model simulated ability in different months

Model	Month	a	b	R^2	Mean relative error (%)	n
Photosynthesis	Jun.	0.8659	4.024	0.9029	9.94	206
	Jul.	0.7852	7.2643	0.8935	9.85	258
	Aug.	0.8214	4.8449	0.9370	10.79	289
Transpiration	Jun.	0.6204	1.2836	0.3034	46.32	206
	Jul.	0.7814	1.3332	0.5339	44.45	258
	Aug.	0.6844	1.296	0.3525	41.18	289

The form of equation was Y_c, simu = $aY_c + b$. Mean relative error (%)=$100\times\Sigma(|Y_c, \text{simu}-Y_c|/Y_c)/n$ ($Y=A$ denotes photosynthesis and $Y=E$ denotes transpiration).

model.

The simulated ability of the model had no obvious difference in different months (shown in table 1). The slope, R^2 and mean relative error of regression line of simulated and observed canopy photosynthesis rate varied from 0.7852, 0.8935 and 9.94% to 0.8659, 0.9370 and 10.79%, respectively. For canopy transpiration rate, they are 0.6024—0.7814, 0.3034—0.5339 and 41.18%—46.32%, respectively. This resulted from the big leaf hypothesis with the same applicability in the growing season at the Changbai Mountains in 2003.

5 Conclusions

In this study, the method of the scale SMPT-SB model from individual leaves to canopy was discussed. Through simulating the canopy light distribution, canopy internal conductance to CO_2 can be scaled from single leaf to canopy by integrating to canopy using the relationship single internal conductance and photosynthetic photon flux density, and the empirical relationship proposed by Ball et al.[3] between canopy stomatal conductance and photosynthesis rate was still useful at canopy scale. Photosynthesis-transpiration coupling model was established at the scale of canopy in terrestrial ecosystem. Using the data observed by eddy covariance from the Changbai Mountains site of ChinaFLUX, the application of the models were examined and their applicability was discussed.

Under no water stress, the photosynthesis model had very high precision for simulating the canopy photosynthesis rate, and can account for 88.92% of canopy photosynthesis rate; it can be used as a basic carbon cycle model of soil-plant-atmosphere continuum. Compared to the photosynthesis model, the transpiration model can only explain 43.55% of canopy transpiration rate, mainly due to no consideration of evaporation from soil and canopy and the different ratios of canopy transpiration to total ecosystem evapotranspiration in different rain courses in the model.

This study was the primary discussion of scaling SMPT-SB model from individual leaves to canopy, and proved its applicability at special conditions, namely at the big leaf hypothesis, high leaf area index, no water stress and in the growing season, 2003 at the Changbai Mountains. But, firstly, how to expand the SMPT-SB model to the early and later periods of growing season and non-growing season, the key problem is how to simulate multi-source processes of substance fluxes in ecosystem under the "special conditions" being absent; secondly, how to better consider the factors affecting the canopy transpiration rate to improve the simulated ability of transpiration model is another problem to be solved; and thirdly, how to scale the SMPT-SB model in other regions and how to set up a series of solutions of parameterization suited for general ecosystems still deserve more study.

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