

## Effects of vertical air temperature distribution within forest canopies on photosynthesis and transpiration

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## Original Article

**Effects of vertical air temperature distribution within forest canopies on photosynthesis and transpiration \***

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**Abstract**

This study examined whether accurately simulating vertical air temperature (AT) distribution within forest canopies is essential for predicting vertical photosynthesis and transpiration distribution using multilayer canopy models. Inspecting earlier observational studies that reported vertical AT distribution within forest canopies, we showed that the common vertical AT difference within forest canopies was lower than 3.0 °C. We showed, using a leaf-scale transpiration-photosynthesis model, that a 3.0 °C AT difference caused smaller differences in leaf-scale photosynthesis and transpiration rates than a common vertical difference in photosynthetic active radiation (PAR) intensity within forest canopies when AT was higher than ca. 15 °C. While, the AT difference caused larger differences in leaf-scale photosynthetic and transpiration rates than the PAR difference when AT was lower than ca. 10 °C. However, the ranges in the rates with changing AT by 3.0 °C were comparable with predictability of a leaf-scale transpiration-photosynthesis model. Thus, we conclude that accurately simulating AT distribution is not essential at this stage for calculating vertical photosynthesis and transpiration distribution using multilayer canopy models.

**Key words:** air temperature; forest canopy; multilayer canopy models; photosynthesis; transpiration; vertical distribution

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\* 林内の気温鉛直分布が蒸散・光合成に与える影響

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## 1. Introduction

Examining forest photosynthesis and transpiration has been a major goal in forest hydrology and ecology, since transpiration and photosynthesis are major components of forest water and carbon cycles, respectively (e.g., Wilson *et al.*, 2001; Gower, 2003). Multilayer canopy models (e.g., Baldocchi and Meyers, 1998; Lai *et al.*, 2000a,b) are useful tools to examine photosynthesis and transpiration processes of forest canopies, because they divide the canopy into many layers and calculate photosynthesis and transpiration in detail at each layer. [Here, we are using the term "canopy" to indicate the whole space between the forest floor and the topmost tree layer, not the tree-crown layer.] Multilayer canopy models calculate or assume vertical distribution of meteorological factors, such as wind speed, radiation intensity, air temperature (AT), and vapor and CO<sub>2</sub> concentrations (e.g., Baldocchi and Meyers, 1998; Lai *et al.*, 2000a,b).

These meteorological factors affect photosynthesis and transpiration at each layer. Though most multilayer canopy models calculate vertical AT distribution based on diffusion theory, they often fail to simulate AT distribution (e.g., Naot and Mahrer, 1989; Baldocchi, 1992; Styles *et al.*, 2002). Furthermore, some multilayer canopy models assume vertically constant AT instead of calculating vertical AT distribution (e.g., Leuning *et al.*, 1995, 2000; Sala and Tenhunen, 1996; Williams *et al.*, 1996, 1998, 2001). Such inaccuracy in simulating AT distribution causes errors in predicting vertical photosynthesis and transpiration distribution.

This study examines whether such inaccuracy in simulating AT distribution is serious for predicting vertical distribution of photosynthesis and transpiration within forest canopies. This examination enables us to judge whether improving model predictability for AT distribution is highly required or not.

This study was comprised of two steps. First, we clarified a common intensity of the vertical maximum AT difference within forest canopies inspecting observational studies that reported AT profiles within forest canopies. Second, we examined effects of the common AT difference on vertical photosynthesis and transpiration distribution using a leaf-scale transpiration-photosynthesis model, that was incorporated in most recent multilayer canopy models. We compared these effects with those of radiation intensity differences within forest canopies which would be the primary factor producing vertical photosynthesis and transpiration distribution.

## 2. AT difference data

AT difference data were obtained from earlier publications. The vertical maximum AT difference  $T_{max} - T_{min}$  was determined for each observation data by defining a typical AT profile in daytime for each observation data. Here,  $T_{max}$  and  $T_{min}$  are

the vertical maximum and minimum ATs for the typical AT profile, respectively. When time-series of AT profiles during one day were illustrated (e.g., Ni, 1997; Ohtani, 2000), AT profiles between 10:00 and 14:00 were averaged to obtain a typical AT profile in daytime. When time-series of AT profiles during several days (e.g., Hosker *et al.*, 1974; Aoki *et al.*, 1975) were illustrated, AT profiles between 10:00 and 14:00 were averaged for each day. Then, the averaged AT profiles for each day were again averaged to obtain a typical AT profile in daytime during the measurement period.

### 3. Leaf-scale transpiration-photosynthesis model

The leaf-scale transpiration-photosynthesis model calculates  $A_l$  and  $E_l$  with inputs of meteorological factors and leaf physiological parameters, where  $A_l$  and  $E_l$  are leaf-scale photosynthetic and transpiration rates. The model is conceptually same as those developed by Collatz *et al.* (1991) and Harley *et al.* (1992). The model comprises of three components, i.e., (1) the biochemical photosynthesis model developed by Farquhar *et al.* (1980), (2) the semi-empirical relationship between stomatal conductance and  $A_l$  originally developed by Ball *et al.* (1987), and (3) CO<sub>2</sub> and H<sub>2</sub>O diffusion equations from the intercellular space of the stomata to ambient air (e.g., Campbell and Norman, 1998). The model assumes complete coupling of the leaf surface to ambient air, as done by Harley *et al.* (1992) and Harley and Baldocchi (1995).

#### 3.1 Model equations

The biochemical photosynthesis model formulates  $A_l$  as (Farquhar *et al.*, 1980)

$$A_l = \min(A_v, A_j) - R_d, \quad (1)$$

where  $A_v$  and  $A_j$  are the gross rate of photosynthesis limited by Rubisco activity and the rate of RuP<sub>2</sub> regeneration through electron transport, and  $R_d$  is the day respiration rate.  $A_v$  in Eq(1) is formulated as

$$A_v = V_{cmax} \frac{c_i - \Gamma_*}{c_i + K_c (1 + o_i/K_o)}, \quad (2)$$

where  $V_{cmax}$  is the maximum catalytic activity of Rubisco in the presence of saturating levels of RuP<sub>2</sub> and CO<sub>2</sub>,  $c_i$  is the intercellular CO<sub>2</sub> concentration,  $\Gamma_*$  is the CO<sub>2</sub> compensation point in the absence of day respiration,  $o_i$  is the intercellular oxygen concentration, and  $K_c$  and  $K_o$  are Michaelis coefficients for CO<sub>2</sub> and O<sub>2</sub>, respectively.  $A_j$  in Eq(1) is formulated as

$$A_j = \frac{J c_i - \Gamma_*}{4 c_i + 2 \Gamma_*}, \quad (3)$$

where  $J$  is the electron transport rate.  $J$  is modeled as (Baldochi and Meyers, 1998)

$$J = \frac{\alpha I}{\sqrt{1 + (\alpha I/J_{max})^2}}, \quad (4)$$

where  $\alpha$  is the quantum yield,  $J_{max}$  is the maximum rate of electron transport, and  $I$  is the incident photosynthetic active radiation (PAR).  $R_d$  in Eq(1) is formulated by Collatz *et al.* (1991) as

$$R_d = 0.015 \cdot V_{cmax}. \quad (5)$$

$V_{cmax}$ ,  $\Gamma_*$ ,  $K_c$ , and  $K_o$  depend on temperature, of which dependency is formulated following the manner described in Leuning *et al.* (1995).

The semi-empirical relationship between stomatal conductance and  $A_l$  is written by Harley *et al.* (1992) as

$$g_{sc} = \frac{m A_l r h}{c_a} + g_0, \quad (6)$$

where  $g_{sc}$  is stomatal conductance for  $\text{CO}_2$ ,  $m$  is the dimensionless slope,  $r h$  is relative humidity of ambient air, and  $c_a$  is the  $\text{CO}_2$  concentration of ambient air.

The  $\text{CO}_2$  diffusion equation from the intercellular space of the stomata to ambient air is written by

$$A_l = g_{sc} (c_a - c_i). \quad (7)$$

The  $\text{H}_2\text{O}$  diffusion equation from the intercellular space of the stomata to ambient air is written by

$$E_l = g_{sw} \{ e_{sat}(T_a) - e_a \}, \quad (8)$$

where  $E$  is the transpiration rate,  $g_{sw}$  is stomatal conductance for  $\text{H}_2\text{O}$ ,  $e_{sat}$  is the saturation vapor pressure,  $T_a$  is AT, and  $e_a$  is air vapor pressure.  $g_{sw}$  is obtained from  $g_{sc}$  using  $g_{sw} = 1.56 \cdot g_{sc}$  (Leuning *et al.*, 1995).

### 3.2 Complete coupling assumption

Besides AT, other meteorological factors such as radiation intensity and wind speed differ vertically (e.g., Aoki *et al.*, 1975; Jarvis *et al.*, 1976). These factors modify leaf temperature through leaf energy balance and therefore affect  $A_l$  and  $E_l$  when the leaf surface is not completely coupled to ambient air (e.g., Monteith and Unsworth, 1990; Campbell and Norman, 1998). When assuming complete coupling of the leaf surface to ambient air, leaf temperature equals to air temperature, resulting in no effect of radiation intensity and wind speed on  $A_l$  and  $E_l$  through leaf energy balance. Thus, the assumption enables us to purely evaluate the AT effect on  $A_l$  and  $E_l$ .

Earlier studies have reported well-coupling at leaf- and canopy-scale on many broad-leaved forests (e.g., Kostner *et al.*, 1992; Herbst, 1995; Granier and Breda, 1996; Granier *et al.*, 1996, 2000) and almost all coniferous forests (e.g., Jarvis and McNaughton, 1986; Martin *et al.*, 1999, 2001; Komatsu, 2003; Komatsu *et al.*, 2006a). However, several studies (Meinzer *et al.*, 1993, 1995, 1997) have reported decoupling of the leaf surface to ambient air on broad-leaved trees with large leaf size under low wind speed conditions. The complete coupling assumption and therefore our conclusions can be invalid under these conditions, although these conditions would not be so common.

## 4. Results and discussion

### 4.1 AT difference intensity

Table 1 shows  $T_{max} - T_{min}$  data summarized from earlier papers. Total sample size was thirty-eight. Eleven samples were from tropical broad-leaved forests. Six and sixteen samples were from temperate broad-leaved and coniferous forests, respectively. One sample and four samples were from a boreal broad-leaved forest and boreal coniferous forests, respectively.

Figure 1 shows a relative frequency of the summarized data classified according to  $T_{max} - T_{min}$  values.  $T_{max} - T_{min}$  ranged between 0.3 °C and 6 °C. The mean and median of  $T_{max} - T_{min}$  were 2.0 °C and 1.8 °C, respectively. 89% data samples satisfied  $T_{max} - T_{min} \leq 3.0^\circ\text{C}$ , while 11% data samples satisfied  $T_{max} - T_{min} > 3.0^\circ\text{C}$ . Thus,  $T_{max} - T_{min}$  was commonly  $\leq 3.0^\circ\text{C}$ .

AT profiles are measured by thermometers that are vertically located at several observation points (e.g., Cabral *et al.*, 1996; Kumagai *et al.*, 2001). Thus, smaller number of observation point can underestimate  $T_{max} - T_{min}$  because of coarse resolution of measurements. When using data with number of observation point  $\leq 5$ ,  $T_{max} - T_{min}$  ranged between 0.6 °C and 5.2 °C ( $n = 22$ ). The mean and median of  $T_{max} - T_{min}$  were 2.1 °C and 1.8 °C, respectively. 86% data samples satisfied  $T_{max} - T_{min} \leq 3.0^\circ\text{C}$ , which 14% data samples satisfied  $T_{max} - T_{min} > 3.0^\circ\text{C}$ . These

Table 1.  $T_{max} - T_{min}$  values summarized from published reports.  $Z_{T_{max}}/H$  and  $Z_{T_{min}}/H$  values are shown, where  $Z_{T_{max}}$  and  $Z_{T_{min}}$  are the heights at which  $T_{max}$  and  $T_{min}$  were recorded and  $H$  represents canopy height.  $Z_{T_{max}}/H$  and  $Z_{T_{min}}/H$  values are defined only when  $T_{max} - T_{min} > 1.0$  °C. Defining these values is not meaningful when  $T_{max} - T_{min}$  values are small.

H (m)	projected LAI	$T_{max}-T_{min}$ (°C)	$Z_{T_{max}}/H$	$Z_{T_{min}}/H$	number of observation point	References
Tropical	broad-leaved					
47	8	5.2	1.00	0.00	6	Aoki <i>et al.</i> (1975)
41	?	1.1	0.80	0.05	5	Baynton <i>et al.</i> (1965)
30	6.0	3.2	1.00	0.07	7	Bouka Biona textit <i>et al.</i> (2001)
35	5.7*1	2.3	0.71	0.14	4	Cabralttextit <i>et al.</i> (1996)
30*2	3.5~4.5*2	0.6	-	-	3	Komatsu <i>et al.</i> (unpublished data)
50	5.1	1.3	0.99	0.10	10	Kumagai <i>et al.</i> (2001)
25	?	1.8	0.85	0.02	5	Loesher <i>et al.</i> (2005)
35	?	2.6	0.87	0.04	4	Shuttleworth <i>et al.</i> (1985)
25	?	2.3	0.84	0.20	3	Szarzynski and Anhof (2001)
40	6.5*3	0.9	-	-	3	Tani (1996)
35	?	1.7	0.86	0.01	12	Thompson and Pinker (1975)
Temperate	broad-leaved					
12	?	2.2	0.83	0.01	6	Chroust (1968) cited in Groβ (1993)
18	?	0.9	-	-	4	Droppo <i>et al.</i> (1973)
25	5~6	2.9	0.88	0.04	4	Elias <i>et al.</i> (1989)
20	3.4	2.6	0.05	1.00	4	Ni (1997)
15	5	0.8	-	-	5	Ohtani (2000)
20	7.1	2.4	1.00	0.02	6	Yabuki <i>et al.</i> (1978)
Temperate	coniferous					
5	?	6	1.00	0.00	?	Baumgartner (1956) cited in Groβ (1993)
24	2.7	0.4	-	-	4	Berbigier <i>et al.</i> (1996)
21	?	1.8	1.00	0.14	5	Daigo (1977)
7.5	?	0.5	-	-	4	Denmead (1969)
20	?	0.8	-	-	7	Denmead and Bradley (1987)
8.5	1.8	1	-	-	9	Ewers and Oren (2000)
8.5	1.9	1	-	-	9	Ewers and Oren (2000)
8.5	3.3	3	0.01	0.71	9	Ewers and Oren (2000)
8.5	3.6	3	0.01	0.71	9	Ewers and Oren (2000)
17	?	1.2	0.18	0.94	6	Green <i>et al.</i> (1984)
12.5	?*4	2.5	0.84	0.01	9	Hayashi <i>et al.</i> (1989)
17	3.3*5	5	0.84	0.07	7	Hosker <i>et al.</i> (1974)
10.5	?	2.3	1.00	0.00	?	Jarvis <i>et al.</i> (1976)
18	3.0*6	0.3	-	-	3	Monji <i>et al.</i> (1994)
10	?	3	0.95	0.02	4	Suzuki and Fukushima (1976)
8*7	3.7*7	0.6	-	-	3	Yoshifuji <i>et al.</i> (unpublished data)
Boreal	broad-leaved					
21.5	2.3*8	2.3	0.09	0.74	7	Gu <i>et al.</i> (1999)
Boreal	coniferous					
12	10	0.6	-	-	5	Amiro (1990)
30	7.6	0.6	-	-	3	Constantin <i>et al.</i> (1998)
20	2.5	1.1	0.10	1.00	10	Halldin and Lindroth (1986)
23	4.3	2.7	0.44	0.02	5	Styles <i>et al.</i> (2002)

\*1 McWilliam *et al.* (1993); Roberts *et al.* (1996)

\*2 Takizawa *et al.* (2001); Komatsu *et al.* (2003, 2005)

\*3 Tani *et al.* (2003)

\*4 Although an LAI value is present, no definition of the LAI is given.

\*5 Estimated by the authors of this paper by dividing the total surface area index by 2.4, which is an intermediate value for conifers (Landsberg and Gower, 1997).

\*6 Tanaka *et al.* (1996)

\*7 Komatsu *et al.* (2006a,b)

\*8 Blanken *et al.* (1997)

results were qualitatively same as those based on all data samples.

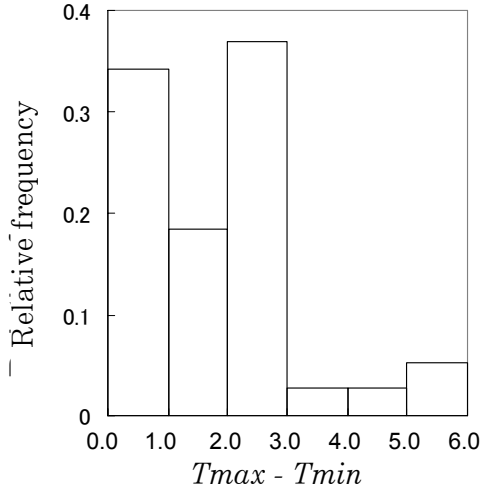


Fig. 1. Relative frequency distribution of summarized data classified according to  $T_{max} - T_{min}$ . Data at the boundary of two succeeding classes were categorized into the class with lower AT. For example, the data from Hosker *et al.* (1974) ( $T_{max} - T_{min} = 5$  °C) were categorized into the class between 4 °C and 5 °C.

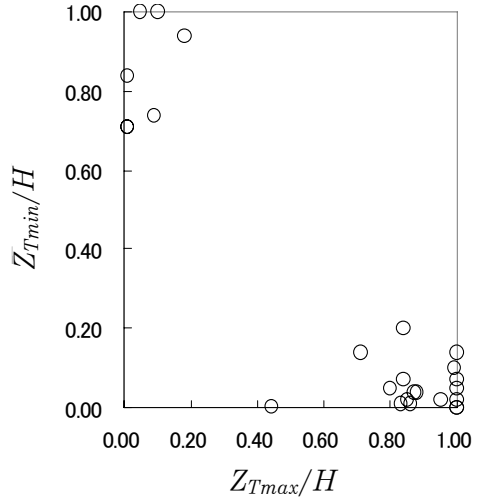


Fig. 2. The relationship between  $Z_{T_{max}}/H$  and  $Z_{T_{min}}/H$ , where  $Z_{T_{max}}$  is height of  $T_{max}$  appearance,  $H$  is canopy height, and  $Z_{T_{min}}$  is height of  $T_{min}$  appearance. Note that two samples from Ewers and Oren (2000) overlap each other.

Figure 2 shows the relationship between  $Z_{T_{max}}/H$  and  $Z_{T_{min}}/H$ , where  $Z_{T_{max}}$  is height of  $T_{max}$  appearance,  $H$  is canopy height, and  $Z_{T_{min}}$  is height of  $T_{min}$  appearance.  $Z_{T_{max}}$  data satisfied  $Z_{T_{max}}/H = 0.71 \sim 1.00$  or  $Z_{T_{max}}/H = 0.01 \sim 0.18$  except for data from Styles *et al.* (2002). When  $Z_{T_{max}}/H = 0.71 \sim 1.00$ ,  $Z_{T_{min}}/H = 0.00 \sim 0.33$ . When  $Z_{T_{max}}/H = 0.01 \sim 0.18$ ,  $Z_{T_{min}}/H = 0.71 \sim 1.00$ . Thus,  $T_{max}$  appeared in the upper canopy or in the lower canopy. When  $T_{max}$  appeared in the upper canopy,  $T_{min}$  appeared in the lower canopy. When  $T_{max}$  appeared in the lower canopy,  $T_{min}$  appeared in the upper canopy.

We found no clear relationships between  $T_{max} - T_{min} > 3.0$ °C appearance (e.g., Hosker *et al.*, 1974; Bouka Biona *et al.*, 2001) and forest properties, such as leaf area index (LAI), leaf type (broad-leaved/coniferous), and canopy height.  $T_{max} - T_{min} > 3.0$ °C appeared both for high-LAI forests (Aoki *et al.*, 1975; Bouka Biona *et al.*, 2001) and a not so high-LAI forest (Hosker *et al.*, 1974). AT data from high-LAI forests did not always show high  $T_{max} - T_{min}$  values (e.g., Tani, 1996; Constantin *et al.*, 1998).  $T_{max} - T_{min} > 3.0$ °C appeared both for broad-leaved (Aoki *et al.*, 1975; Bouka Biona *et al.*, 2001) and coniferous forests (Baumgartner, 1956 cited in Groβ, 1993;



Hosker *et al.*, 1974).  $T_{max} - T_{min} > 3.0^{\circ}\text{C}$  appeared both for tall forests (Aoki *et al.*, 1975; Bouka Biona *et al.*, 2001) and a short forest (Baumgartner, 1956 cited in Gro  $\beta$ , 1993).

We found clear relationships between LAI and  $Z_{T_{max}}/H$  and between LAI and  $Z_{T_{min}}/H$ . Figures 3a and 3b show the relationships between LAI and  $Z_{T_{max}}/H$  and between

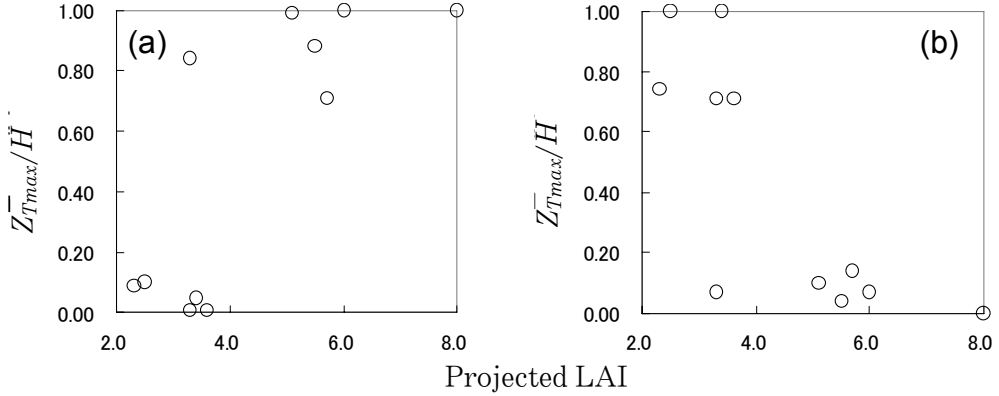


Fig. 3. Relationships between projected LAI and  $Z_{T_{max}}/H$  and between projected LAI and  $Z_{T_{min}}/H$ , where  $Z_{T_{max}}$  is height at which  $T_{max}$  was recorded,  $H$  is the canopy height, and  $Z_{T_{min}}$  is the height at which  $T_{min}$  was recorded.

LAI and  $Z_{T_{min}}/H$ . When projected LAI  $\leq 4.0$ ,  $Z_{T_{max}}/H = 0.01 \sim 0.18$  and  $Z_{T_{min}}/H = 0.71 \sim 1.00$  with only one exception. When projected LAI  $> 4.0$ ,  $Z_{T_{max}}/H = 0.71 \sim 1.00$  and  $Z_{T_{min}}/H = 0.00 \sim 0.33$ . Thus,  $Z_{T_{max}}/H$  tended to be low and  $Z_{T_{min}}/H$  tended to be high when LAI was low, whereas  $Z_{T_{max}}/H$  tended to be high and  $Z_{T_{min}}/H$  tended to be low when LAI was high. According to the Lagrangian dispersion theory (Raupach, 1987, 1989a, b), an AT profile is maximized in the lower canopy and minimized in the upper canopy when an intensive heat source in the upper canopy is absent. The maximum AT in the lower canopy is produced by less active heat diffusion there. While, an AT profile is maximized in the upper canopy and minimized in the lower canopy when an intensive heat source in the upper canopy is present. The maximum AT in the upper canopy is produced by the near-field heat diffusion from the intensive heat source. Greater LAI values indicate more intensive radiation absorption and heat source in the upper canopy, resulting in appearance of the maximum AT there (Fig. 3a).

#### 4.2 Effects on photosynthesis and transpiration

Incident PAR in clear midday of a growing season usually differs by ca.  $1000 \mu \text{mol m}^{-2} \text{s}^{-1}$  between upper and lower canopies. Elias *et al.* (1989) observed incident PAR above and within a forest with projected LAI = 5  $\sim$  6. Incident PAR in clear midday of a growing season is ca.  $1200 \mu \text{mol m}^{-2} \text{s}^{-1}$  above the canopy, and ca.  $50 \mu$

mol m<sup>2</sup> s<sup>-1</sup> near the forest floor. Chen *et al.* (1997) observed incident PAR above and within a forest with projected LAI = 2.3. Incident PAR in clear midday of a growing season is ca. 1500  $\mu$  mol m<sup>2</sup> s<sup>-1</sup> above the canopy, and ca. 300  $\mu$  mol m<sup>2</sup> s<sup>-1</sup> near the ground above the understory vegetation.

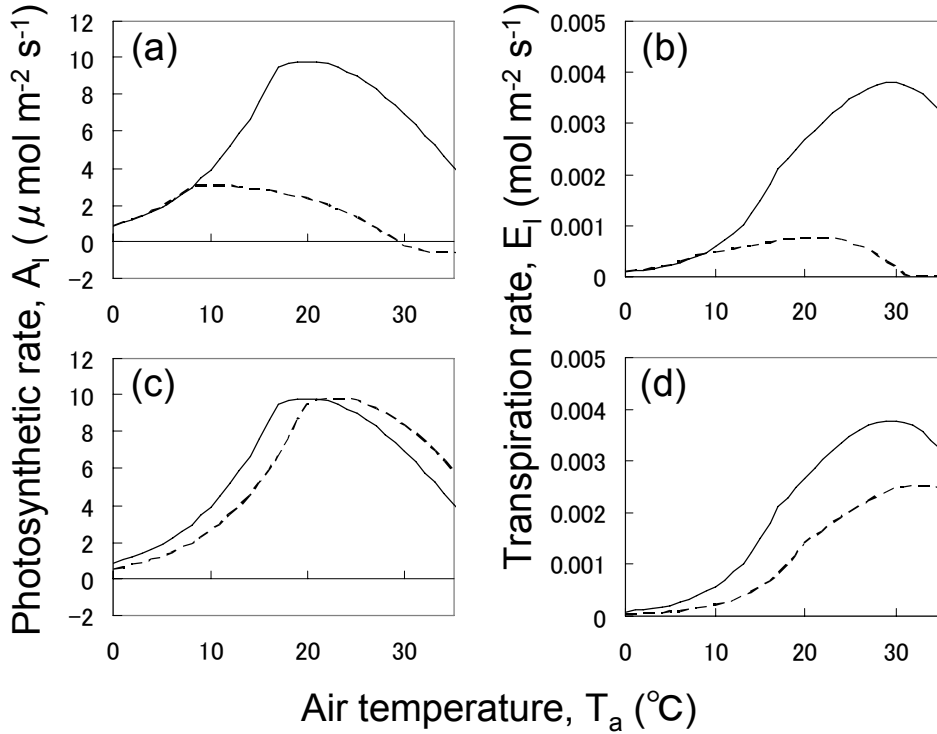


Fig. 4 (a)  $A_l$  and (b)  $E_l$  calculated by the model assuming  $I = 1200 \mu \text{ mol m}^{-2} \text{ s}^{-1}$  (solid lines) and  $I = 300 \mu \text{ mol m}^{-2} \text{ s}^{-1}$  (dotted lines). (c)  $A_l$  and (d)  $E_l$  calculated by the model assuming default AT (solid lines) and AT lower than the default AT by 3.0 °C (dotted lines). Physiological parameters are given as  $V_{\text{cmax}} = 47 \text{ mol m}^{-2} \text{ s}^{-1}$  at  $T_a = 20 \text{ °C}$  (Wullschleger, 1993),  $J_{\text{max}} = 126 \text{ mol m}^{-2} \text{ s}^{-1}$  at  $T_a = 20 \text{ °C}$  (Leuning, 1997),  $\alpha = 0.055$ ,  $m = 9.5$ , and  $g_0 = 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$  (Baldocchi and Meyers, 1998). Meteorological factors are given as relative humidity = 60% and  $c_a = 360 \mu \text{ mol mol}^{-1}$ . Results here were not qualitatively altered assuming physiological parameters that are typical for coniferous trees:  $V_{\text{cmax}} = 25 \text{ mol m}^{-2} \text{ s}^{-1}$  at  $T_a = 20 \text{ °C}$  (Wullschleger, 1993),  $J_{\text{max}} = 67 \text{ mol m}^{-2} \text{ s}^{-1}$  at  $T_a = 20 \text{ °C}$  (Leuning, 1997),  $\alpha = 0.055$ ,  $m = 7.5$ , and  $g_0 = 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$  (Baldocchi and Meyers, 1998). Similarly, the results were not qualitatively altered assuming another relative humidity condition (relative humidity = 40%) and other CO<sub>2</sub> concentration conditions ( $c_a = 300 \mu \text{ mol mol}^{-1}$  and  $c_a = 400 \mu \text{ mol mol}^{-1}$ ).

Figures 4a and 4b show  $A_l$  and  $E_l$  calculated by the model assuming two contrastive PAR conditions ( $I = 1200 \mu \text{ mol m}^{-2} \text{ s}^{-1}$  and  $I = 300 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ ). Figures 4c and 4d show  $A_l$  and  $E_l$  calculated by the model assuming two different AT conditions. These calculations assumed physiological parameters that were typical

for broad-leaved trees and meteorological conditions that were typical for clear midday (see caption of Fig. 4). Note that our conclusions hold when assuming physiological parameters that were typical for coniferous trees and other meteorological conditions (see caption of Fig. 4). Decrease in PAR always causes decrease in  $A_l$  and  $E_l$ . Decrease in AT causes increase in relative humidity, which causes increase in  $g_{sc}$  and  $g_{sw}$ , and therefore it does not always cause decrease in  $A_l$  and  $E_l$ .

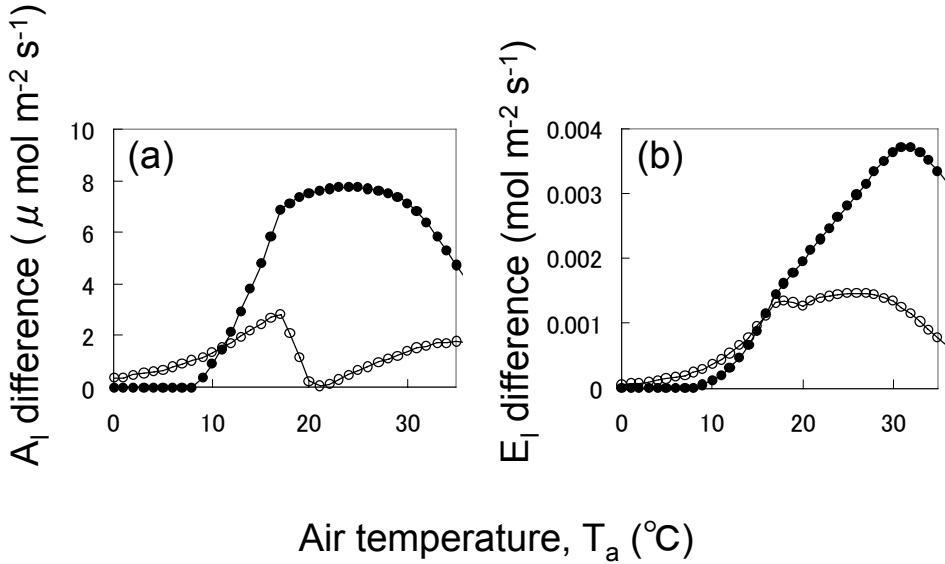


Fig. 5 (a)  $A_l$  and (b)  $E_l$  differences between the two different PAR conditions (closed circles) and between the two different AT conditions (open circles).

Figure 5 shows differences in  $A_l$  (Fig. 5a) and  $E_l$  (Fig. 5b) caused by the PAR difference and by the AT difference. Both  $A_l$  and  $E_l$  differences caused by the AT difference were less significant than those caused by the PAR difference when  $AT \geq$  ca.  $15\text{ }^\circ\text{C}$ . Both  $A_l$  and  $E_l$  differences caused by the AT difference were more significant than those caused by the PAR difference when  $AT \leq$  ca.  $10\text{ }^\circ\text{C}$ .

Our results suggest that vertical  $A_l$  and  $E_l$  distribution is less sensitive to AT distribution than PAR distribution when  $AT \geq$  ca.  $15\text{ }^\circ\text{C}$ . This suggestion does not contradict with earlier studies. Earlier studies have succeeded in simulating whole-canopy photosynthesis and transpiration in growing seasons using multilayer canopy models (e.g., Williams *et al.*, 1996, 1998, 2001; Baldocchi and Meyers, 1998; Ogee *et al.*, 2003), though those models often fail to simulate AT distribution.

While, our results suggest that vertical  $A_l$  and  $E_l$  distribution is more sensitive to AT distribution than PAR distribution when  $AT \leq$  ca.  $10\text{ }^\circ\text{C}$ . However,  $A_l$  and  $E_l$  differences caused by a  $3.0\text{ }^\circ\text{C}$  AT difference (Figs. 5a and 5b) are comparable to predictability for  $A_l$  and  $E_l$  by a leaf-scale transpiration-photosynthesis model. The

model often causes  $> 2.0 \mu \text{ mol m}^{-2} \text{ s}^{-1}$  errors in  $A_l$  estimates and  $> 0.001 \text{ mol m}^{-2} \text{ s}^{-1}$  errors in  $E_l$  estimates (e.g., Fig. 5 of Harley and Baldocchi, 1995; Fig. 4 of Dang *et al.*, 1997). Thus, improvement in AT distribution predictability will not enable much more precise prediction of  $A_l$  and  $E_l$  distribution due to the predictability of a leaf-scale transpiration-photosynthesis model.

## 5 Conclusions

Inspecting earlier observational studies that reported vertical AT distribution within forest canopies, we showed that the common vertical AT difference within forest canopies was smaller than  $3.0 \text{ }^\circ\text{C}$ . We showed, using a leaf-scale transpiration-photosynthesis model, that a  $3.0 \text{ }^\circ\text{C}$  AT difference caused smaller differences in leaf-scale photosynthetic and transpiration rates than a common vertical difference in PAR intensity within forest canopies when AT was higher than ca.  $15 \text{ }^\circ\text{C}$ . While, the AT difference caused larger differences in leaf-scale photosynthetic and transpiration rates than the PAR difference when AT was lower than ca.  $10 \text{ }^\circ\text{C}$ . However, the ranges in the rates with changing AT by  $3.0 \text{ }^\circ\text{C}$  were comparable with predictability for leaf-scale photosynthetic and transpiration rates by the model. Thus, we conclude that accurately simulating AT distribution is not essential at this stage for predicting vertical photosynthesis and transpiration distribution using multilayer canopy models.

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## 林内の気温鉛直分布が蒸散・光合成に与える影響

小松 光・熊谷朝臣・堀田紀文

### 要 旨

本研究では、林内気温鉛直分布を正確に再現することが、林内光合成・蒸散鉛直分布を多層モデルで推定するのに不可欠かどうかを調べた。筆者らは既存文献を踏査して、林内で計測される鉛直方向の気温差が通常 $3.0^{\circ}\text{C}$ 以下であることを示した。つづいて、単葉スケールの蒸散・光合成モデルによる計算によってつぎのことを示した。気温が約 $15^{\circ}\text{C}$ 以上のとき、 $3.0^{\circ}\text{C}$ の気温の差が引き起こす光合成・蒸散量の違いは、林内で通常計測される光合成有効放射量の鉛直方向の差が引き起こす光合成・蒸散量の違いよりも小さい。一方、気温が約 $10^{\circ}\text{C}$ 以下のとき、 $3.0^{\circ}\text{C}$ の気温の差が引き起こす光合成・蒸散量の違いは、林内で通常計測される光合成有効放射量の鉛直方向の差が引き起こす光合成・蒸散量の違いよりも大きい。 $3.0^{\circ}\text{C}$ の気温の差が引き起こす光合成・蒸散量の違いは、単葉スケールの蒸散・光合成モデルの予測精度と同程度である。したがって、現時点において、林内気温鉛直分布を正確に再現することは、林内光合成・蒸散鉛直分布を多層モデルで推定するのに不可欠ではないと結論した。

キーワード：気温；樹冠；多層モデル；光合成；蒸散；鉛直分布

