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

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

Hikaru Komatsu**, Tomo’omi Kimagai **, Norifumi Hotta ***

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

* 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 CO₂ 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$_2$ and H$_2$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)

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

where $A_v$ and $A_j$ are the gross rate of photosynthesis limited by Rubisco activity and the rate of RuP$_2$ regeneration through electron transport, and $R_d$ is the day respiration rate. $A_v$ in Eq(1) is formulated as

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

where $V_{cmax}$ is the maximum catalytic activity of Rubisco in the presence of saturating levels of RuP$_2$ and CO$_2$, $c_i$ is the intercellular CO$_2$ concentration, $\Gamma_*$ is the CO$_2$ 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$_2$ and O$_2$, respectively. $A_j$ in Eq(1) is formulated as
where $J$ is the electron transport rate. $J$ is modeled as (Baldocchi and Meyers, 1998)

$$J = \frac{\alpha I}{1 + \left(\frac{\alpha I}{J_{\text{max}}}\right)^2},$$  \hspace{1cm} (4)

where $\alpha$ is the quantum yield, $J_{\text{max}}$ 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

$$R_d = 0.015 \cdot V_{\text{cmax}}.$$  \hspace{1cm} (5)

$V_{\text{cmax}}$, $\Gamma_*$, $K_c$, 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

$$g_{sc} = \frac{m A_l rh}{c_a} + g_0,$$  \hspace{1cm} (6)

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

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

$$A_l = g_{sc} (c_a - c_i).$$  \hspace{1cm} (7)

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

$$E_l = g_{sw} \{ e_{\text{sat}} (T_a) - e_a \},$$  \hspace{1cm} (8)

where $E$ is the transpiration rate, $g_{sw}$ is stomatal conductance for H$_2$O, $e_{\text{sat}}$ 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 $T_{\text{max}} - T_{\text{min}}$ 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 $T_{\text{max}} - T_{\text{min}}$ values. $T_{\text{max}} - T_{\text{min}}$ ranged between 0.3 $^\circ$C and 6 $^\circ$C. The mean and median of $T_{\text{max}} - T_{\text{min}}$ were 2.0 $^\circ$C and 1.8 $^\circ$C, respectively. 89% data samples satisfied $T_{\text{max}} - T_{\text{min}} \leq 3.0^\circ$C, while 11% data samples satisfied $T_{\text{max}} - T_{\text{min}} > 3.0^\circ$C. Thus, $T_{\text{max}} - T_{\text{min}}$ was commonly $\leq 3.0^\circ$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 $T_{\text{max}} - T_{\text{min}}$ because of coarse resolution of measurements. When using data with number of observation point $\leq 5$, $T_{\text{max}} - T_{\text{min}}$ ranged between 0.6 $^\circ$C and 5.2 $^\circ$C ($n = 22$). The mean and median of $T_{\text{max}} - T_{\text{min}}$ were 2.1 $^\circ$C and 1.8 $^\circ$C, respectively. 86% data samples satisfied $T_{\text{max}} - T_{\text{min}} \leq 3.0^\circ$C, which 14% data samples satisfied $T_{\text{max}} - T_{\text{min}} > 3.0^\circ$C. These
Table 1. Tmax - Tmin values summarized from published reports. ZTmax/H and ZTmin/H values are shown, where ZTmax and ZTmin are the heights at which Tmax and Tmin were recorded and H represents canopy height. ZTmax/H and ZTmin/H values are defined only when Tmax - Tmin > 1.0 °C. Defining these values is not meaningful when Tmax - Tmin values are small.

<table>
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<th>H (m)</th>
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<th>ZTmin/H</th>
<th>number of observation point</th>
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*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 \(T_{\text{max}} - T_{\text{min}}\). 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) \((T_{\text{max}} - T_{\text{min}} = 5 \, ^\circ\text{C})\) were categorized into the class between 4 \(^\circ\text{C}\) and 5 \(^\circ\text{C}\).

Figure 2 shows the relationship between \(Z_{\text{Tmax}}/H\) and \(Z_{\text{Tmin}}/H\), where \(Z_{\text{Tmax}}\) is height of \(T_{\text{max}}\) appearance, \(H\) is canopy height, and \(Z_{\text{Tmin}}\) is height of \(T_{\text{min}}\) appearance. Note that two samples from Ewers and Oren (2000) overlap each other.

We found no clear relationships between \(T_{\text{max}} - T_{\text{min}} > 3.0\, ^\circ\text{C}\) 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. \(T_{\text{max}} - T_{\text{min}} > 3.0\, ^\circ\text{C}\) 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 \(T_{\text{max}} - T_{\text{min}}\) values (e.g., Tani, 1996; Constantin et al., 1998). \(T_{\text{max}} - T_{\text{min}} > 3.0\, ^\circ\text{C}\) 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). $T_{\text{max}} - T_{\text{min}} > 3.0^\circ\text{C}$ appeared both for tall forests (Aoki et al., 1975; Bouka Biona et al., 2001) and a short forest (Baumgartner, 1956 cited in Groβ, 1993).

We found clear relationships between LAI and $Z_{T_{\text{max}}}/H$ and between LAI and $Z_{T_{\text{min}}}/H$. Figures 3a and 3b show the relationships between LAI and $Z_{T_{\text{max}}}/H$ and between LAI and $Z_{T_{\text{min}}}/H$. Figures 3a and 3b show the relationships between LAI and $Z_{T_{\text{max}}}/H$ and between LAI and $Z_{T_{\text{min}}}/H$. When projected LAI $\leq 4.0$, $Z_{T_{\text{max}}}/H = 0.01 \sim 0.18$ and $Z_{T_{\text{min}}}/H = 0.71 \sim 1.00$ with only one exception. When projected LAI $> 4.0$, $Z_{T_{\text{max}}}/H = 0.71 \sim 1.00$ and $Z_{T_{\text{min}}}/H = 0.00 \sim 0.33$. Thus, $Z_{T_{\text{max}}}/H$ tended to be low and $Z_{T_{\text{min}}}/H$ tended to be high when LAI was low, whereas $Z_{T_{\text{max}}}/H$ tended to be high and $Z_{T_{\text{min}}}/H$ 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 $\mu$ mol m$^{-2}$ 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 $\mu$ mol m$^{-2}$ s$^{-1}$ above the canopy, and ca. 50 $\mu$
mol m$^{-2}$ s$^{-1}$ 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 μmol m$^{-2}$ s$^{-1}$ above the canopy, and ca. 300 μmol m$^{-2}$ s$^{-1}$ near the ground above the understory vegetation.

Figures 4a and 4b show $A_l$ and $E_l$ calculated by the model assuming two contrastive PAR conditions ($I = 1200$ μmol m$^{-2}$ s$^{-1}$ and $I = 300$ μmol m$^{-2}$ 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 coniferous trees: $V_{c\text{max}} = 25$ mol m$^{-2}$ s$^{-1}$ at $T_a = 20^\circ$C (Wullschleger, 1993), $J_{\text{max}} = 67$ mol m$^{-2}$ s$^{-1}$ at $T_a = 20^\circ$C (Leuning, 1997), $\alpha = 0.055$, $m = 7.5$, and $g_0 = 0.01$ mol m$^{-2}$ s$^{-1}$ (Baldocchi and Meyers, 1998). Similarly, the results were not qualitatively altered assuming another relative humidity condition (relative humidity = 40%) and other CO$_2$ concentration conditions ($c_a = 300$ μmol mol$^{-1}$ and $c_a = 400$ μmol mol$^{-1}$).
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 $g_{sv}$, and therefore it does not always cause decrease in $A_l$ and $E_l$.

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 °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 °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 °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 °C. However, $A_l$ and $E_l$ differences caused by a 3.0 °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 $> 2.0 \mu$ mol m$^{-2}$ s$^{-1}$ errors in $A_l$ estimates and $> 0.001$ mol m$^{-2}$ 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 °C. We showed, using a leaf-scale transpiration-photosynthesis model, that a 3.0 °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 °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 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

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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℃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℃以上のとき、3.0℃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℃以下のとき、3.0℃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が3.0℃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