Parameterization of *Zelkova serrata* stomatal conductance model to estimate stomatal ozone uptake in Japan

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A B S T R A C T

To parameterize stomatal conductance or ozone uptake modeling in the Eastern Asian tree species *Zelkova serrata*, measurements of stomatal conductance were carried out in several Japanese sites across the growing season. The new parameterization improved the stomatal conductance model performance relative to a previously proposed model. The results were used to compare the spatial distribution of AOT40 and Z. *serrata* stomatal ozone uptake in Japan. Including a soil moisture function improved the model in the short periods with low precipitation. In addition, elevated vapor pressure deficit and soil moisture deficit due to high temperature, and high ozone exposure induced stomatal closure. The consequent decoupling of stomatal ozone uptake from high ozone exposure suggests caution in using AOT40 as a standard for *Z. serrata* protection in Japan.

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1. Introduction

Tropospheric ozone (O₃) is an important phytotoxic air pollutant and is also recognized as a significant greenhouse gas (Bytnierowicz et al., 2007; Serengil et al., 2011). Surface O₃ concentrations are increasing in East Asia because of rapid increases in emission of the main O₃ precursors, Nitrogen oxides and volatile organic compounds (Naja and Akimoto, 2004). Ohara and Sakata (2003) reported that annual average concentrations of photochemical oxidant, mainly O₃, increased at high rate (0.33 ppb year⁻¹) from 1985 to 1999 in Japan.

Phytotoxic nature of O₃ has been well known for decades (e.g., NIES, 1980, 1984; Omasa et al., 2002; Paoletti, 2007). The concentration based approach for O₃ effects on plants (e.g., AOT40: accumulated exposure over a threshold of 40 ppb) has the advantage of being simple and needs only atmospheric O₃ concentrations, i.e., external O₃ exposure, without considering internal O₃ uptake in a leaf. In Japan, Kohno et al. (2005) recommended 8–15 ppm h AOT40 from April to September for sensitive forest species as a critical level, i.e., able to induce a 10% growth reduction. In Europe, the critical level is 5 ppm h AOT40 for forests (Mills et al., 2010) or 9 ppm h AOT40 for any kind of vegetation (European Commission, 2008). However, several studies suggest that AOT40 is not adequate for O₃ risk assessment to plants (Kobayashi, 1999; Matyssek and Innes, 1999; Matyssek et al., 2007). Stomatal O₃ uptake or flux is more closely related to O₃ impacts (Omasa et al., 2002; Paoletti and Manning, 2007; Karlsson et al., 2007). In Europe, critical levels for O₃ risk based on stomatal O₃ uptake have been suggested for potato, tomato, wheat and several tree species (Mills et al., 2010).

Although the stomatal flux-based approach is expected to provide a better assessment of O₃ impacts to plants in East Asia (Watanabe and Yamaguchi, 2011), AOT40 has been recommended for assessments of O₃ impacts in Japan (e.g., Kohno et al., 2005). This is because much precipitation and limited water stress in Japan might be favorable climate for stomatal opening, i.e., not limiting stomatal O₃ uptake. In Japan, however, maximum hourly air temperature exceeding 35 °C often occurred in summer since the 90s (JMA, 2002), which thus may induce high vapor pressure deficit (VPD) and enhance evapotranspiration resulting in soil moisture deficit. Enhanced VPD and soil moisture deficit may limit stomatal O₃ uptake.

Ozone is also known to directly induce stomatal closure as a result of the inhibition of photosynthesis (Wittig et al., 2007). Therefore, stomatal O₃ uptake may be limited under current climate conditions and air quality in East Asia.

Japanese zelkova (*Zelkova serrata*) is one of the typical deciduous broadleaved tree species in Japan, Korea, eastern China, and Taiwan. It is often grown as an ornamental tree in warm temperate climates.
This species is known as a highly O₃-sensitive species (Kohno et al., 2005). A short-term (2-day) previous investigation provided model parameters of stomatal conductance for Z. serrata in western Japan (Kadaira and Yoshida, 2006), but the results were not validated by comparison with data measured over a seasonal course. The model developed in that study is here referred to as “literature-based stomatal conductance model”.

Our main objective was to develop a parameterization of the stomatal conductance model for Z. serrata, and to use it for O₃ uptake modeling in Japan. The re-parameterized model was applied to measured data throughout the growing season and compared with the literature-based model. Because no measured data of soil water content were obtained, the model function of soil water content was tested by using model estimates. Results from the literature-based model and the re-parameterized model were used to map stomatal O₃ uptake, compared with AOT40 maps, and used to discuss whether current climate and O₃ pollution may limit stomatal O₃ uptake in East Asia.

2. Materials and methods

2.1. Estimation of AOT40 and stomatal ozone uptake

AOT40 was estimated by using hourly mean O₃ concentrations during daylight hours from April to September in 2007 (Kohno et al., 2005; Mills et al., 2010), i.e., the growing season of Z. serrata in Japan:

\[ \text{AOT40} = \sum \max (40 - [O₃], 0) \quad \text{if global radiation} > 50 \text{ W m}^{-2} \] (1)

where [O₃] is hourly mean O₃ concentration (ppb).

Stomatal O₃ uptake \((F_{st}; \text{mmol O₃ m}^{-2} \text{s}^{-1})\) was calculated as:

\[ F_{st} = \frac{[O₃]}{[O₃]; \{1/(r_b + r_c)\}; \{\{g_{sw} \times 1.65\}/g_{sw} \times 1.65 + g_{ext}\}} \] (2)

where \(r_b\) is the leaf boundary layer resistance \(\text{mol}^{-1} \text{ m}^2 \text{ s}^{-1}\), \(r_c\) is the leaf surface resistance \(\text{mol}^{-1} \text{ m}^2 \text{ s}^{-1}\), \(g_{sw}\) is the stomatal conductance for water vapor \(\text{mmol H₂O m}^{-2} \text{ s}^{-1}\), and \(g_{ext}\) is the external leaf conductance \(\text{mol}^{-1} \text{ m}^2 \text{ s}^{-1}\). The former accounts for diffusivity of water in air compared with O₃, while the latter accounts for diffusivity of O₃ in air.

Leaf boundary layer resistance \((r_b)\) was calculated from the wind speed, \(u\) \((\text{m} \text{ s}^{-1})\), and the mean leaf length, \(L\) \((0.06 \text{ m})\) for Z. serrata obtained from Hosoi and Omasa, 2007 (Mills et al., 2010):

\[ r_b = 1.3 \times 1500 \times (L/d)^{0.5} \] (3)

where the factor 1.3 accounts for differences in diffusivity between heat and O₃.

In Europe, phytotoxic O₃ dose above a flux threshold of \(Y\) \((\text{POD})\) was recommended to assess O₃ risk for forest species (Mills et al., 2010). It is given by:

\[ \text{POD}_Y = \sum \max (F_{st} - Y, 0) \] (4)

where \(Y\) is a species-specific threshold of stomatal O₃ uptake \(\text{mmol m}^{-2} \text{ s}^{-1}\). As it was not clear which threshold \(Y\) can be applied for this species in Japan, we did not set a threshold for the \(F_{st}\) value \((\text{POD})\) in the present study.

Climate (air temperature, precipitation, air humidity, solar radiation and wind speed) and O₃ concentration data for the year 2007 (Takigawa et al., 2007) were input into our model. The values of the main climate parameters are shown in Table 1. These data were provided by the regional air quality forecasting system (Takigawa et al., 2007). This system consists of global and regional chemistry transport model (CTM). The regional CTM is based on the WRF/Chem model (Grell et al., 2005) provided at 1-h temporal resolution and 15 × 15 km spatial resolution in East Asia (25°–45° N, 120°–150° E). Boundary condition in the regional CTM was provided by the global CTM based on CHASER (Sudo et al., 2002). The model successfully captured the horizontal distribution of the observed surface O₃ concentrations (Takigawa et al., 2007). Distribution of Z. serrata was obtained from the spatial map of tree species in Japan (Horiikawa, 1976). These data allowed to provide an estimation of the leaf-level stomatal O₃ uptake for Z. serrata in each grid square \((15 \times 15 \text{ km})\) with 1-h time steps.

2.2. Literature-based stomatal conductance model

A stomatal conductance model for Z. serrata was previously provided by measurements carried out in western Japan (35°01' N, 135° 46' E) (Kadaira and Yoshida, 2006) over two days in August and October. The model was based on the multiplicative algorithm described by Jarvis (1976):

\[ g_{sw} = g_{max} f_{light} f_{temp} f_{VPD} \] (5)

where \(g_{max}\) is the maximum stomatal conductance \((610 \text{ mmol H₂O m}^{-2} \text{ s}^{-1})\). The other functions are limiting factors of \(g_{max}\) and are scaled from 0 to 1. \(f_{light}, f_{temp}\), and \(f_{VPD}\) are a function of photosynthetically photon flux density at the leaf surface \((\text{PPFD}, \text{μmol photons m}^{-2} \text{ s}^{-1})\), temperature \((T, °C)\), and VPD \((\text{kPa})\), respectively.

These functions are expressed as follows:

\[ f_{light} = \frac{\text{PPFD}}{\text{PPFD} + k} \] (6)

\[ f_{temp} = \left(\frac{T - T_{\min}}{T_{\opt} - T_{\min}}\right) \left(\frac{T_{\max} - T}{T_{\max} - T_{\opt}}\right) \left(\frac{T_{\opt} - T_{\min}}{T_{\max} - T_{\opt}}\right) \] (7)

\[ f_{VPD} = \frac{1}{1 + (\text{VPD} / D_{0.5})^k} \] (8)

where \(k\) is a constant, and \(T_{\opt}, T_{\min},\) and \(T_{\max}\) represent the optimum, minimum, and maximum temperatures for \(g_{sw}\), respectively. \(D_{0.5}\) and \(a\) are constants.

2.3. Reparameterization of the stomatal conductance model

Measurements of \(g_{sw}\) were conducted in the three regions near Tokyo listed in Table 2 (central Tokyo: 35°43’ N, 139°45’ E; south eastern Tokyo: 35°37’ N, 139°42’ E; western Tokyo: 35°44’ N, 139°32’ E). The three regions were chosen as representatives of

<table>
<thead>
<tr>
<th>Grid number</th>
<th>Air temperature (°C)</th>
<th>Precipitation (mm)</th>
<th>Solar radiation (W m⁻²)</th>
<th>VPD (kPa)</th>
<th>O₃ concentration (ppb)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1598</td>
<td>18.8 (3.9)</td>
<td>939 (313)</td>
<td>249.4 (15.5)</td>
<td>0.72 (0.29)</td>
<td>37.2 (3.6)</td>
</tr>
</tbody>
</table>
different polluted area in order to parameterize O3 effects on \( g_{sw} \). Western Tokyo (Tanashi) is a high-polluted area where AOT40 was nearly equaled to 30 ppm h. \( g_{sw} \) was measured using a cycling diffusive porometer (Model AP4, Delta-T devices, Cambridge, UK).

Measurements were carried out on southward sunlit leaves in >10-year-old tree in all sites and on fully sun-exposed healthy leaves at top of the canopy of 10-year-old saplings at western Tokyo (Table 3).

Diurnal courses of \( g_{sw} \) were measured during different stages of the growing seasons of three consecutive years (central Tokyo: April—August in 2009; south eastern Tokyo: July and September in 2008; western Tokyo (Tanashi park): May—August in 2009, and the nearby University of Tokyo Tanashi forest, May—November in 2008, April—August in 2009, and May—September in 2010). All pooled data of 2532 measurements were divided into two subsets, i.e., data for validation and parameterization. A subset for validation (20% of all pooled data, 510 measurements) was extracted by random sampling using Microsoft Excel software. The extracted data included following measurements: 10 June 2009 in central Tokyo, 17 July 2008 in south eastern Tokyo, 13 July 2009 in Tanashi park (western Tokyo), and 11 July 2008, 30 April and 28 August 2009, and 11 June, 2 July and 5 August 2010 in University of Tokyo Tanashi forest (western Tokyo). The rest of data set was used to re-parameterize the stomatal conductance model.

The model was based on the multiplicative algorithm described by Jarvis (1976) and modified by Emberson et al. (2000a):

\[
g_{sw} = g_{max} \cdot \min\left(f_{phen}, f_{O3}\right) \cdot f_{light} \cdot \max\left(f_{min}, \frac{f_{temp} \cdot f_{VPD} \cdot f_{SWP}}{1}ight) \tag{9}
\]

where \( f_{min} \) is the minimum stomatal conductance, \( f_{phen} \) and \( f_{O3} \) are the variation in \( g_{sw} \) with leaf age and premature senescence induced by \( O_3 \), respectively. \( f_{SWP} \) is a function of volumetric soil water potential (MPa).

The response of \( g_{sw} \) to phenology (\( f_{phen} \)) is described as follows:

When \( SGS \leq DOY < SGS + f_{phen,c} \):

\[
f_{phen} = \left(1 - f_{phen,a}\right) \cdot \left(\frac{DOY - SGS}{f_{phen,c}}\right) + f_{phen,a}
\]

When \( SGS + f_{phen,c} \leq DOY \leq SGS + f_{phen,d} \):

\[
f_{phen} = 1
\]

When \( SGS + f_{phen,d} < DOY \leq EGS \):

\[
f_{phen} = \left(1 - f_{phen,b}\right) \cdot \left(\frac{EGS - DOY}{f_{phen,d}}\right) + f_{phen,b}
\]

where DOY is the day of year, SGS and EGS is a date of start and end of growing season, respectively. The parameters \( f_{phen,a} \) and \( f_{phen,b} \) denote the maximum fraction of \( g_{sw} \) at the start and end of the growing season. \( f_{phen,c} \) and \( f_{phen,d} \) are the parameters representing the number of days for \( f_{phen} \) to reach its maximum and the number of days during the decline of \( f_{phen} \) for the minimum value.

The response of \( g_{sw} \) to PPFD, i.e., \( f_{light} \), is described as:

\[
f_{light} = 1 - \exp(a \cdot PPFD)
\]

where \( a \) is a species-specific parameter defining the shape of the hyperbolic relationship.

The function of \( T(\degree C) \) is expressed as:

\[
f_{temp} = \left(\frac{T - T_{min}}{T_{opt} - T_{min}}\right) \left(\frac{T_{max} - T}{T_{max} - T_{opt}}\right)
\]

where \( T_{opt}, T_{min}, \) and \( T_{max} \) represent the optimum, minimum, and maximum temperature for \( g_{sw} \), respectively.

The response of \( g_{sw} \) to VPD (kPa) is given by:

\[
f_{VPD} = \frac{(1 - f_{min}) \cdot (VPD_{min} - VPD)}{VPD_{max} - VPD} + f_{min}
\]

where \( VPD_{min} \) and \( VPD_{max} \) represent the threshold of VPD to reach minimum and full stomatal opening, respectively. If VPD exceeds \( VPD_{min} \), \( f_{VPD} \) is set to \( f_{min} \). If VPD is lower than \( VPD_{max} \), \( f_{VPD} \) is 1.

The function of \( O_3 \) is given as follows, according to Pleijel et al. (2002):

\[
O_3 = \left(1 + \frac{AO TG}{b^c}\right)^{-1}
\]

where \( AO TG \) is the accumulated exposure over a threshold of 0 ppb during daylight hours (ppm h), \( b \) and \( c \) are constants.

Parameterization was carried out using a boundary line analysis. First, the \( g_{sw} \) data were divided into classes with the following step-wise increases for each variable: 200 \( \mu mol \) photons m\(^{-2}\) s\(^{-1}\) for PPFD (when PPFD values were less than 200 \( \mu mol \) photons m\(^{-2}\) s\(^{-1}\), PPFD classes at 50 \( \mu mol \) photons m\(^{-2}\) s\(^{-1}\) steps were adopted), 2 \( \degree C \) for \( T \), 0.2 kPa for VPD and 20 ppm h for \( AO TG \). A function was fitted against each model variable based on 98th percentile values per each class of environmental factors except for \( f_{SWP} \). Because no measurements of soil water content were available, the effect of soil water availability on stomatal \( O_3 \) uptake was accounted for by using model estimates.

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**Table 2**

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>PPFD ((\mu mol m^{-2} s^{-1}))</th>
<th>Air temperature ((\degree C))</th>
<th>VPD (kPa)</th>
<th>AOT40 (ppm h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Tokyo</td>
<td>2009</td>
<td>0–1970 (638)</td>
<td>12.5–33.4 (25.4)</td>
<td>0.8–2.5 (1.6)</td>
<td>6.1</td>
</tr>
<tr>
<td>South eastern Tokyo</td>
<td>2008</td>
<td>60–1660 (491)</td>
<td>25.2–32.8 (29.2)</td>
<td>1.3–2.4 (1.7)</td>
<td>16.6</td>
</tr>
<tr>
<td>Western Tokyo</td>
<td>2008</td>
<td>100–1910 (583)</td>
<td>15.1–35.8 (25.7)</td>
<td>0.9–2.4 (1.6)</td>
<td>28.0</td>
</tr>
<tr>
<td>Western Tokyo</td>
<td>2009</td>
<td>90–1990 (918)</td>
<td>18.9–34.4 (27.6)</td>
<td>0.8–3.2 (1.8)</td>
<td>27.7</td>
</tr>
<tr>
<td>Central Tokyo</td>
<td>2010</td>
<td>60–1950 (1051)</td>
<td>19.8–36.9 (29.6)</td>
<td>0.9–2.8 (1.7)</td>
<td>31.0</td>
</tr>
</tbody>
</table>

* Ozone concentration data was obtained from monitoring stations near the measurement sites (distance between the stations and measurement sites <1.5 km). AOT40 was calculated over April—September.

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**Table 3**

<table>
<thead>
<tr>
<th>Measured leaf position</th>
<th>Site</th>
<th>Year</th>
<th>Number of trees</th>
<th>Number of leaves of each tree</th>
<th>Tree height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southward sunlit leaves</td>
<td>Central Tokyo (Bunkyo-ku)</td>
<td>2009</td>
<td>1</td>
<td>10</td>
<td>15</td>
</tr>
<tr>
<td>(3 m, &gt;10-year-old tree)</td>
<td>South eastern Tokyo (Meguro-ku)</td>
<td>2008</td>
<td>1</td>
<td>10</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Western Tokyo (Tanashi park)</td>
<td>2009</td>
<td>1</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Leaves at top of the canopy</td>
<td></td>
<td>2008–2010</td>
<td>3–5</td>
<td>5</td>
</tr>
<tr>
<td>(5 m, 10-year-old saplings)</td>
<td>Western Tokyo Univ. Tokyo Tanashi forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
of soil water content (see Section 2.4). Meteorological parameters such as PPFD, T and VPD were derived from the pyrometry measurements to estimate the parameters of stomatal conductance model. O3 concentration data was obtained from monitoring stations near the measurement sites (distance between the stations and measurement sites <1.5 km).

2.4. Testing a model function of soil water content

The function of root-zone plant available water (fPAW) has been suggested as a better proxy of soil moisture effects on stomata and can be used instead of the function of soil water potential (fSWP) (Mills et al., 2010). Root-zone plant available water (PAW) is the amount of water in the soil, which is available to the plants. PAW (fraction) is expressed as follows:

\[ \text{PAW} = \frac{\theta - \theta_{\text{WP}}}{\theta_{\text{FC}} - \theta_{\text{WP}}} \] (15)

where \( \theta \) is the current soil water content (mm), \( \theta_{\text{FC}} \) is soil water content at field capacity (mm) and \( \theta_{\text{WP}} \) is soil water content at wilting point (mm).

The \( f_{\text{PAW}} \) is given by the following equations:

When \( \text{PAW}_t < \text{PAW} \)

\[ f_{\text{PAW}} = 1 \]

when \( 0 < \text{PAW} < \text{PAW}_t \)

\[ f_{\text{PAW}} = \frac{\theta - \theta_{\text{WP}}}{\text{PAW}_t} \] (16)

where \( \text{PAW}_t \) is the threshold of PAW (fraction), above which \( g_{\text{sw}} \) is at a maximum.

Root-zone moisture (RM = \( \theta - \theta_{\text{WP}} \)) mm) was estimated by using the simple water budget model (e.g., Lhomme and Katerji, 1991; Mintz and Walker, 1993):

\[ \text{RM} = \text{RM}_{-1} + (P - E_t) - (E_t + E_s) \] (17)

where \( \text{RM}_{-1} \) is the root-zone moisture at the end of the preceding day (mm), \( P \) is the daily precipitation (mm), \( E_t \) is the daily intercepted canopy evaporation (water evaporated from the wet surface of the vegetation and wet surface of the soil, during and following precipitation (mm)), \( E_s \) is the daily transpiration (mm), and \( E_s \) is the daily soil evaporation (mm). Any excess precipitation was assumed to be lost to run-off. Soil water storage capacity (\( \theta_{\text{FC}} - \theta_{\text{WP}} \)) was set to 200 mm (soil type: clay loam; soil depth: 1 m) (Fujieda, 2007). PAW was assumed to be 0.9 at the beginning of the year (De Marco et al., 2010).

\( E_t, E_s \) and \( E_t \) were estimated by Thornthwaite’s method (Thornthwaite and Mather, 1955; Mintz and Walker, 1993):

\[ E_t = \min (P, E_p) \]

\[ E_t + E_s = (E_p - E_t) \cdot \text{PAW} \] (18)

where \( E_p \) is the daily potential evapotranspiration (mm), and given by:

\[ E_p = \begin{cases} 0, & T_a < 0 \degree \text{C} \\ 0.539 \cdot \left( \frac{10 - T_a}{I} \right)^{d} \cdot \frac{h}{T_a} \cdot \frac{T_a}{T_a}, & 0 < T_a < 26.5 \degree \text{C} \\ -13.86 + 1.075 \cdot T_a - 0.0144 \cdot T_a^{2} \cdot \frac{h}{T_a}, & T_a > 26.5 \degree \text{C} \end{cases} \]

\[ I = \sum_{i=1}^{12} i; \quad i = \left( \frac{T_a}{5} \right)^{1.514}, \quad i_{\min} = 0 \]

\[ d = \left( 6.75 \times 10^{-7} I^3 \right) - \left( 7.71 \times 10^{-5} I^2 \right) + \left( 1.79 \times 10^{-2} I \right) + 0.492 \] (19)

where \( T_a \) is daily mean air temperature (\degree C), \( T_m \) is monthly mean air temperature (\degree C), \( h \) is length of daylight hours (h), \( i \) is the annual heat index (no dimension), \( d \) is an empirical coefficient (no dimension). To calculate \( E_p, T_a \) and \( P \) for each site were obtained from nearby monitoring stations of the Japanese climate agency. \( f_{\text{PAW}} \) was fitted by using boundary line analysis based on 98th percentile values per each of PAW, i.e., splitting up the data set into PAW class at 0.1 steps. The stomatal conductance model including \( f_{\text{PAW}} \) was validated by comparison with measurements of \( g_{\text{sw}} \).

2.5. Data analysis

Simple regression analysis was used to test the relationships between measured and estimated \( g_{\text{sw}} \). The analysis was performed using SPSS software (SPSS, Chicago, USA).

Spatial maps of both indices were provided in order to compare AOT40 and PODp. The mapping was achieved using Arc GIS software (ESRI, USA).

3. Results

3.1. Reparameterization of the stomatal conductance model

The \( g_{\text{max}} \) value was set to 465 mmol H2O m-2 PLA s-1 as 98th percentile of \( g_{\text{sw}} \) measurements at all 4 sites (Fig. 1A; Table 4). The \( f_{\min} \) value was set to 0.1 (fraction) corresponding to the 5th percentile values of \( g_{\text{sw}} \) recorded throughout the measurements.

The limiting functions of \( g_{\text{sw}} (f_{\text{phen}}, f_{\text{light}}, f_{\text{temp}}, f_{\text{VPD}}, f_{\text{PAW}} \) and \( f_{\text{O3}} \) were defined by boundary line analysis (Fig. 1B–G; Table 4). The main differences between the literature-based model and the revised model were in \( f_{\text{phen}}, f_{\text{light}}, f_{\text{PAW}} \) and \( f_{\text{O3}} \) (Fig. 1B, D, F, G). In the literature-based model, functions of phenology, soil water and

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Re-parameterized model</th>
<th>Literature-based model</th>
</tr>
</thead>
<tbody>
<tr>
<td>( g_{\text{max}} ) (mmol H2O m-2 PLA s-1)</td>
<td>465</td>
<td>610</td>
</tr>
<tr>
<td>( f_{\min} ) (fraction)</td>
<td>0.1</td>
<td>8</td>
</tr>
<tr>
<td>( f_{\text{phen}} ) (SGS (day of year))</td>
<td>105</td>
<td>27</td>
</tr>
<tr>
<td>( f_{\text{light}} ) (days)</td>
<td>60</td>
<td>2.3</td>
</tr>
<tr>
<td>( f_{\text{light}} ) (c (constant))</td>
<td>–0.0084</td>
<td>k (constant)</td>
</tr>
<tr>
<td>( f_{\text{light}} ) (a (constant))</td>
<td>94</td>
<td>3.5</td>
</tr>
<tr>
<td>( f_{\text{temp}} ) (\degree C)</td>
<td>45</td>
<td>45</td>
</tr>
<tr>
<td>( T_{\text{min}} ) (\degree C)</td>
<td>11</td>
<td>5</td>
</tr>
<tr>
<td>( T_{\text{max}} ) (\degree C)</td>
<td>45</td>
<td>45</td>
</tr>
<tr>
<td>( f_{\text{VPD}} ) (kPa)</td>
<td>1.1</td>
<td>3.5</td>
</tr>
<tr>
<td>( f_{\text{PAW}} ) PAW (fraction)</td>
<td>0.58</td>
<td>0.58</td>
</tr>
<tr>
<td>( f_{\text{O3}} ) (b (constant))</td>
<td>141</td>
<td>141</td>
</tr>
<tr>
<td>( c ) (constant)</td>
<td>3.4</td>
<td>3.4</td>
</tr>
</tbody>
</table>
Fig. 1. Parameterization of stomatal conductance model for Zelkova serrata (A: $g_{\text{max}}$; B: $f_{\text{phen}}$; C: $f_{\text{light}}$; D: $f_{\text{temp}}$; E: $f_{\text{VPD}}$; F: $f_{\text{PAW}}$; G: $f_{\text{O3}}$). $f_{\text{phen}}, f_{\text{light}}, f_{\text{temp}}, f_{\text{VPD}}, f_{\text{PAW}}$ and $f_{\text{O3}}$ are functions of phenology, photosynthetically photon flux density at the leaf surface (PPFD, μmol photons m$^{-2}$ s$^{-1}$), temperature (T, °C), vapor pressure deficit (VPD, kPa), root-zone plant available water (fraction) and AOT0 (ppm h), respectively. Relative $g_{sw}$ was calculated as $g_{sw}$ divided by $g_{\text{max}}$ in each site. Thick and dashed lines are the plots of each function in re-parameterized model and literature-based model, respectively. Larger symbols show 98th percentile values per each class of environmental factors (PPFD: 200 μmol photons m$^{-2}$ s$^{-1}$; except for values less than 200 μmol photons m$^{-2}$ s$^{-1}$ where 50 μmol photons m$^{-2}$ s$^{-1}$ class was chosen; T: 2 °C; VPD: 0.2 kPa; root-zone plant available water: 0.1; AOT0: 20 ppm h).
O$_3$ were not included, i.e., $f_{\text{phen}}$, $f_{\text{PAW}}$ and $f_{O3} = 1$ throughout the growing season.

The reparameterization presented in this study provided a better fit with the measurements for validation than the literature-based model presented by Kadaira and Yoshida (2006) ($R^2 = 0.53$ vs. 0.17) (Table 5). Including $f_{O3}$ improved the model performance (Table 5). Testing a function of soil water showed no change of model performance because $f_{\text{PAW}}$ was 1 in most of the growing seasons, i.e., no limitation to $g_{\text{sw}}$. However, when the re-parameterized model was applied in summer 2010 with low precipitation (27 mm as monthly precipitation in August), $f_{\text{PAW}}$ improved the daily course of estimated $g_{\text{sw}}$ (Fig. 2).

### 3.2. Comparison of POD$_0$ and AOT40 maps

Fig. 3A shows a map of the AOT40 values from April to September 2007 in Japan. There was a strong gradient in the AOT40 values from central Japan to northern and western Japan. The highest AOT40 value of 30 ppm h could be found in Kanto region (around 35° N, 140° E). In contrast, the AOT40 values were relatively low (0–9 ppm h) in Hokkaido region (42°–45° N, 140°–145° E).

POD$_0$ presented in this study was 46–50 mmol m$^{-2}$ in the central part of Japan (Fig. 3B). In Kanto region (around 35° N, 140° E), POD$_0$ was relatively low (28–34 mmol m$^{-2}$) although the highest AOT40 was recorded here. Fig. 4A and B shows averaged $f_{\text{VPD}}$ and $f_{\text{PAW}}$ values in summer (July–August), respectively. In Kanto region, the averaged $f_{\text{VPD}}$ values were <0.8 because of high temperature in summer, $f_{\text{PAW}}$ values were also <0.8 in this region because high temperature increased evaportranspiration and induced soil moisture deficit. Therefore, relatively low POD$_0$ was estimated in this area by the re-parameterized model. The spatial distribution of POD$_0$ by the re-parameterized model differed from estimates based on the literature-based model (Fig. 3B, C). In particular, in Kanto region (around 35° N, 140° E), POD$_0$ was 43–52 mmol m$^{-2}$ and 28–34 mmol m$^{-2}$ when estimated by the literature-based model and the re-parameterized model, respectively. According to the new model, the highest value of POD$_0$ (50 mmol m$^{-2}$) was recorded in central Japan (Fig. 3B).

### 4. Discussion

The new model of $g_{\text{sw}}$ showed a better performance than the literature-based model when compared with the measurements (Table 5). The main discrepancies in model parameters between the literature-based model and the revised model were $g_{\text{max}}$, $f_{\text{phen}}$, $f_{\text{temp}}$, $f_{\text{PAW}}$ and $f_{O3}$ (Fig. 1).

The $g_{\text{max}}$ (610 mmol H$_2$O m$^{-2}$ PLA s$^{-1}$) in the literature-based model was higher than $g_{\text{max}}$ obtained in this study (465 mmol H$_2$O m$^{-2}$ PLA s$^{-1}$). Literature values support $g_{\text{max}}$ presented in this study. Saito et al. (2003) showed a diurnal course of stomatal conductance of 6-year-old Z. serrata saplings and reported around 400–500 mmol H$_2$O m$^{-2}$ PLA s$^{-1}$ as maximum values under saturated light and low VPD conditions. Previous studies have highlighted the importance of $g_{\text{max}}$ in determining the predictive capabilities of the model (e.g. Emberson et al., 2000b; Tuovinen et al., 2007). $g_{\text{max}}$ depends not only on tree and leaf age and canopy position, but also on population and environmental conditions such as nutrient availability and pollution climate (Wieser et al., 2000). Collecting data of $g_{\text{max}}$ is important for identifying the representative value on a regional scale. Although further work is needed, $g_{\text{max}}$ presented in this study was based on a larger data set of measurements than previous exercises and is thus recommended for estimating stomatal O$_3$ uptake of Z. serrata in Japan.

The response of $g_{\text{sw}}$ to phenology was added to the stomatal conductance model according to the Emberson et al. (2000a) approach. $f_{\text{phen}}$ increased from mid-April to May, and gradually decreased from the beginning of September (Fig. 1B). The parameter of $f_{\text{phen}}$ improved the model performance at early spring and late autumn (data not shown). Seasonal course of $f_{\text{phen}}$ differed depending on the sites (Fig. 1B). In western Tokyo, 98th percentile of measured $g_{\text{sw}}$ was 50–70% of $g_{\text{max}}$ from mid-August to September in 2008 to 2010. Western Tokyo is a highly polluted area where AOT40 was 317 ppm h (Table 1). Ozone-induced reductions in stomatal conductance have been widely reported (Wittig et al., 2007). The function of $O_3$, $f_{O3}$, reduced the error of estimated $g_{\text{sw}}$ in the re-parameterized model (Table 5). In summer 2010, low precipitation in Tokyo induced soil moisture deficit resulting in reduction of $g_{\text{sw}}$ (Fig. 2). Including the soil moisture function ($f_{\text{PAW}}$) improved the model performance in summer 2010 (Fig. 2). In most seasons, $f_{\text{PAW}}$ was not a limiting factor to stomatal conductance. In Japan, annual precipitation is elevated and ranges from 1100 mm to 2300 mm. Sirisampan et al. (2003) reported that soil water content had no effect on $g_{\text{sw}}$ of six tree species in central Japan. However, the present study suggests that soil moisture deficit may be a limiting factor in estimating POD$_0$ during short periods of high

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**Table 5**

Results of the regression analysis between measured and estimated $g_{\text{sw}}$ using literature-based model and re-parameterized model.

<table>
<thead>
<tr>
<th>Model</th>
<th>$f_{\text{PAW}}$</th>
<th>$f_{O3}$</th>
<th>$R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Literature-based model</td>
<td>-</td>
<td>-</td>
<td>0.17</td>
<td>111.4</td>
</tr>
<tr>
<td>Re-parameterized model</td>
<td>-</td>
<td>-</td>
<td>0.48</td>
<td>98.0</td>
</tr>
<tr>
<td>Re-parameterized model</td>
<td>-</td>
<td>+</td>
<td>0.54</td>
<td>110.5</td>
</tr>
<tr>
<td>Re-parameterized model</td>
<td>+</td>
<td>-</td>
<td>0.48</td>
<td>98.0</td>
</tr>
<tr>
<td>Re-parameterized model</td>
<td>+</td>
<td>+</td>
<td>0.53</td>
<td>95.5</td>
</tr>
</tbody>
</table>

*: including the function; –: not including the function.

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**Fig. 2.** Examples of the daily trend of measured $g_{\text{sw}}$ (●) and estimated $g_{\text{sw}}$ by the re-parameterized model (□) and re-parameterized model with the soil moisture function (×) at western Tokyo (Univ. Tokyo Tanashi forest) in August 2010. Measured data are mean values ± SD, n = 15 (5 leaves × 3 trees).
soil moisture deficit due to lack of rainfall and/or high temperatures as experienced in August 2010 (Fig. 2). The parameterization of \( \text{f}_{\text{PAW}} \) developed in this study thus improves the calculation of stomatal \( \text{O}_3 \) uptake for Japan.

The function of air temperature, \( \text{f}_{\text{temp}} \), was also significantly changed relative to the literature-based model (Fig. 1D), where the \( T_{\text{opt}} \) was set to more than 40 \(^\circ\)C. High \( T_{\text{opt}} \) may cause strong temperature dependency of \( \text{POD}_0 \) (data not shown). High VPD often occurs in the afternoon together with high air temperature. High ambient \( \text{O}_3 \) concentrations are often associated with occurrence of high VPD leading to stomatal closure (e.g., Grünhage and Jäger, 1994). In general, \( T_{\text{opt}} \) ranges from 20 to 30 \(^\circ\)C for temperate deciduous forest trees (Larcher, 2001). Adequate settings of \( T_{\text{opt}} \) in the re-parameterized model reflected such interactions between atmosphere and stomatal responses.

The highest AOT40 value was 30 ppm h found in Kanto region (around 35°N, 140°E) (Fig. 3A). In contrast, \( \text{POD}_0 \) provided by the re-parameterized model in the same region was relatively low (23–34 mmol m\(^{-2}\) s\(^{-1}\)) (Fig. 3B), because stomatal closure induced by VPD and soil moisture deficit led to limited stomatal \( \text{O}_3 \) uptake (Fig. 4A, B).

In Japan, air temperature increased by 1.0 \(^\circ\)C during the past 100 years (JMA, 2002), which is higher than the world average (0.7 \(^\circ\)C) (IPCC, 2007). Although an increase in air temperature can be clearly found in Japan, no change of annual precipitation was recorded during the past 100 years (JMA, 2002). Air temperature is expected to increase more than 2 \(^\circ\)C in 2081–2100 (Kurihara et al., 2005). This perspective suggests higher frequency of elevated temperature and high VPD conditions in a future climate. Stomatal \( \text{O}_3 \) uptake may be further limited under an expected warming climate.

Risk assessments based on AOT40 and \( \text{O}_3 \) flux may not significantly differ under non-limiting conditions for \( g_{\text{sw}} \) (Schaub et al., 2007). Although annual precipitations are usually very high in Japan, VPD and soil moisture deficit induced by high temperature, and \( \text{O}_3 \) exposure limited stomatal \( \text{O}_3 \) uptake under high ambient \( \text{O}_3 \) levels. As a result, the comparison between \( \text{POD}_0 \) and AOT40 maps revealed that the spatial patterns of \( \text{POD}_0 \) differed from those of AOT40. Therefore, current climate conditions and \( \text{O}_3 \) pollution may limit stomatal \( \text{O}_3 \) uptake and decoupled it from high \( \text{O}_3 \) levels in Japan.

5. Conclusion

There are only a few reports of \( g_{\text{sw}} \) modeling to develop the stomatal flux-based approach in East Asia such as Japan (rice: Oue et al., 2008; wheat: Oue et al., 2009; several tree species: Hoshika et al., 2011a,b). Our results contribute to develop the stomatal flux-based approach in East Asia. A new parameterization of \( g_{\text{sw}} \) for \( \text{Z. serrata} \) was developed on the basis of measured data and improved the performance of the model relative to a previous model (Kadaira and Yoshida, 2006). We demonstrated that stomatal closure induced by VPD, soil moisture deficit and \( \text{O}_3 \) exposure can limit stomatal \( \text{O}_3 \) uptake under high ambient \( \text{O}_3 \) levels. Caution is thus recommended in using AOT40 as a standard for \( \text{Z. serrata} \) protection in Japan. Response data in the field or free-
Acknowledgments

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