



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

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ABSTRACT

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 (O_3) is an important phytotoxic air pollutant and is also recognized as a significant greenhouse gas (Bytnerowicz et al., 2007; Serengil et al., 2011). Surface O_3 concentrations are increasing in East Asia because of rapid increases in emission of the main O_3 precursors, Nitrogen oxides and volatile organic compounds (Naja and Akimoto, 2004). Ohara and Sakata (2003) reported that annual average concentrations of photochemical oxidant, mainly O_3 , increased at high rate ($0.33 \text{ ppb year}^{-1}$) from 1985 to 1999 in Japan.

Phytotoxic nature of O_3 has been well known for decades (e.g., NIES, 1980, 1984; Omasa et al., 2002; Paoletti, 2007). The concentration based approach for O_3 effects on plants (e.g., AOT40: accumulated exposure over a threshold of 40 ppb) has the advantage of being simple and needs only atmospheric O_3 concentrations, i.e., external O_3 exposure, without considering internal O_3 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 O_3 risk assessment to plants (Kobayashi, 1999; Matyssek and Innes, 1999; Matyssek et al., 2007). Stomatal O_3 uptake or flux is more closely related to O_3 impacts (Omasa et al., 2002; Paoletti and Manning, 2007; Karlsson et al., 2007). In Europe, critical levels for O_3 risk based on stomatal O_3 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 O_3 impacts to plants in East Asia (Watanabe and Yamaguchi, 2011), AOT40 has been recommended for assessments of O_3 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 O_3 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 O_3 uptake. Ozone is also known to directly induce stomatal closure as a result of the inhibition of photosynthesis (Wittig et al., 2007). Therefore, stomatal O_3 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.

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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:

$$\text{AOT40} = \sum \max(40 - [\text{O}_3], 0) \quad (1)$$

if global radiation > 50 W m⁻²

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

Stomatal O₃ uptake (F_{st} ; nmol O₃ m⁻² s⁻¹) was calculated as:

$$F_{\text{st}} = [\text{O}_3] \cdot \{1/(r_b + r_c)\} \cdot \{(g_{\text{sw}}/1.65)/(g_{\text{sw}}/1.65 + g_{\text{ext}})\} \quad (2)$$

where r_b is the leaf boundary layer resistance (mol⁻¹ m² s), r_c is the leaf surface resistance (=1/($g_{\text{sw}}/1.65 + g_{\text{ext}}$); s m⁻¹), g_{sw} is the stomatal conductance for water vapor (mmol H₂O m⁻² Projected Leaf Area (PLA) s⁻¹) and 1.65 accounts for the difference in diffusivity of water in air compared with O₃. g_{ext} is the external leaf conductance (s m⁻¹) that indicates negligible or slight adsorption of O₃ on leaf surface (Omasa et al., 2002). g_{ext} was set to 0.0004 m s⁻¹ (Mills et al., 2010).

Leaf boundary layer resistance (r_b) was calculated from the wind speed, u (s m⁻¹), and the mean leaf length, L_d (0.06 m for *Z. serrata* obtained from Hosoi and Omasa, 2007) (Mills et al., 2010):

$$r_b = 1.3 \cdot 150 \cdot (L_d/u)^{0.5} \quad (3)$$

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 (POD_Y) was recommended to assess O₃ risk for forest species (Mills et al., 2010). It is given by:

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

where Y is a species-specific threshold of stomatal O₃ uptake (nmol O₃ m⁻² 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 (POD₀) 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 (Horikawa, 1976). These data allowed to provide an estimation of the leaf-level stomatal O₃ uptake for *Z. serrata* in each grid square (15 × 15 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):

$$g_{\text{sw}} = g_{\text{max}} \cdot f_{\text{light}} \cdot f_{\text{temp}} \cdot f_{\text{VPD}} \quad (5)$$

where g_{max} is the maximum stomatal conductance (610 mmol H₂O m⁻² PLA 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 (PPFD, μmol photons m⁻² s⁻¹), temperature (T , °C), and VPD (kPa), respectively.

These functions are expressed as follows:

$$f_{\text{light}} = \frac{\text{PPFD}}{(\text{PPFD} + k)} \quad (6)$$

$$f_{\text{temp}} = \left(\frac{T - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \right) \left\{ \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right) \left(\frac{T_{\text{max}} - T_{\text{opt}}}{T_{\text{opt}} - T_{\text{min}}} \right) \right\} \quad (7)$$

$$f_{\text{VPD}} = \frac{1}{(1 + (\text{VPD}/D_{0.5})^\alpha)} \quad (8)$$

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 α 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 1

Main climate data (±SD) as an input data (April–September 2007) estimated by Takigawa et al. (2007) to estimate stomatal O₃ uptake in Japan.

Grid number	Air temperature (°C)	Precipitation (mm)	Solar radiation (W m ⁻²)	VPD (kPa)	O ₃ concentration (ppb)
1598	18.8 (3.9)	939 (313)	249.4 (15.5)	0.72 (0.29)	37.2 (3.6)

Table 2Range of main meteorological parameters during g_s measurements (value in brackets indicates mean), and AOT40 in the measurement sites.

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

^a 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.

different polluted area in order to parameterize O_3 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):

$$g_{sw} = g_{max} \cdot \min(f_{phen}, f_{O_3}) \cdot f_{light} \cdot \max\left\{f_{min}, \left(f_{temp} \cdot f_{VPD} \cdot f_{SWP}\right)\right\} \quad (9)$$

where f_{min} is the minimum stomatal conductance. f_{phen} and f_{O_3} 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 $\text{SGS} \leq \text{DOY} < (\text{SGS} + f_{phen,c})$

$$f_{phen} = (1 - f_{phen,a}) \cdot ((\text{DOY} - \text{SGS}) / f_{phen,c}) + f_{phen,a}$$

When $(\text{SGS} + f_{phen,c}) \leq \text{DOY} \leq (\text{EGS} - f_{phen,d})$

$$f_{phen} = 1$$

When $(\text{EGS} - f_{phen,d}) < \text{DOY} \leq \text{EGS}$

$$f_{phen} = (1 - f_{phen,b}) \cdot ((\text{EGS} - \text{DOY}) / f_{phen,d}) + f_{phen,b} \quad (10)$$

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_{max} 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:

$$f_{light} = 1 - \exp(-a \cdot \text{PPFD}) \quad (11)$$

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

The function of T ($^{\circ}\text{C}$) is expressed as:

$$f_{temp} = \left(\frac{T - T_{min}}{T_{opt} - T_{min}}\right) \left\{ \left(\frac{T_{max} - T}{T_{max} - T_{opt}}\right) \left(\frac{T_{max} - T_{opt}}{T_{opt} - T_{min}}\right) \right\} \quad (12)$$

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:

$$f_{VPD} = \frac{(1 - f_{min}) \cdot (\text{VPD}_{min} - \text{VPD})}{\text{VPD}_{min} - \text{VPD}_{max}} + f_{min} \quad (13)$$

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):

$$f_{O_3} = (1 + (\text{AOT0}/b)^c)^{-1} \quad (14)$$

where AOT0 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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for PPFD (when PPFD values were less than 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, PPFD classes at 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ steps were adopted), 2 $^{\circ}\text{C}$ for T , 0.2 kPa for VPD and 20 ppm h for AOT0. 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

Table 3

Summary of target trees in the measurement sites.

Measured leaf position	Site	Year	Number of trees	Number of leaves of each tree	Tree height (m)
Southward sunlit leaves (3 m, >10-year-old tree)	Central Tokyo (Bunkyo-ku)	2009	1	10	15
	South eastern Tokyo (Meguro-ku)	2008	1	10	15
	Western Tokyo (Tanashi park)	2009	1	10	10
Leaves at top of the canopy (5 m, 10-year-old saplings)	Western Tokyo Univ. Tokyo Tanashi forest)	2008–2010	3	3–5	5

of soil water content (see Section 2.4). Meteorological parameters such as PPFD, T and VPD were derived from the porometry measurements to estimate the parameters of stomatal conductance model. O_3 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 (f_{PAW}) 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 (f_{SWP}) (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:

$$PAW = \frac{\theta - \theta_{WP}}{\theta_{FC} - \theta_{WP}} \quad (15)$$

where θ is the current soil water content (mm), θ_{FC} is soil water content at field capacity (mm) and θ_{WP} is soil water content at wilting point (mm).

The f_{PAW} is given by the following equations:

When $PAW_t < PAW$

$$f_{PAW} = 1$$

when $0 < PAW < PAW_t$

$$f_{PAW} = \frac{\theta - \theta_{WP}}{PAW_t} \quad (16)$$

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

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

$$RM = RM_{-1} + (P - E_1) - (E_t + E_s) \quad (17)$$

where RM_{-1} is the root-zone moisture at the end of the preceding day (mm), P is the daily precipitation (mm), E_1 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_t 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 ($\theta_{FC} - \theta_{WP}$) 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_1 was estimated by Thornthwaite's method (Thornthwaite and Mather, 1955; Mintz and Walker, 1993):

$$E_1 = \min(P, E_p)$$

$$E_t + E_s = (E_p - E_1) \cdot PAW \quad (18)$$

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

$$E_p = \begin{cases} 0, & T_a < 0^\circ\text{C} \\ \left[0.533 \cdot \left(\frac{10 \cdot T_a}{I} \right)^d \right] \frac{h}{12}, & 0 < T_a < 26.5^\circ\text{C} \\ \left(-13.86 + 1.075 \cdot T_a - 0.0144 \cdot T_a^2 \right) \frac{h}{12}, & T_a > 26.5^\circ\text{C} \end{cases}$$

$$I = \sum_1^{12} i; \quad i = \left(\frac{T_m}{5} \right)^{1.514}, \quad i_{\min} = 0$$

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

where T_a is daily mean air temperature ($^\circ\text{C}$), T_m is monthly mean air temperature ($^\circ\text{C}$), 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_{PAW} was fitted 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_{PAW} was validated by comparison with measurements of g_{sw} .

2.5. Data analysis

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

Spatial maps of both indices were provided in order to compare AOT40 and POD_0 . The mapping was achieved using Arc GIS software (ESRI, USA).

3. Results

3.1. Reparameterization of the stomatal conductance model

The g_{\max} value was set to $465 \text{ mmol H}_2\text{O m}^{-2} \text{ PLA s}^{-1}$ as 98th percentile of g_{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_{sw} recorded throughout the measurements.

The limiting functions of g_{sw} (f_{phen} , f_{light} , f_{temp} , f_{VPD} , f_{PAW} and f_{O_3}) 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_{phen} , f_{temp} , f_{PAW} and f_{O_3} (Fig. 1B, D, F, G). In the literature-based model, functions of phenology, soil water and

Table 4

Summary of g_{sw} parameters in re-parameterized model and literature-based model for *Zelkova serrata*.

Parameter	Re-parameterized model	Literature-based model
g_{\max} (mmol H ₂ O m ⁻² PLA s ⁻¹)	465 SD = 64.5	610
f_{\min} (fraction)	0.1	
f_{phen} SGS (day of year)	105	
EGS (day of year)	320	
f_{phen_a} (fraction)	0.2	
f_{phen_b} (fraction)	0.5	
f_{phen_c} (days)	56	
f_{phen_d} (days)	60	
f_{light} a (constant)	-0.0084	k (constant) 94
f_{temp} T_{opt} ($^\circ\text{C}$)	27	T_{opt} ($^\circ\text{C}$) 43.9
T_{\min} ($^\circ\text{C}$)	11	T_{\min} ($^\circ\text{C}$) 5
T_{\max} ($^\circ\text{C}$)	45	T_{\max} ($^\circ\text{C}$) 45
f_{VPD} VPD _{max} (kPa)	1.1	$D_{0.5}$ (kPa) 3.5
VPD _{min} (kPa)	4.9	α (constant) 2.3
f_{PAW} PAW _t (fraction)	0.58	
f_{O_3} b (constant)	141	
c (constant)	3.4	

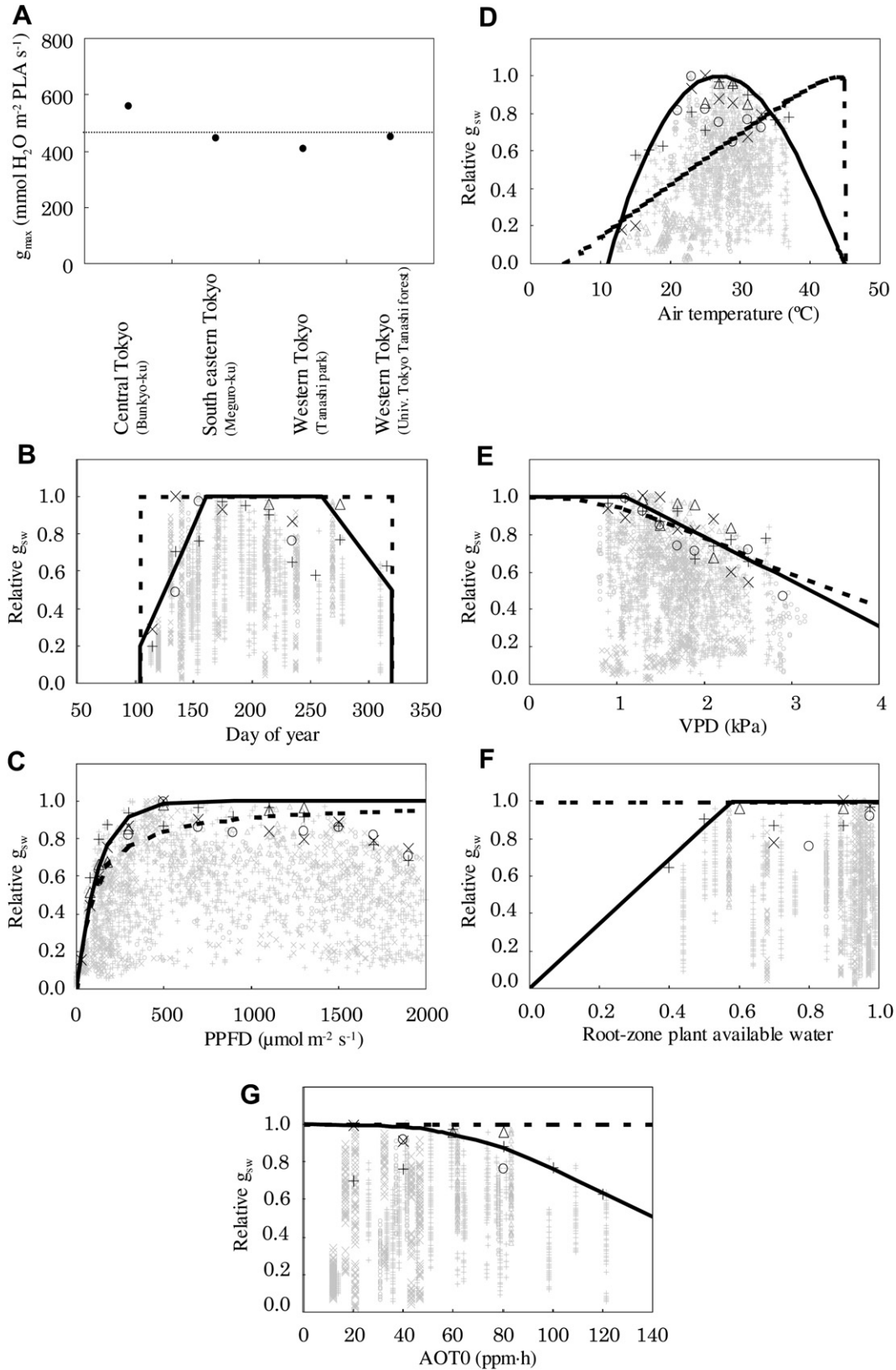


Fig. 1. Parameterization of stomatal conductance model for *Zelkova serrata* (A: g_{max} ; B: f_{phen} ; C: f_{light} ; D: f_{temp} ; E: f_{VPD} ; F: f_{PAW} ; G: f_{O_3}). f_{phen} , f_{light} , f_{temp} , f_{VPD} , f_{PAW} and f_{O_3} are functions of phenology, photosynthetically photon flux density at the leaf surface (PPFD, $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), temperature (T , $^{\circ}\text{C}$), 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_{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 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, except for values less than 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ where 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ class was chosen; T : 2 $^{\circ}\text{C}$; VPD: 0.2 kPa; root-zone plant available water: 0.1; AOT0: 20 ppm h).

Table 5
Results of the regression analysis between measured and estimated g_{sw} using literature-based model and re-parameterized model.

Model	f_{PAW}	f_{O_3}	
Literature-based model	–	–	$R^2 = 0.17$ RMSE = 111.4
Re-parameterized model	–	–	$R^2 = 0.48$ RMSE = 114.9
Re-parameterized model	–	+	$R^2 = 0.54$ RMSE = 98.0
Re-parameterized model	+	–	$R^2 = 0.48$ RMSE = 110.5
Re-parameterized model	+	+	$R^2 = 0.53$ RMSE = 95.5

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

O_3 were not included, i.e., f_{phen} , f_{PAW} and $f_{O_3} = 1$ 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_{O_3} improved the model performance (Table 5). Testing a function of soil water showed no change of model performance because f_{PAW} was 1 in most of the growing seasons, i.e., no limitation to g_{sw} . However, when the re-parameterized model was applied in summer 2010 with low precipitation (27 mm as monthly precipitation in August), f_{PAW} improved the daily course of estimated g_{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_{VPD} and f_{PAW} values in summer (July–August), respectively. In Kanto region, the averaged f_{VPD} values were <0.8 because of high temperature in summer. f_{PAW} values were also <0.8 in this region because high temperature increased evapotranspiration 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_{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_{max} , f_{phen} , f_{temp} , f_{PAW} and f_{O_3} (Fig. 1).

The g_{max} (610 mmol H₂O m⁻² PLA s⁻¹) in the literature-based model was higher than g_{max} obtained in this study (465 mmol H₂O m⁻² PLA s⁻¹). Literature values support g_{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 H₂O m⁻² PLA s⁻¹ as maximum values under saturated light and low VPD conditions. Previous studies have highlighted the importance of g_{max} in determining the predictive capabilities of the model (e.g. Emberson et al., 2000b; Tuovinen et al., 2007). g_{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_{max} is important for identifying the representative value on a regional scale. Although further work is needed, g_{max} presented in this study was based on a larger data set of measurements than previous exercises and is thus recommended for estimating stomatal O₃ uptake of *Z. serrata* in Japan.

The response of g_{sw} to phenology was added to the stomatal conductance model according to the Emberson et al. (2000a) approach. f_{phen} increased from mid-April to May, and gradually decreased from the beginning of September (Fig. 1B). The parameter of f_{phen} improved the model performance at early spring and late autumn (data not shown). Seasonal course of f_{phen} differed depending on the sites (Fig. 1B). In western Tokyo, 98th percentile of measured g_{sw} was 50–70% of g_{max} from mid-August to September in 2008 to 2010. Western Tokyo is a highly polluted area where AOT40 was 31.7 ppm h (Table 1). Ozone-induced reductions in stomatal conductance have been widely reported (Wittig et al., 2007). The function of O₃, f_{O_3} , reduced the error of estimated g_{sw} in the re-parameterized model (Table 5). In summer 2010, low precipitation in Tokyo induced soil moisture deficit resulting in reduction of g_{sw} (Fig. 2). Including the soil moisture function (f_{PAW}) improved the model performance in summer 2010 (Fig. 2). In most seasons, f_{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_{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

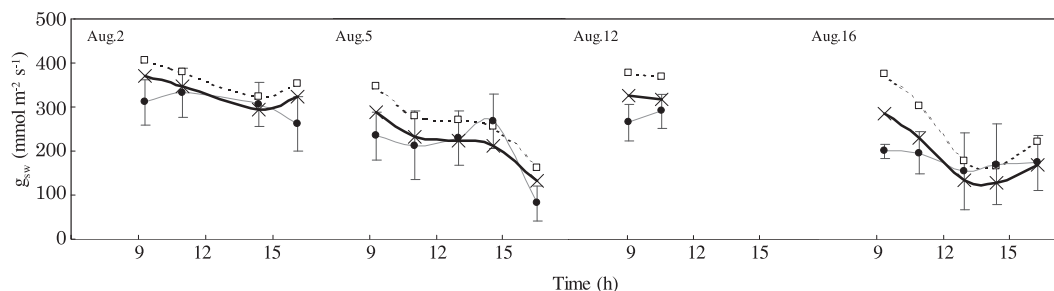


Fig. 2. Examples of the daily trend of measured g_{sw} (●) and estimated g_{sw} by the re-parameterized model (□) and re-parameterized model with the soil moisture function (×) at western Tokyo (Univ. Tokyo Tanashi forest) in August 2010. Measured data are mean values ± SD, $n = 15$ (5 leaves × 3 trees).

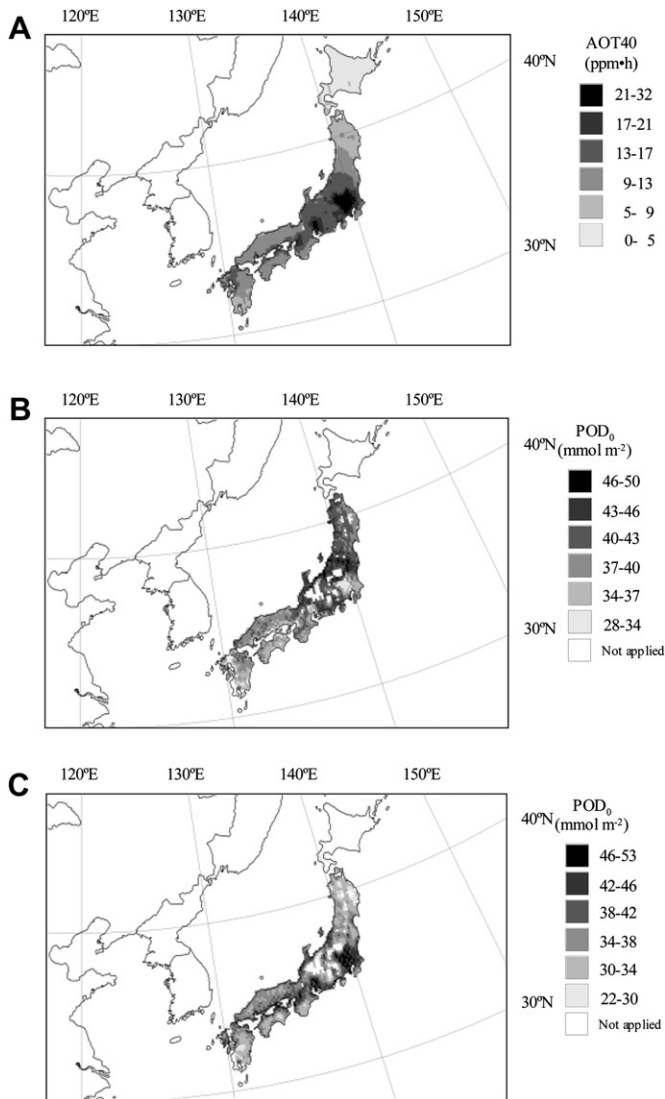


Fig. 3. Maps of estimated AOT40 (accumulated exposure over a threshold of 40 ppb) (A), estimated POD_0 (phytotoxic ozone dose above a flux threshold of $0 \text{ nmol m}^{-2} \text{ s}^{-1}$) for *Zellkova serrata* by the re-parameterized model (B) and the literature-based model (C) in 2007.

soil moisture deficit due to lack of rainfall and/or high temperatures as experienced in August 2010 (Fig. 2). The parameterization of f_{PAW} developed in this study thus improves the calculation of stomatal O_3 uptake for Japan.

The function of air temperature, f_{temp} , was also significantly changed relative to the literature-based model (Fig. 1D), where the T_{opt} was set to more than 40°C . High T_{opt} may cause strong temperature dependency of POD_0 (data not shown). High VPD often occurs in the afternoon together with high air temperature. High ambient O_3 concentrations are often associated with occurrence of high VPD leading to stomatal closure (e.g., Grünhage and Jäger, 1994). In general, T_{opt} ranges from 20 to 30°C for temperate deciduous forest trees (Larcher, 2001). Adequate settings of T_{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, POD_0 provided by re-parameterized model in the same region was relatively low (23 – 34 mmol m^{-2}) (Fig. 3B), because stomatal closure induced by VPD and soil moisture deficit led to limited stomatal O_3 uptake (Fig. 4A, B).

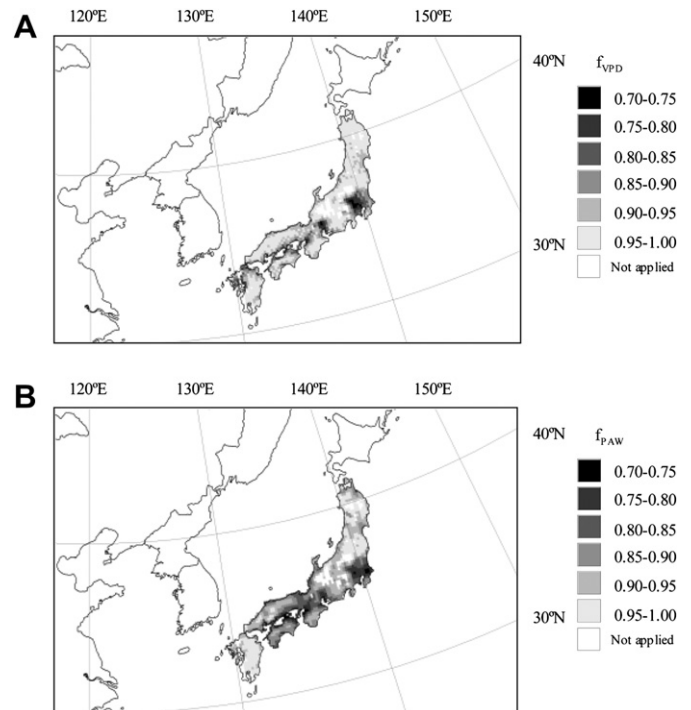


Fig. 4. Spatial distribution of averaged f_{VPD} values (A) and f_{PAW} values (B) of re-parameterized model during summer (July–August) in 2007. f_{VPD} and f_{PAW} show the response of stomatal conductance to vapor pressure deficit and root-zone plant available water, respectively (scaled from 0 to 1).

In Japan, air temperature increased by 1.0°C during the past 100 years (JMA, 2002), which is higher than the world average (0.7°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°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 O_3 uptake may be further limited under an expected warming climate.

Risk assessments based on AOT40 and O_3 flux may not significantly differ under non-limiting conditions for g_{sw} (Schaub et al., 2007). Although annual precipitations are usually very high in Japan, VPD and soil moisture deficit induced by high temperature, and O_3 exposure limited stomatal O_3 uptake under high ambient O_3 levels. As a result, the comparison between POD_0 and AOT40 maps revealed that the spatial patterns of POD_0 differed from those of AOT40. Therefore, current climate conditions and O_3 pollution may limit stomatal O_3 uptake and decoupled it from high O_3 levels in Japan.

5. Conclusion

There are only a few reports of g_{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_{sw} for *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 O_3 exposure can limit stomatal O_3 uptake under high ambient O_3 levels. Caution is thus recommended in using AOT40 as a standard for *Z. serrata* protection in Japan. Response data in the field or free-

air experiments are insufficient in East Asia. Monitoring of O₃ injury and biomass reduction may help to validate the spatial maps of O₃ risks in East Asia and develop the assessment approach in future.

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