

1 **Dependence of stomatal conductance on leaf chlorophyll concentration and**  
2 **meteorological variables**

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1 **Abstract**

2

3 We examined the dependence of stomatal conductance on physiological properties and  
4 meteorological variables using a Jarvis-type stomatal conductance model that included a  
5 function representing leaf chlorophyll concentration as a physiological property. We sampled  
6 the leaves of 5- and 10-year-old *Quercus serrata* trees. A low leaf chlorophyll concentration  
7 imposed a restriction on the opening capacity of the stomata. The stomatal conductance  
8 variability depended markedly on chlorophyll function; the degree of dependence was almost  
9 equal to that on solar radiation or vapour pressure deficit. The characteristics of stomatal  
10 conductance response to meteorological or physiological changes exhibited little seasonal  
11 variation (except relative to temperature). Stomatal conductance variability depended on the  
12 following meteorological parameters in decreasing order: radiation, vapour pressure deficit,  
13 leaf temperature, and soil moisture; this order did not vary seasonally. The dependence of  
14 stomatal conductance variability on the seasonal change in chlorophyll concentration was  
15 larger in spring and autumn than in summer. These results indicate that the consideration of  
16 seasonal changes in plant physiological properties is important in evaluating the water, energy,

1 and CO<sub>2</sub> cycles between plants and the atmosphere.

2

3 *Keywords:* chlorophyll concentration; Jarvis-type model; physiological property; seasonal

4 change; stomatal conductance.

## 1 **1. Introduction**

2

3 Stomata are the primary structures that exchange water and CO<sub>2</sub> between plants and the  
4 atmosphere. Therefore, stomatal conductance ( $g_s$ ) is an important factor in the cycling and  
5 balancing of water, CO<sub>2</sub>, and energy between plants and the atmosphere. Several models of  $g_s$   
6 have been developed. Based on the knowledge that stomata respond to several environmental  
7 variables (*e.g.*, Meidner and Mansfield, 1968; Lange *et al.*, 1971; Neilson and Jarvis, 1975),  
8 Jarvis (1976) empirically expressed  $g_s$  as function of these variables. This model is mainly used  
9 in studies that focus on the stomatal response to environmental conditions. Ball *et al.* (1987)  
10 proposed a semi-empirical model of  $g_s$  based on the close correlation between  $g_s$  and the CO<sub>2</sub>  
11 assimilation rate ( $A$ ). Although there are reports that  $g_s$  is not directly determined by  
12 photosynthetic capacity (*e.g.*, von Caemmerer *et al.*, 2004), many modelling studies of gas  
13 exchange by vegetation use Ball-type models because they can easily be linked with  
14 biochemical photosynthesis models (Farquhar *et al.*, 1980) and can predict  $g_s$  using few  
15 parameters. These models have been extended to the canopy level, and have been used as  
16 sub-models of canopy conductance in land surface models (LSMs) within general circulation

1 models (*e.g.*, Sellers *et al.*, 1996).

2 In addition to meteorological variables such as light, temperature, humidity, ambient CO<sub>2</sub>  
3 concentration, and soil moisture, physiological variables such as leaf ageing and leaf health,  
4 may also affect the seasonal variability in  $g_s$  because stomata are themselves physiological  
5 structures. Nielson and Jarvis (1975) reported that the  $g_s$  of Sitka spruce declines with leaf age  
6 under constant meteorological conditions. The nitrogen and chlorophyll contents of leaves are  
7 often used as parameters of leaf physiological status. In photosynthesis studies, a positive  
8 correlation between photosynthetic activity and leaf nitrogen content has been observed (*e.g.*,  
9 Field and Mooney 1986; Evans 1989). Many studies (*e.g.*, Niinemets and Tenhunen, 1997; Le  
10 Roux *et al.*, 1999; Wilson *et al.*, 2000; Kosugi *et al.*, 2003) use the leaf nitrogen content or  
11 chlorophyll concentration as a function to express the spatial and temporal change in the  
12 maximum carboxylation rate ( $V_{cmax}$ ) in Farquhar-type photosynthesis models. Stomatal studies  
13 report a close relationship between the global-scale distribution of maximum stomatal  
14 conductance and nitrogen content (Schulze *et al.*, 1994). Le Roux *et al.* (1999) included  
15 nitrogen content in a stomatal conductance model. However, although there are studies using  
16 these parameters to explain the spatial distribution of leaf properties on a global- or

1 inner-canopy scale, few studies use it as a parameter affecting seasonal variation in  $g_s$ .  
2 Moreover, the relative importance of physiological properties and meteorological variables in  
3 the temporal behaviour of stomata is also not clear.

4 In this study, we examine the relationship between  $g_s$  and leaf chlorophyll concentration as an  
5 indicator of seasonal leaf physiological properties. We include the function governing this  
6 relationship in a Jarvis-type  $g_s$  model, and examine the dependence of  $g_s$  on leaf physiological  
7 properties and meteorological variables. In addition, we investigate the seasonal difference in  
8 these factors by analysing a seasonally divided dataset.

## 1 List of symbols

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2	<i>Symbol</i>	<i>Definition</i>	<i>Units</i>
3	$A$	net assimilation rate	$\mu\text{mol m}^{-2} \text{s}^{-1}$
4	$C$	total chlorophyll (chl a + chl b) concentration in a leaf	$\text{mg dm}^{-2}$
5	$C_{\text{max}}$	maximum value of $C$	$\text{mg dm}^{-2}$
6	$D_a$	specific humidity deficit in air	$\text{g kg}^{-1}$
7	$D_1$	specific humidity deficit at the leaf surface	$\text{g kg}^{-1}$
8	$D_{10.5}$	value of $D_1$ when $g_s$ is at 50% of $g_{s\text{max}}$	$\text{g kg}^{-1}$
9	$E$	transpiration rate	$\text{mmol m}^{-2} \text{s}^{-1}$
10	$g_s$	stomatal conductance of water vapour	$\text{mol m}^{-2} \text{s}^{-1}$
11	$g_{s\text{max}}$	maximum stomatal conductance	$\text{mol m}^{-2} \text{s}^{-1}$
12	$h$	matric suction of soil at a depth of 20 cm	$\text{cm H}_2\text{O}$
13	$h_{0.5}$	value of $h$ when $g_s$ is at 50% of $g_{s\text{max}}$	$\text{cm H}_2\text{O}$
14	$P$	precipitation	$\text{mm day}^{-1}$
15	$Q$	photosynthetic photon flux density	$\mu\text{mol m}^{-2} \text{s}^{-1}$
16	$S$	SPAD meter value	

1	$T_a$	air temperature at a height of 1.2 m	°C
2	$T_l$	leaf temperature	°C
3	$T_{lmax}$	maximum leaf temperature for stomatal opening	°C
4	$T_{lmin}$	minimum leaf temperature for stomatal opening	°C
5	$T_{lopt}$	optimum leaf temperature for stomatal opening	°C
6	<i>Greek Letters</i>		
7	$\alpha$	degree of contribution of one function to the model accuracy	$\text{mol m}^{-2} \text{s}^{-1}$
8	$\beta$	root mean square error between estimated and observed $g_s$	$\text{mol m}^{-2} \text{s}^{-1}$
9	$\theta$	volumetric soil water content at a depth of 20 cm	%
10	$\theta_r$	volumetric soil water content under air-dried conditions	%
11	$\theta_s$	saturated volumetric soil water content	%

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1 **2. Materials and Methods**

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3 *2.1. Research Site*

4 The research site was the Nagoya University farm situated in the city of Togo, in Aichi, Japan  
5 (35° 6' 33"N, 137° 4' 58"E). Fig. 1 shows the layout of the experimental field. We planted five  
6 *Quercus serrata* (5 years old) widely separated in a fallow field (18 × 8.5 m) in June 2002.

7 These trees were designated samples A-E (tree height: 1.9-2.4 m, stem diameter at 1.2-m  
8 height: 0.8-1.2 cm). In April 2003, 10-year-old trees (samples F-J, tree height: 3.8-4.5 m, stem  
9 diameter at 1.2-m height: 3.9-4.5 cm) were planted in a similar fashion. Each tree was planted  
10 in a pot 50-cm deep and 50-cm diameter. Each tree was individually fully isolated, and the  
11 leaves of each tree were not in contact with each other. There were no objects taller than the  
12 sample trees nearby, and the site was not shadowed throughout the day. *Quercus serrata* is a  
13 common tree in Japanese temperate deciduous broadleaf forests. To examine the effects of soil  
14 moisture conditions on stomatal conductance, we attempted to keep the soil of samples C-E and  
15 H-J dry by placing a cover over the pots to intercept rain. The pot surfaces were only covered  
16 during rainfall events.

1

2 *2.2. Stomatal Conductance, Meteorological Variables, and Chlorophyll Concentration*

3 We made observations on 7 days in 2002 (31 July; 14 August; 25 September; 4, 18, and 31  
4 October; and 18 November) and on 20 days in 2003 (5, 17, and 25 May; 6 and 22 June; 3 July;  
5 13 and 22 August; 12 and 26 September; 3, 10, 19, 25, and 31 October; 4, 12, and 22  
6 November; and 3 and 10 December). These days generally had good weather. The stomatal  
7 conductance ( $g_s$ , mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), transpiration rate ( $E$ , mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), net assimilation  
8 rate ( $A$ , μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), photosynthetic photon flux density (PPFD,  $Q$ ; μmol m<sup>-2</sup> s<sup>-1</sup>), specific  
9 humidity deficit at the leaf surface ( $D_l$ , g kg<sup>-1</sup>), and leaf temperature ( $T_l$ , °C) were obtained for  
10 three leaves per sapling every 1 or 2 hours from early morning until evening using a portable  
11 open-system infrared gas analyser (IRGA; LI-6400; LI-COR, Lincoln, NE, USA). Leaves for  
12 the measurements were chosen randomly from the surface of the tree crowns, although we  
13 avoided worm-eaten and wilted leaves. In order to clarify the diurnal variation in  $Q$ , air  
14 temperature ( $T_a$ , °C), and specific humidity deficit in air ( $D_a$ , g kg<sup>-1</sup>) at a fixed point,  $Q$ ,  $T_a$ , and  
15 relative humidity were observed at a 1.2-m height on a weather observation mast at the  
16 observation site (Fig. 1).  $D_a$  was calculated from  $T_a$  and relative humidity, which were measured

1 and logged at 10-min intervals with a thermo recorder (TR-72S; T&D, Nagano, Japan) placed  
2 in the shelter with a ventilation device. The thermo recorder readings were calibrated with an  
3 Assmann-type ventilation psychrometer (SK-RHG; Sato Keiryoki, Tokyo, Japan).  $Q$  was  
4 measured on the mast using a small photon sensor (IKS-27; Koito Industries, Tokyo, Japan),  
5 and logged with an SQ800 (Grant Instruments, Cambridge, UK). Observations using the  
6 weather mast were only taken on days during which the LI-6400 was operating because of  
7 limited battery power for the ventilation shelter on the mast. Data obtained from the mast were  
8 not used in the model analysis. The precipitation ( $P$ , mm day<sup>-1</sup>) was measured using a  
9 tipping-bucket rain gauge with a resolution of 0.2 mm (Rain Collector 2; Davis Instrument,  
10 Hayward, CA, USA) at the observation site. Only these data were measured continuously  
11 throughout the 2-year observation period. The volumetric soil water content ( $\theta$ , percentage)  
12 was measured using a dielectric aquameter, ECH<sub>2</sub>O EC-20 (Decagon Devices, Pullman, WA,  
13 USA) buried to a depth of 20 cm. As with observations from the weather mast,  $\theta$  was manually  
14 measured only on days during which the LI-6400 was operating. To convert the volumetric soil  
15 water content into matric suction ( $h$ , cm H<sub>2</sub>O), we investigated  $\theta$  when the values of  $h$  were 30,  
16 50, 100, 200, 500, 1000, and 1600 cm H<sub>2</sub>O, using a soil pF gauge (DIK-3420; Daiki Rika

1 Kogyo, Tokyo, Japan) in the laboratory. The volume of the soil sampler for determining matric  
2 suction was 100 cm<sup>3</sup>. In addition, a characteristic soil water curve, as derived below (van  
3 Genuchten, 1980), approximated the results.

$$4 \quad \theta = \theta_r + \frac{\theta_s - \theta_r}{\left\{1 + (k_a h)^{k_b}\right\}^{(1-1/k_b)}} \quad (1)$$

5 where  $\theta_s$  is the saturated soil water content (%),  $\theta_r$  is the soil water content under air-dried  
6 conditions (%), and  $k_a$  and  $k_b$  are constants.  $\theta_s$  and  $\theta_r$  were 52.1-60.0% and 5-13%, respectively,  
7 among saplings.  $k_a$  and  $k_b$  were 0.04-0.07 and 1.3-1.6, respectively, and were calculated using  
8 the non-linear least-squares method using the equation solver in Microsoft Excel that  
9 minimised the root mean square error (RMSE) between the measured and predicted values for  $\theta$ .  
10 The SPAD value ( $S$ , dimensionless), a good indicator of leaf chlorophyll concentration, was  
11 measured using a chlorophyll meter (SPAD-502; Minolta, Tokyo, Japan).  $S$  was observed for  
12 three leaves per sapling every hour, and the daily mean was calculated for each sapling. In 2002,  
13 leaves observed using the LI-6400 were not the same leaves observed using the SPAD meter.  
14 Therefore, the average  $S$  for three leaves was used in the 2002 calculations. In 2003, the same  
15 leaves were observed using the LI-6400 and SPAD meter. Hoshino (1996) derived the

1 following equation from an examination of the relationship between SPAD and the actual leaf  
2 chlorophyll concentration of *Q. serrata*.

$$3 \quad C = 0.0008S^2 + 0.0879S \quad R^2 = 0.98 \quad (2)$$

4 where  $C$  is the leaf chlorophyll-a and -b concentrations ( $\text{mg dm}^{-2}$ ), and  $S$  is the SPAD value  
5 (dimensionless). Although this is a quadratic equation, the relationship between  $S$  and  $C$  is  
6 almost linear. In this study, we converted  $S$  into  $C$  using this equation.

7

### 8 *2.3. Jarvis-type Stomatal Conductance Model*

9 We used the Jarvis-type stomatal conductance model (Jarvis, 1976), which has also been used  
10 as a sub-model describing transpiration from vegetation in the second-generation land surface  
11 model (Pitman, 2003). Jarvis (1976) described the relationship between  $g_s$  and several variables  
12 in a phenomenological model, where the maximum stomatal conductance ( $g_{s\text{max}}$ ) is reduced by  
13 the functions associated with each variable. For environmental variables in the Jarvis-type  
14 model, we used  $Q$ ,  $D_1$ ,  $T_1$ , and  $h$ . To examine the effect of the physiological activity of leaves on  
15  $g_s$ , we used the model shown below, to which the function of  $C$  was added as an indicator of the  
16 seasonal change in leaf physiological properties.

$$1 \quad g_s = g_{smax} f(Q) f(D_1) f(T_1) f(h) f(C) \quad (3)$$

2 where  $g_{smax}$  is the maximum stomatal conductance ( $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ), and  $f(Q)$ ,  $f(D_1)$ ,  $f(T_1)$ ,  $f(h)$ ,  
3 and  $f(C)$  are functions of PPFD ( $Q$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), specific atmospheric humidity deficit ( $D_1$ ,  $\text{g}$   
4  $\text{kg}^{-1}$ ), leaf temperature ( $T_1$ ,  $^\circ\text{C}$ ), soil matric suction ( $h$ ,  $\text{cm H}_2\text{O}$ ), and leaf chlorophyll  
5 concentration ( $C$ ,  $\text{mg dm}^{-2}$ ), respectively. Each function varies independently from 0 to  
6 approximately 1, and each function operates as a reduction factor for  $g_{smax}$ . The functions for  $Q$ ,  
7  $D_1$ ,  $T_1$ , and  $h$  are referred to in many other studies (e.g., Jarvis, 1976; Choudhury and Idso, 1985;  
8 Stewart, 1988; Kosugi *et al.*, 1995; Hanan and Prince, 1997; Strachan and McCaughey, 2002).

9 These functions are expressed as follows:

$$10 \quad f(Q) = \frac{Q}{Q + 1/k_1} \quad (4)$$

$$11 \quad f(D_1) = \frac{1}{1 + (D_1/D_{10.5})^{k_2}} \quad (5)$$

$$12 \quad f(T_1) = \left( \frac{T_1 - T_{1min}}{T_{1opt} - T_{1min}} \right) \left( \frac{T_{1max} - T_1}{T_{1max} - T_{1opt}} \right)^{\left( \frac{T_{1max} - T_{1opt}}{T_{1opt} - T_{1min}} \right)} \quad (6)$$

$$13 \quad f(h) = \frac{1}{1 + (h/h_{0.5})^{k_3}} \quad (7)$$

14 where  $D_{10.5}$  is the  $D_1$  value when  $f(D_1)$  is equal to 0.5;  $T_{1min}$ ,  $T_{1opt}$ , and  $T_{1max}$  are the minimum,

1 optimum, and maximum leaf temperatures, respectively;  $T_{lmin}$  and  $T_{lmax}$  describe the leaf  
2 temperature when  $f(T_l)$  is 0;  $T_{lopt}$  is the leaf temperature when  $f(T_l)$  is 1;  $h_{0.5}$  is the  $h$  value when  
3  $f(h)$  is equal to 0.5;  $k_1$  is the slope of the  $g_s$ - $f(Q)$  curve at the origin; and  $k_2$  and  $k_3$  are constants  
4 that are connected to the curvature of the response curve. The schematic diagrams in Fig. 2  
5 show that each function varies with the parameters.

6

#### 7 *2.4. Function for Chlorophyll Concentration*

8 A detailed function for  $C$  has not previously been proposed. Therefore, we observed the actual  
9 relationship between  $g_s$  and  $C$ . When  $C$  was low,  $g_s$  increased sensitively in proportion to  $C$ .  
10 However,  $g_s$  appeared to reach a maximum under conditions of high  $C$ . Therefore, we adopted  
11 the following equation to describe  $C$ :

$$12 \quad f(C) = \frac{C(C_{max} + k_4)}{C_{max}(C + k_4)}, \quad (8)$$

13 where  $C_{max}$  is the  $C$  value when  $f(C)$  is 1, and  $k_4$  is a constant related to the curvature of the  
14 response curve. This equation is similar to that used in other studies as a function of radiation  
15 (*e.g.*, Stewart, 1988; Ogink-Hendriks, 1995). The curve produced by this function varies as

1 shown in Fig. 2, according to the variation in  $k_4$ .

2

### 3 *2.5. Fitting of Model Parameters*

4 The parameter values were calculated using a non-linear least-squares technique using the

5 equation solver in Microsoft Excel to minimise the root mean square error (RMSE) between

6 measured and predicted values for  $g_s$ . To calculate values that expressed actual phenomena, we

7 imposed the following constraints on the calculations of the parameters:  $g_{s\max}$  cannot be smaller

8 than the maximum  $g_s$  of actual observed data, and  $T_{l\min}$  and  $T_{l\max}$  cannot be less than 0 or greater

9 than 50.

1 **3. Results and Discussion**

2

3 *3.1. Variation of Meteorological Factors and Chlorophyll Concentration*

4 Figure 3 shows the measurements of the meteorological parameters (PPFD,  $Q$ ; air  
5 temperature,  $T_a$ ; specific humidity deficit,  $D_a$ ; and matric suction,  $h$ ) on each observation date,  
6 as well as precipitation ( $P$ ) for the entire year, for 2002 and 2003. The values for  $Q$ ,  $T_a$ , and  $D_a$   
7 were obtained at the weather observation mast and are average values from 11:00-13:00. In Fig.  
8 3,  $Q$ ,  $T_a$ ,  $D_a$  and  $h$  are not necessarily representative seasonal values because observations were  
9 made only on days on which leaf gas exchange was measured. Error bars for  $h$  indicate the  
10 variance among samples. The variance of  $h$  for 10-year-old saplings was larger than that for  
11 5-year-old saplings. Compared with the soil of 5-year-old trees, that of 10-year-old trees was  
12 very dry in September (around day 250 of 2003). This is probably attributable to the higher  
13 evaporation rate of 10-year-old trees, which have many more leaves than do 5-year-old trees.  
14 Figure 4 shows the temporal series for leaf chlorophyll concentration ( $C$ ) in 2002 and 2003.  
15 Error bars for  $C$  indicate the variance among samples. The chlorophyll concentration of leaves  
16 displayed seasonal variability; it gradually increased from spring to summer, reached a steady

1 state in summer, and then decreased from autumn to early winter.

2

### 3 *3.2. Diurnal and Seasonal Variation in Stomatal Conductance, Transpiration and*

#### 4 *Photosynthesis*

5 The variation in stomatal conductance ( $g_s$ ), transpiration rate ( $E$ ), and assimilation rate ( $A$ ) of  
6 sample C (a 5-year-old tree) on five selected observation dates in 2003 is shown in Fig. 5. The  
7 diurnal patterns of each show maximum values in the daytime and minimum values in the early  
8 morning or evening. In detail, the peaks of  $g_s$  and  $A$  appear generally at the same time, although  
9 the time of the peak differed on different dates; the peak of  $E$  sometimes appeared later than  
10 those of  $g_s$  and  $A$  (e.g., on September 26).  $E$  is affected not only by  $g_s$ , but also by the vapour  
11 pressure deficit. The peak vapour pressure deficit on a good-weather day generally appears in  
12 the afternoon, and this may account for the time lag in  $E$ . This diurnal characteristic was seen on  
13 other many observation days.  $g_s$ ,  $E$ , and  $A$  showed a seasonal pattern: low in spring (May) and  
14 late autumn (December), and high in summer and autumn (July-November).

15

### 1 3.3. Relationship among Variables

2 To consider the effects of each variable on stomatal behaviour in a model, we must determine  
3 whether the measured variables are independent. We examined the relationships among PPFD  
4 ( $Q$ ), specific humidity deficit ( $D_1$ ), leaf temperature ( $T_1$ ), matric suction ( $h$ ), and chlorophyll  
5 concentration ( $C$ ), which are used here in the Jarvis-type model. There was no clear relationship  
6 among these variables, except for an apparently proportional relationship between  $T_1$  and  $D_1$ .  
7 This implies that the effects of  $T_1$  and  $D_1$  on stomatal conductance cannot be evaluated  
8 separately. Although there are several studies in which temperature is not used in the models  
9 because of this tendency (*e.g.*, Toda *et al.*, 2000), we used both  $T_1$  and  $D_1$  in the model because  
10 the  $g_s$  response curves to each variable do not take the same form. For example, when  $T_1$  is low,  
11  $D_1$  is also low. However, low  $T_1$  restrains  $g_s$ , while low  $D_1$  does not (see Fig. 2). If  $T_1$  were  
12 omitted from the model, the effect of low temperature may not be considered.

13 A proportional relationship between the vertical distribution of light in the canopy and the  
14 vertical leaf nitrogen concentration by leaf acclimation, and thus photosynthetic capacity, has  
15 been reported (*e.g.*, Le Roux *et al.*, 1999; Meir *et al.*, 2002). However, for a thinned canopy  
16 forest, the leaf chlorophyll content was constant throughout the canopy (Lewandowska and

1 Jarvis, 1977). All the sample trees in our study were widely separated and were not big enough  
2 to result in large vertical light differences among the leaves. Moreover, we observed only leaves  
3 positioned on the surface of the tree crown. Therefore, there was no relationship between  $Q$  and  
4  $C$  in this study, and we can consider  $C$  as an indicator of “seasonal change” in leaf physiological  
5 properties, and as parameter independent of the other meteorological variables.

6

#### 7 *3.4. Model Parameters and Response of Stomata to Variables*

8 Table 1 indicates the parameter values estimated using the method described in section 2.5.  
9 Figure 6 shows the relationships between the environmental variables and  $g_s$ ; the fitted line for  
10 each function for sample C in 2003 is shown as an example of a 5-year-old tree. Each fitted line  
11 is drawn at roughly the upper boundary of the actual observed values, so that this model clearly  
12 expresses the response characteristics of stomata to each variable. Similar features were  
13 observed for the other trees.

14 The maximum stomatal conductances ( $g_{smax}$ ) of the sample trees were between 0.21 and 0.37  
15  $\text{mol m}^{-2} \text{s}^{-1}$  (sample A in 2002 and samples B and C in 2003, respectively), as shown in Table 1.  
16 These  $g_{smax}$  are similar to those reported by Sirisampan *et al.* (2003) for mature *Q. serrata* trees

1 from a forest near our site. Overall, the  $g_{s\max}$  of 5-year-old trees was higher than that of  
2 10-year-old trees.

3 There were no clear differences in the other parameter values related to the responses of  $g_s$  to  
4 each variable for the 5- and 10-year-old trees, except for the response to the soil pressure head  
5 for 10-year-old trees. Although the  $h_{0.5}$  for 10-year-old trees was larger than for 5-year-old  
6 trees, as shown in Table 1, restriction of  $g_s$  by a shortage of soil water was rarely measured for  
7 any tree, so the response to  $h$  may not be accurate. The responses for each variable have the  
8 following general characteristics for each sample:  $g_s$  reached light saturation at approximately  
9  $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ ;  $g_s$  became generally less than 30% of  $g_{s\max}$  as  $D$  became greater than  $20 \text{ g kg}^{-1}$ .  
10 The optimum leaf temperature for stomata ( $T_{\text{lopt}}$ ) ranged between  $20$  and  $27.5^\circ\text{C}$ , and the  
11 stomata closed at low ( $0$ - $5^\circ\text{C}$ ) and high ( $44$ - $50^\circ\text{C}$ ) temperatures. Although these results are  
12 similar to the results obtained from other trees in Japan (*e.g.*, Kosugi *et al.*, 1995; Sirisampan *et*  
13 *al.*, 2003),  $T_{\text{lopt}}$  is higher ( $> 30^\circ\text{C}$ ) in other studies. The maximum chlorophyll concentration was  
14 between  $5.0$  and  $7.0 \text{ mg dm}^{-2}$ .

15 As an example, Fig. 7 shows the diurnal variation in observed  $g_s$  for a leaf of sample C (leaf  
16 C-2 in Fig. 5), the estimated  $g_s$ , and the variation in each function used in the model for five

1 days in 2003. To examine the effectiveness of importing  $f(C)$  to the model, the estimated  $g_s$  was  
2 calculated using two model types, namely, a model constructed from all functions [Eq. (3)] and  
3 a model that did not include  $f(C)$ . We call these models “model A” and “model B”, respectively.  
4 Model B uses the same parameter values for the meteorological functions as does model A.  
5 Both models explain the diurnal variation in  $g_s$  well in the mid-growing season, and there are no  
6 large differences between the two models (*e.g.*, 26 September). From the variation in each  
7 function, it is easily seen that the dominant factors controlling diurnal variation in  $g_s$  are light  
8 and vapour pressure deficit. In morning and evening,  $f(Q)$  is low, and light availability becomes  
9 the limiting factor for  $g_s$ . In the day, although  $f(Q)$  approaches 1, it is not a limiting factor;  $f(D_l)$   
10 is reduced by the increase in vapour pressure deficit and is a greater limiting factor.  
11 By contrast, in spring (2 May) and late autumn (10 December), a distinct difference in  $g_s$   
12 estimated using the two models appears. While model B largely overestimates  $g_s$  in late  
13 autumn, model A expresses the actual  $g_s$  well. This indicates that the leaf chlorophyll  
14 concentration effectively explains the low  $g_s$  in autumn. In spring, although the  $g_s$  estimated  
15 using model A is closer to the value determined using model B, model A still overestimates  $g_s$ .  
16 In addition to chlorophyll content, other parameters may limit  $g_s$  in spring. The features

1 mentioned in this section were commonly observed in all sample trees and on other observation  
2 dates.

3

### 4 3.5. Dependence of the Variability in $g_s$ on other Variables

5 To compare the effect of each variable on the variability in  $g_s$ , and to clarify the contribution of  
6 each function to the model precision, we calculated the RMSE between estimated and observed  
7  $g_s$  values for each of the following models:

8 model without  $f(Q)$ ;  $g_s = g_{smax} f(D_1)f(T_1)f(h)f(C)$ , (9)

9 model without  $f(D_1)$ ;  $g_s = g_{smax} f(Q)f(T_1)f(h)f(C)$ , (10)

10 model without  $f(T_1)$ ;  $g_s = g_{smax} f(Q)f(D_1)f(h)f(C)$ , (11)

11 model without  $f(h)$ ;  $g_s = g_{smax} f(Q)f(D_1)f(T_1)f(C)$ , (12)

12 model without  $f(C)$ ;  $g_s = g_{smax} f(Q)f(D_1)f(T_1)f(h)$ . (13)

13 Here, Eq. (13) is same as model B in section 3.4. When one function is removed from the model  
14 (*i.e.*, model A [Eq. (3)]), the model precision will decline (*i.e.*, increase RMSE), reflecting the  
15 contribution of that function. We define the contribution of one function [*i.e.*,  $f(x)$ ] to the  
16 variability in  $g_s$  ( $\alpha_x$ , mol m<sup>-2</sup> s<sup>-1</sup>) as follows:

1 
$$\alpha_x = \beta_{x\text{-exc}} - \beta_A \tag{14}$$

2 where  $\beta_{x\text{-exc}}$  and  $\beta_A$  are the RMSE of the model in which  $f(x)$  was excluded [*i.e.*, Eq. (9) – (13)  
3  $\text{mol m}^{-2} \text{s}^{-1}$ ], and the RMSE of model A ( $\text{mol m}^{-2} \text{s}^{-1}$ ), respectively.

4 Figure 8 shows the contribution ( $\alpha$ ) of each function for 5-year-old trees in 2003. The order of  
5  $\alpha$  for each environmental function was  $f(Q) > f(D_1) > f(T_1) > f(h)$ . The results obtained for  
6 5-year-old trees in 2002 and for 10-year-old trees in 2003 were similar. Moreover,  
7 Ogink-Hendriks (1995; for surface conductance) and Sirisampan *et al.* (2003) obtained similar  
8 results for the dependence of each function or variable. Although the level of  $\alpha$  for  $f(C)$  differed  
9 among trees, it was very large in all trees, and was similar to or greater than that of  $f(D_1)$ . This  
10 means that, in addition to the meteorological variables, the chlorophyll concentration is also a  
11 very effective parameter expressing seasonal variability in stomatal behaviour.

12

### 13 3.6. Seasonal Change in Stomatal Response

14 The seasonal differences in the values of the model parameters and in the contribution of each  
15 function to the model performance were examined using the 2003 data for 5-year-old trees  
16 because there were sufficient data. We divided the dataset into three seasons (spring, 2 May to 6

1 June; summer, 22 June to 26 September; autumn, 3 October to 10 December). We used these  
2 data in the Jarvis-type model and examined the seasonal differences in the parameter values and  
3 the contributions of the functions. Subdivision of the year-long dataset resulted in a narrow  
4 range of  $T_l$ , not only for  $T_{lmin}$  and  $T_{lmax}$ , but also for  $T_{lopt}$ . Therefore, we inferred that these  
5 parameter values become unreliable when estimated using a subdivided dataset, and assigned  
6 these parameter values as those from the results for the entire year (see Table 1). For the other  
7 parameters, we used the values calculated for the whole-year analysis (Table 1) as the initial  
8 value for each parameter, and calculated the fitted values using the method described in section  
9 2.5.

10 Table 2 gives the fitted parameter values for spring, summer, and autumn, for 5-year-old trees  
11 with fixed values for  $T_l$ . There were no distinct seasonal differences in any parameter except for  
12  $g_{smax}$ , which was lower in spring than in summer and autumn. This probably arises from the fact  
13 that  $g_s$  is low in spring, regardless of the chlorophyll concentration. If we can add the  
14 parameters related to the spring-specific factor limiting  $g_s$  to the model, the resulting  $g_s$  will be  
15 closer to the  $g_s$  in other seasons. Although we did not evaluate seasonal changes in  $T_{lmin}$ ,  $T_{lopt}$ ,  
16 and  $T_{lmax}$ , Nielson and Jarvis (1975) reported that the optimum leaf temperature for  $g_s$  in Sitka

1 spruce changed seasonally.

2 Figures 9a, b, and c show the relative contribution ( $\alpha$ , mol m<sup>-2</sup> s<sup>-1</sup>) of each function to the

3 model performance during spring, summer, and autumn, respectively. The order of the

4 contributions of  $f(Q)$ ,  $f(D_1)$ ,  $f(T_1)$ , and  $f(h)$  was generally similar for each season and for the

5 entire year (Fig. 8), *i.e.*,  $f(Q) > f(D_1) > f(T_1) > f(h)$ , although parameter  $T_1$  was fixed. However,

6 the  $\alpha$  of  $f(C)$  indicated an obvious seasonal change. The  $\alpha$  of  $f(C)$  was very low in summer, but

7 very high in spring and autumn. Figure 7 shows that only  $f(C)$  decreases markedly in spring and

8 autumn, while it remains high in summer. Therefore, chlorophyll was only a major limiting

9 factor for  $g_s$  in spring and autumn.

#### 1 4. Conclusion

2

3 We examined the dependence of stomatal behaviour in *Quercus serrata* on the physiological  
4 properties of leaves and meteorological variables for entire-year and seasonal data using a  
5 Jarvis-type stomatal conductance model and inserting a function of leaf chlorophyll  
6 concentration. Our study produced a number of findings.

7 1. A reduction in the chlorophyll concentration induces a hyperbolic decrease in stomatal  
8 conductance.

9 2. The variability in stomatal conductance depended on meteorological variables in the order  
10 PPFD > specific humidity deficit > leaf temperature > matric suction; this order did not  
11 change seasonally, although it may be location, year, and species specific.

12 3. The dependence of stomatal conductance on physiological properties, as indicated by the  
13 chlorophyll concentration, was as large as that on PPFD or specific humidity deficit, and  
14 was larger in spring and autumn than in summer because the chlorophyll concentration is  
15 relatively stable in summer.

16 4. Although the model that includes chlorophyll is more accurate in autumn compared to the

1 model constructed using meteorological variables only, in spring it is still insufficient to  
2 correct the model, suggesting that other limiting factors may exist.

3 This research suggests that the effect of leaf physiological properties, such as those of  
4 pre-mature and senescent leaves, is important in evaluating stomatal behaviour, and  
5 consequently heat and gas exchange in plants. The model that considered leaf physiological  
6 properties was effective for estimating the seasonal change in stomatal conductance. The  
7 inclusion of plant physiological properties will not only improve leaf-scale models, but also  
8 vegetation-atmosphere gas exchange models. On a canopy scale, remote-sensing techniques  
9 could be used for evaluating canopy physiological properties.

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2

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2

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10 Table 1

11 Fitted parameter values of the model for each sample, and model precision (RMSE; mol H<sub>2</sub>O

12 m<sup>-2</sup> s<sup>-1</sup>).  $g_{smax}$ , maximum stomatal conductance (mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>);  $k_1$ , slope of the  $g_s$ - $f(Q)$  curve

13 at the origin;  $D_{10.5}$ , specific humidity deficit (g kg<sup>-1</sup>) when  $f(D_1) = 0.5$ ;  $T_{lmin}$ ,  $T_{lopt}$ , and  $T_{lmax}$ ,

14 minimum, optimum, and maximum leaf temperatures (°C), respectively;  $h_{0.5}$ , soil matric

15 suction (cm H<sub>2</sub>O) when  $f(h) = 0.5$ ;  $C_{max}$ , maximum chlorophyll concentration (mg dm<sup>-2</sup>);  $k_2$ ,  $k_3$ ,

16 and  $k_4$ , constants reflecting the curvature of the response curve.

	$g_{\text{max}}$	$k_1$	$D_{10.5}$	$k_2$	$T_{1\text{min}}$	$T_{\text{lopt}}$	$T_{\text{lmax}}$	$h_{0.5}$	$k_3$	$C_{\text{max}}$	$k_4$	RMSE
<b>5-year-old saplings in 2002</b>												
A	0.210	0.012	20.0	4.0	1.0	25.0	50.0	1000	3.0	5.0	1.5	0.0409
B	0.330	0.011	18.0	3.5	3.0	26.0	49.0	1500	3.0	5.0	1.5	0.0707
C	0.450	0.010	16.5	5.0	0.0	25.5	45.0	1200	3.0	5.0	1.5	0.0836
D	0.260	0.017	22.0	3.5	0.0	24.0	50.0	1200	3.0	5.0	1.0	0.0614
E	0.235	0.013	22.0	3.3	5.0	27.5	50.0	1200	3.0	5.0	1.3	0.0470
<b>5-year-old saplings in 2003</b>												
A	0.330	0.012	15.0	2.5	5.0	25.0	45.0	1200	3.0	6.0	1.4	0.0655
B	0.370	0.016	16.0	3.0	4.0	24.0	48.0	1200	3.0	6.0	1.3	0.0690
C	0.370	0.018	14.0	2.5	1.0	22.0	45.0	1200	3.0	6.0	1.3	0.0663
D	0.350	0.011	15.0	3.5	3.0	22.0	48.0	1200	3.0	6.5	2.5	0.0640
E	0.310	0.016	16.0	3.0	3.0	24.0	48.0	1200	3.0	6.0	2.0	0.0628
<b>10-year-old saplings in 2003</b>												
F	0.255	0.022	16.0	4.0	5.0	25.0	45.0	4000	2.5	6.0	2.0	0.0640
G	0.260	0.015	13.5	3.5	0.0	21.0	45.0	10000	5.0	6.0	2.0	0.0494
H	0.230	0.013	13.0	2.5	0.0	20.0	45.0	6000	3.0	6.5	2.0	0.0360
I	0.255	0.014	13.0	3.0	4.0	20.0	44.0	7000	3.0	7.0	2.5	0.0358
J	0.240	0.010	13.0	3.0	0.0	21.0	45.0	1200	3.0	6.0	1.0	0.0449

1 Table 2

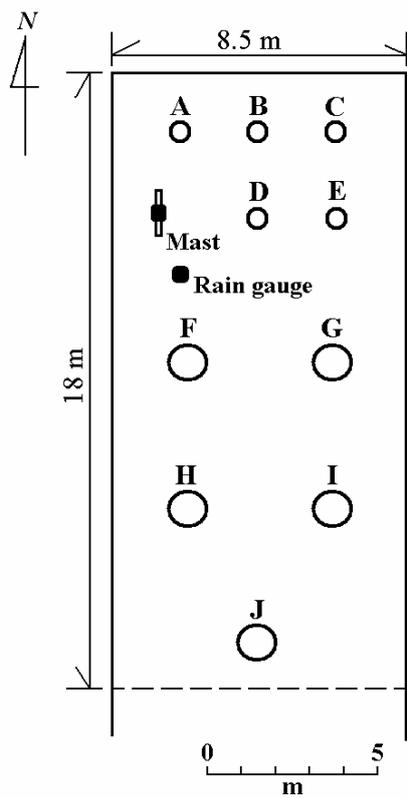
2 Fitted parameter values of 5-year-old trees in spring, summer, and autumn of 2003, and model  
 3 precision (RMSE; mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>).  $g_{smax}$ , maximum stomatal conductance (mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>);  
 4  $k_1$ , slope of the  $g_s$ - $f(Q)$  curve at the origin,  $D_{10.5}$ , specific humidity deficit (g kg<sup>-1</sup>) when  $f(D_i) =$   
 5 0.5;  $h_{0.5}$ , soil matric suction (cm H<sub>2</sub>O) when  $f(h) = 0.5$ ;  $C_{max}$ , maximum chlorophyll  
 6 concentration (mg dm<sup>-2</sup>);  $k_2$ ,  $k_3$ , and  $k_4$ , constants reflecting the curvature of the response curve.

	Spring	Summer	Autumn
$g_{smax}$	0.15–0.21	0.28–0.37	0.31–0.37
$k_1$	0.013–0.019	0.011–0.018	0.011–0.018
$D_{10.5}$	13.0–17.0	13.0–16.0	14.0–16.0
$k_2$	2.5–4.0	2.0–3.5	2.5–3.5
$h_{0.5}$	1200	1200	1200
$k_3$	3.0	3.0	3.0
$C_{max}$	5.0	5.0–6.5	6.0–6.5
$k_4$	1.3–2.5	1.3–2.5	1.3–2.5
RMSE	0.0170–0.0469	0.0410–0.0633	0.0477–0.0582

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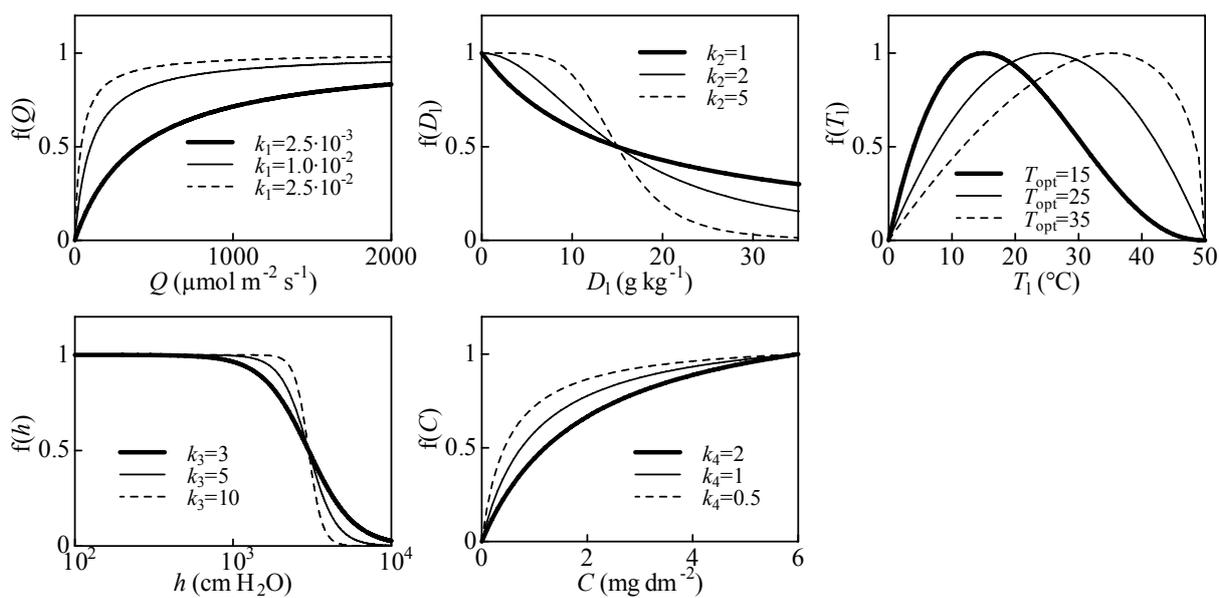
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2 Fig. 1. Layout of the trees, the weather observation mast and the rain gauge in the experimental

3 field. A-E and F-J are 5- and 10-year-old trees, respectively.

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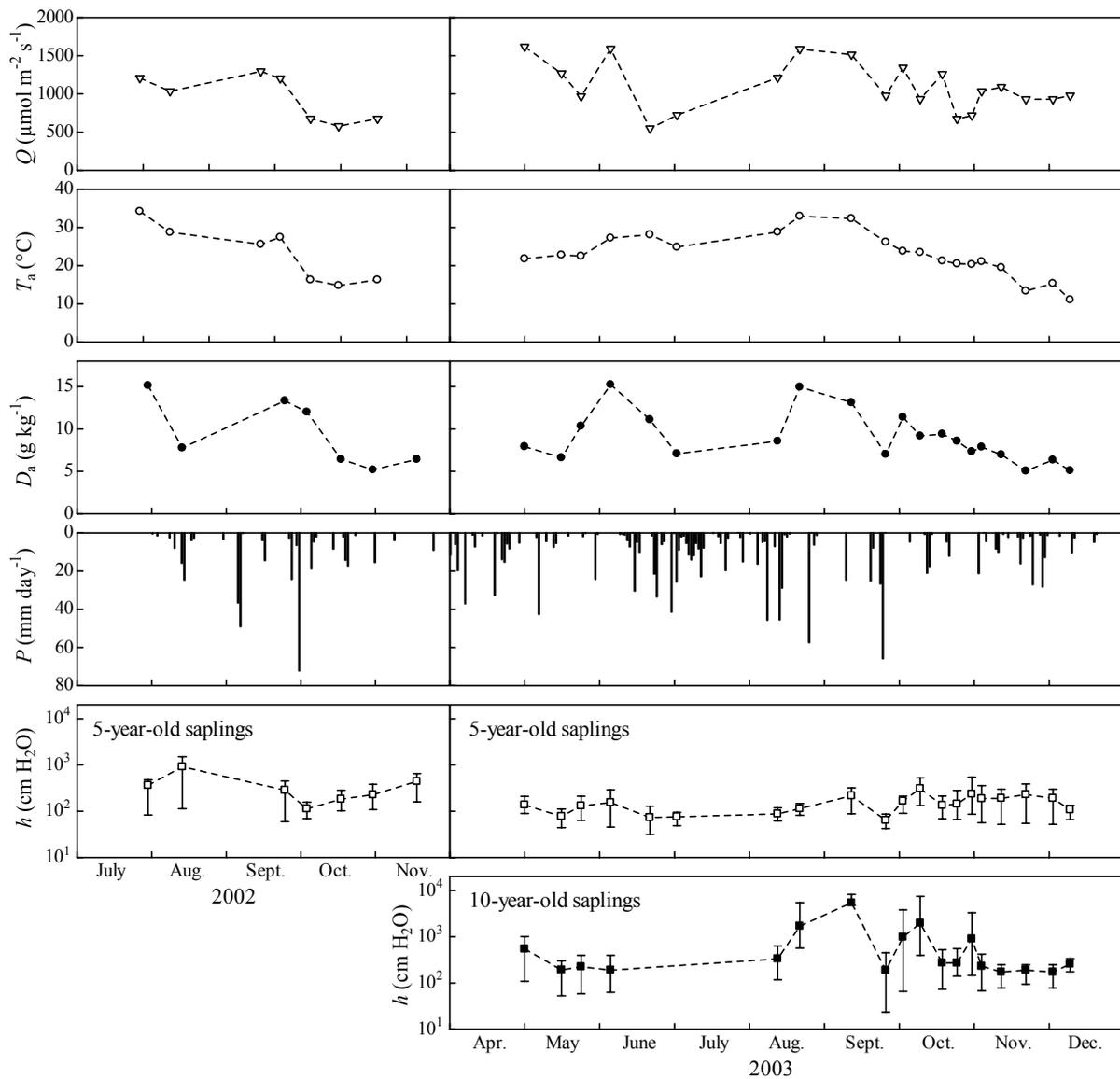
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 2 Fig. 2. Plots of the functions associated with each variable when parameter values were altered.  
 3 PPFD,  $Q$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; specific humidity deficit,  $D_1$ ,  $\text{g kg}^{-1}$ ; leaf temperature,  $T_1$ ,  $^{\circ}\text{C}$ ; soil matric  
 4 suction,  $h$ ,  $\text{cm H}_2\text{O}$ ; and chlorophyll concentration,  $C$ ,  $\text{mg dm}^{-2}$ . Here,  $D_{10.5}$ ,  $T_{1\text{min}}$ ,  $T_{1\text{max}}$ ,  $h_{0.5}$  and  
 5  $C_{\text{max}}$  were fixed at 15, 0, 50, 3000 and 6, respectively.

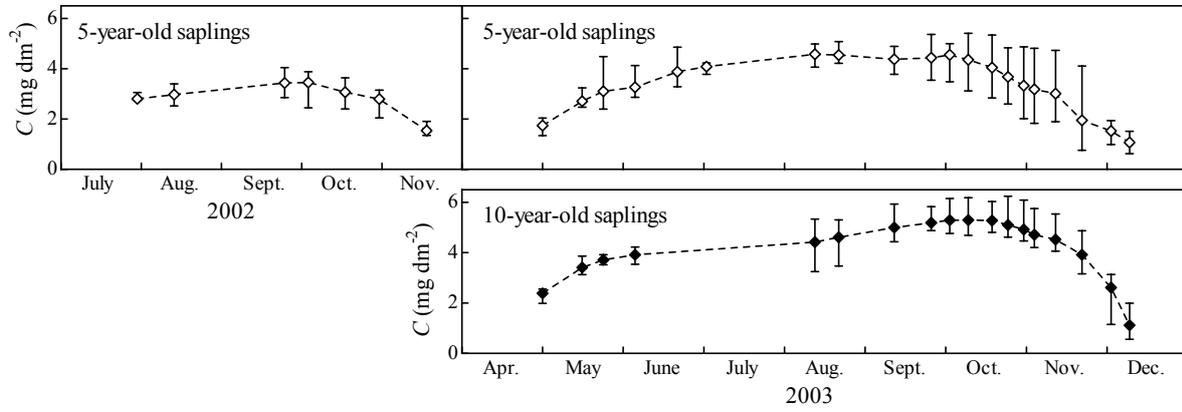
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 2 Fig. 3. Seasonal variation in the daily values of PPFD ( $Q$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), air temperature ( $T_a$ ,  $^{\circ}\text{C}$ ),  
 3 specific humidity deficit of air ( $D_a$ ,  $\text{g kg}^{-1}$ ), precipitation ( $P$ ,  $\text{mm day}^{-1}$ ), observed from the  
 4 weather observation mast (1.2 m height), and soil water potential ( $h$ ,  $\text{cm H}_2\text{O}$ ) in 2002 (left) and  
 5 2003 (right).  $Q$ ,  $T_a$  and  $D_a$  are average values between 11:00 and 13:00. Error bars indicate the  
 6 variance among the five sample trees.

1



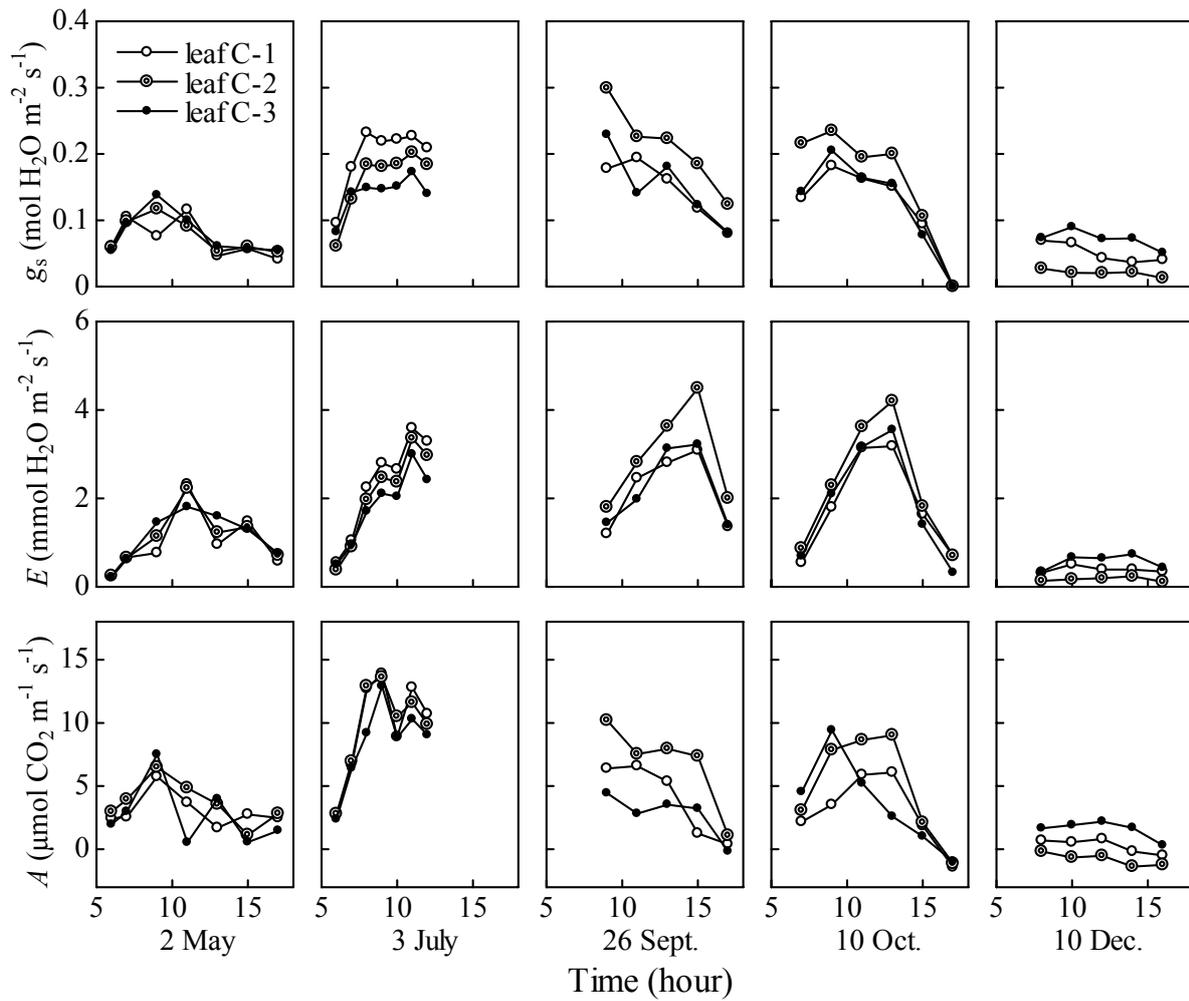
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3 Fig. 4. Seasonal variation in the chlorophyll concentration in leaves ( $C$ ,  $\text{mg dm}^{-2}$ ) in 2002 (left)

4 and 2003 (right). Error bars indicate the variance among the five sample trees.

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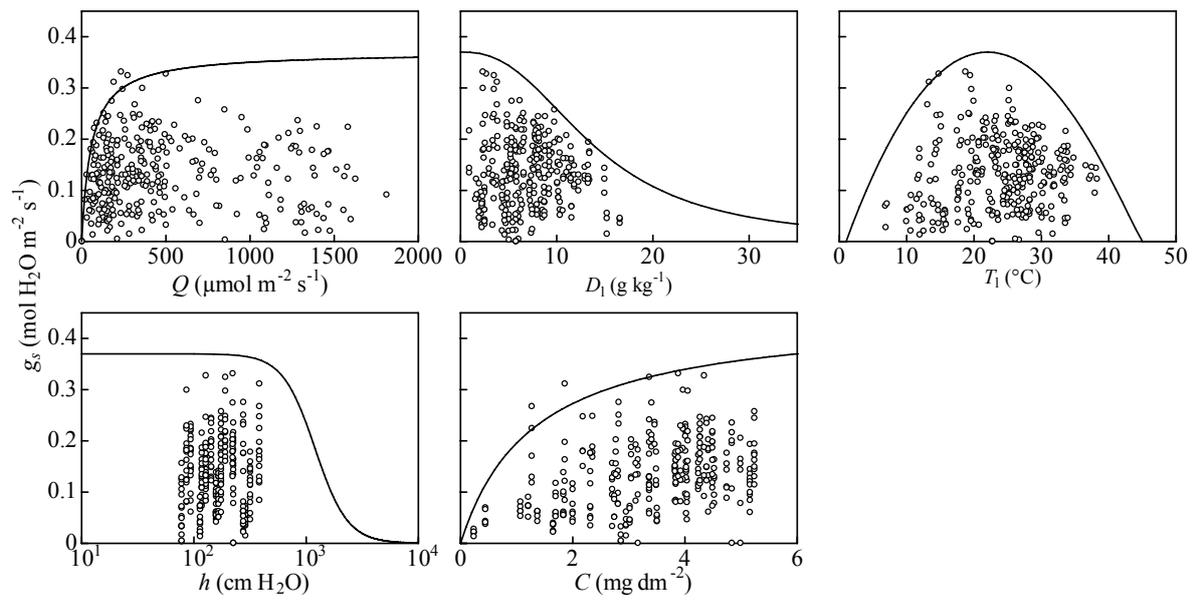


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2 Fig. 5. Diurnal variation of stomatal conductance ( $g_s$ , mol H<sub>2</sub>O m<sup>-2</sup>s<sup>-1</sup>), transpiration rate ( $E$ ,  
 3 mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), and net photosynthesis rate ( $A$ ; μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) for three leaves of sample  
 4 C (C-1, C-2, and C-3; 5-year-old *Quercus serrata*) on 2 May, 3 July, 26 September, 10 October,  
 5 and 10 December 2003.

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2 Fig. 6. Relationships between the distributions of actual observed data and the fitted model

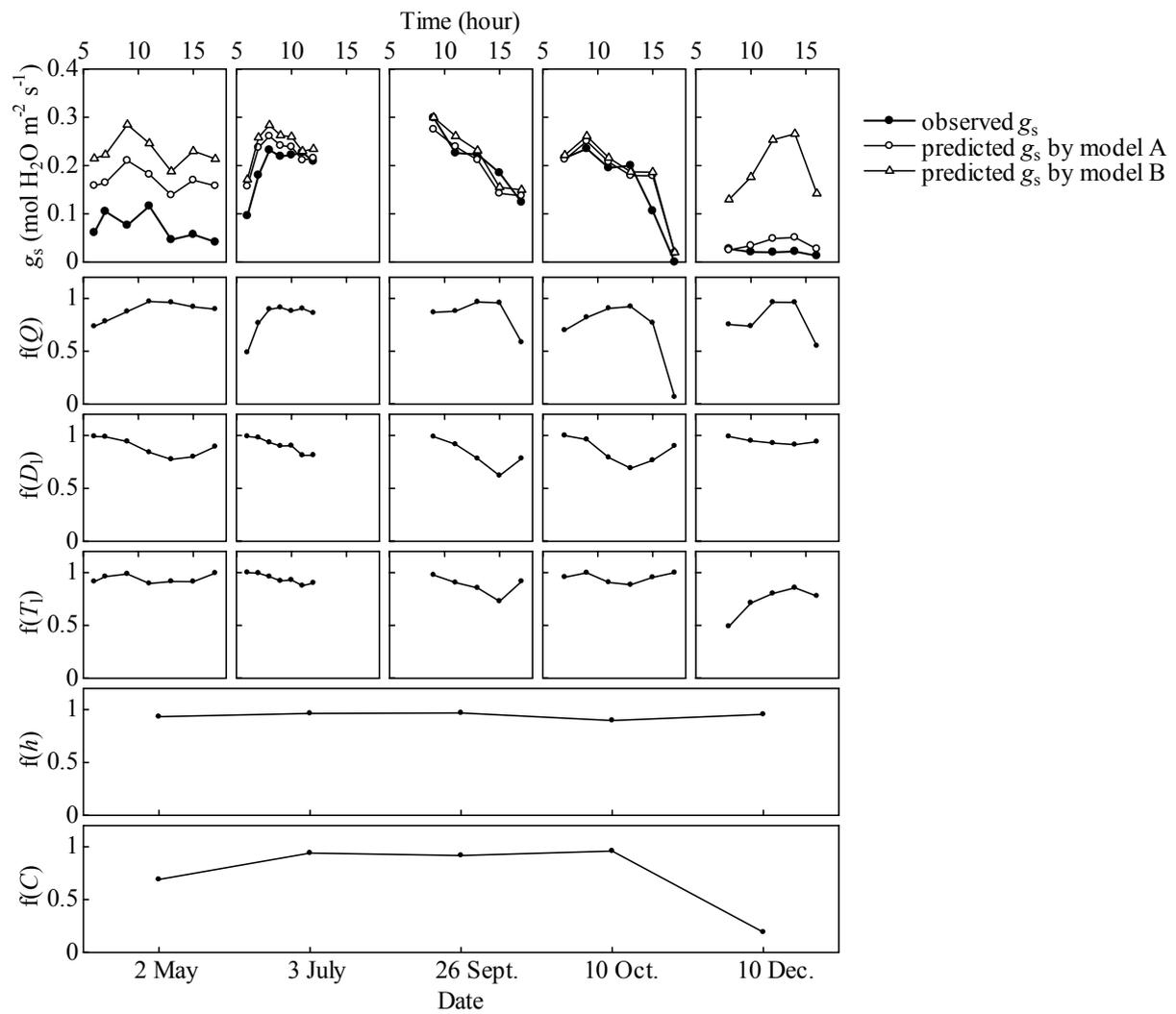
3 equation for each variable (PPFD,  $Q$ ; specific humidity deficit,  $D_l$ ; leaf temperature,  $T_l$ ; matric

4 suction,  $h$ ; and chlorophyll concentration,  $C$ ) for sample C (5-year-old *Quercus serrata*) in

5 2003.

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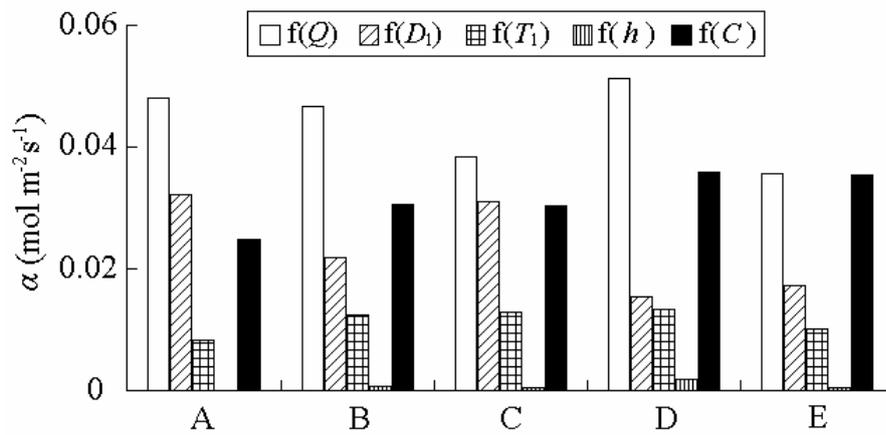
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 2 Fig. 7. Diurnal relationship between observed  $g_s$  for sample C (leaf C-2; 5-year-old *Quercus*  
 3 *serrata*) and predicted  $g_s$  using models with (model A) and without (model B)  $f(C)$ , and varying  
 4 the functions of  $Q$ ,  $D_1$ ,  $h$ , and  $C$  for 2 May, 3 July, 26 September, 10 October, and 10 December  
 5 2003.

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Fig. 8. Relative contributions ( $\alpha$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ) of each function associated with meteorological

3

and physiological variables (PPFD,  $Q$ ; specific humidity deficit,  $D_1$ ; leaf temperature,  $T_1$ ; matric

4

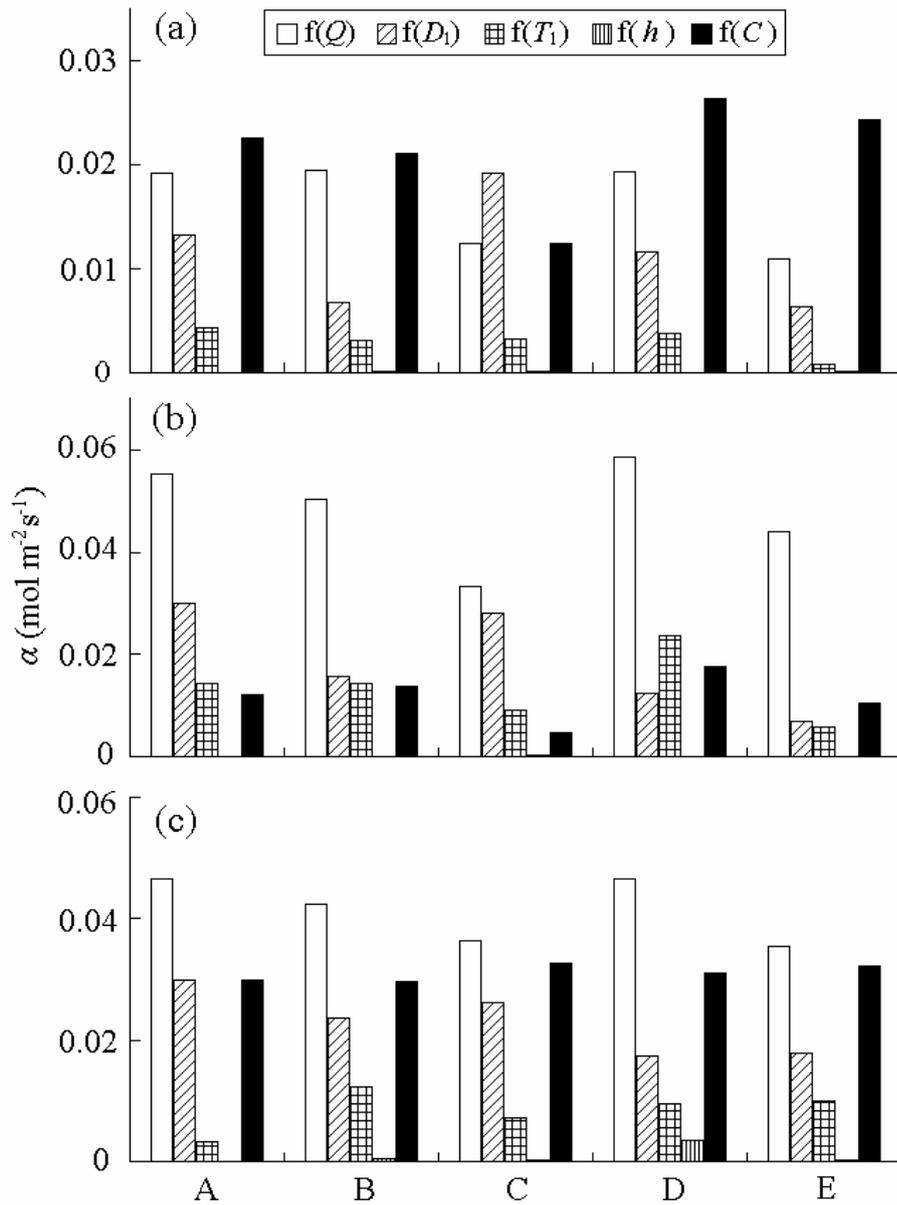
suction,  $h$ ; and chlorophyll concentration,  $C$ ) to the model accuracy in 5-year-old trees (samples

5

A-E) in 2003.

6

7



1

2 Fig. 9. Relative contribution ( $\alpha$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ) of each function associated with meteorological  
 3 and physiological variables (PPFD,  $Q$ ; specific humidity deficit,  $D_1$ ; leaf temperature,  $T_1$ ; matric  
 4 suction,  $h$ ; and chlorophyll concentration,  $C$ ) to the model accuracy in 5-year-old trees (samples  
 5 A-E) in (a) spring, (b) summer, and (c) autumn of 2003.