Responses of canopy conductance to environmental variables in forests in the northern Far East

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Introduction

Canopy conductance (g_c) is an important parameter that controls gas and heat exchanges between vegetation and the atmosphere. Two types of stomatal conductance (g_s) models have been used to express g_c: the Jarvis (1976) type model, which derives g_s empirically as a function of several environmental variables, and the Ball *et al.* (1987) type model, which uses a correlation relationship between g_s and the assimilation rate (A). A Jarvis-type model requires the maximum conductance value and many coefficients related to the stomatal response to environmental variables, while a Ball-type model requires only a dimensionless coefficient. Therefore, many recent land surface schemes have used Ball-type models (*e.g.*, Baldocchi & Meyers, 1998). However, to improve the performance of Ball-type models, modified versions have imported empirical functions for the humidity deficit (Leuning, 1995) and soil moisture (*e.g.*, Moriana *et al.*, 2002). Consequently, the evaluation of the response of canopy conductance to environmental variables is very important for evaluating water, energy, and CO_2 cycles between vegetation and the atmosphere.

Studies have attempted to evaluate the spatial variation in canopy conductance, especially the maximum conductance (*e.g.*, Schulze *et al.*, 1995; Komatsu, 2003). As another parameter, Baldocchi & Meyers (1998) reported that the slope coefficient in the Ball-type model centres on $10 \pm 20\%$ in various vegetation types. These results are effective for modelling global gas exchange. However, the spatial distribution of the response characteristics of g_c or g_s to environmental variables has still not been clarified on a global scale. Although Jarvis-type models have been applied to various canopies and plants, there has been no clear comparison of the parameter values in the models because of the difference in the function form in the models used in different studies and in the investigation periods across studies. To allow a global evaluation of g_c and the water and heat exchanges between vegetation and the atmosphere, the spatial distribution of the parameter values must be clarified.

Here we investigated the variation in g_c in five different forest types, which were distributed from middle to high northern latitudes in the Far East. In addition, we applied a Jarvis-type g_c model to the data for each site for the 2003 or 2004 growing season, and then compared the response characteristics of g_c to environmental factors.

Materials and Methods

Site descriptions

The research sites were five mature forests in the Far East: two boreal forests in eastern Siberia, two sub-boreal (cool temperate) forests in Hokkaido, Japan, and one warm temperate forest in Aichi, Japan.

Siberian sites. Study sites were established in a larch stand (L-YKS; 62˚15'18"N, 129˚37'08"E, 220 m a.s.l.) and a pine stand (P-YKS; 62˚14'29"N, 129˚39'02"E, 220 m a.s.l.) at Spasskaya Pad, located about 20 km north of Yakutsk city in republic of Sakha, Russia. The dominant species in the larch stand was larch (*Larix cajanderi*), a deciduous conifer, while lingonberry (*Vaccinium vitis-ideae*) covered 100% of the ground. The pine forest consisted of evergreen conifer pine (*Pinus sylvestris*) with 50% ground cover by bearberry (*Arctostaphylos uva-ursi*). The effective leaf area index (LAI, measured using an LAI-2000, Li-Cor) of the tree canopy in summer at L-YKS and P-YKS was 1.5 and 1.0, respectively.

Hokkaido sites. The study sites were located in a birch stand (B-HOK; 44°23'03"N, 142°19'07"E, 584 m a.s.l.) on a ridge and in a conifer-hardwood mixed stand (M-HOK; 44°19'19"N, 142°15'41"E, 340 m a.s.l.) in Uryu Experimental Forest of Hokkaido University, located in Hokkaido, Japan. The birch stand was a secondary forest of deciduous broad-leaved birch (*Betula ermanii*), and the ground surface was covered by dense dwarf bamboo (*Sasa kurilensis*). The mixed stand consisted of deciduous broad-leaved trees (*e.g.*, *Betula platyphylla*, *Phellodendron amurense*, *Quercus crispula*, and *Betula ermanii*) and evergreen conifers (*e.g.*, *Picea glehnii* and *Abies sachalinensis*). The forest floor was covered by dense dwarf bamboo (*Sasa senanensis*). The effective LAI of the tree canopy in summer at B-HOK and M-HOK was 2.68 and 3.44, respectively.

Aichi site. This site was established in a mixed deciduous and evergreen stand (M-AICHI) on a ridge in Jokoji Natural Recreational Forest (Aichi Highland Quasi-National Park) located in Aichi, Japan (35°15'29"N, 137°04'54"E, 205 m a.s.l.). The site consisted of deciduous broad-leaved trees (*e.g.*, *Quercus serrata* and *Evodiopanax innovans*), evergreen broad-leaved trees (*e.g.*, *Ilex pedunculosa*, *Symplocos prunifolia*, and *Castanopsis sieboldii*), and an evergreen conifer (*Pinus densiflora*). The forest floor was partly covered with pteridophytes (*e.g.*, *Dicranopteris pedata*) and evergreen shrubs (*e.g.*, *Eurya japonica* and *Osmanthus heterophyllus*). The effective LAI of the tree canopy in summer at M-AICHI was 3.50.

Fluxes and environmental measurements

Micrometeorological observation towers were installed at each site to measure fluxes and meteorological variables. At each site, the towers were 1.5 times higher than the average tree height.

Three-dimensional ultrasonic anemometers and open-path CO_2/H_2O infrared gas analysers were installed at the top of each tower. The water and energy fluxes were calculated using the eddy covariance technique. The sensible (H) and latent (λE) heat fluxes were calculated as half-hourly data from 10-Hz raw data. Extraordinary flux values and flux data measured during and for 5 hours after rainfall events were excluded from the analysis.

Canopy conductance

The canopy conductance (g_c; m s^{-1}) was calculated using the inverted Penman-Monteith equation (big-leaf model):

$$g_c^{-1} = \left[\left(\frac{\Delta}{\gamma}\right)\beta - 1\right]g_a^{-1} + \frac{\rho c_p}{\gamma}\frac{D}{\lambda E} \qquad (1)$$

where Δ is the rate of change of the saturation vapour pressure with air temperature (hPa K^{-1}), γ is the psychrometric constant (hPa K^{-1}), β is the Bowen ratio ($H/\lambda E$), D is the vapour pressure deficit (hPa), and g_a is the aerodynamic conductance (m s^{-1}).

Jarvis-type canopy conductance model

To evaluate the responses of g_c to environmental variables, we applied a Jarvis-type g_c model to the data. This model expresses g_c as a function of several environmental variables. The model form we used is expressed as:

$$g_c = g_{c\,max} f(Q) f(D) f(T) f(W) \qquad (2)$$

where $g_{c\,max}$ is the maximum canopy conductance (m s^{-1}), and $f(Q)$, $f(D)$, $f(T)$, and $f(W)$ are functions of the photosynthetic photon flux density (PPFD; Q, μmol m^{-2} s^{-1}), vapour pressure deficit (D; hPa), air temperature (T; °C), and volumetric soil water content (W; %), respectively. Each function expresses the response curve of g_c to each variable, and varies from 0 to approximately 1. These functions are expressed as

$$f(Q) = \frac{Q}{Q + 1/k_1} \qquad (3)$$

$$f(D) = \left(\frac{1}{1 + (D/D_{0.5})^{k_3}}\right)(1 - k_2) + k_2 \qquad (4)$$

$$f(T) = \left(\frac{T - T_{min}}{T_{opt} - T_{min}}\right)\left(\frac{T_{max} - T}{T_{max} - T_{opt}}\right)^{((T_{max} - T_{opt})/(T_{opt} - T_{min}))} \qquad (5)$$

$$f(W) = 1 - 10^{k_4(W_{min} - W)} \qquad (6)$$

where k_1 is the slope of the Q - $f(Q)$ curve at the origin; k_2 is the minimum constant value of $f(D)$ for high values of D; $D_{0.5}$ is the D value when $f(D)$ is halfway between 1 and k_2; T_{min}, T_{opt}, and T_{max} are the minimum, optimum, and maximum air temperatures for g_c, respectively; W_{min} is the minimum soil water content; and k_3 and k_4 are parameters that are related to the curvature of the response curve. The model was applied to the mid-growing season data only (July and August in 2004 at YKS and HOK, May to September in 2003 at AICHI because lightning damaged the system in 2004), because the seasonal variation in LAI was not obtained. The model was not applied to P-YKS because the soil water content was not measured at this site. The parameters were obtained using a non-linear least-squares technique to minimise the root mean square error between measured and predicted values for g_c. To calculate values that expressed actual phenomena, we imposed several constraints on the parameter calculations.

Results and Discussion

Environment at each site

Although the daily mean Q and T differed markedly among the sites in winter, the values in summer were similar among the sites. The environmental variable with the greatest difference among the sites was the moisture condition in summer. D increased in the order HOK < AICHI < YKS. W decreased in the order HOK > AICHI > YKS.

Seasonal variation in g_c

In mid-summer, the daytime g_c was smallest at YKS, largest at HOK, and intermediate at AICHI. The g_c at HOK and AICHI showed clear seasonal variation and was large in summer and low in winter. At YKS, a temporary decrease in g_c was seen in mid-summer (under very high D, ≥ 20 hPa). In winter, g_c became nearly zero at HOK, while g_c did not quite reach zero at AICHI because of the relatively high temperature in winter. Compared to the difference in g_c among the regions, the difference among the forest types within the same region was not significant.

Response of g_c to the environment

Figure 1 shows the response of g_c to the environmental variables (Q, D, T, W) at each site and the lines of the functions in the model fitted for the data for each site. Each fitted line was drawn at the upper boundary of the actual observed values, so that the relationships shown by the upper boundary can be regarded as the response curves of g_c to the environment. The values of the parameters in the model are shown in Table 1. As seen in Table 1 and Fig. 1, the responses to Q and T were similar across sites. In contrast, there were significant differences in the responses to D and W among sites. However, we also found that the ranges of the observed D and W differed markedly. For example, there were no values in the high dry range at HOK, while there were few values in the humid range at YKS. Therefore, the lines in the range for which there were no values were drawn only for convenience, and may not represent true phenomena. However, we postulated that phenomena in the range for which there were no values at one site could be expressed by the values for other sites. To verify this, we examined the response of g_c for all sites to the environment using a combined figure, which shows that the data for all sites appear to complement each other, as in a jigsaw puzzle (Fig. 2). Furthermore, the results for pooling g_c for all sites could be represented by a single best-fit line (model). It was interesting that the differences in $g_{c\,max}$ for the sites were explained by the lumped fitting line for W. To our knowledge, it has generally been assumed that the gas exchange behaviours of forests are site or forest-type specific. Therefore, we found this result very surprising.

Comparison of the precision of the site-specific and lumped models

Table 1 shows the precision of the site-specific and lumped models. The precision of the lumped model was slightly poorer than that of the site-specific models for three sites. However, the lumped model still expressed the actual g_c well. Therefore, it was clear that the lumped model could be used to estimate g_c at each site.

We believe that the lines in the lumped model represent the rough "potential" response curves of g_c to the environment in mature forests in the northern Far East, even if there are small differences among the forests. If this concept were correct, the g_c of the YKS forests would increase under more humid conditions. Further investigation is necessary to clarify this. However, the fact that one model can explain the g_c of different forests in different climates will be useful for the spatial parameterisation of the heat and gas exchanges between vegetation and the atmosphere over a wide spatial range.

Table 1 The parameter values and precision (root mean square error; RMSE; m s^{-1}) of the site-specific and lumped models.

	$g_{c\,max}$	k_1	k_2	k_3	$D_{0.5}$	T_{min}	T_{opt}	T_{max}	k_4	W_{min}	RMSE	
											Site-sp.	Lumped
L-YKS	0.012	0.0040	0.20	3.5	14	0	20	40	0.18	11	$10.1 \cdot 10^{-4}$	$13.0 \cdot 10^{-4}$
B-HOK	0.039	0.0040	0.10	4.0	12	0	19	40	0.03	15	$47.6 \cdot 10^{-4}$	$47.9 \cdot 10^{-4}$
M-HOK	0.032	0.0040	0.00	5.0	16	0	19	40	0.08	30	$35.7 \cdot 10^{-4}$	$39.9 \cdot 10^{-4}$
M-AICHI	0.020	0.0050	0.00	3.5	25	0	20	40	0.07	10	$20.4 \cdot 10^{-4}$	$19.6 \cdot 10^{-4}$
Lumped	0.039	0.0040	0.10	3.0	15	0	19	40	0.03	10		

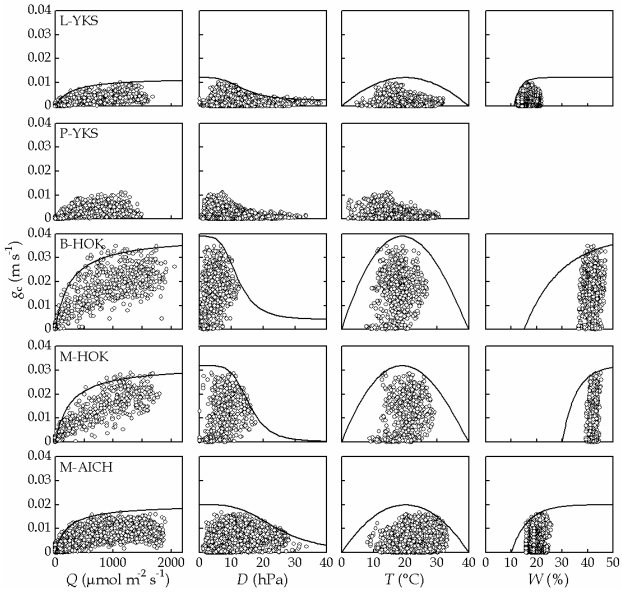

Fig. 1 Relationships between g_c and the environment, and the model-fitting line for the data for each site (the site-specific model).

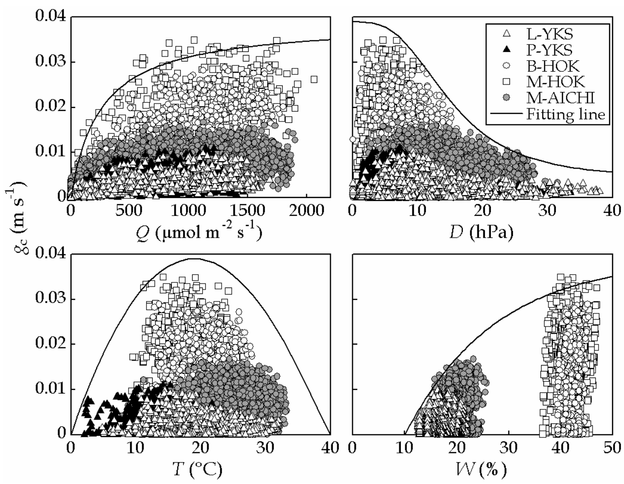

Fig. 2 Figures combining the data in Fig. 1 and the line fitting the data for all sites (the lumped model).

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