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Global diurnal and nocturnal parameters of stomatal conductance in woody plants and major crops

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Stomatal parameters in global woody and crop species

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Abstract

Aim Stomata regulate CO_2 uptake, water-vapor loss, and uptake of gaseous pollutants. Jarvis-type models that apply multiple-constraint functions are commonly used to estimate stomatal conductance (g_s), but most parameters for plant functional types (PFTs) have been estimated using limited information. We refined the data set of key components of the g_s response to environmental factors in global PFTs.

Location Global.

Time period Data published in 1973-2015

Major taxa Woody plants and major crops (rice, wheat, and maize)

Methods We reviewed 235 publications of field-observed g_s for the parameterization of Jarvis-type model in global PFTs. The relationships between stomatal parameters and climatic factors (MAT, mean annual air temperature; MAP, mean annual precipitation) were assessed.

Results We found that maximum stomatal conductance (g_{max}) in global woody plants correlated with MAP rather than MAT. g_{max} of woody plants on average increased from 0.18 to 0.26 mol m^{-2} s^{-1} with an increase in MAP from 0 to 2000 mm. Models, however, can use a single g_{max} across major crops (0.44 mol m^{-2} s^{-1}). We propose similar stomatal responses to light for C3 crops and woody plants, but C4 crops should use a higher light saturation point of g_s. Stomatal sensitivity to vapor-pressure deficit (VPD) was similar across forest PFTs and crops, although desert shrubs had a relatively low sensitivity of stomata to VPD. The optimal temperature for g_s increased by 1 °C for every 3.0 °C of MAT. Stomatal sensitivity to predawn water potential was reduced in hot and dry climate. The fraction of nighttime conductance to g_{max} (0.14 for forest trees, 0.28 for desert shrubs, 0.13 for crops) should be incorporated into the models.

Main conclusions This analysis of global g_s data provides a new summary of g_s

responses and will contribute to modeling studies for plant-atmosphere gas exchange and land-surface energy partitioning.

Key words: *Stomatal conductance, Jarvis-type model, Global plant functional types, Forests, Crops, Nocturnal stomatal conductance*

1. Introduction

Plants influence climate by the exchange of energy, water, carbon dioxide (CO_2), and other chemical species with the atmosphere (Bonan 2008). Stomata, small pores on leaves, regulate the exchange of gas and energy between plants and the atmosphere. Stomatal responses to environmental stimuli are therefore important for terrestrial carbon sinks and the hydrology of ecosystems (Hetherington & Woodward 2003), the partitioning of terrestrial surface energy affecting local and regional climate (Bonan, 2008), and the sensitivity of plants to air pollutants such as ozone (O_3) (Sitch et al., 2007; Matyssek et al., 2013).

The stomatal control of gas exchange at foliar level is quantified as stomatal conductance (g_s). g_s is often empirically modeled based on several environmental factors that affect stomatal aperture (Jarvis 1976; Ball *et al.* 1987; Leuning 1995), but an optimization theory of stomatal functioning (Cowan and Farquhar, 1977; Katul et al., 2009; Medlyn et al., 2011; Hoshika et al., 2013b; Lin et al., 2015) and a hydraulic theory of stomatal regulation (Buckley et al., 2003, 2012; Buckley, 2017) are currently advancing. A common empirical approach is the multiple-constraint functions model, which is a Jarvis-type g_s model (Jarvis 1976; Körner et al. 1995; Emberson *et al.* 2007; Damour et al., 2010). Jarvis-type g_s models can be incorporated into global or regional vegetation-climate models (Zhang et al., 2003; Felzer et al. 2004; Galbraith et al., 2010; Huang et al., 2016). In particular, Jarvis-type g_s models are widely used for the stomatal component of gas deposition in global air-quality models (Zhang et al., 2003) and are recommended by UNECE-CLRTAP (United Nations Economic Commission for Europe Convention on Long-range Transboundary Air Pollution) for calculating stomatal O_3 fluxes and assessing O_3 risks to forest trees and crops in Europe (CLRTAP, 2015). These models adjust the maximum g_s (g_{max}, the maximum value of stomatal conductance, which is achieved under environmental conditions that are favorable for stomatal opening) to changes in plant phenology and environmental variables, e.g. light intensity, air temperature, vapor-pressure deficit (VPD), and soil moisture. A review by Körner (1995) summarized the g_{max} data in globally important biomes and reported that: i. g_{max} does not differ between types of woody plants, and ii. crops have a higher g_{max} than woody plants. Data of g_s summarized by Körner (1995), however, were scarce for some plant types (e.g. tropical trees and desert shrubs). Korner's review (1995) was published more than 20 years ago. An update of the analysis is needed.

Physiological parameters may differ with climatic conditions for growth (Larcher, 2003). Lin et al. (2015) suggested that stomatal behavior may differ with water-use strategy among plant functional types (PFTs), according to the optimal photosynthesis-stomatal theory. The well-known Miami model (Lieth, 1975) indicates that terrestrial carbon assimilation, so-called net primary production (NPP), is associated with precipitation and temperature. Del Grosso et al. (2008), Chapin et al. (2012), and Gillman et al. (2015) provided a support for this relationship globally. g_s is typically correlated with photosynthesis (Larcher, 2003). Therefore, we hypothesized that g_{max} may depend on both precipitation and temperature.

In addition to g_{max}, the parameters of stomatal response to environmental factors in each type of biome are still based on limited information. Current Jarvis-type models, in particular, have ignored the ratio of nighttime conductance to g_{max} (f_{night}) (Emberson et al., 2007; Damour et al., 2010), even though stomatal opening at night shows an important influence on water use and the effects of air pollutants such as O_3 (Grulke et al., 2004; Zeppel et al., 2014).

Our purpose in this literature review was to refine the key components of the response of g_{s} to environmental factors using Jarvis-type g_{s} models of global woody plants, defined as PFTs, commonly used in global vegetation-climatic models (Poulter et al., 2011), and of the major food crops, i.e. rice, wheat, and maize (FAO, 2013). Specifically, we aimed to: 1) quantify the parameters of Jarvis-type multiplicative g_{s} models, i.e. g_{max}, and stomatal responses to light, temperature, vapor-pressure deficit (VPD), and predawn leaf-water potential (ψ_{pd}) as a proxy of soil-water potential (SWP), for estimating g_{s} in different plant types, geographic regions, and environmental conditions; 2) investigate relationships between stomatal and climatic parameters; and 3) summarize current information for f_{night} for possible inclusion into Jarvis-type g_{s} models.

2. Methodology

2.1 Jarvis-type model

We modified the Jarvis-type multiplicative algorithm (Körner et al., 1995; Büker et al., 2015; CLRTAP, 2015) to include various environmental factors that affect g_{s} for woody plants and crops:

$$g_{\text{s}} = g_{\text{max}} \cdot \max\left[f_{\text{night}}, f_{\text{phen}} \cdot f_{\text{light}} \cdot \max\left\{f_{\text{min}}, \left(f_{\text{temp}} \cdot f_{\text{VPD}} \cdot f_{\text{SWP}}\right)\right\}\right] \qquad (1)$$

where g_{max} is the maximum stomatal conductance (mmol H_2O m^{-2} projected leaf area s^{-1}), i.e. the seasonal maximum g_{s} in fully developed but not senescent leaves in their natural environment (Körner, 1995). The other functions are limiting factors of g_{max} and are scaled from 0 to 1: f_{min} is the fraction of minimum daytime stomatal conductance to $g_{\max}$ (e.g. Emberson et al., 2000), f_{night} is the fraction of stomatal conductance at night to $g_{\max}$. f_{phen} is the variation in stomatal conductance with leaf age, and f_{light}, f_{temp}, f_{VPD}, and f_{SWP} are the fractions that depend on photosynthetic photon flux density at the foliar surface (PPFD, µmol photons m^{-2} s^{-1}), air temperature (°C), VPD (kPa), and SWP (MPa), respectively. We did not collect data for f_{phen}. Phenological change of g_s cannot be simply defined from the literature, because f_{phen} varies with several factors such as ageing (Kitajima et al., 2002), soil temperature (Stone et al., 1999), and nighttime temperature (Koike and Sakagami, 1985). In fact, the parameterization of f_{phen} developed for a few species was very complex (e.g. *Quercus ilex*, Alonso et al., 2008). In addition, we assumed $f_{\min}$ to zero because $f_{\min}$ is not easily defined in the model as g_s dynamically decreases with decreasing light intensity before sunset (de Dios et al., 2013; Hoshika et al., 2013b).

The response of g_s to PPFD, f_{light}, is calculated as (Emberson et al., 2000):

$$f_{\text{light}} = 1 - \exp\left(-a \cdot \text{PPFD}\right) \qquad (2)$$

where a is a constant (a = Ln[2]/PPFD$_{50}$) and PPFD$_{50}$ is the PPFD when g_s reaches 50% of $g_{\max}$.

The response of g_s to air temperature is expressed as (Emberson et al., 2007):

$$f_{\text{temp}} = \left(\frac{\mathrm{T} - \mathrm{T}_{\min}}{\mathrm{T}_{\text{opt}} - \mathrm{T}_{\min}}\right)\left\{\left(\frac{\mathrm{T}_{\max} - \mathrm{T}}{\mathrm{T}_{\max} - \mathrm{T}_{\text{opt}}}\right)^{\left(\frac{\mathrm{T}_{\max} - \mathrm{T}_{\text{opt}}}{\mathrm{T}_{\text{opt}} - \mathrm{T}_{\min}}\right)}\right\} \qquad (3)$$

where T_{opt}, $\mathrm{T}_{\min}$, and $\mathrm{T}_{\max}$ denote the optimal, minimum, and maximum temperatures (°C) for g_s, respectively. We focused on T_{opt} only, because $\mathrm{T}_{\max}$ and

T_{min} are rarely measured under field conditions (Larcher, 2003, generally 40 to 50 °C and -5 to 5 °C, respectively) and thus cannot be appropriately defined from the literature.

Oren et al. (1999) suggested a logarithmic function of the response of g_s to VPD:

$$f_{\mathrm{VPD}} = 1 - m \cdot \ln[\mathrm{VPD}] \qquad (4)$$

where m denotes the sensitivity of g_s to VPD ($\ln(\mathrm{kPa})^{-1}$). A hydraulic model, which assumes stomatal regulation of leaf-water potential, suggests that m is ~0.6 (e.g. Oren et al., 1999).

Soil-moisture deficit is also a major limiting factor of g_s in dry and semi-dry climates (Chaves et al., 2002; Alonso et al., 2008), because stomatal closure is the primary physiological response to water limitation (Hinckley et al., 1978). Data for parameterizing the effects of soil water on g_s, however, are limited. Misson et al. (2004) suggested that g_s was affected by, and decreased with, ψ_{pd}. For parameterizing f_{SWP}, we thus assumed that ψ_{pd} was a proxy of SWP, which is a common assumption for calculations of soil-plant water balance (e.g. Hinckley et al., 1978). Following Misson et al. (2004), the function of $f_{\psi pd}$ can be described as:

$$f_{\mathrm{SWP}} \approx f_{\psi\mathrm{pd}} = 1 - b\left(\psi_{\mathrm{pd}} - \psi_{\mathrm{max}}\right) \qquad (5)$$

where b is the slope of the regression line between g_s and ψ_{pd} (mol m^{-2} s^{-1} MPa^{-1}) and ψ_{max} (MPa) is the predawn leaf-water potential under well-watered conditions and is assumed to be zero.

2.2 Database and quantitative research synthesis

Quantitative research synthesis, including a meta-analysis, can integrate findings from many studies in a formal statistical analysis to create one large overview (Ainsworth et al., 2002; Feng et al., 2008; Haworth et al., 2016). Using Scopus and Google scholar, a survey of all peer-reviewed literature published between 1970 and 2015 was made on the basis of the keywords "[stomatal conductance]+[a target PFT]", including researches under natural environmental conditions. The literature was also cross-checked through the list of references included in review papers.

To include an article in this research synthesis, we examined if it met the following criteria: (1) the experimental period was specified and longer than 1 month; (2) the species name was specified; (3) only the papers which measured stomatal conductance by a diffusion porometer or an infra-red gas analyzer using a leaf cuvette or a branch bag were included, i.e. data derived by sap flow measurements were not included; (4) data were obtained from field measurements to represent actual field conditions, i.e. we excluded data from experiments using potted plants and environmental control chambers; (5) data were derived from upper canopy leaves exposed to the sun, because they are the most representative for canopy photosynthesis and the uptake of gaseous pollutants (Emberson et al., 2007); (6) data for tree g_{max} were selected for trees either >10 years old or >10 m in height, because g_{max} can vary with tree size or age (Steppe et al., 2011); (7) data for mean annual air temperature (MAT, °C), mean annual precipitation (MAP, mm), and measurement year were obtained from original sources, which are needed to assess their effect on the stomatal parameters. An article was excluded because its outlier value of MAP = 4000 mm strongly influenced the results of our analysis (Oberbauer et al., 1987). Articles were excluded when the description of experimental design was insufficient to allow an objective assignment, or the data were reported in another article. After excluding articles based on these criteria, a total of 235 publications for woody plants, two major C3 crops (rice and wheat), and one C4 crop (maize) were used for the analysis (Appendix S1). A list of the data sources is available in Appendix 1.

The selected crops are the three most important crops globally, providing 60% of the world's food energy (FAO, 2013). PFTs classify species into ~10-20 groups defined by their growth forms and climatic characteristics and are commonly used in global vegetation-climatic models (Poulter et al., 2011). We used the PFTs for forest trees, although the current classification does not include seasonally dry climates (Zhang et al., 2003; Poulter et al., 2011). For example, temperate deciduous and evergreen trees are distributed in both humid and seasonally dry climates. In temperate humid Asia, soil-water content generally does not affect g_s of tree species (Sirisampan et al., 2003; Hoshika et al., 2012), but trees grown under seasonal drought such as in Mediterranean climates suffer frequent water stress (Alonso et al., 2008). We therefore also compared the parameters of stomatal models between trees in temperate humid and Mediterranean climates, and between evergreen and deciduous taxa.

The g_s parameters for the analysis were obtained: 1) directly from those reported in the literature of Jarvis-type modelling studies (e.g., Alonso et al., 2008; Fares et al., 2013) or 2) from fitting g_s data in the literature. In the latter case, g_{max} was derived as the seasonal maximum g_s in fully developed leaves (Körner, 1995). Stomatal conductance at night was obtained from data measured in relatively dry days (relative humidity<70%), at least 3 h after sunset (Uddling et al., 2005; Hoshika et al., 2013b), and then f_{night} was calculated as the fraction of stomatal conductance at night to g_{max}. The f_{light} parameters were achieved by fitting the g_s data that were measured with VPD < 1.5 kPa in each paper. T_{opt} in

f_{temp} was determined as the temperature at which g_{max} was obtained. f_{VPD} was estimated by fitting the functional form ($1-m\cdot\ln[\mathrm{VPD}]$)) to presumably non light-limiting data (PPFD > 500 μmol m^{-2} s^{-1}). We fitted the $f_{\psi\mathrm{pd}}$ function to mean midday g_{s} data in each paper (e.g., Bréda et al., 1993).

We used linear mixed models (LMM) to investigate the relationships between stomatal and climatic parameters. Our analysis considered estimate errors of g_{max} reported by original articles, which allowed us to quantatively integrate the finding of original articles. All parameters were checked for normality to meet the assumption of statistical model, and thus g_{max} and f_{light} were log-transformed. We fitted LMM to woody plant and crop data separately, and used MAT, MAP, measurement year, and (measurement year)^2 as fixed effects, and article, species, measurement instrument, Mediterranean / temperate humid climate type (only woody plant data), evergreen / deciduous tree (only woody plant data), C3 / C4 crop (only crop data), irrigation (only crop data), as random effects. MAT and MAP were scaled to mean 0 and variance 1, and measurement year were scaled to minimum 0 and maximum 1. The crop data of f_{temp}, f_{VPD}, f_{SWP}, and f_{night} were not analyzed because these data had few sample size (n = 10, 12, 0, and 4, respectively). All statistical analyses were conducted in R 3.4.0 (R Core Team, 2017) and Stan 2.15.1 (Stan Development Team, 2017) to calculate posterior probability obtained by Bayesian inference. We ran three independent chains and retained 5,000 iterations after an initial burn-in of 5,000 iterations. We then thinned the samples every 5 intervals. The convergence of samples was confirmed by monitoring traceplots and checking Gelman-Rubin diagnostic $\widehat{\mathrm{R}} < 1.1$ for each estimate. All Stan codes for our analysis are provided in Appendix S3.

3. Results

3.1 Maximum stomatal conductance (g_{max})

g_{max} showed a range from 0.07 to 0.36 mol m^{-2} s^{-1} in woody plants, and from 0.34 to 0.61 mol m^{-2} s^{-1} in major crops (Table 1). g_{max} significantly varied with the species, and was 37% lower for evergreen trees than for deciduous trees (Table 1; 0.18±0.02 and 0.28±0.02 mol m^{-2} s^{-1}, respectively), although such taxa did not statistically affect g_{max} (Table 2). g_{max} of woody PFTs was significantly correlated with MAP (Table 2, Fig. 1), although g_{max} did not differ between trees in Mediterranean and temperate humid climates (Table 2). The slope of the regression line of log(g_{max}) was 0.090 for MAP, i.e. log(g_{max}) increased by 0.1 with an increase in MAP of 640 mm. MAT, however, was not significantly correlated with the g_{max} of woody PFTs (Table 2). g_{max} was affected by measurement year for woody plants (Table 2), and was lower before 1980s (Fig. 1). However, this may be due to insufficient g_{max} measurements before 1980s. In fact, g_{max} did not change or rather decreased after 1990s, when g_s was widely measured in various PFTs including tropical trees.

3.2 Other parameters

Woody plants and C3 crops reached 50% of g_{max} at a similar PPFD, 100-250 μmol m^{-2} s^{-1} (Table 1), corresponding to approximately 5-10% of maximum daily PPFD. The C4 crop (maize) had a much higher PPFD$_{50}$ (~500 μmol m^{-2} s^{-1}), although this classification of C3 and C4 plants did not statistically affect PPFD$_{50}$.

T$_{opt}$ was 17-30 °C for woody plants and 27-30 °C for crops (Table 1). A significant relationship between T$_{opt}$ and MAT was found in woody plants (Table 2, Fig. S2 in Appendix S2). For example, needleleaved summergreen trees, which are mainly boreal species, had a lower T$_{opt}$ (16.8±3.5 °C) than tropical evergreen trees (29.4±1.8 °C). The slope of the regression line was 2.38, i.e. T$_{opt}$ increased by 1 °C with an increase in MAT of 3.0 °C (Fig. S1).

Stomatal sensitivity to vapor pressure deficit in woody plants was affected by species and MAP (Table 2). In regions with low rainfall, desert shrubs had the lowest m (= 0.37 ln(kPa^{-1})). All the other PFTs had similar m values (average m of ~0.56 ln(kPa^{-1})), independent of functional type and geographic origin (Table 1).

The stomatal sensitivity to ψ_{pd} (represented as the parameter b) was correlated positively with MAP and negatively with MAT in global woody PFTs (Table 2), indicating that relatively low values of b can be found in hot and dry climate. In fact, b was relatively higher in temperate humid climate evergreen/deciduous trees than in Mediterranean climate evergreen/deciduous trees (Table 1).

MAT or MAP did not affect f_{night} (Table 2). f_{night} depended on the species. On average, f_{night} was 0.14 for forest trees, 0.28 for desert shrubs and 0.13 for crops.

4. Discussion

4.1 Maximum stomatal conductance (g_{max})

g_{max} plays an important role in determining the uncertainty of Jarvis-type g_{s} models (Tuovinen et al., 2007). g_{max} was higher for crops than for woody plants (Table 1; 0.44±0.03 and 0.21±0.02 mol m^{-2} s^{-1}, respectively), consistent with Körner (1995), who suggested 0.45 and 0.22 mol m^{-2} s^{-1}, respectively. Crops have been anthropogenically selected and bred for productivity, and opening stomata can increase productivity (Fischer et al., 1998). Assessing the effects of crop varieties on g_{max} was not possible (data not shown), because data in each variety were not sufficient. Further studies using a larger number of data per variety are needed to assess whether different varieties could affect g_{max}.

Körner (1995) reported that g_{max} did not differ among the major woody types. Our analysis, however, found that g_{max} differed among the woody PFTs, relative to leaf longevity and climatic conditions. Short-lived leaves may have a higher

$g_{\max}$ and photosynthetic capacity relative to long-lived leaves of forest tree species (Koike, 1988; Reich et al., 1999; Kikuzawa & Lechowicz, 2011). $g_{\max}$ for woody PFTs was dependent on MAP (Fig. 1). Del Grosso et al. (2008) interestingly reported that NPP of global native vegetation correlated better with precipitation than with temperature. Stomatal adjustments may maximize carbon gain while minimizing water loss under a given water availability to plants (Cowan & Farquhar, 1977; Manzoni et al., 2011). Stomatal behavior in dry environments is likely to be more hydraulically constrained than that in wet environments (Lin et al., 2015). The reduction of $g_{\max}$, especially under severely water-limited conditions, may help to reduce water loss in hot and dry environments, suggesting a limitation of carbon assimilation by water availability. Although this may promote carbon starvation due to continued carbohydrate demand for maintenance of metabolism and defense against stressors, plants tend to maintain xylem water tension below its cavitation threshold to avoid embolism (McDowell & Sevanto, 2010).

In recent years, plant response to global change including rising CO_2 concentration and nitrogen deposition has become an important issue (Peñuelas et al., 2011; Keenan et al., 2013). For example, rising CO_2 concentrations might reduce water use in plants due to stomatal closure (Ellsworth et al., 2012). Our results indicated that $g_{\max}$ of woody plants slightly decreased since g_s was widely measured in the 1990s. This is supported by Keenan et al. (2013), suggesting that latent heat, a surrogate for transpiration, in boreal and temperate forests tended to decrease from 1990 to 2010 because of increasing CO_2 concentration in the atmosphere.

4.2 Light limitation (f_{light})

C4 plants potentially have a significant advantage over C3 plants in hot, arid, and bright habitats (Pearcy & Ehleringer, 1984; Yamori et al., 2014). The relatively higher PPFD$_{50}$ of g_s in the C4 crop (maize) indicated a different photosynthetic light response between C3 and C4 species. Maize does not light-saturate even in full sunlight, while C3 photosynthesis saturates at intermediate light intensities (Larcher, 2003).

4.3 Temperature limitation (f_{temp})

The observed range of T$_{opt}$ of g_s corresponded to the optimal range for photosynthesis, generally 20-30 °C globally (Larcher, 2003). The optimal temperature for photosynthesis generally increased with the growth temperature MAT (Table 2), because such an acclimation contributes to higher productivity (Hikosaka et al., 2006, 2007). T$_{opt}$ was slightly lower for trees in the Mediterranean than in temperate humid climates, although the difference was not statistically significant (Table 2). g_{max} in Mediterranean climates often occurs earlier in the season (May-June) when water availability is higher than in summer (July-August) (Rhizopoulou & Mitrakos, 1990; Manes et al., 1997).

4.4 Vapor pressure deficit limitation (f_{VPD})

Except for desert shrubs, our finding was consistent with the theory by Oren et al. (1999) that assumes stomatal regulation of leaf water potential and suggests an m of ~0.6 based on a hydraulic model. The parameter m did not differ significantly between the C4 crop (maize) and the C3 crops, consistent with the report for two C3 and two C4 grass species by Morison & Gifford (1983). Stomatal sensitivity to VPD (m=0.37) was slightly lower for desert shrubs (Table 2). Desert shrubs generally show very deep roots, enabling them to tap water in deep soil layers (Canadell et al., 1996). Kropp & Ogle (2015), however, suggested that this lower sensitivity of g_s to VPD for desert shrubs might be associated with reduced access to water, which is restricted by the neighboring plants. The neighboring plants might influence the root distribution of desert shrubs, which determines water availability and affects stomatal response (Kropp & Ogle, 2015).

4.5 Leaf water potential limitation ($f_{\psi pd}$)

Stomatal closure associated with soil moisture deficits reduces water vapor loss and photosynthetic carbon gain (Chaves et al., 2002). This stomatal closure also provides some protections to plants from the negative effects of O_3 exposure (Tingey & Hogsett, 1985; CLRTAP, 2015). The $f_{\psi pd}$ function is therefore critical under water-limited conditions. Although dewfall and fog might affect predawn water relations (e.g., Limm et al. 2009), the relationship between g_s and ψ_{pd} generally indicates stomatal response to soil-moisture deficits (Misson et al., 2004). The slope (b) of the relationship, representing the sensitivity of stomata to ψ_{pd}, was correlated with MAP and MAT in global PFTs (Table 2). Higher b indicates an avoidance of drought stress by early stomatal closure (Castel & Terradas, 1995; Picon et al., 1996; Teixeira Filho et al., 1998). Conifers, beeches, and birches (representative of the boreal/temperate summergreen type) generally have shallow root systems (Peterken & Mountford, 1996; Mauer & Palatova, 2003; Anderson, 2005) and may need to drastically reduce water loss by stomatal closure during drought (Castel & Terradas, 1995). The lower sensitivity of stomata to ψ_{pd} implies that trees in Mediterranean climates have developed mechanisms for drought tolerance and are able to maintain a higher g_s during water-stressed conditions (Tenhunen et al., 1987). These tolerance mechanisms may be associated with morphological/anatomical adjustments, leading to an increase in the apoplastic water fraction (Serrano & Peñuelas, 2005; Serrano et al., 2005). Increased cell wall elasticity of sclerophyllous leaves contributes to drought resistance by an increased range of positive pressure potential of twigs

(Serrano & Peñuelas, 2005). Interestingly, stomata of trees in tropical savanna had a similar sensitivity to ψ_{pd} (b=~0.40 MPa^{-1}: Eamus, 1999; Thomas & Eamus, 1999) compared to those of trees in Mediterranean climate.

4.6 Nighttime stomatal conductance (f_{night})

Current Jarvis-type models assume that f_{night} is zero (Emberson et al., 2007; Damour et al., 2010), but several studies detected 5-30% of g_{max} rates at night relative to daytime (Caird et al., 2007; Zeppel et al., 2014). The value of f_{night} (a ratio of nighttime stomatal conductance to g_{max}) was larger in desert shrubs (Table 1). However, absolute values of nighttime stomatal conductance and g_{max} are relatively low in this PFT (Fig. 1; Table S1). Although Ogle et al. (2012) suggested a potential for significant nocturnal transpiration in desert plants, underlying mechanisms or biological significance of the nocturnal transpiration in those plants are still unknown. To our knowledge, information is not available for f_{night} in tropical trees at foliar level. Measurements of nocturnal sap flow suggest that f_{night} might be higher in tropical evergreen/raingreen trees than in temperate evergreen/summergreen trees (Zeppel et al., 2014), although we should note that nocturnal sap flow consists of not only nocturnal transpiration but also hydraulic recharge of trees (Caird et al., 2007) and may also be affected by guttation (Fisher et al., 1997). de Dios et al. (2015) suggested that the actual magnitude of nocturnal transpiration may be higher than the nocturnal evapotranspiration currently predicted by vegetation-climatic models (typically ~1-2% of global evapotranspiration, e.g. Greve et al. 2014). Nocturnal water loss may thus contribute a substantial fraction of total daily water use and thereby affect the water balance of ecosystems (Zeppel et al., 2014).

Also, nocturnal stomatal opening may enhance the deleterious effects of gaseous air pollutants such as O_3. Matyssek et al. (1995) showed that a 24-h exposure to O_3, including exposure at night, caused a stronger decrease in growth relative to daytime exposure only, for European birch (*Betula pendula*), and concluded that nighttime O_3 exposure should be included in the calculation of daily O_3 flux. Ozone concentration can remain elevated at night, particularly in mountainous areas (Musselmann & Minnick, 2000), and plants can be more susceptible to O_3 at night than during daytime, because plant defenses are lower at night (Musselmann & Minnick, 2000). f_{night} is affected by several environmental factors (de Dios et al., 2013), but a parameterization is not yet available.

5. Conclusions

Our review synthesized a wide range of published data for g_{s} and examined the patterns of stomatal response among PFTs. The empirical evidence will contribute to the further development of modeling studies for plant-atmosphere gas exchange and land-surface energy partitioning.

Our review provided a new summary of g_{max} and the stomatal responses to environmental factors across global woody plants and major crops based on Jarvis-type models. The results confirmed the concluding remarks about g_{max} by Körner’s review (1995), suggesting that crops have a higher g_{max} than woody plants. However, contrary to Körner’s summary (1995), g_{max} differed between types of woody plants, likely because of the influence of MAP. We recommend that g_{max} for global woody PFTs should be estimated as a function of precipitation (approximately 0.18 to 0.26 mol m^{-2} s^{-1} within the range of 0-2000 mm MAP). A higher g_{max} (0.44 mol m^{-2} s^{-1}) can be used for crops than for woody plants. T_{opt} and the stomatal response to ψ_{pd} (i.e. the slope parameter b) also varied with the growth environment for global woody plants. T_{opt} of crops ranged from 27 to 30 °C. A parameterization of $f_{\psi\mathrm{pd}}$ is not yet available for global major crops. In contrast, we recommend a single parameter for the stomatal responses to light (average $PPFD_{50}$ of 140 μmol m^{-2} s^{-1} for C3 plants and ~500 μmol m^{-2} s^{-1} for C4 crop (maize)) and VPD (average m of 0.56 ln(kPa^{-1})) for all forest PFTs and crops, in agreement with many land-surface models that do not differentiate between g_s model parameters for these stomatal responses among PFTs (De Kauwe et al., 2015). However, we should note that m of desert shrubs may be lower (0.37 ln(kPa^{-1})). f_{night} was 0.14 across forest tree types, i.e. 14% of g_{max}. f_{night} of desert shrubs was higher (28% of g_{max}). f_{night} was ~0.13 across the crops.

Our analysis identified major gaps in our understanding of stomatal responses to soil moisture and phenological changes in both woody and crop species and of the responses to light and temperature in tropical raingreen trees, tundra shrubland, and desert shrubland. More research is also recommended for g_{max} of tropical raingreen and boreal needleleaved summergreen trees and tundra shrubland, because only less than 10 values were available for these PFTs. Information for f_{night} is still limited, particularly for tropical evergreen/raingreen, needleleaved summergreen, Mediterranean trees, tundra shrubs, and crops. Interest in the role of f_{night} in the optimization of g_s (Cirelli et al., 2016) and in the uptake of O_3 (Grulke et al., 2007; Hoshika et al., 2013a) is increasing. If increasing water loss at night leads to higher total daily water use, then soil water content may decrease, leading to drier soils and lower rates of transpiration during the resultant dry periods (Zeppel et al., 2014). We therefore propose to incorporate f_{night} into Jarvis-type models (see Eq. 1).

The empirical responses in the models may also be altered in plants grown at elevated levels of CO_2 (Heath & Kerstiens 1997; Heath 1998; Bobich et al., 2010) and O_3 (Pearson & Mansfield, 1993; Paoletti & Grulke, 2005; Wilkinson & Davies, 2010; Hoshika et al., 2013b). Further experimental evidence at elevated CO_2 and/or O_3 levels will improve the empirical models of g_s under such future changing environments, which are incorporated into global climatic models to assess land-atmosphere carbon and water exchanges.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data set for the analysis.

Appendix S2 Supplementary figures

Appendix S3 Stan codes for the statistical analysis

Biosketch

Y. Hoshika is a post-doctoral researcher at the National Research Council (CNR) of Italy. His current research interest is modeling of environmental botany of plant species as affected by ozone stress.

Author contributions: Y.H., A.DM., J.P. and E.P. conceived the study. Y.H.

collected data, and wrote the first draft of the manuscript. Y.H. and Y.O. undertook the statistical analyses. Y.O. conducted the programming by R software for statistical analysis. Y.O., A.DM., J.P. and E.P. revised the manuscript and contributed to the final version.

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Appendix 1: Data Sources

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