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Summary

When the rate of photosynthesis is greatly diminished, such as during severe drought, extreme temperature or low light, it seems advantageous for plants to close stomata and completely halt water loss. However, water loss continues through the cuticle and incompletely closed stomata, together constituting the leaf minimum conductance (g_{min}). In this review, we critically evaluate the sources of variation in g_{min}, quantitatively compare various methods for its estimation, and illustrate the role of g_{min} in models of leaf gas exchange. A literature compilation of g_{min} as measured by the weight loss of detached leaves is presented, which shows much variation in this trait, which is not clearly related to species groups, climate of origin or leaf type. Much evidence points to the idea that g_{min} is highly responsive to the growing conditions of the plant, including soil water availability, temperature and air humidity – as we further demonstrate with two case studies. We pay special attention to the role of the minimum conductance in the Ball–Berry model of stomatal conductance, and caution against the usual regression-based method for its estimation. The synthesis presented here provides guidelines for the use of g_{min} in ecosystem models, and points to clear research gaps for this drought tolerance trait.

Key words: cuticular conductance, drought tolerance, ecosystem modeling, plant water relations, stomatal conductance model.

I. Introduction

Plants face a dilemma in constructing leaves that minimize water loss, whilst allowing the uptake of CO_2. As a membrane that is permeable to CO_2, but not H_2O, has never evolved, all land plants have stomata in their leaves, which disrupt the cuticle and allow CO_2 uptake. It is well known that stomata open and close in response to changes in light intensity, humidity and CO_2 concentration at the leaf surface. To avoid desiccation and ultimate death, stomata typically close during periods of water stress. When stomata are closed, water loss continues at a greatly diminished rate through the cuticle. After accounting for evaporative demand, this rate of water loss is expressed as the minimum conductance of a leaf. There is increasing recognition that the minimum conductance plays an important role in estimating the water fluxes in plant canopies (Barnard & Bauerle, 2013), during heat waves (Kala *et al.*, 2016) and in models of plant drought response (Blackman *et al.*, 2016; Martin-StPaul *et al.*, 2017).

A comprehensive review of g_{min} with the goal to improve functional model representation is made difficult by the fact that literature data arise from various methods, and represent distinct processes. The absolute minimum attainable water loss rate is through the cuticle only, which is typically measured on isolated cuticles of the adaxial (nonstomatal) side of the leaf. Other measurements allow for the estimation of water loss through incompletely closed and broken stomata. Of particular interest because of its simplicity is the method in which leaves are detached from the plant, their weight loss monitored over time and expressed as the minimum conductance (g_{min}). This method (mass loss of detached leaves, MLD) aims to simulate field conditions during severe drought, when water supply to the leaf has practically ceased, although it proceeds much more quickly (typically 0.5–2 d, compared with weeks or even months in field conditions). This measurement also includes both surfaces of the leaf – not just the adaxial side. A comprehensive compilation of estimates of g_{min} is currently lacking, and is needed, not just to parameterize models, but also to study sources of variation in this overlooked plant trait.

In this review, we discuss the role of the minimum conductance in models of plant water use, and critically evaluate sources of variation in this parameter. Previous reviews of the minimum conductance have largely focused on the biology of the plant cuticle, and detailed physiology and anatomy of water transport across cuticles (Kerstiens, 1996a; Riederer & Muller, 2006; Fernández *et al.*, 2017; Schuster *et al.*, 2017). Other work has focused on a different definition of the minimum conductance (g_0): the value that should be used in models of plant water use (e.g. Barnard & Bauerle, 2013; Lombardozzi *et al.*, 2017), which includes both g_{min} and a 'stomatal residual' because of the fact that stomata do not completely close during periods of zero photosynthesis (De Kauwe *et al.*, 2015). This discussion often centers around leaf conductance during the night (Lombardozzi *et al.*, 2017), but we must also consider appropriate values for the minimum conductance during the day, for example during very high (or low) temperature, transient low light and extreme drought. Thus, there is a lack of connection between the detailed understanding of the plant cuticle (Riederer & Muller, 2006) and the very simple assumptions made when using leaf conductance in global vegetation models (GVMs).

We aim to improve the connection between the physiology of minimum conductance, empirical approaches and model implementations by synthesizing the state of knowledge. Our goals are as follows: (1) to quantitatively compare various definitions of g_{min}, which have sometimes been assumed to be equal; (2) to present a new compilation of minimum conductance measurements, which we use to test for ecologically meaningful patterns, and demonstrate the large acclimatory potential of this trait to environmental drivers; and (3) to demonstrate the need to include a nonzero minimum conductance in models of water use efficiency and drought responses.

II. Comparison of various definitions and measurement techniques of minimum conductance

Measurements of minimum conductance, after stomatal closure is either induced or assumed, can be broadly divided into the following categories: conductance of the cuticle only, conductance of detached leaves, and gas exchange measurements during conditions leading to presumed stomatal closure (Table 1). The absolute minimum conductance attained by leaves is that through the cuticle only. Measurements of cuticular conductance (g_{cuti}) are typically made on isolated nonstomatal cuticles (Riederer & Schreiber, 2001) via special gas exchange techniques (Boyer *et al.*, 1997), or via MLD by sealing the side with stomata (Kerstiens, 1996a). We further discuss some important aspects of cuticular conductance in Section III.

The minimum conductance of intact leaves is typically measured by MLD. In this method, leaves are detached and leaf mass is monitored over time as the leaf dries out. Early work by Hygen (1951) showed that, after a leaf is detached, initial water loss rates are high, but, after some time, a constant low rate is achieved. From this minimum transpiration rate (sometimes described as the 'residual transpiration' or 'epidermal transpiration'), the minimum conductance (g_{min}) can be estimated using the measured vapor pressure deficit (VPD) (Sinclair & Ludlow, 1986). Although this method resembles the conditions that plants may experience during a dry-down or periods of extreme stress, some uncertainties regarding the methods of measurement remain. In our own work, we have found that, in some leaves, the water loss rate increases (rather than decreases) sometime after leaf detachment (see Supporting Information Methods S1). It is likely that the relatively rapid dry-down sometimes causes artifacts, and must be carefully avoided (see also Heinsoo & Koppel, 1998).

We quantitatively compared g_{cuti} and g_{min} by synthesizing existing data. In addition, we compiled data on leaf conductance when photosynthesis rates are low or zero during nondrought conditions: night-time conductance (g_{dark}) (further discussed in subsection VI.4), conductance at low photosynthetically active radiation (PAR) (0–40 µmol m^{-2} s^{-1}) during the day, and conductance during conditions in which photosynthesis rates are very low (< 1 µmol m^{-2} s^{-1}) (but excluding low PAR and drought).

Table 1 Definitions of minimum conductance

Variable	Definition
g_{cuti}	Conductance of an isolated nonstomatal cuticle
g_{min}	Minimum conductance measured from the weight loss of detached leaves
g_{dark}	Night-time conductance, or conductance after significant dark adaptation
g_0	Intercept in the Ball–Berry-type stomatal conductance model, that is, g_s when A_n approaches zero

Measurements of conductance of isolated, nonstomatal cuticles (g_{cuti}) were taken from the compilations by Kerstiens (1996a) and Schuster *et al.* (2017) (both also include g_{min} data, but these were not used as they included no metadata). Data on minimum conductance (g_{min}) from MLD were compiled from 40 original papers (see Methods S2 for description and references). For the compilation, we returned to all original papers mentioned in the review by Kerstiens (1996a), and added many newer sources (see Methods S2 for full details of the compilation). The database includes a total of 221 species (136 Angiosperm, 49 Gymnosperm, 1 Pteridophyte) from 57 taxonomic families, with woody species making up *c.* two-thirds of the data.

All conductance values were converted to per unit projected surface area, allowing direct comparison with stomatal conductance data which are typically presented in these units. Estimates of g_{dark} were taken from Lombardozzi *et al.* (2017), who compiled measurements of *c.* 150 species during the night (we selected only gas exchange-based measurements from their database). Daytime values ($g_{low\ PAR}$ and $g_{low\ A}$) were estimated from an update to the Lin *et al.* (2015) database by taking the appropriate subsets and averaging the g_s values by species within the study. All data and code to reproduce the database and analyses are available online (see the Acknowledgements section).

The results of the quantitative comparison are presented in Fig. 1. From this compilation, a few striking differences among the estimates are apparent. Cuticular conductance averaged 0.45 mmol m^{-2} s^{-1}, 10-fold lower than g_{min} (4.9 mmol m^{-2} s^{-1}). This result is in line with the methods comparison of Kerstiens (1996a). More recently, Schuster *et al.* (2017) argued, based on data for eight species, that g_{min} from MLD is comparable with g_{cuti}. However, in the same study, a literature compilation of hundreds of values showed that g_{cuti} was 10-fold lower than g_{min}, although this finding was not reported by Schuster *et al.* (2017) (see also Fernández *et al.*, 2017) and, instead, g_{min} and g_{cuti} were pooled in their analysis. Nonetheless, the comparison between g_{cuti} and g_{min} should be viewed with some caution as Kerstiens (1996a) argued that measurements of g_{cuti} may be too low because of the low water content of the cuticle after detachment from the leaf and storage in often dry-air conditions. Boyer *et al.* (1997) suggested that this decline in the cuticular permeability could be a result of stretching of the wax layer at full saturation and tightening of the wax structure as the turgor releases.

Conductance in the dark (g_{dark}) (mean = 41.4 mmol m^{-2} s^{-1}) was, on average, eight-fold higher than g_{min}. It is not a new observation that stomata do not close fully in the dark (further discussed in subsection VI.4). Previous studies have directly compared g_{dark} and g_{min} in the same species, and generally concluded that g_{dark} is much higher than g_{min} (Hygen & Midgaard, 1954; Körner, 1994; Walden-Coleman *et al.*, 2013), but an exception is Cavender-Bares *et al.* (2007), who found that the two rates are similar in oaks. In turn, g_{dark} could not be differentiated from stomatal conductance measurements during daytime in very low light (mostly just after dawn or before sunset) ($g_{low\ PAR}$) or during conditions in which photosynthetic rates were very low (as a result of very high temperature, VPD or other factors) ($g_{low\ A}$). These comparisons demonstrate that g_s values during nondrought

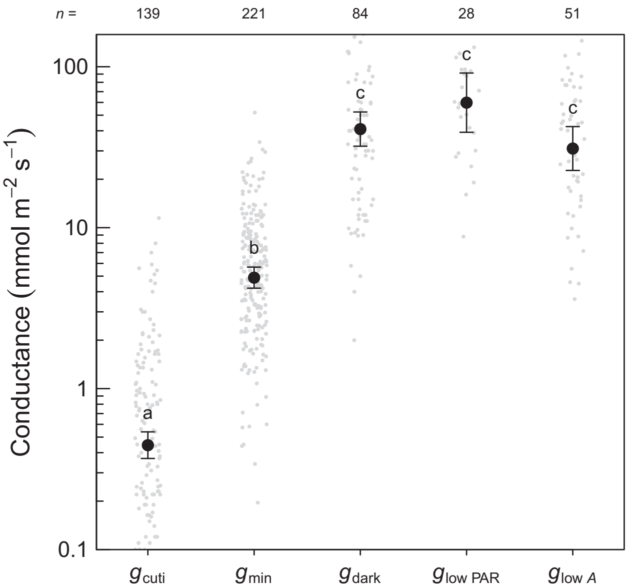

Fig. 1 Comparison of various estimates of the (presumed) minimum conductance. Error bars are 95% confidence intervals. Gray dots are the original data (but a few data points occur outside the figure range). Different letters denote significant differences (at $\alpha = 0.05$). g_{cuti}, conductance of isolated cuticles; g_{min}, minimum conductance measured with mass loss of detached leaves; g_{dark}, leaf conductance during the night or after dark adaptation; $g_{low\ PAR}$, leaf conductance during low light (PAR, photosynthetically active radiation); $g_{low\ A}$, leaf conductance during periods of very low photosynthesis. See Section II for data sources and methods.

conditions when photosynthetic rates are zero or negligible are much higher than the minimum reached in simulated drought conditions (g_{min}).

III. Cuticular conductance

A review of cuticular transport mechanisms, biochemical composition and formation of cuticular waxes is well outside the scope of this review, as these topics have been well described elsewhere (Kerstiens, 1996a, 2006; Schreiber & Riederer, 1996; Schreiber, 2001; Shepherd & Wynne, 2006; Schuster *et al.*, 2016). However, a few key points should be summarized as they are relevant to the current discussion, in particular when we aim to interpret the variation in literature values of g_{min} (Section V).

Although we use the term ‘cuticular conductance’ freely, this transport pathway does not represent a true conductance, as water does not diffuse as a gas through the cuticle. Instead, it dissolves into the medium of the cuticle, diffuses through the solid matrix and is desorbed at the outer edge of the cuticle (Kerstiens, 1996a; Schreiber & Riederer, 1996; Riederer & Schreiber, 2001). The main barrier to diffusion is actually a very thin layer of wax at the leaf surface. Because most of the resistance is located in such a thin layer, g_{cuti} does not correlate with the thickness of the cuticle (Priestley, 1943; Riederer & Schreiber, 2001; Anfodillo *et al.*, 2002; Schuster *et al.*, 2016). Nonetheless, there is considerable variation in cuticle thickness among plant species (Schuster, 2016), along altitudinal transects (DeLucia & Berlyn, 1984) and even with increasing height in the canopy of very tall trees (Woodruff *et al.*, 2010). If the cuticle thickness does not directly affect its conductance, what is the value of a thicker cuticle?

It is important to bear in mind the many other functions of the cuticle, including the attenuation of radiation, as a barrier to fungal pathogens, various interactions with insects, including signaling and herbivory resistance (Kerstiens, 1996b; Riederer & Muller, 2006; Müller, 2008), and foliar water uptake (Fernández *et al.*, 2017). The thickness of the cuticle may also confer mechanical strength, as Onoda *et al.* (2012) reported that thicker cuticles are more resistant to tearing (the force to tear was proportional to the cuticle thickness). As such, thick cuticles may be advantageous in exposed environments to avoid excessive damage (Blackman *et al.*, 2005). Prolonged exposure to wind has been shown to increase the conductance of the cuticle (Grace, 1974; Hadley & Smith, 1983; van Gardingen *et al.*, 1991) by dislodging cuticular compounds by abrasion (Rogge *et al.*, 1993). Similarly, exposure to simulated rain damages the cuticle and increases its conductance (Baker & Hunt, 1986), most dramatically demonstrated in an ice storm, leading to much higher g_{min} (Boyce *et al.*, 2003).

Despite considerable work on the topic, no clear relationship between the chemical composition or structure of the cuticle and its conductance has emerged. Recently, Schuster (2016) presented a comprehensive study of cuticle chemical composition, but was able to explain only some of the wide range of g_{cuti} measured across different plant species. Similarly, Hauke & Schreiber (1998) found no relationship between the gradual decrease in g_{cuti} in *Hedera helix* during leaf maturation and cuticle wax amount, mean chain lengths or cuticle weight.

IV. Contribution of stomata

The minimum leaf conductance includes two pathways: across the cuticle and through the (potentially incompletely closed) stomata. Only a few studies have directly quantified the stomatal component of minimum conductance, in contrast with the wealth of information on the cuticular component. A detailed study of *Hedera helix* concluded that 35% of water loss occurred across the stomatal pores (although closed) and 65% across the nonstomatal part of the cuticle, despite the fact that the stomata presumably covered only a small fraction of the leaf (Šantruček *et al.*, 2004). For 10 *Sorghum* genotypes, Muchow & Sinclair (1989) reported a strong positive correlation between stomatal density and g_{min}, suggesting that leaky stomata contribute substantially to g_{min}. For seven conifer species, Brodribb *et al.* (2014) reported that 50–94% of water loss of detached leaves originated from the stomatal side, concluding that stomata must be very leaky, and probably incompletely closed. However, Šantruček *et al.* (2004) found that the cuticle of the stomatal side (but excluding the stomata themselves) in *Hedera helix* was many times more permeable than the nonstomatal side, thus providing another potential explanation for this difference. Either way, the water loss rates of intact leaves cannot be simply explained by the permeability of isolated nonstomatal cuticles, the contribution of leaky stomata and the potentially more permeable cuticle on the abaxial side, and probably varies among species.

One key question is whether incomplete stomatal closure is under the plant's control, or whether it is an unavoidable consequence of imperfect stomata, damage, blocking by particles, etc. For example, endophytic fungi, which commonly colonize plant leaves, have been shown to prevent stomatal closure and greatly increase water use (Arnold & Engelbrecht, 2007). As discussed in the next section, there is ample evidence to suggest that stomata not only stay open in the dark, but that plants actively control stomatal conductance during the night. During severe drought, there is less evidence for such active control, and it seems likely that incomplete closure is not under the plant's control as there is no obvious reason to keep stomata open. Some conditions (especially rapid drying conditions) may lead to excessive drying of the epidermis, which can physically pull apart the stomata ('mechanical advantage', Buckley, 2005).

V. Environmental and ecological variation in minimum conductance

1. Minimum conductance is highly variable among species

In the following sections, we review the quite substantial literature on g_{min} measured with the MLD technique, stretching back to the 1930s (Pisek & Berger, 1938), focusing on environmental and ecological determinants. We also further analyze the literature compilation of g_{min} (Fig. 2), and separately analyze crop species and their genotypic variation. Comparing all available data, we did not find significant relationships between g_{min} and climate of origin, nor were there meaningful relationships with other traits (see Methods S1). We thus found it difficult to explain the variation in g_{min} among species. A simple breakdown by taxonomic order (Fig. 2b) revealed that grasses (Poales) have a higher g_{min} compared with other orders, and conifers (especially Pinales) tend towards the lower range of values (but are only significantly different from Poales).

Very few studies have found meaningful correlations between g_{min} and environmental factors or ecological categories. Based on their own compilation of the literature, Schuster *et al.* (2017) concluded that there were no significant differences in g_{min} or g_{cuti} (analyzed together) by plant growth form. One notable exception was Brodribb *et al.* (2014), who showed a correlation with rainfall at species origin (of the driest quarter), but these authors used a gas exchange approach (over many weeks), not MLD. This correlation did not hold across the species in our database. Of particular note, *Eucalyptus* species ($n = 11$, included in Myrtales) – all measured on the driest continent of Australia – have g_{min} values slightly higher than the average (Fig. 2b).

In crop science, g_{min} has long been identified as a key drought tolerance trait (Sinclair & Ludlow, 1986). A number of studies have targeted g_{min} as a key trait for the breeding of more drought-tolerant crops, leading to comparisons of g_{min} across genotypes grown in the same conditions. For example, James *et al.* (2008) compared g_{min} in 58 soybean (*Glycine max*) genotypes, and found more than two-fold variation that could not be easily explained by other traits. In Fig. 2(c), we have compiled a number of studies in crops, demonstrating not just variation in g_{min} among crops, but also

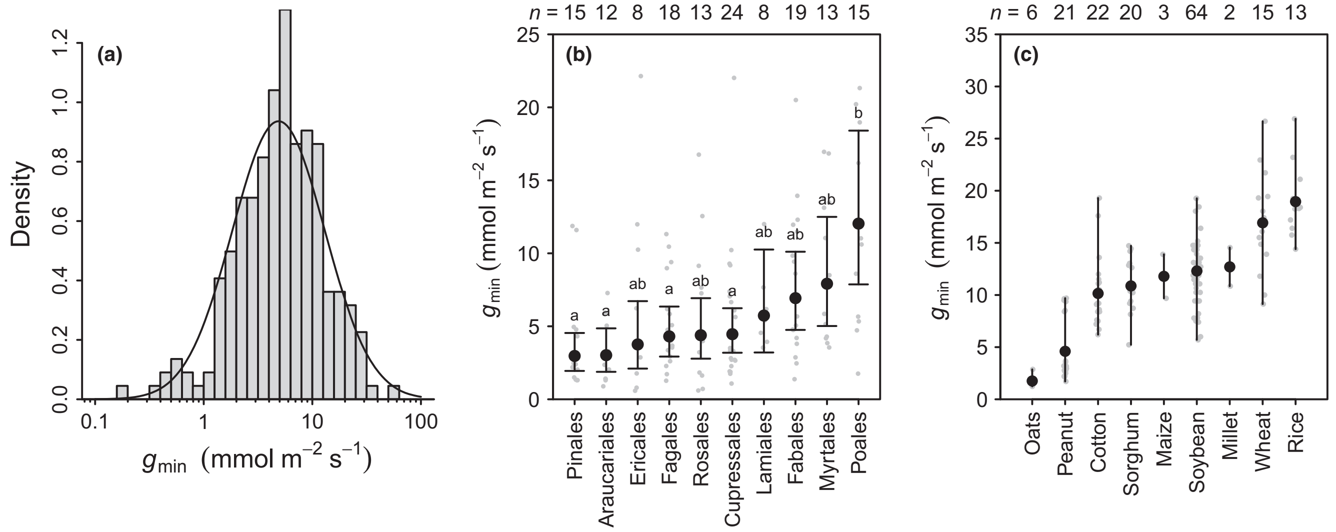

Fig. 2 Analysis of a literature compilation of minimum conductance (g_{min}) estimates, as measured with mass loss of detached leaves. (a) Histogram (probability density) of all estimates (after averaging by species, $n = 221$), with a log-normal distribution curve (mean = 4.89, SD = 2.67). (b) g_{min} averaged by phylogenetic order (including only the top 10 orders in the database). Bars are 95% confidence intervals. Numbers above the figure refer to the number of species. Different letters denote significant differences (at $\alpha = 0.05$, adjusted for multiple comparisons) and gray symbols are species-level data. (c) g_{min} estimates for crops only, averaged by genotype. Bars denote the range, illustrating the wide range in g_{min} among genotypes for a particular crop species. Numbers above the figure refer to the number of genotypes included.

the wide range in g_{min} among genotypes. Again, it is striking that the wide variation in g_{min} cannot be easily explained by variation in leaf or other traits, or chemical and structural components of the cuticle (Bengtson *et al.*, 1978; James *et al.*, 2008; Saito & Futakuchi, 2010), suggesting a significant role of incomplete stomatal closure.

2. Acclimation to the environment

Although there is clearly considerable variation in g_{min} among species, a number of lines of evidence suggest that g_{min} also has great potential for plasticity. Here, we summarize the literature on the acclimation of g_{min} to drought conditions, to changes in temperature and humidity, and the change in g_{min} with leaf age, altitude and other factors. This discussion is directly relevant to the use of g_{min} in models, because, if the degree of plasticity is large, it complicates model parameterization.

There is a general tendency for a decreased g_{min} in plants acclimated to drought stress (James *et al.*, 2008). The magnitude of the decrease in g_{min} with acclimation to drought stress varies from −4 to −70% (across 10 studies, see Table S1), with a typical decrease on the order of 30–40%. In each of the studies summarized, plants were grown in well-watered or drought conditions, and, in one case, a difference in g_{min} was demonstrated after just 4 d of drought exposure (Bengtson *et al.*, 1978). We also demonstrate drought acclimation via a case study on 11 *Hakea* species grown in two watering treatments (Fig. 3). All 11 species showed a decrease in g_{min} in the drought treatment (see Methods S3 for experimental details). This significant change in g_{min} with drought acclimation is probably an important component of the overall drought hardening of plants.

The idea that water limitation causes a reduction in g_{min} (via changes in the chemical composition of the cuticle) can be tested by inspecting the response to factors that increase evaporative demand. As one of the very few studies testing this idea, Fanourakis *et al.* (2013) reported much lower g_{min} in *Rosa* sp. plants grown in 60% vs 95% relative humidity. The difference could be attributed largely to a change in stomatal anatomy and lack of closure during desiccation, not to changes in the cuticle *per se*. Also relevant is Sack

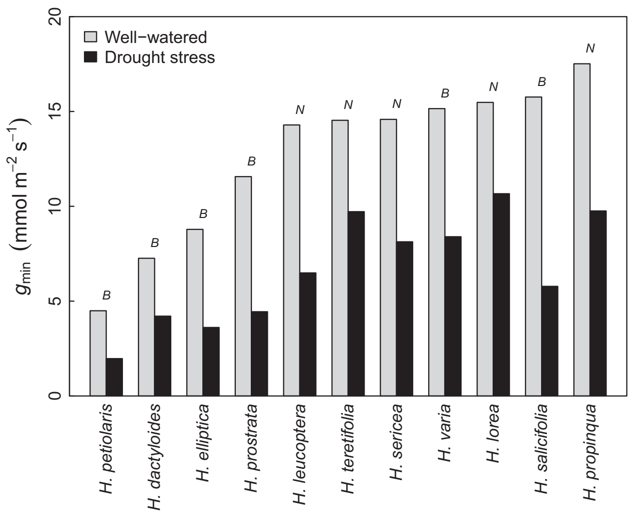

Fig. 3 Minimum conductance (g_{min}) measured by mass loss of detached leaves on a variety of *Hakea* species, a genus native to Australia. Plants were grown in containers in a grow house, and supplied with ample water or subjected to long-term (8 months) mild drought stress. Bars are labeled by leaf form (broadleaf (*B*) or needle-like (*N*)) and ordered by g_{min} in the well-watered treatment. For drought-treated plants, g_{min} was higher for species with needle-like leaves (Wilcoxon test, $P = 0.02$), but not for well-watered plants ($P = 0.14$).

et al. (2003), who reported lower g_{min} in sun leaves (for two of four species) compared with shade leaves, again a lower g_{min} for leaves acclimated to high evaporative conditions.

A number of studies have attempted to attribute the drought-induced acclimation in g_{min} to a change in the chemical composition of the cuticle. Bengtson *et al.* (1978) reported lower g_{min} in six oat varieties in response to drought, and an increase in the amount of cuticular waxes, but could not find a relationship between the two and the response was highly genotype specific. However, Premachandra *et al.* (1992) found that the epicuticular wax load increased on leaves of nonirrigated *Sorghum* cultivars and was positively correlated with cuticular conductance and cell membrane stability. Macková *et al.* (2013) found that the addition of abscisic acid (ABA, simulating drought stress) to *Lepidium sativum* increased the chain length of cuticular waxes (but not the total amounts). Bi *et al.* (2017) also reported that drought caused a change in cuticular wax production and chemical composition, but again in a highly genotype-specific way. Thus, it can be concluded that the cuticle indeed changes substantially after a change in plant-available water, but in a complex, species-specific manner that is yet to be connected directly to changes in g_{min}.

The response of g_{min} to temperature is more complex; it shows both a response to instantaneous changes in temperature, as well as an acclimatory response to growth temperature. Riederer & Schreiber (2001) and Schuster *et al.* (2016) have both demonstrated a steep nonlinear instantaneous response of g_{cuti} to temperature, with the response becoming especially steep at higher temperatures (> 40°C). In *Eucalyptus haemastoma*, the response of g_{min} to temperature was so steep that the proportion of cuticular to total transpiration increased from 2–3% at 20°C to 40% at 38°C (Eamus *et al.*, 2008). The mechanism of the instantaneous temperature response is complex and highly species specific, and we refer to Schuster *et al.* (2016) for a detailed investigation. The rapid increase in g_{min} at high temperature may well be a crucial component of the ability of plants to tolerate heat waves (Drake *et al.*, 2018). In support of the link between g_{min} and heat tolerance, Schuster (2016) reported a negative relationship between thermal tolerance and g_{min} across nine species, such that species with improved tolerance to very high temperature had a low g_{min}.

Less well established is the acclimatory potential of g_{min} to changes in growth temperature. We present a case study on *Eucalyptus parramattensis* grown in whole-tree chambers (see Methods S3 for experimental details). The chambers either tracked ambient conditions, or were subjected to a + 3°C warming treatment. After several months of growth in the treatments, g_{min} was measured at various temperatures, ranging from 17.5 to 27.5°C. We found a 56% decrease in g_{min} in the elevated temperature trees, but there was no clear pattern with measurement temperature (Fig. 4). This decrease in g_{min} is consistent with the drought response because, again, g_{min} is reduced in leaves that are subjected to conditions that increase evaporative demand (VPD was higher in the elevated temperature treatment, see Drake *et al.*, 2018). The direction of this response is consistent with Duarte *et al.* (2016), who reported lower g_0 and g_{dark} in a heat wave treatment in *Pseudotsuga menziesii*, which persisted for some time. Responses across temperature gradients are more complex. In particular, the change in g_{min} with altitude has been well studied, and it is commonly reported that g_{min} increases with altitude (e.g. DeLucia & Berlyn, 1984; Herrick & Friedland, 1991; Anfodillo *et al.*, 2002). Fernández *et al.* (2017) discuss the literature on altitude responses in detail and argue that the short growing seasons at high altitude are insufficient for complete maturation of leaf cuticles.

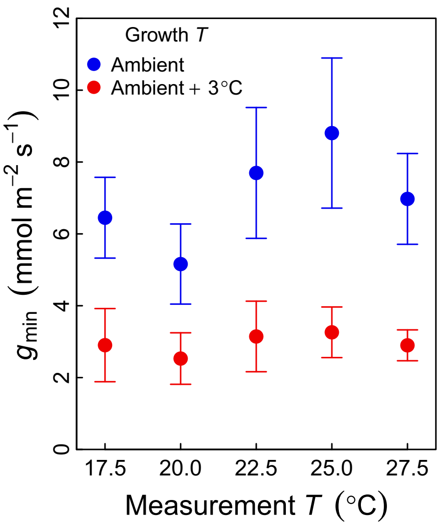

Fig. 4 Minimum conductance (g_{min}) measured with mass loss of detached leaves on *Eucalyptus parramattensis* grown in whole-tree chambers. Trees were grown following ambient conditions or in an elevated temperature treatment (+ 3°C) (see Drake *et al.*, 2018). Measurements of g_{min} were carried out at five different temperatures on replicate leaves. There was no consistent effect of measurement temperature on g_{min}, but leaves of trees grown in elevated temperature showed, on average, a 45% reduction in g_{min} ($P < 0.01$, linear mixed-effects model). Error bars denote 95% confidence intervals.

Finally, we mention the striking effect of leaf age on g_{min}. We have summarized five studies in Fig. S1, all of which reported an increased g_{min} for older leaves for the majority of species studied. The data reported by Jordan & Brodribb (2007) are particularly impressive, as g_{min} in the woody shrub *Agastachys odorata* gradually increased with leaf age up to *c.* 10 yr. If this effect is caused by properties of the cuticle alone, a possible explanation for the increase in g_{min} is the continued exposure to wind, rain and abrasives, which have been shown to damage the cuticle and increase its conductance (see discussion in Section III). Another possibility is that the contribution of stomata to g_{min} increases with leaf age, as reported by Jordan & Brodribb (2007). In plants that maintain several cohorts of leaves, the identification of an appropriate value of g_{min} for use in models must take into account the leaf age effect.

VI. Use of minimum conductance in models

1. Models of water use efficiency

Most current-generation, process-based GVMs use a version of the Ball–Berry class of 'stomatal' (technically including both stomata and the cuticle) conductance (g_s) models characterized by the dependence on assimilation rate, CO_2 and humidity (Eqn 1).

$$g_s = g_0 + g_1 \frac{A_n}{C_a} f(D) \quad \text{Eqn 1}$$

where g_1 is a 'slope' parameter, A_n is the leaf net photosynthetic rate, C_a is the atmospheric CO_2 concentration, $f(D)$ is some function of the VPD D (or relative humidity in the case of the model of Ball *et al.* (1987); see Damour *et al.* (2010) for a list of functions) and g_0 is the value of g_s when A_n is zero. The g_1 parameter is directly related to the water use efficiency: large values of g_1 indicate low water use efficiency. In this article, we refer to Eqn 1 as 'the Ball–Berry model', thus including all model formulations that include different $f(D)$ functions besides that proposed by Ball *et al.* (1987). Much attention has been paid to the quantification and interpretation of the variation in the g_1 parameter (Medlyn *et al.*, 2011; Prentice *et al.*, 2014; Lin *et al.*, 2015; Miner *et al.*, 2017), but the g_0 parameter has been studied in much less detail. For example, a recent comprehensive review of stomatal conductance models did not mention g_0 or any similar minimum conductance (Damour *et al.*, 2010). The original description of Eqn 1 as published by Ball *et al.* (1987) did not include an intercept term. It was first introduced in the unpublished manuscript of Ball *et al.* (1987) as an 'intercept' without further discussion of the role that it plays in the model. In practice, g_0 is usually estimated from a regression of Eqn 1 with leaf gas exchange data, but, as shown here, this approach may lead to inaccurate values, as pointed out by Barnard & Bauerle (2013), but not explained in detail.

In the Ball–Berry-type framework of stomatal conductance models, the effects of the photosynthetic photon flux density (PPFD) and leaf temperature on g_s are both assumed to enter via the dependence of A_n on these drivers. Here, we show that the g_0 parameter not only sets a minimum value of g_s in the model (when A_n is zero), but it also modifies the behavior of Eqn 1 after it has been coupled to the Farquhar–von Caemmerer–Berry model of photosynthesis (the so-called 'coupled leaf gas exchange model'). Leuning (1990) defined g_0 as g_s when A_n approaches zero as PPFD approaches the light compensation point, and pointed out that g_0 is necessary to simulate the increase in A_n/g_s (and C_i) at low light (see also Leuning, 1995). Similarly, Collatz *et al.* (1992) showed that the inclusion of g_0 affects the response of g_s to relative humidity in the coupled leaf gas exchange model. Despite these early reports, the exact role of g_0 in models is often overlooked.

In this review, we focus on the cuticle as a barrier to water loss, but point out that previous work has shown that the cuticle is much less permeable to CO_2 than H_2O (Boyer *et al.*, 1997; Boyer, 2015). This finding, if indeed generally true, has a large effect on the calculation of various gas exchange parameters (Hanson *et al.*, 2016). Manzoni *et al.* (2011) recalculated leaf water use efficiency for drought-treated plants assuming that CO_2 is blocked by the cuticle, but the uncertainty of this approach is the effect of leaky and incompletely closed stomata. Because g_0 includes not just the cuticle, but also incompletely closed stomata, we ignore this effect in the model simulations that follow.

Within the model framework, g_0 is reached when photosynthesis (A_n) goes to zero. However, A_n can approach zero for many different reasons, including low light, high temperature, low humidity and drought, and it is unclear whether the same g_0 is reached in each of these cases. In the application of the Ball–Berry model, it is frequently assumed that g_0 must equal g_s at night, simply because no photosynthesis occurs at night (Uddling *et al.*, 2005; Barnard & Bauerle, 2013; Lombardozzi *et al.*, 2017). An alternative common assumption is that g_0 is equal to the absolute minimum conductance achievable for a leaf, the 'cuticular conductance' (g_{cuti}) (Baldocchi, 1997; Egea *et al.*, 2011; Manzoni *et al.*, 2011), which technically is the conductance of the cuticle alone, ignoring leaky and incompletely closed stomata. Photosynthesis also ceases at very high temperature, but stomata do not appear to always close in proportion to this decrease in photosynthesis, if at all (Urban *et al.*, 2017; Drake *et al.*, 2018).

A popular approach in thinking about how stomata 'should' respond to environmental drivers is the idea that stomatal conductance is varied to maximize total photosynthesis for a given amount of water use (Cowan & Farquhar, 1977). The consequence is that stomata tend to open during periods that are favorable for photosynthesis (high light, optimal temperature) and close when photosynthesis drops to zero (darkness, very high temperature). Clearly, in this optimality framework, there is no place for g_0, as it is always suboptimal to open stomata (i.e. spend water) when there is no photosynthetic gain. Indeed, early work on optimal stomatal conductance models ignored the possibility of $g_s > 0$ when $A_n = 0$ (Cowan & Farquhar, 1977; Cowan, 1978; Hari *et al.*, 1986, 1999). More recent work derives the optimal g_s, and simply adds a g_0 to the solution (Medlyn *et al.*, 2011).

As pointed out by Leuning (1990, 1995), g_0 needs to be > 0, otherwise the ratio of intercellular CO_2 to atmospheric CO_2 concentration (C_i/C_a) does not vary with PAR, as is typical in leaf gas exchange data (although other mechanisms can also be employed to simulate this pattern, see Dewar *et al.*, 2018). When PAR approaches the light compensation point, clearly C_i needs to approach C_a, as no photosynthesis is occurring that draws down C_i. To see this point, we can rearrange Eqn 1 to give:

$$A_n/g_s = C_a f(D)/g_1 \quad \text{Eqn 2}$$

and, using the diffusion constraint (Fick's law) $A_n = g_s/1.6(C_a - C_i)$, we obtain an expression for C_i/C_a:

$$C_i/C_a = 1 - \frac{f(D)}{1.6 \cdot g_1} \quad \text{Eqn 3}$$

Eqn 3, derived using zero g_0, thus does not give any dependence on PAR.

Using the coupled leaf gas exchange model, we show in Fig. 5 how A_n/g_s and C_i depend on PPFD with three values of g_0 (0, 0.01 and 0.03 mol m^{-2} s^{-1}). We also demonstrate the effect of g_0 on modeling of the T_{leaf} response. In this simulation, T_{leaf} and VPD are assumed to co-vary with an empirical relationship as used by Duursma *et al.* (2014). Over the entire range of T_{leaf}, the inclusion of a nonzero g_0 obviously increases leaf transpiration, but at a slightly higher rate than just due to g_0. This effect arises because the additional conductance allows slightly higher rates of photosynthesis, which, in turn, increase g_s via Eqn 1.

2. Models of plant desiccation

When plants are sufficiently water stressed so that stomata are mostly closed, water loss still continues at a rate determined by the minimum conductance. Thus, models that aim to predict when plants desiccate and die must include a minimum conductance term. A classic study by Pisek & Winkler (1953) calculated the length of time needed to desiccate leaves to some critical low water content, given the minimum transpiration rate and the saturated water content of the leaves. Based on that work, Burghardt & Riederer (2006) reported a direct correlation between g_{min} and the survival time of leaves. Sinclair (2000) presented the minimum conductance as a key drought tolerance trait, and used it as a basis for the prediction of crop mortality during severe drought. More recently, Gleason *et al.* (2014) and Blackman *et al.* (2016) have proposed that embolism resistance together with whole-plant capacitance and minimum transpiration rates all contribute to define the time to desiccation. Building on this work, Martin-StPaul *et al.* (2017) demonstrated, in a whole-plant model of hydraulic failure, that g_{min} was one of the key parameters to explain the drop in water potential below the cavitation threshold, because stomata generally close well before this threshold. Applying the *Sureau* model presented in Martin-StPaul *et al.* (2017), we illustrate the critical role of g_{min} in defining the desiccation time (Fig. 6).

3. Problems with the estimation of g_0 from regression

The previous section discussed and compared methods for more or less direct measurements of minimum conductance according to various definitions. The approach taken by the majority of vegetation models is, however, very different. Usually, g_0 (for use in Eqn 1) is estimated from regression, with g_s as the response variable and the right-hand side of Eqn 1 as the predictor (a combination of measured photosynthesis rate, air humidity and CO_2 concentration). The g_0 parameter is thus estimated as the intercept. Here, we briefly discuss some statistical aspects of this estimation procedure, and draw the general conclusion that g_0 is poorly estimated by this method. The difficulty of the estimation can already be anticipated from the fact that: (1) many studies set g_0 to some assumed value rather than fitting it (e.g. Leuning (1995) uses 0.01 mol m^{-2} s^{-1} for all species, presumably because

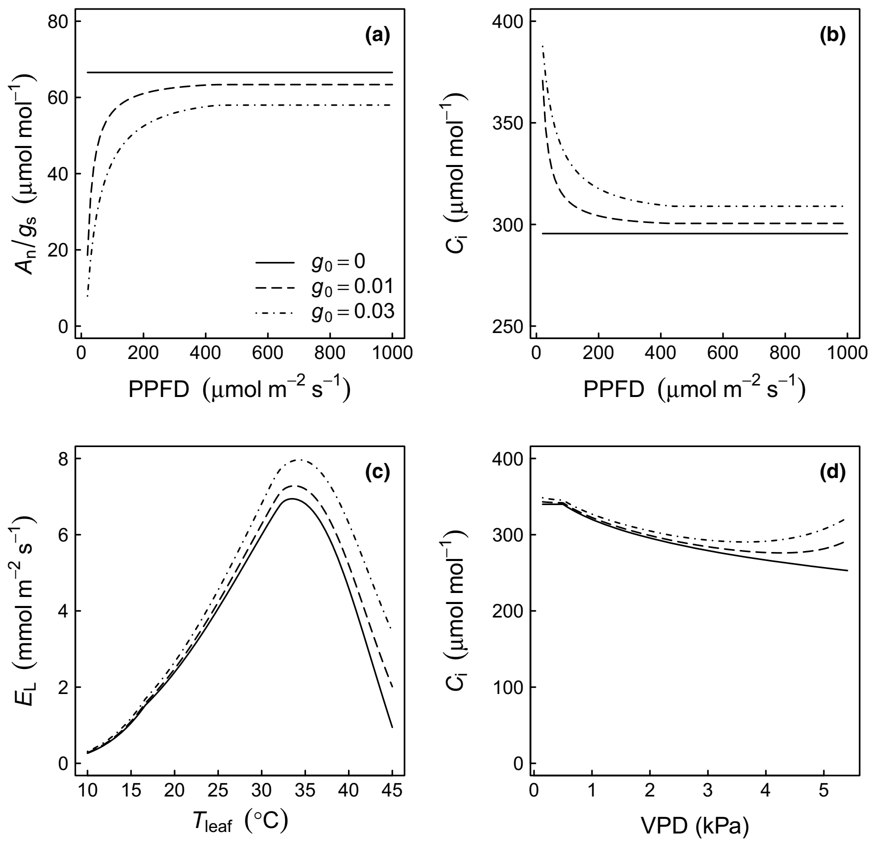

Fig. 5 Simulations with a coupled leaf gas exchange model (Duursma, 2015), demonstrating the effect of inclusion of the g_0 parameter (Eqn 1) on leaf fluxes. (a) Intrinsic water use efficiency (A_n/g_s) as a function of the photosynthetic photon flux density (PPFD), holding other environmental drivers constant, for three values of g_0. (b) The same simulations as in (a), but showing the intercellular CO_2 concentration (C_i). (c) Leaf transpiration (E_L) simulations, where the vapor pressure deficit (VPD) and air temperature (T_{air}) were covaried based on an empirical relationship (Duursma *et al.*, 2014), reflecting typical covariation in field conditions. (d) The same simulations as in (c), but showing C_i. Note how C_i increases at high VPD and T_{air}, only when $g_0 > 0$. For all simulations, it is assumed that T_{leaf} is equal to T_{air}, and we ignore the differential permeability of the cuticle to CO_2 and H_2O (Hanson *et al.*, 2016).

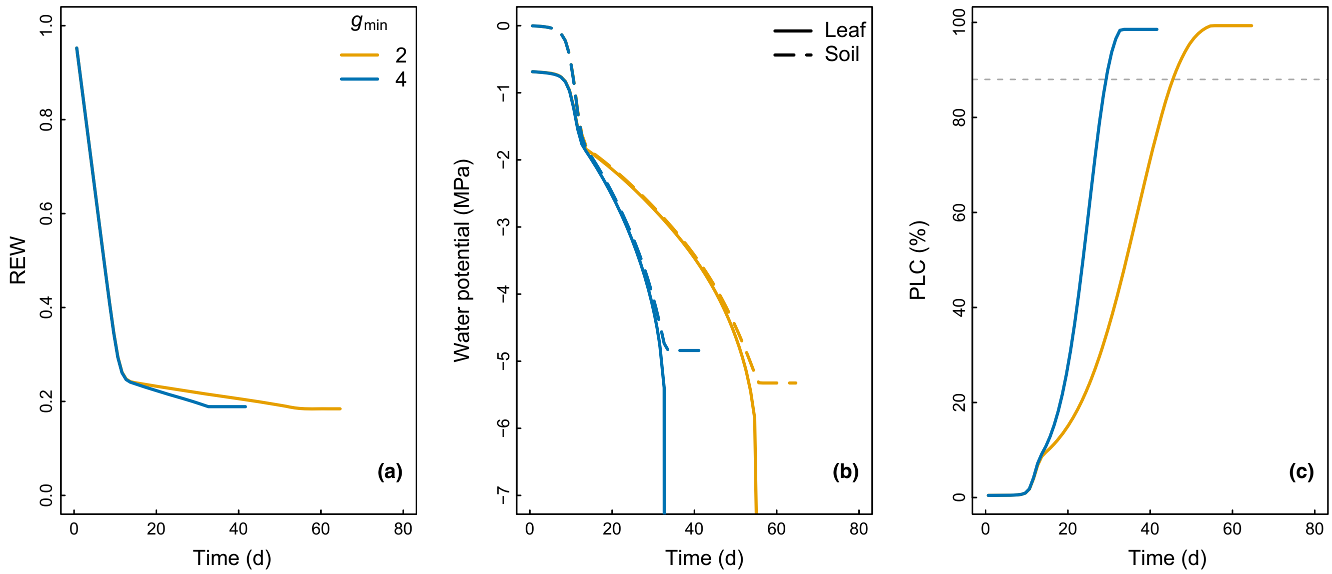

Fig. 6 Simulations with the *Sureau* model demonstrating the effect of g_{min} on the desiccation tolerance of plants. The *Sureau* model simulates water transport in the soil–plant–atmosphere continuum, and includes a detailed representation of capacitance in stem and leaf tissues. (a) Soil relative extractable water (REW; 1 = field capacity, 0 = permanent wilting point) for the two simulations, using a minimum conductance (g_{min}) of 2 or 4 mmol m^{-2} s^{-1} – all other parameters were equal. (b) Water potential in the soil and leaf as the dry-down progresses. (c) Progression of percent loss conductivity (PLC) of the xylem. Dashed line is at a PLC of 88%, indicating possible mortality.

unreliable estimates were obtained); and (2) negative g_0 estimates from regression are commonly reported (Leuning, 1995; Heroult *et al.*, 2013; Miner *et al.*, 2017), although it is clearly nonsensical to suggest negative conductance values. Barnard & Bauerle (2013) also mentioned the difficulty of fitting Eqn 1 to estimate g_0, but did not present specific details. The following analysis builds on their work by demonstrating statistical uncertainties.

It is also telling that there are few reports on the intraspecific plasticity or interspecific variation of g_0, perhaps because it is so poorly estimated. An exception is Duarte *et al.* (2016), who found a lower g_0 in a heat wave treatment in *P. menziesii* (although g_1 was unaffected), but, in their case, g_0 was very accurately estimated by careful multi-point light response curves. Another exception is Misson *et al.* (2004), who reported a close negative correlation between predawn leaf water potential and g_0 in Ponderosa pine (again, the g_1 parameter was unaffected).

In the following, we demonstrate that the fitting process is problematic for three reasons: (1) the estimates of g_0 and g_1 are highly correlated; (2) the precision for g_0 is generally much lower than for g_1; and (3) for data that have a worse fit overall, the g_0 estimates are elevated. We thus conclude that g_0 should not be estimated from regression, although this is the most common method applied. In addition, it is difficult – and generally not recommended – to accurately measure low fluxes with a portable gas exchange system, and great care must be taken to arrive at reasonable estimates of g_0 in this way.

Typically, gas exchange data are collected across a range of conditions, and are used to plot g_s vs a combined term including photosynthesis rate, CO_2 concentration and air humidity. An example dataset is shown in Fig. 7(a), together with a fitted linear regression line. We show in Fig. 7(b) that estimates of g_0 and g_1 are statistically correlated, that is, their confidence intervals are not independent. Thus, large estimated values for g_1 lead to low estimates for g_0, and vice versa. The consequence is that we cannot use estimates of g_0 from this approach in a compilation, because these estimates depend on g_1. The correlation between slopes and intercepts is not unique to Eqn 1, but a general property of linear models (Stapleton, 1995; Becker & Wu, 2007).

Next, we study the values obtained when fitting Eqn 1 to many datasets, basing our work on the large database collected by Lin *et al.* (2015) and the compilation of Miner *et al.* (2017). The (updated version of) the Lin *et al.* (2015) database includes >15 000 gas exchange measurements on over 300 species. After selecting species/site combinations with $n > 15$, we produced 78 estimates of g_1 and g_0 with nonlinear regression of the Medlyn *et al.* (2011) model of stomatal conductance. The compilation by Miner *et al.* (2017) includes 233 estimates of g_0 and m (they compiled parameters for the original Ball–Berry model, equivalent to g_1) for 172 species (including woody plants and crops).

For both databases, estimates of g_0 are inflated when the model fits poorly (Fig. 8a,b). This can be understood by considering that a poor fit often results in the flattening out of the regression line, thus giving a large value for the intercept. A poor fit is often obtained when there is little variation in the right-hand side of Eqn 1, usually because there is low variation in environmental conditions (humidity, light, temperature). We confirm this by showing that the standard error (SE) of g_0 increases when the coefficient of variation of the right-hand side of Eqn 1 is lower (Fig. 8c).

4. Night-time conductance

A number of studies have assumed that g_0 in the Ball–Berry model equals the night-time conductance (g_{dark}) (Barnard & Bauerle, 2013; Lombardozzi *et al.*, 2017), simply because it is a condition in

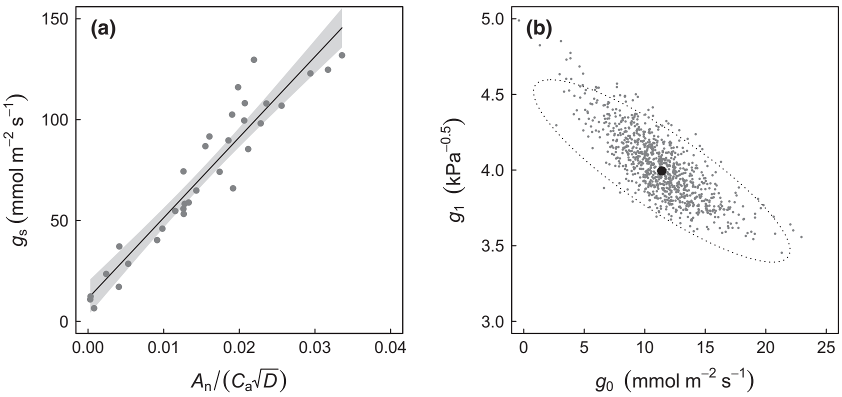

Fig. 7 (a) Example linear regression of stomatal conductance (g_s) against a combination of terms, in this case the linearized version of the model of Medlyn *et al.* (2011) applied to a leaf gas exchange dataset of Martin-StPaul *et al.* (2012). This example shows a very good fit between g_s and the stomatal index, and was selected from the database of Lin *et al.* (2015). The solid line is the regression line, and the shaded area is the 95% confidence interval for the mean. (b) The correlation between the estimated slope (g_1) and intercept (g_0) of the regression shown in (a). The dotted ellipse is a bivariate 95% confidence interval for slope and intercept. The symbols represent 1000 bootstrap samples of the coefficients.

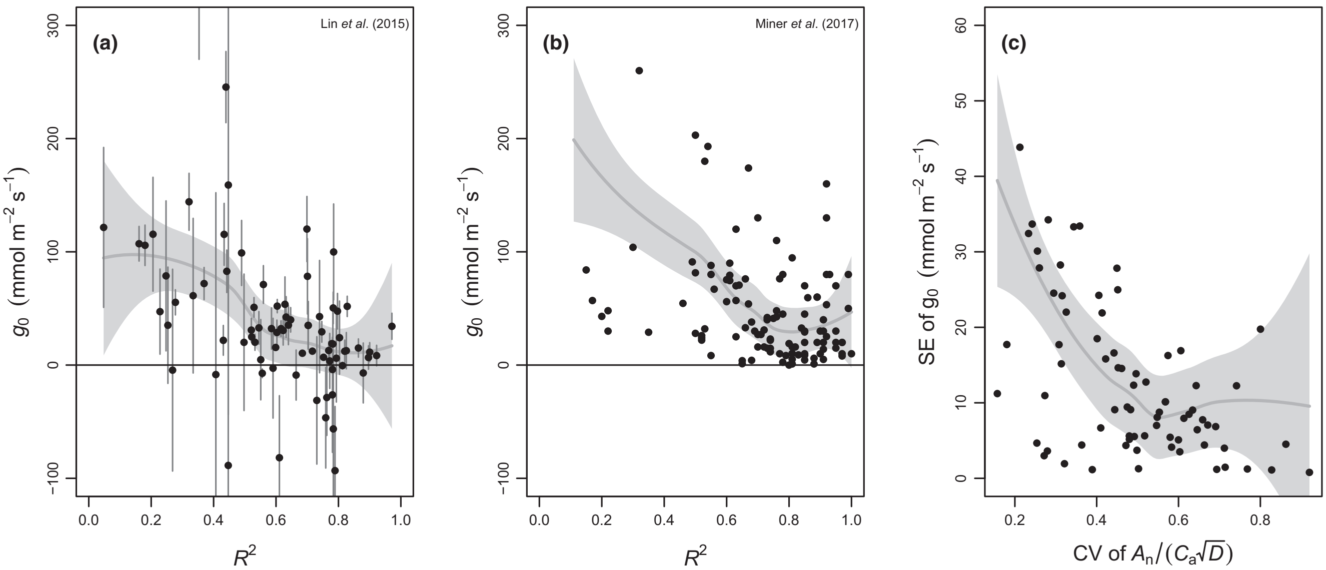

Fig. 8 Statistical uncertainty in the estimation of g_0 from regression, demonstrated with two parameter databases. (a) We fitted the linearized form of the Medlyn *et al.* (2011) model to each of the datasets in the Lin *et al.* (2015) leaf gas exchange database, showing that, for poorly fitted relationships (low R^2), inflated estimates of g_0 are obtained. Vertical lines are 95% confidence intervals. The gray line is a fitted loess smoother with 95% confidence interval. Note the wide confidence intervals and frequent negative values. (b) Similar to (a), but using the published compilation by Miner *et al.* (2017). The gray line is a fitted loess smoother with 95% confidence interval. (c) Using the fits from (a), a demonstration that the standard error (SE) of g_0 is much higher when the coefficient of variation (CV) of the predictor (i.e. right-hand side of the equation being fitted) is lower.

which net photosynthesis is zero. We provide some caution to the assumption that g_{dark} can be used in models of daytime leaf conductance. First, ample observations suggest that g_{dark} is not a fixed rate, but varies tremendously during the night. Caird *et al.* (2007) (and references therein) described how, for many species, g_{dark} is not stable throughout the night period. Instead, endogenous, gradual increases in stomatal opening during predawn hours have been reported in many species under natural field conditions, as well as in controlled environments (Rawson & Clarke, 1988). Resco de Dios *et al.* (2016) showed that, in *Eucalyptus camaldulensis*, g_{dark} in the period just after sunset was much lower than pre-dawn g_{dark}. Strong evidence for endogenous regulation of g_{dark} was reported by Resco de Dios *et al.* (2013), who showed that g_{dark} fluctuated throughout the night, despite environmental conditions being held constant in whole-tree chambers. In addition, g_{dark} can show a clear response to VPD (Barbour & Buckley, 2007) during night-time conditions. Finally, g_{dark} is under strong genetic control independent of daytime water use – at least in grapevine (Coupel-Ledru *et al.*, 2016). Clearly, g_{dark} is an actively controlled process that cannot be adequately summarized by a single constant g_0, and should be modeled in a separate framework that is yet to be identified.

5. Towards a new model formulation

We suggest that the minimum conductance in the Ball–Berry model should include both a g_0 and a g_{min} term, as g_0 represents the minimum reached during low light and conditions of low photosynthesis, and g_{min} represents the minimum reached during severe drought. Moreover, we suggest that the minimum conductance is not simply added to the photosynthesis-dependent term (right-hand side of Eqn 1), but used as an actual minimum. Thus:

$$g_s = \max\left[\max(g_{min}, g_0), g_1 \frac{A_n}{C_a} f(D)\right] \quad \text{Eqn 4}$$

This model for g_s will converge to g_0 during periods of low photosynthesis, and to g_{min} during drought, if we further include a model for the dependence of g_0 on water availability (see, for example, Misson *et al.*, 2004) – as long as the right-hand term (including g_1) is reduced under drought as well (Zhou *et al.*, 2013). Another advantage is that independent estimates of g_0 can be used, not those obtained via regression, which produces the undesirable correlation with estimates of g_1. The above formulation is yet to be tested against data, but we propose that this test should be performed with data from drought and nondrought conditions.

VII. Conclusions

In a pioneering publication on stomatal conductance, Jarvis (1976) stated that 'we have assumed in the following equations that when stomata are closed the leaf conductance is zero because field data are generally inadequate to define a cuticular conductance'. Similarly, given the poor statistical properties of g_0 estimated from regression, we conclude that g_0 should not be estimated from regression on leaf gas exchange data for use in models. Then, how should g_0 be estimated? It is clear from our review and synthesis of available data that there is no single minimum conductance. Leaves maintain much higher g_{dark} (itself an actively controlled process) than the minimum conductance measured on intact detached leaves. Thus, when modeling night-time or low-light conductance, a different g_0 should be used than when modeling the drought response of plants. We suggest a new model form that includes both g_0 and g_{min} with some desirable properties in Section VI.

Finally, we conclude that g_{min} displays a large amount of variation among species that could not be explained by traits, and remarkable plasticity to growing conditions. Perhaps this plasticity is the reason that g_{min} does not vary predictably among species. Another possibility is that the lack of standardized methods for measurement preclude clear comparisons among species. Future studies should compare g_{min} on many species grown in the same conditions to better understand the adaptive value of the minimum water loss rate of leaves.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 Effects of leaf age on g_{min}.

Table S1 Effects of drought stress on g_{min}

Methods S1 Methodological issues with the measurement of g_{min}.

Methods S2 Literature compilation of g_{min} estimates.

Methods S3 Methods description for case studies.