On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls

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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.

I. Introduction

Plants face a dilemma in constructing leaves that minimize water loss, whilst allowing the uptake of CO₂. As a membrane that is permeable to CO₂, but not H₂O, has never evolved, all land plants have stomata in their leaves, which disrupt the cuticle and allow CO₂ uptake. It is well known that stomata open and close in response to changes in light intensity, humidity and CO₂ 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-StrPaul et al., 2017).

A comprehensive review of $g_{\text{min}}$ 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 ($g_{\text{min}}$). 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 $g_{\text{min}}$ 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 $g_{\text{min}}$ 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 $g_{\text{min}}$ 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 ($g_{\text{cuti}}$) 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 ($g_{\text{min}}$) 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 $g_{\text{cuti}}$ and $g_{\text{min}}$ 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 ($g_{\text{dark}}$) (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

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
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<tr>
<td>$g_{\text{cuti}}$</td>
<td>Conductance of an isolated nonstomatal cuticle</td>
</tr>
<tr>
<td>$g_{\text{min}}$</td>
<td>Minimum conductance measured from the weight loss of detached leaves</td>
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<tr>
<td>$g_{\text{dark}}$</td>
<td>Night-time conductance, or conductance after significant dark adaptation</td>
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<tr>
<td>$g_0$</td>
<td>Intercept in the Ball–Berry-type stomatal conductance model, that is, $g_{\text{a}}$ when $A_{\text{a}}$ approaches zero</td>
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Measurements of conductance of isolated, nonstomatal cuticles ($g_{cut}$) 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 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 150 species during the night (we selected only gas exchange-based measurements from their database). Daytime values ($g_{low \text{ PAR}}$ and $g_{low A}$) were estimated from an update to the Lin et al. (2015) database by taking the appropriate subsets and averaging the $g$ 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 $g_{cut}$. However, in the same study, a literature compilation of hundreds of values showed that $g_{cut}$ 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 $g_{cut}$ were pooled in their analysis. Nonetheless, the comparison between $g_{cut}$ and $g_{min}$ should be viewed with some caution as Kerstiens (1996a) argued that measurements of $g_{cut}$ 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) ($g_{low \text{ PAR}}$) 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 $g$ values during nondrought 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, $g_{cut}$ 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 within...
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 \( \frac{g_{\text{min}}}{g_{\text{cuti}}} \) (Boycce 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 \( g_{\text{cuti}} \) measured across different plant species. Similarly, Hauke & Schreiber (1998) found no relationship between the gradual decrease in \( g_{\text{cuti}} \) 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 (Santrůček et al., 2004). For 10 Sorghum genotypes, Muchow & Sinclair (1989) reported a strong positive correlation between stomatal density and \( g_{\text{min}} \), suggesting that leaky stomata contribute substantially to \( g_{\text{min}} \). 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, Santrůček 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 \( g_{\text{min}} \) 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 \( g_{\text{min}} \) (Fig. 2), and separately analyze crop species and their genotypic variation. Comparing all available data, we did not find significant relationships between \( g_{\text{min}} \) 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 \( g_{\text{min}} \) among species. A simple breakdown by taxonomic order (Fig. 2b) revealed that grasses (Poales) have a higher \( g_{\text{min}} \) 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 \( g_{\text{min}} \) 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 \( g_{\text{min}} \) or \( g_{\text{cuti}} \) (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 \( g_{\text{min}} \) values slightly higher than the average (Fig. 2b).

In crop science, \( g_{\text{min}} \) has long been identified as a key drought tolerance trait (Sinclair & Ludlow, 1986). A number of studies have targeted \( g_{\text{min}} \) as a key trait for the breeding of more drought-tolerant crops, leading to comparisons of \( g_{\text{min}} \) across genotypes grown in the same conditions. For example, James et al. (2008) compared \( g_{\text{min}} \) in 58 soybean (\( G_{\text{lycine max}} \)) 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 \( g_{\text{min}} \) among crops, but also
the wide range in $g_{\text{min}}$ among genotypes. Again, it is striking that the wide variation in $g_{\text{min}}$ 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 $g_{\text{min}}$ among species, a number of lines of evidence suggest that $g_{\text{min}}$ also has great potential for plasticity. Here, we summarize the literature on the acclimation of $g_{\text{min}}$ to drought conditions, to changes in temperature and humidity, and the change in $g_{\text{min}}$ with leaf age, altitude and other factors. This discussion is directly relevant to the use of $g_{\text{min}}$ in models, because, if the degree of plasticity is large, it complicates model parameterization.

There is a general tendency for a decreased $g_{\text{min}}$ in plants acclimated to drought stress (James et al., 2008). The magnitude of the decrease in $g_{\text{min}}$ 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 $g_{\text{min}}$ 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 $g_{\text{min}}$ in the drought treatment (see Methods S3 for experimental details). This significant change in $g_{\text{min}}$ with drought acclimation is probably an important component of the overall drought hardening of plants.

The idea that water limitation causes a reduction in $g_{\text{min}}$ (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 $g_{\text{min}}$ 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. 2 Analysis of a literature compilation of minimum conductance ($g_{\text{min}}$) 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) $g_{\text{min}}$, 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) $g_{\text{min}}$ estimates for crops only, averaged by genotype. Bars denote the range, illustrating the wide range in $g_{\text{min}}$ among genotypes for a particular crop species. Numbers above the figure refer to the number of genotypes included.

Fig. 3 Minimum conductance ($g_{\text{min}}$) 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 $g_{\text{min}}$ in the well-watered treatment. For drought-treated plants, $g_{\text{min}}$ 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 \( g_{min} \) 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 \( g_{min} \) 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.

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 (\( g \)) models characterized by the dependence on assimilation rate, \( CO_2 \) and humidity (Eqn 1).
where \( g_i \) is a ‘slope’ parameter, \( A_n \) is the leaf net photosynthetic rate, \( C_i \) 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 \( g_i \) when \( A_n \) is zero. The \( g_i \) parameter is directly related to the water use efficiency: large values of \( g_i \) 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 \( g_i \) 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 \( g_i \) 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 \( g_i \) 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 \( g_i \) 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 \( A_n/g_i \) (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 \( g_i \) 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\(_2\)O (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 \( g_i \) 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’ \( (g_{cut}) \) (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 \( g_0 > 0 \) when \( A_n = 0 \) (Cowan & Farquhar, 1977; Cowan, 1978; Hari et al., 1986, 1999). More recent work derives the optimal \( g_i \), 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 \( (C_i/C_0) \) 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 \( C_0 \), as no photosynthesis is occurring that draws down \( C_i \). To see this point, we can rearrange Eqn 1 to give:

\[
A_n/g_i = C_0 f(D)/g_i \quad \text{Eqn 2}
\]

and, using the diffusion constraint (Fick’s law)

\[
A_n = g_i/1.6(C_i-C_0) \]

we obtain an expression for \( C_i/C_0 \):

\[
C_i/C_0 = 1 - f(D)/1.6 \cdot g_i \quad \text{Eqn 3}
\]

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 \( A_n/g_i \) 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 \( g_i \) 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 & 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 $g_{\text{min}}$ 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 $g_{\text{min}}$ 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

![Image](https://example.com/image.png)

**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 ($A_0/g_s$) 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 ($T_{\text{air}}$) 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 $T_{\text{air}}$, only when $g_0 > 0$. For all simulations, it is assumed that $T_{\text{leaf}}$ is equal to $T_{\text{air}}$, and we ignore the differential permeability of the cuticle to CO$_2$ and H$_2$O (Hanson et al., 2016).
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 \( g \) vs a combined term including photosynthesis rate, \( \mathrm{CO}_2 \) 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 >15000 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 (\( g_{\text{dark}} \)) (Barnard & Bauerle, 2013; Lombardozzi et al., 2017), simply because it is a condition in
which net photosynthesis is zero. We provide some caution to the assumption that $g_{\text{dark}}$ can be used in models of daytime leaf conductance. First, ample observations suggest that $g_{\text{dark}}$ is not a fixed rate, but varies tremendously during the night. Caird et al. (2007) (and references therein) described how, for many species, $g_{\text{dark}}$ 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*, $g_{\text{dark}}$ in the period just after sunset was much lower than pre-dawn $g_{\text{dark}}$. Strong evidence for endogenous regulation of $g_{\text{dark}}$ was reported by Resco de Dios et al. (2013), who showed that $g_{\text{dark}}$ fluctuated throughout the night, despite environmental conditions being held constant in whole-tree chambers. In addition, $g_{\text{dark}}$ can show a clear response to VPD (Barbour & Buckley, 2007) during night-time conditions. Finally, $g_{\text{dark}}$ is under strong genetic control independent of daytime water use – at least in grapevine (Coupel-Ledru et al., 2016). Clearly, $g_{\text{dark}}$ 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.

![Figure 7](image_url) 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.

![Figure 8](image_url) 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.
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 $g_{\text{min}}$ term, as $g_0$ represents the minimum reached during low light and conditions of low photosynthesis, and $g_{\text{min}}$ 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:

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

Eqn 4

This model for $g_s$ will converge to $g_0$ during periods of low photosynthesis, and to $g_{\text{min}}$ 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 $g_s$) 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 $g_s$. 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 $g_{\text{dark}}$ (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 $g_{\text{min}}$ with some desirable properties in Section VI.

Finally, we conclude that $g_{\text{min}}$ 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 $g_{\text{min}}$ 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 $g_{\text{min}}$ on many species grown in the same conditions to better understand the adaptive value of the minimum water loss rate of leaves.

Acknowledgements

This work was made possible by the ARC Linkage Project LP140100232. R.L. was supported by a Marie Curie fellowship (FP7-IOF 624473). All raw data, code and a fully reproducible workflow which generated the figures, the manuscript and all analyses are available at https://www.github.com/remkoduursma/g0paper, archived at Zenodo (doi: 10.5281/zenodo.1313588).

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References


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 $g_{\text{min}}$.

**Table S1** Effects of drought stress on $g_{\text{min}}$.

**Methods S1** Methodological issues with the measurement of $g_{\text{min}}$.

**Methods S2** Literature compilation of $g_{\text{min}}$ estimates.

**Methods S3** Methods description for case studies.

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