



## Review

## Mesophyll diffusion conductance to CO<sub>2</sub>: An unappreciated central player in photosynthesis

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## ABSTRACT

Mesophyll diffusion conductance to CO<sub>2</sub> is a key photosynthetic trait that has been studied intensively in the past years. The intention of the present review is to update knowledge of  $g_m$ , and highlight the important unknown and controversial aspects that require future work. The photosynthetic limitation imposed by mesophyll conductance is large, and under certain conditions can be the most significant photosynthetic limitation. New evidence shows that anatomical traits, such as cell wall thickness and chloroplast distribution are amongst the stronger determinants of mesophyll conductance, although rapid variations in response to environmental changes might be regulated by other factors such as aquaporin conductance.

Gaps in knowledge that should be research priorities for the near future include: how different is mesophyll conductance among phylogenetically distant groups and how has it evolved? Can mesophyll conductance be uncoupled from regulation of the water path? What are the main drivers of mesophyll conductance? The need for mechanistic and phenomenological models of mesophyll conductance and its incorporation in process-based photosynthesis models is also highlighted.

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**1. Introduction**

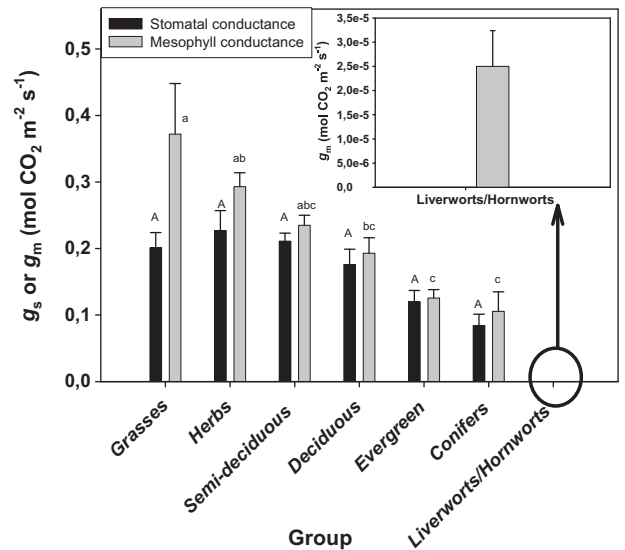
Photosynthesis in plants has been considered for decades to be limited only by two factors: the velocity of diffusion of CO<sub>2</sub> through stomata and the capacity of photosynthetic machinery to convert light energy to biochemical energy and fix CO<sub>2</sub> into sugars. Diffusion is a passive physical process, but in plants can be regulated. According to Fick’s law, diffusion depends on substance (e.g. CO<sub>2</sub>) diffusivity, temperature, the nature (mainly viscosity) of the media in which diffusion occurs (e.g. water, air, etc.), and the distance of diffusion. The mesophyll pathway comprises a series of ‘physical barriers’ to CO<sub>2</sub> diffusion, including air, cell walls, lipid membranes and liquid cytoplasm and stroma. The ‘physical barriers’ differ in nature and size (i.e. ‘distance’) among leaves, and thus there is a large variation among leaves in diffusion conductance to CO<sub>2</sub> in the mesophyll ( $g_m$ ).

Early studies already suggested that the diffusion of CO<sub>2</sub> from sub-stomatal cavities to the sites of carboxylation inside chloroplasts could limit photosynthesis (e.g., [1–3]). These early studies and most subsequent examinations of  $g_m$  are dependent on several methods for the estimation of  $g_m$  – including a method based on <sup>13</sup>C-discrimination during photosynthesis[4], a method combining chlorophyll fluorescence and gas exchange measurements [5,6] and model-based methods [6–8]. For details on methods for  $g_m$  estimation, the required precautions when using them and specific strategies of adjustment, see references [9–11]. The pioneering early studies [1–3] and a raft of subsequent studies have highlighted that  $g_m$  is the third major player in the process of photosynthesis, together with stomatal conductance and biochemical capacity.

The current understanding on  $g_m$  has been recently reviewed [12]. In addition, specific reviews on the mechanisms regulating  $g_m$  [13], and on the ecophysiological and ecological significance of  $g_m$  [14–16] have been published. These papers are recommended as the best introduction to the importance of  $g_m$  in plant physiology. As there has been rapid gain in understanding of  $g_m$ , the aims of the present paper are: (1) to update information accumulated after the recent reviews; (2) to discuss the most obscure/controversial aspects on  $g_m$  function and regulation, such as its response to CO<sub>2</sub>, or how much it limits photosynthesis; and (3) to highlight the obvious gaps in knowledge on this subject and the future research needs.

**2. How different is  $g_m$  among phylogenetically distant groups and how have mechanisms controlling  $g_m$  evolved?**

The rate of diffusion conductance to CO<sub>2</sub> in the mesophyll ( $g_m$ ) has now been estimated for more than 100 species, and it is now possible to search for phylogenetic/evolutionary patterns. The vast majority of estimates of  $g_m$  are for Spermatophytes [14] (angiosperms and gymnosperms), with only very few data for liverworts and hornworts [17]. Most surprisingly there are



**Fig. 1.** Mesophyll conductance is greatest the more a species is phylogenetically evolved. Average ± S.E. values for  $g_s$  and  $g_m$  in different pooled groups of plants. Data from liverworts and hornworts from [17], data for all other groups from [14]. Only data at light saturation and ambient temperature were considered. Capital letters indicate differences between means for  $g_s$  and lower case letters for  $g_m$  (Tuckey test,  $p < 0.05$ ,  $n = 3, 21, 2, 11, 25$  and  $6$  for grasses, herbs, semi-deciduous, deciduous, evergreen and conifer species, respectively).

no measurements available for phylogenetically intermediate groups such as mosses, lycophytes, equisetophytes, or ferns. This constitutes a serious gap in our knowledge that precludes driving any broad conclusion as for the evolution of mechanisms controlling  $g_m$ .

Some valuable information can nevertheless be obtained by comparing the existing data for liverworts and hornwort gametophytes with those for Spermatophytes belonging to different phylogenetic and/or functional groups (Fig. 1). At first sight, it is evident that there are variations in the average rate of  $g_m$  among different plant groups, and that these variations are more closely correlated with evolutionary advancements than stomatal conductance ( $g_s$ ) which, indeed, did not show any significant difference among groups despite some apparent declining tendency from herbs and grasses to conifers. The largest values for  $g_m$  are found among non-woody angiosperms, whereas grasses present somewhat higher  $g_m$  values than annual dicots (Fig. 1). The lowest values are found in liverworts and hornworts for which  $g_s$  is set as zero as they lack stomata, and CO<sub>2</sub> has to diffuse through the cuticle and epidermis. Among Spermatophytes, conifers show the lowest values. An evolutionary trend towards larger  $g_m$  than  $g_s$  values is plausible given that angiosperms are evolutionary more recent than gymnosperms and non-Spermatophytes (the earliest fossil records for conifers dating back to 290 Myr as compared

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