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Comment on “Was atmospheric CO_2 capped at 1000 ppm over the past 300 million years?” by McElwain J. C. et al. [Palaeogeogr. Palaeoclimatol. Palaeoecol. 441 (2016) 653–658]

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ABSTRACT

Franks et al. (2014) developed a model for estimating the concentration of atmospheric CO_2 (c_a) that can be applied to most stomata-bearing plant fossils. In a recent paper, McElwain et al. (2016a) proposed changes to two of the key inputs: mesophyll conductance to CO_2 (g_m) and CO_2 assimilation rate at a known c_a (A_0). These proposed changes lead to increases in the model-estimates of c_a. Here we show a lack of support for these proposed changes. First, the downward revision of g_m is the result of a mathematical error by McElwain et al. (2016a) when describing the relationship between CO_2 assimilation rate (A_n) and g_m. Once corrected, values for g_m are very similar to the values recommended by Franks et al. (2014). Second, the proposed ~2-fold upward revision of A_0 is not supported by data from extant analogs or by hydraulic constraints from fossils. Moreover, the modelled estimates of A_n from Franks and Beerling (2009) are in fact most consistent with the modelled A_n in Franks et al. (2014) using their recommended A_0 values, not those proposed by McElwain et al. (2016a). These results provide further support for the strategy of model implementation outlined in Franks et al. (2014).

1. Introduction

In a recent paper, McElwain et al. (2016a) evaluate how the new palaeo-atmospheric CO_2 model by Franks et al. (2014) responds to changes in three of its input parameters. As expected, the model calculates different atmospheric CO_2 concentrations (c_a, or pCO_2 in McElwain et al., 2016a) with the altered input parameters, highlighting the importance of accurate parameterization. Franks et al. (2014) described in detail how the input parameters are theoretically determined and empirically validated, and gave default representative values for use when direct determination is difficult. Incorporating a full error propagation analysis within their model, Franks et al. (2014) showed the model outputs were robust to realistic deviation of the input parameters from their mean and, critically, that unbounded errors characteristic of other proxy methods were eliminated. McElwain et al. (2016a) conclude that the Franks et al. (2014) model can derive more robust and accurate c_a estimates than other proxy methods. However, they also propose revisions to two of the input parameters, the mesophyll conductance (g_m) and the reference CO_2 assimilation rate at a known c_a value (A_0, conventionally taken as A_n at current ambient c_a), the latter leading to significantly higher calculated c_a than with the default values suggested by Franks et al. (2014).

Here we correct two errors in the analysis by McElwain et al. (2016a) and, as a result, show that their proposed revisions to g_m and A_0 are not well supported.

2. Correcting a mathematical error in the formulation of g_m leads to almost identical estimates of c_a

In their formulation of g_m, McElwain et al. (2016a) have made a mathematical error in translating the equation from their nonlinear regression of g_m on CO_2 assimilation rate (A_n). Franks et al. (2014) propose that g_m can be estimated from its general relationship with A_n and, using linear regression through the multi-species compilation in Evans and von Caemmerer (1996), suggest the following equation for g_m:

$$g_m = 0.013 \times A_n, \tag{1}$$

which is Eq. S1 in Franks et al., 2014. Using a similar approach, McElwain et al. (2016a) fitted a power function through the multi-species compilation of g_m vs A_n from Niinemets et al. (2009), arguing that the data of Niinemets et al. (2009) represent a more diverse

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group of plants and the equation resulting from this regression might therefore be more generally applicable. The equation that McElwain et al. (2016a) give for their regression of g_m on A_n using the data of Niinemets et al. (2009) is

$$g_m = 0.0099 \times A_n^{1.0965}. \tag{2}$$

After purportedly running the Franks et al. (2014) model with Eq. (2), McElwain et al. (2016a) find that, compared to model runs using Eq. (1), the resulting c_a estimates are higher by 10% plus 150.28 ppm. McElwain et al. (2016a) conclude from this that the original formulation of g_m by Franks et al. (2014) underestimates c_a, and they advocate using a revised equation for g_m (Eq. (2)) in the Franks et al. (2014) model.

Although there is a semantic argument as to whether Eq. (1) results in underestimates of c_a when used in the Franks et al. (2014) model, or whether in fact the use of Eq. (2) results in overestimates, there is a fundamental mathematical error in the analysis by McElwain et al. (2016a) that renders this argument irrelevant. The equation for g_m used by McElwain et al. (2016a) to generate the results in their Fig. 1B is not Eq. (2) but rather

$$g_m = (0.0099 \times A_n)^{1.0965}. \tag{3}$$

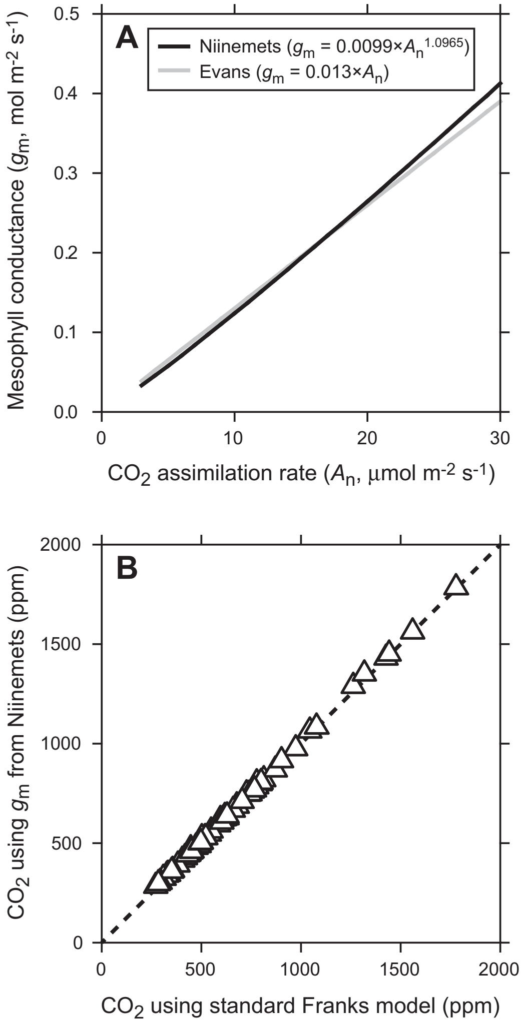

Fig. 1. Two independent formulations for mesophyll conductance (g_m) give similar atmospheric CO$_2$ concentration estimates (c_a) from the Franks et al. (2014) model. (A) Relationship between g_m and CO$_2$ assimilation rate (A_n) from Evans and von Caemmerer (1996) and Niinemets et al. (2009). The former was used by Franks et al. (2014) and the latter proposed by McElwain et al. (2016a). (B) Comparisons of estimated CO$_2$ from the Franks et al. (2014) model based on the two formulations for g_m. The data come from 71 extant species of angiosperms, gymnosperms, and ferns measured in the field or from growth-chamber experiments. A dashed 1:1 line is shown.

Using Eq. (3) it is possible to reproduce the 10% + 150.28 ppm disparity reported by McElwain et al. (2016a). However, as correctly stated by McElwain et al. (2016a), it is Eq. (2), not Eq. (3), that results from a power function regression through the data of Niinemets et al. (2009). Over the normal range of A_n, plots of g_m vs A_n using Eqs. (1) and (2) are almost indistinguishable (Fig. 1A). Similarly, when we compare outputs from the Franks et al. (2014) model using Eq. (1) and Eq. (2) we find that the c_a estimates are virtually identical (mean difference = 1.5%; Fig. 1B).

A positive outcome from this is that, once the above mathematical error is corrected, the generality of the original equation for g_m given by Franks et al. (2014), Eq. (1) above, is independently validated in the work of McElwain et al. (2016a).

3. Parameterization of A_0 in Franks et al. (2014) is not low

McElwain et al. (2016a) state that incorrectly low parameterization of A_0 by Franks et al. (2014) resulted in underestimation of c_a for the Phanerozoic. To support this, McElwain et al. (2016a) draw upon two lines of argument. The first is that A_0 values for their fossil species from the Devonian, Carboniferous and Triassic should be around double the default values recommended by Franks et al. (2014) based on ecologically similar extant species. The second is that the modelled A_n values used for the Phanerozoic reconstruction of c_a in Franks et al. (2014) are much lower than the A_n values reported in the reconstruction of plant gas exchange capacity for the Phanerozoic by Franks and Beerling (2009). We show below that the first argument is not supported empirically, and the second is incorrect because of an erroneous comparison.

3.1. Little evidence for high A_0 in extant lycophytes

The closest living ecological analog for the two Devonian fossil species used in McElwain et al. (2016a) is observed in the lycophytes. In fact one of them, *Aglaophyton major*, a member of the now extinct rhyniophytes, is said to closely resemble a more basal plant group, the bryophytes, on account of it not having true vascular tissue (Edwards et al., 1998). Having more limited vascular capacity than a lycophyte, it is likely that *Aglaophyton major* also had lower photosynthetic capacity.

To justify their use of double the recommended default A_0 value for lycophytes (6 rather than 3 µmol m^{-2} s^{-1}), McElwain et al. (2016a) refer to observations of A_0 for lycophytes in Brodribb and Holbrook (2006) (here, for simplicity, we define measurements of CO$_2$ assimilation rate at or near current-day c_a as representative of A_0). We note that one of the species in the paper by Brodribb and Holbrook (2006) is incorrectly labeled (*Lygodium venustrum* is a fern, not a lycophyte). For the remaining six lycophyte species in Brodribb and Holbrook (2006), the mean A_0 is 3.73 µmol m^{-2} s^{-1}. We conducted similar measurements on an additional epiphytic, sun-adapted lycophyte, *Huperzia prolifera*, and found A_0 to be 2.33 µmol m^{-2} s^{-1} (mean of four plants). Furthermore, Brodribb and Holbrook (2006) provide independent measures of leaf hydraulic conductance (k_{leaf}), which scales roughly with A_0 and can be used as an indirect means to estimate A_0. McElwain et al. (2016a) used this scaling method to estimate A_0 for their four seed fern species (see below), but not the Devonian lycophyte or rhyniophyte. Applying the scaling equation of McElwain et al. (2016a, 2016b) for A_0 as a function of k_{leaf} (their equation for A_{max}, which they equate to A_0), the mean calculated A_0 for the six lycophyte species in Brodribb and Holbrook (2006) is 2.40 µmol m^{-2} s^{-1}. Taken together, the above evidence supports use of the Franks et al. (2014) default A_0

value of 3 μmol m^{-2} s^{-1} for lycophytes. There is little justification for using A_0 values as high as 6 μmol m^{-2} s^{-1} for lycophytes, as suggested by McElwain et al. (2016a).

3.2. Extant fern photosynthesis and vein density modelling do not support the proposed high A_0 values for fossil seed ferns

For the four seed ferns from the Carboniferous and Triassic periods, McElwain et al. (2016a) propose A_0 values of between 10 and 16 μmol m^{-2} s^{-1}, whereas Franks et al. (2014) recommend a default value of 6 μmol m^{-2} s^{-1} for seed ferns and ferns. The recommendation by Franks et al. (2014) is based on direct measurement of A_0 on extant ferns, but McElwain et al. (2016a) have derived their A_0 values indirectly by applying scaling equations that correlate A_0 with anatomical traits inferred from fossil images. The key anatomical traits used by McElwain et al. (2016a) are vein density (D_v) and an abstract quantity called "mean maximum linear mesophyll path length from veins to stomata", termed D_m, which was invoked by Brodribb et al. (2007). Despite several claims in the literature of a correlation between D_v and A_0, and the intuitive suggestion that involvement of D_v in water transport should link it somehow to gas exchange capacity, the empirical evidence for a strong general correlation between D_v and A_0 remains vague (see Fig. 8 in Sack et al., 2013), so applying a general equation to predict A_0 from D_v is risky. Calculation of D_m requires careful measurement of linear distances in two planes and various unverifiable assumptions about the unique pathways of water movement in leaves of anatomically diverse species. Brodribb et al. (2007) found a correlation between D_m and k_{leaf} in some species, but no relationship in others, indicating extreme caution with this method. McElwain et al. (2016a) provide little information on how they determined A_0 from D_v or how they obtained the critical measurements to determine D_m in their fossil material. However, given the difficulties highlighted above, and that the resulting indirectly determined A_0 values given in McElwain et al. (2016a) are so much larger than the average for direct measurements on extant ferns, there is not a strong case for doubling or tripling the default A_0 value for ferns and seed ferns recommended by Franks et al. (2014). We note also that the mean D_v for the seed ferns in McElwain et al. (2016a) is about 2.6 mm mm^{-2}, and the modelling by Brodribb et al. (2007) predicts this would correspond to a mean A_0 of about 7 μmol m^{-2} s^{-1}, which is very close to the default 6 μmol m^{-2} s^{-1} for seed ferns recommended by Franks et al. (2014).

3.3. Phanerozoic A_n values in Franks et al. (2014) are consistent with previous modelling

To help justify their proposal for using much higher A_0 values than those recommended by Franks et al. (2014), McElwain et al. (2016a) have compared the output from two different models. McElwain et al. (2016a) suggest in their Fig. 3 that the upper theoretical boundary of A_n (modelled by Franks and Beerling, 2009) should align with the actual operational A_n (modelled by Franks et al., 2014). However, these are not the same thing. The critical difference is that the plotted lines in Fig. 7A of Franks and Beerling (2009) (henceforth F&B 2009) were generated using *maximum* stomatal conductance to CO$_2$ ($g_{c(max)}$, from maximum stomatal aperture, a_{max}) for observed combinations of stomatal size and density in fossils. This means that the plotted lines in F&B 2009 each represent a theoretical maximum CO$_2$ assimilation rate ($A_{n(max)}$) for four constraining conditions: the upper and lower ranges in the spatial envelope of fossil stomatal length and density combinations (termed "upper bound" and "lower bound"), and either fixed or variable temperature and atmospheric oxygen (O$_2$) concentration. They do not represent the operational A_n, which in theory could be anywhere under each respective curve in F&B 2009.

Consistency between the Phanerozoic A_n from Franks et al. (2014) and the independently modelled Phanerozoic A_n from F&B 2009 should increase confidence in both the estimated range of A_n and the recommended A_0 values in Franks et al. (2014). However, this comparison is not straightforward. It first requires conversion of the modelled $A_{n(max)}$ in F&B 2009 to A_n by subtracting the "stomatal limitation" from $A_{n(max)}$. As noted by Franks et al. (2014), and confirmed independently (Dow et al., 2014; McElwain et al., 2016b), operational stomatal conductance ($g_{c(op)}$) is typically about 20% of $g_{c(max)}$. As a result, A_n is about 30–50% lower than $A_{n(max)}$ under ideal conditions, with further limitation from stomatal closure under environmental stress such as drought (Farquhar and Sharkey, 1982). For the condition of variable temperature and O$_2$ in F&B 2009 (the more realistic of the two presented), the effective range of A_n with stomatal limitation imposed on $A_{n(max)}$ is illustrated by the blue shaded area in Fig. 2.

Next, because the modelled $A_{n(max)}$ in F&B 2009 was generated using prescribed c$_a$ values from Berner (2006), the upper and lower bound of $A_{n(max)}$ (blue solid and dashed lines in Fig. 2) and the derived A_n range (blue shaded area in Fig. 2) correspond to those prescribed c$_a$ values for each time interval (noting that A_n is a function of c$_a$). However, the Phanerozoic A_n values in Franks et al. (2014) correspond to the simultaneously modelled c$_a$ values in Franks et al. (2014), which differ slightly from Berner (2006). Therefore, the Phanerozoic A_n values in Franks et al. (2014) need to be adjusted to correspond with the Berner (2006) c$_a$ values before they can be compared with the A_n range determined for F&B 2009. The simplest approach is to force the Franks et al. (2014) model with the prescribed c$_a$ values for corresponding time intervals in Berner (2006). This gives A_n values (yellow triangles, method 1, in Fig. 2) that closely resemble the original A_n values from Franks et al. (2014), except that instead of a range of A_n values there is only a single A_n value per plant group for each time interval, corresponding to the single prescribed c$_a$ value.

Another approach that aligns better with the method in F&B 2009 is to use the form of the relationship between A_n and c$_a$ observed in extant members of each plant group to extrapolate to A_n at the prescribed Berner CO$_2$. This can be approximated by multiplying the original Phanerozoic A_n values in Franks et al. (2014) by the ratio of relative A_n at the

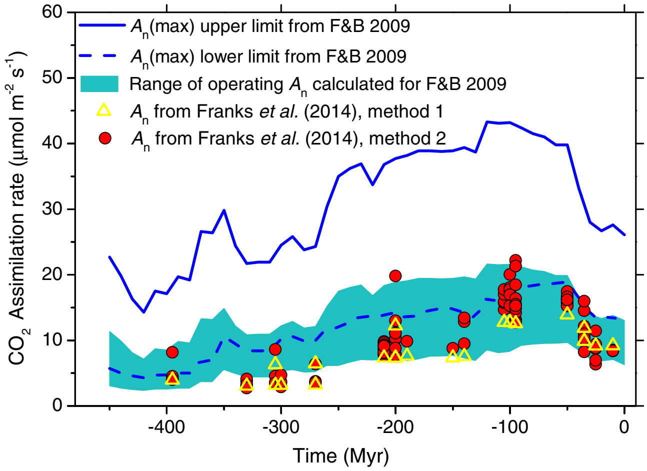

Fig. 2. Validation of recommended A_0 values for the Franks et al. (2014) model. To estimate atmospheric CO$_2$ concentration (c$_a$) the Franks et al. (2014) model calculates the average operating CO$_2$ assimilation rate (A_n) for the fossils using a reference CO$_2$ assimilation rate at ambient atmospheric CO$_2$ concentration (A_0) as one of the input variables. The range of A_n calculated for the Phanerozoic in Franks et al. (2014) (yellow symbols with method 1, red symbols with method 2) is similar to that calculated from the model of Franks and Beerling (2009) (termed F&B 2009; blue shaded area) which uses a different methodology to determine A_n from prescribed c$_a$ values. Close agreement between these two independently determined Phanerozoic A_n ranges supports the recommended A_0 values in Franks et al. (2014). To enable comparison, A_n from Franks and Beerling (2009) was determined from the modelled upper and lower limits of maximum A_n ($A_{n(max)}$; see text), and A_n from Franks et al. (2014) was adjusted to correspond with the prescribed c$_a$ values in Franks and Beerling (2009).

c_a in Berner (2006) to relative A_n at the c_a in Franks et al. (2014). For typical conditions, relative A_n ($A_{n(rel)}$) as a function of c_a can be described by the empirical relationship

$$A_{n(rel)} = A_1 + A_2 e^{\left(-\frac{c_a}{t}\right)}, \tag{4}$$

where $A_{n(rel)}$ is A_n as a fraction of its RuBP-regeneration-limited rate at high c_a (e.g. when c_a is 2000 ppm) and A_1, A_2 and t are fitted constants. For this demonstration (results shown as red symbols, method 2, in Fig. 2), we measured $A_{n(rel)}$ vs c_a in extant representatives of the four plant groups used in Franks et al. (2014). With Group 1, we used two species, *Huperzia prolifera* (a lycophyte) and *Equisetum laevigatum* (a horsetail), depending on which was a closer match to the fossil species; for Group 2, *Cycas thouarsii* (a cycad); for Group 3, *Tsuga canadensis* (a conifer); for Group 4, *Arabidopsis thaliana* (an angiosperm). For A_1, A_2 and t the respective values were 1.14, −1.26 and 880 for *H. prolifera*; 1.03, −1.21 and 496 for *E. laevigatum*; 1.03, −1.20 and 488 for *C. thouarsii*; 1.07, −1.21 and 563 for *T. Canadensis*; 1.01, −1.27 and 302 for *Arabidopsis thaliana*.

After adjusting Phanerozoic A_n in Franks et al. (2014) to the same c_a in F&B 2009, a comparison of the two studies shows that they are in close agreement (compare red and yellow symbols with blue shaded area in Fig. 2). This, together with the evidence for typical values of A_0 in extant analogs (see above), adds further support for use of the recommended values for A_0 in Franks et al. (2014).

4. Conclusions

It is important that new proxy methods such as Franks et al. (2014) are independently tested and validated. However, the study by McElwain et al. (2016a) contains two errors that weaken two of their interpretations about the formulation of g_m and the default A_0 values in Franks et al. (2014). We show that, once these errors are corrected, the study by McElwain et al. (2016a) largely validates the model of Franks et al. (2014), including the formulation of g_m and A_0.

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