**Title: A derivation error that affects carbon balance models exists in the current implementation of the Johnson et al. (1942) modified Arrhenius function**

**Running Title: Derivation error in modified Arrhenius model**

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**Abstract**

Understanding biological temperature responses is crucial to predicting global carbon fluxes. The current approach to modeling temperature responses of photosynthetic capacity in large scale modeling efforts uses a modified Arrhenius equation. We rederived the modified Arrhenius equation from the source publication and uncovered a missing term that was dropped between 1942 and 2002. We compare fitted temperature response parameters between the new and old derivation of the modified Arrhenius equation. We find that most parameters are minimally affected, though activation energy is impacted quite substantially. We then scaled the impact of these small errors to whole plant carbon balance and found that the impact of the rederivation of the Arrhenius on modelled daily carbon gain causes a meaningful deviation of ~18%. This suggests that the error in the derivation of the modified Arrhenius equation has impacted the accuracy of predictions of carbon fluxes at larger scales.

*Keywords: Arrhenius, temperature, photosynthesis, gas exchange, modeling, carbon balance*

**Introduction**

Globally, photosynthesis and autotrophic respiration are the largest biological carbon fluxes, with photosynthesis removing ~120 Gt C year-1 from the atmosphere and autotrophic respiration releasing ~60 Gt C year-1 back to the atmosphere (Amthor, 2000; Ciais et al., 2013). Given the temperature sensitivity of these large carbon fluxes (Lombardozzi et al., 2015), understanding how photosynthesis and respiration respond on acute, acclimatory, and adaptive timescales is crucial for predicting vegetative and carbon cycle responses to future global climates (Rogers et al., 2017; Stinziano et al. 2018). Biological temperature responses including photosynthesis and respiration are typically assumed to be exponential or peaked (Way and Yamori, 2014; Smith & Dukes, 2017; Kumarathunge et al., 2019). Exponential responses are usually modelled based on an Arrhenius-type curve (Arrhenius, 1915):

Equation 1, or equivalently,

Equation 2

where f(T) is the rate of the process at temperature T, A is a pre-exponential factor, T in K, k25 is the rate of the process at 298.15 K, Ea is the activation energy in J mol-1, R is the universal gas constant of 8.314 J mol-1 K-1, and 298.15 is the reference temperature in K. As for peaked responses, while a few options are available (Kruse et al., 2008; Hobbs et al., 2013; Heskel et al., 2016), the most commonly implemented version is the modified Arrhenius model of Johnson et al. (1942) as presented in Medlyn et al. (2002):

Equation 3

where Hd is the deactivation energy in J mol-1, and ΔS is the entropy of the process in J mol-1 K-1.

Equation 3 is used for modeling the temperature responses of photosynthetic capacity (i.e. maximum carboxylation capacity of rubisco, Vcmax, maximum electron transport capacity, Jmax, and triose phosphate utilization capacity (TPU); see Rogers et al., 2017 for a review of models using Equation 3). These parameters are then used in ecophysiological studies to understand thermal acclimation of photosynthesis (see Kattge & Knorr, 2007; Smith & Dukes, 2017; and Kumarathunge et al., 2019 for examples). Furthermore, this equation is also used in terrestrial biosphere models to predict the future carbon cycling (e.g. Rogers et al., 2017).

Due to the ubiquity of Equation 3 in modeling temperature responses and the thermal acclimation of photosynthetic capacity (e.g. Kattge & Knorr, 2007; Rogers et al., 2017; Smith & Dukes, 2017; Kumarathunge et al., 2019), we revisited the original Johnson et al. (1942) modified Arrhenius function to rederive Equation 3. In the process of this rederivation, we uncovered a term that was dropped sometime between Johnson et al. (1942) and Medlyn et al. (2002) which causes a systematic error in the application of Equation 3 for modeling photosynthetic capacity in individual species (e.g. Medlyn et al., 2002) to modeling global scale carbon uptake (e.g. Rogers et al., 2017). We then refit a freely available dataset (Kumarathunge et al., 2019), with both versions of the modified Arrhenius model, and fed the temperature response fits through a carbon balance model to estimate the impact of the derivation error on modelled plant carbon balance. We predicted that the derivation error would cause substantial variation in fitted temperature response parameters, and that these differences would propagate through to modelled daily carbon balance.

**Materials & methods**

**Rederivation of the modified Arrhenius equation**

Johnson et al. (1942, equation 24) describe the temperature response of the light intensity of a luciferase reaction as:

Equation 4

where I is the intensity of the luciferase reaction, c’’ is not explicitly defined in Johnson et al. (1942), but presumably represents a constant based on the derivation in the study, T is the temperature in K, R is the universal gas constant of 8.314 J mol-1 K-1, ΔH‡ is the activation energy in J mol-1, ΔH is the deactivation energy in J mol-1, and ΔS is the entropy in J mol-1 K-1. We can relativize the equation to a reference temperature by dividing Equation 4 at a hypothetical temperature by Equation 4 at a standard temperature (i.e. 25 °C):

Equation 5

Next, rearrange fractions for clarity:

Equation 6

Cancel out c’’, use exponent rules to simplify:

Equation 7

Simplify further by setting a common denominator within exponential terms:

Equation 8

Simplify exponential terms further:

Equation 9

Harmonizing the notation scheme to that typically used in plant ecophysiology:

Equation 10

Note the difference between Equations 3 and 10: the term T / 298.15 is missing from Equation 3. There are several alternative expressions of Equation 4 (e.g. Farquhar et al., 1980; Harley et al., 1986; Harley et al., 1992; Harley & Baldocchi, 1995; Lloyd, 1995), however when relativized to a common temperature, the equations presented in Farquhar et al. (1980), Harley et al. (1992), Harley & Baldocchi (1995), and Lloyd (1995) are all identical to Eq. 3, while the Harley et al. (1986) equation is identical to our derivation when relativized to a common temperature (Appendix A). This introduces multiple systematic errors. First, errors are introduced into the fitted parameters Ea, Hd, and ΔS. Second, k25 is scaled using the wrong equation, introducing an error in f(T). And third, acclimation equations describing Ea, Hd, and ΔS will then be in error due to errors in the fitted parameters at each temperature.

Here we focus on the impact of 1 and 2 on modeling whole-plant carbon balance.

**Data analysis**

Using A-Ci curve data compiled in Kumarathunge et al. (2019), available from the Kumarathunge et al. (2018) repository, we used the {fitacis} function from the R package {plantecophys} (Duursma, 2015), setting fitmethod = “bilinear”, Tcorrect = FALSE, and fitTPU = TRUE, to obtain Vcmax and Jmax. We then fit Equations 3 and 10 to the data, allowing Hd to be fit. To ensure that the curves could be fit (i.e. that there were enough data to fit 4 parameters), we only used data where A-Ci curves were measured at 5 or more temperatures. This reduced the number of candidate temperature responses from 729 to 403. We used the R package {minpack.lm} (Elzhov et al., 2016), using Equation 2 to obtain starting values for Ea and k25, while the other initial parameters were ΔS = 0.650 kJ mol-1, and Hd varying from 1 to 1000 kJ mol-1, followed by the {BIC} function to select the best model based on Bayesian Information Criteria. We obtained 341 and 337 successful Vcmax temperature response curve fits for Equations 3 and 10, respectively, and 241 and 242 successful Jmax temperature response curve fits for Equations 3 and 10, respectively. This resulted in a total of 547 fitted temperature response curves which we filtered further, requiring that Ea, ΔS, and Hd were all positive values and that the Vcmax and Jmax data were paired, resulting in 196 complete pairs of Vcmax and Jmax temperature responses for analysis..

**Modeling**

We modelled the impact of the equations 3 and 10 on daily net plant carbon balance. Data for leaf area, root and shoot masses, as well as leaf dark respiration at 25 °C were taken for white spruce (*Picea glauca*) from Stinziano & Way (2017), while stomatal conductance model parameters were calculated with the gas exchange data reported in Stinziano & Way (2017). Briefly, Stinziano and Way (2017) grew white spruce in growth chambers under a simulated autumn treatment based on temperatures and photoperiods from Trenton, ON, with weekly harvesting of biomass and gas exchange measurements across 17 weeks as a control treatment, along with a warming treatment where temperatures were +5 °C of the control, a constant summer day/night temperature with declining photoperiod, and a constant summer photoperiod with ambient changes in temperature. Here we only used data from Stinziano & Way (2017) that were from the control treatment. Mean data were taken from the control treatment at weeks 0 and 12 to provide contrasting biomass allocation patterns such that week 0 is a low respiration scenario and week 12 is a high respiration scenario. These different respiration scenarios were used to reduce bias in any conclusions regarding the impact of Equations 3 and 10 on carbon balance, as the ratio of photosynthesis to respiration may alter the sensitivity of net carbon balance to the Arrhenius equation used. Root respiration for white spruce was taken from Weger and Guy (1991) and we assumed that stem respiration was equal to root respiration (Table 1).

**Table 1. Parameters used in modeling daily carbon gain.**

|  |  |  |  |
| --- | --- | --- | --- |
| Parameter | Group | Value | Reference |
| Respiration | Rdark | 2.78 μmol m-2 s-1 | Stinziano & Way, 2017 |
|  | Rday | 0.7 \* Rdark | Ayub et al., 2011 |
|  | Rroot | 0.0095 μmol g-1 s-1 | Weger & Guy, 1991 |
|  | Rstem | 0.0095 μmol g-1 s-1 | Assumed |
|  | Q10 | 2.015 | Atkin & Tjoelker, 2003 |
| Γ\* | 25 °C | 42.75 μmol mol-1 | Bernacchi et al., 2001 |
|  | Ea | 37.83 kJ mol-1 | Bernacchi et al., 2001 |
| Km | 25 °C | 718.4 μmol mol-1 | Bernacchi et al., 2001 |
|  | Ea | 65.51 kJ mol-1 | Bernacchi et al., 2001 |
| α |  | 0.8 | Norman & Campbell, 1998 |
| φ |  | 0.08 | Norman & Campbell, 1998 |
| Leaf Area | Low R | 0.015 m2 | Stinziano & Way, 2017 |
|  | High R | 0.025 m2 | Stinziano & Way, 2017 |
| Stem Mass | Low R | 0.496 g | Stinziano & Way, 2017 |
|  | High R | 2.523 g | Stinziano & Way, 2017 |
| Root Mass | Low R | 0.498 g | Stinziano & Way, 2017 |
|  | High R | 5.072 g | Stinziano & Way, 2017 |

**Q10: thermal sensitivity coefficient; Γ\*: photorespiratory CO2 compensation point; Km: apparent Michaelis-Menten constant for rubisco carboxylation in 21% O2/air (i.e. Kc,air); α: absorbance of photosynthetically activation radiation; φ: maximum quantum efficiency of photosynthetic electron transport; Ea: activation energy; Rdark: leaf respiration in the dark; Rday: leaf respiration in the light; Rroot: root respiration; Rstem: stem respiration; Low R: low respiration scenario; High R: high respiration scenario.**

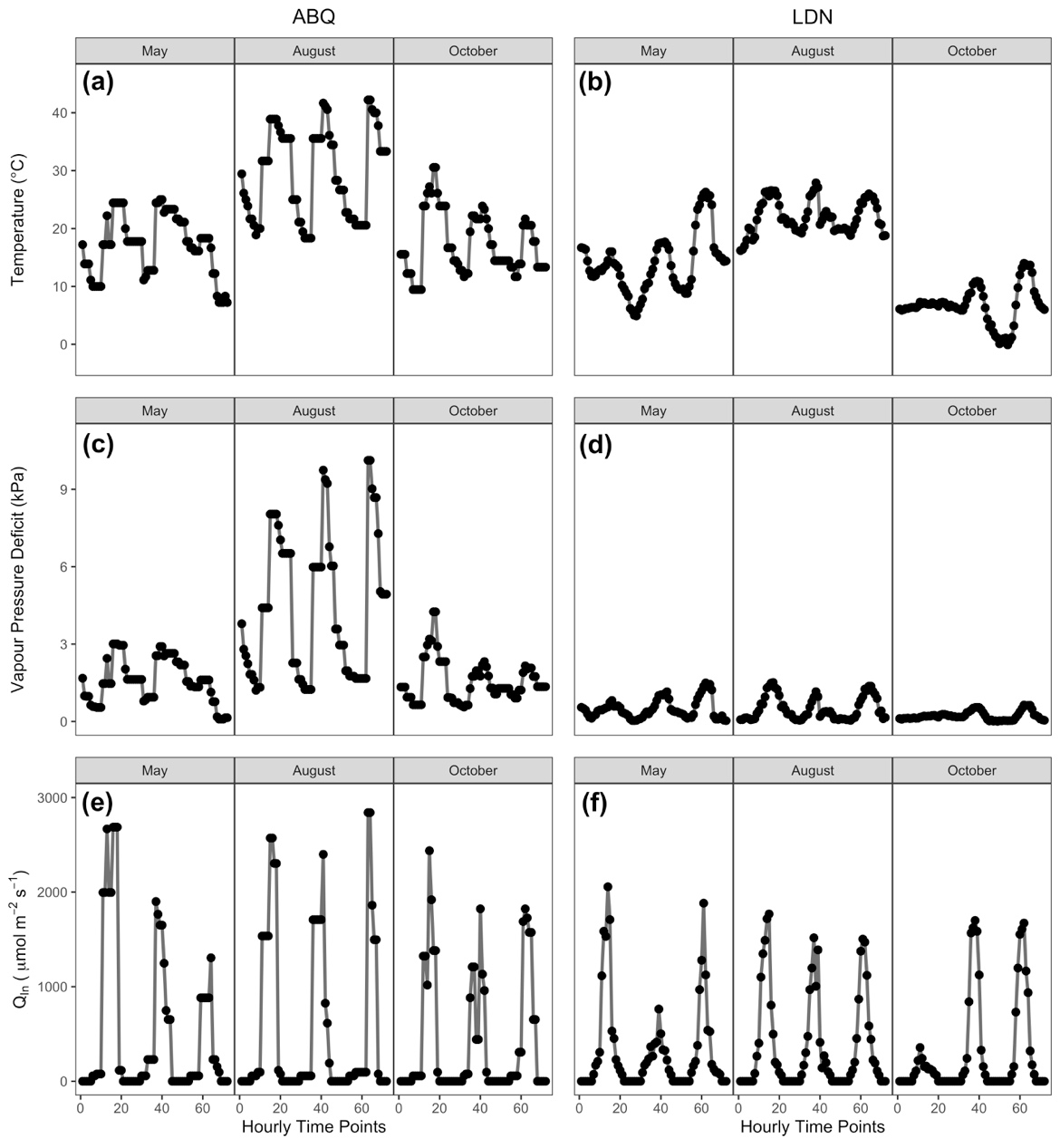
For the full model structure and equations, please see the accompanying R package {arrhenius.comparison} (“arrhenius.comparison\_1.0.0.tar.gz”; Stinziano & Murphy, 2020) (see Table 2 for equations). Briefly, we linked the Medlyn et al. (2011) stomatal conductance model with the Farquhar et al. (1980) C3 photosynthesis model, assuming infinite mesophyll conductance to CO2 as these assumptions were used in fitting the data from Kumarathunge et al. (2018). Photosynthetic capacity, both maximum rubisco carboxylation capacity, Vcmax, and maximum electron transport rate, Jmax were scaled to temperature using either Equation 3 or 10, while respiration was scaled according to (Atkin & Tjoelker, 2003). Photosynthesis and respiration were summed across each modelled day to calculate daily plant carbon assimilation.

**Table 2. Equations used in modeling daily carbon uptake.**

|  |  |
| --- | --- |
| Equation | Reference |
|  | Atkin & Tjoelker, 2003 |
|  | Arrhenius, 1915 |
|  | Johnson et al., 1942; Medlyn et al., 2002 |
|  | Johnson et al., 1942; this study |
|  | Farquhar et al., 1980 |
|  | Farquhar et al., 1980; Way et al., 2011 |
| Where J is calculated as the minimum root of: | |
|  |  |
|  |  |
|  | Medlyn et al., 2011 |
|  |  |
|  |  |
|  |  |

**f(T): rate of a process at a given temperature; T: temperature in K; k25: rate of a process at 25 °C; Q10: thermal sensitivity coefficient; Ea: activation energy in kJ mol-1; ΔS: entropy parameter in kJ mol-1; Hd: deactivation energy in kJ mol-1; R: universal gas constant in 0.008314 kJ mol-1 K-1; Wc: rate of CO2-limited carboxylation in μmol m-2 s-1; Wj: rate of RuBP regeneration-limited carboxylation in μmol m-2 s-1; Vcmax: maximum rate of rubisco carboxylation capacity in μmol m-2 s-1; Jmax: maximum rate of electron transport in μmol m-2 s-1; Ci: intercellular CO2 concentration in μmol mol-1; Γ\*: photorespiratory CO2 compensation point in μmol mol-1; Km: Michaelis-Menten constant for rubisco in μmol mol-1; α: absorbance of photosynthetically active radiation; φ: maximum quantum efficiency of electron transport; Qin: incident photosynthetically active radiation; Agross: gross CO2 assimilation in μmol m-2 s-1; Anet: net CO2 assimilation in μmol m-2 s-1; Rday: leaf day respiration in μmol m-2 s-1; gs: stomatal conductance to water in mol m-2 s-1; go: intercept for the Medlyn et al. 2011 model; g1: slope for the Medlyn et al. 2011 model; VPD: vapor pressure deficit in kPa; Ca: CO2 concentration at the leaf surface in μmol mol-1; Aplant: whole plant net CO2 assimilation; LA: leaf area in m-2; Rdark: leaf dark respiration in μmol m-2 s-1; Rstem: stem respiration in μmol m-2 s-1; Rroot; root respiration in μmol m-2 s-1; SM: stem mass in g; RM: root mass in g; Cbalance: whole plant daily carbon balance in g plant-1 day-1.**

Modeling was performed on 18 total days of environmental data, with three days of data from three months (17th – 19th of May, August, and October, 2019) obtained from external irradiance sensors at the Biotron Experimental Climate Change Research Centre at the University of Western Ontario and the remaining environmental data from Environment Canada historical climate data for South London (43.01°N, 81.27°W, altitude: 251 m) and the rooftop greenhouse at the University of New Mexico (35.08°N, 106.62°W, altitude: 1587 m) to capture different levels of environmental variability (Fig. 1).



**Fig. 1. Environmental data used to drive the model in Table 1 covering 3 days (17th, 18th, and 19th) of 3 months. (a,c,e) Albuquerque, NM, USA (ABQ); (b,d,e) London, ON, Canada (LDN).**

Overall, the modeling approach allows us to assess the relative differences between Equations 3 and 10 under a low- and high- respiration scenario, fixing versus fitting Hd, and across different ranges of seasonal variability.

*Statistical analysis*

Data were analyzed using the {lm} function in R v.3.6.1 (R Core Team, 2019), regressing the data obtained from Equation 3 against the data obtained from Equation 10 for each of Vcmax,25, Jmax,25, Ea,Vcmax, Ea,Jmax, ΔSVcmax­, ΔSJmax, Hd,Vcmax, Hd,Jmax, BIC values for the fits of Equations 3 and 10, daily photosynthesis, daily net carbon balance, and daily photosynthesis : daily respiration ratios. Intercepts in the regression, when significant, were interpreted as a bias in the parameter, while deviations in slope from a 1:1 relationship where interpreted as percentage over- or under- estimation of the parameter (i.e. [parameter slope – 1] ∙ 100 = % estimation error). All p-values were corrected for multiple testing using the p.adjust() function in R with Holm’s method. All code and data will be made freely available on GitHub upon publication in the {arrhenius.comparison} R package (Stinziano & Murphy, 2020).

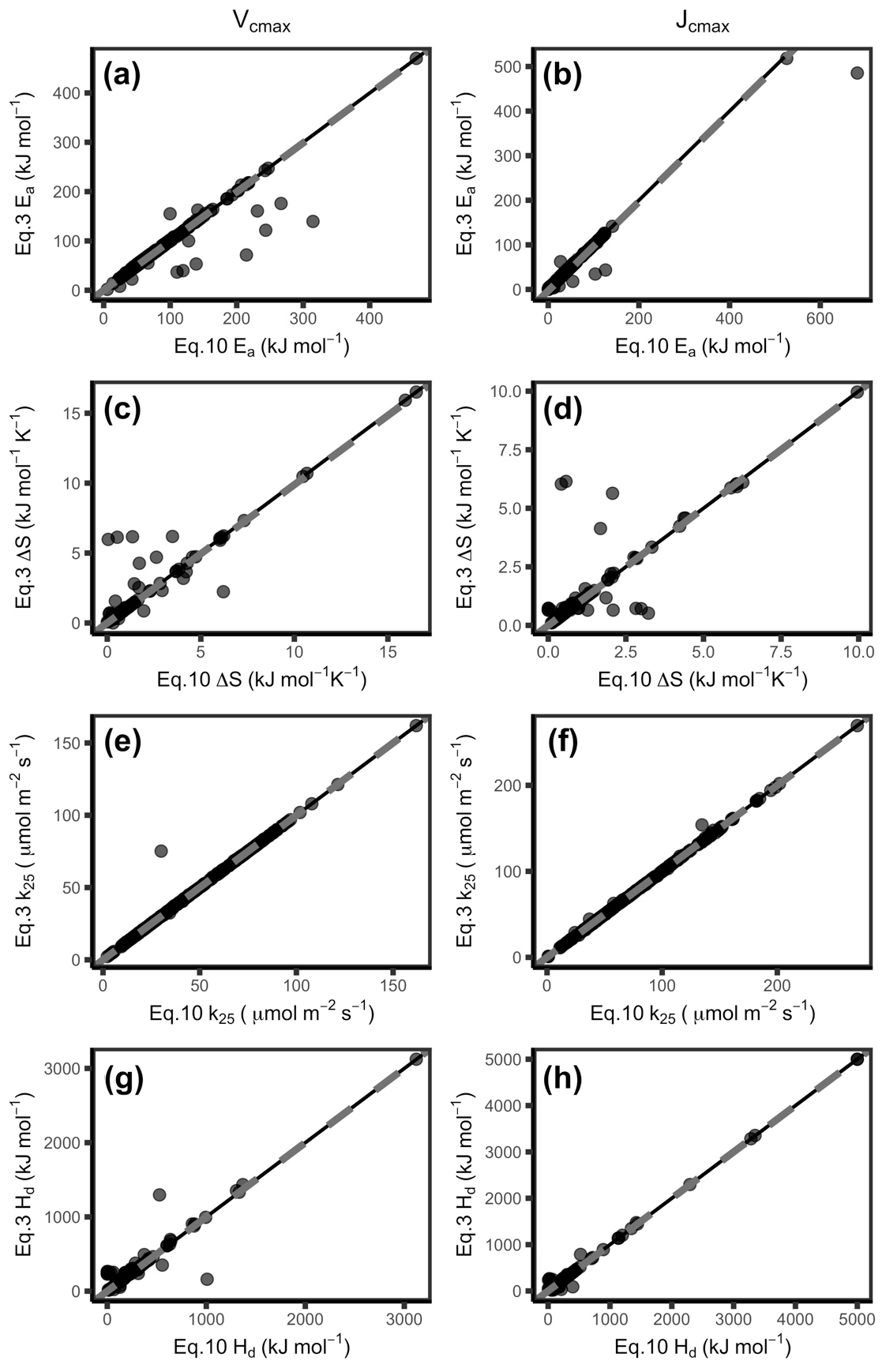
**Results**

*Equations 3 and 10 exhibited similar performance*

The performance between Equations 3 and 10 for fitting Vcmax temperature responses were essentially identical when assessed based on BIC, with a slope of 1.001 ± 0.001 (*F1,195* = 5.52 ∙ 105, *R2* = 0.9996, *P* < 2.2 ∙ 10-16; Fig 2a), as was the case for Jmax with a slope of 1.001 ± 0.001 (*F1,195* = 2.43 ∙ 106, *R2* = 0.9999, *P* < 2.2 ∙ 10-16; Fig. 2b). However, while some fitted temperature responses appeared identical, there were some cases where the fitted shape differed (Figs. 2c-f).

**Figure 2. Relative performance and fit for Equations 3 and 10 for the temperature responses of Vcmax and Jmax based on a,b) Bayesian Information Criterion (BIC), and c-f) visual inspection of curve fits.**

Estimates of Vcmax,25 were essentially identical between the Equation 3 fitting (y-axis) and the Equation 10 fitting (x-axis) with a slope of 1.002 ± 0.004 (*F1,195* = 5.84 ∙ 104, *R2* = 0.9967, *P* < 2.2 ∙ 10-16; Fig 3e), as was the case for Jmax,25 with a slope of 1.001 ± 0.001 (*F1,195* = 6.56 ∙ 105, *R2* = 0.9997, *P* < 2.2 ∙ 10-16; Fig 3f). Ea,Vcmax was generally underestimated with a slope of 0.847 ± 0.024 and a positive bias of 9.73 ± 2.59 kJ mol-1 when using Equation 3 (*F1,194* = 1202, *R2* = 0.8610, *P* < 2.2 ∙ 10-16; Fig. 3a), while Ea,Jmax was underestimated with a slope of 0.832 ± 0.013 and a positive bias of 5.98 ± 1.06 kJ mol-1 (*F1,194* = 3834, *R2* = 0.9518, *P* < 2.2 ∙ 10-16; Fig. 3b). ΔSVcmax was essentially identical between Equation 3 and 10 with a slope of 1.000 ± 0.0233 (*F1,195* = 1849, *R2* = 0.9046, *P* < 2.2 ∙ 10-16; Fig. 3c), as was the case with ΔSJmax with a slope of 0.988 ± 0.033 (*F1,195* = 904, *R2* = 0.8226, *P* < 2.2 ∙ 10-16; Fig. 3d). Hd,Vcmax was also essentially identical between Equation 3 and 10 fittings with a slope of 1.002 ± 0.005 (*F1,195* = 4.12 ∙ 104, *R2* = 0.9953, *P* < 2.2 ∙ 10-16; Fig. 3g), although Hd,Jmax was underestimated with a slope of 0.952 ± 0.024 and a positive bias of 31.48 ± 8.93 kJ mol-1 (*F1,194* = 1592, *R2* = 0.8914, *P* < 2.2 ∙ 10-16; Fig. 3h).

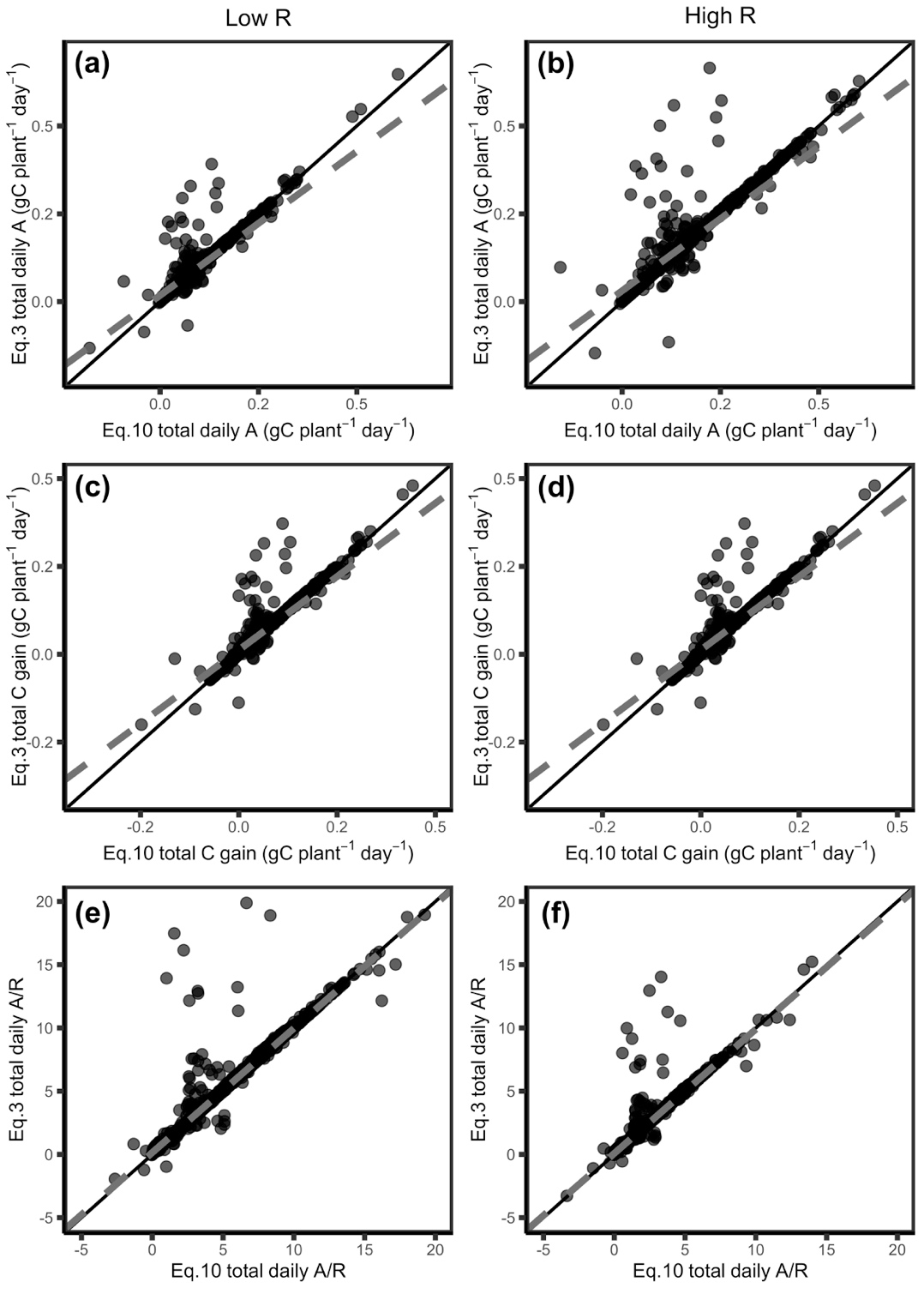


**Fig. 3. The modified Arrhenius equation with the missing term (Equation 10) gives**

**similar temperature response parameters as Equation 3 for Ea (a,b), ΔS (c,d), k25 (e,f) and Hd (f, g) for both Vcmax (a, c, e, g) and Jmax (c, d, f, h) under scenarios where Hd is allowed to vary. Ea: activation energy, ΔS: entropy parameter, k25: rate of the process at 25 °C, Hd: deactivation energy, Vcmax: maximum capacity of rubisco carboxylation, Jmax: maximum rate of electron transport. Black line indicates 1:1 line and grey dashed line indicates respective modeled slopes and intercepts.**

*Impacts on modelled net carbon balance*

In general, the differences in thermal response parameters were amplified when integrated at the whole-plant level. For daily photosynthesis (A) measured at a variable Hd, the slope for the low respiration model was 0.819 ± 0.013 and the intercept was 0.018 ± 0.002 (approximately 18% of modeled A) (*F*1,3523 = 4.168 ∙ 103, R2 = 0.5418; *P* < 2.2 ∙ 10-16) (Fig. 4**a**). For the high respiration model of daily A, the slope was 0.819 ± 0.013and the intercept was 0.031 ± 0.003 (approximately 18% of modeled A) (*F*1,3523 = 4.168 ∙ 103, R2 = 0.5418; *P* < 2.2 ∙ 10-16) (Fig. 4**b**). The low respiration model of total daily carbon (C) gain had a slope of 0.836 ± 0.012 and an intercept of 0.012 ± 0.001 (approximately 16% of modeled C gain) (*F*1,3523 = 4.539 ∙ 103, R2 = 0.5629; *P* <2.2 ∙ 10-16) (Fig. 4**c**). The high respiration of total C gain similarly had a slope of 0.859 ± 0.012 and an intercept of 0.011 ± 0.002 (approximately 14% of modeled C gain) (*F*1,3523 = 5.364 ∙ 103, R2 = 0.6035; *P* <2.2 ∙ 10-16) (Fig. 4**d**). The ratio of the total daily photosynthesis: respiration (A/R) was also considered when comparing models. The low respiration model of A/R had a slope of 0.982 ± 0.007 and the intercept was 0.146 ± 0.031 (approximately 2% of modeled A/R) (*F*1,3523 = 2.096 ∙ 104, R2 = 0.8561; *P* <2.2 ∙ 10-16) (Fig. 4**e**). The high respiration model had a similar slope of 0.982 ± 0.007 and the intercept was 0.082 ± 0.017 (approximately 2% of modeled A/R) (*F*1,3523 = 2.097 ∙ 104, R2 = 0.8562; *P* <2.2 ∙ 10-16) (Fig. 4**f**).



**Fig. 4. The modified Arrhenius equation with the missing term (Equation 10) gives differences in modeled daily carbon fluxes compared to Equation 3 for low R (a,c,e) and high R (b,d,f) under scenarios where Hd is allowed to vary. Modeled carbon fluxes include: a,b) Total daily photosynthesis; c,d) total daily C gain; and e,f) total daily A/R. A: photosynthesis, R respiration, Low R: low respiration, High R: high respiration. Black line indicates 1:1 line and grey dashed line indicates respective modeled slopes and intercepts.**

**Discussion**

We sought to determine whether the missing term in Equation 3 had a meaningful impact on fitted temperature response parameters due to its prevalence in photosynthetic temperature response data and vegetation modeling (Kattge & Knorr, 2007; Duursma & Medlyn, 2012; Rogers et al., 2017; Smith & Dukes, 2017; Stinziano et al., 2018; Stinziano et al., 2019; Kumarathunge et al., 2019). Our present analysis suggests that there is a large impact on Ea for both Vcmax and Jmax, however there were minimal impacts on k25, Hd, and ΔS (though note that Hd for Jmax was underestimated) (Fig. 3). In general, fitting Equation 3 instead of Equation 10 results in Ea reductions of around 15% with positive bias. These findings are promising in that one of the parameters to which modelled carbon gain is particularly sensitive, Hd (Stinziano et al., 2018), is minimally affected by the missing term. However, since temperature responses are non-linear, small changes in the shape of an accelerating curve can have a strong impact on the integral of the response (Jensen, 1906). Despite fit performance being nearly identical, the differences due to Ea values between the equations led to an 18% reduction in modeled daily photosynthesis for Equation 3 compared to Equation 10, leading ~14-16% reduction in modeled net daily carbon gain. Overall, comparisons of low-respiration to high-respiration scenarios resulted in similar percent changes in daily C balance with similar variation.

Based on the above analysis, the impact of the missing term in the modified Arrhenius equation substantially alters Ea and net daily carbon balance at a whole-plant level. However, given that carbon balance is the time integral of net CO2 assimilation, this may lead to substantial impacts over a long time period. It is thus possible that the differences we observed could accumulate to even larger carbon flux errors across large spatial and temporal scales with fluctuating temperatures. We therefore recommend the switch from Equation 3 to Equation 10 because: 1) Equation 3 is the result of a derivation error, and 2) Equations 3 and 10 lead to quite difference net daily carbon estimates due to the derivation error.

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**Additional Information**

A version of this manuscript was posted on bioRxiv (manuscript ID: BIORXIV/2020/921973).

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**Supplementary Information**

*Instructions for installing {arrhenius.comparison} in R for review purposes*

1. Download the arrhenius.comparison.tar.gz file
2. Set working directory in R to the directory that holds the arrhenius.comparison.tar.gz file using setwd()
3. Run:  
   install.packages("arrhenius.comparison\_1.0.0.tar.gz", repos = NULL, type = "source")  
   library(arrhenius.comparison)