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Photosynthetic responses to temperature across the tropics: a meta-analytic approach

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Publication Date

2024-12-12

DOI

10.1093/aob/mcae206

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1   Original Article

2

3   Photosynthetic responses to temperature across the tropics: a meta-analytic approach

4

5   Running title: Tropical photosynthesis responses to temperature

6

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54
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57

66 **Abstract**
67
68 **Background and Aims**

69 Tropical forests exchange more carbon dioxide (CO_2) with the atmosphere than any other

70 terrestrial biome. Yet, uncertainty in the projected carbon balance over the next century is

71 roughly three-times greater for the tropics than other ecosystems. Our limited knowledge of

72 tropical plant physiological responses, including photosynthetic, to climate change is a

73 substantial source of uncertainty in our ability to forecast the global terrestrial carbon sink.

74

75 **Methods**

76 We used a meta-analytic approach, focusing on tropical photosynthetic temperature responses, to

77 address this knowledge gap. Our dataset, gleaned from 18 independent studies, included leaf-

78 level light saturated photosynthetic (A_{sat}) temperature responses from 108 woody species, with

79 additional temperature parameters (35 species) and rates (250 species) of both maximum rates of

80 electron transport (J_{max}) and Rubisco carboxylation (V_{cmax}). We investigated how these

81 parameters responded to mean annual temperature (MAT), temperature variability, aridity, and

82 elevation, as well as also how responses differed among successional strategy, leaf habit, and

83 light environment.

84

85 **Key Results**

86 Optimum temperatures for A_{sat} (T_{optA}) and J_{max} (T_{optJ}) increased with MAT but not for V_{cmax}

87 (T_{optV}). Although photosynthetic rates were higher for "light" than "shaded" leaves, light

88 conditions did not generate differences in temperature response parameters. T_{optA} did not differ

89 with successional strategy, but early successional species had ~4 °C wider thermal niches than

90   mid/late species. Semi-deciduous species had ~1 °C higher T_{optA} than broadleaf evergreen. Most

91   global modeling efforts consider all tropical forests as a single "broadleaf evergreen" functional

92   type, but our data show that tropical species with different leaf habits display distinct

93   temperature responses that should be included in modeling efforts.

94

95   **Conclusions**

96   This novel research will inform modeling efforts to quantify tropical ecosystem carbon cycling

97   and provide more accurate representations of how these key ecosystems will respond to altered

98   temperature patterns in the face of climate warming.

99

100

101

102   **Key Words:** A-C_i curves; Maximum rate of photosynthetic electron transport (J_{max}); Maximum

103   rate of Rubisco carboxylation (V_{cmax}); Meta-analysis; Photosynthesis; Temperature Response;

104   Tropics

105

106   **Introduction**

107   Tropical forests have been characterized as one of the biomes with the greatest

108   uncertainty regarding the accuracy of large-scale models in estimating carbon fluxes (Booth *et*

109   *al.* 2012; Cavaleri *et al.* 2015; Lombardozzi *et al.* 2015; Mercado *et al.* 2018). Addressing this

110   information gap is critical because tropical forests have high biomass and cycle large amounts of

111   carbon (Dixon *et al.* 1994; Pan *et al.* 2013; Tagesson *et al.* 2020), thus alterations in tropical

112   forest carbon uptake would likely significantly affect global carbon cycling (Anderegg *et al.*

113   2015). In addition, these forests are projected to surpass their historical climate margin, entering

114   into novel climate conditions within the next quarter century (Williams *et al.* 2007; but see

115   Jaramillo *et al.* 2010), a trend anticipated to occur sooner for the tropics than other global regions

116   (Diffenbaugh and Scherer 2011; Mora *et al.* 2013; Doughty *et al.* 2023). Some tropical forests

117   are already believed to be operating near or beyond their photosynthetic thermal optima

118   (Doughty and Goulden 2008; Vårhammar *et al.* 2015; Mau *et al.* 2018; Dusenge *et al.* 2021;

119   Doughty *et al.* 2023), making them particularly vulnerable to the effects of climate warming on

120   carbon uptake.

121   Due to the significant uncertainties around how the tropical forest biome will respond to

122   continued global change, better representation of vegetation processes is needed to more

123   accurately inform Earth system and dynamic vegetation models (Friedlingstein *et al.* 2006;

124   Matthews *et al.* 2007; Booth *et al.* 2012; Rogers *et al.* 2017; Fisher *et al.* 2018). In particular,

125   quantifying photosynthetic temperature responses of tropical species will help to reduce model

126   uncertainty (Matthews *et al.* 2007; Booth *et al.* 2012). Photosynthesis has a peaked response to

127   temperature, where the rate of photosynthesis increases and then declines after the optimum

128   temperature (T_{optA}; Table 1) is reached. The components of photosynthetic decline beyond the

129   thermal optimum can be examined by exploring stomatal conductance and the underlying

130   biochemical processes that control photosynthesis. These biochemical processes include the

131   maximum rate of carbon dioxide (CO_2) fixation by Rubisco (V_{cmax}) and the maximum rate of

132   photosynthetic electron transport *(J_{max})*, both of which are derived by a well-established

133   biochemical model (Farquhar *et al.* 1980; von Caemmerer and Farquhar 1981). Global

134   vegetation models use the temperature response parameters of these biochemical processes

135 controlling photosynthesis to predict carbon uptake at wider scales (Kattge *et al.* 2009; Lin *et al.*

136 2012; Smith and Dukes 2013; Mercado *et al.* 2018; Oliver *et al.* 2022).

137   Considerable efforts have been made to quantify these photosynthetic response

138 parameters at the global scale (Medlyn *et al.* 2002; Kattge and Knorr 2007; Yamori *et al.* 2014;

139 Kumarathunge *et al.* 2019; Crous *et al.* 2022). These studies show that species can (but may not)

140 acclimate to their growth environment, and algorithms developed in Kattge and Knorr (2007)

141 have been implemented in some Earth system and vegetation models for more accurate

142 representation of photosynthetic acclimation (e.g. Arneth *et al.* 2012; Lombardozzi *et al.* 2015;

143 Smith *et al.* 2016; Mercado *et al.* 2018). However, Kattge and Knorr (2007) did not have enough

144 data to represent tropical species in their meta-analysis. As a result, carbon models are likely

145 biased in projecting tropical biome temperature responses. More recently, Kumarathunge *et al.*

146 (2019) published updated algorithms including six datasets from tropical forests which will

147 undoubtedly improve global carbon models (Zarakas *et al.* 2024). Even so, because tropical

148 forests cycle a disproportionate amount of carbon, specific investigations of tropical

149 photosynthetic responses to temperature based on plant function and growth strategy will further

150 minimize uncertainty for this crucial biome (Booth *et al.* 2012).

151   There is strong evidence suggesting that, across the globe, T_{opt} is determined by the

152 plant's current growth temperature (Berry and Björkman 1980; Kattge and Knorr 2007;

153 Kumarathunge *et al.* 2019). Genetic variation also plays an important role in determining

154 species' ability to acclimate and adjust to their growth temperatures (Berry and Björkman 1980;

155 Yamori *et al.* 2014; Crous *et al.* 2022; but see Kumarathunge *et al.* 2019). However, it is still

156 unclear whether this holds true within tropical ecosystems. Studies of photosynthetic temperature

157 responses of tropical forest species provide evidence that T_{opt} is either closely associated with

158   mean (Vargas and Cordero 2013, Kositsup *et al.* 2009, Tan *et al.* 2017) or maximum air

159   temperature (Read 1990; Slot and Winter 2017a; Mau *et al.* 2018). Historically, these forests

160   have been thought to have little capacity to acclimate to temperature changes because they have

161   evolved under low variability in diurnal, seasonal, and inter-annual ambient air temperature

162   (Janzen 1967; Read 1990; Battaglia *et al.* 1996; Cunningham and Read 2002). More recent

163   studies have found evidence that tropical leaves are capable of acclimation to the temperature

164   where they are grown (Scafaro *et al.* 2017; Slot and Winter 2017b; Choury *et al.* 2022;

165   Wittemann *et al.* 2022; Cox *et al.* 2023), but not for all species (Cunningham and Read 2003;

166   Slot *et al.* 2014; Varhammar *et al.* 2015; Carter *et al.* 2020, 2021; Dusenge *et al.* 2021; Crous *et*

167   *al.* 2022; Kullberg *et al.* 2023) and successional strategy likely influences the response

168   (Mujawamariya *et al.* 2023). The few studies investigating J_{max} optimum temperature (T_{optJ}) and

169   V_{cmax} optimum temperature (T_{optV}) on tropical species suggest that both traits are closely

170   associated with their home climate and most are unable to adjust to warmer growth temperatures

171   (Slot and Winter 2017b; Dusenge *et al.* 2021; but see Wittemann *et al.* 2022). Additionally, a

172   common garden study by Vårhammar *et al.* (2015) found that tropical species that originate from

173   areas with lower temperatures have lower optimum temperatures for J_{max} than species that

174   originate from warmer areas. This variation of photosynthetic temperature responses in tropical

175   forests suggests that, in order to accurately model global carbon fluxes, we need to better

176   understand the drivers of temperature responses for critical photosynthetic parameters in tropical

177   systems.

178   Growth conditions and ecological successions can also affect plant photosynthetic

179   responses to temperature (Yamori *et al.* 2014; Dusenge *et al.* 2019), and these differences are

180   rarely incorporated into vegetation models (Lombardozzi *et al.* 2015; Smith *et al.* 2016; Mercado

181   *et al.* 2018). Growth strategies are often characterized by their successional strategy, with some

182   forms, such as early successional species and lianas, incorporating fast growth as juveniles, while

183   late successional and evergreen species employ slower growth as juveniles (Bloom *et al.* 1985,

184   Box *et al.* 1996; Wright *et al.* 2004; Michaletz *et al.* 2016). Due to higher radiation reaching

185   deeper into the canopy, early successional forests have more variable land surface temperature

186   fluxes than late successional forests (Cao and Sanchez-Azofeifa 2017), suggesting that seedlings

187   adapted to this environment may have a greater plasticity to adjust T_{opt} to their fluctuating growth

188   environment. Studies of canopy species in Panama found that early successional seedlings had a

189   higher T_{opt} than late successional seedlings (Slot *et al.* 2016, Slot and Winter, 2018). However,

190   those results were not replicated for mature canopy trees (Slot and Winter 2017a), suggesting

191   that successional type T_{opt} differences are primarily driven by trees at the immature seedling and

192   sapling stages.

193   Tropical trees with differing leaf habits (i.e., evergreen vs. deciduous) may also employ

194   different temperature responses. For example, species with shorter-lived leaves have a greater

195   variability in leaf phenotypes, making them more responsive to seasonal changes (Kitajima *et al.*

196   1997). Compared to longer-lived evergreen leaves, shorter-lived deciduous leaves are

197   hypothesized to have broader photosynthetic temperature response curves (i.e., thermal niches;

198   Michaletz *et al.* 2016). Broad- and needle-leaf evergreen species have been found less able to

199   increase their growth rates in warmer temperatures than deciduous species (Way and Oren 2010;

200   Way and Yamori 2014; Yamori *et al.* 2014; Reich *et al.* 2022). Recently, Crous *et al.* (2022)

201   found that needleleaf evergreen species' photosynthetic and respiration rates declined more with

202   warming compared to broadleaf evergreen species. This, in addition to longer-lived leaves

203   having lower photosynthetic capacity (Niinemets 2007), and lower rates of photosynthesis

204 (Wright *et al.* 2004), suggests that evergreen and deciduous species may have different

205 capabilities to respond to their growth environment.

206   Light availability may also play a role in modulating plant photosynthetic responses to

207 temperature (Niinemets 2007). Models of canopy photosynthesis and global primary productivity

208 often separate leaves into 'sun' and 'shade' leaves, as they have different photosynthetic

209 responses to irradiance (Sinclair *et al.* 1976; De Pury and Farquhar 1997; Wang and Leuning

210 1998; Ryu *et al.* 2011). Because leaf temperature is strongly influenced by irradiance (Rey-

211 Sánchez *et al.* 2016; Fauset *et al.* 2018; Miller *et al.* 2021; Crous *et al.* 2023), it should follow

212 that sun leaves that have developed under higher irradiance are acclimated to operate at higher

213 temperatures. However, comparisons of leaves growing in different light environments in

214 tropical forests have found large differences in photosynthetic capacity but little to no differences

215 in photosynthetic temperature response (Pearcy 1987; Hernández *et al.* 2020), or

216 thermotolerance (Slot *et al.* 2019), between sun and shade leaves. The limited evidence that we

217 have comparing tropical temperature responses of sun and shade leaves suggests that light may

218 play a large role in determining overall carbon gain but only a minor role for leaves'

219 photosynthetic temperature responses.

220   Rainfall and moisture regimes also play a role in controlling plant photosynthesis, which

221 can lead to restrictions on temperature response parameters. In general, drier conditions can

222 induce stomatal closure, slowing the rate of photosynthesis and decreasing tropical forest

223 productivity (Cavaleri *et al.* 2017; Santos *et al.* 2018; Van Schaik *et al.* 2018; Kumarathunge *et*

224 *al.* 2020; Mujawamariya *et al.* 2023). However, drier conditions are also associated with less

225 rainfall and cloud cover, and a higher light environment can directly increase ecosystem

226 productivity (Carswell *et al.* 2002). Ecosystem scale studies show gross primary productivity

227 (GPP) can either increase in the dry season (Goulden *et al.* 2004; Yan *et al.* 2013; Wu *et al.*

228 2016; Green *et al.* 2020) or remain constant between seasons (Carswell *et al.* 2002; Yan *et al.*

229 2013; Guan *et al.* 2015), suggesting that tropical forests can sustain higher GPP during the higher

230 dry-season atmospheric water stress if they are not stomatal conductance limited. Across two

231 Panamanian tropical systems, a leaf level study showed that, when compared to a wet forest,

232 seasonally dry forests can have higher rates of photosynthesis and higher optimum temperatures

233 that correspond to their higher growth temperatures (Slot and Winter 2017a). Within a Puerto

234 Rican tropical forest, drier soil was associated with higher optimum temperatures but lower rates

235 of photosynthesis (Carter *et al.* 2020). These studies suggest that optimum temperatures could be

236 positively correlated with drier tropical systems.

237   In order to better understand tropical net photosynthetic and biochemical responses to

238 temperature, we used a meta-analytic approach to quantify how photosynthetic temperature

239 response parameters respond to different climate and growth environment factors using already

240 established temperature response functions (Medlyn *et al.* 2002; June *et al.* 2004). We

241 hypothesize that (1) light saturated photosynthetic optimum temperatures (T_{optA}) will be

242 positively correlated with mean annual temperatures (MAT) due to positive shifts in V_{cmax}

243 temperature response parameters. We similarly hypothesize that, due to indirect environmental

244 effects of higher light availability, (2) temperature optima will decrease with rising aridity index

245 (*AI*) (decrease in wetter ecosystems). We also compare temperature response variables of leaves

246 grown in different light environments (sun vs. shade), growth environments (*in situ* vs. *ex situ* or

247 field vs chamber/glasshouse), leaf habits (evergreen vs. drought semi-deciduous), and

248 successional strategy (early vs. mid-late). We predicted that (3) sun leaves would have higher

249 photosynthetic rates than shade leaves; but that T_{opt} would not differ between different light

250   environments. Additionally, we predicted that (4) early successional species T_{opt} will not differ

251   from late successional species and (5) broadleaf evergreen leaves would have a narrower thermal

252   niche and lower T_{opt} than semi-deciduous species. Lastly, we aimed to estimate the most

253   important individual environmental drivers to best predict the temperature parameters of both net

254   photosynthesis and the biochemical reactions driving photosynthesis.

255

256   ***Methods***

257

258   *Meta-analysis data collection and selection*

259   For this meta-analysis, we gathered datasets where photosynthetic measurements were

260   collected at different leaf temperatures on woody (trees, shrubs, and lianas) tropical species.

261   These data come in the form of net photosynthesis measured at saturating light conditions (A_{sat})

262   vs. leaf temperature (T_{leaf}) response curves, A_{sat} vs. T_{leaf} estimated from photosynthetic light

263   response curves at different temperatures, biochemical parameters (V_{cmax} and J_{max}) vs. T_{leaf}

264   response curves (estimated from net assimilation response to different leaf internal CO_2

265   concentrations, A-C_i curves, measured at different temperatures), and measurements of A_{sat} and

266   A-C_i curves at multiple ambient temperatures through time. Data were gathered from woody

267   species in forested systems within the tropical latitudes (23°26'10.6" N, 23°26'10.6" S),

268   including tropical montane systems. We obtained our data by approaching research groups for

269   unpublished data and searching "photosynthesis" "tropical" "temperature" on Web of Science

270   (Fig S1). This resulted in 18 datasets with representation in Africa (2), Oceana (6), North

271   America (8), and South America (3). No studies were identified from the Asian continent. Site-

272   specific climate data from the years 1970-2000 were collected from the WorldClim database

273   (Fick and Hijmans, 2017) using provided latitude and longitudinal data. Latitude and longitude

274   were designated as the location where plants grew, except for data from Read (1990), which

275   were obtained with plants that were grown in a chamber. In this specific case, seeding source

276   location was used for latitude and longitude and mean annual temperature (MAT) was

277   designated as the growth chamber temperature. Data were extracted from the WorldClim

278   database using the 'getData' function in the 'raster' package in R version 3.5.0 (R Core Team

279   2020). Aridity index (*AI*) was calculated as mean annual precipitation divided by mean annual

280   potential evapotranspiration (Greve and Seneviratne 2015), where both variables were collected

281   from WorldClim. Higher *AI* indicates a less arid system. *AI* was only used from *in situ* datasets,

282   i.e.*,* we excluded greenhouse, growth chamber, and arboretum grown individuals from this

283   analysis. Successional stage and leaf habit (raingreen semi-deciduous or evergreen; Poulter *et al.*

284   (2015)) were either provided by the contributing data author or extracted from the literature.

285   Species that were classified as "pioneer" and "shade-intolerant" were designated as "early

286   successional". If the species was classified as "shade-tolerant" the species was considered

287   "mid/late successional". When light environment information was available, we used author

288   designations or classified ourselves; where growth chamber, greenhouse, "open" or "upper"

289   canopy was considered "sun," and "understory" was considered shade. All samples grown in

290   growth chambers, greenhouses, or transplant studies in arboretums were considered "*ex situ*". All

291   other growth environments (i.e., "field collected") were designated as "*in situ*". We gathered

292   photosynthetic data in two ways: 1) raw data in the form of photosynthetic response curves or 2)

293   extraction from published articles. Data were digitized from published articles using Digitize It

294   2016 version 4.2.0 software (Alcasa). Raw data were provided from both published and

295   unpublished sources. Some of the datasets that were shared with us also included a 'warming'

296   treatment. For these data, we only used leaves grown in the 'control' environment.

297

298   *Net photosynthesis parameter extraction*

299   Within individual datasets, means of different species and canopy class (shaded or sun)

300   from the same study were treated as separate, independent samples (Curtis and Wang 1998).

301   The net photosynthetic temperature optimum of each sample was extracted from a peaked

302   curve (June *et al.* 2004):

$$A_{sat} = A_{opt} \times e^{-\left(\frac{T_{leaf} - T_{optA}}{\Omega}\right)^2} \tag{1}$$

304

305   where A_{sat} (μmol m^{-2} s^{-1}) is the rate of net assimilation at the leaf temperature (T_{leaf}) in °C, T_{optA}

306   (°C) is the optimum temperature for photosynthesis, and A_{opt} (μmol m^{-2} s^{-1}) is the rate of

307   photosynthesis at T_{optA}. Ω, or net photosynthetic thermal niche, is the temperature difference

308   from T_{optA} where photosynthesis declines to 37% of A_{opt}. Ω (° C) describes the width of the

309   response curve peak, where wide curves have a higher Ω and narrower curves have a lower Ω.

310   Prior to fitting Equation 1, A_{sat} from each dataset was individually inspected for outliers. Outliers

311   were removed only when they were clearly erroneous, such as $A_{sat} < 0$ μmol m^{-2} s^{-1} that were not

312   clearly caused by high temperatures. In addition, data points with $C_i < 0$ were removed as they

313   were considered bad measurements. In total, we removed 402 data points, 2.79% of our A_{sat} data.

314   To compare the rates of net photosynthesis across studies, we extracted the rate at 25 °C

315   (A_{25}) by allowing T_{leaf} to equal 25 in Equation 1 for each set of extracted temperature parameters.

316   This standard temperature was selected because it is similar to the average MAT (25.5 °C) in our

317   dataset and is often used as a standard so photosynthetic rates are widely comparable across

13

318   studies. Using similar methods as Kumarathunge *et al.* (2019), we further increased the size of

319   our dataset by extracting A_{sat} values from photosynthetic response to internal CO_2 concentration

320   (A-C_i) curves. For these data, we extracted the first data point taken at ambient CO_2

321   concentrations and saturating irradiance. Values of A_{sat} were kept only if the C_i values were

322   between 275 and 410 ppm. 40 additional curves were added to the A_{sat} dataset using this method.

323   One dataset measured light response curves at different temperatures. A_{sat} was estimated by

324   extracting the light saturated photosynthetic rate from light response curves using a non-

325   rectangular curve (Marshall and Biscoe 1980), and fitting A_{sat} to Equation 1. A total of 111 A_{sat}

326   temperature response curve samples were successfully fit using Equation 1.

327

328   *Biochemical parameter extraction*

329   Biochemical rates, J_{max} and V_{cmax}, were estimated from A-C_i curves. Most datasets

330   collected A-C_i curves starting at an ambient CO_2 concentration, 360-410 ppm. A-C_i curves were

331   obtained by gradually decreasing the CO_2 below ambient concentrations (to as low as zero ppm).

332   CO_2 concentrations were then brought back up to ambient levels and then gradually increased to

333   saturating concentrations (up to 2100 ppm). Prior to fitting the A-C_i curves, data points outside 0

334    $< C_i < 2200$ ppm were removed from the dataset as they were beyond the range of CO_2

335   concentration given to the leaf. We further removed datapoints where A_{sat} was smaller than -10

336   and greater than 70 μmol m^{-2} s^{-1} as they were not considered reasonable A_{sat} rates. In total we

337   removed less than 0.5% of total A-C_i datapoints. J_{max} and V_{cmax} were obtained using the default

338   fit method with "Tcorrect = FALSE" in the 'fitaci' function from the 'plantecophys' package

339   (Duursma 2015) in R version 3.5.0 (R Core Team, 2020), which extracts parameters using the

340   Farquhar, von Caemmerer, and Berry model (FvCB model; (Farquhar *et al.* 1980, von

341 Caemmerer and Farquhar 1981). We further looked at the fitted A-C_i curves and individually

342 removed curves with poor fits. We further removed curves where fitted J_{max} and V_{cmax} values

343 were less than 0 µmol m^{-2} s^{-1}, as this is not possible for correctly fit curves. After the initial data

344 exclusion, we removed outliers where J_{max} or V_{cmax} were clearly erroneous by looking at qqplots

345 and histograms of each dataset. In total, 7.8% or 102 A-C_i curves were removed from the initial

346 dataset.

347   Biochemical temperature response parameters for J_{max} and V_{cmax} were extracted using the

348 peaked Arrhenius function (Medlyn *et al.* 2002):

349

350
$$(T_k) = (k_{opt}) \frac{H_d \exp\left(\frac{E_a(T_k - T_{opt})}{(T_k R T_{opt})}\right)}{H_d - E_a\left[1 - \exp\left(\frac{H_d(T_k - T_{opt})}{(T_k R T_{opt})}\right)\right]} \tag{2}$$

351

352 where T_k is the measured leaf temperature in Kelvin, (k_{opt}) is the value of J_{max} or V_{cmax} at the

353 optimum temperature (µmol m^{-2} s^{-1}), E_a is the activation energy in the Arrhenius function (kJ

354 mol^{-1}), or exponential increase in J_{max} or V_{cmax} before T_{opt}, H_d is the deactivation energy of J_{max} or

355 V_{cmax} after T_{opt} (kJ mol^{-1}), and R is the universal gas constant (8.314 JK^{-1}mol^{-1}). To avoid over-

356 parameterization of the temperature response function, we set $H_d = 200$ kJ mol^{-1} and estimated

357 T_{opt}, k_{opt}, and E_a from Equation 2. Each individual curve was examined and curves were removed

358 if T_{opt}, k_{opt}, or E_a values were over or underestimated, e.g. visually estimated T_{opt} was clearly

359 higher or lower than model estimations which was often due to too few temperatures used to

360 produce the curve, resulting in 35 V_{cmax} and 35 J_{max} temperature response curves.

361 We extracted the rate of V_{cmax} (V_{25}) and J_{max} (J_{25}) at 25 °C from A-C_i curves measured from

362 temperatures ranging from 20-30 °C by setting Tcorrect = "TRUE" in the "fitaci" function. The

363   ratio between J_{25} and V_{25} ($J{:}V$) was calculated by dividing J_{25} by V_{25} for each individual sample.

364   This resulted in 295 samples in our V_{25} and J_{25} datasets. Version 1.4 of the "plantecophys"

365   package defaults to using temperature fitting parameters estimated from a global analysis of

366   photosynthetic temperature responses that estimated values using (Medlyn *et al.* 2002):

367

$$T_k = k_{25} exp\left[\frac{E_a(T_k-298)}{(298RT_k)}\right] \frac{1+exp\left(\frac{298\Delta S - H_d}{298R}\right)}{1+exp\left(\frac{T_k\Delta S - H_d}{T_kR}\right)} \tag{3}$$

369

370   Where ΔS is an entropy term. We estimated J_{25} and V_{25} using the default "global" parameters

371   and this study's tropical estimations of E_a and ΔS (Table S3) and made comparisons of the two

372   fitting estimations.

373

374   *Meta-analytic statistical analyses*

375   Biases for sample size were accounted for by weighting each extracted parameter with

376   the number of observations that were used in each temperature response curve. The weighting

377   factor was calculated as (Hedges and Olkin 1985; Gurevitch *et al.* 1992):

378

$$J = 1 - \left(\frac{3}{4(n-1)}\right) \tag{4}$$

380

381   where J is the weighting factor and n is the number of data points used to fit each temperature

382   response curve (Fig. S2). The weighted mean was incorporated into the linear model by adding J

383   into the 'weights' weighting factor component of the 'lmer' function the 'lme4' package in R

384   (Bates *et al.* 2015). All data analyses were performed in R version 3.5.0 (R Core Team, 2021).

385   Mixed effects models were used to compare global and tropical V_{cmax} and J_{max} activation

386   energies (E_{aV} and E_{aJ}, respectively) and entropy terms (ΔS_V and ΔS_J, respectively), where data

387   source was used as the random intercept. Mixed effects models were also used to investigate

388   relationships between A_{sat} and biochemical parameters (T_{opt}, T_{optJ}, T_{optV}, A_{25}, V_{25}, J_{25}, Ω, E_{aV}, and

389   E_{aJ}) and individual climate variables. We found high collinearity between MAT and elevation

390   (Fig. S3); therefore, elevation was removed from the individual bivariate regression models. We

391   removed elevation as a continuous variable and grouped the data into four elevational groups (0-

392   500m, 501-1000m, 1001-2000m, and >2000m) to visually show the role that elevation played in

393   our climate range for all bivariate regressions. Mixed effect models were also used to compare

394   leaf habit, successional type, and growth conditions, using an $\alpha < 0.05$. Due to available

395   characterizations for our dataset, light environment (sun or shade) and leaf habit (deciduous or

396   evergreen) were compared only for A_{sat} parameters. Successional type (early or late) and growth

397   environment (*in* or *ex situ*) were compared for both A_{sat} and biochemical parameters (summary of

398   samples used in each categorical analysis included in Table S2). Estimated J_{25} and V_{25} were

399   compared between the default "plantecophys" package and our parameter estimates using a

400   mixed effects model as described above.

401   High variance inflation factors (VIF), a means of identifying potential collinearity, were

402   assessed when we included both MAT and elevation in the same multivariate model, where full

403   models that included all four climate variables (MAT, AI, T_{range}, elevation) had at least one

404   variable VIF > 2 (VIF range 2.02-648.53). VIF on the full model was calculated using "vif"

405   function in base R. Therefore, we used hierarchical partitioning to quantify which climate

406   variable had the highest explanatory power on parameter (T_{opt}, T_{optJ}, T_{optV}, A_{25}, V_{25}, J_{25}, Ω, E_{aV},

407   and E_{aJ}) variance using the "rdacca.hp" package in R (Lai *et al.* 2022). Hierarchical partitioning

408   is used in instances of high VIF because it estimates individual importance of predictors in all

409   model subsets, where the subsets also include the full model (Lai *et al.* 2022). The individual

410   effects were estimated via hierarchical partitioning and were calculated from the sum of the

411   calculated unique and shared contribution to the overall model's adjusted R^2, where the model

412   includes all individual variables of interest. The individual effect can be negative if the unique or

413   shared contribution is negative due to high multicollinearity. In this calculation, the individual

414   effects were added to equal the total adjusted R^2.

415

416   **Results**

417   *Comparisons of biochemical estimations from global and tropical parameters*

418   Global estimates of biochemical activation energies and entropy terms yielded higher

419   biochemical parameter rates compared to tropical data derived estimates, suggesting that studies

420   in tropical systems would overestimate V_{25} and J_{25} if using global values. V_{25} and J_{25} estimated

421   from global datasets were both approximately 7% higher than those from tropical parameters

422   (Table S3; Fig. S4A-B), resulting in no discernible difference in JV between parameter estimates

423   (Fig. S4C).

424

425   *Primary climate variable influences on temperature parameters*

426   In bivariate regressions, the net photosynthetic and electron transport optimum

427   temperature increased with increasing temperature, while the maximum Rubisco carboxylation

428   optimum temperature did not. T_{optA} was positively related with MAT, with MAT alone

429   explaining 37% of T_{optA} variance (Fig. 1A; Table 2). T_{optA} did not strongly respond to *AI* or T_{range}

430   (Figs. 2B, S5A). T_{optV} did not respond to any of the three climate variables (Figs. 1C-D, S5B;

431   Table 2). T_{optJ} increased with rising MAT, which explained 14% variation, and T_{optJ} did not

432   respond to AI or T_{range} (Figs. 1E-F, S5C).

433   While net photosynthetic rate did not show clear relationships with climate variables, the

434   rates of photosynthetic biochemical reactions decreased with a warmer climate. A_{25} did not

435   respond to with MAT, AI, or T_{range} (Figs. 2A-B, S6A; Table 2). V_{25} decreased as MAT rose

436   (marginal $R^2 = 0.20$; Fig. 2C), did not respond to AI (Fig. 2D), and decreased with wider T_{range}

437   (marginal $R^2 = 0.18$; Fig. S6B). Similarly, J_{25} decreased as MAT increased (marginal $R^2 = 0.41$;

438   Fig. 2E), did not respond to AI (Fig. 2F), and increased as T_{range} increased (marginal $R^2 = 0.28$;

439   Fig. S6C). The ratio between J_{max} and V_{cmax} at 25 °C ($J{:}V$) decreased with rising MAT (marginal

440    $R^2 = 0.28$; Fig. 3A), did not respond to AI (Fig. 3B; Table 2), and slightly increased with a wider

441   T_{range} (marginal $R^2 = 0.06$; Fig. 3C). Neither net photosynthetic thermal niche (Ω) nor the

442   activation energy for V_{cmax} and J_{max} responded to any climate variables (Fig. S7; Table 2).

443

444   *Growth environment influences on temperature response parameters*

445   Variables describing the rate of a photosynthetic process were higher in sun compared to

446   shade leaves, but temperature response parameters did not differ. Sun and shade leaf T_{optA} were

447   not significantly different from one another (Satterthwaite's method; p = 0.786; Fig. 4A). A_{25} of

448   sun leaves was 1.5 times higher than shade leaves (p = 0.008; Fig. 4B). Similar to T_{optA}, there

449   was no difference in Ω between the two light environments (p = 0.210; Fig. 4C). V_{25} and J_{25} of

450   sun leaves were 88% and 63% higher than the rate of shade leaves, respectively, (both p < 0.001;

451   Fig. 4D-E), and $J{:}V$ was slightly (~10%) higher in shade than sun leaves (p = 0.022; Fig. 4F).

452   Plants grown *in situ* had higher biochemical response rates than *ex situ* grown plants, but

453   that did not lead to differences in A_{sat} rates or parameters. There were no clear differences

454   between plants grown *in* or *ex situ* for A_{sat} parameters and rates T_{optA} (p = 0.085), A_{25} (p = 0.096),

455   or Ω (p = 0.313; Figs. S8A-C). T_{optV} (p = 0.974; Figs. S7D) and E_{aV} (p = 0.102; Figs. S8F) did

456   not differ between *in* and *ex situ*, but plants grown *ex situ* had 40% higher V_{25} (p = 0.030; Figs.

457   S8E). T_{optJ} did not differ between growth environments (p = 0.802; Fig. S8G), J_{25} for plants

458   grown *ex situ* trended 48% higher than those grown *in situ* (p = 0.054; Fig. S8H), and E_{aJ} was

459   around double in *in situ* than *ex situ* grown plants (p =0.002; Fig. S8I). Lastly, *J:V* also was not

460   different between the two growth environments (p = 0.696; Fig. S8J).

461

462   *Effects of plant functional type on temperature response parameters*

463   T_{optA} was higher in drought (semi-) deciduous, or raingreen, species compared to

464   broadleaf evergreen species, but other net photosynthetic temperature response rates and

465   variables did not differ between the two leaf habits. T_{optA} was ~1 °C higher in drought (semi-)

466   deciduous compared to evergreen species (p = 0.009; Fig. 5A). There were no differences

467   between evergreen and deciduous species for A_{25} (p = 0.347; Fig. 5B) or Ω (p = 0.197; Fig. 5C).

468   Optimum temperatures of photosynthesis did not vary between successional types, but

469   rates of photosynthetic responses and the width of the photosynthetic responses were higher in

470   early compared to mid/late successional species. Early and mid/late successional species did not

471   differ in T_{optA} (p = 0.955; Fig 6A). A_{25} and Ω (both p < 0.001; Fig. 6B-C) in early successional

472   species were ~83% and 32% higher than in mid/late successional species, respectively. T_{optV} did

473   not differ between successional types (p = 0.502; 6D) but, in terms of rates, mean early

474   successional V_{25} was 61% higher than late successional species (p < 0.001; Fig. 6E). There were

475   no differences between successional types for *J:V* (p = 0.936; Fig. 6F). T_{optJ} did not differ

476   between successional types (p = 0.644; Fig 6G) but early successional species J_{25} was around

477   double that of late successional species (p < 0.001; Fig. 6H).

478

Hierarchical Partitioning

480   Except for T_{optA}, hierarchical partitioning revealed that no single climate or growth

481   environment variable explained a high amount of variation in our photosynthetic parameters. The

482   strongest predictor for T_{optA} variation was the elevation (individual adj $R^2 = 0.159$; Fig 7A). With

483   a full model $R^2 = 0.018$, climate was not a strong predictor for A_{25}; however, MAT (adj $R^2 =$

484   0.017) had a slightly stronger individual effect on A_{25} than other predictors (Fig. 7B). Ω was

485   more strongly predicted by T_{range} (adj $R^2 = 0.170$; Fig. 7C). T_{optV} was most strongly predicted by

486   AI (adj $R^2 = 0.032$; Fig. 7D), V_{25} was slightly more predicted by MAT (adj $R^2 = 0.053$; Fig. 7E),

487   and E_{aV} was most strongly predicted by MAT (adj $R^2 = 0.128$, Fig. 7F). T_{optJ} was not well

488   predicted by any climate variables; however, T_{range} explained slightly higher variation than other

489   variables (adj $R^2 = -0.040$; Fig. 7G). Variance of J_{25} was more strongly explained by MAT (adj

490    $R^2 = 0.125$; Fig. 6H). E_{aJ} was more strongly driven by MAT (adj $R^2 = 0.068$; Fig. 7I). $J{:}V$ was

491   best explained by elevation (adj $R^2 = 0.060$; Fig. 7J).

492

Discussion

494   *Climate drivers of the optimum temperature of photosynthesis*

495   Globally (Kattge and Knorr 2007; Kumarathunge *et al.* 2019; Crous *et al.* 2022) and in

496   tropical ecosystems (Tan *et al.* 2017), studies have found that the photosynthetic optimum

497   temperature of net photosynthesis increases as growth temperatures increase. In partial support

498   of our first hypothesis, the optimum temperatures of net photosynthesis (T_{optA}) and

21

499 photosynthetic electron transport (T_{optJ}) rose with increasing mean annual temperature (MAT;

500 Fig. 1A,E); however, the optimum temperature of Rubisco carboxylation (T_{optV}) did not (Fig 1C).

501 The slope of our tropical species responses to MAT (T_{optA} slope: 0.59 ± 0.15 °C °C^{-1}; Table 3), is

502 similar to and has overlapping standard error with a global analysis of T_{optA} response to growth

503 temperature (T_{optA} slope: 0.62 ± 0.1 °C per increase in growth temperature; Kumarathunge *et al.*

504 2019), providing no evidence that different algorithms should be used to model tropical and

505 global T_{optA} responses. T_{optJ} in our study also had a similar positive response as the global

506 analysis (current study: T_{optJ} slope: 0.38 ± 0.17MAT; Kumarathunge: T_{optJ} slope: $0.63 \pm$

507 $0.2T_{growth}$; Kumarathunge *et al.* 2019). Our results for the optimum temperatures of V_{cmax} were

508 not as consistent with Kumarathunge *et al.* (2019), where our T_{optV} did not respond to MAT (T_{optV}

509 slope: 0.26 ± 0.21MAT; Table 3), but the global analysis showed a positive relationship with

510 increasing growth temperature (T_{optV} slope: $0.71 \pm 0.2T_{growth}$: Kumarathunge *et al.* 2019). We

511 note, however, that our meta-analysis of tropical species' biochemical parameters (19.6 – 27.5

512 °C) has narrower temperature range than the global meta-analysis (~3.0 – 30.0 °C;

513 Kumarathunge *et al.* 2019) which, along with the high variation in parameter values at each point

514 along the MAT axis, might limit our ability to detect data trends. Additionally, the lower T_{optV}

515 MAT slope response provides some support for the common hypothesis that tropical species

516 have adapted to more narrow climate envelopes and do not strongly respond to variations in

517 growth temperature, potentially resulting in a reduced capability to acclimate to warmer

518 temperatures (Janzen 1967; Cunningham and Read 2003; Dusenge *et al.* 2021). This idea is

519 further supported by Kumarathunge *et al.* (2019) which found optimum temperature responses to

520 growth temperature were more strongly driven by acclimation to growth temperature than

521 adaptation to climate of origin. In a recent analysis across latitudes, Crous *et al.* (2022) found

522   more negative photosynthetic responses to warmer temperatures in the tropics compared to

523   cooler climates, suggesting constrained acclimation. Our J_{max} and V_{cmax} temperature response

524   datasets cover MAT across a reduced range (19.6 – 27.5 °C) than our A_{sat} dataset (11.8 – 30.0

525   °C). Additional studies investigating these biochemical parameters would enable the assessment

526   of whether tropical forest species have systematically different temperature responses of these

527   parameters than extra-tropical species.

528   Contrary to our hypothesis, aridity index alone was not a strong predictor of

529   photosynthetic temperature responses. None of our photosynthetic parameters or rates responded

530   to aridity index (Figs. 1, 2, 3, S7). Compared with trees in temperate zones, fewer studies in the

531   tropics have investigated how rainfall affects T_{opt}. T_{optA} was found to increase as soils dry in a

532   Puerto Rican tropical forest (Carter *et al.* 2020) and a savanna grassland ecosystem (Ma *et al.*

533   2017). However, Kumarathunge *et al.* (2020) found that the optimum temperature for tropical

534   tree growth increases with water addition. Hierarchical partitioning showed aridity index as the

535   most important measured climate component controlling T_{optV}; however, the individual aridity

536   index effect on T_{optV} was very low (Fig. 7D). To date, the few studies that have investigated

537   large-scale environmental controls on the biochemical components of photosynthesis focus

538   solely on how temperature controls these important model parameters (Kattge and Knorr 2007;

539   Tan *et al.* 2017; Kumarathunge *et al.* 2019; Crous *et al.* 2022). Even though these results suggest

540   that aridity does not play a key role in controlling photosynthetic temperature responses, both

541   temperature and rainfall play significant roles in modeled reductions in carbon gain in the

542   Amazon rainforest (Galbraith *et al.* 2010). Future studies should investigate how other climate

543   factors, such as aridity, influence photosynthetic optimum temperatures, as we know that a key

544 constraint on photosynthetic optimization is the balance of carbon gain against water loss

545 (Bloom *et al.* 1985; Wang *et al.* 2017).

546

547 *Biochemical limitations at high temperatures*

548   Limitations to the optimum temperature of net photosynthesis at moderate growth

549 temperatures are often attributed to limitations of Rubisco carboxylation temperature response

550 parameters (Lin *et al.* 2012; Yamaguchi *et al.* 2016), although not always (Wise *et al.* 2004; Cen

551 and Sage 2005). When plants are grown at elevated temperatures, measured photosynthesis is

552 increasingly limited by carboxylation as temperature rises, a trend that is driven both by stomatal

553 limitations on CO_2 substrate and by the high temperature sensitivity of Rubisco carboxylation

554 (Brooks and Farquhar 1985; Hikosaka *et al.* 2006). However, optimality theory of photosynthetic

555 capacity suggests that resources allocated to J_{max} and V_{cmax} at 25 °C are disproportionally reduced

556 under warmer temperatures, resulting in reduced *J:V* (Smith and Keenan 2020; Wang *et al.*

557 2020). The limitation to J_{max} is due to high temperatures reducing electron transport through PSII

558 (Havaux 1996), and a greater investment in Rubisco carboxylation relative to electron transport

559 to counteract the increased photorespiration at higher temperatures (Smith and Keenan 2020).

560 This is supported by global meta-analyses showing declining *J:V* with increasing growth

561 temperature (Kumarathunge *et al.* 2019; Crous *et al.* 2022). Our results support this, where both

562 V_{25} and J_{25} decreased with increasing MAT but J_{25} declined at a steeper rate (Fig. 2), resulting in

563 a decreasing *J:V* with rising MAT (Fig. 3). Across our temperature range, our results are not

564 consistent with those of previous global meta-analyses (Medlyn *et al.* 2002; Hikosaka *et al.*

565 2006; Kattge and Knorr 2007; Kumarathunge *et al.* 2019), where neither of our activation energy

566 terms of J_{max} (E_{aJ}) or V_{cmax} (E_{aV}) responded to temperature (Fig S8). E_{aV} activation energy is a

567   driver of V_{cmax} adjustment and is consistently found to increase with warmer growth temperatures

568   (Yamori *et al.* 2005; Hikosaka *et al.* 2006). The rate of E_{aV} rise declines at temperatures that

569   exceed mid 30 °C, limiting V_{cmax} at higher temperatures (Scafaro *et al.* 2023). The disparity

570   between our results of no E_{aV} response to growth temperature and *J:V* results that are in line with

571   global analyses could be due to the narrower temperature in our E_{aV} dataset. Also, of note, this

572   study does not consider effects of rising CO_2 concentrations on photosynthetic temperature

573   responses. Elevated CO_2 can result in a positive shift in T_{opt} (Long 1991; Šigut *et al.* 2015), and

574   this has been supported in studies on a subtropical tree species (Sheu and Lin 1999) and a

575   tropical mangrove species (Reef *et al.* 2016). This response occurs because higher CO_2

576   concentrations can counteract the increased photorespiration rates that occur at higher

577   temperatures, resulting in decreased *J:V* (Long 1991; Hikosaka *et al.* 2006; but see Fauset *et al.*

578   2019 in a tropical species). More CO_2 fertilization studies should be conducted in tropical forests

579   to further elucidate interactions between tropical species CO_2 and temperature interaction

580   responses.

581

582   *Photosynthetic differences between growth conditions, deciduousness, and successional types*

583   We found that the rate of photosynthesis was higher in sun leaves but there were no T_{opt}

584   differences between sun and shade leaves (Fig. 4), similar to the few studies that have

585   investigated differences in *in situ* tropical photosynthetic responses to different canopy light

586   conditions (Pearcy 1987; Slot *et al.* 2019; Hernández *et al.* 2020; but see Carter *et al.* 2021).

587   Other biomes show similar results, and studies investigating differences in T_{optA} between upper

588   canopy and understory leaves have found that T_{optA} either does not differ (Carter and Cavaleri

589   2018), or T_{optA} is higher in the upper canopy leaves (Jurik *et al.* 1988). Niinemets *et al.* (1999)

590   showed that the optimum temperature of electron transport is higher in the upper canopy (higher

591   incident radiation on average) compared to lower canopy leaves (lower spectral quality, lower

592   average incident radiation), suggesting that the biochemical process of photosynthesis associated

593   with light can adjust to different light conditions and higher temperatures. Within the tropics,

594   Carter *et al.* (2021) found that T_{optA} decreased as canopy height and light increased, likely due to

595   VPD induced stomatal limitations. Hernández *et al.* (2020) found trends toward higher T_{optV} in

596   Panamanian sun leaves, yet T_{optJ} did not differ between light conditions. We did not have enough

597   V_{cmax} or J_{max} data classified as "shaded" and were unable to make a robust sun-shade comparison

598   within our dataset. Even though we were able to make a comparison between A_{sat} sun and shade

599   leaves, we only had eight samples where shade leaves were measured (Table S2), suggesting we

600   need much more temperature response measurements comparing sun and shade leaves in tropical

601   forests. Even so, the growing evidence in tropical forests suggests that light conditions do not

602   strongly control tropical T_{opt}, and we may not need to distinguish between sun and shade leaves

603   when modeling temperature responses in tropical forest canopies.

604   Even though leaf habits, such as evergreen and deciduous species, often have different

605   photosynthetic temperature responses (Yamori *et al.* 2014), global vegetation models usually do

606   not implement separate temperature response parameters for different plant functional types due

607   to insufficient data (Lombardozzi *et al.* 2015; Smith *et al.* 2016; Mercado *et al.* 2018). In the

608   current study, A_{25} did not differ but evergreen leaves had a slightly lower T_{optA} than semi-drought

609   deciduous leaves (Fig. 5A,B). This suggests that global models should differentiate between

610   "broadleaf evergreen tropical" and "semi-deciduous raingreen tropical" forests (Poulter *et al.*

611   2015), rather than considering all tropical regions as "broadleaf evergreen tropical. Although we

612   did find a trend toward higher T_{optA} in semi-deciduous species, we note that all species labeled as

26

613 'semi-deciduous' came from the same study (Slot and Winter 2017a), which had the highest

614 MAT (26.6 °C) of all the study sites included in the A_{sat} dataset. No species in our A-C_i dataset

615 was characterized as either 'deciduous' or 'semi-deciduous' (Table S1), preventing any analysis

616 on differences between leaf habit for J_{max} and V_{cmax} data. Greater efforts should be made to better

617 characterize differences between different plant functional types within the tropics and these data

618 should be used to assess how vegetation models define tropical forest plant functional types.

619   Generally, fast growing, early successional species have higher rates of photosynthesis

620 (Wright *et al.* 2004). Our results agreed with this theory and, similar to Ziegler *et al.* (2020) and

621 Mujawamariya *et al.* (2023), we found higher A_{25}, V_{25}, and J_{25} in early successional species.

622 Additionally, early successional species in a tropical dry forest were found to reside in higher

623 temperature environments due to the higher light environment and more open forest structure in

624 an early successional forest (Cao and Sanchez-Azofeifa 2017), suggesting that early successional

625 seedlings and saplings might have higher optimum temperatures. However, our study that

626 combined all species growth stages found no differences between successional types for T_{optA}

627 (Fig. 6). Our results support a lack of clear differences between canopy species of different

628 successional types in Slot and Winter (2017b) but differ from the results of Slot *et al.* (2016),

629 which found higher optimum temperatures in early successional seedlings. Here, we highlight

630 that Slot *et al.* (2016) was conducted on seedlings instead of canopy trees (Slot and Winter,

631 2017b). Future work should investigate differences in early successional seedling vs mature

632 canopy tree optimum temperatures. We did find that the net photosynthetic thermal niche (Ω)

633 was broader for early successional species than late successional species (Fig 6C). This is

634 consistent with theory on 'fast' species with high rates of photosynthesis, as these species tend to

635 invest in traits that allow productivity under a wide range of temperatures (Michaletz *et al.*

636   2016). A wider thermal niche is likely beneficial to early successional forests that experience a

637   wider, more dynamic range of temperatures (Holbo and Luvall 1989).

638

639   *Opportunities for better parameterized functions*

640   We present trends for the temperature parameters of net photosynthetic and biochemical

641   processes of net photosynthesis in tropical regions. However, both stomatal conductance and

642   daytime respiration can also play large roles in controlling photosynthetic temperature responses

643   (Lin *et al.* 2012). Stomatal conductance, or vapor pressure deficit (VPD) which is the primary

644   climate variable controlling stomatal conductance (Farquhar and Sharkey 1982), have been

645   estimated to be the strongest predictors of photosynthetic decline with climate warming in the

646   tropics (Lloyd and Farquhar 2008; Wu *et al.* 2017; Smith *et al.* 2020; Slot *et al.* 2024). This

647   relationship between temperature, moisture, and stomatal conductance should also be

648   investigated across tropical forests and is critical to understand photosynthetic responses to

649   temperature as tropical forests become hotter and drier (Malhi *et al.* 2008). Further, our

650   hierarchical partitioning could be further improved if we had included leaf functional traits. Most

651   of our photosynthetic parameters were not well explained by any environmental factors. A meta-

652   analysis by Atkin *et al.* (2015) found that plant functional types (broadleaf, conifer, grass type,

653   shrubs) had the most explanatory power for predicting the rate of respiration globally. In

654   addition, other plant trait factors, such as leaf nitrogen and leaf mass per area also improved their

655   predictive models (Atkin *et al.* 2015). Including other factors, such as leaf habit or growth type

656   (e.g., evergreen or deciduous; successional type) could provide valuable information for tropical

657   biome photosynthesis modeling, and substantial efforts should be made to collect a larger

658   variation of these data types, which were not available for many of the studies we analyzed. We

659   also note that this study presents results that under-represent African and Asian tropical forests.

660   Data from these regions could improve photosynthetic temperature response models.

661

662   *Conclusions*

663   This study reports new predictive equations that describe photosynthetic temperature responses

664   of tropical trees to different climate factors and describes pan-tropic differences related to plant

665   growth conditions, growth habits, and successional strategies. Our novel analysis focusing on

666   tropical woody species shows that T_{optA} and T_{optJ} responses to mean temperatures tended to align

667   with global meta-analyses; however, the optimum temperature of T_{optV} did not align with results

668   found globally. A lower slope of photosynthetic biochemical parameter's T_{opt} against MAT for

669   tropical ecosystems suggests a lower capacity for these ecosystems to keep apace of climate

670   change. While global carbon models should consider acclimation of the temperature response of

671   photosynthetic parameters in order to allow for plant plasticity, the lower capacity for this

672   response in tropical ecosystems should also be considered when making projections of

673   ecosystem responses to climate change. Importantly, we did not find different temperature

674   optimums between sun/shade leaves or successional types, but we did find differences between

675   evergreen and semi-deciduous species' optimum temperatures. Vegetation models often define

676   these systems solely as "broadleaf evergreen tropical", but functional types within tropical

677   biomes have distinct temperature responses between "broadleaf evergreen tropical" and "semi-

678   deciduous raingreen tropical" that should be considered to accurately represent tropical or global

679   carbon dynamics.

680

681   **Acknowledgements**

29

682   Author contributions: KRC, MAC, AR, SPS, KSE, RJN, APW, PBR, SCR, TEW conceived of

683   and designed the study, KRC and ECS organized and analyzed the data. KRC and MAC wrote

684   the manuscript. KRC, AR, KSE, OA, NHAB, AWC, ZC, KYC, CED, MED, JRE, JFS, JWGK,

685   ACM, BEM, PM, JR, MS, EST, JU, AV, KW, JW collected and contributed data to the study.

686   All authors contributed to writing and editing the final manuscript.

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688   **Funding Information**

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1056   **Figure 1** The optimum temperature of net photosynthesis and biochemical responses to mean

1057   annual growth temperature and aridity index. T_{optA} response to A) MAT and B) aridity index.

1058 T_{optV} response to C) MAT and D) aridity index. T_{optJ} response to E) MAT and F) aridity index.

1059   Regression equations are weighted by number of observations that are used to calculate each

1060   temperature response mean. Size of data point depicts weight of each mean where larger data

1061   points carry a greater weight. Line represents linear regression fits (Table 2). Shaded area around

1062   line represents confidence intervals. Color represents altitude groupings of < 500m (blue-green),

1063   500-999m (turquoise), 1000-2000m (beige), NA (gray).

1064

1065   **Figure 2** The rate of net and the biochemical components of photosynthesis at 25 °C responses

1066   to three primary climate variables. A_{25} response to **A)** MAT, **B)** aridity index where higher

1067   aridity index indicates wetter conditions. V_{25} response to **D)** MAT, **E)** aridity index. J_{25} response

1068   to **G)** MAT, **H)** aridity index. Regression equations are weighted by number of observations used

1069   to calculate each temperature response mean. Size of data point depicts weight of each mean

1070   where larger data points carry a greater weight. Solid line represents significant linear regression

1071   fits (Table 2). Shaded area around line represents confidence intervals. Color represents altitude

1072   groupings of < 500m (blue-green), 500-999m (turquoise), 1000-2000m (beige), >2000m (black),

1073   NA (gray).

1074

1075   **Figure 3** The ratio between rate of J_{max} and V_{cmax} responses to three primary climate variables.

1076   The ratio between the rate of J_{max} at 25 °C and V_{cmax} at 25 °C (JV) responses to **A)** mean annual

1077   temperature (MAT), **B)** aridity index, and **C)** mean annual temperature range (T_{range}). Regression

1078   equations are weighted by number of observations that are used to calculate each temperature

1079 response mean. Size of data point depicts the sample size used to weight each mean where larger

1080 data points carry a greater weight. Shaded area around line represents confident intervals. Color

1081 represents altitude groupings of < 500m (blue green), 500-999m (turquoise), 1000-2000m

1082 (beige), >2000m (black), NA (gray).

1083

1084 **Figure 4** Boxplots displaying the net photosynthetic and biochemistry at 25 °C parameter

1085 differences with leaf light environment. The distribution of shade and sun growth leaves for **A)**

1086 T_{optA}, **B)** A_{25}, **C)** Ω, **D)** V_{25}, **E)** J_{25}, and F) the ratio of J_{max} to V_{cmax}. Ω indicates the difference in

1087 T_{opt} and the temperature where the rate of photosynthesis is 37% of $T_{opt.}$ The boxes display

1088 median and interquartile range. The whiskers represent 1.5 times the interquartile range. Data

1089 beyond the whiskers are outside of 1.5 times the interquartile range. Asterisks denotes significant

1090 differences between treatments based on a Satterthwaite test, * $p < 0.05$, ** $p < 0.01$, *** $p <$

1091 0.001. A_{max}: sun n $= 89$ shade n $= 6$; k_{25}: sun n $= 248$, shade n $= 23$.

1092

1093 **Figure 5** Boxplots displaying the net photosynthetic parameter differences between species of

1094 different leaf habit. The distribution of evergreen and semi-deciduous species for **A)** T_{optA}, **B)**

1095 A_{25}, and **C)** Ω. The boxes display median and interquartile range. The whiskers represent 1.5

1096 times the interquartile range. Data beyond the whiskers are outside of 1.5 times the interquartile

1097 range. Asterisks denotes significant differences between treatments based on a Satterthwaite test,

1098 ** $p < 0.01$. evergreen n $= 45$, semideciduous n $= 23$.

1099

1100 **Figure 6** Boxplots displaying the net photosynthetic parameter differences between successional

1101 stratus. The distribution of early and late successional species for **A)** T_{optA}, **B)** A_{25}, and **C)** Ω, **D)**

40

1102 T_{optV}, **E)** V_{25}, **F)** JV, **G)** T_{optJ}, **H)** J_{25}. The boxes display median and interquartile range. The

1103 whiskers represent 1.5 times the interquartile range. Data beyond the whiskers are outside of 1.5

1104 times the interquartile range. Asterisks denotes significant differences between treatments based

1105 on a Satterthwaite test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. A_{max}: early n = 20, mid/late n =

1106 22; k_{25}: early n = 14, shade n = 17; A-C_i: early n = 8, shade n = 7.

1107

1108 **Figure 7** Hierarchical partitioning results for relative individual importance of individual climate

1109 variables on T_{optA} (A), A_{25} (B), Ω (C), T_{optV} (D), V_{25} (E), H_{aV} (F), T_{optJ} (G), J_{25} (H), H_{aJ} (I), JV

1110 (J). Individual effects sums to the calculated total explained variation (adj R^2).

1112 **Table 1** Abbreviations and descriptions

Variable	Description	Units
ACi	Refers to the net photosynthetic assimilation at a range of leaf internal CO_2 concentrations	unitless
AI	Aridity Index, calculated as the mean annual precipitation divided by the mean annual evaoptranspiration	unitless
A_{sat}	Light saturated photosynthesis, estimated from light response curves	$\mu mol\ m^{-2}\ s^{-1}$
A_{opt}	The value of A_{net} at the optimum temperature	$\mu mol\ m^{-2}\ s^{-1}$
A_{25}	Rate of net photosynthesis at 25 ºC	$\mu mol\ m^{-2}\ s^{-1}$
E_{aV}	The activation energy of the V_{cmax} temperature response curve	$kJ\ mol^{-1}$
E_{aJ}	The activation energy of the J_{max} temperature response curve	$kJ\ mol^{-1}$
g_s	Stomatal conductance	$mol\ m^{-2}\ s^{-1}$
J_{max}	The maximum rate of photosynthetic electron transport	$\mu mol\ m^{-2}\ s^{-1}$
J_{25}	The rate of J_{max} at 25 ºC	$\mu mol\ m^{-2}\ s^{-1}$
$J{:}V$	The ratio between J_{25} and V_{25}	unitless
k_{opt}	The value of J_{max} or V_{cmax} at the optimum temperature	$\mu mol\ m^{-2}\ s^{-1}$
MAT	Mean annual temperature	ºC
T_{leaf}	Leaf temperature	ºC
T_{optA}	The optimum temperature for net photosynthesis	ºC
T_{optJ}	Optimum temperature of photosynthetic electron transport	ºC
T_{optV}	Optimum temperature for Rubisco carboxylation	ºC
T_{range}	Mean annual temperature range	ºC
V_{cmax}	Maximum rate of Rubisco carboxylation	$\mu mol\ m^{-2}\ s^{-1}$
VPD	Vapor pressure deficit	kPa
V_{25}	The rate of V_{cmax} at 25 ºC	$\mu mol\ m^{-2}\ s^{-1}$
Ω	The difference in T_{opt} and the temperature where the rate of photosynthesis is 37% of T_{opt}	ºC

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1115   **Table 2** Regression equations for each photosynthetic parameter response to individual climate variables.

	Coefficients						
	Intercept	MAT Slope	Aridity Index Slope	T_{range} Slope	marginal r^2	conditional r^2	p-value
T_{opt}	**13.62 ± 3.79**	**0.59 ± 0.15**			**0.37**	**0.78**	**<0.001**
	30.39 ± 1.04		-0.82 ± 0.45		0.02	0.62	0.066
	24.72 ± 2.45			0.25 ± 0.17	0.03	0.82	0.396
A_{25}	1.67 ± 4.61	0.28 ± 0.19			0.05	0.27	0.139
	8.35 ± 1.58		-0.46 ± 0.82		0.00	0.13	0.573
	9.38 ± 3.11			$-8.02 \times 10^{-2} \pm 24.24 \times 10^{-2}$	0.00	0.26	0.741
Ω	11.15 ± 7.77	0.14 ± 0.31			0.01	0.70	0.651
	15.35 ± 2.35		0.91 ± 0.82		0.01	0.80	0.268
	11.30 ± 4.00			0.26 ± 0.29	0.01	0.69	0.380
T_{optV}	32.83 ± 5.26	0.26 ± 0.21			0.08	0.18	0.216
	34.76 ± 3.68		2.36 ± 1.86		0.08	0.14	0.203
	35.91 ± 2.15			0.35 ± 0.24	0.10	0.25	0.156
V_{25}	**75.26 ± 6.67**	**-1.36 ± 0.25**			**0.20**	**0.55**	**<0.001**
	42.75 ± 3.78		-1.02 ± 1.33		0.01	0.26	0.443
	13.82 ± 6.76			**2.16 ± 0.40**	**0.18**	**0.62**	**<0.001**
E_{aV}	57.22 ± 89.50	1.54 ± 3.57			0.01	0.45	0.668
	139.82 ± 69.15		-17.14 ± 33.39		0.02	0.44	0.608
	145.29 ± 45.95			-3.87 ± 3.47	0.09	0.45	0.264
T_{optJ}	**26.56 ± 4.32**	**0.38 ± 0.17**			**0.14**	**0.14**	**0.025**
	36.63 ± 2.86		0.95 ± 1.49x		0.02	0.02	0.520
	31.73 ± 3.33			0.35 ± 0.26	0.09	0.24	0.170
J_{25}	**182.95 ± 13.12**	**-4.37 ± 0.49**			**0.41**	**0.64**	**<0.001**
	76.39 ± 9.46		-0.91 ± 2.91		0.00	0.39	0.755

	Intercept	MAT	Aridity index	Temperature range	Marginal r^2	Conditional r^2	p-value
	-8.29 ± 14.68			**6.43 ± 0.82**	**0.28**	**0.73**	**<0.001**
E_{aJ}	-0.82 ± 91.11	3.08 ± 3.63			0.06	0.40	0.396
	108.84 ± 40.26		-11.00 ± 20.61		0.02	0.13	0.594
	130.67 ± 48.49			-4.20 ± 3.64	0.08	0.41	0.249
$J{:}V$	**2.41 ± 0.16**	**-0.02 ± 0.01**			**0.10**	**0.53**	**<0.001**
	1.85 ± 0.14		$7.64 \times 10^{-3} \pm 3.14 \times 10^{-2}$		0.00	0.62	0.808
	1.50 ± 0.16			$\mathbf{2.84 \times 10^{-2} \pm 9.34 \times 10^{-3}}$	**0.06**	**0.60**	**0.002**

1116 Photosynthetic parameters are: the optimum temperatures of net photosynthesis (T_{optA}; °C), the rate of net photosynthesis at 25 °C

1117 (A_{25}; µmol m^{-2} s^{-1}) at 25 °C, photosynthetic thermal niche or width of the temperature response curve (Ω; °C), the optimum

1118 temperatures of the maximum rate of Rubisco carboxylation (V_{cmax}) and photosynthetic electron transport (J_{max}) (T_{optV}, T_{optJ}

1119 respectively; °C), the rate of V_{cmax} (V_{25}; µmol m^{-2} s^{-1}) and J_{max} (J_{25}; µmol m^{-2} s^{-1}) at 25 °C, and the activation energy term for V_{cmax}

1120 (E_{aV}; kJ mol^{-1})and J_{max} (E_{aJ}; kJ mol^{-1}). Climate variables are mean annual temperature (MAT; °C), aridity index, and the mean annual

1121 temperature range from the maximum temperature of the warmest month and the minimum temperature of the coldest month.

1122 Intercepts and slopes are given as means ± standard error. Bolded values indicate regression results with p-values < 0.05. Marginal r^2

1123 provides the model variance of only the model fixed effect, whereas, conditional r^2 provides variance of the model with both the fixed

1124 and random effects.

A

$$y = 2.41 - 0.02x$$
$$R^2 = 0.1$$
$$p < 0.001$$

B

$$y = 1.85 - 0.008x$$
$$R^2 < 0.01$$
$$p = 0.808$$

Elevation
- <500m
- 500-999m
- 1000-2000m
- >2000m

C

$$y = 1.50 + 0.03x$$
$$R^2 = 0.06$$
$$p = 0.002$$