

1 **Co-variations between plant functional traits emerge from constraining**
2 **parameterization of a terrestrial biosphere model.**

3 **Running title:** Functional traits variability inferred from data assimilation

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82 **Key words:** Plant functional traits, ORCHIDEE, terrestrial model, optimization, data
83 assimilation, plant acclimation.

84

85 **Abstract**

86 **Aim**

87 Mechanisms of plant trait adaptation and acclimation are still poorly understood and
88 consequently lack a consistent representation in terrestrial biosphere models (TBMs). Despite
89 the increasing availability of geo-referenced trait observations, current databases are still
90 insufficient to cover all vegetation types and environmental conditions. In parallel, the
91 growing number of continuous eddy-covariance observations of energy and CO₂ fluxes has
92 enabled modelers to optimize TBMs with these data. Past attempts to optimize TBMs
93 parameters mostly focused on model performance overlooking the ecological properties of
94 ecosystems. The aim of this study is to assess the ecological consistency of optimized trait-
95 related parameters while improving the model performances for gross primary productivity
96 (GPP) at sites.

97 **Location**

98 World

99 **Time period**

100 1992-2012

101 **Major taxa studied**

102 Trees and C3 grasses

103 **Methods**

104 We optimized parameters of the ORCHIDEE model against 371 site-years of GPP estimates
105 from the FLUXNET network and we looked at global co-variation among parameters and
106 with climate.

107 **Results**

108 The optimized parameter values are shown to be consistent with leaf-scale traits, in particular
109 well-known trade-offs observed at the leaf level, echoing the leaf economic spectrum theory.
110 Results show a marked sensitivity of trait-related parameters to local bio-climatic variables
111 and reproduce observed relationships between traits and climate.

112 **Main conclusions**

113 Our approach validates some biological processes implemented in the model and enables us
114 to study ecological properties of vegetation at the canopy level, as well as some traits that are
115 difficult to observe experimentally. This study stresses the need for 1) implementing explicit
116 trade-offs and acclimation processes in TBMs, 2) improving the representation of processes to
117 avoid model-specific parameterization as well as 3) performing systematic traits
118 measurements at FLUXNET sites in order to gather information on plant ecophysiology and
119 plant diversity, together with micro-meteorological conditions.

120

121 **Introduction**

122 Terrestrial biosphere models (TBMs) describe the different processes controlling exchanges
123 of energy and trace gases between the atmosphere and the biosphere. Process-based TBMs are
124 useful tools for understanding the dynamics of ecosystems under changing environment, for
125 present-day to future conditions.

126 In most TBMs, the worldwide vegetation is divided into plant functional types (PFTs) based
127 on general characteristics of the photosynthetic pathways, phenology, structure and
128 physiology. Different PFTs usually share the same equations but use different parameter
129 values to describe generic processes (photosynthesis, respiration), while biome-specific
130 equations may be used for phenology and allocation. Therefore, for a given PFT, only the
131 differences in climate and soil properties can determine spatial and temporal gradients in
132 ecosystem state variables.

133 The prescribed values of PFT-specific parameters are derived from discrete observations
134 obtained at varying spatial scales (organs, individuals, ecosystems; Reich *et al.*, 2007; Kattge
135 *et al.*, 2009) and in specific environmental conditions, despite the modulation of real world
136 plant traits by climate (Wright *et al.*, 2005; Ordoñez *et al.*, 2009; van Ommen Kloeke *et al.*,
137 2012; Maire *et al.*, 2015) and soil properties (Fisher *et al.*, 2012). In addition, some TBM
138 parameters relate to traits that are difficult to measure experimentally (e.g. root turnovers or
139 carbon allocation), or are model-specific. These parameters can hardly be directly optimized
140 from observations and their adjustment to varying environmental conditions can only be
141 determined by labor intensive multi-factorial ecosystem manipulation experiments (Luo *et al.*,
142 2017). This rigid determination of parameter values, combined with the use of single PFT to
143 cover a range of different species (Peaucelle *et al.*, 2016), hinders a realistic representation of
144 the past, present and future ecosystem dynamics both at the local or regional scale, and their

145 response to global drivers such as climate, elevated CO₂ and nutrient fertilization (Hartig *et*
146 *al.*, 2012, Atkin *et al.*, 2015; Kroner & Way, 2016; Reich *et al.*, 2016).

147 To overcome the rigidity of the PFT representation, various approaches have been proposed
148 to provide continuous distributions of plant functional traits related to model parameters.
149 These approaches range from extrapolating trait observations across spatial gradients
150 (Verheijen *et al.*, 2015), to estimating optimal trait values according to ecological theories and
151 plant-centered approaches (Reu *et al.*, 2011; Pavlick *et al.*, 2013; Prentice *et al.*, 2014). The
152 drawback of these different approaches is that they require both spatial and temporal
153 observations for model calibration and/or validation. Despite the increasing number of geo-
154 referenced trait observations (Kattge *et al.*, 2011), current databases are insufficient to cover
155 all vegetation types and environmental conditions for projections at the ecosystem level
156 (Musavi *et al.*, 2015, 2016). Moreover, trait observations should be co-located with process
157 and meteorology data to understand linkages between traits and ecosystem function (Law *et*
158 *al.*, 2008), which is rare in existing databases although increasingly addressed for some
159 biomes (Bjorkman *et al.*, 2018). Long-term monitoring of functional traits is needed to assess
160 the adjustments to climate. As such information is still lacking, approaches have been
161 developed that confound the spatial and temporal dimensions of trait variability.

162 Another modeling strategy consists in optimizing TBMs against observed variables sensitive
163 to ecosystem-level parameters in order to overcome these limitations. This approach assumes
164 that the model structure is unbiased, so that realistic parameters values can be estimated when
165 model simulations best match observations. Because biometric variables are sparse and often
166 depend on processes not represented in models (Thum *et al.*, 2017), energy and trace gas flux
167 measurements are more appealing to optimize TBM parameters. Eddy-covariance data
168 provide near-continuous observations of CO₂, latent heat and sensible heat fluxes, and are
169 therefore well suited for better constraining photosynthesis, respiration, transpiration and

170 carbon phenology model parameters. Eddy-covariance measurements have been extensively
171 used to improve specific performances of TBMs, i.e. their ability to reproduce specific
172 observed ecosystem behaviors (Carvalhais *et al.*, 2010; Kuppel *et al.*, 2012; Santaren *et al.*,
173 2014; Schürmann *et al.*, 2016). However, such model calibrations are disconnected, by
174 construction, from ecological theory or trait-based relationships, and do not exploit the full
175 potential of continuous flux observations across the globe, which provide both spatial and
176 temporal information.

177 In this study, we aim at assessing the consistency of model trait parameters optimized against
178 eddy-covariance flux tower measurements of growth primary productivity (GPP) using the
179 state-of-the-art ORCHIDEE land surface model (Krinner *et al.*, 2005). In addition to classical
180 optimization analyses (i.e. looking for the optimal parameter sets resulting in the highest
181 model improvement), we focus here on the variability of optimized parameter values and on
182 inter-traits correlations or trait-environment correlations. By doing so, we address the
183 following research questions: 1) Are the parameters retrieved by optimizing the model against
184 flux tower records consistent with known relationships between traits (i.e. trade-offs) ? or 2)
185 between traits and environmental variables? and 3) What new relationship can be identified
186 with this approach?

187

188 **Methods**

189 *The ORCHIDEE model*

190 The land surface model ORCHIDEE (v1.9.6, without nitrogen cycle) computes biosphere-
191 atmosphere exchanges, consistently with water and carbon storage using ordinary differential
192 equations (Krinner *et al.*, 2005) (Figure1). Given meteorological forcing, plant and soil
193 conditions, the model simulates photosynthesis, all components of the surface energy budget
194 and hydrological processes at a half-hourly time step, while the dynamics of carbon storage
195 are calculated daily. In ORCHIDEE, the land surface is discretized into 12 plant functional
196 types (PFT) and bare soil (Table S1.1, Appendix S1). All PFTs share the same equations, but
197 use different parameter values, except for phenology (budburst/senescence), which is PFT-
198 specific (Botta *et al.*, 2000).

199

200 *Eddy-covariance GPP*

201 We used half-hourly flux observations from eddy-covariance sites within the FLUXNET
202 network (<https://fluxnet.fluxdata.org>). The sites were selected on the basis of spatial
203 homogeneity and the dominance of a vegetation type that could easily be matched to one of
204 the PFTs in ORCHIDEE, excluding crops and C₄ grasses. The vegetation type information at
205 each site was obtained from <http://fluxnet.ornl.gov>. The list of analyzed FLUXNET sites (98
206 sites, 371 site-year) and the corresponding PFTs is given in Appendix S2. The following
207 analyses rely on GPP derived from net ecosystem exchange (NEE; reference with variable
208 USTAR threshold) after accounting for ecosystem respiration calculated using the method of
209 Reichstein *et al.*, (2005) provided in the FLUXNET dataset. Years with less than 80% of
210 available half hourly observations were discarded.

211

212 *Meteorological data*

213 Because ORCHIDEE needs continuous half-hourly meteorological forcing, we gap-filled time
214 series of weather variables using the interpolation algorithm developed by Vuichard & Papale
215 (2015). Linear interpolation was applied between available observations when the gap-
216 duration in the meteorological data was less than six hours. Otherwise, the variables were
217 interpolated and bias corrected using the ERA-interim reanalysis (~80km, Dee *et al.*, 2011).
218 Snow and rain were identified according to air temperature (threshold for snow being 0°C).

219

220 *Data assimilation procedure*

221 The parameters of ORCHIDEE were optimized with the ORCHIDAS package developed by:
222 Kuppel *et al.*, (2012); Bacour *et al.*, (2015); MacBean *et al.*, (2015) and Peylin *et al.*, (2016);
223 (<https://orchidas.lsce.ipsl.fr/>; Figure 1). Gaussian distributions of parameter and observation
224 errors being assumed, a gradient-based approach was used to minimize the Bayesian cost
225 function J (Tarantola, 2005):

$$J(x) = \frac{1}{2} \left[(\mathbf{y} - H(x))^T \mathbf{R}^{-1} (\mathbf{y} - H(x)) + (\mathbf{x} - \mathbf{x}_b)^T \mathbf{B}^{-1} (\mathbf{x} - \mathbf{x}_b) \right] \quad (1)$$

226 This function quantifies the difference between observations (\mathbf{y}) and simulations ($H(x)$) (here
227 GPP), and between *a priori* (\mathbf{x}_b) and optimized parameters (\mathbf{x}). The B and R matrices are the
228 prior error covariance matrices for parameters and observations, respectively (including in the
229 latter case eddy-covariance measurement and model errors).

230 Both R and B were taken as diagonal, as discussed in Kuppel *et al.* (2012). The $J(x)$ function
231 was iteratively minimized with the L-BFGS-B algorithm (Byrd *et al.*, 1995), which notably
232 allows bounding the range of variation of the parameters to optimize. After model calibration
233 (i.e. minimizing J), the posterior error covariance matrix (A), providing the full statistical
234 distribution of the optimized parameters was estimated by:

$$A = [H^T R^{-1} H + B^{-1}]^{-1} \quad (2)$$

235 where H is the Jacobian of model at the minimum of J (Tarantola, 2005). The covariances of
236 errors between parameters contained in the non-diagonal terms of A inform about the ability
237 of observations given the structure of H to solve for parameters individually, or in
238 combination. High error covariance between two parameters relates to the equifinality
239 problem, whereby different values of these parameters result in model outputs equally
240 matching the observations (relative to R).

241

242 *Optimized parameters*

243 We restricted our exercise to the parameters involved in the assimilation of CO_2 following
244 previous sensitivity analyses from Kuppel (2012). We analyzed 14 parameters controlling
245 long-term and inter-annual GPP variability (Table 1). The key equations involving each
246 optimized parameter as well as their effect on the simulated GPP are described in Table S1.2
247 (Appendix S1). The parameters were related to photosynthetic capacity, phenology, carbon
248 allocation and the water budget. Photosynthetic capacity parameters were the maximal rate of
249 carboxylation limited by CO_2 (V_{cmax}), the ratio between the maximal rate of carboxylation
250 limited by light and V_{cmax} (V_j/V_c), the optimal temperature of photosynthesis (T_{opt}) and the
251 slope of the Ball-Berry model for stomatal conductance ($gslope$). Parameters driving
252 phenology were the specific leaf area (SLA), leaf longevity ($Lage$), summer maximal leaf area
253 index (LAI_{max}) and the temperature for leaf senescence ($Csenes$). Allocation parameters were
254 the minimal fraction of LAI_{max} for the use of carbohydrate reserves ($Klai$) and the period
255 after budburst during which the use of carbohydrates is allowed ($tauleaf$) for the formation of
256 new leaves. Finally, two parameters involved in the water status of the plant were the
257 exponential factor describing the root profile and length ($Kroot$) and the minimal threshold at
258 which photosynthesis becomes limited by minimum water potential ($Wlim$). In addition, two

259 scaling factor *Kbm* (initial biomass of leaves for evergreen species) and *bbdate* (spring
260 burdburst date) were added in the optimization to allow adjusting the seasonal timing of GPP.

261 The range in variation of the three parameters corresponding to observable traits (*SLA*, *Vcmax*
262 and *Lage*) was set from the TRY database for each PFT (Niinemets *et al.*, 1999; Deng *et al.*,
263 2004; Meir *et al.*, 2007; Kattge *et al.*, 2009, 2011; Domingues *et al.*, 2010; Cernusak *et al.*,
264 2011; Azevedo & Marenco, 2012; van de Weg *et al.*, 2012; Nascimento & Marenco, 2013).
265 Species from the TRY database were assigned to corresponding PFTs based on available
266 metadata about plant structure, leaf phenology and climate information extracted from
267 species' latitude and longitude coordinates. We chose as a reference range the 2.5 - 97.5
268 percentile of the trait distributions from TRY. The variation ranges for the other parameters
269 were fixed based on expert judgment (Kuppel *et al.*, 2014).

270

271 *Simulations and assimilation set-up*

272 At each flux tower site, we assumed that the eddy-covariance flux footprint was entirely
273 composed by a single PFT (Appendix S2). The model was forced by local meteorological
274 observations (see *Meteorological data* section) and soil texture from the harmonized
275 worldwide soil database (Nachtergaele *et al.*, 2012) to define the residual and saturation water
276 contents, and the saturated hydraulic conductivity in the soil model (Ducoudré *et al.*, 1993;
277 Krinner *et al.*, 2005) based on Van Genuchten (1980). Initial soil carbon pools in equilibrium
278 with local climate were obtained with an analytical spin-up procedure (Lardy *et al.*, 2011; Xia
279 *et al.*, 2012). Initial biomass was simulated until reaching equilibrium (generally after a ~300
280 year-long simulations using the studied year meteorological data and constant CO₂ set to level
281 of the year), thus different from the real stand age observed at each site.

282

283 We optimized GPP averaged over 15 days using moving windows to avoid noise from high
284 frequency variations in the parameter optimization that could induce convergence issues
285 (Bacour *et al.*, 2015). As far as test data from eddy-covariance measurements are concerned,
286 high frequency variations in fluxes include also variation in the boundary layer that are
287 unrelated to the fluxes at the surface (Ibrom *et al.*, 2006). Santaren *et al.* (2007) estimated that
288 for parameters related to photosynthesis and phenology, optimization based on half-hourly
289 observations did not improve the results. For each site, the optimizations were conducted
290 year-by-year to account for trait variability over time (Wu *et al.*, 2013).

291 Following MacBean *et al.* (2015), each calibration (site-year) used ten replicates representing
292 different starting parameter sets with values randomly picked within their allowed variation
293 range (Table S1.3). Only the best calibration out of these ten replicates was retained for
294 analyses. This procedure increases the chances of finding the global minimum of J as
295 Santaren *et al.* (2014) showed that the gradient-based algorithm was sensitive to initial
296 conditions with a non-linear and complex model such as ORCHIDEE.

297

298 *Analyses*

299 We only retained calibrations for which the optimized model reproduced GPP observations
300 with high precision. The rationale for this was that optimized parameters from model runs
301 which agreed poorly with GPP observations provided little or no useable information. The
302 filtering was performed using a two-step procedure.

303 First, the criterion for ‘improved GPP simulation’ was the relative site-year posterior RMSE
304 ($RMSE_{re}$) between observed and optimized GPP:

$$RMSE_{re} = \frac{RMSE}{mean(GPP_{obs})} \quad (4)$$

305 Whenever the value of $RMSE_{re}$ was higher than the all- $RMSE_{re}$ median plus one interquartile
306 range (IQR), the site-year was removed from the analysis. We also discarded sites with
307 ‘inconsistent parameters values’, i.e. with too large differences between the ten replicates at
308 the same site reflecting convergence issues (equifinality) of the algorithm.

309 Secondly, for sites with at least two $RMSE_{re}$ below 10 % among the ten replicates, we
310 estimated the coefficient of variation (CV) of parameters across the replicates. We retained
311 only years for which the median CV was below the median of all CV plus one IQR of their
312 distribution. This filtering provided optimized parameters from 371 site-years (over 516
313 initially considered) for 98 sites (over 116; Appendix S2) spanning seven PFTs located in
314 boreal, temperate and tropical areas (Table S3.4; Appendix S3).

315

316 For each parameter, we calculated the uncertainty reduction (UR) as:

$$UR = 1 - \frac{\sigma_{post}}{\sigma_{prior}} \quad (5)$$

317 With σ_{post} and σ_{prior} being the *posterior* and *prior* parameter uncertainties (square root of the
318 diagonal elements of A and B). We then separated in the analysis the well- from the poorly-
319 constrained parameters. Well-constrained parameters are defined as those with 1) UR higher
320 than the median of UR distributions for all parameters and 2) a low correlation of error with
321 other parameters (from the A matrix, Eq. 2). Note that a strong error correlation making two
322 parameters poorly constrained individually is still an interesting result as it indicates a range
323 of possible tradeoffs between these two parameters.

324 The optimized parameter values were regressed against the local background bio-climatic
325 variables (Table 2) for each site, and against the soil relative water content (volume of water
326 by volume of soil) simulated by ORCHIDEE. Bio-climatic variables were averaged over the
327 whole year and over the length of the growing season (GSL). For temperate sites, the growing

328 season was defined as the period with daily temperature above 5°C and relative soil water
329 content above 0.2 (Violle *et al.*, 2015). In some tropical regions, the growing season length is
330 potentially limited by water availability (wet/dry seasons), we thus kept the same definition as
331 for temperate ecosystems. For boreal sites, we adapted the definition of the growing season
332 such as weekly temperature must be above 0°C. Analyses were performed with the R.3.2
333 software (R Core Team, 2016) and standardized major axis (SMA) analyses were performed
334 with the 'lmodel2' package (Legendre, 2014). Because we sought to compare simulated
335 correlations with common ecological properties observed at the global scale, we analyzed
336 different groups of PFTs: all PFTs together; deciduous versus evergreens; needleleaves versus
337 broadleaves; and C₃ grasses (Table S1.1). Regressions were performed both with and without
338 a logarithmic transformation of the data.

339 **Results and comparison to existing literature**

340 *Optimization performances*

341 A full description of the optimization performances and parameter uncertainty reduction can
342 be found in Appendix S3.

343 In all cases, the optimized GPP time series better agrees with observations than the prior ones,
344 with the RMSE being reduced by 76.6 ± 13.0 % (Table S3.4; Appendix S3). The median
345 posterior $RMSE_{re}$ is 0.19 and the IQR is 0.11. The median CV over all parameters is 0.24
346 (IQR=0.13). After optimization, the parameter uncertainty (Eq. 5) is reduced by 30 % on
347 average (Table S3.5; Appendix S3).

348 The posterior error correlation matrix A (Eq.2) reveals a positive correlation between V_{cmax}
349 and several other parameters including (Figure 2): $Topt$ ($r=0.57\pm0.05$); $gslope$ ($r=-0.37\pm0.04$);
350 $Kroot$ ($r=0.24\pm0.07$) and Vj/Vc ($r=-0.31\pm0.04$). There also exists a negative correlation
351 between $Kroot$ and $gslope$ ($r=-0.38\pm0.08$), between $Kroot$ and $Wlim$ ($r=-0.30\pm0.09$) and
352 between LAI_{max} and $Klai$ ($r=-0.37\pm0.16$) (Figure 2).

353 Jointly analyzing information from the uncertainty reduction (Appendix S3) and the cross-
354 parameter error correlation enables to distinguish between: 1) well constrained parameters
355 ($Lage$ and SLA for evergreens/ $Lage$ and $Csenes$ for deciduous); 2) well constrained
356 parameters with a risk of equifinality ($gslope$, $Kroot$, LAI_{max} , $Topt$ and V_{cmax}); and 3) poorly
357 constrained parameters (Vj/Vc , $Klai$, $Tauleaf$ and $Wlim$; Table 1). In the following analyses,
358 trait co-variations have to be interpreted in respect to confidence intervals (posterior error) in
359 parameter estimates.

360 *Co-variation between parameters*

361 We analyzed cross-site correlations between optimized parameters in relation to expected trait
362 relationships. The co-variation between all parameters is illustrated in Figure S4.2 (Appendix

363 S4). For more clarity and considering the large number of parameters, we only describe here
364 the relationships involving four parameters related to phenology (*SLA*, *Lage*) and
365 photosynthesis (*Vcmax*, *gslope*). All relationships are provided in Table S4.6 (Appendix S4).

366 We observed a negative correlation between *SLA* and *Lage* for all PFTs ($r=-0.63$; Table 3) as
367 well as for evergreens ($r=-0.67$) and broadleaves PFTs ($r=-0.53$), separately. The slope of the
368 emerging relationship between *LMA* ($1/SLA$) and *Lage* (1.91; 1.63-2.24 95% confidence
369 interval; $p < 0.05$) for all PFTs was close to the observed slope from field observations (1.71;
370 1.62-1.82; Wright *et al.* 2004). Results highlighted other co-variations between *Lage* and
371 *Vcmax* ($r=-0.59$ overall PFTs), *gslope* and *Lage* ($r=-0.7$ for broadleaves), *LAI*_{max} and *SLA*
372 ($r=0.6$ for needleleaves), and between *SLA* and *Vcmax* ($r=-0.55$ for evergreens). Here again,
373 the slope between *Lage* and *Vcmax* emerging for broadleaves PFTs (-1.69) was close to
374 observations (-1.13; Xu *et al.* 2017).

375 No relationships were reported between *gslope* and *Lage* or between *gslope* and *SLA*, but a
376 trade-off between the stomatal conductance (*gs*) and *Lage* was observed experimentally
377 (Reich *et al.*, 1992; Poorter & Bongers, 2006), as well as a positive correlation between *gs*
378 and *SLA* (Poorter & Bongers, 2006). The optimizations showed opposite relationships
379 between *gslope* and *SLA* depending on the PFT: a positive significant correlation was
380 obtained for deciduous PFTs and a negative significant correlation for evergreens and grasses
381 (Table 3).

382 The positive relationship between *SLA* and *LAI*_{max} emerging from optimized parameters for
383 coniferous PFTs was consistent with the positive correlation between *LAI* and *SLA* reported
384 by Pierce *et al.* (1994) for coniferous forests. Finally, a negative correlation between *SLA* and
385 *Vcmax* has been observed experimentally for two gymnosperms species (Niinemets *et al.*,
386 2007), confirming the negative relationships found in our study for needleleaves. Despite the

387 equifinality risk between *gslope* and the soil water stress *Wlim* in Figure 2, the positive
388 correlation observed for broadleaves ($r=0.7$) and evergreens ($r=0.52$) was comparable to
389 observations from independent data compiled by Lin *et al.* (2015).

390 Other significant correlations from the optimized parameters (Table S4.6, Figure S4.2;
391 Appendix S4) could not be verified against observations because of the correlation of errors
392 observed in Figure 2 or because of the scarcity of ecological data preventing us to conclude
393 about the true nature of those correlations, as for example between *gslope* and *Vcmax*.

394

395 *Variation of trait-related parameters with climate*

396 We analyzed correlations between parameters and climate variables (Table 4, Figure S5.4;
397 Appendix S5). As for co-variations between parameters, we only described here those
398 implying *SLA*, *Lage*, *Vcmax* and *gslope*. All relationships are listed in Table S5.7 and more
399 detailed analysis are available in Appendix S5.

400 We found a strong negative correlation between leaf lifespan (*Lage*) and temperatures (*MAT*,
401 *TMIN*; $r=-0.78/-0.65$; Figure 3a) for evergreen PFTs. This correlation was independently
402 reported at global scale (Wright *et al.*, 2005; van Ommen Kloeke *et al.*, 2012) and confirmed
403 by Reich *et al.* (2014) who showed higher needle longevity with cold temperatures for boreal
404 species. However, the observed positive correlation between *Lage* and *MAT* at the global
405 scale for deciduous PFTs (Wright *et al.*, 2005; van Ommen Kloeke *et al.*, 2012) was not
406 found specifically for deciduous systems in our study. Nevertheless, a positive correlation was
407 observed for C₃ grasses and broadleaves (including deciduous). We also found a strong
408 negative correlation between *Lage* and the mean annual precipitations (*MAP*) for evergreens
409 PFTs ($r = -0.65$), consistent with field data (van Ommen Kloeke *et al.*, 2012). In addition, a

410 negative correlation between *Lage* and incident shortwave radiation (*SW*) for evergreens was
411 obtained, consistent with field observations (Poorter & Bongers, 2006).

412

413 Regarding *SLA*, we found opposite sensitivities to *MAT* for evergreen ($r=0.65$) and deciduous
414 forests ($r=-0.55$). This result is consistent with independent leaf-scale data showing a positive
415 correlation between *SLA* and *MAT* for evergreen species (Figure 3b) and a negative
416 correlation for deciduous ones (Wright *et al.* 2005). The model calibration also resulted in a
417 positive correlation between the relative precipitation (*RELP*; Table 2) and *SLA* for deciduous
418 trees ($r = 0.60$; Figure 3c). Regarding the positive correlations obtained between *SLA* with
419 *Kroot* or *gslope* (Table 3), it suggests that *SLA* is highly sensitive to water stress for deciduous
420 trees. For evergreens, positive correlation between *SLA* and precipitation also emerges when
421 considering the length of the growing season (*MAPgs*, $r = 0.57$; Table 4); which is consistent
422 with trait data (Wright *et al.*, 2005). For evergreens, *SLA* was positively correlated to *SW*
423 ($r=0.53$), a relationship observed by Givnish *et al.* (2004) and Poorter & Bongers (2006).

424

425 In their meta-analysis of stomatal conductance parameters from observations of several PFTs,
426 Lin *et al.* (2015) showed that the slope of the stomatal conductance is positively correlated to
427 the mean air temperature over the growing period and to soil moisture stress. Here, our results
428 show the same correlation between *gslope* and soil moisture during the growing season
429 ($r=0.71$; Figure 3d) and relative precipitation ($r=0.66$) for deciduous or broadleaved PFTs. On
430 the contrary, we find that *gslope* is negatively correlated with mean annual precipitation for
431 C_3 grasses ($r=-0.59$), and with shortwave radiation for broadleaved PFTs ($r=-0.63$). Medlyn *et*
432 *al.* (2011) suggested that *gslope* is proportional to the photosynthesis compensation point for
433 CO_2 , and consequently to growth temperatures of the plant (Bernacchi *et al.*, 2001). This

434 assumption is supported by the data from Lin *et al.* (2015). In our study, the relationship
435 between *gslope* and temperature was not supported.

436

437 Finally, *Vcmax* is mostly sensitive to temperature and light for broadleaved PFTs, with a
438 negative correlation observed with *MAT* ($r=-0.52$) and *SW* ($r=-0.54$). This result contradicts
439 previous observations by Ali *et al.* (2015), who suggested a positive correlation between
440 *Vcmax* and seasonal temperature and light variations.

441

442 **Discussion**

443 *Uncertainties and shortcomings of the approach*

444 This section provides an overview of possible shortcomings of our approach that may explain
445 some residual mismatch between model and observations. Several factors can impact the
446 optimized value of the parameters, potentially aliasing the observed relationships: 1) flux
447 measurements errors and errors in ecosystem respiration estimates used to derive gap-filled
448 GPP; 2) optimization protocol/setup errors; and 3) model systematic errors deriving from
449 absent or poorly represented processes in the model.

450 First, we restricted our analysis to GPP. This flux is not directly measured but estimated from
451 NEE measured using the eddy-covariance method with an estimate of ecosystem respiration
452 determined using empirical models (Reichstein *et al.*, 2005), and thus can be biased by
453 several factors (see Appendix S3 for a list of these factors). We chose GPP over a
454 combination of NEE and latent heat or evapotranspiration fluxes, which has often been used
455 to optimize ORCHIDEE (Kuppel *et al.*, 2012; Bacour *et al.*, 2015; Peylin *et al.*, 2016),
456 because it implies the optimization of more parameters related to soil, respiration and energy
457 budget, and therefore increases the risk of equifinality. To reduce the uncertainties, it is

458 necessary to lower the correlation of errors between parameters by assimilating
459 complementary biophysical variables. For example, assimilating both GPP and LAI estimates
460 at the site level could improve the evaluation of parameters such as *SLA* or *Lage*, and
461 consequently improve the estimation of photosynthesis parameters.

462 Second, the Bayesian framework is based on the assumption that the model/observation errors
463 are random and that the model structure is “true”. Any bias of model structure is expected to
464 be aliased onto the estimated parameters (MacBean *et al.*, 2016) and might therefore impact
465 the retrieved correlations. For instance, missing processes would be compensated during the
466 optimization by adjusting parameters (e.g. light attenuation, vertical distribution of LAI,
467 diffuse light, horizontal light distribution in the stand) to non optimal values. Also, while
468 traits are usually measured at the leaf level, our approach rather focuses on traits at the canopy
469 level (given the structure of ORCHIDEE and the assumed exponential attenuation of light and
470 LAI from top to bottom of canopy (Krinner *et al.* 2005; Table S1.2), and the assimilation of
471 GPP data). As an additional test, we conducted the above analyses using multi-year instead of
472 single-year observations in order to add more constraints on parameters (see Figure S4.3 &
473 S5.5). The same relationships were found as with single-year observations, thus strengthening
474 our conclusions, showing that spatial correlations are observed even when taking into account
475 a possible temporal variability of traits.

476 Finally, a wrong representation of species and the lack of representation of representation of
477 traits variability within a community in ORCHIDEE can affect simulated processes, which
478 will ultimately impact the estimated parameter values (see Appendix S3 for a discussion on
479 initial site conditions). Especially, the C₃ grass PFT represents diverse grasslands, with
480 different species, ecophysiology (Adams *et al.*, 2016) and management practices (Merbold *et*
481 *al.*, 2014). This results in an increased variability and a high range of estimated plant
482 functional traits (Figure S3.1). A refinement of the PFT definition may improve the

483 robustness of optimizations (for instance by separating natural or semi-managed biomes), or
484 by distinguishing genera or major species (Peaucelle *et al.*, 2016).

485 In order to decrease the impact of uncertainty in PFT composition and reduce the correlation
486 errors between parameters, the use of concomitant observations of traits and carbon fluxes at
487 the FLUXNET sites would enable a) to constrain known parameters and b) to validate
488 optimized traits. However, functional trait observations at FLUXNET sites as well as a
489 precise description of species composition are not yet systematic (Musavi *et al.*, 2015, 2016).

490

491 *Ecological consistency of trait relationships*

492 The optimization of model parameters managed to reproduce many known ecological
493 properties. The optimized parameters consistently matched the well-known relationships
494 resulting from the leaf economic spectrum theory (LES, Reich *et al.*, 1999; Wright *et al.*,
495 2004). Particularly our results align with the trait theory that long lived canopies are
496 metabolically less active and are consistent with the LES empirical evidence that plants invest
497 either in structure or photosynthesis (Liu *et al.*, 2010; Reich, 2014).

498 Our results also reproduced several observed trait-climate relationships at the PFT level.
499 Globally, evergreen PFT parameters showed a strong dependency on mean annual
500 temperature and radiation, while parameters for deciduous PFTs exhibited a strong sensitivity
501 to precipitation and soil moisture over the growing season (Figure S5.4). As postulated by
502 Reich (2014), climate exerts a control on the average leaf characteristics at the community
503 level. The observed relationships obtained at the PFT level might reflect, not only differences
504 in plant response to climate, but also differences in plant community composition (Shi *et al.*,
505 2015). These results suggest that both the development of acclimation processes and trait-

506 based approaches are needed in TBMs if we seek to capture the effect of biogeography on
507 ecosystem characteristics (Lu *et al.*, 2017; Fisher *et al.*, 2018).

508

509 Finally, while the results clearly highlight that photosynthesis and phenological mechanisms
510 implemented in ORCHIDEE are robust enough to reproduce known behaviors of several
511 vegetation species, belowground processes still appear poorly represented, which resulted in
512 weakly constrained parameters and trait co-variations inconsistent with literature. These
513 discrepancies are primarily due to a lack in eco-physiological knowledge reflecting the actual
514 difficulty to study belowground ecological processes. The rooting system uses model-specific
515 parameters (*Kroot*) that are hardly comparable to measured functional traits.

516

517 **Concluding remarks and recommendations**

518 The approach presented in this study is a new and effective way to validate the processes
519 implemented in TBMs, to better define vegetation response to climate (Liang *et al.*, others,
520 2018), and could help improving existing data assimilation frameworks (Kaminski *et al.*,
521 2013; LeBauer *et al.*, 2013; Arsenault *et al.*, 2018) by bringing ecological constraints. The
522 availability of continuous observations from eddy-covariance flux measurements gives a
523 unique opportunity to resolve the different components of the short and long-term variability
524 of traits through this approach.

525 Our results show that optimized leaf-related parameters align with plant trait theory, and
526 highlight the need to implement acclimation processes and trait-based approaches in models
527 instead of using constant parameters to reduce uncertainties in spatio-temporal patterns of the
528 modeled carbon fluxes. A first step would be to assess the behavior of the model at the global
529 scale when trait-climate relationships characterized in this study are explicitly implemented.

530 In parallel, relationships highlighted in this study may help to develop or validate new
531 methods to simulate plant acclimation. Used in a prognostic way, this approach could enable
532 to study correlations at the canopy scale and to assess the behavior of trait-related parameters
533 that are difficult to observe experimentally.

534 Several known ecological properties, observed at the site/leaf scale, emerged from model-data
535 assimilation. However, quantitative comparisons with observations were possible only for two
536 of them, *SLA* and *Lage*, which are also the two most studied traits. This is mainly because
537 TBMs use model-specific parameters that cannot be directly compared to standard trait
538 observations, but also because concomitant observations of functional traits, both in space and
539 time, are scarce in the literature. A recommendation to the TBM community would be to
540 make use of parameters (and processes) that can be related directly to observations in order to
541 unit vegetation model and functional traits (for instance the use of the Specific Root Length
542 for belowground processes).

543 We argue that co-located systematic and standardized trait observations (starting with key
544 traits related to phenology -*SLA*, *LAI*-, photosynthesis -*Vcmax*, *Jmax*, *Topt*-, water transport -
545 *gs*- and allocation -*Carbon:Nitrogen ratio*, *shoot/root*-; (Law *et al.*, 2008) along with
546 biometric data are needed at the FLUXNET sites or within other environmental observation
547 networks such as ICOS (Integrated Carbon Observation System) or NEON (National
548 Ecological Observatory Network) if we seek to distinguish temporal and spatial components
549 of trait variability across biomes and climates. The creation of a FLUXNET trait database
550 could improve our comprehension of trait acclimation and help us to disentangle the
551 differences observed at regional and local scales, to improve the up-scaling of processes from
552 the leaf to the canopy/ecosystem level and to properly calibrate/validate ecosystem models.

553 **Supporting information**

554 **Appendix S1:** Description of PFTs, model parameters and equations

555 Table S1.1: List of plant functional types.

556 Table S1.2: List of main equations involving optimized parameters.

557 Table S1.3: Default parameter value and range allowed by the optimization algorithm.

558 **Appendix S2:** List of FLUXNET sites used for the analyses (xlsx file).

559 **Appendix S3:** Optimization performances

560 Figure S3.1: Distribution of optimized parameter values.

561 Table S3.4: Mean *a priori* and *a posteriori* RMSE between observations and simulations.

562 Table S3.5: Mean parameter uncertainty reduction between *prior* and *posterior* simulations.

563 **Appendix S4:** Relationships between traits

564 Figure S4.2: Correlation matrices between traits optimized against site-year GPP.

565 Figure S4.3: Correlation matrices between traits optimized against site GPP.

566 Table S4.6: Extended Table 3 with all relationships

567 **Appendix S5:** Relationships between traits and climate

568 Figure S5.4: Correlation matrices between traits and environmental variables optimized
569 against site-year GPP

570 Figure S5.5: Correlation matrices between traits and environmental variables optimized
571 against site GPP

572 Table S5.7: Extended Table 4 with all relationships

573

574 **Data accessibility**

575 All FluxNet data can be downloaded at: <https://fluxnet.fluxdata.org>

576 Information about the ORCHIDEE model, source code and contact: <http://orchidee.ipsl.fr/>

577 Information about the data assimilation system ORCHIDAS: <https://orchidas.lsce.ipsl.fr/>

578

579

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Table 1: Description of the 14 optimized parameters and associated processes. All the parameters are common to each PFT. Kbm and bdate are scaling factor added in the model to improve the optimization of the seasonal cycle of the GPP but are not analyzed in the study. (See Table S1.2; Appendix 1 for the detailed equations involving each parameter).

Parameter	Description	Processes involved
SLA	Specific leaf area ($\text{m}^2 \text{gC}^{-1}$)	Photosynthesis, Phenology, Allocation
Lage	Leaf lifespan (days)	Photosynthesis, Phenology
Vcmax	Maximal carboxylation rate limited by CO_2 ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Photosynthesis
Vj/Vc	Ratio between the maximal carboxylation rate limited by light and Vcmax	Photosynthesis
Topt	Optimal temperature of the photosynthesis ($^{\circ}\text{C}$)	Photosynthesis
gslope	Slope of the Ball-Berry relationship for the stomatal conductance	Photosynthesis, energy budget
LAImax	Maximal leaf area index	Photosynthesis, Phenology, Allocation
Klai	Minimal fraction of LAI _{max} for the use of carbohydrate reserves	Allocation
bdate	Budburst date (day of the year)	Phenology
tauleaf	Period after budburst during which the use of carbohydrates is allowed	Allocation
Csenes	Temperature for leaf senescence (used only for deciduous)	Phenology
Kbm	Multiplicative factor for the initial leaf biomass (used only for evergreens)	Phenology, Allocation
Kroot	Exponential factor describing the root profile and depth	Water budget, Photosynthesis
Wlim	Minimal threshold at which the photosynthesis becomes limited by water availability	Photosynthesis

Table 2: Description of bio-climatic variables calculated at each site and for each year.

Variable	Description	Units
LAT	Latitude	°N
MAT	Mean annual temperature	Celsius
TMAX	Mean temperature of the warmest month of the year	Celsius
TMIN	Mean temperature of the coldest month of the year	Celsius
TVAR	Temperature difference between TMAX and TMIN	Celsius
DTR	Yearly average of diurnal temperature range	Celsius
MAP	Mean annual precipitation	mm y ⁻¹
REH	Mean annual relative humidity	%
SW	Mean annual downward shortwaves radiation (visible and near IR)	W m ⁻²
PDRY	The driest quarter of the year is determined (to the nearest week), and the total precipitation over this period is calculated.	mm y ⁻¹
RELP	PDRY divided by MAP	fraction
SHUM	Yearly averaged soil humidity	fraction
GSL	MAT _{gs} , DTR _{gs} , SW _{gs} , MAP _{gs} , REH _{gs} and SHUM _{gs} are the same variables averaged during the growing season of the plant	-

Table 3 : Relationships between trait-related parameters. For some relationships, values are log-transformed (x). For each relationship is the number of sites, as well as the correlation coefficient (r, blue when negative; red when positive). Only relationships with an absolute and significant (p-value<0.05) correlation coefficient higher than 0.5 are listed for the different groups of PFT : all, broadleaves (bro ; TroEB, TemEB, TDB, BDB), needleleaves (need ; TEN, BEN), evergreens (ever ; TroEB, TemEB, TEN, BEN), deciduous (dec ; TDB, BDB) and C3 grasses (gra). Note that evergreens include needleleaves and that broadleaves include deciduous. The type of relationship is given for each trait: 0= verified with ecological observations; 1=partially verified on similar data or 3= different from observations. When available, the reference for verification is given. Well constrained parameters are in bold, parameters with a risk of equifinality are normal, poorly constrained parameters are in italics. Refer to Table 1 for the description of each parameter.

Parameters		r	PFT	log	SMA slope	n sites	references	Type
Lage	SLA	-0.67	ever	x	-1.39	49		0
		-0.53	bro	x	-3.47	37	(Reich <i>et al.</i> , 1999); (Wright <i>et al.</i> , 2004)	0
		-0.63	All	x	-1.92	98		0
Lage	Vcmax	-0.90	Bro	x	-1.69	37		0
		-0.65	Dec		-2.15	23	(Xu <i>et al.</i> , 2017)	0
		-0.59	All	x	-3.13	98		0
gslope	Lage	-0.70	Bro	x	-0.74	37	(Reich <i>et al.</i> , 1992)	1
		-0.57	Grass		0.00	26	(Poorter & Bongers, 2006)	1
gslope	SLA	-0.62	Ever		-534.01	49		3
		0.52	Dec		418.99	23	(Poorter & Bongers, 2006)	1
		-0.51	Grass		-235.65	26		3
LAlmax	SLA	0.60	Need		422.11	35	(Pierce <i>et al.</i> , 1994)	1
SLA	Vcmax	-0.55	Ever	x	-1.28	49		1
		-0.53	Need	x	-0.75	35	(Niinemets <i>et al.</i> , 2007)	1
gslope	<i>Wlim</i>	0.70	Bro	x	1.61	37		3
		0.52	Ever	x	1.47	49	(Lin <i>et al.</i> , 2015)	3

Table 4: Relationships between trait-related parameters and climate variables. For some relationships, traits values are log-transformed (x). For each relationship is given the correlation coefficient (r). Only relationships with an absolute (and significant p-value<0.05) correlation coefficient higher than 0.5 are listed for the different groups of PFT : all, broadleaves (bro ; TroEB, TemEB, TDB, BDB), needleleaves (need ; TEN, BEN), evergreens (ever ; TroEB, TemEB, TEN, BEN), deciduous (dec ; TDB, BDB) and C3 grasses (gra). The type of relationship is given for each trait: 0= verified with ecological observations; 1=partially verified on similar data; 2= not verified or, 3=different from observations. When available, the reference for verification is given. Well constrained parameters are in bold, parameters with a risk of equifinality are normal. Refers to Table 1 and 2 for the description of each parameter and climate variables respectively.

Trait	Climat	r	PFT	log	SMA slope	Référence	Type
Lage	LAT	0.59	ever		24.90	(Reich <i>et al.</i> , 2014)	0
		-0.56	bro		-13.44	-	2
	MAP	0.66	grass		1.14	-	2
		-0.65	need	x	-0.66	(van Ommen Kloeke <i>et al.</i> , 2012)	0
	MAT	-0.78	ever	x	-16.95	(Wright <i>et al.</i> , 2005; van Ommen Kloeke <i>et al.</i> , 2012; Reich <i>et al.</i> , 2014)	0
		-0.62	need	x	-17.93		0
		0.54	grass	x	107.81	-	2
		0.53	bro	x	30.14	-	2
	SW	-0.53	ever	x	-1.84	(Poorter & Bongers, 2006)	1
		0.52	bro	x	3.85	-	2
TMIN	-0.65	ever	x	-30.99	(Wright <i>et al.</i> , 2005; van Ommen Kloeke <i>et al.</i> , 2012; Reich <i>et al.</i> , 2014)	1	
SLA	MAP	0.54	need	x	0.37	(Wright <i>et al.</i> , 2005)	0
	MAP _{gs}	0.57	ever	x	0.47		0
	MAT	0.65	ever	x	12.16		0
	MAT _{gs}	-0.63	bro	x	-0.86	(Wright <i>et al.</i> , 2005)	0
		-0.55	dec	x	-0.96		0
	RELP	0.60	dec	x	0.25	-	2
		0.59	bro		0.08	-	2
SW	0.53	ever		0.00	(Givnish <i>et al.</i> , 2004; Poorter & Bongers, 2006; Reich <i>et al.</i> , 2014)	1	
gslope	MAP	-0.59	grass	x	-1.12	-	2
	PDRY	0.58	dec		0.02		1
	REH	0.64	dec		19.24		1
	RELP	0.66	bro		42.67	(Lin <i>et al.</i> , 2015)	1
		0.58	dec		29.05		1
	SHUM _{gs}	0.71	dec		20.53		1
	SW	-0.63	bro		-0.10	-	2
SW _{gs}	-0.55	dec		-0.08	-	2	
Vcmax	MAT	-0.52	bro		-4.77	(Ali <i>et al.</i> , 2015)	3
	RELP	0.60	bro		511.72	-	2
	SW	-0.54	bro		-1.15	(Ali <i>et al.</i> , 2015)	3

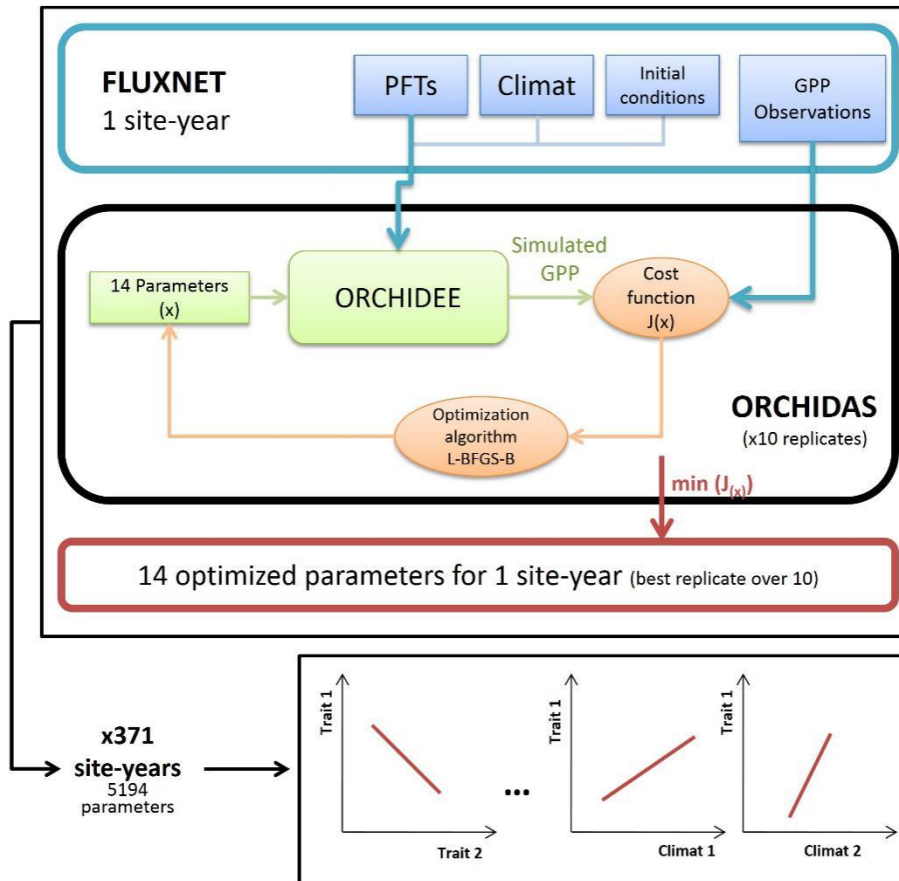


Figure 1: Schematic representation of the modeling protocol followed in this study. For each FLUXNET site-year (blue), the model ORCHIDEE (green) was calibrated with the data assimilation system ORCHIDAS (red) in order to reproduce GPP observations. The ORCHIDAS system uses a gradient-based approach (L-BFGS-B) to reduce the cost function $J(x)$. For each site-year, 14 parameters (listed in Table 1) were optimized 10 times with different initial values. The best calibration, i.e. leading to the minimum value of $J(x)$, was retained. This procedure was repeated for each site-year, resulting in 371 sets of 14 independently optimized parameters. Finally, correlations between optimized parameters and climate were explored using standardized major axis regressions.

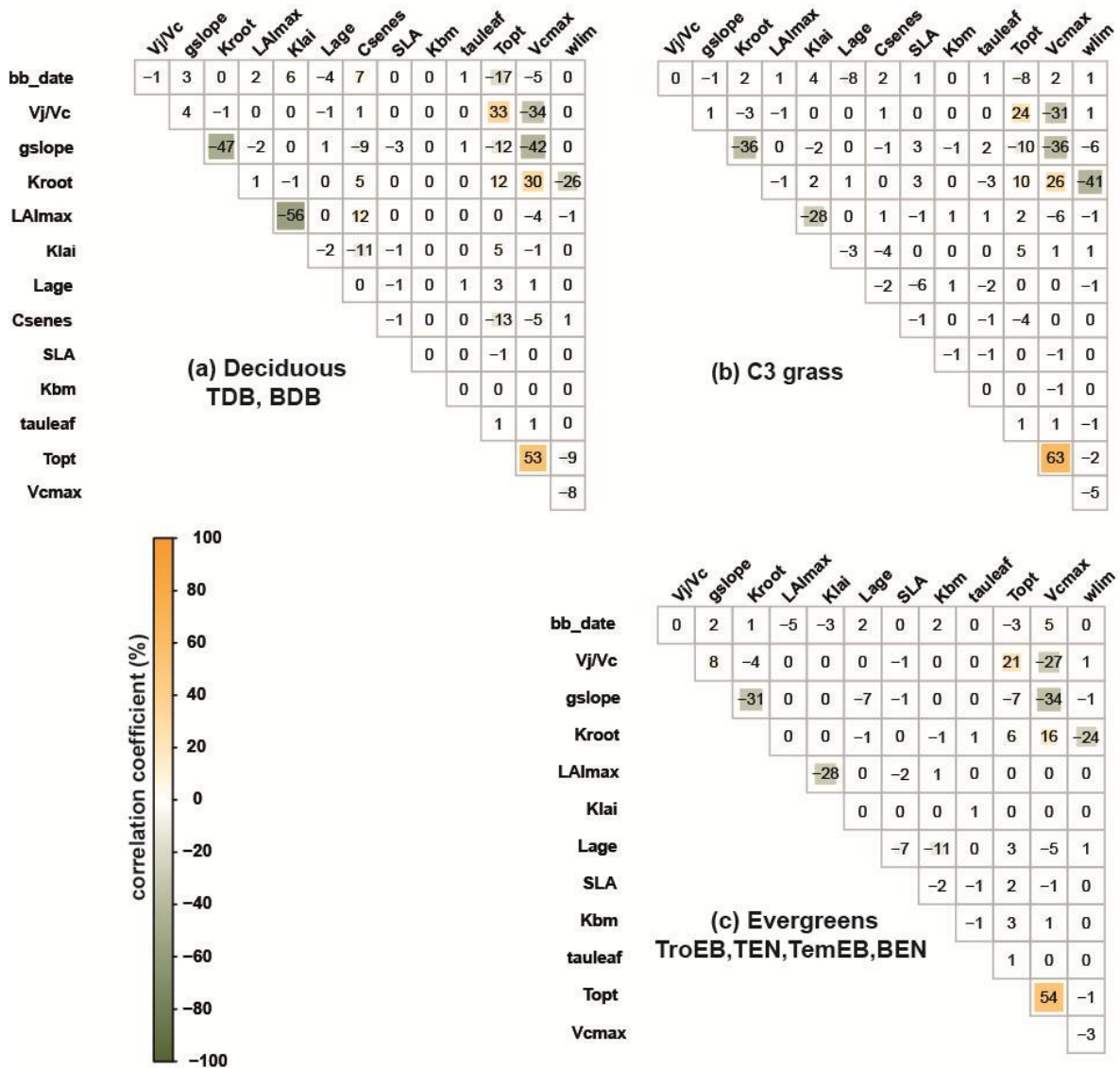


Figure 2: Error correlation between optimized parameters (derived from the A matrix) averaged over deciduous trees, evergreen trees, and C3 grass. The color scale gives the error correlation coefficient. For more clarity, the coefficient is indicated in % in each matrix cell. The description of each parameter is listed in Table 1.

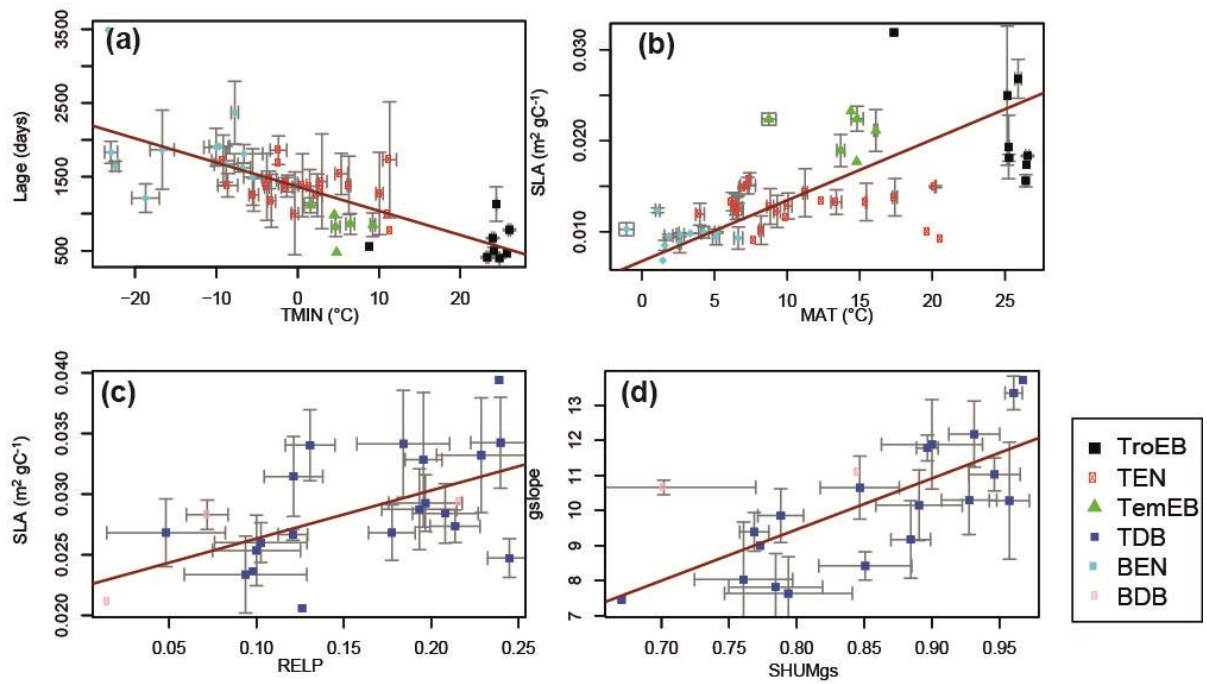


Figure 3: Four examples of co-variations obtained between optimized parameters (Table 1) and environmental conditions (Table 2) of the sites for PFTs TroEB (black square), TEN (red square), TemEB (green triangle), TDB (blue square), BEN (cyan dots) and BDB (pink dots). Each point represents the mean optimized parameter (environmental variable) value for one site while the error bars represent the inter-annual variability (no bars means only one year of measurement). The red line represents the slope of the standardized major axis regression.