Response to reviewer comments for
"Leveraging leaf-level optimality processes with explicit acclimation improves global GPP representation in an individual-based DGVM (LPJ-GUESS v4.1.1)"
M. Forrest et al., egusphere-2026-3273 (under review for GMD)

We thank both the reviewer for taking the time to review our manuscript. The comments are copied verbatim below, our responses are in blue, suggested revision to the text are in green. Line numbers refer to the initial version of the manuscript.

Reviewer 1

General comment

The authors implemented eco-evolutionary optimality principles into the LPJ-GUESS vegetation model, by merging the model with an adapted version of the P-model for photosynthesis. They then evaluated the performance of the model against in-situ eddy covariance fluxtower measurements and global data products of GPP, as well as existing global biome distribution maps. While the metrics show only a small (but significant) improvement compared to the standard version of LPJ-GUESS, these new simulations are based on highly reasonable optimality constraints, which allow the model to use less (often poorly constrained) parameters and assumptions. I think this is a very interesting approach and a very useful and meaningful contribution to the development of LPJ-GUESS and dynamic vegetation models in general. I do have a few (minor) questions and concerns, especially regarding the different values for leaf-to-canopy scaling factor and comparison with a nitrogen-limited version of standard LPJ-GUESS. However, I could see the article being published close to its current form.

We are glad the reviewer sees merit in the approach and the study.

Specific comments

- L194-216: These lines are sligthly confusing at first read, because it seems Eqs. (3) and (4) should be connected like Eqs. (1) and (2) are. However, when puzzling everything together further in the section it becomes clear that the relationship between GPP_{indiv} and $I_{abs,indiv}$ is more complex in LPJ-GUESS. Maybe consider rephrasing a bit to make this clear earlier on? Maybe starting from Eq. (4) could help, and then introduce Eq. (3) only later when it's needed. And maybe don't mention Eqs (1) and (2) at all, because they are not really used? Just a suggestion.

Yes, we see your point. We propose to swap equations (3) and (4), which will give better consistency with equations (1) and (2), and starts the description in earnest from equation (4) (now equation 3) as you suggested. However, we do want to keep equations (1) and (2) as they give important background of how GPP is calculated via light use efficiency and are also important for our later discussion of the effect fAPAR and its error on GPP. And we feel

it makes sense keep equation (3) towards the beginning as I_{abs} is a fundamental driver. The opening of the section will then read:
"Conceptually, GPP is calculated as the product of light use efficiency and absorbed photosynthetically active radiation (I_{abs}):

$$GPP = I_{abs} \cdot LUE \quad (1)$$

where I_{abs} is in turn calculated the product of incoming solar radiation (PAR, mol s^{-1} m^{-2}), the fraction absorbed of PAR absorbed by a vegetation (fAPAR, dimensionless) and the canopy-to-leaf scaling parameter, α_a (dimensionless), which accounts for inefficiencies in the canopy absorption of PAR (i.e. losses due to absorption by woody tissues and gap in the canopy), i.e.

$$I_{abs} = PAR \cdot fAPAR \cdot \alpha_a \quad (2)$$

However, in practical terms, LPJ-GUESS photosynthesis is calculated per individual and in terms of A_{indiv} (mol s^{-1} m^{-2}), the assimilation rate of a vegetation individual. Accordingly, the daily GPP of one individual (gC m^{-2} day^{-1}) for one day is defined as

$$GPP_{indiv} = A_{indiv} \cdot C_{mass} \cdot daylength \quad (3)$$

where C_{mass} is the molar mass of carbon and daylength is the number of seconds in day. Grid cell total GPP is then the sum of all GPP_{indiv}.

In LPJ-GUESS, each individual intercepts its own share the incoming solar radiation depending on its position in the canopy, thus giving rise to its own I_{abs}, i.e.

$$I_{abs,indiv} = PAR \cdot fAPAR_{indiv} \cdot \alpha_a \quad (4)$$

where $fAPAR_{indiv}$ is calculated following LPJ-GUESS's standard light interception scheme (Smith et al., 2001)."

- L342: Why is this extremely rare? Aren't such drought conditions rather common, especially when you do global simulations? Is this also extremely rare in Standard LPJ-GUESS? To which degree does the P-model capture the diversity in stomatal regulation (e.g. isohydry)?

  Yes, drought conditions are common, but we realise now that text was unclear. Full drought conditions, i.e. the situation where there is precisely zero soil water available, are common, but in this case the model logic is clear and unequivocable – there should be zero photosynthesis. However, the text is discussing the timestep of the *onset* of full drought, i.e. the point where available soil moisture goes from "just a bit left" to "absolutely zero" due to photosynthesis/transpiration. The frequency of this is much less, partly because it will typically only happen once per dry season, partly because the low soil moisture and VPD progressively reduce transpiration, and partly because LPJ-GUESS's phenology scheme sets the grass and raingreen PFTs (that

tend to dominate in seasonally dry areas) to a phenologically dormant state (with zero photosynthesis) as the soil dries but *before* it dries out completely.

We propose to simply modify the text at line 342 to read:

"In the rare case that available soil water was above zero but insufficient to satisfy the P-model demand at a given time step, photosynthesis is scaled down proportionally to the fraction of the demand satisfied by the available water"

We did output the amount of "transpiration deficit" i.e. the amount by which demand exceed supply at the timestep where the available soil moisture is reduced to zero, see Figure R1 below, and never greater than 1 mm/y.

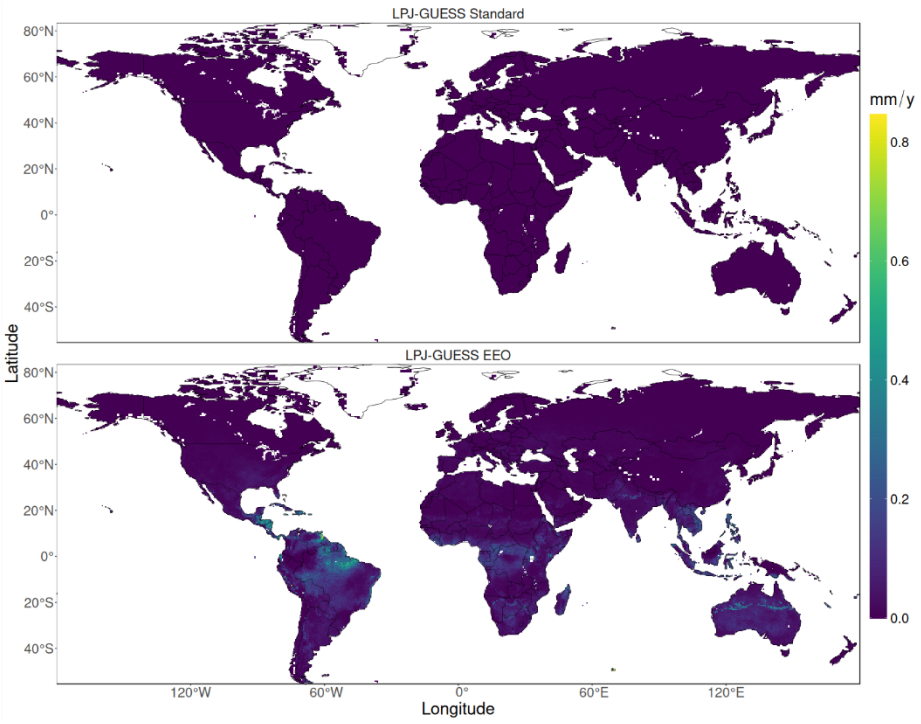


Fig. R1: Annual soil moisture deficit (transpirational demand – available soil water) on model timesteps at which soil moisture is depleted (average 1990-2010).

Note that the model still conserves water, and no photosynthesis happens without associated transpiration. The key point is that in this rare circumstance, photosynthesis and transpiration are linearly scaled by the fraction of the demand available (which is model implementation choice, not a feature of the P-model).

Concerning standard LPJ-GUESS, the construction of its water demand function doesn't produce this scenario at all (confirmed in the Figure R1).

- L349-350: Regarding the SMART scheme producing somewhat better results, is this in general, or in your simulations? What do you have to back up this statement? E.g. if in general, do you have a reference for this?

  In our simulations it improved spatial GPP NME by 0.01 compared to the standard ROOTDIST. The Lapides et al. (2024) reference shows more concrete improvements in late summer ET at their study site. We propose to modify the "somewhat" to "slightly" and reference the text as follows:

  "The SMART scheme also produces slightly better results than other water uptake schemes in LPJ-GUESS with the P-model enabled (data not shown) and improved the representation of late summer ET in Lapides et al. (2024)."

- L359: Correct me if I'm wrong, but as far as I know the leaf-to-canopy scaling factor (α_a) can have quite a large impact on the simulated GPP and carbon stocks in LPJ-GUESS. I understand that you set this parameter a-priori (ie. you did not tune it afterward to get a good result) even though the new value is still "an initial guess that appears more plausible" (L668-669). Still, is it fair to compare two versions of LPJ-GUESS that have a different value for this? How much of the model difference is due to this parameter, compared to the difference introduced by the EEO approach alone? See also my next comment for a similar concern.

  You are not wrong; this parameter has a very large effect and has historically been used as something of a tuning parameter. Alternatively, it can be understood as a place to absorb missing limitation processes. For example, with the introduction of N limitation, α_a was increased from 0.5 to its current value of 0.6. Yes, it is not ideal to compare model versions with different values of α_a but, given its role as a tuning parameter and its high associated uncertainty, it is in sense the only fair thing to do. Testing either configuration with the value from the other would be unfair. And we feel this is sufficient for the study here, particularly as the selected value works well and is plausible.

  We did test the standard photosynthesis model with a lower value of α_a to bring global GPP down the ballpark of the GOSIF global total. For this, we needed to bring of α_a down to 0.45 and then NPP collapsed to 50 PgC/year, a value we considered to be unfeasibly low.

- L371-373: The standard simulations have N limitation activated, but your EEO-model does not. Similarly to the previous comment, I wonder how this affects the model comparison, e.g. how much of the difference in model output can be explained by this? Doesn't this difference obscure the effect of the EEO approach on its own? I understand that you want to compare the "default versions" of both models (ie. the standard model has N-limitation by default, and your model does not) and that is

totally valid (same for alpha_a). However, it also seems a bit "unfair" to compare a model with N-limitation to a model without it? See also next comment. I also see you discuss this in Sect 4.5 where you give good reasons to doubt the causal relationship between soil N and V_{cmax}, and you provide future pragmatic approach to include N limitation. But this also makes me wonder whether it would make sense to (also) compare your model against a version of LPJ-GUESS where N-limitation on $V_{c,max}$ is turned off?

Yes, the lack of any form of N limitation is a gap in the current EEO configuration. And, yes, it may be that this lack of N limitation is obscuring the effect of EEO approach. However, despite this, the model results are still improved over the standard version. Introducing N limitation along the lines we suggested in the text may well improve the model by further reducing the positive bias in the much of the temperature and boreal zones. However, this is just speculation at this stage and there are also many other relevant factors (see the answers to the next point below). And so, for the purposes of this publication, we feel it is sufficient to show that even without N limitation, the results are still an improvement on the standard version.

Just for interest, we did follow your suggestion and tested the old photosynthesis scheme without N limitation (using the corresponding value of $\alpha_a = 0.5$). This produced worse results than the standard model with N limitation. GPP came in higher at 179.9 PgC $year^{-1}$, and spatial NME was much worse at 0.59. So, we can conclude that the N limitation does improve the standard Haxeltine and Prentice (1996) photosynthesis scheme (although we would not necessarily say for the right reason). However, as this configuration is now rarely used, and has not been developed or evaluated for several years, it is more of a legacy version and doesn't really form a fair comparison. We feel its inclusion would muddy the narrative and lengthen the paper to little practical gain, so we prefer not to mention it in the manuscript.

- L444: Similar to the previous comment, the standard model version produces a higher annual total, even though it is N limited. I wonder what N limitatation would have on the P-model? Maybe it will underestimate GPP? See also Table 2 (and text from L534) which shows that C stocks, leaf area and NPP were overall a bit lower in EEO version, despite not having N limitation.

  Yes, it will be very interesting to include N limitation in the EEO configuration. However, we don't want to speculate on its effect on global GPP totals or derived variables because there are a lot of moving pieces which should be nailed down first. On the theoretical side there has recently been a revised formulation of the quantum yield of photosynthesis which significantly raises P-model GPP (Sandoval et al., 2026). There is also the role of phenology and fAPAR, a quantity which LPJ-GUESS over-estimates but for which there is now well-performing EEO theory (Zhou et al., 2025).

And then there is the role of α_a and other parameters and processes which may require re-examination in tandem with further changes such the introduction of new N limitation scheme. Even on the data side there are quite a range on estimates (see summary in Sandoval et al., 2026). In short, there is a lot to do to improve the robustness of DGVM calculations of GPP and other quantities!

L690: Is this really a fundamental part of the P-model on its own?

True, it is a not really a part of the P-model *per se*, but rather a consequence of our implementation. We propose to rephrase the text at line 690 to:

"One change introduced by our EEO implementation is that photosynthetic rates are no longer directly affected by nutrient availability as they are in standard LPJ-GUESS,…"

Technical corrections

- L124-125: Maybe rephrase? A bit hard to read in one breath

  Yes, indeed, and it could also link better with the previous sentence. We will rephrase to:

  "These replicate patches differ due to the stochastic processes of establishment, mortality and disturbance, and so represent landscape heterogeneity driven by succession dynamics."

- L37,L135: The term "mitochondrial respiration" is only used twice in this paper, while it's called dark respiration otherwise. Consider harmonising this terminology throughout the paper.

  Yes, done.

- L145: Typo in "LPJ-GUES"

  Thanks, corrected.

- L165: It could be nice to refer to the three EEO hypotheses in the later part of this section, so we know which part of the theory (which formula) corresponds to which hypothesis, ie. from line 196

  Yes, this would be nice, but it is a bit tricky because hypotheses are used together to derive the specific equations of the P-model, so there is not always a good correspondence between hypotheses and equations in the paper. However, equations (5) and (6) are directly derived from the Least Cost Hypothesis so we now mention this (see text in answer to point below). The other equations cannot be

cleaning attributed because their derivation uses the Coordination Hypothesis, the Optimal J_{max} Hypothesis, and equations from the FvCB standard model of photosynthesis together with a good chunk of algebra.

- L218: What is ξ? It has not been defined before. I do see that you define ξopt in eq. (6) however. Or did you maybe mean the ratio χ on this line, as in L174-175?

  Yes, apologies, this wasn't clear. ξ is the sensitivity parameter in the P-model's optimal stomatal relationship, setting how strongly a plant's stomatal behaviour responds to VPD as the air dries. It is optimised, and that in turn gives the optimal χ at a given VPD. And whilst we did originally mean ξ and not χ at line 218, it actually makes sense to introduce optimal χ first (since that is what is needed in the FvCB equations) and then introduce ξ as the means of obtaining this χ. So, to clarify all this, we propose to modify the text starting at line 218 as follows:

"To calculate A_{indiv} we require acclimated values for the photosynthetic capacities V_{cmax} and J_{max}, and for χ, the ratio of leaf-internal to ambient CO_2 concentration, also represented as $c_i{:}c_a$, where c_i is the leaf internal CO_2 partial pressure and c_a is the atmospheric CO_2 partial pressure (calculated as $c_a = [CO_2] \cdot p \cdot 10^{-6}$). Calculating these requires first calculating daily optimal values (which we denote $V_{cmax,opt}$, $J_{max,opt}$ and χ_{opt}) via the P-model based on the daily temperature (*T*), vapour pressure deficit (*D*), and atmospheric pressure (*p*). These optimal values are done separately for C_3 and C_4 photosynthesis but apply to all vegetation individuals of a given photosynthesis pathway as all individuals are assumed to experience the same daily *T*, *D* and *p*.

In the P-model, χ, is calculated via ξ, the parameter that controls how strongly stomatal behaviour responds to VPD. It is in fact ξ that is optimised, and following the Prentice et al. (2014) application of the Least Cost Hypothesis, optimal ξ and χ are given by

$$\chi_{opt} = \frac{\Gamma*}{c_a} + \left(1 - \frac{\Gamma*}{c_a}\right) \cdot \frac{\xi_{opt}}{\xi_{opt} + \sqrt{D}} \quad (5)$$

where

$$\xi_{opt} = \sqrt{\frac{\beta \cdot (K + \Gamma*)}{1.6 \cdot \eta*}} \quad (6)"$$

- L324: Word and maybe a comma missing?

  Yes, this formulation was clumsy, we suggest to change it to:

  "Program control was modified using a single switch which enables both the P-model photosynthesis and the EEO leaf dark respiration."

- L473-474: ...but for many of these biomes still better than the standard model, right? (from Table B2)

  Yes, you are right, we are underselling the new implementation here. So, we propose to change the text to:

  "Model performance was generally poorer in grassland, shrubland, and savanna biomes than in the seasonal forests, but the EEO configuration generally outperformed the standard model (Table B2, Fig. C1)."

- L476: The reference to Fig. 6 comes before the first reference to Fig. 5 as far as I can tell. Maybe reorder the figures?

  Yes, you are right. We will reorder the figures.

- L804: I guess the bold values in Table B2 mean the "better" value. Maybe add that to the caption.

  Yes indeed. We propose to add:
  "Bold text indicates better agreement."

- L551: "lower left and upper right quadrants"?

  Yes, that is nicer terminology, we have adjusted the text accordingly.

Reviewer 2

The authors applied an eco-evolutionary optimality (EEO) approach for calculation of assimilation rates in the LPJ-GUESS DGVM. Additionally, an acclimation process was implemented. This alternative approach has two major advantages: It saves computation time and gives better agreement between observed and modelled GPP. They used for LPJ-GUESS mode in individual mode and see an improvement in model performance and better agreement with observational data. In general, the paper is well written and structured and fits into the scop of the journal.

The model is run with modelling individual trees. it might be interesting to see the performance in run time and quality of the average individual model mode. This mode is significantly faster and is best suited for coupling to Earth system models. `The authors state, however, that acclimation must be calculated on an individual level. A short discussion how this approach can be applied to average individual models should be added.

Yes, we didn't consider the "population mode" (so named because one average individual represents the whole population in a gridcell). This mode is now very rarely used, even coupled configurations use the cohort mode (confirmed for EC-Earth, RCA-GUESS, EMAC-GUESS, LPJ-GUESS-LSM). The logic is that although cohort mode is computationally heavier, it is still a very small fraction of compute time compared to a full atmospheric simulation and

so worth including for the added realism. Furthermore, all model development and tuning is done with cohort mode and the mostly recently integrated fire model, SIMFIRE-BLAZE, doesn't run in population mode.

To satisfy the reviewers curiosity we did run the model in population mode (with the GlobFIRM fire model). It indeed very much faster, around 10x (from a little over 5 hours on 384 AMD 7763 CPU to only 30 mins). Global GPP increased modestly 143 PgC/year in the EEO configuration but to a rather large 196 PgC/year in Standard config. Interestingly the spatial NME was unchanged for the EEO config (0.41) but was very much worse for the standard configuration (0.65). This is actually pretty interesting and useful. Based on this, we propose to add the following text on how the approach might be applied to average individual models.

"Although LPJ-GUESS's "population mode" (which uses a single average individual per PFT instead of the full cohort structure) is now very rarely used and has not been developed for quite some time, we tested it with EEO configuration to give some indication of how the EEO formulations might work with average-individual type models. The global total GPP increased moderately to 143 PgC/year and the spatial NME remained unchanged at 0.41 (data not shown). This rather good performance indicated that the EEO approach works well with an average individual representation, which is perhaps to be expected as the EEO formulations were mostly developed and tested at the ecosystem, as opposed to individual plant, level."

The authors compare the LPJ-GUESS model with EEO photosynthesis and acclimation to the unchanged model. It would be interesting to see the impact of different acclimation times on the model performance to see how important the addition of acclimation is.

Yes, that could be interesting to see how time plays out in the DGVM. However, such an exercise would be confounded by other model processes and errors, such as errors in phenology and soil moisture, and would thus be rather specific to LPJ-GUESS. The cleaner studies and more broadly useful studies are the Mengoli et al. (2022) and Ren et al., (2024) papers, especially as they use higher quality site data, and we don't feel we would be able to usefully add to those results.

More specific remarks:

Line 292: Soil moisture is denoted as Theta, identical to the co-limitation parameter Theta in Table 1.

Ah, yes, that is inconvenient. The original sources both use Theta and we would like to be consistent with both. We propose to add change the "(θ)" on line 292 to:

"(θ, distinct from the parameter in Table 1)"

Line 279: One question. Does this correspond to the original photosynthesis model setting the co-limitation factor Theta=1? Are there any justifcati9on to assume this?

Essentially yes, but they apply at different time scales and for slightly different purposes. The colimitation factor Theta is applied to daily or monthly average rates. The minimum at line 279 applies to the instantaneous rates (although these do happen to be daily average rates in this case). The P-model avoids the need for a Theta by using the Coordination Hypothesis, which is well supported (Maire et al., 2012) and essentially assumes that the two rates are equal under typical growth conditions. The (Mengoli et al., 2022) approach goes further and assumes the rates are equal specifically under midday conditions and separates the acclimation timescale from the instantaneous timescale. The minimum term is then applied as instantaneous conditions *deviate* from the midday conditions. In contrast, the Theta is used to co-limit using the two average rates under average conditions without invoking the Coordination Hypothesis.

Please add unit of GPP and R_d in the figure captions.

Yes, done.

The authors use 500 yrs of spin up of the model. The carbon and nitrogen pool should be in equilibrium after the spin up period It might be in particular for the boreal and polar regions that the pools are in disequilibrium because of the low temperatures leading to very low decomposition rates This might not be important for evaluation of GPP values bit for soil pools it is important. Also nitrogen limitation might change.

Ah yes, we didn't mention in the description that LPJ-GUESS has a soil pool extrapolation functionality which acts during spinup and uses 200 years of modelled fluxes to extrapolate C and N pools for 40,000 years to a long term equilibrium specifically to address this. We propose to remedy this by adding the following the end of section 2.5:

"Following standard LPJ-GUESS protocol, soil C and N pools were extrapolated to an estimate of their long-term equilibrium using 200 years of modelled fluxes recorded during spin up."

The author claims that an error in the fAPAR values propagate directly to the GPP value due to its linear relationship. The fAPAR dynamics is also affected by the phenology. LPJ-GUESS has an annual update of the carbon pools distributing the assimilated carbon to all vegetation carbon pools. The phenology function determines the intra-annual the intra-annual variability of leaf carbon changing the fAPAR value. A discussion should be added.

Yes, we were a little brief on the fAPAR and phenology discussion, although we do mention the role of phenology at line 574. We proposed to add additional text discussing the role of fAPAR and phenology at line 626 in the discussion:

"Dynamics of fAPAR are controlled by LAI in LPJ-GUESS and LAI in turn has two controls; the allometry scheme, which determines the carbon allocated to leaves and therefore seasonal maximum leaf area, and the phenology scheme, which determines how leaf area responds to soil moisture and temperature. Both of these could be targeted to improve LAI and

consequently fAPAR and GPP. Recent EEO theory about the controls on LAI (Zhou et al., 2025) may prove informative for both aspects."

The authors claim to have a faster model using the EEO approach. Pleas gives some numbers for a typical configuration on an HPC cluster.

Happily. We propose to modify the text at line 683 to:
"Model runtime was reduced by ~23% for the global simulations presented here, from 7 h for the standard simulation to 5 h 22 min for the EEO simulation on 384 AMD 7763 CPU cores."
15 patches are normally considered sufficient for LPJ-GUESS, so the 30 patch simulations used here are computationally heavier than strictly-speaking necessary.

References

Maire, V., Martre, P., Kattge, J., Gastal, F., Esser, G., Fontaine, S., & Soussana, J.-F. (2012). The Coordination of Leaf Photosynthesis Links C and N Fluxes in C3 Plant Species. *PLOS ONE*, *7*(6), e38345. https://doi.org/10.1371/journal.pone.0038345

Mengoli, G., Agustí-Panareda, A., Boussetta, S., Harrison, S. P., Trotta, C., & Prentice, I. C. (2022). Ecosystem Photosynthesis in Land-Surface Models: A First-Principles Approach Incorporating Acclimation. *Journal of Advances in Modeling Earth Systems*, *14*(1), e2021MS002767. https://doi.org/10.1029/2021MS002767

Ren, Y., Wang, H., Harrison, S. P., Prentice, I. C., Atkin, O. K., Smith, N. G., Mengoli, G., Stefanski, A., & Reich, P. B. (2024). Reduced global plant respiration due to the acclimation of leaf dark respiration coupled with photosynthesis. *New Phytologist*, *241*(2), 578–591. https://doi.org/10.1111/nph.19355

Sandoval, D., Flo, V., Morfopoulos, C., & Prentice, I. C. (2026). Environmental influences on the maximum quantum yield of terrestrial primary production. *New Phytologist*, *251*(4), 1709–1722. https://doi.org/10.1111/nph.71303

Zhou, B., Cai, W., Zhu, Z., Wang, H., Harrison, S. P., & Prentice, I. C. (2025). A General Model for the Seasonal to Decadal Dynamics of Leaf Area. *Global Change Biology*, *31*(3), e70125. https://doi.org/10.1111/gcb.70125