

Response to Reviewer #2

In this manuscript, Yao et al. examine drought legacy effects on carbon and water fluxes using eddy-covariance observations and a process-based model for a temperate forest in the central US. The manuscript is generally well written and reflects considerable effort in the model experiments and data analysis. It has the potential to contribute to the literature by providing a data-model fusion framework for understanding drought legacy effects and improving the representation of post-drought recovery of carbon and water fluxes. I only have several concerns that should be addressed before publication.

[Response]

We thank the Reviewer's positive feedback on our study. Below, we provide a point-by-point response. Reviewer comments are shown in *italics*, and our responses are provided in blue.

Major comments:

1) The overall structure of the methodology is understandable, but some key details are missing. The equations for how GPP, ET, leaf water potential, and hydraulic conductance are calculated should be included. They are important for readers to understand how the water stress factor affects the dynamics of these variables.

[Response]

We thank the Reviewer for pointing this out. The calculations of key variables, including GPP, transpiration, leaf water potential, and hydraulic conductance, are summarized below. To address this issue, we will incorporate these descriptions into the revised Methods section.

The leaf net photosynthetic rate is computed using the classic C3 photosynthesis model (Farquhar et al., 1980). For the optimality-based stomatal model, the criterion is to maximize the difference between leaf-level carbon gain and hydraulic risk, with risk represented through leaf hydraulics and their coupling to photosynthesis (Eq. 1).

$$g_s = \operatorname{argmax}\left(A_{\text{net}} - A_{\text{net}} \frac{E}{E_{\text{crit}}}\right) \text{ Eq. (1)}$$

where E is the leaf-level transpiration rate, and E_{crit} is the critical transpiration rate at which the leaf xylem hydraulic conductance decreases to 0.1% of the maximum value (namely at 99.9% loss of hydraulic conductance). A_{net} is the net photosynthesis rate.

In the Medlyn stomatal model, β can be added either into the g_1 (Eq. 2) or V_{cmax} (Eq. 3).

$$g_s = g_0 + 1.6 \cdot \beta \cdot \left(1 + \frac{g_1}{\sqrt{D}}\right) \cdot \frac{A_{net}}{c_s} \quad \text{Eq. (2)}$$

$$g_s = g_0 + 1.6 \cdot \left(1 + \frac{g_1}{\sqrt{D}}\right) \cdot \frac{A_{net}(\beta)}{c_s} \quad \text{Eq. (3)}$$

c_s is the CO₂ concentration at the leaf surface. D is leaf-to-air vapour pressure deficit. g_0 and g_1 are empirical parameters.

Then leaf net photosynthesis is solved by putting the stomatal model and Farquhar model together using Eq. 4.

$$A_{net} = V_{cmax} \frac{c_i - \Gamma^*}{c_i + K_m} = g_s \cdot (C_a - c_i) \quad \text{Eq. (4)}$$

V_{cmax} is the maximum rate of Rubisco activity and K_m is the Michaelis-Menten coefficient for Rubisco kinetics. Γ^* is the CO₂ compensation point in the absence of dark respiration and R_d is the dark respiration rate. c_i is the intercellular CO₂ concentration.

Transpiration is computed following Fick's law of diffusion (Eq. 5).

$$T = \sum_{i=1}^{n_{canopy}} g_s \cdot D \cdot LAI_i \quad \text{Eq. (5)}$$

LAI_i is the leaf area index of i^{th} layer.

Hydraulic conductance is updated following the Weibull function (Eq. 6).

$$K = K_{max} \cdot e^{-1 \cdot \left(\frac{-\psi}{b}\right)^c} \quad \text{Eq. (6)}$$

K_{max} is maximum hydraulic conductance. b and c are empirical parameters. ψ is leaf water potential.

Leaf water potential is updated following Darcy's law based on vertical water flow and leaf hydraulic conductance (Eq. 7).

$$\psi(t + 1) = \psi(t) - \frac{F}{K} \quad \text{Eq. (7)}$$

F is water flow within one layer.

2) The authors show the comparison of GPP and ET between observations and model simulations under different scenarios across drought stages in an aggregated way. It would be great to show the temporal dynamics in more detail by showing the daily time series, which could help convey the messages more clearly to readers. In addition, the time series of the water stress and hydraulic conductance under the partial recovery scenario could be worth showing to demonstrate the role of the partial recovery of hydraulic conductance in the recovery of carbon and water fluxes.

[Response]

We thank the Reviewer for pointing this out. We have added time series of GPP and ET (Figure R1) and now also show how water stress and hydraulic conductance recover under the partial recovery scenario (Figure R2).

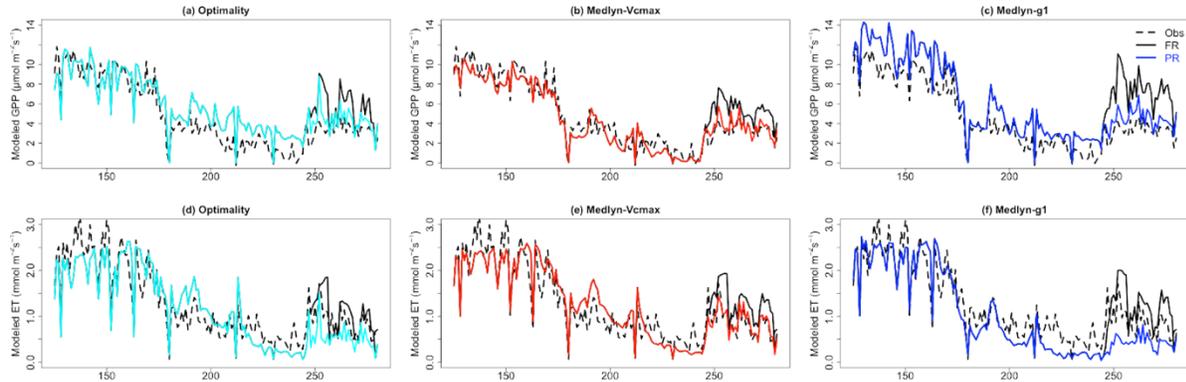


Figure R1 Time series of GPP and ET between observations and model simulations.

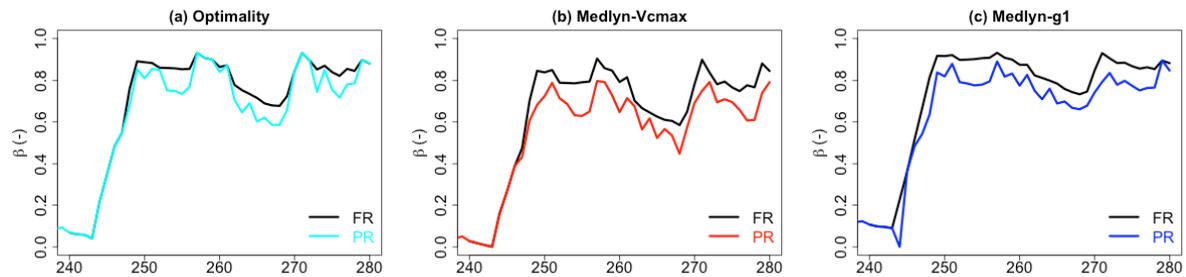


Figure R2 Time series of water stress (β) under the full-recovery and partial-recovery scenarios.

3) Because the model does not simulate soil evaporation and re-evaporation of rainfall interception, the authors assume a fixed T/ET ratio to link transpiration (T) to observed ET . However, this is a strong assumption in the context of drought legacy effects on ET . Because, given the same conditions of water and energy availability, the reduced T due to legacy effects could be compensated by the soil evaporation, resulting in a similar magnitude of ET . Therefore, the result that the ET simulation under the full-recovery assumption is closer to the observation than the non-recovery assumption could be confounded by this compensation effect. This could also question the finding that a quicker resumption of ET , but a slower recovery of GPP . Given that the model used can not simulate soil evaporation, I suggest authors try to use an ET partitioning

method (e.g., Nelson et al., 2020) to estimate transpiration and directly compare it with model simulations.

[Response]

Following the Reviewer's suggestions, we used the uWUE method from Nelson et al. (2020) for ET partitioning and compared the partitioned T against model simulations. To solve this issue, we will add the below uWUE method and model performance comparison into the revised version.

Method description

$$uWUE = \frac{GPP \cdot \sqrt{D}}{ET} \quad \text{Eq. (1)}$$

The potential uWUE (uWUE_p) is calculated at an annual scale using a 95th percentile regression between $GPP \cdot \sqrt{D}$ and ET, representing the conditions with the highest carbon gain to water loss and thus $T = ET$. The apparent uWUE (uWUE_a) is estimated directly from Equation (1) when estimating at half-hourly resolution.

$$\frac{T}{ET} = \frac{uWUE_a}{uWUE_p} \quad \text{Eq. (2)}$$

Using the partitioned transpiration (T) as the observation constraint, we find model simulations overestimate the recovery of both T and GPP (Figure R3). After applying the partial recovery setup, we find that it is still incorporating biochemical limitations (Medlyn-V_cmax) that yields the minimum model-observation mismatch (Figure R4).

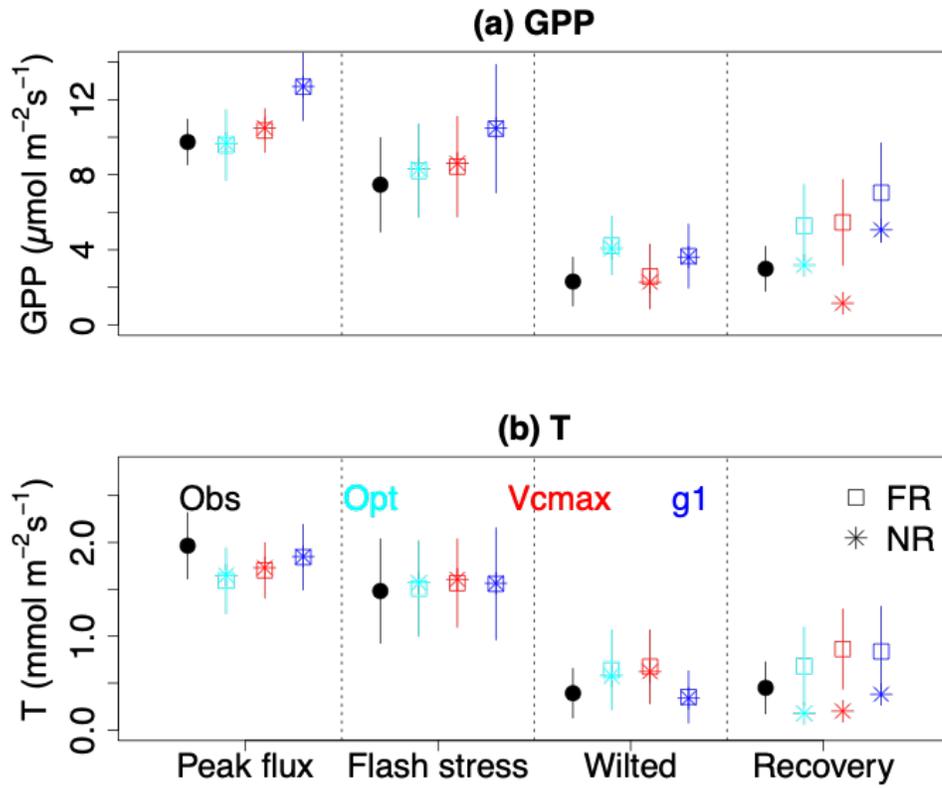


Figure R3 Model performance for GPP and T across four periods in 2012. Curves show the optimality-based stomatal model (cyan) and the Medlyn model with the water-stress factor applied to V_{cmax} (red) or to g_1 (blue). FR, full recovery; NR, no recovery. Error bars indicate variability within each period.

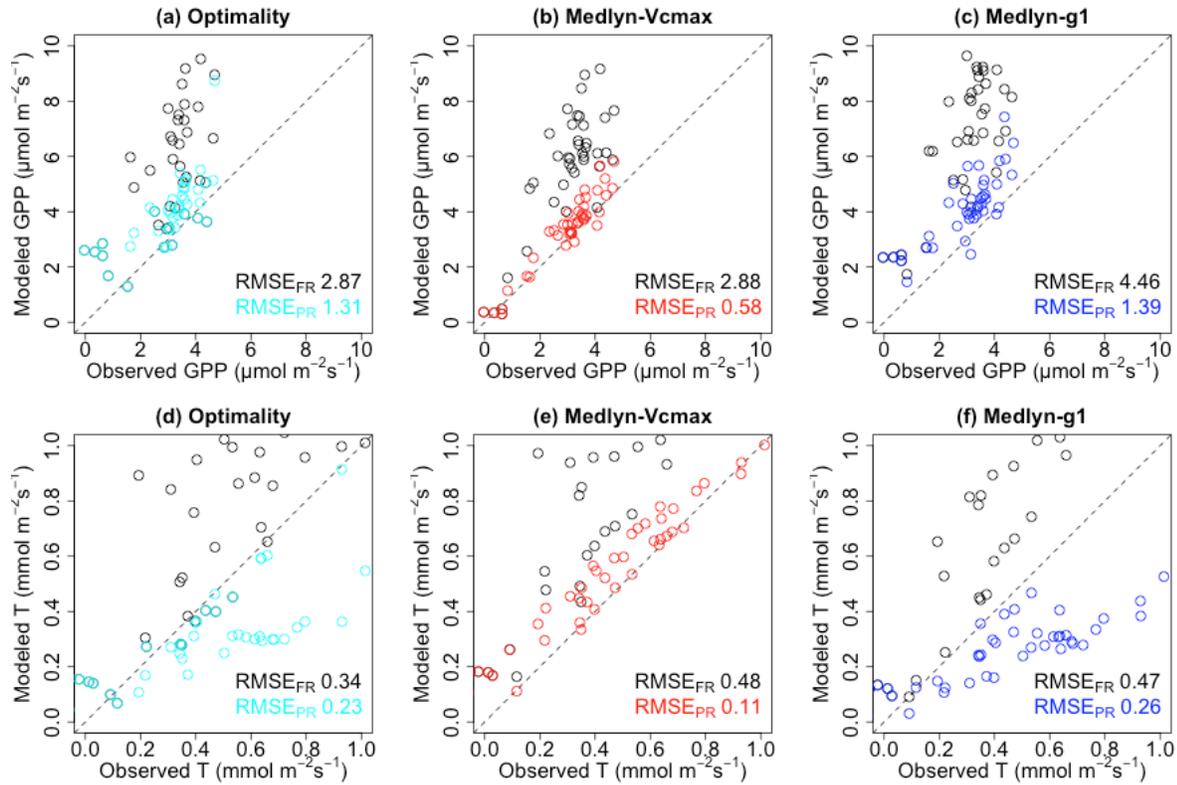


Figure R4 Improvement in model performance after accounting for drought legacy effects (recovery period only). Scatterplots compare RMSE under the partial-recovery scenario (RMSE_{PR}) against the full-recovery baseline (RMSE_{FR}) for GPP and T. Symbols denote simulations assuming full recovery (black circles) and partial recovery using the optimality-based model (cyan) or the Medlyn model with the water-stress factor applied to Vcmax (red) or g1 (blue). RMSEs are computed against flux observations; lower values indicate better fit.

4) I am a little confused about the true mechanisms investigated in this study. The authors design three hydraulic conductance recovery scenarios and use a water stress factor (β), which gives the impression that the effect of partial recovery of hydraulic conductance is examined. However, in the analysis, this β factor is used to adjust Vcmax to account for the down-regulation of photosynthetic capacity, and in the discussion later, the significance of Vcmax impairment in shaping the delayed recovery of carbon fluxes is highlighted. Is the down-regulation of photosynthetic capacity the consequence of the loss of hydraulic conductance? Or they jointly contribute to drought legacy effects. There seems to be a mixture of these two processes. It would be great if this point could be clarified throughout the manuscript.

[Response]

We thank the Reviewer for pointing this out and apologize for the lack of clarity. Drought stress can reduce V_{cmax} through declines in Rubisco activity and nitrogen allocation, and metabolic inhibition under low leaf water potential, resulting in biochemical limitations that may persist beyond the subsidence of meteorological water stress. In our Medlyn– V_{cmax} model framework, V_{cmax} is reduced through a water-stress factor β , and this biochemical limitation is allowed to recover more slowly than environmental conditions. In our framework, drought legacy effects can arise from both incomplete recovery of hydraulic conductance due to embolism/cavitation and reduced biochemical capacity associated with impaired Rubisco activity. The water-stress factor β is used to represent the recovery state of both processes, and these two components jointly contribute to the simulated drought legacy effects. We will clarify this mechanism and its implementation in the revised manuscript.

Line-by-line comments:

Line 4: repeated numbers

[Response]

We removed the number.

Line 23: timing? You mean duration?

[Response]

Yes. This sentence is changed as:

Further research to mechanistically represent dynamic recovery processes, particularly their **duration** and magnitude, is essential for improving the modeling of global carbon and water fluxes.

Line 35: From my understanding, Ciais et al. (2005) did not include legacy effects. Also, it is unclear if drought legacy effects could shift ecosystems from carbon sinks to carbon sources. Maybe consider rephrasing this sentence.

[Response]

We rephrased this part as:

This lagged recovery, often referred to as the drought legacy effect, has been documented in drought-induced tree mortality (Matusick et al. 2018), carbon fluxes (Haberstroh et al. 2025), and tree growth (Anderegg et al., 2015).

Line 149: Where is Figure S1? The entire supplement seems to be missing.

[Response]

We apologize for the missing SI. We will upload SI during the revision stage.

Lines 172-173: It would be great if the equation of the optimality stomatal model or more details could be provided. How to apply β to it?

[Response]

We will add the equation and explanation in the revised version as below.

Optimality stomatal model:

$$g_s = \operatorname{argmax}(A_{net} - A_{net} \frac{E}{E_{crit}}) \text{ Eq. (1)}$$

where E is the leaf-level transpiration rate, and E_{crit} is the critical transpiration rate at which the leaf xylem hydraulic conductance decreases to 0.1% of the maximum value (namely at 99.9% loss of hydraulic conductance).

Table 1: Where is V_{cmax}?

[Response]

V_{cmax} is used in the calculation of net photosynthesis rate. Photosynthesis is solved by using both the Farquhar model and the diffusion model as below.

$$A_{net} = V_{cmax} \frac{C_i - \Gamma^*}{C_i + K_m} = g_s \cdot (C_a - C_i)$$

Line 229: just curious. Why 63% instead of 50%?

[Response]

The classical Weibull cumulative distribution function (CDF) is

$$F(x) = 1 - e^{-\left(\frac{x}{\beta}\right)^k}$$

β is a scale parameter. k is the shape parameter. If we evaluate it at $x=\beta$, $F(\beta)=1-e^{-1}\approx 0.632$. The scale parameter corresponds to the point where the cumulative probability reaches ~63.2%.

When mapping to hydraulic vulnerability curve, PLC is computed as:

$$\frac{K}{K_{max}} = e^{-\left(\frac{-\psi}{b}\right)^c}$$

$$PLC = 1 - \frac{K}{K_{max}} = 1 - e^{-\left(\frac{-\psi}{b}\right)^c}$$

This is mathematically identical to the Weibull CDF.

When $|\psi| = b$, $PLC = 1 - e^{-1} \approx 0.632$

Figure 1b): would be great to show the related equations to better understand this figure. Also see the first major comment.

[Response]

The equations related to Figure 1b are shown here. We will add them to the revised version.

$$K = K_{max} \cdot e^{-1 \cdot \left(\frac{-\psi}{b}\right)^c}$$

K_{max} is maximum hydraulic conductance. b and c are empirical parameters. ψ is leaf water potential.

$$T = \sum_{i=1}^{n_{canopy}} g_s \cdot D \cdot LAI_i$$

LAI_i is the leaf area index of i^{th} layer.

Leaf water potential is updated using vertical water flow (F) and leaf hydraulic conductance.

$$\psi(t + 1) = \psi(t) - \frac{F}{K}$$

Figure 4: Why is the difference between RMSEFR in b and c so large? They should be based on the same model without β , right?

[Response]

Under full recovery (FR) assumption, β was included and applied to different locations. Panel (b) and (c) used the same Medlyn stomatal model, but applied the β to either V_{cmax} or g_l part. Applying the water-stress factor β to V_{cmax} represents a biochemical limitation, directly reducing photosynthetic capacity and indirectly constraining stomatal conductance through reduced assimilation. This formulation leads to a stronger and more persistent reduction in GPP, with comparatively weaker impacts on transpiration. In contrast, applying β to g_l represents a non-biochemical (stomatal) limitation, directly reducing stomatal conductance and CO_2 diffusion, thereby suppressing transpiration and secondarily reducing photosynthesis. This means when

model performance on transpiration is similar between two setups, which was the case here as transpiration was used in the error function to optimize K_{max} , photosynthesis in Medyn-g1 would be slightly higher than that in Medlyn-V c_{max} . These two parameterizations therefore produce distinct responses of carbon and water fluxes under drought and during recovery as shown in Figure 4.

Lines 384-390: see the 3rd major comment.

[Response]

We conducted additional model simulations using observation-based partitioned transpiration as a constraint (please see our response to the 3rd major comment). The results do not change our conclusion that delayed recovery can be effectively captured by incorporating biochemical limitations.

Lines 484-485: see the 3rd major comment.

[Response]

We agree with the Reviewer that soil evaporation may compensate for reduced transpiration, potentially leading to a rapid recovery of ET. To account for this, we used observation-based partitioned transpiration as a constraint and repeated the model simulations. We find that during the recovery period, the full-recovery scenario overestimates both GPP and transpiration, although this does not alter our conclusion that incorporating biochemical limitations helps resolve the model-observation mismatch. We have therefore removed the description “quick resumption of ET” from the manuscript.

Lines 488-489: From my understanding, under the partial recovery scenario, the model needs to be calibrated by observations during the recovery phase. Would this prevent it from applying to the case where the observation is not available?

[Response]

Yes, calibrating the model against observations is required to optimize its ability to capture the extent of partial recovery. Regarding generalizability, the proposed method can be applied at sites with eddy-covariance observations to derive general constraints on vegetation recovery processes, which can then be transferred to sites lacking eddy-covariance measurements. For example, key

recovery characteristics, such as the time required for the release of accumulated water deficit and the upper bound of hydraulic conductance recovery, can be derived from existing eddy-covariance observations. These features can then be related to commonly available environmental variables using nonlinear regression or machine-learning approaches, enabling their prediction at sites without eddy-covariance data. We will add this to the revised Discussion section.

References

- Haberstroh, S., Christen, A., Sulzer, M., Scarpa, F., & Werner, C. (2025). Recurrent hot droughts cause persistent legacy effects in a temperate Scots Pine forest. *Plant Biology*. doi: 10.1111/plb.70066
- Matusick, G., Ruthrof, K. X., Kala, J., Brouwers, N. C., Breshears, D. D., & Hardy, G. E. S. J. (2018). Chronic historical drought legacy exacerbates tree mortality and crown dieback during acute heatwave-compounded drought. *Environmental Research Letters*, 13(9), 095002.