Response letter

Reviewer 1

Comment 1: In their revised manuscript, Tang et al. addressed most of my comments, but there are still some issues with clarity of presentation and interpretation of the results.
Response: We appreciate Dr. Manzoni's comments, which helped us improve the manuscript's clarity and readability significantly. We below address his new comments point by point and highlight our changes.

Comment 2: I should apologize up front, as one of my comments was wrong and might have created some confusion. I contrasted "deterministic" vs. "chaotic" in my comment, but of course a chaotic trajectory can still be deterministic (i.e., not stochastic). However, the authors use the term "deterministic relationship" meaning "unique relationship" (L101, L182); I think the latter wording is more appropriate.

Response: Based on your suggestion and our intended message, we now use "static relationship" for a more accurate description of the common practice that a one-to-one function is used to formulate the relationship between CUE and its controlling factors, while the relationship really should be dynamic in that multiple CUE values may occur under a given set of controlling factor values.

Comment 3: The authors explained in their response that at steady state, the "CUE of each model becomes a function of microbial parameters […] and is independent of substrate supply rate." This is an important result that in my opinion deserves to be presented and discussed. The fact that varying carbon input rate—and thus substrate supply and organism growth—in the long-term does not shift CUE suggests a lack of response of aggregated traits representing microbial or plant physiology to e.g. elevated CO2, which would promote both photosynthesis and litterfall. This might also mean—I am speculating here—that even missing some features of the short-term CUE-growth relation might not have consequences for long-term predictions, if anyway the system adjusts so that CUE is independent of source supply.

Response: We clarify in the revision that the above-mentioned conclusion is true only for constant environmental conditions, including carbon inputs. In effect, this is a feature of deterministic modeling of microbial dynamics, that given identical conditions, the steady-state state variables are uniquely determined.

Comment 4: The introduction might benefit from some additional work, as some terms are introduced but not defined (e.g., structural and reserve biomass, introduced in L37 but defined only in L43-44) and microbial and plant processes are sometimes mixed up (e.g., L58-59 on plants in a paragraph on microbes).
Response: We now re-organized the text, so that the concepts of structural and reserve biomass are defined before they are used. Specifically, in the introduction, we now wrote:

Moreover, based on observations that biological activity, such as the hatching of an egg or the germination of a plant seed, continues for a significant period of time in the absence of carbon uptake from the environment, variable internal storage models differentiated between structural and reserve biomass (e.g., Tang and Riley, 2015; Kooijman, 2009; Nev and Van Den Berg, 2017). Specifically, the structural biomass refers to DNA, cell wall and membrane material, and any biomass that requires maintenance to support an organism's normal function, while reserve biomass includes lipids, glycogen, circulating metabolites, short-lived RNA and any biomass that stores energy and acts as a precursor of structural biomass. Consequently, the variable internal storage models reasoned that, since only the structural biomass requires maintenance, CUE can be either defined with respect to the growth of structural biomass or total biomass. Further, because plants drive growth using photosynthates (that is already stored in cells), the variable internal storage models fit plant growth naturally. However, many models do not differentiate between structural biomass and reserve biomass (e.g., (1) all microbe-implicit soil BGC models; Koven et al., 2013; Parton et al., 1988; Jenkinson, 1990), (2) the Pirt model (Pirt, 1982), and (3) the Compromise model (Beeftink et al., 1990; Wang and Post, 2012)), and implicitly assume an equal CUE for structural and total biomass growth.

Comment 5: I see the point of leaving much of the technical details in the supplementary materials, but some more information in the main text would help to understand the approach and results. For example, in Section 2.2, without a short description of the soil carbon model, the meaning of the scenarios is hard to grasp and later in the manuscript, the interpretation of the results is difficult without continuously flipping between main text and supplement.
Response: We now added high level description of the soil carbon model, while leaving the technical details in the supplemental material. Specifically, we now wrote:

For models used in the 50-year simulations of soil carbon dynamics, we detail their mathematical formulations and parameterizations in section F of the supplemental material and provide here only a high-level description. Specifically, each of the six models describes the dynamics of one microbial population that feeds on one fast C pool and one slow C pool. Note that the use of fast and slow pools here simply means the former carbon substrate is kinetically more favorable than the latter to the microbes, and they do not have the same meaning as in microbe-implicit models, which are directly associated with turnover times (Parton et al., 1988). We formulated the substrate uptake based on the argument in Tang et al. (2024), i.e., a form that resembles the competitive Michaelis-Menten kinetics as simplified using equilibrium chemistry approximation (ECA) kinetics (Tang and Riley, 2013). In these models, the fast and slow C pools increase due to external inputs, and all microbial biomass from mortality is added to the slow pool C.

Comment 6: Figures 3-6: the message that there is no unique relation between CUE and growth is clear, but the reasons why these cycles emerge are not explained. Why does a positive CUE-growth relation turn negative and then loops back? What are the variables that introduce this hysteretic behavior? Some explanations of the processes represented in the soil carbon model that drive these patterns would help readers understand the Results.

Response: We now added appropriate explanations to the results. Specifically, we wrote for Figure 3:

In contrast, the representation of reserve biomass makes the other four models predict multiple total biomass CUE values for each specific growth rate (Figure 3b, c), which gradually converge to a closed curve due to repeating growth pattern (Figure S2d) driven by the temporal response of reserve biomass to the fixed seasonal pattern of carbon input.

And for Figure 5:

However, the curves still gradually close on themselves due to the temporal response of reserve biomass to the fixed seasonal pattern of carbon input and temperatures.

General comments on language and presentation:
Comment 7: Please check that all symbols are defined—e.g., in Table 1: R and B_V in the modified Droop model, and B_X and in the VIS model are not listed in Table A1.

Response: We corrected the biomass variables for the mDroop model (to ensure consistency with the supplemental material) and added the missing variables to Table A1.

Comment 8: The term “population” is used to refer to “community” (or at least I interpret it that way when reading); it would be good to refer to “population” when there is a single species

Response: We double checked to ensure the proper use of “population” and “community”.

Comment 9: I wonder if the description of the shapes of the CUE vs. growth relations (baguettes, kiwi fruits, mussels etc.) can be misleading. The shape appearance depends mostly on the scaling of the figure axes, so a baguette shape would become closer to a kiwi fruit with a less stretched x-axis or an expanded y-axis.

Response: We now reduced the use of these “fun words”, and added context when needed.

Other specific comments:
Comment 10: L48, confusing sentence, I am not quite sure I understand what it means that “biomass focuses on…”

Response: For precision, we revised the sentence as “Specifically, is it the structural biomass CUE that designates population growth, or is it the total biomass CUE that designates biomass growth?”

Comment 11: Table 1, delete extra “is” in the first line of the description of the mDroop model; in the fourth line of the same paragraph, is an equal sign missing after j_A?

Response: We deleted extra "is". Also, we assure that there is not an equal sign after j_A. Rather, it says the substrate dependent j_A is modified by the cellular carbon quota via $\frac{Q_{max-Q}}{Q_{max}-Q_{min}}$ and total structural biomass B_V.

Comment 12: Figure 2 caption: I would clarify that CUE and growth rate are normalized
Response: These are now made clear.

Comment 13: Figure 3: there is a lot of empty space in these panels; I would cut off the x-axis below 0.8 and above 1.2, and the y-axis below 0.42, to help focus on the area in the plots where the trajectories are located

Response: We revised the figure to decrease the empty space for each panel.

Comment 14: L137: perhaps I would not call calibrated parameters "inappropriate"—they are "effective parameters" that might not have a clear biological/physical meaning, but they are "appropriate" in the sense of producing reasonable predictions.

Response: We have now label them "physically unrealistic" so that it implies the model needs correction.

Comment 15: L166: does this hypothesis imply that there are no DEB models for plants? I am not up to speed with the recent literature, but I thought Glenn Ledder and Roger Nisbet were working in that direction

Response: We now added the reference Russo et al. (2022) and Kooijman (2009) to indicate that such efforts exist. Specifically, we wrote: Some prototype applications of the sDEB model to plant growth are in (Russo et al., 2022; Kooijman, 2009).

Comment 16: L190: this work does not really show that considering moisture and temperature effects on the kinetics of individual processes is better than using multipliers; I don't disagree with the point made, but that does not seem to be what this manuscript is about (or it is not clear how the statement is supported by the Results presented here)

Response: We made this assertion partly based on findings in Tang and Riley (2015), which showed using a multiplicative Q10 approach overestimated the temperature sensitivity when considering high frequency variations in temperature. Additionally, the multiplier approach assumes independence between different factors, thus excluding the causal constraint between them. These together led us to believe the multiplier approach should be used more cautiously. To address the reviewer's concern, we have now written:

Therefore, considering that our previous analysis based on the sDEB model (Tang and Riley, 2015) showed that treating the temperature effect as a multiplier led to significant overestimation of warming induced soil carbon loss (see Figure 3 there), we contend that, in order to robustly simulate the emergent carbon use efficiency dynamics and its consequent influence on ecosystem biogeochemistry, models should represent biological growth as sink-driven, and the effect of controlling factors like temperature and moisture should not be applied as multiplier functions, rather they should be applied to directly modify the kinetic parameters of different metabolic processes.

Other minor comments:

L82, L87: spread of what? (in L87 "spread is…")

L182: "by Lipson et al. (2015)"

L109: "wider"
Response: We corrected the typos and removed redundant words.

Reviewer 2:

Comment: Thank you for the revision. The manuscript has been substantially improved. However, I still have some concerns about the Introduction.
In my view, the Introduction still does not define the central research gap as clearly and as directly as it could. It brings together several relevant topics—reserve versus structural biomass, differences among empirical CUE measurements, plant CUE, and the thermodynamic analogy—but these elements are not yet organized into a sufficiently focused line of argument. As a result, the main research questions are stated clearly near the end of the Introduction, but they do not emerge as naturally as they could from the preceding background. To me, the key gap is that current biological growth models differ fundamentally in whether they distinguish reserve from structural biomass, and therefore structural from total biomass CUE, yet the consequences of these differences for the predicted CUE–growth relationship have not been systematically compared. I encourage the authors to sharpen the Introduction around this central point.

Relatedly, I still find the paragraph on plant CUE somewhat abrupt. Although this section has been improved, the transition from microbial CUE definitions to whole-plant CUE and then to the thermodynamic framework is still not fully smooth. It would help if the authors explained more explicitly why plant CUE is introduced here. For example, they could clarify that the purpose is not to review plant physiology itself, but to show that the distinction among growth, storage, and maintenance is a general feature of biological systems and that plant growth theory provides a useful conceptual reference for microbial growth modeling.

Response: We appreciate Dr. He's comments, which further help to improve the clarity of our manuscript. In the revision, we improved the logical flow of the introduction by reducing the distance between the description of a new concept and its use. Specifically, for the structural biomass and reserve biomass concepts, we now write:

Moreover, based on observations that biological activity, such as the hatching of an egg or the germination of a plant seed, continues for a significant period of time in the absence of carbon uptake from the environment, variable internal storage models differentiated between structural and reserve biomass (e.g., Tang and Riley, 2015; Kooijman, 2009; Nev and Van Den Berg, 2017). Specifically, the structural biomass refers to DNA, cell wall and membrane material, and any biomass that requires maintenance to support an organism's normal function, while reserve biomass includes lipids, glycogen, circulating metabolites, short-lived RNA and any biomass that stores energy and acts as a precursor of structural biomass. Consequently, the variable internal storage models reasoned that, since only the structural biomass requires maintenance, CUE can be either defined with respect to the growth of structural biomass or total biomass. Further, because plants drive growth using photosynthates (that is already stored in cells), the variable internal storage models fit plant growth naturally. However, many models do not differentiate between structural biomass and reserve biomass (e.g., (1) all microbe-implicit soil BGC models; Koven et al., 2013; Parton et al., 1988; Jenkinson, 1990), (2) the Pirt model (Pirt, 1982), and (3) the Compromise model (Beeftink et al., 1990; Wang and Post, 2012)), and implicitly assume an equal CUE for structural and total biomass growth.

We now include plant growth (as early as) in the first sentence of the introduction, and (throughout the text) ensured that plant CUE and microbial CUE are introduced initially before they are discussed in detail. Additionally, at the end of the model description section 2.2, we now write explicitly that: "Additionally, since the Pirt model, Thornley's model, and the sDEB model have also been adopted for modeling plant growth (Thornley, 1972; Russo et al., 2022; Thornley, 2011), the assertions we draw below can also be more generally extended to plants."