

Interactive comment on “Reviews and syntheses: Carbon use efficiency from organisms to ecosystems – Definitions, theories, and empirical evidence” by Stefano Manzoni et al.

Anonymous Referee #1

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Manzoni et al reviewed and synthesized patterns in carbon use efficiency (CUE) across scales. This is a large effort that can help reconciling previously identified differences in CUE. The authors go into the details of the different definitions that have been used and clarify some of the misunderstandings in the past. I think this could become an important contribution to the field, as differences in definitions and equations for CUE have been mostly ignored and confusion exists on what CUE should reflect. However, I do not fully agree on the presented definitions and think the manuscript still fails to fully resolve discrepancies. The current manuscript does not accurately represent what CUE is, where the term originates from and how it has been used in the past. As the manuscript reads now, I find it a missed opportunity to resolve the confusion that is

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associated with this topic.

About the definitions:

From a plant perspective, theory indicates that $CUE = NPP/GPP$, with $NPP = \text{the synthesis of organic compounds} = GPP - R$. Hence, $CUE = 1 - R/GPP$. ($NPP = \text{net primary production}$; $GPP = \text{gross primary production}$, $R = \text{respiration}$)

This corresponds more or less to equation 3 ($CUE = 1 - \text{outputs/inputs}$) used by Manzoni et al. However, Manzoni et al consider egestion (EG) and exudation (EX, including symbionts) as part of the outputs, and not as part of NPP. Consequently, the CUE considered here is actually biomass production efficiency (biomass production/inputs = BPE) instead of CUE. Both CUE and BPE are meaningful terms – CUE focusses on the C cycle, while BPE targets the biomass that is produced. In the past, both terms have been rarely distinguished though and they have also not been used consistently. Correct use can be critical, however, as CUE and BPE may respond differently to environmental changes. For example, an increase in BPE could be associated with unaltered CUE if the partitioning to EX is the sole responsible of the change in BPE (i.e., R unchanged). Such understanding becomes important for example when comparing models with observations. Model evaluation assuming observed $BPE = \text{modeled } CUE (=1 - R/GPP)$ can lead to serious flaws, as illustrated by the following hypothetical example. Assuming modeled CUE should equal observed BPE, a (hypothetical) decrease of BPE with increasing CO₂ concentration would suggest an increase in R/GPP whereas in reality the decrease in BPE may be solely due to an increase of EX while R/GPP, and hence true CUE, remain unaltered. In this hypothetical example, adjusting the model to reflect observed BPE in modeled CUE would lead to an overestimation of the response of CUE and R to elevated CO₂.

The above problem related to the assumption that $BPE = CUE$ is more prominent at some levels (e.g. vegetation) than at others (e.g. bacteria). Hence, differences among levels may in part be due to differences in the definition used. This is somewhat

acknowledged by the authors, but it would be much clearer and more accurate if BPE and CUE were clearly distinguished throughout the manuscript and if it was made clear in the figures and tables where BPE is calculated, where CUE is calculated and perhaps also where $BPE \sim CUE$.

Specific comments: I.26 and I.50: I don't think biomass production/C uptake is the consensus definition of CUE (see above). Intro: I suggest to review the history of the definitions for CUE more elaborately. Where was it first used, what was the exact definition, how have definitions been applied in different fields,...? I. 160: clearly define the difference between uptake and assimilation to help the reader in following the different equations I.175: define overflow respiration. Ion uptake respiration is not mentioned. Is it considered part of growth respiration? See for example Lambers et al 1983, *Physiologia Plantarum*, 58: 556-563. I.200: replace 'reduces' with 'can be simplified to'. I.222: add 'and to EX' after 'exports to other parts of the plant'. I.295: I suggest to replace 'lower estimates of CUE' by 'an underestimation of CUE'. I.444: 'for a given uptake rate' seems more logical than 'for a given respiration rate'.

I think the authors missed some relevant publications. Cotrufo et al 2013 (*Global Change Biology* 19, 988-995) discuss the influence of substrate quality on microbial substrate use efficiency (another alternative for CUE), and consequences for soil C storage. This framework deserves at least a mention. Campioli et al 2015 (*Nature Geoscience* 8, 843-846) provide an update of Luysaert et al 2007 and Vicca et al 2012 (both cited in the manuscript), and include also other vegetation types than forests. Data are provided in the supplementary files. I suggest considering including these data, or at least refer to them.

Table 2: Cannell and Thornley 2000 actually used the definition $CUE = 1 - Ra/GPP$. DeLucia et al 2007 used data on biomass production/GPP but termed it NPP/GPP (hence ignoring other NPP components such as exudates and symbionts). This is part of the confusion and I suggest the authors take the opportunity to clarify this. Fig. 2: CUE_{plant} is defined as NPP/GPP , but NPP is undefined. In line with my earlier

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comments, I suggest to clearly define NPP. Figs. 6 and 7: clarify where the data originate from (refer to SI).

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