Environment & Ecology PERSPECTIVE

Digging deeper into microbial carbon use efficiency in soil: Perspectives from microbial growth and respiration

Jiacong Zhou,[1,2] Ji Liu,[1] Bruce A. Hungate,[3] Pete Smith,[4] Robert L. Sinsabaugh,[5] Yakov Kuzyakov,[6,7] Asko Noormets,[8] and Ji Chen[1,2,9,*]

[1]State Key Laboratory of Loess Science, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an 710061, China
[2]Guanzhong Plain Ecological Environment Change and Comprehensive Treatment National Observation and Research Station, Xi'an 710061, China
[3]Department of Biological Sciences, Northern Arizona University, Flagstaff Arizona 86011, USA
[4]Institute of Biological and Environmental Sciences, School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK
[5]Department of Biology, University of New Mexico, Albuquerque New Mexico 87131, USA
[6]Department of Soil Science of Temperate Ecosystems, Department of Agricultural Soil Science, University of Goettingen, Göttingen 37077, Germany
[7]Peoples Friendship University of Russia (RUDN University), Moscow 117198, Russia
[8]Department of Ecology and Conservation Biology, Texas A & M University, College Station Texas 77843, USA
[9]Institute of Global Environmental Change, Department of Earth and Environmental Science, School of Human Settlements and Civil Engineering, Xi'an Jiaotong University, Xi'an 710049, China
*Correspondence: chenji@ieecas.cn

Received: June 1, 2025; Accepted: October 14, 2025; Published Online: October 16, 2025; https://doi.org/10.59717/j.xinn-geo.2026.100183

Citation: Zhou J., Liu J., Hungate B. A., et al. (2026). Digging deeper into microbial carbon use efficiency in soil: Perspectives from microbial growth and respiration. *The Innovation Geoscience* **4**:100183.

Microbial carbon use efficiency (CUE), a key regulator of soil organic carbon (SOC) dynamics, reflects carbon allocation between microbial growth and respiration. Separate investigation of microbial growth and respiration helps to clarify the role of CUE in the carbon balance and consequently, in the carbon cycle in soil. First, in terms of microbial resource acquisition, the drivers of microbial growth and respiration differ: microbial growth is primarily regulated by synergistic availability of carbon, nitrogen, and phosphorus, whereas respiration is more strongly influenced by substrate quality, such as the carbon-to-nitrogen ratio. Second, synchronized responses of microbial growth and respiration rates under climate change (e.g., warming, drought, elevated CO_2) often mask underlying CUE regulatory mechanisms. Thus, we propose: (1) explicitly representing microbial growth and respiration in models to raise the precision of SOC dynamics predictions; and (2) applying approaches such as isotope probing and metagenomic functional annotation to resolve CUE mechanisms from the community to the single-species level. Overall, decoupling CUE into its growth and respiration components establishes a mechanistic framework that explicitly links CUE to microbially mediated SOC dynamics.

Microbial carbon use efficiency (CUE) is the ratio of carbon channeled into microbial growth to the carbon that is taken up,[1] serving as a pivotal indicator governing the initial step of organic matter utilization by microorganisms that can have some relevance for soil organic carbon (SOC) accrual.[2] CUE increases as more carbon is allocated to microbial growth than to respiration, and CUE declines when respiratory costs rise. Because CUE combines two processes, growth and respiration, we suggest that understanding these two components (fluxes) independently will improve our representation of the role of CUE in the soil carbon cycle. For example, growth and respiration rates may vary in concert, as when both processes increased in response to climate change factors, causing no change in CUE.[3]

Indeed, an improved understanding of microbial growth and respiration is crucial to raise our comprehension of CUE and its driving factors. For example, a meta-analysis reported that microbial growth rate increased with contents of SOC, total nitrogen, and total phosphorus, while these factors showed no direct relationship with CUE.[4] Regarding microbial resource acquisition, microbial growth is generally driven by the availability and accessibility of carbon and nutrient resources in soil. Carbon serves as both the energy source and the structural substrate of microbial biomass. Nitrogen is critical for structural protein and nucleic acid synthesis, and phosphorus supports nucleic acid production and energy metabolism. Together, these elements establish a three-dimensional resource limitations framework that governs microbial growth.[1] In contrast, respiration is more directly regulated by SOC quality (e.g., substrate carbon-to-nitrogen ratio, labile and stable SOC pools) than by the availability of carbon or nitrogen, because the stoichiometric balance of SOC determines the enzymatic activity and energy investment required for organic matter decomposition, which in turn directly affects the rate of microbial respiration.[5] This distinction is supported by a meta-analysis showing that nitrogen or combined nitrogen–phosphorus additions altered CUE primarily by affecting microbial growth rather than respiration.[6] Soil microorganisms may adjust their physiological processes and metabolic pathways to alter their growth and respiration under resource limitations, further complicating the factors affecting CUE. For example, in soils with a high carbon availability but low phosphorus levels, microorganisms accelerate phosphorus recycling within biomass to sustain growth or trigger overflow respiration.[7] Thus, the differential driving mechanisms of microbial growth and respiration may explain the lack of consistent relationships between CUE and other factors.

Gaining more knowledge on the components of CUE can deepen our understanding of CUE in response to climate change. A meta-analysis revealed that warming did not affect CUE, but strongly decreased microbial growth rate due to substrate limitation, declined soil moisture and higher maintenance metabolism investments.[8] Microorganisms can invest resources for growth only after the costs for maintenance (e.g., respiration) are covered. Additionally, CUE was not sensitive to the interactive effects of drought, elevated CO_2 concentration, and warming, while both microbial growth and respiration rates were increased by their interactions.[3] These synchronous changes in microbial growth and respiration rates reflect an intrinsic regulatory mechanism that underpins their adaptation strategies to long-term climate change.[3] Therefore, focusing on microbial growth and respiration instead of CUE helps to uncover the regulatory mechanisms of climate change on CUE, as well as the driving factors.

Breaking down CUE into two observable pathways, microbial growth and respiration, can improve the accuracy of soil carbon models. Current models simplify CUE as a constant or a temperature-dependent parameter, which result in unrealistic predictions for SOC dynamics, as CUE varies across ecosystems, temporal scales, and environmental factors.[3,4] To better align with current understanding of microbial physiology, CUE should be represented not as a fixed input parameter but as an emergent property arising from multiple interacting microbial processes.[9,10] Explicitly modeling microbial growth and respiration as separate, dynamic modules allows simulations to capture their asynchronous responses and directly match empirical CUE measurements from isotope-labeling studies, thereby substantially reducing model uncertainties.[9] Furthermore, linking microbial growth to the associated necromass accumulation rather than associating CUE with SOC accumulation, as in the Century model, provides a more mechanistic understanding of the varied relationships between CUE and SOC.[2]

Emerging advanced molecular biotechnologies will help understanding the CUE components. Of these two CUE components, microbial growth is the less studied than respiration, as respiration is well documented. DNA- and RNA-based stable isotope probing enables direct tracking of isotopically labelled substrates into specific microbial taxa, allowing quantification of growth rates and corresponding CUE at both community and single-species

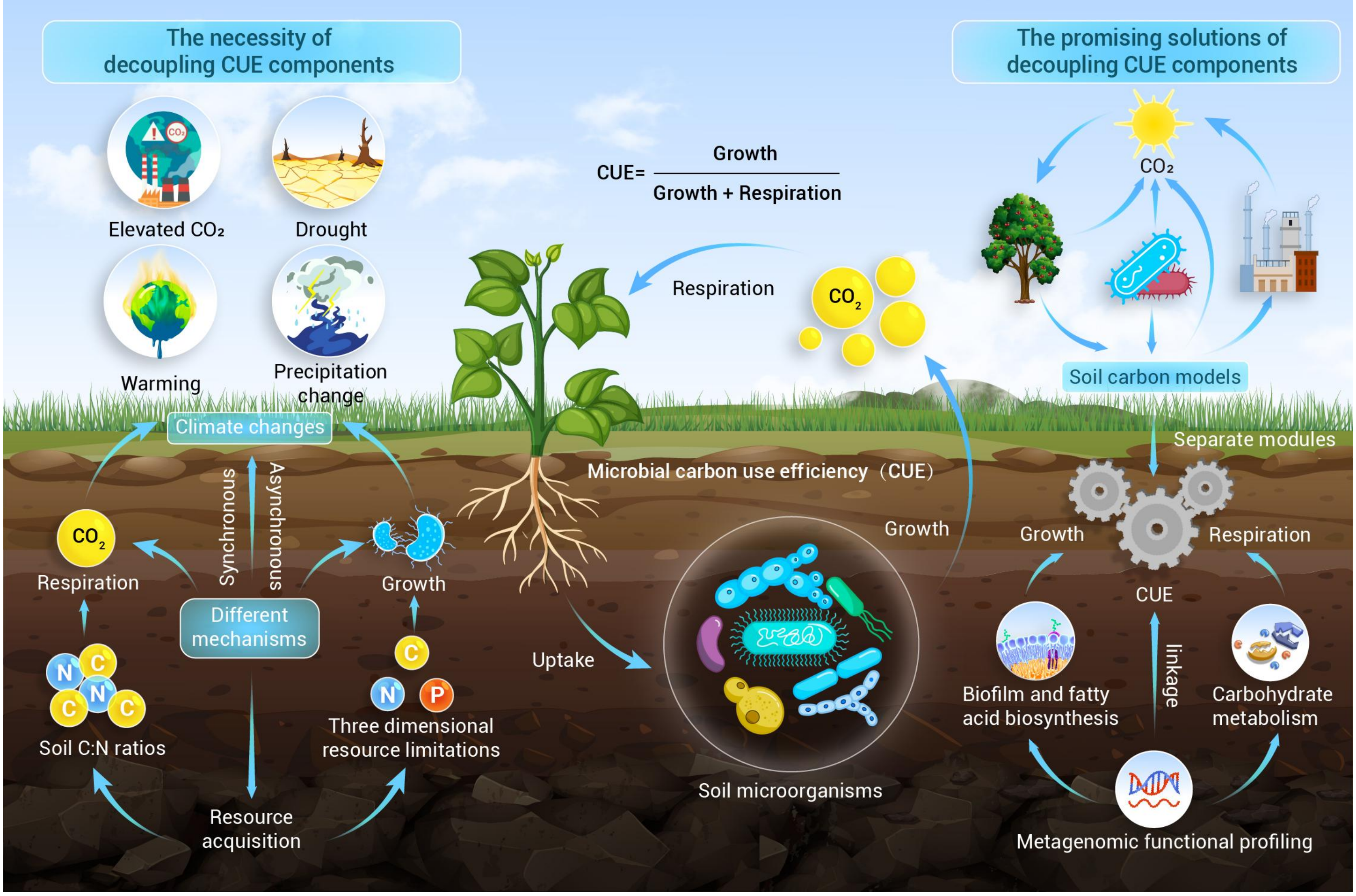

Figure 1. The conceptual diagram illustrates the necessity and promising solutions of decoupling microbial carbon use efficiency (CUE) into growth and respiration components.

scales.[10] For example, stable isotope probing coupled with high-throughput sequencing has been used to identify growing bacterial and fungal taxa, revealing which microbial groups dominate carbon assimilation and how their growth dynamics contribute to overall microbial CUE.[10] Metagenomic functional annotation provides insights into the potential functions of microbial communities, linking gene abundance in growth-related pathways (e.g., biofilm formation, fatty acid biosynthesis) and in respiration-associated pathways, such as carbohydrate metabolism (e.g., lignin, chitin, cellulose).[2] These technological innovations offer the possibility of exploring CUE components from the community to the single-species level, thereby opening promising pathways for advancing understanding of CUE and its ecological impacts.

However, the interpretations of microbial respiration and growth remain some limitations. First, current methods for estimating microbial growth rates rely primarily on isotope tracing techniques, which track the synthesis of key biomolecules such as DNA, lipids, or proteins.[10] These approaches typically involve the incorporation of stable isotopes (e.g., ^{13}C, ^{2}H, ^{18}O) into microbial biomolecules over a defined period, from which gross microbial growth rates can be inferred. Accurate isotope recovery requires controlled incubation conditions to minimize interference from environmental variability. However, technical constraints currently prevent the direct application of these methods in field settings. As a result, the potential rates of microbial respiration and growth measured under optimized incubation conditions do not correspond to *in-situ* rates. Second, widely used proxies, such as biomass carbon accrual and DNA synthesis, may systematically underestimate CUE by neglecting non-growth anabolic processes (e.g., extracellular polymeric substances production and the repair of damaged cell structures).[1] Third, CUE estimation methods based on various microbial growth proxies may produce divergent or even contradictory results, especially under climate change.[2] For example, the addition of ^{13}C-labelled substrates alleviated substrate limitation caused by nitrogen deposition, activating dormant microorganisms and thereby reducing CUE estimates, which contradicts results obtained using the $H_2^{18}O$ labelling method.[6] Therefore, selecting appropriate microbial CUE measurement methods under climate change is essential to minimize methodological artifacts. Fourth, interspecific interactions within microbial communities (e.g., predation, cross-feeding, endo- vs exoenzymes) can substantially modulate microbial respiration and growth dynamics, yet these processes remain underexplored.[4,10] To address these uncertainties, developing direct and *in-situ* measurement techniques, combined with investigating microbial interactions within the soil food web, is essential.

Altogether, decoupling CUE into growth and respiration components establishes a mechanistic framework that explicitly links apparent CUE to microbially mediated SOC dynamics (Figure 1). However, current methodologies for measuring CUE components, particularly the quantification of microbial growth rate, remain technically constrained. Future research should integrate multi-omics approaches to microbial physiology, cross-scale spatiotemporal observations, and process-explicit models to test conceptual and quantitative frameworks of how CUE components will determine overall variations in CUE and the associated the soil carbon cycling.

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FUNDING AND ACKNOWLEDGMENTS

This work was supported by the National Natural Science Foundation of China (Grant No. 32301405, 32471685), the Shaanxi Province Postdoctoral Science Foundation (Grant No. 2024BSHYDZZ018), and the Shaanxi Province Natural Science Foundation for Distinguished Young Scholar (Grant No. 2024JC-JCQN-32). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

AUTHOR CONTRIBUTIONS

Jiacong Zhou conceptualized the study and drafted the manuscript. Ji Chen led the overall direction and planning of the paper, and provided revisions of the manuscript. All authors contributed to the writing and editing process. All authors reviewed and approved the final version of the manuscript.

DECLARATION OF INTERESTS

Yakov Kuzyakov is an Editorial Board member of The Innovation Geoscience and was blinded from reviewing or making final decisions on the manuscript. Peer review was handled independently of this member and their research group. The other authors declare no conflicts of interest.