

Variation of soil microbial carbon use efficiency (CUE) and its Influence mechanism in the context of global environmental change: a review

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Soil microbial carbon utilization efficiency (CUE) is the efficiency with which microorganisms convert absorbed carbon (C) into their own biomass C, also referred to as microorganism growth efficiency. Soil microbial CUE is a critical physiological and ecological parameter in the ecosystem's C cycle, influencing the processes of C retention, turnover, soil mineralization, and greenhouse gas emission. Understanding the variation of soil microbial CUE and its influence mechanism in the context of global environmental change is critical for a better understanding of the ecosystem's C cycle process and its response to global changes. In this review, the definition of CUE and its measurement method are reviewed, and the research progress of soil microbial CUE variation and influencing factors is primarily reviewed and analyzed. Soil microbial CUE is usually expressed as the ratio of microbial growth and absorption, which is divided into methods based on the microbial growth rate, microbial biomass, substrate absorption rate, and substrate concentration change, and varies from 0.2 to 0.8. Thermodynamics, ecological environmental factors, substrate nutrient quality and availability, stoichiometric balance, and microbial community composition all influence this variation. In the future, soil microbial CUE research should focus on quantitative analysis of trace metabolic components, analysis of the regulation mechanism of biological-environmental interactions, and optimization of the carbon cycle model of microorganisms' dynamic physiological response process.

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Abstract

Soil microbial carbon utilization efficiency (CUE) is the efficiency with which microorganisms convert absorbed carbon (C) into their own biomass C, also referred to as microorganism growth efficiency. Soil microbial CUE is a critical physiological and ecological parameter in the ecosystem's C cycle, influencing the processes of C retention, turnover, soil mineralization, and greenhouse gas emission. Understanding the variation of soil microbial CUE and its influence mechanism in the context of global environmental change is critical for a better understanding of the ecosystem's C cycle process and its response to global changes. In this review, the definition of CUE and its measurement methods are reviewed, and the research progress of soil microbial CUE variation and influencing factors is primarily reviewed and analyzed. Soil microbial CUE is usually expressed as the ratio of microbial growth and absorption, which is divided into methods based on the microbial growth rate, microbial biomass, substrate absorption rate, and substrate concentration change, and varies from 0.2 to 0.8. Thermodynamics, ecological environmental factors, substrate nutrient quality and availability, stoichiometric balance, and microbial community composition all influence this variation. In the future, soil microbial CUE research should focus on quantitative analysis of trace metabolic components, analysis of the regulation mechanism of biological-environmental interactions, and optimization of the carbon cycle model of microorganisms' dynamic physiological response process.

Introduction

It is the worldwide agreement to deal with climate change by jointly controlling and slowing global warming by effectively increasing carbon (C) retention and reducing C emissions in a reasonable manner [1]. It is critical to accurately simulate and predict the interaction between global warming and the earth's ecosystems, particularly the feedback effects and mechanisms of

terrestrial ecosystems on global warming, to formulate effective measures to increase sinks [2], [3]. A large number of studies have found that global warming encourages the release of soil carbon, resulting in positive feedback on global warming [2], [4]. Microorganisms, on the other hand, are increasingly being discovered to play a key role in regulating the feedback of terrestrial ecosystems to global changes, and may even alter the expected feedback effects [5]–[7]. Long-term warming, for example, reduces the decomposition of soil organic carbon by inhibiting microbial biomass and enzyme activity. Microorganisms' physiological metabolic processes, as well as their responses and adaptations to changes in the external environment, have become crucial to the terrestrial ecosystem's feedback effect [5].

Soil microbes are involved in almost all material transformation processes in the soil and connect the material circulation of the soil, biosphere, atmosphere, hydrosphere, and lithosphere. The carbon utilization efficiency of soil microorganisms (Microbial carbon use efficiency, CUE), that is, the microorganisms' ability to convert absorbed carbon into biomass carbon, is directly related to their growth. The microbial CUE is set as a constant in many soil C cycle models [8]–[10]. Field observations and indoor cultivation experiments, on the other hand, contradict this hypothesis. Changes in the external environment and nutrient conditions can have a significant impact on soil microbial CUE. According to studies, soil microbial CUE increases as soil nutrient availability increases [11], [12] and decreases as temperature rises [5], [13]. However, there is a lack of consensus on the impact of these potential factors. Water stress, for example, inhibits the growth of microorganisms and CUE, according to studies conducted on the prairies of North America [14]. [15] discovered, however, that lowering soil water content did not affect soil microbial CUE. These disparate findings reflect a lack of understanding of soil microbial CUE variation and the mechanisms that influence it, limiting accurate simulation and prediction of terrestrial ecosystem feedback [16].

Laboratory data, conceptual and quantitative models, and, to some extent, field-based experiments are all contributing to the development of microbial CUE concepts [1]–[3]. However, in order to effectively incorporate agricultural C sequestration, this information must be applied to the complexities and variation of soil microbial carbon use efficiency (CUE) and its impact mechanism in the light of global environmental change. In this light, we illustrate areas where information is missing, such as the complexities of microbial population abiotic, biotic, and interaction interactions, which may be crucial in accurately predicting management outcomes of soil microbial CUE. We think about these uncertainties in terms of influence mechanisms that could improve CUE in soil ecosystems. Many methodological problems have recently been discussed [4] but here we concentrate on the wider influences of other factors on CUE that continue to challenge C sequestration in soil ecosystems

The purpose of this current review is to provide a comprehensive understanding of the variation characteristics of soil microbial CUE and its influencing factors, and highlights the focus of future research, by combing and analyzing the existing literature, all to improve the current earth system model and provide a theoretical foundation for scientist, researchers and relevant stakeholders to predict future climate change.

Survey methodology

To ensure an inclusive and unbiased analysis of literature and to accomplish the review's objectives, a comprehensive analysis of published articles on soil microbial carbon use efficiency was conducted using the Science Direct (<http://sciencedirect.com>) database, Web of Science, and Google Scholar. The following keywords were used to retrieve relevant literature: "soil microbial carbon use efficiency", "soil microorganisms", "ecological stoichiometry", "microbial community", and "nutrient limitation in soil ecosystem". While current publications between 2014 and 2019 were considered, publications that did not fall within this time period but contained critical information and were relevant to the review's objectives were also considered. Additionally, the reference lists of the retrieved literature were combed for additional pertinent publications. It is worth noting that this review presents a cross-section of studies on soil microbial carbon use efficiency and does not include all studies on the subject.

Definition of soil microbial carbon utilization rate

Through photosynthesis, vegetation converts CO₂ in the atmosphere into organic matter, forming the ecosystem's net primary productivity. To realize the biogeochemical cycle of materials and energy in the ecosystem, the majority of vegetation productivity must be reduced to inorganic nutrients by decomposer-soil microbial decomposition and mineralization, and then absorbed and used by vegetation. Microorganisms' physiological metabolic process is a combination of assimilation and alienation metabolism. Microorganisms convert part of the photosynthesis of plants into microbial biomass, while the rest is released into the atmosphere via respiratory metabolism. Microbial carbon utilization efficiency [12], [17], also known as microbial growth efficiency or substrate utilization efficiency, is the efficiency with which microorganisms convert vegetation productivity into microbial biomass in this process [18]–[20]. Soil microbial CUE is an important ecological parameter in the soil C cycling process. It has a direct impact on the ecosystem's C retention time and turnover rate, as well as the soil's C storage capacity [7], [21], [22].

In ecological research, microbial CUE is usually expressed as the ratio of microbial growth (μ) to absorption (U) [12], [17], that is, $CUE = \mu/U$. Microorganisms absorb C from the outside world mainly for microbial growth (μ), respiratory metabolism (R), secretion of extracellular enzymes and metabolites (EX), and microbial death (BD) (Figure 1). According to the principle of conservation of mass, microorganism U is expressed as;

$$U = \mu + R + EX + BD$$

Among them, soil microbial respiration (R) includes the respiration produced by microorganisms for growth (R_G), maintenance (R_M), extracellular enzyme production (R_E), and overflow process (R_O) [12], and is expressed as:

$$R = R_G + R_M + R_E + R_O$$

According to the definition of CUE and the mass conservation equation, the microbial CUE is expressed as:

$$CUE = \frac{\mu}{U} = \frac{\mu}{\mu + R_G + R_M + R_E + R_O + EX + BD}$$

In natural ecosystems, EX and BD are usually difficult to determine and relative to growth and respiration. The amount of EX and BD is very small and often considered negligible [12]. Therefore, CUE is generally considered to be a balanced relationship between the two processes of μ and R, that is,

$$CUE = \frac{\mu}{U} = \frac{\mu}{\mu + R}$$

This definition is widely used in current microbial metabolism and soil carbon cycle models [12], [17].

Determination method of soil microbial carbon utilization

Indoor culture, in combination with a mass conservation method and a marker tracing method, is the most common method for determining soil microbial CUE. The method of mass conservation entails directly measuring the change in mass or concentration of a substance and calculating the CUE using the principle of substance conservation. The purpose of the marker tracking method is to effectively track the substrate's utilization path by labeling it and calculating the ratio of substrate used for growth and respiration for determination. It is currently a widely used method. Existing analysis methods can be roughly divided into methods based on microbial growth rate measurement, methods based on microbial biomass measurement, methods based on substrate absorption rate measurement, and methods based on substrate concentration change determination based on different research methods and research objects (microorganisms or substrates). Each method has its own set of benefits, drawbacks, and application range (Table 1).

The growth rate method

One of the earliest measurement methods is the growth rate method. It determines the microbial CUE by measuring the rate of microbial biosynthesis and respiration directly. Using ^3H -thymidine, ^3H -leucine, and other labeling substrates, the synthesized nucleic acid or protein is separated using trichloro-acetic acid digestion, combined with radioisotope analysis, and it is determined that microorganisms synthesize ^3H -thymidine into DNA. Alternatively, the rate at which ^3H -leucine is converted to protein [23]–[25]. This method is simple and precise, and it is primarily used in aquatic ecosystems. Use heavy water H_2^{18}O labeled with ^{18}O for cultivation in terrestrial soils, measure the amount of DNA synthesized by microorganisms from the water of ^{18}O , and calculate the soil microbial CUE by combining the microbial DNA and biomass C conversion coefficients. This method can directly measure a microorganism's biosynthesis rate, but it's mostly used for short-term cultivation [26], [27].

Biomass method

CUE is typically calculated in terrestrial ecosystems, such as soil, based on changes in microbial biomass. To determine the change in microbial biomass, a labeled activated organic carbon is added as a substrate for indoor culture, along with a chloroform fumigation method. This method is easy to use and maneuver, and it is a widely used standard method. However, because capturing the growth of microbial communities and maintaining respiration in a short period is difficult, the rate of conversion of active markers to biomass measured by this method in a short period is not completely equivalent to the growth rate of microorganisms, but rather the absorption rate of the community, resulting in the phenomenon of overestimation [28]–[30].

Substrate absorption rate method

The substrate absorption rate method is used to calculate the CUE by observing how the substrate changes over time. ³H-thymidine, ³H-leucine, and other labeling substrates are used in this method, and a short-term indoor culture is used to determine the rate of absorption and utilization. This method, unlike the microbial biomass measurement method, accounts for the loss of microbial products. However, determining the absorption rate of the substrate is usually difficult and is only appropriate for short-term indoor culture analysis.

Substrate concentration change method

The substrate concentration change method, like the substrate absorption rate method, measures CUE in terms of substrate change. After a period of indoor culture, this method adds high concentrations of substrates (glucose, acetic acid, etc.), measures the changes in substrate concentration, and calculates CUE based on the respiratory volume during the same period. This method usually does not necessitate isotope labeling of the substrate, but it does necessitate a substrate medium with a high concentration. The metabolism and secretion processes of microbial products are taken into account because this method necessitates a certain amount of culture time.

Stoichiometric method

The stoichiometric method calculates CUE based on the stoichiometric limit theory of elements and does not require direct measurement of CUE. It's widely used in models of soil and litter decomposition [17], [31]. According to the stoichiometric balance theory, when the ratio of essential elements (such as N, P) and carbon in exogenous nutrients is lower than the N/P: C element ratio threshold required for optimal microorganism growth, these Constraints on the effectiveness of elements will affect microorganism growth. $CUE = A_E \times B_{C:E} / TER_{C:E}$ is a first-order functional relationship between CUE and the nutrient element measurement ratio. A_E stands for absorption efficiency of essential elements (E), $B_{C:E}$ stands for the C: E ratio of microbial biomass, and $TER_{C:E}$ stands for the C: E ratio threshold required for optimal microorganism growth [32]–[34]. Although this method has a theoretical foundation, does not

require experimental measurements, and can be parameterized and simulated, it is an empirical relationship that is primarily used in the simulation of soil carbon cycle process models.

Variability of soil microbial carbon utilization rate

Soil microbial CUE is not constant in natural ecosystems. Microorganisms would only assimilate organic matter and completely assimilate the substrate in an ideal state, so the carbon utilization rate would be 1. Microorganisms' growth, on the other hand, is always accompanied by the consumption of respiratory metabolic products. Microorganisms have a maximum CUE (CUE_{max}) of less than 1 due to thermodynamic constraints [35], [36]. Microorganisms' actual growth is governed by their stoichiometric balance, which shows that CUE varies with changes in essential element absorption efficiency (E), the microorganisms' C: E ratio, and the optimal growth C: E ratio threshold. When the nitrogen absorption efficiency $A_N=1$, the soil microbial CUE can approach the maximum CUE when the C: N ratio threshold $TER_{C:N}$ is 15 ($CUE_{max} = 0.6$); when the $TER_{C:N}$ is 30, the soil microbial CUE drops to 1/2 of CUE_{max} ($CUE_{max}/20.3$). Because A_N is usually less than one in the real world, it's difficult for microorganisms' actual CUE to reach CUE_{max} . The results of three different methods of ATP generation, electron transfer, and energy conversion show that the actual maximum CUE of microorganisms is around 0.6 due to thermodynamic limitations [35]. After accounting for the maintenance of metabolic consumption by microorganisms, [28] found that the maximum thermodynamic CUE is around 0.55.

The soil microbial CUE can range from 0.2 to 0.8, according to the integration results based on measured data. [28], [37] used a stoichiometric model of ecological enzyme activity, biomass composition, and nutrient concentration to find that the average soil microbial CUE is around 0.29, which is close to $CUE_{max}/2$. The average soil microbial CUE is about 0.270.11, according to the estimation result based on the C: N element stoichiometric equilibrium equation, which is similar to the estimation result based on the C: P element stoichiometric equilibrium equation (0.250.12) [17]. However, the results of the experiments show that the microbial CUE in different soil layers varies. For example, the CUE of microorganisms in the mineral layer (0.2840.005) is higher than the CUE of microorganisms in the organic layer (0.2050.008) [38]. The CUEs of different microbial populations are also different. Based on an integrated analysis of experimental observation data, [39] discovered that the CUE of bacteria is around 0.3360.213, which is higher than that of fungi (0.3260.196). The CUE of soil microbial varies depending on the type of vegetation. The research and study of [40] on Siberian vegetation transects revealed that the CUE of soil microorganisms decreased as they progressed from the meadow steppe to the Taiga forest and tundra.

Soil microbial CUE is usually set as a parameter in the current large number of biogeochemical cycle models, with values ranging from 0.25 to 0.6. (Table 2). Because different substrate compositions and other influences are taken into account in different biogeochemical models, the CUE parameter values vary. For example, the decomposition of underground and above-ground organic matter in the CENTURY model uses different soil microbe CUs of 0.45 and 0.55,

respectively [8]. The Daisy, NCSOL, ICBM, and other models take carbon pool activity into account. CUE is 0.6 for activated carbon pools and less than 0.6 for inert carbon pools [9], [10], [41] (Table 2). However, [31] pointed out that measured soil microbial CUE results are frequently lower than the model's preset value, implying that the current model understates the true hetero-oxygen respiration flux to some extent.

Influencing factors of soil microbial carbon utilization.

Thermodynamics, physiology, and ecology, as well as environmental factors like temperature and moisture, soil texture, substrate, and nutrient availability, and microbial community composition, influence soil microbial CUE.

Thermodynamic limit

Microorganisms' carbon absorption process is a combination of assimilation and alienation. Microorganisms convert photosynthesis from vegetation into their biomass, but this is always accompanied by the metabolic consumption of their respiration. Microorganisms have a theoretical maximum CUE of about 0.8 at the thermodynamic limit [36]. This indicates that microorganisms can use no more than 80% of absorbed organic C for their growth and that at least 20% of the C must be used to maintain the energy consumption of breathing. However, the actual soil microbial CUE is difficult to reach the theoretical maximum because the microbes still need to invest more energy in processes like respiration and nutrient absorption due to physiological and ecological environmental constraints.

Limits of ecological environmental factors

Temperature, humidity, precipitation, and soil moisture all influence microbial metabolism, altering the balance between and R and thus affecting CUE [5], [12]. [5], [12], [13], [42], [43] have found that soil microbial CUE has a negative feedback on temperature increase, with CUE decreasing as temperature rises. This is because, when the temperature is controlled, microorganisms' growth and metabolic rate increase as the temperature rises [44]–[46]. However, the temperature sensitivity of microbial respiration metabolism is higher than that of growth response [44], and microbial respiration increases faster than microbial growth, reducing CUE [5], [43], [47]. According to [48], soil microbial CUE decreased by about 0.009 for every 1°C increase in temperature. Under high-temperature stress, the negative feedback effect of microbial CUE is more pronounced [42]. According to the simulation results, 30 years of continuous temperature rise has reduced the proportion of absorbed C used for microbial growth, lowering the CUE from 0.31 to 0.23. [5]. However, some studies have found that the soil microbial CUE does not change significantly as the temperature rises [49], [50]. The composition of the substrate and the metabolic stage influence the response of soil microbial CUE to temperature. The CUE of soil microorganisms under the supply of a single-molecule structure substrate decreases with increasing temperature, while the CUE of soil microorganisms under the supply of a polymer structure substrate does not change with increasing temperature,

according to [51]. Long-term warming, according to some studies, will make microorganisms adaptable. Long-term warming will cause microorganisms to reduce their basal respiration rate [52]. The continuous warming experiment in Harvard Forest revealed that a 5°C increase in temperature over 18 years reduced the degree of soil microbial CUE, with an increasing temperature lower than the warming effect of two consecutive years [6]. Because microorganisms' thermal adaptability is linked to changes in microbial community composition, reduced nutrient availability, and changes in microbial metabolic pathways, as well as substrates and observation methods, there are still many unknowns about how microorganisms respond to temperature and how they do so.

Another important environmental factor that influences microorganism growth and respiration, and thus CUE, is soil moisture and water availability [14]. The effect of soil water availability on CUE is complex and variable, similar to the effect of temperature, and is influenced by intensity, duration, soil type, and soil water stress. Short-term water stress stimulates a microbial response to water stress, promotes microbes to reduce the impact of drought by increasing osmotic pressure regulation or short-term dormancy, and increases soil microbial CUE, according to studies [15], [53]. Long-term water stress, on the other hand, reduces the solubility and absorption of soil substrates, inhibiting microorganism growth [12], [54]. Long-term water stress, on the other hand, will increase the metabolic consumption of microorganisms, lowering CUE [14]. The CUE of soil microorganisms in an anaerobic environment is lower than in an aerobic environment, according to studies [55]. The metabolites of soil microorganisms are released from CO₂ to CH₄, which cannot be completely oxidized, and CUE decreases in an anaerobic environment [56].

Substrate quality and effectiveness

Microorganisms use soil organic carbon and vegetation litter as a source of food. Soil microbial CUE will be affected significantly by substrate quality [16]. The different material compositions of the substrate, the decomposition process, the degree of reducibility, and the effectiveness all contribute to this effect. Complex substrates (such as lignin and phenols, for example) necessitate more enzymatic decomposition reactions, which increases microorganism respiratory metabolism and lowers CUE [51], [57]. Degradation of refractory substrates increases extracellular enzyme metabolism and lowers CUE [58]. The geographic distribution of soil microorganism CUE is primarily influenced by differences in the quality of the soil substrate at various points, according to [40].

The degree of C reduction of the substrate (γ_S) is another important factor that affects the CUE of soil microorganisms. The degree of C reducibility refers to the chemical energy per mole of C and is usually expressed by the electron equivalent per mole of C. The γ_S of the main substrate used by microorganisms is usually in the range of 3-5 (such as organic acids, glucose, carbohydrates, and lipids), which is equivalent to the degree of C reduction of soil microorganisms ($\gamma_B \approx 4.2$) [35]. When the γ_S of the substrate is lower than the microbial γ_B , the CUE of soil microorganisms is lower because the energy per unit of the substrate cannot meet

the energy requirement of a unit of biomass production [35], [36]. The analysis results of 16 substrates CUE with different degrees of reduction showed that sugar CUE (0.667) > amino sugar CUE (0.601) > amino acid CUE (0.551) > organic acid CUE (0.498).

The availability of substrate nutrients will also have an impact on soil microbial CUE. Microorganisms will respond to nutrient changes by changing the carbon assimilation pathways regulated by their chemical enzymes when the availability and composition of nutrients changes [59], [60]. A large number of studies have found that as nutrient availability increases, soil microbial CUE increases [11], [12]. The microbial carbon absorption rate and nutrient concentration have a saturation function relationship. Microorganisms will maintain the optimal carbon absorption rate to meet the absorption system's resource consumption when resources are limited [37], [60]. When the availability of nutrients increases and the nutrient concentration exceeds the microorganisms' equilibrium concentration, carbon absorption increases, increasing CUE. Nutrient restriction, on the other hand, will lower CUE. The microorganism's decomposition and synthesis, as well as the coupled metabolic process, will be altered by nutrient restriction, which will increase metabolites such as extracellular enzymes and polysaccharides, and a decrease in CUE [61], [62]. This has also been proven by a large number of N addition experiments. The addition of nutrients such as nitrogen can either stimulate or inhibit microorganism activity and respiration metabolism. Microbes have a high CUE, especially in environments limited by N elements [19], [63]–[65]. The addition of nitrogen boosts microorganisms' ability to use active carbon [65]. Studies have also shown that after long-term N addition, the active C pool decomposes gradually, and the microbial community becomes restricted by energy such as C, lowering the CUE of soil microorganisms. More in-depth long-term observational studies are needed to reveal how microorganisms respond and adapt to changes in nutrient availability, as most nutrient addition experiments are still limited in time. Soil microorganisms will adjust and redistribute resources within cells to meet the demand for a variety of nutrient elements, which will further affect microorganism growth and CUE [66]–[68]. When microorganisms are restricted by a nutrient, they will expend more energy to obtain the missing nutrient elements, inhibiting microorganism growth and CUE [11], [12]. When microorganisms are restricted by the P element, for example, they will increase the input for P element resource acquisition, lowering CUE [28]. Experiments have shown that nutrient deficiency inhibits microorganism growth and lowers CUE [51]. This nutrient scarcity is usually the result of the availability of multiple nutrients being constrained at the same time [28].

Limits of ecological stoichiometry

Changes in the stoichiometric ratio of the substrate's elements have a significant impact on microorganism growth and CUE [12], [69]. Decomposer microbes have a stable stoichiometric ratio of elements, which differs from the external environment's and the decomposing substrate's stoichiometric composition. According to studies, soil microorganisms have a C/N ratio of about 7–8.6 [69]–[71], which is higher than plankton (6.6) and aquatic organisms (8.3) but lower than soil organic carbon (12.3). (18.2–75). Soil microorganisms have a C/P ratio of about 23–60 [69],

[70], which is much lower than plankton (106), aquatic ecosystems (166), soil organic carbon (72), and vegetation litter (100-837) [69]–[73]. To help maintain their stoichiometric balance, soil microorganisms will preferentially absorb and utilize the elements that are most suitable for their growth, according to the stoichiometric restriction theory. It is conducive to the mineralization of elements when the ratio of the C content of the substrate to the essential element E content (C: E) is lower than the threshold value of the element ratio required for optimal microorganism growth (TERC: E); in TERC: E, it is conducive to the retention of elements. Soil microorganisms are C-limited when decomposing substrates with high N and P element content, and CUE is higher. When the content of N and P elements in the decomposition substrate is low, soil microorganisms may respond in one of two ways: they may inhibit substrate C and nutrient absorption, or they may release excess C through overflow respiration or metabolic secretions [34]. The first reaction does not affect microbial CUE, but the second reaction reduces microbial CUE in the soil due to increased respiratory metabolism and secretion.

There is a negative correlation between soil microbial CUE and soil organic matter, C: N, and C:P ratios, according to numerous studies [32], [38], [39]. The soil microbial CUE in farmland and deciduous forest decreased as soil soluble C: N increased, according to [64]. [40] investigated the variation of soil microbial CUE at various altitudes and found that as the latitude increased, the soil C: N increased, and the soil microbial CUE decreased.

Composition of microbial community

Because different microbial populations decompose and absorb the organic matter at different rates, the structure and composition of the microbial community have an impact on soil microbial CUE [74], [75]. Fast-growing microorganisms that use the 'opportunity' growth strategy are more adapted to high-nutrient environments and have lower CUE than slow-growing microorganisms [76], [77]. The CUE of a microbial community dominated by fungi is often higher than that of a microbial community dominated by bacteria, according to [78]. Fungi have a wider C: N:P variation range than bacteria, and their C: N ratio is higher than bacteria's, which has a higher requirement for C and has a high CUE [76]. However, some studies have found that the CUE of soil communities does not differ significantly [18], [19]. [19] found no significant difference in CUE between communities with a high fungi/bacteria ratio and communities with a low fungi/bacteria ratio, which was 0.59 ± 0.02 and 0.61 ± 0.01 , respectively, in a study of farmland ecosystems. Increased substrate C: E can also increase the CUE of the fungal community while decreasing the CUE of the bacterial community, according to studies [76]. The microbial community's interspecific competition will reduce the microorganisms' CUE [79].

Because the microbial community's composition is highly susceptible to changes in the external environment and human activities, as well as changes in the substrate's quality and composition, quantifying the differences in the composition of different communities remains a work in progress [18], [76].

Conclusions

Problems and Prospects

Analysis of Research Scales

Microbial CUE generally refers to the efficiency of microorganisms in absorbing and using C and converting it into their products, but it has specific time and space properties [80]. Microbial CUE is divided into three levels by [81]: population CUE (CUE_p), community CUE (CUE_c), and ecosystem CUE (CUE_e). These three levels of CUE describe the biosynthesis efficiency of microorganisms at various scales, from population to ecosystem, and include a variety of physiological and chemical processes in microbes. [81]. A large number of early studies concentrated on microbial CUE at the population and community levels. More and more research has recently focused on changes in the ecosystem-scale CUE and how it responds to the environment [82], [83]. The comparison of CUE results obtained under various research scales, observation stages, and measurement conditions will make the analytical results more difficult and uncertain [80]. For accurate comparison and application in future CUE research, it is critical to more clearly identify the specific research scale and process of microbial CUE.

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Analysis of metabolic components

The current soil CUE calculation method is not consistent, and there is an overestimation problem. Microorganisms' respiration is made up of several components, including growth respiration for growth, maintenance respiration for organism operation, secreting extracellular enzymes respiration, and overflow respiration. Extracellular enzymes and overflow respiration components are rarely considered in most current microbial CUE studies, which mostly focus on growth or growth and maintenance respiration of microorganisms [12]. As a result, CUE is overestimated, and the CUE calculation results are extremely disparate. The loss of extracellular enzymes and overflow respiration must be fully considered in future research. Select an appropriate culture time to observe the entire process, including the metabolism and secretion of microbial products, in the measurement process of indoor culture, for example. Enzyme

production and conversion are also measured using a combination of isotope labeling and metabolomics.

Research on multi-element interactions

The impact of environmental changes on soil microbial CUE, as well as the response and feedback of soil microbial CUE to global changes, remain highly uncertain due to the complex soil-plant-microbe interaction. Is the soil microbial CUE, for example, decreasing as the temperature rises? Is it possible to adjust the temperature? How will long-term exogenous nutrient input affect soil microbial CUE? Because the response and adaptation of soil microbial CUE to environmental changes is complicated and variable due to differences in substrate quality, effectiveness, element stoichiometric composition, microbial activity, and community composition [47], it is necessary to integrate and discuss the physiological response process of microbial CUE in future process mechanism research.

Optimization of soil carbon cycle model

In the soil C cycle model, microbial CUE is an important parameter. Many existing models assume CUE is constant or only take it into account infrequently, making it impossible to accurately simulate the dynamic response process of soil microbial CUE to changes in external environmental conditions and its impact on the soil C cycle [7], [84]. Some models represent microbial CUE as a first-order functional relationship between temperature, nutrient availability, or nutrient element ratio, ignoring physiological processes such as changes in microbial metabolic pathways, community composition, and inter-species relationships. Furthermore, the microbial respiration process is generally considered to be mainly related to the microbial C balance, but not to the N balance, in a large number of biogeochemical models, and it lacks consideration of the dynamic changes of the P element [28], [34]. The balance of elements, the dynamic response process of microorganisms to changes in external environmental conditions, and changes in physiological processes such as microbial metabolic pathways, community composition, inter-species relationships, and microbial turnover must all be considered in the future optimization of the soil C turnover model.

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Table 1(on next page)

tables

Table 1. Different microbial carbon use efficiency measurement methods

Measurement	Microbe			Substrate		Model
Measurement principle	Based on growth rate		Based on changes in biomass	Based on absorption rate	Based on absorption rate	Based on stoichiometric ratio
expression	$CUE = \frac{\mu}{\mu + R}$		$CUE = \frac{\Delta C_B}{\Delta C_B + R_{CUM}}$	$CUE = \frac{U}{U - R}$	$CUE = \frac{\Delta C_S - R_{CUM}}{\Delta C_S}$	$CUE = \frac{\Delta A_E}{TER_{CE}}$
Measurement parameters	Microbial growth rate and respiration		Changes and accumulation of microbial biomass respiration	Substrate absorption rate and respiration	Changes in substrate concentration and cumulative respiration	Element E absorption rate, microbial C:E and the threshold element for optimal growth of microbes
Substrate	³ H-thymidine, ³ H-leucine	¹⁸ O-H ₂ O	¹⁸ C-glucose, ¹⁴ C-acetate	¹³ C-glucose, ¹⁴ C-acetate, ³ H-thymidine	sugars, amino sugars, amino acids and organic acids	
Label needed	needed	needed	needed	needed	not needed	
time scale	short time	short time	short time	short time	Long time	
Advantages	Direct measurement of microbial biosynthesis rate	Direct measurement of microbial biosynthesis rate	Simple and easy to operate	Consider microbial productivity flow	Consider the loss of microbial productivity	No measurement required
Disadvantages	Unsuitable for soil	Only suitable for short-term determination	Need to be converted into biomass, overestimating CUE	Only suitable for short-term determination	Need to measure the adsorption of the substrate and provide a high concentration of the substrate	There are model assumptions, empirical coefficients
Application field	Waters	land	land	land	land	
Reference	[23]–[25]	[26], [27]	[15], [28]	[29]	[13], [14]	[30]

CUE, carbon utilization; μ , microbial growth rate; R, total microbial respiration rate; U, substrate absorption rate; ΔC_B , change in microbial biomass; ΔC_S , change in substrate concentration; R_{CUM} , cumulative respiration rate; A_E , The absorption efficiency of element (E); BC: E, the ratio of C: E of microbial biomass to the C; $TER_{C:E}$, C: required for optimal growth of microorganisms

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Table 2. Variation of microbial carbon use efficiency

Type of model	Carbon use efficiency	Attributes	References
Measured values	0.39		[44]
	0.58		[45]
	0.44-0.73		[46]
	0.58-0.70		[47]
	0.26-0.68		[48]
	0.45-0.75		[28]
	0.46-0.62		[15]
	0.35-0.83		[14]
	0.24±0.08		[49]
	0.49-0.79		[16]
	0.42-0.84		[42]
Stoichiometric model	0.29		[39]
Q-model	0.25		[50]
	0.45	Decomposition of underground organic matter	[8]
CENTURY-model	0.55	Decomposition of surface organic matter	[8]
Daisy, NCSOIL, ICBM model	0.6	Activated carbon pool	[9], [10], [43]
Daisy, NCSOIL, ICBM model	<0.6	Most inert carbon pools	[9], [10], [43]

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Figure 1

Figure 1. microbial metabolic components and equilibrium equation

Sketched according to the definition of soil microorganism CUE and the mass balance equation of soil microorganism metabolism proposed by [12] ; U, microbial carbon absorption; μ , microbial growth; R_G , microbial growth respiration; R_m , microbial maintenance respiration; R_E , extracellular enzyme Respiration; R_O , overflow respiration; EX, secretion of extracellular enzymes and metabolites; BD, microbial death.

