Advancing the mechanistic understanding of the priming effect on soil organic matter mineralisation

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TITLE

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SUMMARY **(320 Words)**

1 The priming effect (PE) is a key mechanism contributing to the carbon balance of the soil ecosystem. Almost 100 years of research since its discovery in 1926 have led to a rich body of scientific publications to identify the drivers and mechanisms involved. A few review articles have summarised the acquired knowledge; the last major one was published in 2010. Since then, knowledge on the soil microbial communities involved in PE and in PE + C sequestration mechanisms has been considerably renewed.

2 This article reviews current knowledge on soil PE to state to what extent new insights may improve our ability to understand and predict the evolution of soil C stocks. We propose a framework to unify the different concepts and terms that have emerged from the international scientific community on this topic, report recent discoveries, and identify key research needs.

3 Seventy percent of the studies on the soil PE were published in the last 10 years, illustrating a renewed interest for PE, probably linked to the increased concern about the importance of soil carbon for climate change and food security issues. Among all the drivers and mechanisms proposed along with the different studies to explain PE, some are named differently but actually refer to the same object. This overall introduces “artificial” complexity for the mechanistic understanding of PE, and we propose a common, shared terminology. Despite the remaining knowledge gaps, consistent progress has been achieved to decipher the abiotic mechanisms underlying PE, together with the role of enzymes and the identity of the microbial actors involved. However, including PE into mechanistic models of SOM dynamics remains challenging as long as the mechanisms are not fully understood. In the meantime, empirical alternatives are available that reproduce observations accurately when calibration is robust.

4 Based on the current state of knowledge, we propose different scenarios depicting to what extent PE may impact ecosystem services under climate change conditions.

KEY WORDS

Soil, Priming effect, Carbon cycle, minerals, enzymes, microbial actors, models, ecosystem services

1 INTRODUCTION

Soils host one of the main carbon (C) stores of our planet, around three times more than the atmosphere does (2,400 *vs*. 800 GtC) (Friedlingstein et al., 2019). Most of this C is stored in organic matter whose turnover controls soil fertility through the release of nutrients for plants. Soil Organic Matter (SOM) also releases huge amounts of CO_2 into the atmosphere, 7-fold more than anthropogenic emissions (Schlesinger and Andrews, 2000). Given the huge size of the soil organic C pool, any change in the soil C content and its dynamics at a global scale – even if tiny – is associated to great impacts in terms of food security and climate change (Dignac et al., 2017; Minasny et al., 2017). Consequently, preserving and even increasing organic carbon in soils is of prime importance to meet the food security challenge and mitigate greenhouse gas emissions (Minasny et al., 2017). This requires getting insights into the determining mechanisms of the soil carbon balance – i.e. mineralisation *vs.* sequestration.

The priming effect (PE) is a key mechanism contributing to the ecosystem carbon balance (Fontaine et al., 2007; Guenet et al., 2018). It corresponds to a change in the rate of SOM-C mineralisation by soil microorganisms resulting from the input of fresh organic matter (FOM) (Bingeman et al., 1953). The definition was later extended to almost any variation of microbial activities after an addition of molecule (e.g., toxic compounds; Kuzyakov et al. 2000), but the present review will focus on ~~C-related~~ PE as previously defined, and more precisely on the plant induced priming effect (PIPE) which includes the rhizosphere priming effect (RPE) but also more generally all priming induced by plant originated carbon inputs (Box 1). The PE occurs everywhere, but it has mainly been studied in soils (Bengtsson et al., 2018; see supporting information). It has long been viewed as a net soil C loss since the most frequent effect reported in the literature is a stimulation of native SOM mineralisation, up to 400 % according to the type of environment and/or soil conditions (Guttière et al., 2021; Chen et al., 2019; Perveen et al., 2019, Blagodatskaya & Kuzyakov, 2008). However, it can also be negative, with up to 50% reductions in soil carbon emissions (Lyu et al., 2018; Chen et al., 2019). As the PE is a complex process, its impact on global C fluxes is hard to grasp and should be considered as a whole, integrating feedbacks between the different and sometimes contrasting effects it causes: for example, the increase of SOM mineralisation has negative consequences on climate change, and the nutrients released from organic matter may be leached down the soil profile; but when the released nutrients are taken up by plants, the PE indirectly contributes to plant growth and additional C sequestration in the plant-soil system. Thus, the effect of PE variation on the net soil C balance is not trivial, particularly in the context of climate change because C inputs may globally increase through enhanced plant productivity, while soil C mineralisation may increase too due to higher temperature (Nishina et al., 2014). Consequently, better knowledge of the mechanisms involved in PE is of fundamental importance to improve our ability to control and predict the evolution of soil C stocks (Guenet et al., 2018; Chen et al., 2019), in agreement with the 2019 IPCC report on land (Shukla et al. 2019) that pointed out the need to better understand how PE will respond to climate change.

Since the pioneering studies that evidenced it (Löhnis, 1926) and due to its importance for C cycling, the PE has prompted a large body of research work to identify the drivers and mechanisms involved (Kuzyakov et al., 2000; Blagodatskaya & Kuzyakov, 2008). A bibliometric analysis of the scientific articles published in the field during the last 50 years shows however that 70% of all the articles are recent, *i.e.* published during the last ten years, and mainly motivated by the rising concern about the importance of soil carbon for climate change and food security issues. We provide as supplementary information a brief report of the main outputs of this analysis highlighting the dynamics of publication, the extent of the associated scientific network and the topical drivers of the publications (Supplementary information available from Zenodo: https://doi.org/10.5281/zenodo.6326056).

Based on these studies, it is clear today that the PE involves different microbial processes sometimes driven in opposite ways by environmental parameters. Soil properties, climate, land use (Bastida et al., 2019; Siles et al., 2022), but also the nature of the substrates entering the soil (*e.g.*, simple compounds, complex compounds, plant residues or living roots) and the way they are added (*e.g.* continuous *vs.* puse) all impact the intensity of priming effect. A few reviews have been published to summarise knowledge in the field. The last major one was published in 2010 (Kuzyakov, 2010). However, in the last ten years, studies aimed at characterising the microbial communities involved in soil processes such as PE have benefited from considerable technical progress providing deeper insights into microbial diversity and activity (Bouchez et al., 2016). In the same time span, the understanding of C sequestration mechanisms has undergone a paradigm change (Lehmann & Kleber, 2015). Therefore, it appeared important to update knowledge on PE mechanisms by integrating the findings of the last 10 years, which was the first objective of the present review. The second objective was to unify the different concepts and terms that emerged from the international literature on this topic. Finally, we identified and focused on specific points that need to be more deeply examined to evaluate and predict the size and the impact of the different mechanisms across space and over time.

2 UNIFYING THE DIFFERENT GENERATION MECHANISMS.

A large number of mechanisms have been proposed to explain PE generation (Table 1). Some of them are similar or even equivalent but have been named differently. This section (i) aims to clarify the different denominations, (ii) groups them according to their effect on C fluxes, and (iii) integrates them on a time scale. Box 1 gathers the terminology associated to the different pools of organic matter and types of PE on which we based our discussion.

2.1 Let's clarify the denomination of the different mechanisms.

The PE is usually measured as the difference between the CO_2-C released from an amended soil (excluding CO_2-C originating from the amendment itself) and from a non-amended control soil over a certain time period, leading to a "positive" or "negative" PE (Kuzyakov et al., 2000).

Negative PE have been attributed to "preferential FOM substrate utilization" by regular native SOM decomposers (Cheng 1999). SOM decomposers can also switch from SOM decomposition to the decomposition of FOM-decomposer necromass after intense predation (Cui et al. 2020). This process has been called "necromass recycling" and also leads to reduced SOM decomposition and mineralisation over time. Viral lysis has been suggested to generate more microbial necromass than predation by protists or nematodes (Kuzyakov and Mason-Jones, 2018), but nobody has yet published on the link between bacteriophages and PE.

Positive PE processes can be called "apparent" PE when they only result from the replacement of microbial cell C by C from the new substrate (labile fraction). Apparent PE have been described under 3 complementary processes (triggering effect, microbial activation, and pool substitution), depending on the amount of labile FOM added compared to the total microbial biomass (Blagodatskaya and Kuzyakov, 2008 – see Table 1).

Real positive PE have been attributed to multiple processes. Those called "stoichiometric decomposition" (Chen et al., 2014), and "mechanism 1" (Fontaine et al., 2003) refer to an acceleration of SOM decomposition generated by the increase in extracellular enzymes produced by FOM decomposers (Table 1). This implies that certain FOM and SOM compounds have chemical similarities (*e.g.*, a plant origin). Therefore, FOM should be at least partly polymerised (such as in residues, litter or dead roots). Both processes occur when N is not limiting, but SOM catabolites benefit SOM decomposers in "Mechanism 1", and FOM decomposers in "stoichiometric decomposition". Processes called "N-mining" (Chen et al., 2014) and "mechanism 2" (Fontaine et al., 2003) result from the energy brought by FOM catabolites, for SOM decomposers to break down biochemically recalcitrant SOM for nutrients. For both processes, the targeted SOM pool was supposed to be also of plant origin. One process has been called "co-metabolism" in different papers and corresponds to the assimilation of FOM and SOM catabolites by either FOM or SOM decomposers, without being aimed at N acquisition (Kuzyakov, 2000; Yu et al., 2018). Therefore, in terms of carbon, this process overlaps with previously-described mechanisms (either Mechanism 1 or Mechanism 2 and nutrient mining) and thus is not discriminant.

A new mechanism of positive PE has been proposed recently to explain the rhizosphere PE (Keiluweit et al., 2015). Roots can exude organic acids, which cause the release of labile organic compounds from protective associations with minerals, and then these compounds can be decomposed by microbes. As a large part of this mineral-associated organic matter (MAOM) is derived from microbial necromass – with a low C:N ratio – through the so-called "entombing effect" (Liang et al., 2017), many nutrients, historically considered as a relatively passive reservoir, can be remobilised by this process, that we called "Abiotically mediated PE" (see section 3).

2.2 Gathering mechanisms according to their effect on C fluxes

Two important parameters have to be considered to evaluate the impact of the different PE generation mechanisms on the dynamics and the fate of primed C.

Firstly, native SOM is a mixture of different pools characterised by different turnover rates depending on their biochemical nature and their accessibility to enzymes. The organic matter that enters the soil is mainly of vegetal origin. Plant tissues are composed of molecules easily (hemicellulose, cellulose) or less easily (lignins, polyphenols, phytates) broken down by microbial extracellular enzymes, hence fast to medium-long turnover rates (a few days to a few years – Derrien et al., 2006). In contrast, the SOM pools showing the lowest turnover rate (centuries) are composed of compounds from both plant and microbial sources, protected from enzymes by mineral association (Lehman & Kleber, 2015). Carbon primed from a SOM pool with a fast turnover rate should impact long-term carbon sequestration less than C remobilised from a pool with a long residence time.

Secondly, PE is often evaluated based on the change in CO_2 mineralisation rate, but respiration can be accompanied by incorporation of C into cell biomass (growth) (see Geyer et al., 2016 for a review). The efficiency of carbon incorporation into biomass (*i.e.*, carbon use efficiency, CUE) is calculated as the amount of microbial biomass produced *per* unit of resource consumed. The CUE of cells can vary between 0 (no growth but alive) to 0.85 (growth but still needing some energy for cell growth and maintenance) depending on their physiology and life strategy. The link between life strategy and CUE depends on the physiological status of microbes. R-strategists are actually less efficient than K-strategists in using their assimilated C during a resting phase, due to a costlier basal metabolism. But as these populations have higher maximal growth rates, during the growth phase when substrate is not limiting, a higher proportion of C is allocated to biomass instead of respiration. This leads to a globally higher CUE than that of K-strategists (Geyer et al., 2016). As PE generation mechanisms are consequences of organic matter decomposition, they are more related to growth phases of different populations than to their resting phases. Thus we consider that during a PE event, r-strategists have high CUE while K-strategists have low CUE. Therefore, primed SOM assimilated by high-CUE populations is likely converted into microbial biomass rather than mineralised into CO_2, and further stabilized via the so-called “entombing effect” (Lehman & Kleber, 2015; Liang et al., 2017). As a result, high-CUE populations increase the chance of moving C from a fast- or a medium-turnover SOM pool to a slow-turnover pool.

We classified the different processes proposed in the literature according to both previously-described parameters: the turnover rate of targeted SOM pool and the CUE of microbial populations assimilating its derived C (Table1). It is interesting to note that, to date, no study has revealed the SOM pool impacted by the negative PE.

2.3 Time scale integration of PE generation mechanisms.

When FOM enters the soil, its nitrogen content will help cells synthesize new enzymes for further FOM or SOM depolymerization. This phase of microbial turnover (apparent PE) first concerns high-CUE microbial populations and low-CUE populations depending on the size of the labile fraction of FOM (Figure 1). If the labile FOM pool exceeds the total microbial biomass and under non limiting N, SOM-decomposers will prefer the FOM substrate (negative PE) decreasing the regular SOM-C flux to the atmosphere. If the labile FOM pool is exhausted before the available N, FOM decomposer exoenzymes, liberated against the polymerized part of FOM will also attack SOM of vegetal origin. High-CUE populations will be more competitive than low-CUE populations under such conditions and will increase their biomass (stoichiometric PE). High-CUE population necromass will be rapidly recycled by low-CUE populations or stabilised by mineral association (Figure 1). When the soil or FOM-available N is exhausted, FOM catabolites will bring some energy to microbial populations able to catabolise recalcitrant SOM for N (N-mining), or to dissociate N-rich SOM from minerals, both population types having a low CUE. Nitrogen remobilised from SOM increases the soil nitrogen status and allows for a next phase driven by high-CUE populations (Fang et al., 2018; Vain et al., 2021).

3 ABIOTICALLY MEDIATED PE: CONCEPTS AND MECHANISMS

3.1 Mineral-associated organic matter (MAOM)

In models of organo-mineral associations, mineral phases involved in organo-mineral associations can be classified into three main categories: well-crystallised minerals, short-range order phases, and metallic monomers. Each category is associated with a distinct conceptual model of organo-mineral association (Figure 2):

- *Adsorption*: organic molecules are adsorbed onto the mineral surface of well-crystallised minerals (*e.g.*, smectite, vermiculite or goethite) (Kleber et al., 2007).
- *Coprecipitation*: organic molecules are coprecipitated with short-range order phases or amorphous small polymers of Al, Fe and Si (Basile-Doelsch et al., 2015; Tamrat et al., 2019). Co-precipitation is thought to be the dominant model as regards the amount of stabilised C (Rasmussen et al., 2018).
- *Complexation and bridging*: organic molecules are bound to monomers (single ions). The main metals involved in complexation are Al and Fe in acidic soils. At higher pH, Ca dominates the organo-mineral associations by cation bridging (Rowley et al., 2018). Cations surrounded by organic molecules form a tertiary structure described as “supramolecular aggregates” (Sutton & Sposito, 2005).

The existence of these different types of organo-mineral models should be taken into account when studying MAOM in order to understand PE mechanisms.

In each type of organo-mineral association model described above, an additional degree of complexity comes from the binding energies. Regardless of the model, the five following types of organic-inorganic bonds can be present: covalent bonding, electrostatic cation bridges, hydrophobic interactions, Van der Waals forces, and H bonding (von Lutzow et al., 2006). The binding strength varies very strongly depending on the type of bond (Newcomb et al., 2017). Therefore, the energy required to break these bonds and destabilise organic molecules is also a very important parameter in the control of the MAOM PE. However, while this parameter seems thermodynamically easy to conceptualise, its consideration in PE experiments is still in its infancy (Li et al., 2021).

The mineral-associated organic matter is less accessible but not fully inaccessible. The bonds between organic molecules and inorganic phases slow down OM degradation. Incubation studies have shown that MAOM is more difficult to mineralise than free OM, whatever the model (adsorption, coprecipitation or complexation) (*e.g.* Jones & Edwards, 1998; Saidy et al., 2015). The proportion of C mineralised during MAOM incubations reached a plateau which, depending on the compounds, barely reached the same proportion as in the control where OM was not associated with mineral phases. These experiments showed that (i) part of MAOM remained accessible to microorganisms but mineralisation was slowed down, and (ii) depending on the nature of the organic compounds and the nature of the mineral (*i.e.*, depending on the nature of the chemical bond), part of MOAM was not mineralised by microorganisms. Thus, rather than use a binary terminology tending to say that OM is stabilised or not in organo-mineral associations, a stabilisation gradient concept should be preferred and considered as a key parameter driving the potential of abiotically mediated PE.

3.2. Priming effect of mineral-associated organic matter

The above-mentioned experiments did not take the full complexity of soil functioning into account. When the physicochemical conditions of the soil solution are modified (changes in pH, redox conditions, ionic strength, composition), the speciation of the mineral phases and organic molecules can be modified, leading to an altered configuration of organo-mineral associations. During these changes, if OM becomes more easily accessible to microbial enzymes, accelerated decomposition (*i.e.*, a PE) may be observed.

The biotic impact on the physico-chemical parameters of MAOM leads to a direct and indirect PE pathways. Roots and microorganisms play an essential role in controlling the physicochemical conditions of the soil solution (Figure 2). Multiple factors impact these conditions. For example, vascular plant roots, fungi and bacteria release low-molecular-weight organic acids. These are mainly carboxylic acids like formic, oxalic, and acetic acid, but also aliphatic and aromatic acids (Clarholm et al., 2015 and references therein). Microorganisms may decrease the pH locally in microsites (Bonneville et al., 2011). Roots also release some easily metabolisable simple sugars (*e.g.*, glucose). They can stimulate microbial activity and growth, which may in turn lower the pH and the redox potential (Mabuza et al., 2020). These various examples show that the factors driving the destabilisation of MAOM are multiple and may be dependent on each other. The factors directly controlled by plant functioning are referred to as "direct (non-microbial) pathways". Conversely, in "indirect (microbial) pathways" root exudates mobilise MAOM indirectly through a sugar-mediated pathway dependent on microbial intermediaries (Keiluweit et al., 2015; Jilling 2021; Finley et al., 2018; Li et al., 2021). Whether the pathway is direct or indirect, whether it is located in the rhizosphere or in the residuesphere, it appears that the functioning of the biotic compartment (roots, bacteria and fungi) is a source of low-molecular-mass organic acids, and pH and Eh variations, all of which are likely to modify the bonding equilibrium of the organo-mineral associations and can be accompanied by an abiotically mediated PE.

The conceptual mechanisms of abiotically mediated PE include three types of reactions releasing mineral-bound C and making the compounds accessible to the extracellular enzymes of microorganisms (Figure 2):

- *Mineral dissolution* can be promoted by exudates. Ligand-promoted dissolution is accelerated by strong ligands such as organic acids (Wang et al., 2014; Li et al., 2018). Protonation of a mineral surface can also weaken metal-oxygen bonds and dissolve minerals (Stumm, 1997). Reductive dissolution can be driven by organic reducing agents such as phenols and aromatic acids (Vermeire et al., 2019). However, as Al is not very sensitive to redox variation, these redox processes mainly impact Fe-bearing mineral phases.
- *Replacement* is promoted by strong ligands such as organic acids, which sorb onto mineral surfaces and displace or release previously sorbed organic compounds from minerals (Li et al., 2021). Other metabolites are also implied in the release of MAOM through displacement of weakly bound compounds (Leineman et al., 2018; Mikutta et al., 2019; Jiang et al., 2021).
- *Direct depolymerisation* of mineral-bound organic compounds by extracellular enzymes can also occur on weakly bound OM, bypassing the desorption step (Wang et al., 2020).

4 ROLE OF ENZYMES IN PE

4.1 Enzymes involved in priming effect mechanisms

The type of enzyme involved in PE depends on (i) the chemical composition of the added substrate, (ii) the chemical composition of the native SOM, (iii) the nutrient availability, and (iv) the functional requirements of microorganisms, which differ amongst microbial communities. When the environment is not nutrient limited, FOM input is expected to increase the activity and biomass of high-CUE microbial communities presenting a high growth yield due to an increased activity of the FOM depolymerizing enzymes (Fanin et al., 2014; Fanin & Bertrand, 2016; Malik et al., 2019). For example, additions of plant residues stimulate plant cell-wall-degrading hydrolytic enzymes, and the resulting PE is directly related to enhanced degradation of plant-derived residues of the native SOM (Chen et al., 2014). Increased activity of microbial communities can also enhance the degradation of native SOM as a result of co-metabolism, *i.e.*, hydrolase activity yields enough energy and monomers to produce a panel of other enzymes degrading FOM, or/and the non-complex and accessible SOM (Blagodatskaya & Kuzyakov, 2008; Pascault et al., 2013).

When the environment is nutrient limited, microbial communities shift from high to low CUE, notably because nutrient limitation affects the community metabolism and reduces growth yield, while it favours investment in resource acquisition (Malik et al., 2020; Fanin et al., 2020). In this context, another type of co-metabolism directed to N-containing SOM is induced when N is not available or becomes exhausted at the late stages of decomposition. It is characterised by a high expression level of enzymes degrading N-containing compounds (Moorhead & Sinsabaugh, 2006; Chen et al., 2014), including hydrolytic chitinases and oxidases, which release N associated to complex aromatic compounds (Derrien et al., 2014). The resulting PE is directly related to enhanced degradation of N-rich SOM compounds that differ chemically from those of the added substrate.

4.2 Energy cost and return on investment

The activity of enzymes involved in PE implies benefits and costs. The major benefit from enzyme activity is the release of mineral nutrients and organic monomers and oligomers that can be taken up and assimilated by microbes. On the other hand, the costs of enzyme production include the C and nutrients necessary to build the backbone structure of the enzyme itself, but also the metabolic energy required for protein synthesis and enzyme excretion (Allison et al. 2014). Because extracellular enzymes have a short lifespan, a return on investment is necessary to maintain microbial growth, especially when resources are scarce in the environment. Nevertheless, the impact of the energy balance associated to enzymes involved in PE is still unknown.

A critical factor influencing the energy balance related to enzymes is the distance between the substrate and the enzyme producer. While some enzymes are directly attached to the plasma membrane of microbial cells or grouped into multi-enzyme complexes (named 'membrane enzymes' hereafter), like the cellulosomes dedicated to cellulose degradation, other enzymes are excreted far away from the cells (named 'exoenzymes' hereafter). When microbes are relatively near their substrates, the monomers produced by membrane enzymes are directly recognised by cell-wall receptors and transported into microbial cells, and this optimises resource uptake from the soil solution. The benefits of enzyme production often exceed the costs thanks to a high return on investment, and allow for microbial growth (Schimel & Weintraub, 2003). By contrast, exoenzymes are sent far away from microbial cells, up to a few mm (Gaillard et al., 1999; Poll et al., 2006; Védère et al., 2020). A significant portion of labile C released through enzymatic action may be lost to the enzyme producer (*i.e.*, leached to deeper soil horizons, immobilised in soil aggregates and/or taken up by other microorganisms) (Allison, 2005; Burns et al., 2013). As a consequence, microbes may invest in chemical defenses (i.e., antibiotics) or produce more enzymes to optimize enzyme foraging (Hiscox & Boddy, 2017).

For these reasons, the degradation of substrates by membrane enzymes may potentially have a stronger positive feedback on SOM decomposition and biomass growth (and thus on PE) than exoenzymes. Therefore, we propose that the distance between microbes and their substrates as well as substrate accessibility to enzymes should be considered as primary factors driving the magnitude of PE across various soil types. This could be tested by implementing random mutagenesis, gene complementation and functional assays (as performed by Picard et al., 2021) to identify how any mutation affecting the production of membrane-cellulosomes or exo-cellulases of a microbe community inoculated on a sterile soil impacts SOM decomposition and microbial growth after the addition of cellulose. Batch experiments with spatially localized applications of decomposers and of fresh cellulose on a sterile soil (as performed by Pinhero et al., 2015) could also allow the investigation of the effect of varying distances between substrate and decomposers on PE intensity.

4.3 PE induced by enzymes sorbed to minerals

Exoenzymes circulating in soil pores exhibit a strong affinity for mineral surfaces and can sorb onto them (Olagoke et al., 2019; Olagoke et al., 2020). This mechanism protects them from degradation and accounts for their persistence in the soil. Mineral-associated exoenzymes are suspected to contribute to the depolymerisation of freshly added substrate, even if their activity is diminished due to changes in conformation after binding to mineral surfaces. They are beneficial to the cost:benefit ratio of the PE because the released monomers are cost-free for the microorganisms that assimilate them.

The monomers taken up into microbe cells are either directed towards microbial biosynthesis, or oxidised into CO_2 by endoenzymes, as reported by CUE. Under aerobic conditions, the aerobic oxidation of monomers also generates energy in the form of adenosine triphosphate. Endoenzymes may be involved in a PE when they are released from dead microbial cells, attached to mineral surfaces, and maintained their activity outside the cell, with electron transfer to O_2 potentially ensured by soil particles due to their electric charge (Maire et al., 2013; Trevors et al., 1982).

5 MICROBIAL ACTORS OF PE

5.1 Actors proposed in the literature

Using molecular approaches, various studies have linked certain PE generation mechanisms to specific bacterial or fungal taxonomic groups listed in Table 2.

Bacterial taxa have been much better documented than fungal ones, probably because of methodological limitations. While a hyphal section is at the microbial scale, its prospected soil volume exceeds the cubic meter. Therefore, current molecular techniques are better adapted to single cell microbial populations (Ranjard et al., 2003). Yet, saprotrophic fungi are believed to have a preponderant role in PE generation, especially in the N-mining process. Their hyphal physiognomy allows them to co-metabolise FOM and SOM very easily, and they appear to be more competitive than bacteria for cellulose decomposition and in turn use cellulose C as an energy source for N-mining. In addition, some fungi have strong enzymatic capacities to break down recalcitrant compounds and access trapped N (Fontaine et al., 2011).

Kingdom or phylum levels do not seem appropriate to associate taxa to specific PE generation mechanisms. Bacterial and fungal taxa have been assigned to all the different PE generation mechanisms (Table 2). Bacteria are roughly considered as r-strategists and fungi as K-strategists, but the reality is more complex (Ho et al., 2017; Tardy et al., 2015). The genus level shows a better correspondence except for *Bacillus*, which gathers both true oligotrophic (*i.e.*, K-strategist) and copiotrophic (*i.e.*, r-strategist) species (Morrissey et al., 2017).

Some interpretations have suffered from a lack of knowledge on poorly described phyla like the Gemmatimonadetes, classified as oligotrophic by some authors (Pascault et al., 2013) but copiotrophic by others (Yu et al., 2020). Increasing efforts in culturomics (Sarhana et al. 2019) and also in large-scale studies of soil microbial diversity will provide precious information to confer functional attributes to microbial taxa (Karimi et al., 2018).

The r-to-K or oligotroph-to-copiotroph concepts refer to a continuum, and many central taxa can develop a certain physiological flexibility depending on (i) environmental conditions, and (ii) competition or complementarity with the other taxa present in each assemblage. These taxa can therefore participate to different PE generation mechanisms according to local conditions (Bernard et al., 2009).

5.2. A trait-based approach

Proposing taxa associated with the different PE generation mechanisms requires to directly focus on functional traits linked to the different PE generation mechanisms described so far. Data retrieved from the application of -omics techniques to environmental samples and recent developments in culturomics have provided and will continue to provide precious information about the genes and enzymes associated with particular taxa.

Different bacterial genomic traits have been proposed to be related to maximum growth rates, and therefore to maximal CUE (linked to stoichiometric decomposition PE), like a high copy number of the ribosomal operon (Klappenbach et al., 2000), a small genome size (Saifuddin et al., 2019), vicinity of the ribosomal operon and the chromosomal origin of replication (Viera-Silva & Rocha, 2010), and the translation efficiency, (Weissman et al., 2021). Some genera sharing those traits are *Burkholderia* sp., *Flavobacterium* sp. and some *Bacillus* sp. (Fierer et al., 2017). The highest maximal fungal growth rates are shared by some well-known saprotrophic fungi that solely use simple sugars and produce spores (Ho et al., 2017), like *Acremonium, Alternaria, Aureobasidium, Cladosporium, Cephalotrichum, Mucor, Rhizopus,* and *Thysanophora*. Decomposition of polymers like cellulose and chitin is widespread and shared by copiotrophic bacterial and fungal species. Genes associated to simple sugar metabolism and ß-glucosidase activity were recently shown to drive PE in forest soils (Ren et al., 2021).

Obligate low-CUE bacteria should be characterised by opposite genomic traits, as adapted to oligotrophy by adopting a small size, a high adsorption capacity of substrate monomers. They should not produce depolymerising enzymes because maintaining these genes is costly (Lynch & Marinov 2015). Therefore, key species implied in nutrient-mining PE should first share a high diversity of genes coding for acquisition systems of poorly accessible substrates. White- and brown-rot saprotrophic fungi and certain bacterial species (*Nocardia* sp., *Streptomyces viridosporum* and other sp., *Amycolatopsis* sp., *Xanthomonas* sp., *Rhodococcus jostii., Novosphingobium* sp. and *Sphingomonas* sp.) share various peroxidases and laccases (Brown & Chang, 2014). All these bacterial genera have between 2 and 6 copies of the ribosomal operon in their genomes (https://rrndb.umms.med.umich.edu), suggesting that they can be physiologically flexible and adapt their CUE to the quality of the substrates they are decomposing. This is also the case of bacterial and fungal species able to weather minerals by producing ligands or chelating agents and who might be good candidates for the abiotically mediated PE, like *Arthrobacter, Janthinobacterium, Leifsonia, Polaromonas* and *Burkholderia* (see Uroz et al., 2015 for a review). As phosphorus and organic matter compete for sorption sites on minerals (Spohn et al. 2022), P-solubilising bacteria could also have an effect on SOM sorption. *Bacillus subtilis* can desorb P from gibbsite by mineral adhesion of the cells themselves (Hong et al., 2016).

6 HOW TO INTRODUCE PE INTO MODELS

Priming is difficult to model, like any other observed but not fully understood phenomenon. To develop a mechanistic model, equations describing the phenomenon are needed, and the very first step is obviously an in-depth understanding of observations. With priming, the situation is somehow slightly uncomfortable for modellers because the debate about the drivers of priming is still ongoing (Chen et al., 2014). Nevertheless, the ubiquity of priming and its potential importance in the soil C balance in a climate change context (Terrer et al., 2021) urge modellers to include priming in their models. We can basically split the modelling objective related to priming into two categories, *i.e.*, (i) understanding the phenomenon, and (ii) quantifying it because observations have shown that priming plays a major role in the C balance of ecosystems. Both objectives can be considered as independent or linked depending on the authors (Blagodatsky et al., 2010; Guenet et al., 2018; Neill & Gignoux, 2006; Perveen et al., 2014). These categories are often associated with different spatio-temporal scales (Figure 3): most of the models aim at understanding priming at small scales and over short time periods, whereas models aimed at quantifying the importance of priming on the SOM balance are developed at larger scales and over longer time periods.

Priming being defined as a change in the SOM mineralisation rate induced by FOM additions (Kuzyakov et al., 2000), we can consider that classic models describing SOM mineralisation using first-order kinetics – *e.g.*, CENTURY or RothC (Coleman et al., 1997; Parton et al., 1987) – implicitly include priming in their decomposition parameter values. Nevertheless, this is associated with implicit assumptions that the relative importance of priming is fixed in space and over time. In particular, an important implicit assumption of first-order kinetic models is that the microbial community is stable. This hypothesis is not verified in a context of global change (climate, CO_2 + land use) (Carney et al., 2007), and priming will play a major role on future C balances (Terrer et al., 2021). Therefore, it is necessary to understand and quantify priming to represent it in models instead of just considering it implicitly.

To represent priming following the classic definition, the FOM and SOM compartments must interact directly or indirectly. This can be done simply by implementing SOM rate modifiers depending on FOM (Guenet et al., 2013) or by changing the SOM CUE according to FOM availability without modifying the decomposition rate (Zhang et al., 2018). Priming can also be represented by models that consider explicit microbial mechanisms, with the effect of FOM on SOM considered through microbial biomass (Fontaine & Barot, 2005; Huang et al., 2018; Perveen et al., 2014; Wieder et al., 2015). These different views on priming representation in models should not be seen as contradictory or opposed, but complementary. It would be unrealistic to consider that a complete representation of priming will soon be included in large-scale models (Eyring et al., 2016); simple and semi-empirical approaches are needed. However, it would also be quite unrealistic to believe that semi-empirical approaches will help to develop a deep understanding of priming. In our opinion, the main difficulty in both cases is related to the parameters used in the equation. Increasing model complexity is most often associated with an increased number of parameters and reduced linear responses of the models (Huang et al., 2021). Therefore, the more complex a model is, the higher the number of possible model trajectories. To avoid unrealistic model behaviors, it is of prime importance to constrain the model parameters using observations. Complex models associated with short time periods and small scales can be constrained by observations coming from incubations under controlled conditions (Neill & Guenet, 2010). Nevertheless, applying complex models and finding suitable parameter values for different soil types, climates, plant covers, etc. is an important challenge that requires a large dataset of incubations like those recently published by Bastida et al. (2019). Even though such large datasets of incubations are now published in single studies or in meta-analyses (Luo et al., 2016), laboratory incubations are still carried out in controlled environments, and upscaling the parameters obtained at this scale to the ecosystem or even the global level is not straightforward. At the end of the calibration process, upscaling may increase model prediction uncertainties compared to less mechanistic models because the uncertainties associated with parameter estimation and upscaling are large. Semi-empirical approaches with a limited number of parameters are an intermediate approach that make it possible to add priming explicitly and to study its effect at larger scales (Guenet et al., 2016; Perveen et al., 2014; Sulman et al., 2014). These models do not catch the entire complexity of the priming response, but they are robust enough to estimate the importance of priming on the SOM balance at large scales.

Different models may involve different, equally accurate or equally uncertain approaches. Therefore, uncertainty remains concerning our prediction capacities. To solve this problem, a promising approach consists in working in close collaboration with experimenters to set up trials aimed at better understanding priming, developing the associated equations and estimating the parameters. But current models can also be compared in the short term. This approach has been fruitful in many fields such as climate sciences (IPCC 2013), biogeochemistry applied to large scales (Ito et al., 2020), and SOM dynamics (Farina et al., 2021). Therefore, using model intercomparison exercises is an interesting alternative to provide robust estimations. This is particularly important when such estimations are key information for stakeholders and policy makers and robust estimations by soil scientists are expected in the near future (Shukla et al., 2019).

Another difficulty in including priming into large-scale models representing plant growth and phenology, water cycles and energy fluxes (Cramer et al., 2001; Sitch et al., 2003) is related to the feedbacks between all the model (Goll et al., 2014; Zaehle et al., 2010; Zhu et al., 2019). A promising research avenue aiming to incorporate complex models with reduced feedbacks but not yet implemented in soil science to our knowledge is the use of a model emulator (Fer et al., 2018). Such approach can help large-scale models to consider priming based on a complex mechanistic approach. Representing priming in models is still a challenge with a large diversity of approaches that should be considered as complementary and able to tackle highly different situations, from a deep understanding of priming at small scales to the quantification of the importance of priming in the global C budget.

7 CONSEQUENCES OF PE ON ECOSYSTEM SERVICES UNDER GLOBAL CHANGE CONDITIONS

Due to various technical constraints related to the measurement of PE such as isotopic labelling of contributed OM, PE studies are often conducted in the laboratory in soil incubations with pure chemical compounds (e.g., glucose) making any extrapolation to the ecosystem scale very complicated. However, some studies have quantified PE and its impacts on C and N fluxes in soil-plant systems (see review of Cheng et al., 2014), often involving heavy infrastructure in order to guarantee the reliability of measurements (Cros et al., 2019). These studies show a massive change in SOM decomposition rate in their rhizosphere induced by plants, from a 50% reduction to a 280% increase (Cheng et al., 2014; Huo et al., 2017). This plant induced priming effect (PIPE) results from the combination of several rhizosphere processes such as plant C inputs (litter rhizodepositions) as well as root uptake of nutrients and water intensifying drying-rewetting cycles and breakage of soil aggregates (Dijkstra et al., 2021). Most if not all ecosystem services and disservices related to SOM dynamics are impacted by the PIPE. For example, the PIPE has been suggested to increase disservices such as soil C loss (Carney et al., 2007; Henneron et al., 2020a) and nitrate leaching (Liu et al., 2008), as well as services such as soluble nutrient supply to plants sustaining greater plant production and CO_2 fixation (Henneron et al., 2020a; 2020b).

Understanding the response of the PIPE and SOM dynamics to current global environmental changes (atmospheric CO_2 increase, global warming and land use changes) is crucial to predict the long-term evolution of the related (dis)services. The task appears very complex because global change can act on priming processes in multiple ways. For example, global warming can impact the intensity of PIPE through its effects on soil enzyme activity, soil microbial populations (Fanin *et al.* in this Special Issue) and plant communities, and in turn determine the quantity and quality of plant C inputs into soils. This complexity is increased by the fact that other processes than PIPE control SOM dynamics (*e.g.*, SOM formation) and have their own response to global change. We suggest a framework that reduces this complexity to three scenarios describing the effect of GC on PIPE, SOM dynamics and four ecosystem (dis)services (Figure 4). This framework is based on the assumptions that (i) plants can drive SOM dynamics to meet their soluble nutrient needs, and (ii) global change can degrade this effect.

It is increasingly recognised that plants can modulate the PIPE and SOM dynamics to adjust the microbial supply of soluble nutrients to their demand. In a common garden experiment comparing 12 grassland plant species, SOM mineralisation rates have been found to be adjusted to the demand of each species (Henneron et al., 2020b). Enhanced plant photosynthesis and nutrient demand under elevated CO_2 increase the PIPE, soil organic N mineralisation and plant N uptake in many different contexts (de Graaff et al., 2009; Kuzyakov, 2019). In contrast, decreased plant photosynthesis (plant demand) in response to plant shading/cutting induces reduced SOM mineralisation (Shahzad et al., 2012; Tang et al., 2019). In temperate ecosystems, the mineralisation/immobilisation ratio changes throughout the season in line with plant demands; immobilisation dominates in winter (low demand), whereas mineralisation dominates in spring (high demand) (Bardgett et al., 2005; Yokobe et al., 2018). Plants control the storage and release of C and nutrients from SOM through their C inputs and soluble nutrient uptake, and this alters the activity of high-CUE and low-CUE microbes (Figure 5). Based on this knowledge on plant control of SOM dynamics, our framework suggests three scenarios of ecosystem response to global change. These scenarios should be considered as attempts to summarise current knowledge, to make it easier to include PE in models and identify priorities for further investigations on the effects of global change on ecosystem C and nutrient cycles.

***Scenario 1: Control by plants is maintained – Global change affects plant production*.** The effects of GC on plant-soil systems are moderate in that plants keep their ability to adjust SOM dynamics to their nutrient needs. Therefore, the ecosystem response to global change is determined by the plant response to global change. More specifically, plant production is modified by global change, while plant biomass remains unchanged. For example, in grasslands under elevated CO_2, primary production is strongly stimulated but the amounts of C and nutrients stored in plant biomass barely change (Terrer et al., 2021) as a consequence of the low storage capacity of herbaceous plants (compared to trees) and continuous grazing. Our framework suggests that the change in primary production modifies the turnover rate of SOM, not the SOM stock. The higher (or lower) plant nutrient demand is expected to increase (or decrease) PIPE and SOM mineralisation. However, an equivalent amount of organic nutrients is expected to return to the soil through litter fall and rhizodeposition if no biomass is exported; this replenishes the SOM stock during periods of low plant demand (Figure 5). In sum, the soil C and ecosystem C stocks as well as nutrient losses remain unchanged, while plant production is changed, meaning there is no feedback effect on global change.

Scenario 2: Control by plants is maintained – Global change affects standing biomass. The sole difference with scenario 1 is that global change also affects the standing plant biomass, as in forests submitted to elevated CO_2 or moderate warming (+ 1 or 2 °C) where primary production and tree biomass often increase (Melillo et al., 2002; Terrer et al., 2021). The increase or decrease in plant biomass induces a parallel and opposite change in the SOM stock (a decrease or an increase, respectively). Given that plants drive the PIPE and SOM dynamics as a function of their nutrient demand, SOM behaves as a nutrient source or sink according to whether plant biomass accumulates or loses nutrients. This nutrient redistribution between plant biomass and SOM affects the ecosystem

C stock since these two compartments have different carbon:nutrient ratios (*e.g*., redistribution of nutrients towards plant biomass increases ecosystem C). In sum, plant production, the soil C stock and the ecosystem are modified, while nutrient loss remains unchanged. In other words, an increase in plant biomass leads to negative feedback and therefore attenuation of climate change, whereas a decrease in plant biomass leads to a runaway positive feedback on climate change.

Scenario 3: Global change degrades plant control of SOM dynamics. This scenario considers more extreme impacts of global change on plant-soil systems leading to a partial or total degradation of the control of SOM dynamics by plants. For example, extreme climatic events such as droughts or heatwaves can block plant nutrient uptake while soil microbes continue to mineralise SOM and release soluble N that accumulates in soils (Deng et al., 2021). Degradation of plant control of the PIPE and SOM dynamics leads to periods of excess soluble nutrients on the short term; these excess nutrients increase nutrient loss and environmental pollution, and periods of nutrient deficiency limit plant production. On the long term, the increased nutrient loss contributes to progressive soil impoverishment and ecosystem decline (loss of plant biomass and production, lower ecosystem C stock). This scenario leads to a runaway positive feedback on global change (climate change and disruption of nutrient cycles)

Several experimental studies support our scenarios. The higher plant C input to soil in response to elevated CO_2 intensifies PIPE and SOM turnover (Scenario 1) (Kuzyakov, 2019; Perveen et al., 2014). Moreover, a recent meta-analysis (Terrer et al., 2021) showed that the effect of elevated CO_2 on SOM stocks was best explained by a negative relationship with plant biomass (Scenario 2): when plant biomass is strongly stimulated by elevated CO_2, SOM storage declines; conversely, when biomass decreases, SOM storage increases. Although plant-soil interactions play a major role in the response of the PIPE to global change, it is important to note that some factors of global change may act on the PIPE and related services independently of soil-plant interactions. For example, moderate atmospheric N depositions have been shown to decrease the microbial production of oxidative enzymes (and the intensity of PIPE leading to SOM accumulation (Hagedorn et al., 2003; Ramirez et al., 2012; Perveen et al., 2014; Liu et al., 2018).

In sum, we propose that global change can deeply impact PIPE, with consequences ranging from a change in plant production to the progressive decline of ecosystems and their services. The consequences of global change on ecosystem services would mostly depend on the ability of plants to keep driving the PIPE and SOM dynamics in a global change context.

8 CONCLUSION AND PERSPECTIVES

After more than 70 years of research on PE, the way it will respond to climate change and impact the flux of C to the atmosphere is still unclear. Research has been strongly intensified these last ten years but a strong global international coordination is still lacking. PE are generated by multiple mechanisms, but many studies continue to focus on the global flux without considering the underlying processes. Various processes have been proposed throughout the literature, following context-dependant nomenclature, thus introducing some confusion in subsequent work. Moreover, while the environmental drivers of these mechanisms are roughly known, their respective output on the C cycle merit to be more deeply studied. We have proposed a classification of the different mechanisms according to their putative impact on the soil C balance between sequestration and mineralization. This classification is based on two factors which have to be taken into account: the putative turnover rate of the primed SOM pool and the putative CUE of the microbial populations respiring the primed C. Future studies have to verify these assumptions as some SOM pools, especially the MAOM, are likely characterised by a wider range of turnover rates than previously thought, depending on the organo-mineral association model and the chemical bonds involved. While wide metagenomic and culturomic studies will continue to increase our knowledge on functional attributes of poorly described microbial populations, the CUE of populations respiring the primed C cannot be extrapolated from the sole identity of present taxa. Actually, many key actors are probably characterized by a wide physiological flexibility, adjusting their CUE and driving different PE generation mechanisms following environmental conditions. Increasing our knowledge on C fluxes driven by the different PE mechanisms will help to introduce the PE into models of SOM dynamics, thus predicting its behavior in response to climate change. Developing *in situ* experiments should also represent a decisive step forward to complete actual knowledge mostly based on incubation experiments. But we are convinced that the PE will not respond directly, but likely through plants, which are the main producers of fresh organic matter generating soil PE. Therefore, the concomitant elevated CO_2, and plant nutrient requirements, also have to be taken into account.

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SUPPORTING INFORMATION

Appendix S1: History of priming effect exploration.

Table S1: List of PE publications from 1973 to April 2021

Figure S1: Network of the international scientific community working on the soil priming effect

Figure S2: Main topics tackled in articles focused on soil priming effect, as deduced from network analysis

TABLES AND FIGURES

TABLE 1 List of the main PE generation mechanisms proposed by the literature, with their given name, definition, drivers and reference articles. SOM: Soil Organic Matter; FOM: Fresh Organic Matter. For each mechanism, the last two columns indicate whether microbial populations assimilating the primed carbon are characterized by high or low carbon use efficiency (CUE), assuming that r-strategists (or copiotrophs) have high CUE while K-strategists (or oligotrophs) have low CUE, and whether the primed SOM pool has a fast, medium or low turnover rate. Generation mechanisms have been colored to follow a proposed gradient of implication in the fate of soil C: from C gain (brown) to C loss (blue).

TABLE 2 List of bacterial and fungal taxonomic groups identified in the literature as associated to FOM mineralization and/or to one of the main PE generation mechanisms: negative PE or positive PE (supposed to involve high CUE or low CUE actors). PE generation mechanisms have been colored to follow a proposed gradient of implication in the fate of soil C: from C gain (brown) to C loss (blue). FOM mineralization was not considered in this gradient and was colored in green. In the colored cells, names correspond to the specific FOM that generated PE in the different publications.

FIGURE 1 **PE-generation mechanisms occurrence** according to (1) the quality of the fresh organic matter (FOM) in terms of lability vs recalcitrance (L:R) and of carbon to nitrogen ratio (C:N), and to (2) the availability of mineral nitrogen in the soil solution. Each PE process is evaluated on a C gain or loss scale depending on the CUE of its actors and the turnover rate of the targeted SOM pool. Basically, the labile fraction of FOM and available N will favor preferential substrate use (negative PE), necromass recycling, entombing effect and PE by stoichiometric decomposition (positive PE), which likely lead to a C gain and an incorporation of N into newly formed biomass. Recalcitrant compounds of FOM will favor Nutrient mining and Abiotically mediated PE specific to low-CUE populations, likely leading to a C loss from SOM and a recycling of N from a low turnover pool to a faster one (biomass and even soil solution). Abiotically mediated PE can also be generated by production of HCO3- H+ during the intense decomposition of FOM, leading to a loss of C from MAOM by microbial populations of unknown CUE.

FIGURE 2 **MAOM and PE.** Conceptual scheme of the abiotically mediated PE of mineral associated organic matter

FIGURE 3 **Constraints on priming effect models**. The level of detail in modeled mechanisms generally depends on the scale considered with more mechanistic models at small scales and more empirical models at large scales. The objectives also depend on the scale, models developed at small scales generally aim at understanding the priming effect whereas models developed at larger scales aim at quantifying its impacts.

FIGURE 4 **Global Change effect on PIPE:** The three main scenarios describing the effect of global change on the plant-induced priming effect (PIPE), soil organic matter (SOM) dynamics and four related ecosystem (dis)services (plant production, soil carbon storage, ecosystem carbon storage, nutrient leaching). N = nutrient. The two first scenarios consider that plants maintain their control on SOM dynamics and microbial supply of soluble nutrients while the last scenario considers that plant control is degraded by global change.

FIGURE 5 **Plant control on SOM dynamics:** Mechanisms by which plants can modulate soil organic matter (SOM) dynamics in order to adjust the microbial supply of soluble nutrients to plant demand. The plant nutrient demand corresponds to the amount of nutrients needed to convert the carbohydrates produced by photosynthesis into biomass. The nutrient supply corresponds to the release of soluble nutrients by the low-CUE microbial community that is stimulated by plant carbon inputs (plant-induced priming effect, PIPE). Plant C inputs also supply the high-CUE microbial community that builds SOM (storing nutrients and carbon) when plant nutrient demand is low or inexistent. The relative abundance and activity of low-CUE and high-CUE communities is driven by plant uptake of soluble nutrients and carbon inputs (quantity & quality). The numbers indicate the chronology of events.

Box 1: Shared terminology

FOM: Fresh Organic Matter relates to organic matter entering the soil and which will generate a PE on organic matter already present in soil (SOM). It can derive from plants like rhizodeposits (exudates or mucus or dead apical cells) or dead roots, leaves, crop residues or dead animals.

SOM: Soil Organic Matter gathers all type of dead organic matter present in the soil before the input of new FOM, from small molecular dissolved compounds to plants residues.

MAOM: Mineral Associated Organic Matter designates organic compounds associated to minerals, from small molecules to microbial or plant cell tissues. MAOM is a specific fraction of SOM.

PE: In the present review, the Priming Effect is a change in the rate SOM-C mineralization induced by an input of FOM.

RPE: The Rhizosphere Priming Effect is the PE generated by live roots and associated rhizosphere organisms when compared to SOM-C mineralisation from rootless soils under the same environmental conditions.

PIPE: The plant Induced Priming Effect is the PE induced by whole plants on SOM-C, including RPE but also PE induced by dead roots and aerial parts of plants like litter or crop residues.

Table 1

PE generation mechanisms			definition	Drivers	References	Microbial CUE	SOM pool turnover rate
SOM decomposition deceleration (negative PE)	real	preferential substrate utilisation	Microbial populations decomposing SOM switch to FOM decomposition.	Labile part of added substrate > 2x microbial biomass Nutrient concentration (soil + substrate) should meet microbial demand	Cheng 1999; Kuzyakov 2000	**High and low**	**?**
		Necromass recycling	Microbial populations decomposing SOM switch to the decomposition of the necromass of FOM-decomposers.	Microbial necromass can also be sorbed on minerals. Clays and metals in the soil can compete with microbes for available necromass (Creamer et al. 2019).	Cui et al. 2020		
SOM decomposition acceleration (positive PE)	apparent	triggering effect	Acceleration of internal microbial metabolism by trace amounts of substrate with an immediate (several minutes to several hours) increase in the respiratory activity	labile part of added substrate < microbial biomass	Blagodatskaya & Kuzyakov 2008	**High and low**	**Fast**
		microbial activation	The N content of the soluble part of the amended substrate will be used to produce first extracellular enzymes. It can also correspond to N-containing root exudates in the rhizosphere.	labile part of added substrate < microbial biomass N rich FOM	Kuzyakov 2002		
		pool substitution	acceleration of the turnover of the whole microbial biomass (several days or weeks)	labile part of added substrate = microbial biomass	Blagodatskaya & Kuzyakov 2008		
	real	stoichiometric decomposition	FOM increases biomass and general enzymatic activity, accompanied by domination of r-strategists and increase in SOM decomposition.	FOM complexity with nutrient availability (Plant residues)	Chen et al. 2014	**High**	**Fast to medium**
		cometabolism	Assimilation of FOM and SOM by similar populations. FOM brings the energy to decompose less available SOM compounds.	labile part of added substrate superior to microbial biomass; Nutrient availability (substrate and dissolved) slighly inferior to microbial demand	Kuzyakov 2000; Blagodatskaya & Kuzyakov 2008; Yu et al. 2018	**High or low**	
		mechanism 1	Enzymes produced by r-strategists in order to decompose FOM may be partially efficient for SOM degradation	FOM complexity with nutrient availability (Plant residues)	Fontaine et al. 2003	**Low**	
		mechanism 2	K-strategists mineralizing SOM, with slow growth rates, may benefit from FOM polymerised substrates which have a long residence time in soil. Thus K-strategist populations and associated enzyme production increase, causing PE.	labile energy rich substrate with nutrient depletion	Fontaine et al. 2003	**Low**	**Medium**
		N-mining	FOM supply increases the biomass and enzymatic activity of K-strategists and increases SOM decomposition.	labile energy rich substrate with N depletion	Chen et al. 2014		
		Abiotically mediated	Plant roots exudate organic acids, which desorb labile MOS associated to minerals (MAOM). Liberated compounds will be accessible to microbial decomposition. Fungi and bacteria are also able to produce organic acids or chelatants and could generate such PE	N-limitation	Keiluweight et al. 2015 ; Fang et al. 2018	**High and or low ?**	**Slow**

TABLE 2

phylogenetic affiliation						FOM mineralization	Negative PE	High-CUE PE	Low-CUE PE	References
Kingdom		Phylum	Order	Family	Genus					
Bacteria	Gramm-						Grass residue	Urea, cellulose		Hamer et al. 2009; Potthast et al. 2010; Blagodatskaya et al. 2014
		G- (16:1w7c)						Glucose		Derrien et al. 2014
		G- (18:1w7c)							Glucose	Derrien et al. 2014
		Proteobacteria				Alfalfa residue				Pascault et al. 2013
		Proteobacteria			Unclassified			Wheat residue		Razanamalala et al. 2018a
		beta-Proteobacteria				Wheat residue		Glucose, wheat residue		Bernard et al. 2012, Razanamalala et al. 2018b; Fang et al. 2018
			Burkholderiales	Comamonadaceae	Variovorax	Wheat residue			Wheat residue	Bernard et al. 2007; 2009
					Ramlibacter			Wheat residues		Bernard et al. 2007
					Acidovorax				Wheat residue	Bernard et al. 2009
					Aquabacterium			Wheat residues	Wheat residue	Bernard et al. 2007; 2009
				Oxalobacreaceae	Massilia	Wheat residue				Bernard et al. 2007; Liu et al. 2021
					Janthinobacterium				Wheat residue	Bernard et al. 2009
					Noviherbaspirillum				Wheat residue	Liu et al. 2021
				Burkholderiaceae	Burkholderia	Glucose; wheat residue				Arcand et al. 2017; Liu et al. 2021
					Ralstonia				Wheat residue	Liu et al. 2021
					Methylibium				Wheat residue	Bernard et al. 2009
		gamma-Proteobacteria				Wheat residue		Wheat residues, glucose		Razanamalala et al. 2018a, 2018b; Maron et al. 2018
			Pseudomonadales	Pseudomonadaceae	Pseudomonas	Wheat residue				Bernard et al. 2007
			Xantomonadales	Rhodanobacteraceae	Dyella				Wheat residue	Liu et al. 2021
		alpha-Proteobacteria				Wheat residue		Wheat residues		Razanamalala et al. 2018a, Maron et al. 2018
			Sphingomonadales	Sphingomonadaceae		Wheat residue				Bernard et al. 2009
					sphingosinicella				Wheat residue	Bernard et al. 2007
					Kaistobacter				Wheat residue	Bernard et al. 2007
					sphingomonas	Glucose				Arcand et al. 2017
			Rhizobiales	Methylobacteriaceae		Wheat residue				Bernard et al. 2009
				Bradyrhizobiaceae	Bradyrhizobium				Wheat residue	Liu et al. 2021
			Hyphomicrobiales	Nitrobacteraceae	Rhodoplanes	Glucose				Arcand et al. 2017
			Micropepsales	Micropepsaceae	Rhizomicrobium				Wheat residue	Liu et al. 2021
		Bacteroidetes					Biochar	Wheat , alfalfa residues, glucose		Bernard et al. 2012; Pascault et al. 2013; Arcand et al. 2017
			Chitinophagales	Chitinophagaceae	Flavisolibacter	Wheat residue				liu et al. 2021
		Acidobacteria					Tree leaves		rice & wheat residue; Glucose; tree leaves	Pascault et al. 2013; Razanamalala et al. 2018a,b; Maron et al. 2018; Fang et al. 2018; Yu et al. 2020
			GP2					Wheat residues		Razanamalala et al. 2018a
			GP6					Wheat residues		Razanamalala et al. 2018a
			GP4						Wheat residue	Razanamalala et al. 2018a
			GP1						Wheat residue	Liu et al. 2021
		Verrucomicrobia				Glucose	Tree leaves	Rice and wheat residue	Wheat residue, tree leaves	Pascault et al. 2013; Morrissey et al. 2017; Razanamalala et al. 2018b; Yu et al. 2020
		Gemmatimonadetes					Biochar		Wheat residue	Pascault et al. 2013; Razanamalala et al. 2018b; Maron et al. 2018; Yu et al. 2020
			Gemmatimonales	Gemmatimonaceae	Gemmatimonas				Wheat residue	Liu et al. 2021
		Planktomycetes						Wheat residues	Wheat residue, Glucose	Razanamalala et al. 2018a,b; Maron et al. 2018
			Planctomycetales	Isosphaeraceae	Aquisphaera				Wheat residue	Liu et al. 2021
		Chloroflexi						Rice and wheat residue	Wheat residue	Razanamalala et al. 2018a,b; Maron et al. 2018
	Gramm+							Bracken	Cellulose, litter, rice straw and roots	Potthast et al. 2010; Blagodatskaya et al. 2014; Wang et al. 2014, 2020
		Actinobacteria				Wheat residue, Glucose		Glucose	Wheat residue	Razanamalala et al. 2018a,b; Maron et al. 2018; Arcand et al. 2017; Liu et al. 2021; Bernard et al. 2009
			Actinomycetales			Glucose			Glucose, wheat residue	Garcia-Pausas et al. 2011; Bernard et al. 2012; Morissey et al. 2017
				microccocaceae	Arthrobacter	Glucose				Mau et al. 2015
					Sinomonas	Wheat residue				Liu et al. 2021
				Streptomycetaceae		Glucose				Morrissey et al. 2017
						Glucose				Arcand et al. 2017
					Streptomyces	Wheat residue				Liu et al. 2021
			Micromonosporales	micromonosporaceae		Glucose				Morrissey et al. 2017
			Propionibacteriales	Nocardioidaceae		Glucose				Morrissey et al. 2017
			Hyphomicrobiales	Hyphomicrobiaceae		Wheat residue				Bernard et al. 2009
			Acidimicrobideae						Wheat residue	Bernard et al. 2007
			Gaiellales	Gaiellaceae	Gaiella				Wheat residue	liu et al. 2021
		Firmicutes				Wheat residue		Glucose, Alfalfa, rice and wheat residues		Pascault et al. 2013; Razanamalala et al. 2018a,b; Maron et al. 2018; Fang et al. 2018; Yu et al. 2020
			Bacillales	Bacillaceae	Bacillus	Wheat residue			Glucose	Mau et al. 2015; Arcand et al. 2017; Liu et al. 2021
				Paenibacillaceae	Paenibacillus				Glucose	Arcand et al. 2017
				Alicyclobacillaceae	Alicyclobacillus				Wheat residue	Liu et al. 2021
		Unknown							Wheat residue	Razanamalala et al. 2018a
fungi							Tree leaves	Urea, cellulose, bracken	Glucose, cellulose, litter, tree leaves, Rhizosphere PE	Hamer et al. 2009; Potthast et al. 2010; Garcia-Pausas et al. 2011; Blagodatskaya et al. 2014; Wang et al. 2014; Shahzad et al. 2018; Tian et al. 2019; Fang et al. 2018; Yu et al. 2020
	saprotrophic							Cellulose		Blagodatskaya et al. 2014
	saprotrophic	Leothiomycota							Biochar	Yu et al. 2018
		Ascomycota							Wheat residue	Maron et al. 2018
			Pezizomycotina	Sordariomycetes					Biochar	Yu et al. 2018
		Basidiomycota				Wheat residue				Maron et al. 2018
			Agaricomycotina	Tremellomycetes					Biochar	Yu et al. 2018
		Zygomycota					Biochar			Yu et al. 2018

FIGURE 2

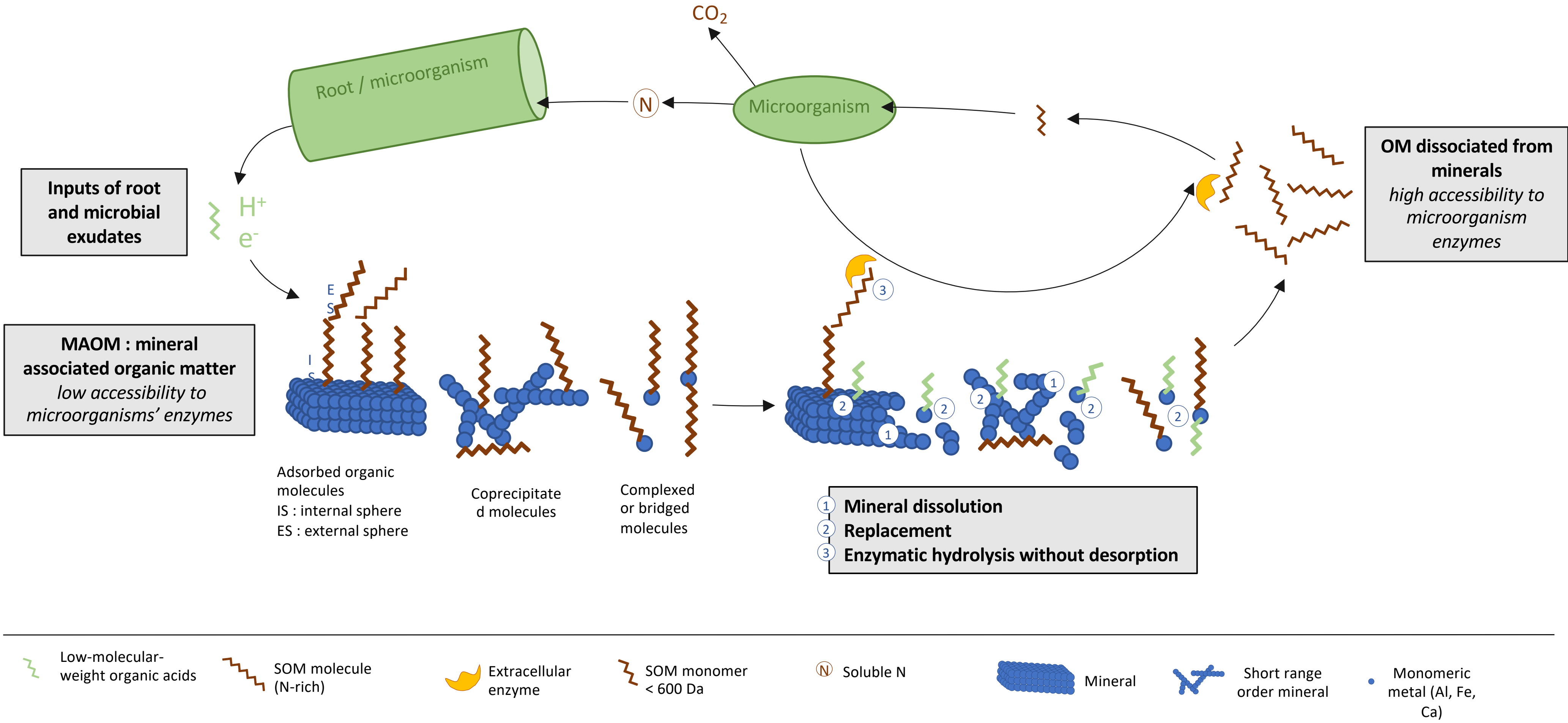

CO$_2$
Root / microorganism
N
Microorganism
Inputs of root and microbial exudates
H$^+$
e$^-$
OM dissociated from minerals
high accessibility to microorganism enzymes
MAOM : mineral associated organic matter
low accessibility to microorganisms' enzymes
ES
IS
Adsorbed organic molecules
IS : internal sphere
ES : external sphere
Coprecipitated molecules
Complexed or bridged molecules
1
2
3
① Mineral dissolution
② Replacement
③ Enzymatic hydrolysis without desorption
Low-molecular-weight organic acids
SOM molecule (N-rich)
Extracellular enzyme
SOM monomer < 600 Da
Ⓝ Soluble N
Mineral
Short range order mineral
Monomeric metal (Al, Fe, Ca)

FIGURE 1

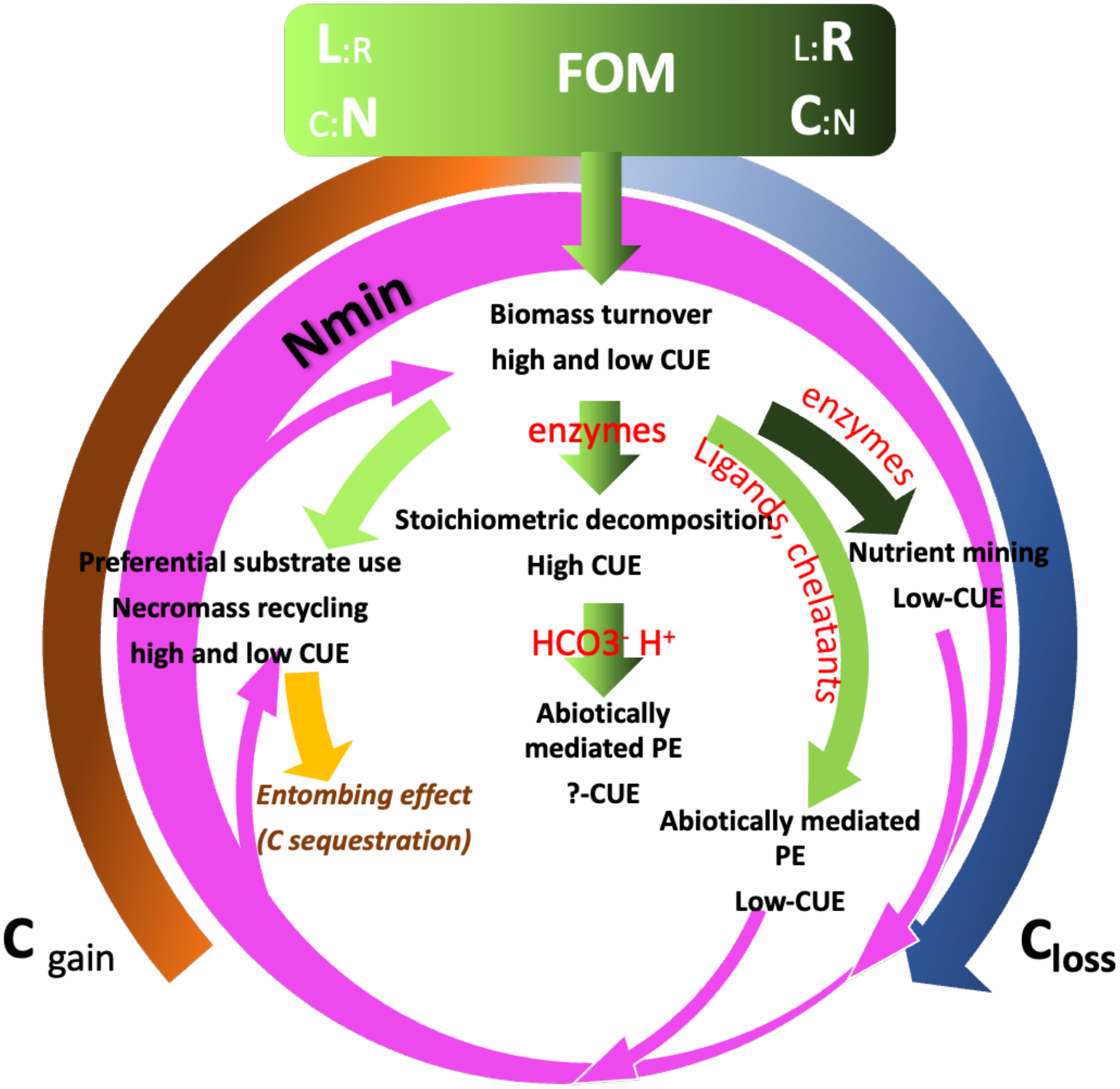

L:R
C:N
FOM
L:R
C:N
Nmin
Biomass turnover
high and low CUE
enzymes
Stoichiometric decomposition
High CUE
HCO3⁻ H⁺
Abiotically mediated PE
?-CUE
Preferential substrate use
Necromass recycling
high and low CUE
Entombing effect
(C sequestration)
Ligands, chelatants
enzymes
Nutrient mining
Low-CUE
Abiotically mediated PE
Low-CUE
C gain
C loss

FIGURE 3

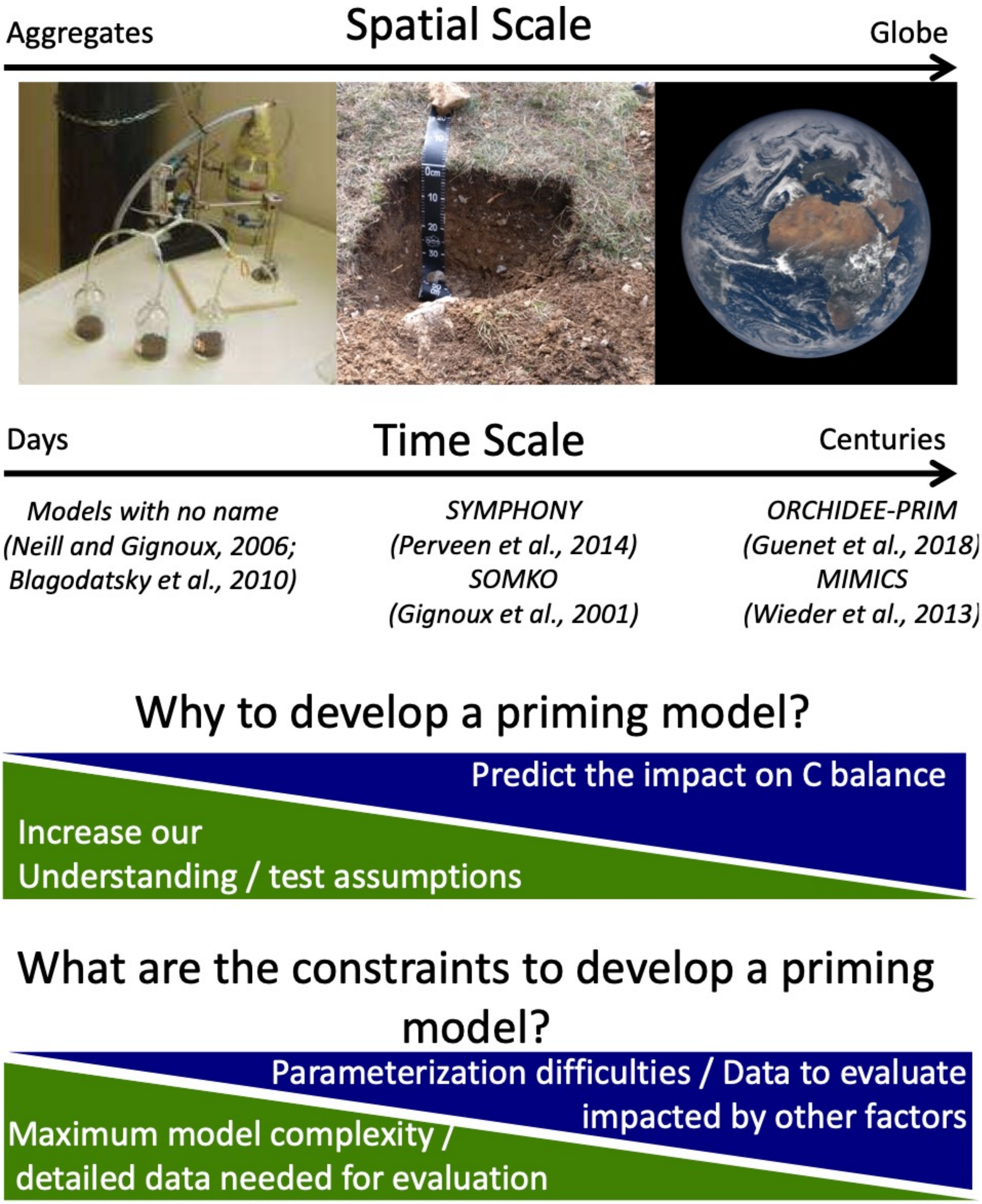
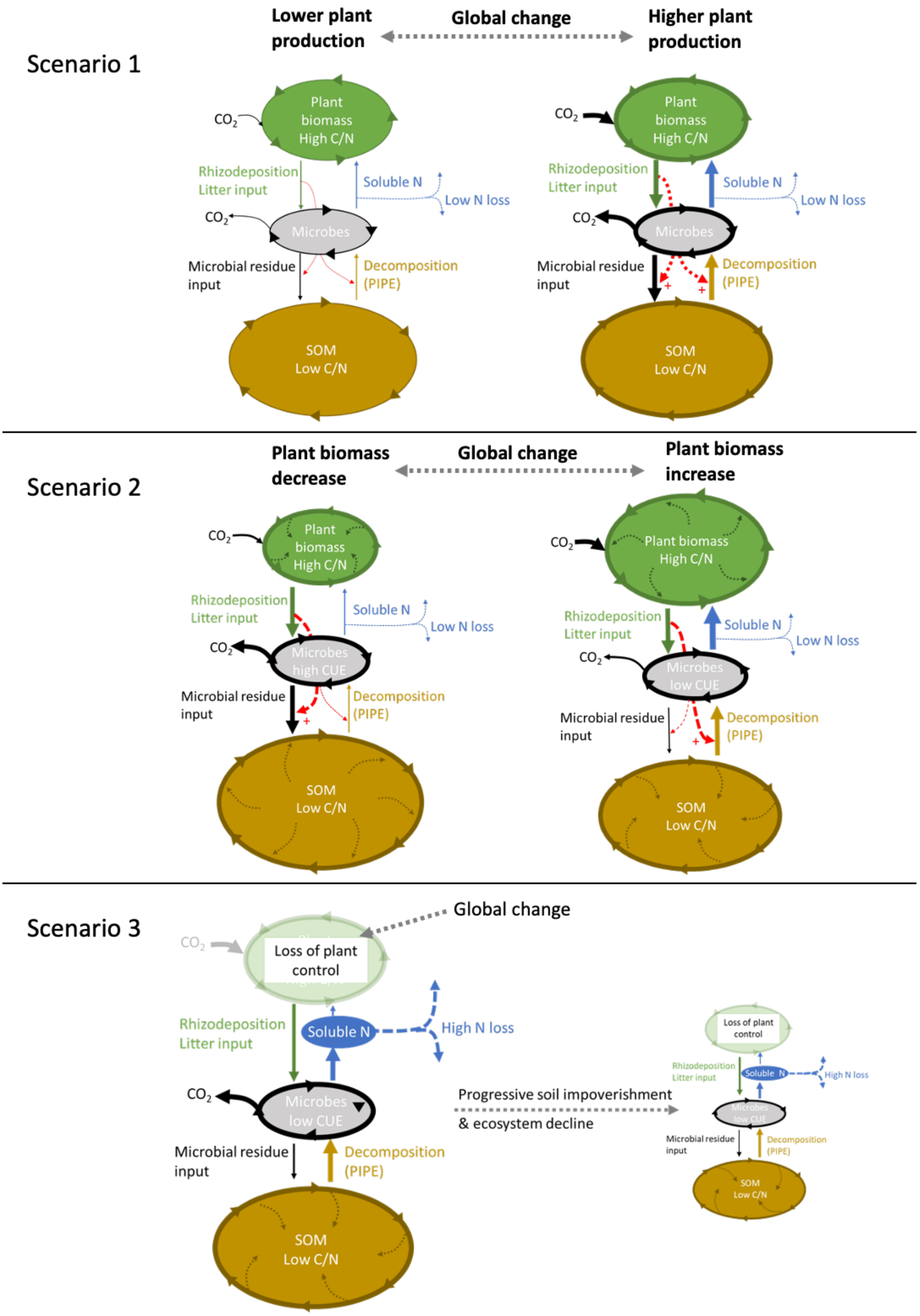
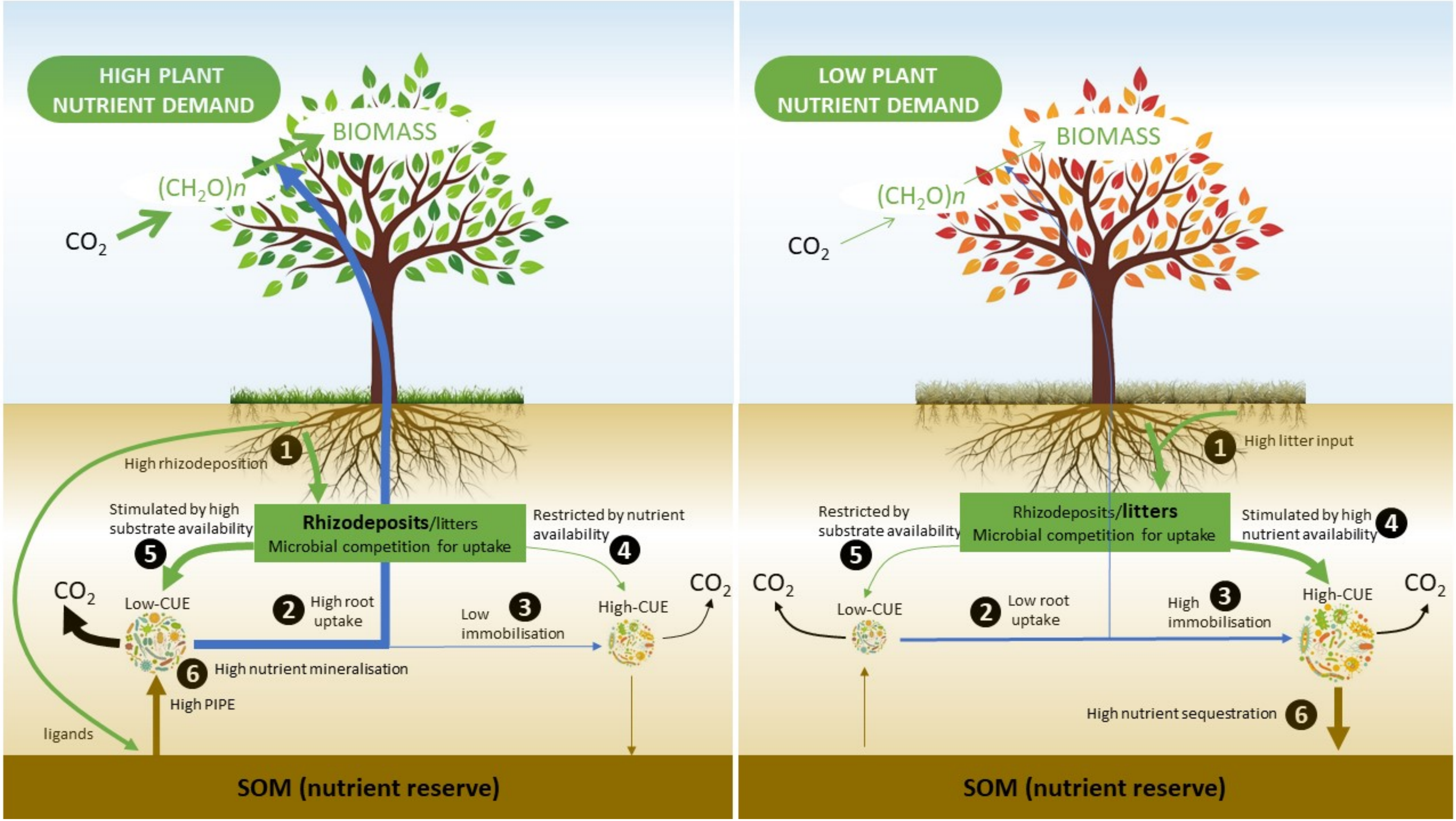

Aggregates
Spatial Scale
Globe
Days
Time Scale
Centuries
Models with no name
(Neill and Gignoux, 2006;
Blagodatsky et al., 2010)
SYMPHONY
(Perveen et al., 2014)
SOMKO
(Gignoux et al., 2001)
ORCHIDEE-PRIM
(Guenet et al., 2018)
MIMICS
(Wieder et al., 2013)
Why to develop a priming model?
Predict the impact on C balance
Increase our
Understanding / test assumptions
What are the constraints to develop a priming model?
Parameterization difficulties / Data to evaluate
impacted by other factors
Maximum model complexity /
detailed data needed for evaluation

FIGURE 4


Scenario 1
Lower plant production
Global change
Higher plant production
CO_2
Plant biomass High C/N
Rhizodeposition
Litter input
Soluble N
Low N loss
CO_2
Microbes
Microbial residue input
Decomposition (PIPE)
SOM Low C/N
CO_2
Plant biomass High C/N
Rhizodeposition
Litter input
Soluble N
Low N loss
CO_2
Microbes
Microbial residue input
+
+
Decomposition (PIPE)
SOM Low C/N
Scenario 2
Plant biomass decrease
Global change
Plant biomass increase
CO_2
Plant biomass High C/N
Rhizodeposition
Litter input
Soluble N
Low N loss
CO_2
Microbes high CUE
Microbial residue input
+
Decomposition (PIPE)
SOM Low C/N
CO_2
Plant biomass High C/N
Rhizodeposition
Litter input
Soluble N
Low N loss
CO_2
Microbes low CUE
Microbial residue input
+
Decomposition (PIPE)
SOM Low C/N
Scenario 3
Global change
CO_2
Loss of plant control
Rhizodeposition
Litter input
Soluble N
High N loss
CO_2
Microbes low CUE
Microbial residue input
Decomposition (PIPE)
SOM Low C/N
Progressive soil impoverishment & ecosystem decline
Loss of plant control
Rhizodeposition
Litter input
Soluble N
High N loss
Microbes low CUE
Microbial residue input
Decomposition (PIPE)
SOM Low C/N


HIGH PLANT NUTRIENT DEMAND
BIOMASS
(CH$_2$O)n
CO$_2$
1
High rhizodeposition
Stimulated by high substrate availability
5
Rhizodeposits/litters
Microbial competition for uptake
Restricted by nutrient availability
4
CO$_2$
Low-CUE
2
High root uptake
Low immobilisation
3
High-CUE
CO$_2$
6
High nutrient mineralisation
High PIPE
ligands
SOM (nutrient reserve)
LOW PLANT NUTRIENT DEMAND
BIOMASS
(CH$_2$O)n
CO$_2$
1
High litter input
Restricted by substrate availability
5
Rhizodeposits/litters
Microbial competition for uptake
Stimulated by high nutrient availability
4
CO$_2$
Low-CUE
2
Low root uptake
High immobilisation
3
High-CUE
CO$_2$
High nutrient sequestration
6
SOM (nutrient reserve)