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1 TITLE

2

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

4

5

6 SUMMARY (320 Words)

7

8 1 The priming effect (PE) is a key mechanism contributing to the carbon balance of the soil
9 ecosystem. Almost 100 years of research since its discovery in 1926 have led to a rich body
10 of scientific publications to identify the drivers and mechanisms involved. A few review
11 articles have summarised the acquired knowledge; the last major one was published in
12 2010. Since then, knowledge on the soil microbial communities involved in PE and in PE +
13 C sequestration mechanisms has been considerably renewed.

14 2 This article reviews current knowledge on soil PE to state to what extent new insights may
15 improve our ability to understand and predict the evolution of soil C stocks. We propose a
16 framework to unify the different concepts and terms that have emerged from the
17 international scientific community on this topic, report recent discoveries, and identify key
18 research needs.

19 3 Seventy percent of the studies on the soil PE were published in the last 10 years, illustrating
20 a renewed interest for PE, probably linked to the increased concern about the importance
21 of soil carbon for climate change and food security issues. Among all the drivers and
22 mechanisms proposed along with the different studies to explain PE, some are named
23 differently but actually refer to the same object. This overall introduces “artificial”
24 complexity for the mechanistic understanding of PE, and we propose a common, shared
25 terminology. Despite the remaining knowledge gaps, consistent progress has been
26 achieved to decipher the abiotic mechanisms underlying PE, together with the role of
27 enzymes and the identity of the microbial actors involved. However, including PE into
28 mechanistic models of SOM dynamics remains challenging as long as the mechanisms are
29 not fully understood. In the meantime, empirical alternatives are available that reproduce
30 observations accurately when calibration is robust.

31 4 Based on the current state of knowledge, we propose different scenarios depicting to what
32 extent PE may impact ecosystem services under climate change conditions.

33

34

35 KEY WORDS

36

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

38

39 1 INTRODUCTION
40

41 Soils host one of the main carbon (C) stores of our planet, around three times more than the
42 atmosphere does (2,400 vs. 800 GtC) (Friedlingstein et al., 2019). Most of this C is stored in organic
43 matter whose turnover controls soil fertility through the release of nutrients for plants. Soil Organic
44 Matter (SOM) also releases huge amounts of CO₂ into the atmosphere, 7-fold more than
45 anthropogenic emissions (Schlesinger and Andrews, 2000). Given the huge size of the soil organic C
46 pool, any change in the soil C content and its dynamics at a global scale – even if tiny – is associated to
47 great impacts in terms of food security and climate change (Dignac et al., 2017; Minasny et al., 2017).
48 Consequently, preserving and even increasing organic carbon in soils is of prime importance to meet
49 the food security challenge and mitigate greenhouse gas emissions (Minasny et al., 2017). This requires
50 getting insights into the determining mechanisms of the soil carbon balance – i.e. mineralisation vs.
51 sequestration.

52

53 The priming effect (PE) is a key mechanism contributing to the ecosystem carbon balance (Fontaine et
54 al., 2007; Guenet et al., 2018). It corresponds to a change in the rate of SOM-C mineralisation by soil
55 microorganisms resulting from the input of fresh organic matter (FOM) (Bingeman et al., 1953). The
56 definition was later extended to almost any variation of microbial activities after an addition of
57 molecule (e.g., toxic compounds; Kuzyakov et al. 2000), but the present review will focus on ~~C-related~~
58 PE as previously defined, and more precisely on the plant induced priming effect (PIPE) which includes
59 the rhizosphere priming effect (RPE) but also more generally all priming induced by plant originated
60 carbon inputs (Box 1). The PE occurs everywhere, but it has mainly been studied in soils (Bengtsson et
61 al., 2018; see supporting information). It has long been viewed as a net soil C loss since the most
62 frequent effect reported in the literature is a stimulation of native SOM mineralisation, up to 400 %
63 according to the type of environment and/or soil conditions (Guttière et al., 2021; Chen et al., 2019;
64 Perveen et al., 2019, Blagodatskaya & Kuzyakov, 2008). However, it can also be negative, with up to
65 50% reductions in soil carbon emissions (Lyu et al., 2018; Chen et al., 2019). As the PE is a complex
66 process, its impact on global C fluxes is hard to grasp and should be considered as a whole, integrating
67 feedbacks between the different and sometimes contrasting effects it causes: for example, the
68 increase of SOM mineralisation has negative consequences on climate change, and the nutrients
69 released from organic matter may be leached down the soil profile; but when the released nutrients
70 are taken up by plants, the PE indirectly contributes to plant growth and additional C sequestration in
71 the plant-soil system. Thus, the effect of PE variation on the net soil C balance is not trivial, particularly
72 in the context of climate change because C inputs may globally increase through enhanced plant

73 productivity, while soil C mineralisation may increase too due to higher temperature (Nishina et al.,
74 2014). Consequently, better knowledge of the mechanisms involved in PE is of fundamental
75 importance to improve our ability to control and predict the evolution of soil C stocks (Guenet et al.,
76 2018; Chen et al., 2019), in agreement with the 2019 IPCC report on land (Shukla et al. 2019) that
77 pointed out the need to better understand how PE will respond to climate change.

78

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

88

89 Based on these studies, it is clear today that the PE involves different microbial processes sometimes
90 driven in opposite ways by environmental parameters. Soil properties, climate, land use (Bastida et al.,
91 2019; Siles et al., 2022), but also the nature of the substrates entering the soil (*e.g.*, simple compounds,
92 complex compounds, plant residues or living roots) and the way they are added (*e.g.* continuous vs.
93 pulse) all impact the intensity of priming effect. A few reviews have been published to summarise
94 knowledge in the field. The last major one was published in 2010 (Kuzyakov, 2010). However, in the
95 last ten years, studies aimed at characterising the microbial communities involved in soil processes
96 such as PE have benefited from considerable technical progress providing deeper insights into
97 microbial diversity and activity (Bouchez et al., 2016). In the same time span, the understanding of C
98 sequestration mechanisms has undergone a paradigm change (Lehmann & Kleber, 2015). Therefore,
99 it appeared important to update knowledge on PE mechanisms by integrating the findings of the last
100 10 years, which was the first objective of the present review. The second objective was to unify the
101 different concepts and terms that emerged from the international literature on this topic. Finally, we
102 identified and focused on specific points that need to be more deeply examined to evaluate and
103 predict the size and the impact of the different mechanisms across space and over time.

104

105 2 UNIFYING THE DIFFERENT GENERATION MECHANISMS.

106

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

112

113 2.1 Let's clarify the denomination of the different mechanisms.

114 The PE is usually measured as the difference between the CO₂-C released from an amended soil
115 (excluding CO₂-C originating from the amendment itself) and from a non-amended control soil over a
116 certain time period, leading to a "positive" or "negative" PE (Kuzyakov et al., 2000).

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

124

125 Positive PE processes can be called "apparent" PE when they only result from the replacement of
126 microbial cell C by C from the new substrate (labile fraction). Apparent PE have been described under
127 3 complementary processes (triggering effect, microbial activation, and pool substitution), depending
128 on the amount of labile FOM added compared to the total microbial biomass (Blagodatskaya and
129 Kuzyakov, 2008 – see Table 1).

130

131 Real positive PE have been attributed to multiple processes. Those called "stoichiometric
132 decomposition" (Chen et al., 2014), and "mechanism 1" (Fontaine et al., 2003) refer to an acceleration
133 of SOM decomposition generated by the increase in extracellular enzymes produced by FOM
134 decomposers (Table 1). This implies that certain FOM and SOM compounds have chemical similarities
135 (*e.g.*, a plant origin). Therefore, FOM should be at least partly polymerised (such as in residues, litter
136 or dead roots). Both processes occur when N is not limiting, but SOM catabolites benefit SOM
137 decomposers in "Mechanism 1", and FOM decomposers in "stoichiometric decomposition". Processes
138 called "N-mining" (Chen et al., 2014) and "mechanism 2" (Fontaine et al., 2003) result from the energy
139 brought by FOM catabolites, for SOM decomposers to break down biochemically recalcitrant SOM for
140 nutrients. For both processes, the targeted SOM pool was supposed to be also of plant origin. One

141 process has been called “co-metabolism” in different papers and corresponds to the assimilation of
142 FOM and SOM catabolites by either FOM or SOM decomposers, without being aimed at N acquisition
143 (Kuzyakov, 2000; Yu et al., 2018). Therefore, in terms of carbon, this process overlaps with previously-
144 described mechanisms (either Mechanism 1 or Mechanism 2 and nutrient mining) and thus is not
145 discriminant.

146

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

154

155 2.2 Gathering mechanisms according to their effect on C fluxes

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

158

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

168

169 Secondly, PE is often evaluated based on the change in CO₂ mineralisation rate, but respiration can be
170 accompanied by incorporation of C into cell biomass (growth) (see Geyer et al., 2016 for a review). The
171 efficiency of carbon incorporation into biomass (*i.e.*, carbon use efficiency, CUE) is calculated as the
172 amount of microbial biomass produced *per* unit of resource consumed. The CUE of cells can vary
173 between 0 (no growth but alive) to 0.85 (growth but still needing some energy for cell growth and
174 maintenance) depending on their physiology and life strategy. The link between life strategy and CUE
175 depends on the physiological status of microbes. R-strategists are actually less efficient than K-

176 strategists in using their assimilated C during a resting phase, due to a costlier basal metabolism. But
177 as these populations have higher maximal growth rates, during the growth phase when substrate is
178 not limiting, a higher proportion of C is allocated to biomass instead of respiration. This leads to a
179 globally higher CUE than that of K-strategists (Geyer et al., 2016). As PE generation mechanisms are
180 consequences of organic matter decomposition, they are more related to growth phases of different
181 populations than to their resting phases. Thus we consider that during a PE event, r-strategists have
182 high CUE while K-strategists have low CUE. Therefore, primed SOM assimilated by high-CUE
183 populations is likely converted into microbial biomass rather than mineralised into CO₂, and further
184 stabilized via the so-called “entombing effect” (Lehman & Kleber, 2015; Liang et al., 2017). As a result,
185 high-CUE populations increase the chance of moving C from a fast- or a medium-turnover SOM pool
186 to a slow-turnover pool.

187

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

192

193 2.3 Time scale integration of PE generation mechanisms.

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

208 3 ABIOTICALLY MEDIATED PE: CONCEPTS AND MECHANISMS

209

210 3.1 Mineral-associated organic matter (MAOM)

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

215 - *Adsorption*: organic molecules are adsorbed onto the mineral surface of well-crystallised minerals
216 (e.g., smectite, vermiculite or goethite) (Kleber et al., 2007).

217 - *Coprecipitation*: organic molecules are coprecipitated with short-range order phases or
218 amorphous small polymers of Al, Fe and Si (Basile-Doelsch et al., 2015; Tamrat et al., 2019). Co-
219 precipitation is thought to be the dominant model as regards the amount of stabilised C
220 (Rasmussen et al., 2018).

221 - *Complexation and bridging*: organic molecules are bound to monomers (single ions). The main
222 metals involved in complexation are Al and Fe in acidic soils. At higher pH, Ca dominates the
223 organo-mineral associations by cation bridging (Rowley et al., 2018). Cations surrounded by
224 organic molecules form a tertiary structure described as “supramolecular aggregates” (Sutton &
225 Sposito, 2005).

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

228

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

237

238 The mineral-associated organic matter is less accessible but not fully inaccessible. The bonds between
239 organic molecules and inorganic phases slow down OM degradation. Incubation studies have shown
240 that MAOM is more difficult to mineralise than free OM, whatever the model (adsorption,
241 coprecipitation or complexation) (e.g. Jones & Edwards, 1998; Saidy et al., 2015). The proportion of C
242 mineralised during MAOM incubations reached a plateau which, depending on the compounds, barely
243 reached the same proportion as in the control where OM was not associated with mineral phases.
244 These experiments showed that (i) part of MAOM remained accessible to microorganisms but

245 mineralisation was slowed down, and (ii) depending on the nature of the organic compounds and the
246 nature of the mineral (*i.e.*, depending on the nature of the chemical bond), part of MOAM was not
247 mineralised by microorganisms. Thus, rather than use a binary terminology tending to say that OM is
248 stabilised or not in organo-mineral associations, a stabilisation gradient concept should be preferred
249 and considered as a key parameter driving the potential of abiotically mediated PE.

250 3.2. Priming effect of mineral-associated organic matter

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

257
258 The biotic impact on the physico-chemical parameters of MAOM leads to a direct and indirect PE
259 pathways. Roots and microorganisms play an essential role in controlling the physicochemical
260 conditions of the soil solution (Figure 2). Multiple factors impact these conditions. For example,
261 vascular plant roots, fungi and bacteria release low-molecular-weight organic acids. These are mainly
262 carboxylic acids like formic, oxalic, and acetic acid, but also aliphatic and aromatic acids (Clarholm et
263 al., 2015 and references therein). Microorganisms may decrease the pH locally in microsites
264 (Bonneville et al., 2011). Roots also release some easily metabolisable simple sugars (*e.g.*, glucose).
265 They can stimulate microbial activity and growth, which may in turn lower the pH and the redox
266 potential (Mabuza et al., 2020). These various examples show that the factors driving the
267 destabilisation of MAOM are multiple and may be dependent on each other. The factors directly
268 controlled by plant functioning are referred to as "direct (non-microbial) pathways". Conversely, in
269 "indirect (microbial) pathways" root exudates mobilise MAOM indirectly through a sugar-mediated
270 pathway dependent on microbial intermediaries (Keiluweit et al., 2015; Jilling 2021; Finley et al., 2018;
271 Li et al., 2021). Whether the pathway is direct or indirect, whether it is located in the rhizosphere or in
272 the residuesphere, it appears that the functioning of the biotic compartment (roots, bacteria and fungi)
273 is a source of low-molecular-mass organic acids, and pH and Eh variations, all of which are likely to
274 modify the bonding equilibrium of the organo-mineral associations and can be accompanied by an
275 abiotically mediated PE.

276

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

280 - *Mineral dissolution* can be promoted by exudates. Ligand-promoted dissolution is accelerated by
281 strong ligands such as organic acids (Wang et al., 2014; Li et al., 2018). Protonation of a mineral
282 surface can also weaken metal-oxygen bonds and dissolve minerals (Stumm, 1997). Reductive
283 dissolution can be driven by organic reducing agents such as phenols and aromatic acids
284 (Vermeire et al., 2019). However, as Al is not very sensitive to redox variation, these redox
285 processes mainly impact Fe-bearing mineral phases.

286 - *Replacement* is promoted by strong ligands such as organic acids, which sorb onto mineral
287 surfaces and displace or release previously sorbed organic compounds from minerals (Li et al.,
288 2021). Other metabolites are also implied in the release of MAOM through displacement of
289 weakly bound compounds (Leineman et al., 2018; Mikutta et al., 2019; Jiang et al., 2021).

290 - *Direct depolymerisation* of mineral-bound organic compounds by extracellular enzymes can also
291 occur on weakly bound OM, bypassing the desorption step (Wang et al., 2020).

292

293 4 ROLE OF ENZYMES IN PE

294

295 4.1 Enzymes involved in priming effect mechanisms

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

308 When the environment is nutrient limited, microbial communities shift from high to low CUE, notably
309 because nutrient limitation affects the community metabolism and reduces growth yield, while it
310 favours investment in resource acquisition (Malik et al., 2020; Fanin et al., 2020). In this context,
311 another type of co-metabolism directed to N-containing SOM is induced when N is not available or

312 becomes exhausted at the late stages of decomposition. It is characterised by a high expression level
313 of enzymes degrading N-containing compounds (Moorhead & Sinsabaugh, 2006; Chen et al., 2014),
314 including hydrolytic chitinases and oxidases, which release N associated to complex aromatic
315 compounds (Derrien et al., 2014). The resulting PE is directly related to enhanced degradation of N-
316 rich SOM compounds that differ chemically from those of the added substrate.

317

318 4.2 Energy cost and return on investment

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

327

328

329 A critical factor influencing the energy balance related to enzymes is the distance between the
330 substrate and the enzyme producer. While some enzymes are directly attached to the plasma
331 membrane of microbial cells or grouped into multi-enzyme complexes (named 'membrane enzymes'
332 hereafter), like the cellulosomes dedicated to cellulose degradation, other enzymes are excreted far
333 away from the cells (named 'exoenzymes' hereafter). When microbes are relatively near their
334 substrates, the monomers produced by membrane enzymes are directly recognised by cell-wall
335 receptors and transported into microbial cells, and this optimises resource uptake from the soil
336 solution. The benefits of enzyme production often exceed the costs thanks to a high return on
337 investment, and allow for microbial growth (Schimel & Weintraub, 2003). By contrast, exoenzymes are
338 sent far away from microbial cells, up to a few mm (Gaillard et al., 1999; Poll et al., 2006; Védère et al.,
339 2020). A significant portion of labile C released through enzymatic action may be lost to the enzyme
340 producer (*i.e.*, leached to deeper soil horizons, immobilised in soil aggregates and/or taken up by other
341 microorganisms) (Allison, 2005; Burns et al., 2013). As a consequence, microbes may invest in chemical
342 defenses (*i.e.*, antibiotics) or produce more enzymes to optimize enzyme foraging (Hiscox & Boddy,
343 2017).

344 For these reasons, the degradation of substrates by membrane enzymes may potentially have a
345 stronger positive feedback on SOM decomposition and biomass growth (and thus on PE) than
346 exoenzymes. Therefore, we propose that the distance between microbes and their substrates as well

347 as substrate accessibility to enzymes should be considered as primary factors driving the magnitude
348 of PE across various soil types. This could be tested by implementing random mutagenesis, gene
349 complementation and functional assays (as performed by Picard et al., 2021) to identify how any
350 mutation affecting the production of membrane-cellulosomes or exo-cellulases of a microbe
351 community inoculated on a sterile soil impacts SOM decomposition and microbial growth after the
352 addition of cellulose. Batch experiments with spatially localized applications of decomposers and of
353 fresh cellulose on a sterile soil (as performed by Pinhero et al., 2015) could also allow the investigation
354 of the effect of varying distances between substrate and decomposers on PE intensity.

355

356 4.3 PE induced by enzymes sorbed to minerals

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

363 The monomers taken up into microbe cells are either directed towards microbial biosynthesis, or
364 oxidised into CO₂ by endoenzymes, as reported by CUE. Under aerobic conditions, the aerobic
365 oxidation of monomers also generates energy in the form of adenosine triphosphate. Endoenzymes
366 may be involved in a PE when they are released from dead microbial cells, attached to mineral surfaces,
367 and maintained their activity outside the cell, with electron transfer to O₂ potentially ensured by soil
368 particles due to their electric charge (Maire et al., 2013; Trevors et al., 1982).

369

370 5 MICROBIAL ACTORS OF PE

371

372 5.1 Actors proposed in the literature

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

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

382 addition, some fungi have strong enzymatic capacities to break down recalcitrant compounds and
383 access trapped N (Fontaine et al., 2011).

384

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

391

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

397

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

403

404 5.2. A trait-based approach

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

410

411 Different bacterial genomic traits have been proposed to be related to maximum growth rates, and
412 therefore to maximal CUE (linked to stoichiometric decomposition PE), like a high copy number of the
413 ribosomal operon (Klappenbach et al., 2000), a small genome size (Saifuddin et al., 2019), vicinity of
414 the ribosomal operon and the chromosomal origin of replication (Viera-Silva & Rocha, 2010), and the
415 translation efficiency, (Weissman et al., 2021). Some genera sharing those traits are *Burkholderia* sp.,
416 *Flavobacterium* sp. and some *Bacillus* sp. (Fierer et al., 2017). The highest maximal fungal growth rates

417 are shared by some well-known saprotrophic fungi that solely use simple sugars and produce spores
418 (Ho et al., 2017), like *Acremonium*, *Alternaria*, *Aureobasidium*, *Cladosporium*, *Cephalotrichum*, *Mucor*,
419 *Rhizopus*, and *Thysanophora*. Decomposition of polymers like cellulose and chitin is widespread and
420 shared by copiotrophic bacterial and fungal species. Genes associated to simple sugar metabolism and
421 β -glucosidase activity were recently shown to drive PE in forest soils (Ren et al., 2021).

422

423 Obligate low-CUE bacteria should be characterised by opposite genomic traits, as adapted to
424 oligotrophy by adopting a small size, a high adsorption capacity of substrate monomers. They should
425 not produce depolymerising enzymes because maintaining these genes is costly (Lynch & Marinov
426 2015). Therefore, key species implied in nutrient-mining PE should first share a high diversity of genes
427 coding for acquisition systems of poorly accessible substrates. White- and brown-rot saprotrophic
428 fungi and certain bacterial species (*Nocardia* sp., *Streptomyces viridosporum* and other sp.,
429 *Amycolatopsis* sp., *Xanthomonas* sp., *Rhodococcus jostii*, *Novosphingobium* sp. and *Sphingomonas*
430 sp.) share various peroxidases and laccases (Brown & Chang, 2014). All these bacterial genera have
431 between 2 and 6 copies of the ribosomal operon in their genomes
432 (<https://rrndb.umms.med.umich.edu>), suggesting that they can be physiologically flexible and adapt
433 their CUE to the quality of the substrates they are decomposing. This is also the case of bacterial and
434 fungal species able to weather minerals by producing ligands or chelating agents and who might be
435 good candidates for the abiotically mediated PE, like *Arthrobacter*, *Janthinobacterium*, *Leifsonia*,
436 *Polaromonas* and *Burkholderia* (see Uroz et al., 2015 for a review). As phosphorus and organic matter
437 compete for sorption sites on minerals (Spohn et al. 2022), P-solubilising bacteria could also have an
438 effect on SOM sorption. *Bacillus subtilis* can desorb P from gibbsite by mineral adhesion of the cells
439 themselves (Hong et al., 2016).

440

441 6 HOW TO INTRODUCE PE INTO MODELS

442

443 Priming is difficult to model, like any other observed but not fully understood phenomenon. To
444 develop a mechanistic model, equations describing the phenomenon are needed, and the very first
445 step is obviously an in-depth understanding of observations. With priming, the situation is somehow
446 slightly uncomfortable for modellers because the debate about the drivers of priming is still ongoing
447 (Chen et al., 2014). Nevertheless, the ubiquity of priming and its potential importance in the soil C
448 balance in a climate change context (Terrer et al., 2021) urge modellers to include priming in their
449 models. We can basically split the modelling objective related to priming into two categories, *i.e.*, (i)
450 understanding the phenomenon, and (ii) quantifying it because observations have shown that
451 priming plays a major role in the C balance of ecosystems. Both objectives can be considered as

452 independent or linked depending on the authors (Blagodatsky et al., 2010; Guenet et al., 2018; Neill
453 & Gignoux, 2006; Perveen et al., 2014). These categories are often associated with different spatio-
454 temporal scales (Figure 3): most of the models aim at understanding priming at small scales and over
455 short time periods, whereas models aimed at quantifying the importance of priming on the SOM
456 balance are developed at larger scales and over longer time periods.

457
458 Priming being defined as a change in the SOM mineralisation rate induced by FOM additions
459 (Kuzyakov et al., 2000), we can consider that classic models describing SOM mineralisation using first-
460 order kinetics – *e.g.*, CENTURY or RothC (Coleman et al., 1997; Parton et al., 1987) – implicitly include
461 priming in their decomposition parameter values. Nevertheless, this is associated with implicit
462 assumptions that the relative importance of priming is fixed in space and over time. In particular, an
463 important implicit assumption of first-order kinetic models is that the microbial community is stable.
464 This hypothesis is not verified in a context of global change (climate, CO₂ + land use) (Carney et al.,
465 2007), and priming will play a major role on future C balances (Terrer et al., 2021). Therefore, it is
466 necessary to understand and quantify priming to represent it in models instead of just considering it
467 implicitly.

468
469 To represent priming following the classic definition, the FOM and SOM compartments must interact
470 directly or indirectly. This can be done simply by implementing SOM rate modifiers depending on
471 FOM (Guenet et al., 2013) or by changing the SOM CUE according to FOM availability without
472 modifying the decomposition rate (Zhang et al., 2018). Priming can also be represented by models
473 that consider explicit microbial mechanisms, with the effect of FOM on SOM considered through
474 microbial biomass (Fontaine & Barot, 2005; Huang et al., 2018; Perveen et al., 2014; Wieder et al.,
475 2015). These different views on priming representation in models should not be seen as
476 contradictory or opposed, but complementary. It would be unrealistic to consider that a complete
477 representation of priming will soon be included in large-scale models (Eyring et al., 2016); simple and
478 semi-empirical approaches are needed. However, it would also be quite unrealistic to believe that
479 semi-empirical approaches will help to develop a deep understanding of priming. In our opinion, the
480 main difficulty in both cases is related to the parameters used in the equation. Increasing model
481 complexity is most often associated with an increased number of parameters and reduced linear
482 responses of the models (Huang et al., 2021). Therefore, the more complex a model is, the higher
483 the number of possible model trajectories. To avoid unrealistic model behaviors, it is of prime
484 importance to constrain the model parameters using observations. Complex models associated with
485 short time periods and small scales can be constrained by observations coming from incubations
486 under controlled conditions (Neill & Guenet, 2010). Nevertheless, applying complex models and

487 finding suitable parameter values for different soil types, climates, plant covers, etc. is an important
488 challenge that requires a large dataset of incubations like those recently published by Bastida et al.
489 (2019). Even though such large datasets of incubations are now published in single studies or in meta-
490 analyses (Luo et al., 2016), laboratory incubations are still carried out in controlled environments,
491 and upscaling the parameters obtained at this scale to the ecosystem or even the global level is not
492 straightforward. At the end of the calibration process, upscaling may increase model prediction
493 uncertainties compared to less mechanistic models because the uncertainties associated with
494 parameter estimation and upscaling are large. Semi-empirical approaches with a limited number of
495 parameters are an intermediate approach that make it possible to add priming explicitly and to study
496 its effect at larger scales (Guenet et al., 2016; Perveen et al., 2014; Sulman et al., 2014). These models
497 do not catch the entire complexity of the priming response, but they are robust enough to estimate
498 the importance of priming on the SOM balance at large scales.

499
500 Different models may involve different, equally accurate or equally uncertain approaches. Therefore,
501 uncertainty remains concerning our prediction capacities. To solve this problem, a promising
502 approach consists in working in close collaboration with experimenters to set up trials aimed at
503 better understanding priming, developing the associated equations and estimating the parameters.
504 But current models can also be compared in the short term. This approach has been fruitful in many
505 fields such as climate sciences (IPCC 2013), biogeochemistry applied to large scales (Ito et al., 2020),
506 and SOM dynamics (Farina et al., 2021). Therefore, using model intercomparison exercises is an
507 interesting alternative to provide robust estimations. This is particularly important when such
508 estimations are key information for stakeholders and policy makers and robust estimations by soil
509 scientists are expected in the near future (Shukla et al., 2019).

510
511 Another difficulty in including priming into large-scale models representing plant growth and
512 phenology, water cycles and energy fluxes (Cramer et al., 2001; Sitch et al., 2003) is related to the
513 feedbacks between all the model (Goll et al., 2014; Zaehle et al., 2010; Zhu et al., 2019). A promising
514 research avenue aiming to incorporate complex models with reduced feedbacks but not yet
515 implemented in soil science to our knowledge is the use of a model emulator (Fer et al., 2018). Such
516 approach can help large-scale models to consider priming based on a complex mechanistic approach.
517 Representing priming in models is still a challenge with a large diversity of approaches that should
518 be considered as complementary and able to tackle highly different situations, from a deep
519 understanding of priming at small scales to the quantification of the importance of priming in the
520 global C budget.

521

524 Due to various technical constraints related to the measurement of PE such as isotopic labelling of
525 contributed OM, PE studies are often conducted in the laboratory in soil incubations with pure
526 chemical compounds (e.g., glucose) making any extrapolation to the ecosystem scale very
527 complicated. However, some studies have quantified PE and its impacts on C and N fluxes in soil-plant
528 systems (see review of Cheng et al., 2014), often involving heavy infrastructure in order to guarantee
529 the reliability of measurements (Cros et al., 2019). These studies show a massive change in SOM
530 decomposition rate in their rhizosphere induced by plants, from a 50% reduction to a 280% increase
531 (Cheng et al., 2014; Huo et al., 2017). This plant induced priming effect (PIPE) results from the
532 combination of several rhizosphere processes such as plant C inputs (litter rhizodepositions) as well as
533 root uptake of nutrients and water intensifying drying-rewetting cycles and breakage of soil aggregates
534 (Dijkstra et al., 2021). Most if not all ecosystem services and disservices related to SOM dynamics are
535 impacted by the PIPE. For example, the PIPE has been suggested to increase disservices such as soil C
536 loss (Carney et al., 2007; Henneron et al., 2020a) and nitrate leaching (Liu et al., 2008), as well as
537 services such as soluble nutrient supply to plants sustaining greater plant production and CO₂ fixation
538 (Henneron et al., 2020a; 2020b).

539
540 Understanding the response of the PIPE and SOM dynamics to current global environmental changes
541 (atmospheric CO₂ increase, global warming and land use changes) is crucial to predict the long-term
542 evolution of the related (dis)services. The task appears very complex because global change can act on
543 priming processes in multiple ways. For example, global warming can impact the intensity of PIPE
544 through its effects on soil enzyme activity, soil microbial populations (Fanin *et al.* in this Special Issue)
545 and plant communities, and in turn determine the quantity and quality of plant C inputs into soils. This
546 complexity is increased by the fact that other processes than PIPE control SOM dynamics (*e.g.*, SOM
547 formation) and have their own response to global change. We suggest a framework that reduces this
548 complexity to three scenarios describing the effect of GC on PIPE, SOM dynamics and four ecosystem
549 (dis)services (Figure 4). This framework is based on the assumptions that (i) plants can drive SOM
550 dynamics to meet their soluble nutrient needs, and (ii) global change can degrade this effect.

551
552 It is increasingly recognised that plants can modulate the PIPE and SOM dynamics to adjust the
553 microbial supply of soluble nutrients to their demand. In a common garden experiment comparing 12
554 grassland plant species, SOM mineralisation rates have been found to be adjusted to the demand of
555 each species (Henneron et al., 2020b). Enhanced plant photosynthesis and nutrient demand under
556 elevated CO₂ increase the PIPE, soil organic N mineralisation and plant N uptake in many different

557 contexts (de Graaff et al., 2009; Kuzyakov, 2019). In contrast, decreased plant photosynthesis (plant
558 demand) in response to plant shading/cutting induces reduced SOM mineralisation (Shahzad et al.,
559 2012; Tang et al., 2019). In temperate ecosystems, the mineralisation/immobilisation ratio changes
560 throughout the season in line with plant demands; immobilisation dominates in winter (low demand),
561 whereas mineralisation dominates in spring (high demand) (Bardgett et al., 2005; Yokobe et al., 2018).
562 Plants control the storage and release of C and nutrients from SOM through their C inputs and soluble
563 nutrient uptake, and this alters the activity of high-CUE and low-CUE microbes (Figure 5). Based on this
564 knowledge on plant control of SOM dynamics, our framework suggests three scenarios of ecosystem
565 response to global change. These scenarios should be considered as attempts to summarise current
566 knowledge, to make it easier to include PE in models and identify priorities for further investigations
567 on the effects of global change on ecosystem C and nutrient cycles.

568

569 **Scenario 1: Control by plants is maintained – Global change affects plant production.** The effects of
570 GC on plant-soil systems are moderate in that plants keep their ability to adjust SOM dynamics to their
571 nutrient needs. Therefore, the ecosystem response to global change is determined by the plant
572 response to global change. More specifically, plant production is modified by global change, while
573 plant biomass remains unchanged. For example, in grasslands under elevated CO₂, primary production
574 is strongly stimulated but the amounts of C and nutrients stored in plant biomass barely change (Terrer
575 et al., 2021) as a consequence of the low storage capacity of herbaceous plants (compared to trees)
576 and continuous grazing. Our framework suggests that the change in primary production modifies the
577 turnover rate of SOM, not the SOM stock. The higher (or lower) plant nutrient demand is expected to
578 increase (or decrease) PIPE and SOM mineralisation. However, an equivalent amount of organic
579 nutrients is expected to return to the soil through litter fall and rhizodeposition if no biomass is
580 exported; this replenishes the SOM stock during periods of low plant demand (Figure 5). In sum, the
581 soil C and ecosystem C stocks as well as nutrient losses remain unchanged, while plant production is
582 changed, meaning there is no feedback effect on global change.

583

584 **Scenario 2: Control by plants is maintained – Global change affects standing biomass.** The sole
585 difference with scenario 1 is that global change also affects the standing plant biomass, as in forests
586 submitted to elevated CO₂ or moderate warming (+ 1 or 2 °C) where primary production and tree
587 biomass often increase (Melillo et al., 2002; Terrer et al., 2021). The increase or decrease in plant
588 biomass induces a parallel and opposite change in the SOM stock (a decrease or an increase,
589 respectively). Given that plants drive the PIPE and SOM dynamics as a function of their nutrient
590 demand, SOM behaves as a nutrient source or sink according to whether plant biomass accumulates
591 or loses nutrients. This nutrient redistribution between plant biomass and SOM affects the ecosystem

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

597

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

609

610 Several experimental studies support our scenarios. The higher plant C input to soil in response to
611 elevated CO₂ intensifies PIPE and SOM turnover (Scenario 1) (Kuzyakov, 2019; Perveen et al., 2014).
612 Moreover, a recent meta-analysis (Terrer et al., 2021) showed that the effect of elevated CO₂ on SOM
613 stocks was best explained by a negative relationship with plant biomass (Scenario 2): when plant
614 biomass is strongly stimulated by elevated CO₂, SOM storage declines; conversely, when biomass
615 decreases, SOM storage increases. Although plant-soil interactions play a major role in the response
616 of the PIPE to global change, it is important to note that some factors of global change may act on the
617 PIPE and related services independently of soil-plant interactions. For example, moderate atmospheric
618 N depositions have been shown to decrease the microbial production of oxidative enzymes (and the
619 intensity of PIPE leading to SOM accumulation (Hagedorn et al., 2003; Ramirez et al., 2012; Perveen et
620 al., 2014; Liu et al., 2018).

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

625

626 8 CONCLUSION AND PERSPECTIVES

627

628 After more than 70 years of research on PE, the way it will respond to climate change and
629 impact the flux of C to the atmosphere is still unclear. Research has been strongly intensified
630 these last ten years but a strong global international coordination is still lacking. PE are
631 generated by multiple mechanisms, but many studies continue to focus on the global flux
632 without considering the underlying processes. Various processes have been proposed
633 throughout the literature, following context-dependant nomenclature, thus introducing some
634 confusion in subsequent work. Moreover, while the environmental drivers of these
635 mechanisms are roughly known, their respective output on the C cycle merit to be more
636 deeply studied. We have proposed a classification of the different mechanisms according to
637 their putative impact on the soil C balance between sequestration and mineralization. This
638 classification is based on two factors which have to be taken into account: the putative
639 turnover rate of the primed SOM pool and the putative CUE of the microbial populations
640 respiring the primed C. Future studies have to verify these assumptions as some SOM pools,
641 especially the MAOM, are likely characterised by a wider range of turnover rates than
642 previously thought, depending on the organo-mineral association model and the chemical
643 bonds involved. While wide metagenomic and culturomic studies will continue to increase our
644 knowledge on functional attributes of poorly described microbial populations, the CUE of
645 populations respiring the primed C cannot be extrapolated from the sole identity of present
646 taxa. Actually, many key actors are probably characterized by a wide physiological flexibility,
647 adjusting their CUE and driving different PE generation mechanisms following environmental
648 conditions. Increasing our knowledge on C fluxes driven by the different PE mechanisms will
649 help to introduce the PE into models of SOM dynamics, thus predicting its behavior in
650 response to climate change. Developing *in situ* experiments should also represent a decisive
651 step forward to complete actual knowledge mostly based on incubation experiments. But we
652 are convinced that the PE will not respond directly, but likely through plants, which are the
653 main producers of fresh organic matter generating soil PE. Therefore, the concomitant
654 elevated CO₂, and plant nutrient requirements, also have to be taken into account.

655

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1197 SUPPORTING INFORMATION

1198 Appendix S1: History of priming effect exploration.

1199 Table S1: List of PE publications from 1973 to April 2021

1200 Figure S1: Network of the international scientific community working on the soil priming effect

1201 Figure S2: Main topics tackled in articles focused on soil priming effect, as deduced from network
1202 analysis

1203

1204 TABLES AND FIGURES

1205 TABLE 1 List of the main PE generation mechanisms proposed by the literature, with their given
1206 name, definition, drivers and reference articles. SOM: Soil Organic Matter; FOM: Fresh Organic Matter.
1207 For each mechanism, the last two columns indicate whether microbial populations assimilating the
1208 primed carbon are characterized by high or low carbon use efficiency (CUE), assuming that r-strategists
1209 (or copiotrophs) have high CUE while K-strategists (or oligotrophs) have low CUE, and whether the
1210 primed SOM pool has a fast, medium or low turnover rate. Generation mechanisms have been colored
1211 to follow a proposed gradient of implication in the fate of soil C: from C gain (brown) to C loss (blue).

1212

1213 TABLE 2 List of bacterial and fungal taxonomic groups identified in the literature as associated
1214 to FOM mineralization and/or to one of the main PE generation mechanisms: negative PE or positive
1215 PE (supposed to involve high CUE or low CUE actors). PE generation mechanisms have been colored to
1216 follow a proposed gradient of implication in the fate of soil C: from C gain (brown) to C loss (blue). FOM
1217 mineralization was not considered in this gradient and was colored in green. In the colored cells, names
1218 correspond to the specific FOM that generated PE in the different publications.

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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 HCO_3^- 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

1254 release of soluble nutrients by the low-CUE microbial community that is stimulated by plant carbon
1255 inputs (plant-induced priming effect, PIPE). Plant C inputs also supply the high-CUE microbial
1256 community that builds SOM (storing nutrients and carbon) when plant nutrient demand is low or
1257 inexistent. The relative abundance and activity of low-CUE and high-CUE communities is driven by
1258 plant uptake of soluble nutrients and carbon inputs (quantity & quality). The numbers indicate the
1259 chronology of events.
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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) slightly 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 chelators and could generate such PE	N-limitation	Keiluweight et al. 2015 ; Fang et al. 2018	High and or low ?	Slow	

FIGURE 2

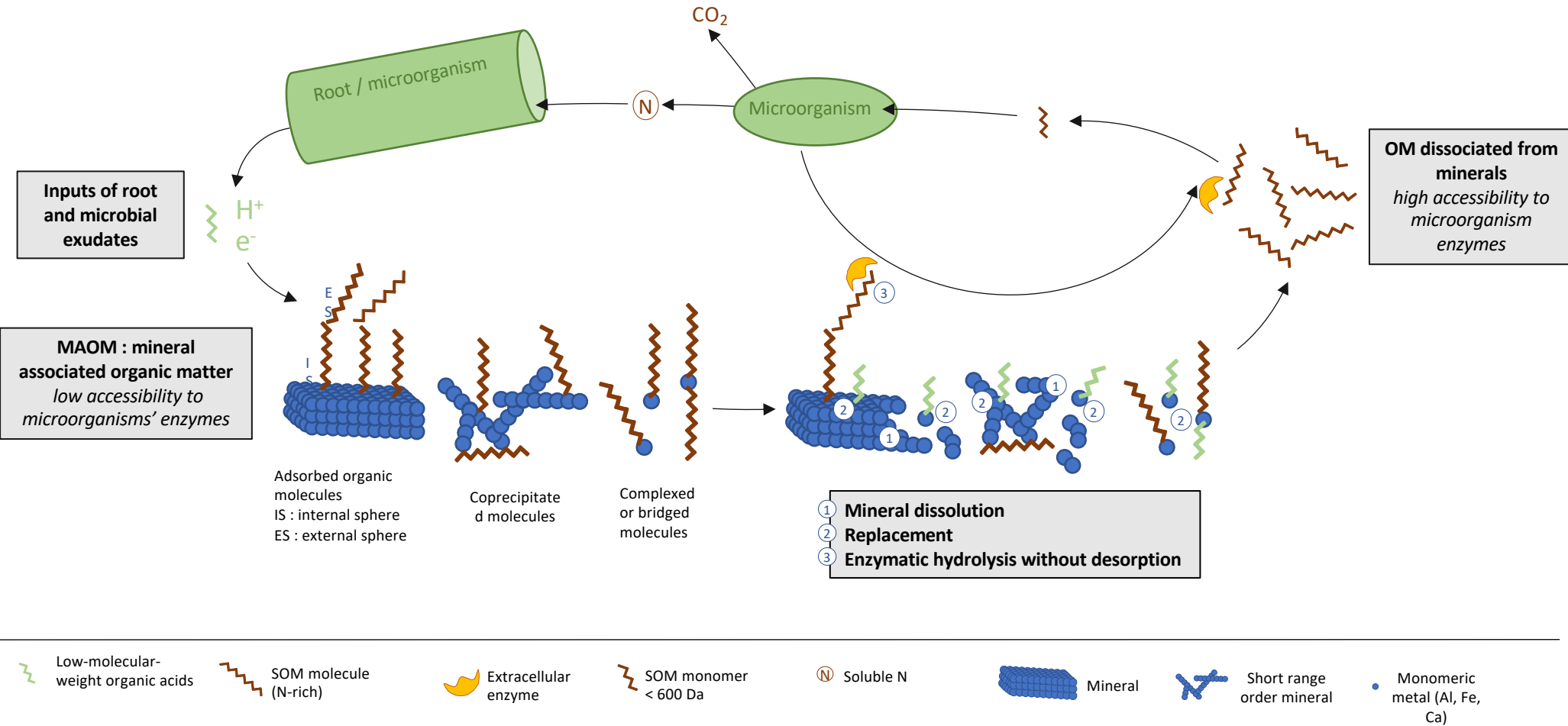


FIGURE 1

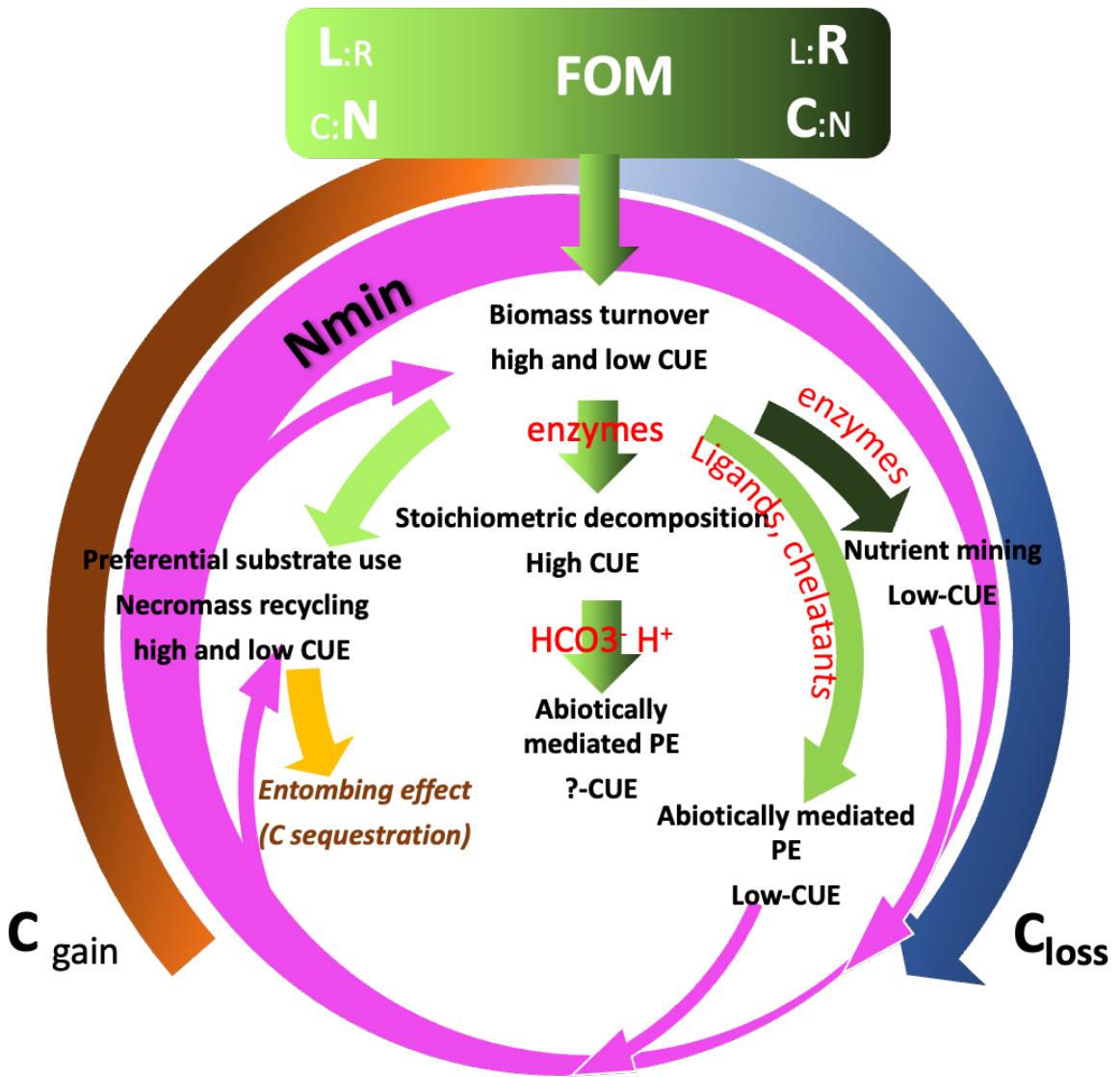
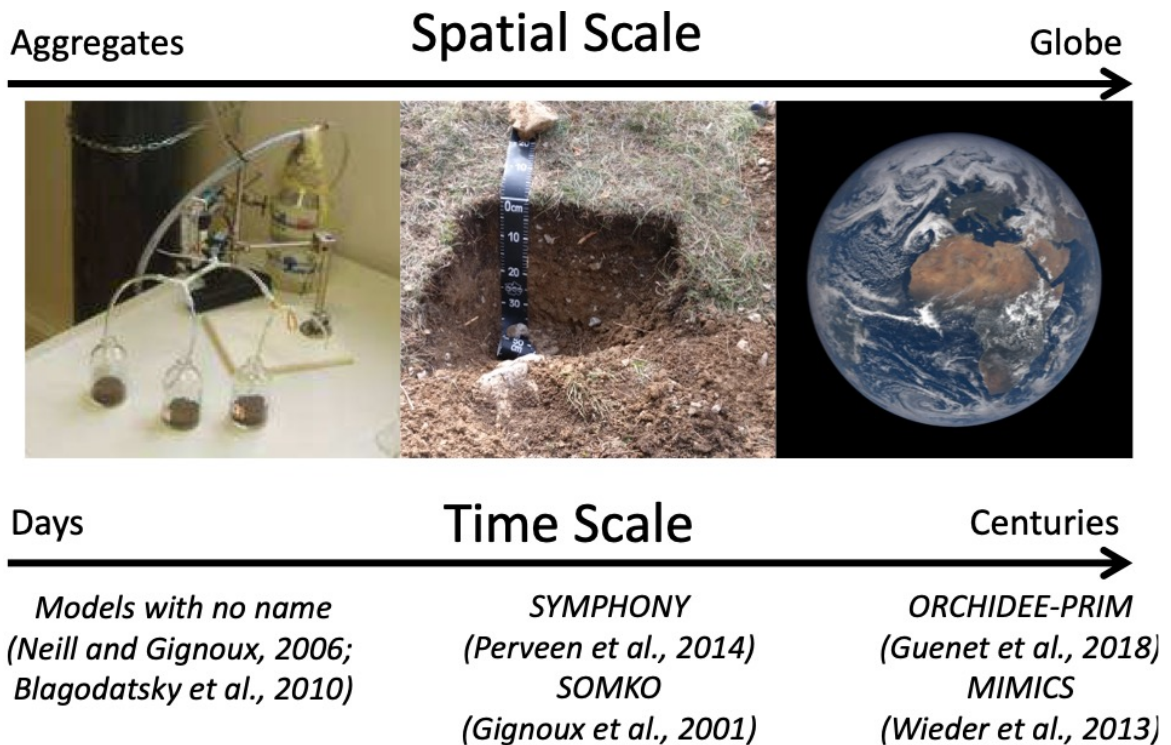


FIGURE 3



Why to develop a priming model?



What are the constraints to develop a priming model?



FIGURE 4

