

1 [A paradigm shift for rhizosphere priming effects to unearth new potential for](#)
2 [more sustainable plant production](#)

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6 [Abstract](#)

7 During photosynthesis, plants fix carbon dioxide from the atmosphere and transform it into
8 bioavailable molecules like primary sugars and more complex molecules like cellulose. A
9 significant fraction of these molecules is transferred to the soil in the plant root zone, where
10 organic carbon compounds serve as food source for soil microorganisms and thus direct their
11 metabolic activity. Increased microbial activity can lead to higher turnover rates of native soil
12 organic matter (positive priming), while microbes can also shift their energy and nutrient
13 acquisition from soil materials to fresh organic inputs, which reduces rates of soil organic
14 matter mineralisation (negative priming). Here, an ecological perspective integrates both
15 positive and negative rhizosphere priming effects as ubiquitous processes in vegetated
16 terrestrial ecosystems linking carbon, nutrient and water cycles. It is suggested that in the
17 mid- to long-term rhizosphere priming effects contribute to synchronising carbon and nutrient
18 supply and demand between plants, soils and microbes, with a neutral carbon balance. Future
19 research could address these rhizosphere plant-soil-microbe interactions in an agronomical
20 context, for example by implementing exudation patterns and rhizosphere priming potential
21 as specific plant-traits to provide new levers for land management strategies that reduce
22 nutrient losses and the need for mineral fertiliser, while also increasing the potential for soil
23 carbon storage.

24 [Keywords](#)

25 Carbon cycle, exudates, microbial mineralisation, nitrogen mining, nutrient cycling, plant
26 nutrition, plant-soil feedback, plant-soil-microbe interaction, rhizosphere priming effect, soil
27 carbon

28 1 Introduction

29 Microbial mineralisation of soil organic matter (SOM) is a continuous process in all soils. It
30 is driven by diverse communities of soil organisms that break organic compounds down into
31 simpler substances, ultimately leaving behind inorganic forms of carbon (C) and various
32 mineral nutrients. This process of decomposition occurs in several stages. Most organic
33 matter primarily enters the soil in form of dead plant material like leaves, stems, roots, animal
34 remains and/or organic materials added as compost, mulch or manure. Easily decomposable
35 compounds are rapidly broken down, releasing simple sugars, amino acids, and other organic
36 molecules. In later slower stages of decomposition, more complex and recalcitrant
37 compounds such as cellulose or lignin are broken down, which also releases phenolic and
38 organic acids. In all these processes, microorganisms, primarily bacteria and fungi, play a
39 crucial role in breaking down the different forms of organic matter into their smallest units
40 (Bot & Benites, 2005). The metabolism of most soil microbes and decomposers is based on
41 the Krebs cycle, in which energy is released from organic compounds through the oxidation
42 of acetyl-CoA, while carbon dioxide (CO₂) is respired (Bore et al. 2017). Some of this CO₂
43 from soil respiration is immediately taken up by nearby plants during photosynthesis,
44 completing a cycle of carbon flow between the atmosphere, plants, organic matter, and
45 microorganisms. Closely coupled to the C cycle is the flow of essential elements such as
46 nitrogen (N), phosphorus (P), potassium (K) and sulphur (S), which are released into the soil
47 when microorganisms decompose organic matter or break-up soil minerals. These nutrients
48 are thus made available to plants and other organisms in the ecosystem, contributing to soil
49 fertility and ecosystem functioning. Rates of SOM mineralisation naturally fluctuate as a
50 function of the catabolic and anabolic activity of the soil microbial community carrying out
51 decomposition. The sum of microbial metabolism is governed by abiotic and biotic factors
52 such as temperature, pH, humidity, the quality and quantity of organic compounds available

53 and the collaborative and competitive interactions between different soil organisms, and
54 between soil organisms and plants (Kuzyakov, 2002; Fontaine et al. 2003; Blagodatskaya &
55 Kuzyakov, 2008; Yin et al. 2018; Liu et al. 2020; Bernard et al. 2022).

56 2 Brief history of “(rhizosphere) priming effects” research

57 Almost a century ago, a particular observation caught the attention of soil scientists: they
58 observed that when adding mineral N fertiliser, glucose or green manure to soil, instead of
59 reducing rates of SOM-mineralisation because fresh nutrients had just been provided, such
60 substrate addition would unexpectedly enhance, or ‘prime’, the rate of natural SOM-
61 mineralisation. They first termed this observation ‘added nitrogen interaction’, and later
62 ‘priming effect’ (Löhnis, 1926; Jenkinson, 1966; Dalenberg & Jager, 1981; Jenkinson et al.
63 1985). In its origins, ‘priming effect’ referred specifically to the case of ‘positive priming
64 effect’, that is an increase in SOM mineralisation. However, the opposite case is also
65 frequently observed, that is a reduction in SOM mineralisation rates following labile organic
66 inputs, referred to as a ‘negative priming effect’ (reviewed in Kuzyakov, 2000). Positive and
67 negative priming effects are not mutually exclusive, and both commonly occur in ecosystems
68 as a function of plant and microbial supply and demand of carbon and nutrients (Bastida et al.
69 2019; Feng & Zhu, 2021). A common misperception is that positive priming is more
70 important and/or frequent than negative priming, but this view is heavily influenced by
71 publication bias and more recent studies increasingly report negative priming (Siles et al.,
72 2022; Verbrügge et al., 2022; Linkosalm et al., 2023; Wild et al., 2023; Michel et al., 2025).
73 In many studies, observations include both positive and negative priming either depending on
74 experimental condition, or sometimes substrate amendments also result in mixed positive,
75 negative and/or no priming within one unique modality (Chen et al. 2014; Qiao et al. 2016;
76 Heitkötter et al. 2017; Hicks et al. 2019; Michel et al., 2023). Individual priming effects are
77 mostly short-term phenomena, but continuously occur in the rhizosphere of living plants,

78 where active root exudation provides energy-rich labile carbon to soil microbes, while
79 rhizodeposition also supplies more complex substances like cellulose to the soil (Canarini et
80 al. 2019; Villarino et al. 2021; Michel et al., 2024). Given the diversity of substances in the
81 rhizosphere, priming effects constantly oscillate between positive and negative priming,
82 while microbial communities alternate between nutrient mining and preferential substrate
83 use, making it difficult to parametrise priming effects (Fig. 1). Researchers agree that they are
84 the results of the interactions between the quality and quantity of added substrate and the
85 composition and functional capacity of the microbial community, but priming also depends
86 on abiotic factors like temperature, humidity and pH, and the composition of present SOM
87 fractions, (Kuzyakov, 2002; Fontaine & Barot, 2005; Blagodatskaya & Kuzyakov, 2008;
88 Garcia-Pausas & Paterson, 2011; Chen et al. 2014; Bastida et al. 2019; Feng & Zhu, 2021). It
89 has not yet been possible to determine the relative importance of each of the potential drivers,
90 as individual effects are not additive and not many fully replicated multifactorial studies have
91 been conducted. Therefore, researchers proposed certain ‘mechanisms’ to predict priming
92 based on a set of conditions, like nutrient and energy supply and demand.

93

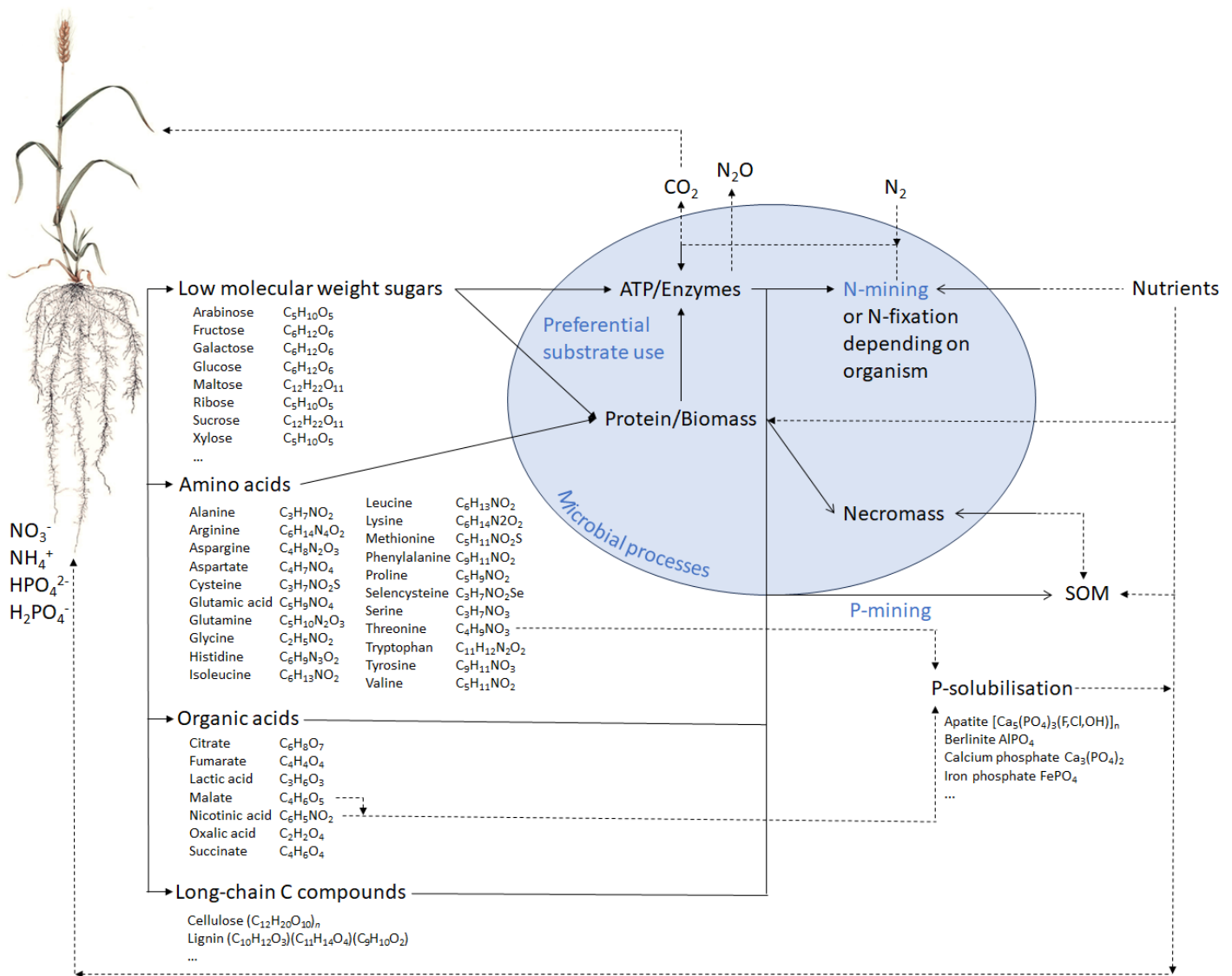


Figure 1: Major groups of molecules present in the rhizosphere and their relation to microbial metabolism, plant available nutrients and greenhouse gas emissions (here only N_2O and CO_2). Rhizosphere priming effects (RPE) are changes in SOM-mineralisation rates, where positive priming describes enhanced rates of SOM mineralisation quantified as an increases proportion of SOC released in CO_2 from soil respiration, and negative priming effects describe reduced rates of SOM-mineralisation, for example when microbes primarily feed on freshly provided root exudates like sugars rather than SOM.

94

95 3 Mechanisms of positive and negative (rhizosphere) priming effects

96 Different mechanisms have been proposed relating the direction of priming effects to

97 different microbial strategies of resource acquisition (Table 1). A positive priming effect

98 describes a situation where supplying soil microbes with labile organic compounds fuels

99 these microbes to degrade more SOM. It is theorised that this occurs when microbes are

100 supplied with proportionally more C than nutrients, so that the microbial demand for nutrients
101 increases and is compensated by enhancing SOM-mineralisation to release nutrients, so
102 called ‘microbial N-mining’ (Schimel and Weintraub 2003; Craine et al. 2007). However, N-
103 mining alone doesn’t explain all positive priming, as enhanced SOM-mineralisation is also
104 dependant on the microbial energy balance of enzyme synthesis and microbial biomass
105 turnover (Mason-Jones et al. 2018). On the other hand, a negative priming effect describes a
106 situation where rates of native SOM-mineralisation decrease following the addition of
107 organic substrates. This is attributed to microbes switching their energy and nutrient
108 acquisition from SOM to substrate when it stoichiometrically meets their metabolic
109 requirements, and is termed ‘preferential substrate use’ (Cheng 1999; Kuzyakov & Bol, 2006;
110 Blagodatskaya et al. 2011). When microbes start feeding on substances of a energetically
111 more beneficial stoichiometry, for example compounds of low C:N with low binding energy,
112 so called ‘selective N-targeting’, this can also change CO₂-emissions from soil as such, but
113 does not necessarily affect rates of SOM-mineralisation (Murphy et al. 2015; Rousk et al.
114 2016).

115 4 Priming effects ≠ rhizosphere priming effects

116 ‘Priming effects (PE)’ refer to interactions between soils, soil microbes and added substances,
117 while ‘rhizosphere priming effects (RPE)’ more specifically describe the interactions between
118 living plant roots, their exudation and other rhizodeposition, rhizosphere microbes and
119 rhizosphere soils. It is important to distinguish between the two, because there are differences
120 between the driving factors. For example, priming effects are caused by a static source of
121 substrate input, while rhizosphere priming effects are driven by a dynamic source, and
122 simultaneous sink, of carbon and nutrients (a plant). Hence, several plant physiological
123 parameters like rate of photosynthesis and exudation are also determinant for rhizosphere
124 priming effects (Dijkstra et al. 2013; Yin et al. 2018; Tang et al. 2019). Rhizosphere priming

125 effects are a function of carbon supply from plants to soil microbes, but at the same time
126 depend on the plant nutrient demand. Carbon is the key source of energy for heterotrophic
127 organisms, including most soil microbes, and one of the most abundant simple carbon
128 sources in the rhizosphere is low molecular weight (LMW) compounds like glucose (Landi et
129 al. 2006; de Deyn et al. 2011; Gunina & Kuzyakov 2015). Microbes in the rhizosphere obtain
130 most of their carbon from plants, which transfer between 50-80% of the photosynthetically
131 fixed CO₂ to soil microbes either via active exudation of for example LMW sugars, or via
132 turnover of plant biomass (Kuzyakov & Domanski 2000; Jones et al. 2009; Pausch et al.,
133 2013; Guyonnet, et al. 2018; Tang et al. 2019). In addition to energy, microbes, like plants,
134 need a suit of other elements to build biomass and perform cellular processes, these include
135 N, P, K, S and many more. In the case of positive priming, the idea is that plants supply
136 microbes with extra energy in form of labile organic carbon compounds, which microbes in
137 turn invest into SOM-mineralisation to release extra nutrients (microbial N-mining), which in
138 turn also releases extra CO₂ as soil microbes are heterotrophic organisms and respire more
139 when they work harder. Plants can also directly provide microbes with nutrients, such as N in
140 the form of amino acids (Canarini et al. 2019). However, usually plants also are in demand of
141 nutrients themselves, so both plants and microbes strive to extract extra nutrients from soil
142 minerals and soil organic matter (Dijkstra at al. 2013). This can be done by several pathways,
143 including excretion of charged ions to modify the pH of the soil solution to weaken mineral
144 binding and excretion of enzymes that break down soil minerals (Schimel & Weintraub,
145 2003; Sinsabaugh at al. 2005). In the case of negative priming effects, microbes are supplied
146 with labile organic substances without a need for additional nutrients. They can hence feed
147 primarily on the supplied organic substance, which reduces rates of SOM-mineralisation
148 (preferential substrate use). This process not only reduces rates of SOM-mineralisation, but
149 when microbes are supplied with ample carbon over time, their biomass increase can also

150 contribute to soil C-sequestration (Liang et al. 2019; Pommer et al. 2019). Different priming
151 effects can easily complement each other to integrate into a unifying framework where
152 direction and magnitude of priming effects fluctuate as a function of plant and microbial
153 supply and demand of C and nutrients. In reality, both positive and negative priming are
154 short-term phenomena, that vary on the small scale along one single root according to the
155 different areas, timing and kind of root exudation, and on the large scale according to plant
156 growth stage and/or season. Alternating positive and negative priming effects from root to
157 ecosystem scale can aid to synchronise carbon and nutrient flows between plants, soils and
158 microbes over time (Liu et al. 2017; Dijkstra et al. 2021; Holz et al. 2023).

159 5 Rhizosphere priming effects and the C-balance

160 Given the limitations in the scalability of short-term reductionist laboratory soil incubations
161 to represent ecosystem processes involving living plants, a thought experiment as an
162 alternative approach to estimate the impact of priming effects in the context of ecosystems
163 was performed in which the magnitude of C-fluxes from priming effects was compared with
164 other ecosystem process. In their comprehensive test of glucose-induced priming effects in
165 global soils, Bastida et al. (2019) found that the average glucose-induced priming effect
166 across terrestrial ecosystems was $0.026 \pm 0.935 \mu\text{g CO}_2\text{-C g}^{-1} \text{ soil day}^{-1}$. The magnitude of
167 these priming effects seems to be on the same scale or smaller than autotrophic CO_2 -fixation
168 by Archaea and some bacteria, which is also an important but underestimated process in soils
169 (Kramer & Gleixner, 2006; Berg et al. 2010; Šantrůčková et al. 2018). In a temperate forest
170 soil for example, dark microbial CO_2 fixation can account for $0.32 \mu\text{g C g}^{-1} \text{ soil day}^{-1}$
171 (Spohn et al. 2019). While rhizosphere processes and priming can account for up to one-third
172 of the total C and N mineralized in temperate forest soils (Finzi et al., 2014), several studies
173 upscaling priming effects over longer time scales and to areas of several hectares indicate that
174 priming effects may not change overall C-budgets. For example, Schiedung et al. (2023)

175 evaluated priming effects along a 20-year chronosequence of land inversion in New Zealand
176 to identify the dependence of priming effects on root-derived C in topsoil and sub soils. Even
177 though positive priming was reported, overall, carbon losses with priming never exceeded
178 new root-derived carbon inputs. Similar observations were made by Yin et al. (2019) who
179 studied rhizosphere priming effects and microbial biomass carbon dynamics of two wheat
180 genotypes grown under two temperatures and found no net soil organic C loss or gain as C
181 loss caused by higher RPE was counteracted by increased microbial growth/turnover.
182 Similarly, Cardinael et al. (2015) used a 52-year long field experiment where SOC stocks of
183 fallow fields were compared to SOC stocks of fields regularly receiving fresh or composted
184 straw to show that no significant difference in SOC stocks dynamics occurred over the 52
185 years, suggesting no long-term impact of priming effect.

186 6 Priming from a plant perspective

187 While the patterns of magnitude and direction of rhizosphere priming effects observed in
188 different studies may seem contradictory, at ecosystem scale it is possible to integrate the
189 ensemble of positive and negative priming effects, and the varying underlying mechanisms,
190 into a framework of coupled carbon and nutrient cycling between the atmosphere and soils
191 over time (Fig. 2). The eco-evolutionary purpose of priming effects may be to synchronise
192 ecosystem processes governed by supply and demand of carbon and nutrients between plants,
193 soils and soil micro-organisms (Myers et al. 1994; Crews & Peoples 2005; Valencia et al.
194 2020). In this regard, positive rhizosphere priming effects are a mechanism to synchronise
195 SOM-mineralisation rates to enhanced plant nutrient demand via provision of labile carbon to
196 soil microbes to trigger SOM-mineralisation and thereby nutrient provision (Holz et al.
197 2023). Negative priming effects serve to preserve the soil C stock when plant activity and
198 nutrient demand are low. Positive and negative rhizosphere priming effects can thus be
199 regarded as complementary mechanisms stabilising the ecosystem C-balance over time

200 (Cheng et al. 2013). In this regard, seasonality may play an important role (Fig. 2). Positive
201 priming occurs when plants and microbes are in higher demand of nutrients, for example in
202 summer or more generally, during the peak growing season or diurnally when photosynthesis
203 is highest (Kaiser et al. 2010; Dijkstra et al. 2014). When net primary production (NPP) is
204 high, increased plant growth increases plant nutrient demand. Plants trigger positive priming
205 by increasing exudation of substances that fuel microbial degradation of SOM to release
206 nutrients from SOM, for example nitrogen (Kaiser et al. 2011; Holz et al. 2023; Pausch et al.,
207 2024). On the other hand, when the present supply of organic substances meets microbial
208 metabolic requirements, negative priming occurs. This may be observed in autumn, or
209 generally under low NPP and low plant nutrient demand, for example at plant senescence,
210 when plant nutrient demand is concordantly reduced and quality and quantity of
211 rhizodeposition changes (Nguyen 2009; Thomas 2013). Microbes might obtain more
212 complex, but nutrient-rich, molecules resulting from plant developmental turnover. This may
213 reduce rates of SOM-mineralisation via negative priming effects and increase microbial
214 necromass if the microbial community previously feeding on the simpler energy-rich
215 substances is no longer sustained, which can aid soil carbon sequestration through
216 accumulation of microbial necromass (Buckeridge et al. 2020; Liang et al. 2023; Mason-
217 Jones et al. 2023).

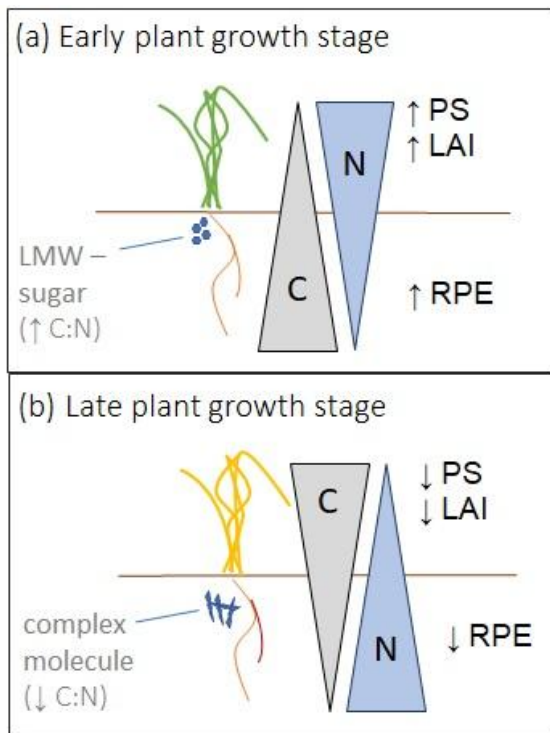


Figure 2: Plant growth stage as a factor of nutrient demand (a) in juvenile stages plant nutrient demand is higher to enable biomass production, so photosynthesis (PS) and leaf area index (LAI) increase. Exudation of low molecular weight (LMW) compounds provides soil microbes with energy to mineralise SOM to release nutrients (rhizosphere priming effect (RPE) increases) (b) at later plant growth stages and during senescence, plant biomass turnover releases more complex organic molecules into the soil like cellulose. These compounds take longer to mineralise, but have higher N-content in return, so that thanks to N-remobilisation less SOM-mineralisation is required to obtain nutrients (rhizosphere priming effect (RPE) decreases). Abbreviations: PS: photosynthesis, LAI: leaf area index, RPE: rhizosphere priming effect, C:N: carbon to nitrogen ratio.

219

220 7 How are (rhizosphere) priming effects measured?

221 The common method to study priming effects of either direction is to supply organic
 222 substance to soils where the element of interest is isotopically labelled. The isotopic label
 223 usually consists in an enrichment of the heavy isotope. Most commonly used are ^{13}C and ^{14}C ,
 224 which can be tracked against the naturally more abundant ^{12}C , and ^{15}N , which is used to track
 225 against the naturally more abundant ^{14}N . Subsequently, the known amount and isotopic
 226 composition of labelled input, the amount and isotopic composition of un-labelled pre-
 227 existing soil organic carbon and the amount and isotopic composition of CO_2 soil respiration
 228 in treated and untreated control soils are used in a two-end-member mass balance to compare
 229 the amount of soil organic carbon that is respired in treated and untreated soils. The
 230 difference in the fraction of soil organic carbon that is found in soil respiration in treated
 231 versus untreated soils is used as a quantitative estimate of the priming effect (Staddon 2004;
 232 Subke et al. 2006; Kuzyakov 2011). The most manageable implementation of such isotope-

233 labelling and mass-balance is to incubate soils with labelled substrates (in the absence of
234 living plants), and the majority of priming studies follows this approach. This kind of study is
235 best suited to investigate short-term responses of soil microbes to changed inputs and allows
236 to quantify priming effects and the involved pools and fluxes more easily as conditions are
237 controlled. However, it should be seen critical that these studies usually use soil samples that
238 have been stored at 4°C and then rewarmed, that have been dried/reweted and that have been
239 sieved. All these pre-incubation treatments can impact microbial community composition and
240 functioning and hence their response to substrate inputs (Subke & Bahn 2010; Thomson et al.
241 2010; Datta et al. 2014) and the observed conditions are not representative of field conditions,
242 where soil has a given bulk density, and fluctuating moisture content and temperatures.
243 Substrate additions also most often use individual molecules like simple sugars, which is not
244 representative of the plethora of substances found in soils (Fig. 1).

245 To study more specifically rhizosphere priming effects, the presence of living plants and their
246 roots is required. Plant-soil mesocosms or field studies are more suited to understand carbon
247 and nutrient cycling at scale, but require more extensive and expensive set-ups and longer
248 time scales. To trace the carbon inputs from living plants to soil microbes, it is necessary to
249 either label the CO₂-atmosphere in which the plants are grown, either by continuous labelling
250 or by pulse labelling with depleted or enriched ¹³C or ¹⁴C-CO₂, or by using the difference in
251 natural abundance of ¹²C and ¹³C in C₃ plants (δ¹³C ~-15) and C₄ plants (δ¹³C ~ -30),
252 introducing a C₃-plant to soils that have been continuously grown with C₄-plants or vice
253 versa (Balesdent et al. 1987; Blagodatskaya et al. 2011). Each of these approaches has
254 advantages, disadvantages, and uncertainties (Cros et al. 2019; Jian & Bengtson 2022).
255 Inaccuracy, which translates into uncertainty of the quantitative estimate of the (rhizosphere)
256 priming effect, is inherent to all of these approaches, because the two end-members of ‘plant-
257 C’ and ‘soil-C’ are variable over time in terms of the availability and isotopic composition of

258 different C fractions (Paul et al. 2001; Kramer & Gleixner, 2006; Villarino et al. 2020). For
259 example, plant carbon compounds in form of exudates or turnover of root tissues comprise a
260 plethora of different molecules (Fig. 1), which are mostly not accounted for in laboratory soil
261 incubations; and in plant-soil experiments pose a problem because these different carbon
262 compounds also have different isotopic compositions due to various carbon isotopic
263 fractionation processes (Blagodatskaya et al. 2011; Wang et al. 2015). In addition, a
264 challenge for both soil incubations and plant-soil mesocosm experiments is that microbes not
265 only respire CO₂, but also capture carbon in their biomass, which can give rise to so called
266 ‘apparent priming effects’ where soil CO₂-emissions change without changing SOM-
267 mineralisation rates (Blagodatskaya & Kuzyakov, 2008). The microbial communities that
268 consume C and mineralise soil organic matter and organic inputs are another source of
269 uncertainty because they are highly flexible and community composition can change rapidly,
270 which can affect the functional capacity of the microbial community to mineralise C and
271 eventually modifies C-fluxes (Lauber et al. 2013, Zechmeister-Boltenstern et al. 2015).

272 [8 Technical challenges and limits to upscaling](#)

273 The research on priming effects started with laboratory soil incubations, but here we showed
274 that we clearly need to include plants if we want to talk about rhizosphere priming effects. To
275 understand on what kind of experiments our current and predominant knowledge about
276 (rhizosphere) priming effects is based on, a systematic literature search was performed to
277 summarize the ‘common practice’ of empirical experiments of the two main types: laboratory
278 soil-substrate incubations and plant-soil mesocosm/field experiments (supplementary data
279 S1). Real ecological insights can only be obtained when the purpose that each respective
280 experimental setup serves is clearly defined. Laboratory soil incubations serve best to unravel
281 mechanisms behind biochemical reactions between soil particles and microbes at a given time
282 and conditions. However, the often artificial set-up of most laboratory soil incubations, where

283 small amounts of top or sub-soil samples are cooled, rewarmed, dried, rewetted and sieved
284 before the incubation render them less suitable to represent field conditions or even
285 ecosystem processes. Standardised soil incubation conditions make comparisons between
286 studies easier, however soils in natural environments are not always and constantly at 73% of
287 their maximum water holding capacity and temperatures fluctuate on daily and annual cycles.
288 Pre-incubation soil treatments like dry-rewetting and cool-rewarm cycles and sieving may be
289 particularly critical because these treatments impact the microbial community in the soil
290 sample and thus may change the priming response (Moinet et al. 2018). Therefore, it needs to
291 be clearly acknowledged that reductionist laboratory soil incubations are incomplete
292 representations of complex natural environments and cannot be extrapolated to ecosystem
293 processes in the same way as plant-soil experiments. While it is possible to gain mechanistic
294 insights of soil microbial processes in isolated conditions via such soil incubation
295 experiments, nutrient dynamics and the carbon balance of entire ecosystems are inherently
296 misrepresented. For example, soil incubations cannot account for key energy and matter
297 flows occurring between plants, soils and microbes in natural ecosystems over time (Fig. 2),
298 such as continuous plant root exudation of different many compounds (Fig. 1) and
299 rhizospheric nutrient uptake belowground and plant photosynthetic C-fixation and biomass
300 production aboveground. Therefore, results of studies on the priming effect cannot be
301 transposed to rhizosphere priming effects, which needs to be taken into account when
302 interpreting results of such studies. Here, it also needs to be noted that many soil incubation
303 studies don't consider the net C balance, that is accounting comprehensively for organic C
304 inputs that have been added but not respired as CO₂-C, such as C incorporated into microbial
305 biomass or simply un-metabolised C. Often, the amount of experimentally added C exceeds
306 the amount of additional C respired from SOM, so that C losses caused by positive priming
307 are cancelled out or even reversed (Liang et al. 2018). Especially in laboratory soil

308 incubations, the amounts of added substances often largely exceed any priming effects (Liang
309 et al., 2018, Qin et al., 2024). This means that there is no net loss of C from the system even
310 though positive priming is observed. In addition, a critical limitation to upscaling most of all
311 priming studies to the carbon cycle, including those studies involving living plants and run
312 over representative time scales, is that they are commonly quantifying the decomposition of
313 SOM, but not the simultaneous formation of organic matter. Thus, these studies misrepresent
314 the soil-C pool and cannot be considered as estimates of its evolution without further
315 measurements (Bradford et al. 2008). To improve our understanding of the impact of
316 rhizosphere priming effects on the C balance, future experiments therefore need to measure
317 not only CO₂ emissions, but also trace the fraction of organic inputs that is not entering
318 catabolic processes in microbes, but for example immobilised in microbial and mesofauna
319 biomass, and the fractions of C that enter the pools of dissolved organic carbon (DOC) and
320 mineral-associated organic carbon (MAOC), and their respective residence times *ibidem*. To
321 improve the accuracy of the two end-member mass balance approach, it is further necessary
322 to evaluate the different turnover times of the different C-pools in soils and in how far they
323 are affected by isotopic fractionation processes, as they occur in plants and soil biota (Tiunov
324 2007).

325 9 Further studies and possible implementations

326 While the impact of priming on CO₂-effluxes has been extensively studied, the rates of SOM-
327 formation following labile organic inputs remain relatively unknown. To complement our
328 knowledge about rhizosphere priming effects, future studies could focus empirical efforts on
329 the C-sequestration potential of unmetabolized organic inputs (Panchal et al. 2022) and
330 microbial biomass turnover (Buckeridge et al. 2020) and the soil C-preservation side of
331 negative priming effects. If we're aiming to understand the impact of rhizosphere priming
332 effects on carbon cycling at the scale of entire ecosystems, it is obligatory for future studies

333 to involve living plants and quantify not only C-effluxes, but also C-influxes to the soil and
334 plant nutrient uptake. In this regard, identifying compounds in exudates that trigger either
335 biomass/SOM-formation or SOM-mineralisation could be an essential puzzle piece to both
336 mechanistic modelling and practical field applications like nature-based biostimulants. It is
337 possible that plants can tailor their exudation to trigger the heterotroph microbes that have the
338 metabolic capacity to degrade SOM to obtain nutrients as needed to meet both plant and
339 microbial nutrient demands, while energy is provided through the plants' autotroph
340 metabolism (Sasse et al. 2018). Further, future studies could test the hypothesis that quantity
341 and quality of root exudates change as a function of plant primary production and soil
342 nutrient availability to stimulate different functional groups of microbes with different SOM-
343 mining capacities. Unravelling the priming-potential of different plant species or specific
344 plant traits like root system architecture could also be useful to implement them in
345 agricultural cropping systems to find species and trait combinations that harmonise together
346 to reduce the need for synthetic fertiliser by purposefully inducing natural SOM-
347 mineralisation processes when high plant productivity is envisaged and promote negative
348 priming on the other hand when plant productivity is low. Further possible implementations
349 include combining plants with complementary priming potential in mixed cropping systems
350 and crop rotations and assessing the impact of different field management practices like cover
351 cropping and switching from annual to perennial plant species on the sum of positive and
352 negative rhizosphere priming effect and the cropping systems' carbon and nutrient balance.

353 10 Conclusions

- 354 1. Every soil incubation study addressing priming effects should imperatively report a
355 net C balance, and provide the elements needed for the reader to estimate the
356 dynamics in the different C pools: amount of soil used, amount of substrate C added,
357 amount of total CO₂-C respired, amount of substrate CO₂-C respired, ideally also

358 change in microbial biomass C. CO₂ of untreated controls also need to be reported to
359 enable estimation of effect sizes across studies.

- 360 2. Studies on rhizosphere priming effects determine changes in rates of SOM-
361 mineralisation and CO₂-emissions from soils, but should also account for
362 simultaneous organic carbon formation and the coupling of nutrient and water
363 availability in the soil with priming effects and above- and belowground biomass
364 production and CO₂-fixation. To reduce the uncertainty of RPE estimates calculated
365 via mass-balance, future research could address the chemical composition of plant
366 carbon inputs to soil and their isotopic composition. Diurnal and seasonal variation of
367 RPE is another research gap. To gain mechanistic insights at ecosystem level, studies
368 should link rhizosphere priming effects *in vivo* to carbon, water and nutrient cycling.
- 369 3. Beyond carbon cycling, future research could address the potential of rhizosphere
370 priming effects to improve plant nutrient uptake by triggering SOM-mineralisation
371 when plant NPP is high. When plant nutrient demand is low, microbial community
372 turnover and the build-up of microbial necromass could help restore soil carbon and
373 nutrient pools after periods of high nutrient demand.
- 374 4. In order to develop practical implementations for land management strategies,
375 different plant species could be characterised by linking specific plant traits like root
376 system architecture and root exudate profiles to their respective potential to induce
377 positive or negative rhizosphere priming effects to purposefully implement these trait
378 combinations in agroecosystems.

379 [Statements and Declarations](#)

380 [Competing interests](#)

381 There are no competing interests to declare.

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