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Influence of cover crop residue traits on phosphorus availability and subsequent uptake by plants

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Statements and Declarations

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Data availability

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29 **Abstract**

30 Cover crops are typically thought to increase the P nutrition of crops. However, there
31 are mixed reports on this with some studies reporting a negative effect. An improved
32 understanding of cover crop residues and their P release dynamics could offer new
33 insight with the benefit of improved management for optimal P availability in cropping
34 systems. Here, we examined the influence of cover crop residue traits for six different
35 crop types on soil P availability and subsequent plant (ryegrass) P uptake over a
36 four-month period in a soil with moderate P availability. Among the residue traits
37 examined (residue P concentration, N concentration, C:P ratio, C:N ratio, N:P ratio
38 and specific leaf area), only residue P concentration and C:P ratio were related to soil
39 P availability and subsequent crop P uptake. Important short-term effects of residue
40 C:P ratio on P availability were highlighted. Strong to moderate negative correlations
41 between residue C:P ratio and subsequent crop P uptake (R^2 between 0.4 and 0.8)
42 were observed. Decreases in subsequent crop uptake of up to 43 % compared to
43 unfertilized pots occurred for residues with high C:P ratios for the first cut, strongly
44 suggesting microbial P immobilization. Effects faded with time, with most cover crop
45 residue additions having little to no influence on ryegrass P uptake over a four month
46 period. Residues with the highest C:P ratio nonetheless resulted in a 22 % decrease
47 in cumulative P uptake compared to unfertilized pots. Our study highlighted that
48 cover crop C:P ratio should be managed in order to ensure minimized adverse
49 effects of microbial P immobilization. The observed low effects of cover crop residues
50 on P uptake in a subsequent crop suggest that improving P availability in context with
51 moderate P limitations via cover cropping may require relying on other services
52 provided by cover crops such as mobilization of sparingly available P pools.

53 **Abbreviations**

54 0P: Control treatment without phosphorus addition

55 BraC: *Brassica carinata*

56 FagE: *Fagopyrum esculentum*

57 LenC: *Lens culinaris*

58 minP: Treatment with addition of 15 mg P kg⁻¹ soil mineral fertilizer (KH₂PO₄)

59 PhaC: *Phacelia tanacetifolia*

60 P_{mic}: Soil microbial P content based on difference method between fumigated and
61 unfumigated resin extracts.

62 P_{res}: Soil available P content as extracted by anion exchange resins

63 SLA: Specific leaf area

64 VicF: *Vicia faba*

65 VicV: *Vicia villosa*

66 **1. Introduction**

67 Low bioavailability of soil phosphorus (P) in most agroecosystems often requires the
68 addition of P fertilizer. However, a large portion of the added P is sorbed onto soil
69 mineral surfaces, reducing plant P uptake and resulting in low P fertilizer use
70 efficiencies (Richardson et al., 2011). Over time, the regular addition of P fertilizer
71 results in the accumulation of sparingly-soluble forms of soil P (Bouwman et al.,
72 2017). Improving crop utilisation of sparingly-soluble forms of soil P could lead to
73 increased P cycling efficiency and reduced dependency on declining resources of
74 phosphate rocks (Faucon et al., 2015; Richardson et al., 2011; Simpson et al., 2011).
75 Several strategies are used by plants to mobilize pools of sparingly-soluble soil P
76 (Richardson et al., 2011). Selection for targeted traits in crops or selection of suitable
77 species in multispecies systems such as cover crops, could lead to improved P
78 cycling efficiency in agroecosystems (Faucon et al., 2015; Honvault et al., 2021).

79 Cover crops can be selected to offer many ecosystem services, such as carbon (C)
80 sequestration, enhanced nutrient cycling, or atmospheric nitrogen (N) fixation
81 (Daryanto et al., 2018). Lately cover crops have also been increasingly suggested to
82 play an important role in enhancing or maintaining P availability (Damon et al., 2014;
83 Hallama et al., 2019; Hansen et al., 2021). Some studies have reported increases of
84 up to 50 % in crop P uptake for the subsequent crop after cover-cropping when
85 compared to bare soil (Hallama et al., 2019). However, the cover-cropping effects on
86 P uptake by the subsequent crop is highly variable across pedoclimatic conditions,
87 with several studies reporting neutral to negative effects (Hallama et al., 2019). This
88 might be explained by the wide range of traits among cover crop species (Alamgir et
89 al., 2012; Hansen et al., 2022; Maltais-Landry and Frossard, 2015; Noack et al.,
90 2012). In addition, cover crop effects on P availability are also modulated by initial

91 soil P availability, possibly contributing to this wide range of effects (Damon et al.,
92 2014; Hallama et al., 2019; Hansen et al., 2022).

93 Cover crops can acquire P from soil P pools of varied spatial and chemical
94 availability, based on differences in their architectural, physiological and
95 morphological traits (Richardson et al., 2011). Root morphological traits may improve
96 P foraging, supporting higher crop yield and P uptake at low concentrations of soil P
97 fertility (Haling et al., 2018; Ma et al., 2018; Pang et al., 2010). Release of exudates
98 such as carboxylates or acidifying agents can mobilize sparingly-soluble soil P by
99 decreasing P sorption on mineral surfaces or solubilizing calcium phosphate in
100 calcareous soils (Li et al., 2017; Wang and Lambers, 2020; White and Hammond,
101 2008). Exudation of enzymes may also improve the mineralization of slowly
102 mineralizing organic P pools (Nobile et al., 2019; Richardson et al., 2011). Through
103 these traits cover crops can substantially increase soil P availability (Hansen et al.,
104 2021), but also accumulate significant amounts of P in their biomass from the diverse
105 soil P pools (e.g., 5-30 kg P ha⁻¹) (Damon et al., 2014; Maltais-Landry and Frossard,
106 2015; Ruis et al., 2019; Wendling et al., 2016). During decomposition of the
107 unharvested cover crop biomass left on the field, P acquired by cover crops is then
108 released, potentially resulting in improved P nutrition in subsequent crops (Dube et
109 al., 2017). However, the contribution of P release from cover crop residues to soil P
110 availability has been proposed to be agronomically significant only in conditions
111 where large amounts of P is acquired and later released by cover crops (Damon et
112 al., 2014; Thibaud et al., 1988). Large variability in the potential contributions of cover
113 crop residues to P availability underline the need to further investigate the factors
114 involved in the fate of residue P in order to optimize cover crops composition and
115 management for enhanced benefits on soil P availability (Faucon et al., 2015).

116 Phosphorus release from crop residues during their decomposition is a complex
117 process generally involving a pattern of rapid initial P leaching of inorganic P from
118 residues to the soil solution followed by a slower release of P (Prescott, 2005). Upon
119 release, P can either remain plant available, be adsorbed onto soil particles, or
120 become immobilized by soil microorganisms (Alamgir et al., 2012; Damon et al.,
121 2014; Prescott, 2005; Simpson et al., 2011). If the amount of soluble P does not meet
122 microbial requirements, residue P can be immobilized into microbial biomass, to be
123 later released during microbial turnover typically within a few days to a month after
124 residue addition (Damon et al., 2014; Spohn and Widdig, 2017).

125 Many factors influence P release from residues among which residue C, N but
126 especially P concentration. In general, a rapid release of P from residues can be
127 expected for concentrations higher than 2.5 to 3 g P kg⁻¹, while concentrations below
128 2.4 g P kg⁻¹ are expected to result in a slower P release or even P immobilization
129 (Kwabiah et al. 2003; Alamgir et al. 2012; Damon et al. 2014). However, much
130 uncertainty remains on these general threshold values (Kwabiah et al. 2003). While
131 less investigated, there is increasing evidence that residue architecture reflected in
132 part by traits such as specific leaf area (SLA) also play a central role in residue
133 decomposition and nutrient release (Freschet et al., 2013; Perez-Harguindeguy et al.,
134 2013; Zuskwert and Prescott, 2017). Tissue architecture may be important in residue
135 degradation and later nutrient release due to its role in early leaching dynamics and
136 later decomposer access (Lindedam et al., 2009; Zuskwert and Prescott, 2017).
137 Specific leaf area has for instance been observed to strongly relate to residue
138 decomposition rates across a range of natural ecosystems (Liu et al., 2018; Santiago,
139 2007). Lower SLA may slow residue decomposition and nutrient release due to
140 reduced surface area per mass slowing early leaching dynamics and reducing

141 decomposer access (Lindedam et al., 2009; Zukswert and Prescott, 2017). Reduced
142 surface area for larger residue pieces has for instance been proposed to explain a
143 slower release of residue P (Noack et al. 2014).

144 Stoichiometric ratios between residue C, N and P have also been highlighted to play
145 an important role in residue decomposition and nutrient release. Indeed soil
146 microorganisms tend to be primarily C-limited, and co-limited by elements necessary
147 to decompose C-sources (Smith and Paul, 1990). Negative correlations have been
148 observed between nutrient ratio such as C:N or C:P and residue decomposition due
149 to microbial N and P requirements to decompose C-sources (de la Riva et al., 2019;
150 Freschet et al., 2013; Lin et al., 2020). However, much uncertainty remains as to how
151 much P is taken up by microbial biomass during residue decomposition with values
152 ranging from 1.5 to 3 mg P g⁻¹ DM (Kwabiah et al., 2003). Residues with C:P ratios
153 higher than 300 were reported to lead to microbial P immobilization, while this
154 threshold value tends to vary greatly with reports of values between 60 and 700
155 (Espinosa et al., 2017). Residues' C:P ratio effects on P availability via microbial P
156 immobilization in turn can be inconsistent and potentially misleading according to the
157 various organic P compounds in residues (Enwezor, 1976; Umrit and Friesen, 1994;
158 White and Ayoub, 1983).

159 Key factors influencing P release from residues and their effect on P availability for
160 the subsequent crop have yet to be fully investigated for cover crop residues
161 (Espinosa et al., 2017; Hansen et al., 2022). Most studies focused on residue from
162 mature crops (Alamgir et al., 2012; Noack et al., 2014), possibly underestimating the
163 effects of vegetative stage residues such as cover crop residues (Maltais-Landry and
164 Frossard, 2015). Alongside the different range of traits of young rather than mature
165 residues, morphological traits influence has received little attention ignored due to the

166 use of milled residues (Damon et al., 2014; Noack et al., 2014). Furthermore,
167 relationships between leaf traits and nutrient dynamics identified in ecosystems (de la
168 Riva et al., 2019) are rarely investigated due to limitations using whole-plant milled
169 residues. Leaves nonetheless often present higher nutrient concentrations and
170 constitute a large part of residues. Effects of leaf traits may be partly masked when
171 leaves get mixed with stems. The large range of contribution from residue to the P
172 taken up by subsequent crop, from 1 to 45 % (Nachimuthu et al., 2009; Noack et al.,
173 2012; Thibaud et al., 1988) reported prompts further investigation in the role of cover
174 crop traits in driving P release dynamics from residues and their contribution to P
175 uptake by the subsequent crop. Getting a better understanding of key cover crop
176 traits involved in these dynamics could offer to manage and select cover crops for
177 enhanced P cycling efficiency in agrosystems (Espinosa et al., 2017; Faucon et al.,
178 2015).

179 We investigated the influence of cover crop residues traits on the fate of residue P in
180 the plant-soil-microbe system during a greenhouse and an incubation experiment.
181 The effects on P uptake by the following crop (Italian ryegrass, *Lolium multiflorum* L.)
182 were investigated in a greenhouse experiment with six cover crop species selected
183 for their gradient of traits. The effects on soil P pools (resin extractable and microbial
184 P pools) were investigated with an incubation experiment. We tested the hypotheses
185 that i) residues with high P concentration or high SLA will release more P faster,
186 contributing more to soil P availability and subsequent plant uptake than residues
187 with lower P concentration or SLA, ii) residues with higher C:P ratio will result in
188 delayed or reduced contribution to soil P availability and subsequent plant uptake
189 compared to residues with lower C:P ratio.

190 **2. Material and methods**

191 **2.1 Soil collection and preparation**

192 A Retisol soil (formerly called Albeluvisol) (IUSS Working Group, 2006) at a depth of
193 5 to 20 cm was collected from a cultivated field in north-eastern France (48° 54' 37"
194 N, 3° 43' 57" E). The surface layer (0-5 cm) was removed prior to collection in order
195 to obtain soil with lower concentrations of 'plant-available' P. The soil was dried at
196 ambient temperature for 60 days and then passed through a 2 mm sieve. Dried soil
197 was stored in the dark for about a year before use in the experiment. The
198 concentration of Olsen-P in the collected soil was 16.3 mg Olsen-P kg⁻¹, which is
199 considered moderately P limited (Hansen et al., 2022) (Table 1). Soil organic C was
200 12.8 g C kg⁻¹ and pH_{KCl} was 7.4.

201

Table 1: Chemical and physical properties of the soil used in the study.

Soil properties	
Clay (g kg ⁻¹)	256
Silt (g kg ⁻¹)	676
Sand (g kg ⁻¹)	68
Total N ^a (g kg ⁻¹)	1.42
Organic C ^b (g kg ⁻¹)	12.8
C/N	9
CEC (cmolc kg ⁻¹)	10.5
Exchangeable Ca ^c (g kg ⁻¹)	3.30
Exchangeable K ^c (g kg ⁻¹)	0.28
Exchangeable Mg ^c (g kg ⁻¹)	0.14
Olsen P ^d (mg kg ⁻¹)	16.3
HCl P ^e (mg kg ⁻¹)	76.7
Total P ^f (mg kg ⁻¹)	600

202 ^a Dumas method (NF ISO 13 878, AFNOR 1998)203 ^b Sulfochromic oxidation (NF ISO 14235, AFNOR 1998)204 ^c Exchangeable, Extracted with ammonium acetate 0.5 M, EDTA 0.02 M pH 4.65 (NFX 31-108, AFNOR 2002)205 ^d According to Olsen (1954)206 ^e HCl P as extracted with 1 M HCl from solid residue after initial extraction with NaOH 1 M as defined in García-Albacete et al. (2012)207 ^f ICP-AES after total solubilization with hydrofluoric and perchloric acid (NF X 31-147, AFNOR 1996)

208

209

210 **2.2 Preparation of crop residues**

211 Residues from six cover crop species were selected for their diverse phylogenetic
 212 lineages and traits (Brassicaceae: *Brassica carinata* (BraC) A. Braun; Polygonaceae:
 213 *Fagopyrum esculentum* (FagE) Moench.; Fabaceae: *Lens culinaris* (LenC) Medik.,
 214 *Vicia faba* (VicF) L., *Vicia villosa* (VicV) Roth.; Hydrophyllaceae: *Phacelia*
 215 *tanacetifolia* (PhaC) Benth.) (Table 2). Cover crop residues were obtained from crops
 216 grown in the glasshouse on the aforementioned Retisol soil diluted with washed sand
 217 (22% mass) to further decrease concentrations of plant-available soil P. Cover crops
 218 were grown in multiple periods of approximately 2.5 months each in a replicated
 219 random design. At harvest, plants were mostly toward the end of their vegetative
 220 stage with the first onset of flowering visible. Growth conditions were set at a
 221 photoperiod of 14 hour day⁻¹, with 22°C at day and 18°C at night. Plants were
 222 watered twice a week to maintain soil humidity approx. between 60 and 50% of soil
 223 water holding capacity. The biomass of each batch was combined and homogenized.

224 After homogenisation, the dried cover crop residues were divided into two portions.
225 Leaves for the 'leaf residues' treatment were collected in one portion. The other
226 portion, consisting of both leaves and stems was used in the 'aboveground residues'
227 treatment. Leaf specific area of residues was determined via scanning leaves issued
228 from the homogenised biomass pool before separation using an Epson Scanner
229 perfection V800 to produce a 600 dpi image. The image was then analysed using
230 imageJ software (version 1.53) to determine leaf area. After 48 hours drying at 55°C,
231 scanned leaves were weighed to calculate their SLA (in $\text{mm}^2 \text{mg}^{-1}$). The residues
232 were then manually cut into pieces to replicate mechanical shredding in the field. In
233 order to conserve mass to area ratio of cover crops (SLA) and examine its effects,
234 residues were manually cut into pieces of 25 mm^2 . This was done to examine the
235 effect of morphology on the fate of residue P in the plant-soil system.

236 **2.3 Experimental design**

237 To investigate the influence of residue traits, namely residue P, N and C
238 concentration, C:P ratio, C:N ratio, N:P ratio and SLA, on the fate of residue P in the
239 plant-soil-microbe system, a glasshouse and an incubation experiment were
240 established. Experimental treatments included the addition of two types of plant
241 residues to the soil (i.e., the residues of (i) leaves and that of (ii) aboveground
242 biomass) from six cover crop species, the addition of mineral P fertilizer (minP), and
243 an unfertilized control (0P). Aboveground residues consisting of leaves and stems
244 were investigated as most representative of field cover crops residues. Leaf residues
245 alone were also examined as leaves are known as one of the main drivers of
246 nutrients dynamic in ecosystems. However, the effects of leaf traits (SLA, P, C:P)
247 may be partly masked when leaves get mixed with stems. Relationships between
248 residue traits and the fate of residue P in the plant-soil-microbe system were

249 examined separately per biomass type (i.e., leaf residues or aboveground residues)
250 as well as for all residues regardless of biomass type. All plant residues and the
251 mineral fertilizer were added to supply 15 mg P kg⁻¹ soil. This rate corresponds to a
252 field productivity of 6.5 t DM ha⁻¹ for residues with a P concentration of 3 mg P kg⁻¹
253 (assuming 1300 t soil ha⁻¹), and is similar to that reported in previous studies
254 (Maltais-Landry and Frossard, 2015; Noack et al., 2014). The experiment was
255 arranged in a factorial randomized complete design and replicated four times.

256 **2.3.1 Pot experiment set up**

257 The aforementioned soil was rewetted at gravimetric water content (GWC) of 156 g
258 H₂O kg⁻¹ soil, which is equivalent to 41 % of the soil's maximum water holding
259 capacity (WHC), in order to increase microbial activity. After 10 days of incubation,
260 the soil for the glasshouse and incubation experiment was labelled with a carrier free
261 ³³P H₃PO₄ radiotracer at 2.1 MBq kg⁻¹ soil. Briefly, 1 kg of dry-weight equivalent soil
262 was weighed and a 10 mL aliquot of 216 MBq L⁻¹ carrier free ³³P H₃PO₄ solution was
263 added evenly across the soil. The soil was then mixed for 2 minutes, adjusted to 60
264 % of its WHC, and then left to equilibrate.

265 After 18 days the P treatments were added to the soil and mixed for 2 minutes. This
266 included the aforementioned crop residues or 10 mL of a solution of 1.5 g P L⁻¹
267 mineral fertilizer as KH₂PO₄. The unfertilized control was also mixed for 2 minutes
268 with 10 mL distilled water, as for the fertilized treatments. A direct labelling control
269 treatment was also included, adding 10 mL of a solution containing 1.5 g P L⁻¹
270 mineral fertilizer and 205 MBq L⁻¹ carrier free ³³P H₃PO₄ (Approx. SA 137 kBq mg⁻¹
271 P). Lastly, all soils simultaneously received basal nutrients except for P at the
272 following rates (mg kg⁻¹ soil): 120 N, 250 K, 40 Ca, 50 Mg, 1 Fe, 150 Cl, 1 B, 2 Mn, 1

273 Zn, 2 Cu, 1 Mo (as NH_4NO_3 , K_2SO_4 , MgSO_4 , CaCl_2 , MnSO_4 , ZnSO_4 , CuSO_4 ,
274 Na_2MoO_4 , H_3BO_3 and $\text{C}_{10}\text{H}_{12}\text{FeN}_2\text{NaO}_8$).

275 Italian ryegrass (*Lolium multiflorum* L.) seeds (0.5 g) were added to each pot and
276 placed 10 mm below the soil surface. This corresponded to an input of 1.6 mg P kg^{-1}
277 soil, which is approximately 10 % of the P contained in the added crop residues. Soils
278 were kept between 50 and 60 % of their WHC (during ryegrass growth) with distilled
279 water. Growth conditions were set at a photoperiod of 14 hour day^{-1} , with $24 \text{ }^\circ\text{C}$ at
280 day and $18 \text{ }^\circ\text{C}$ at night. Pots were randomized weekly.

281 Ryegrass shoots were harvested five times 2 cm above the soil surface (day 35, 47,
282 70, 91 and 110 after the treatment application). After each harvest, the plants were
283 supplied with all nutrients except for P at the following rates (mg kg^{-1} soil): 120 N, 250
284 K, 40 Ca, 50 Mg, 1 Fe, 150 Cl, 1 B, 2 Mn, 1 Zn, 2 Cu, 1 Mo (as NH_4NO_3 , K_2SO_4 ,
285 MgSO_4 , CaCl_2 , MnSO_4 , ZnSO_4 , CuSO_4 , Na_2MoO_4 , H_3BO_3 and $\text{C}_{10}\text{H}_{12}\text{FeN}_2\text{NaO}_8$).
286 Nitrogen was added in two equal doses of 60 mg kg^{-1} one week apart.

287 **2.3.2 Plant analyses and calculations**

288 All ryegrass shoots were dried at $45 \text{ }^\circ\text{C}$ for 72 hours, weighed, and then ground to
289 powder using an MM 300 Mixer Mill (Qiagen, USA). Concentrations of total P in shoot
290 material were determined using the method of Hoenig (2001). Briefly, 0.2 g of shoot
291 material was digested with 2 mL HNO_3 69 % (v/v) for 1 hour at $200 \text{ }^\circ\text{C}$ with a MLS
292 Turbowave (MWS GmbH, Heerbrugg, Switzerland) and then diluted in 10 mL of
293 distilled water. Concentrations of P in digests were then determined via colorimetry
294 using malachite green (Ohno and Zibilske, 1991). Concentrations of total C and N in
295 shoot material were determined via dry combustion.

296 The ^{33}P activity in plant material was determined via scintillation counting after mixing
297 2 mL of the plant digests with 5 mL of scintillation liquid (Ultima Gold AB, Packard
298 Instrument Co.). The specific activity (SA) was then calculated based on measured P
299 concentration in biomass and dry biomass weight. Specific activity in the first two cuts
300 was corrected for 60 % seed P uptake in the first cut and 20 % seed P uptake in the
301 second cut (Hansen et al., 2022; Nanzer et al., 2014; Noack et al., 2014) as follows:

$$SA_{Ryegrass} = \frac{\text{Plant Activity (Bq)}}{\text{Plant P (mg P)} - \text{Correction factor} * \text{Seed P (mg P)}}$$

302 $SA_{Ryegrass}$: Corrected specific activity in ryegrass biomass

303 Plant activity: Activity in ryegrass digest (Bq)

304 Plant P: Ryegrass P uptake (mg P)

305 Correction factor: Correction factor for seed P uptake, 60 % for the first cut and 20 %
306 for the second

307 Seed P: Total seed P content (mg P)

308 P derived from fertilizer (Pdff) was calculated for the direct labelling control, adding
309 10 mL of a solution of 1.5 g P L⁻¹ mineral fertilizer containing 205 MBq L⁻¹ carrier free
310 $^{33}\text{P H}_3\text{PO}_4$, was calculated as follow:

$$Pdff = SA_{Plant} / SA_{Fertilizer} \times \text{Plant P uptake (mg P)}$$

311 Pdff: P derived from fertilizer (mg P)

312 SA_{Plant} : SA of P in plants grown with ^{33}P labeled mineral fertilizer (kBq mg⁻¹ P)

313 $SA_{Fertilizer}$: SA of applied labeled mineral fertilizer (kBq mg⁻¹ P)

314 To assess the nutritional status of plants, the nitrogen nutrition index (NNI) and P
315 nutrition index (PNI) of shoots were calculated according to the methods described in
316 Lemaire et al. (2008) and Duru and Ducrocq (1996). Nitrogen nutrition index was
317 calculated as follows:

$$NNI = \frac{Na}{Nc} = \frac{Na}{4.8 \times DM^{-0.32}}$$

318 With

319 Na: N content (g 100 g⁻¹)

320 Nc: Critical N content, as calculated as function of dry matter (g 100 g⁻¹)

321 DM: Plant dry biomass (t ha⁻¹)

322 And PNI as follows:

$$PNI = \frac{Pa}{Pc} = \frac{Pa}{0.15 + 0.065 \times Na}$$

323 With

324 Pa: P content (g 100 g⁻¹)

325 Pc: Critical P content, as calculated as a function of N content (g 100 g⁻¹)

326 Na: Actual N content (g 100 g⁻¹)

327 For NNI calculation ryegrass biomass per pot (1 kg soil) was converted to t ha⁻¹ with

328 the same assumptions as for P addition rate calculations ie 1300 t soil ha⁻¹.

329 **2.3.3 Soil incubation design and set up**

330 Soil in the incubation experiment was amended at the same rates as for the

331 glasshouse experiment. Soil portions for the incubation were of 100 g dry soil. Soil

332 was labelled with a carrier free ³³P H₃PO₄ radiotracer at 2.1 MBq kg⁻¹ soil and mixed

333 for 2 minutes. Soil then was adjusted to 60 % of its WHC, and left to equilibrate for 18

334 days before amendment with P treatments. During soil amendment with the P

335 treatments, the soil also received basal nutrients except for P at the following rates

336 (mg kg⁻¹ soil): 120 N, 250 K, 40 Ca, 50 Mg, 1 Fe, 150 Cl, 1 B, 2 Mn, 1 Zn, 2 Cu, 1 Mo

337 (as NH₄NO₃, K₂SO₄, MgSO₄, CaCl₂, MnSO₄, ZnSO₄, CuSO₄, Na₂MoO₄, H₃BO₃ and

338 C₁₀H₁₂FeN₂NaO₈). The soil was then mixed for 2 minutes before being kept in the

339 dark under identical experimental conditions as for the previously mentioned pot

340 experiment. Soil was then sampled 10 and 59 days after amendment. Any remaining

341 visible residue pieces were separated from the soil using a pair of tweezers before
342 resin P and microbial P measurement (as detailed in 2.3.4). A subsample of soil from
343 every treatment was used for gravimetric water content determination.

344 **2.3.4 Soil analyses**

345 Microbial P (P_{mic}) was determined via the difference in P concentration between
346 hexanol fumigated and non-fumigated soil extracts using anion exchange resins
347 (Bünemann et al., 2007). After preparation with 0.5 M NaHCO_3 , the anion exchange
348 strips were shaken for 16 h with 2 g equivalent dry soil and 30 mL deionised water.
349 Each incubated soil was extracted in triplicate, one (i) with or (ii) without the addition
350 of 1 mL hexanol as a fumigant, and one (iii) that received a P spike of a known
351 amount of inorganic P (15 mg P kg^{-1} as KH_2PO_4) to correct for P sorption. The anion-
352 exchange strips (VWR, 551642S) were then rinsed with deionised water before
353 having their P extracted by shaking 1 h in 30 mL 0.5 M HCl. For the second
354 extraction after 59 days resins were eluted with 10 mL 0.5 M HCl instead to ensure
355 measurable amount of radioactivity. To compensate for sorption of microbial P
356 released after fumigation, P recovery (58 % of the added 15 mg P kg^{-1} on average
357 for soil amended with organic amendments) was calculated based on spiked samples
358 otherwise extracted identically to non-fumigated samples. Extracted P in the three
359 extracts was measured via malachite green colorimetry (Ohno and Zibilske, 1991).
360 Microbial P was calculated as the difference between fumigated and non-fumigated
361 samples, and corrected for the P recovery of added P:

$$P_{mic} = \frac{(P_{fum} - P_{res})}{P_{recovery}}$$

362 With

363 P_{mic} : Microbial P (mg P kg^{-1})

364 P_{fum} : P in fumigated extract (mg P kg^{-1})

365 P_{res} : P in unfumigated resin extract (mg P kg^{-1})

366 P recovery: fraction of P recovered in spiked extracts

367 Radioactivity was measured by scintillation counting after mixing 1 ml of extract with
368 5 ml of scintillation liquid (Ultima Gold AB, Packard Instrument Co.). Specific activity
369 in microbial extracts was calculated based on SA difference between fumigated and
370 resin extracts. Prior to calculation SA in the fumigated extract was corrected for P
371 sorption with the same factor as for microbial P, assuming similar sorption between
372 ^{31}P and ^{33}P .

373 **2.4 Statistical analysis**

374 To examine the overall effects of treatments and time since amendment on ryegrass
375 biomass and P uptake, linear mixed models with random effects at pot level due to
376 repeated measurements were used. Models with treatment, time and their
377 interactions were selected based on lowest Akaike information criterion (AIC) and
378 normal residual distribution. Differences between treatments per time point (ie. 35,
379 47, 70, 91 or 110 days after addition for the greenhouse experiment and 10 and 59
380 days after addition for the incubation experiment) were examined with one-way
381 analyses of variance (ANOVAs) and post hoc tests of Tukey or Kruskal-Wallis tests
382 and post hoc test of Mann Whitney if ANOVA requirements were not met. Tests were
383 performed separately per residue type (leaf or aboveground residues) as ANOVAs
384 and Kruskal-Wallis tests showed significant effects of residue types.

385 To examine relationships between residue traits and ryegrass P uptake and soil P
386 availability, correlations were examined via Pearson correlation tests (r) on log
387 transformed data or Spearman correlation tests (r_s) for variables not normally
388 distributed after log transformation. Correlations between residue traits and P uptake
389 and availability were first examined separately per residue type. Correlations
390 between the same residue traits and P uptake (or P availability) were identified for
391 both residue types. Residue traits effects were then simultaneously examined on

392 both residue types. This also allowed assessing the relationships over a wider trait-
393 range. To further investigate the relationship between residue traits and P uptake,
394 linear models were produced. Residue traits correlated with P uptake were tested as
395 predictors of P uptake in ryegrass. Soil P pools were also tested as predictors of P
396 uptake in ryegrass as well as combinations of residue traits and soil P pools.
397 Significant models were compared based on adjusted R^2 with the highest relative
398 value considered the best fit. All tests were performed in R version 3.6.0 and the
399 packages Rcmdr (2.8-0, Fox and Bouchet-Valat, 2022), multcomp (1.4-20, Hothorn et
400 al., 2008), nmlr (3.1-160, Pinheiro et al., 2020), ggplot2 (3.4.0, Wickham, 2016),
401 vegan (2.6-4, Oksanen et al., 2022) with a significance level of 0.05.

402 3. Results

403

404 3.1 Cover crop residue properties

405 Concentrations of P in cover crop residues ranged from 1.28 g P kg⁻¹ for VicV
 406 aboveground residues to 3.07 g P kg⁻¹ for VicF leaf residues (Table 2). The C:P
 407 ratios of the cover crop residues ranged from 137 for VicF leaf residues to 316 for
 408 VicV aboveground residues, which corresponded to the addition of 2.1 g C kg⁻¹ to 4.7
 409 g C kg⁻¹. Aboveground residues of FagE resulted in the lowest N addition rate of 47
 410 mg N kg⁻¹ soil and VicV aboveground residues the highest of 264 mg N kg⁻¹. BraC
 411 had the lowest observed SLA of 21.7 mm² mg⁻¹, while the highest SLA of 38.8 mm²
 412 mg⁻¹ was observed for VicV.

413 **Table 2: Cover crop residue traits and inputs for each residue treatment (all inputs designed to add 15 mg**
 414 **P kg⁻¹ soil)**

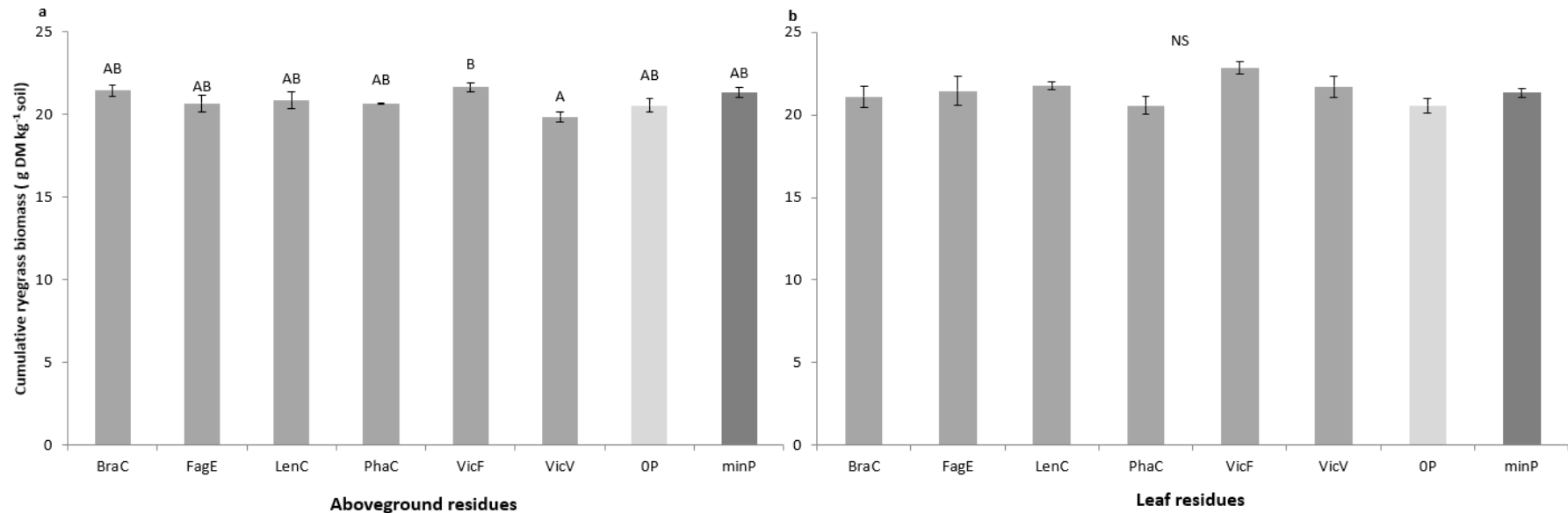
Residues	Species	P g kg ⁻¹ DM	N	C	C:N	C:P	N:P	SLA mm ² mg ⁻¹	N added mg kg ⁻¹ soil	C added mg kg ⁻¹ soil
Aboveground	BraC	2.44	18.6	400	21.5	164	7.6	21.7	114	2456
	FagE	2.49	9.2	403	43.9	162	3.7	47.4	55	2434
	LenC	2.26	23.0	429	18.7	189	10.1	31.3	152	2842
	PhaC	2.73	8.6	379	44.0	139	3.2	24.2	47	2083
	VicF	1.85	26.3	415	15.8	224	14.2	38.5	213	3362
	VicV	1.28	22.5	404	18.0	316	17.6	38.8	264	4739
Leaf	BraC	1.86	25.2	404	16.0	217	13.6	21.7	203	3257
	FagE	2.41	24.4	377	15.5	156	10.1	47.4	152	2347
	LenC	2.71	35.1	423	12.0	156	13.0	31.3	194	2340
	PhaC	2.54	18.4	352	19.2	139	7.2	24.2	109	2082
	VicF	3.07	49.9	422	8.5	137	16.2	38.5	244	2060
	VicV	2.04	35.1	414	11.8	204	17.2	38.8	259	3054

415 SLA : Specific leaf area. BraC: *Brassica carinata*; FagE: *Fagopyrum esculentum*; LenC: *Lens culinaris*; PhaC:
 416 *Phacelia tanacetifolia*; VicF: *Vicia faba*; VicV: *Vicia villosa*.

417 3.2 Effect of cover crop residues on ryegrass growth, biomass and nutrition

418 Cumulative ryegrass biomasses were largely similar across all treatments at the end
 419 of the experiment (Figure 1). Average ryegrass biomass per cut decreased with time,
 420 from 4.4 g kg⁻¹ soil after 35 days to 3.5 g kg⁻¹ soil after 110 days. Significantly lower
 421 cumulative ryegrass biomass was only observed in pots amended with VicV

422 aboveground residues as compared to VicF aboveground residues (19.9 g kg⁻¹ soil
423 compared to 21.7 g kg⁻¹ soil) (Figure 1a). Significant differences in ryegrass biomass
424 were observed for the first harvest, after which little to no differences were observed
425 (Supplementary table S1).



426
427

Fig. 1 Ryegrass biomass after amendment with cover crop residues

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430

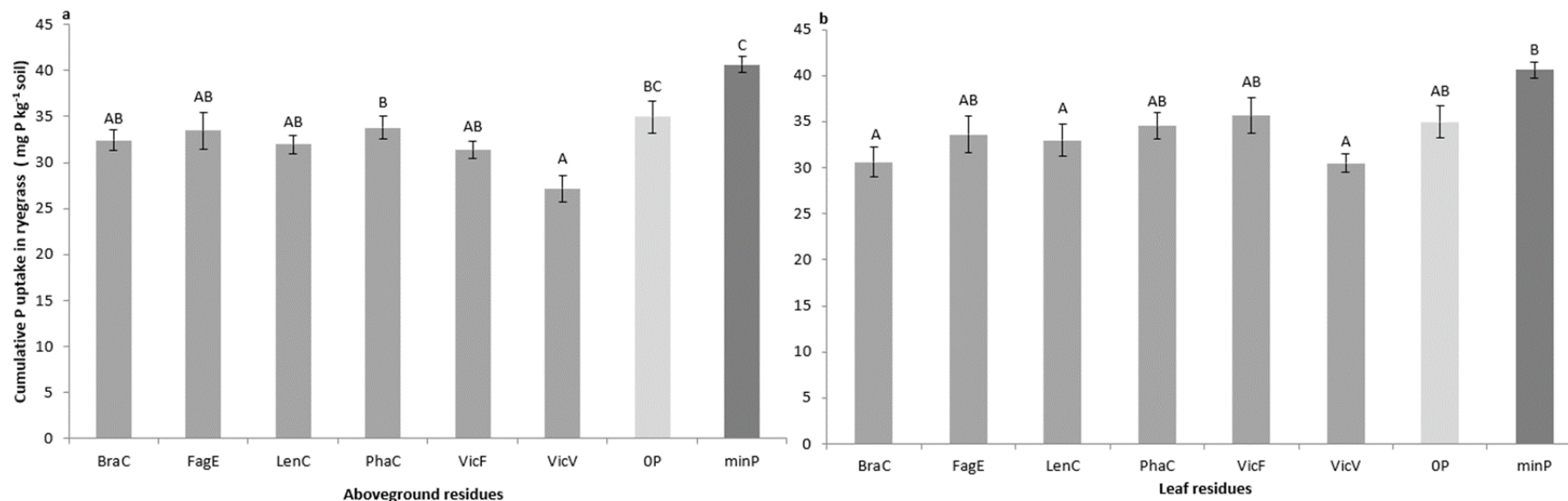
a : Cumulative biomass after 110 days after amendment with aboveground residues; b : Cumulative biomass after 110 days after amendment with leaf residues. ± standard error. Sum of 5 harvests. Letters above the bars represent statistically significant differences among treatments within the same residue type. NS : Not significant. BraC: *Brassica carinata*; FagE: *Fagopyrum esculentum*; LenC: *Lens culinaris*; PhaC: *Phacelia tanacetifolia*; VicF: *Vicia faba*; VicV: *Vicia villosa* ; OP: Control without P addition; minP: control with 15 mg P kg⁻¹ mineral P

431

432 The P nutrition index (indicative of a plant P limitation), averaged 50 % across all
433 harvests, decreasing over time from 53% to 43% on average. Average ryegrass P
434 concentrations ranged between 2.9 and 0.6 g P kg⁻¹. The PNI differed significantly
435 between treatments only until 70 days after amendment (Supplementary table S2).
436 The NNI averaged at 91% across all harvests, first decreasing with time until 70 days
437 after amendment (112 % on average after 35 days, 77 % on average after 70 days).
438 The NNI increased thereafter (94 % on average after 110 days) (Supplementary table
439 S3). The PNI was not significantly correlated to ryegrass biomass for most harvests.
440 The NNI was not correlated to ryegrass biomass until 70 days after amendment.

441 **3.3 Effect of cover crop residues on ryegrass P uptake**

442 Few significant differences between treatments were observed in total cumulative P
443 uptake by ryegrass over the course of the experiment (Figure 2). However, cover
444 crop residues significantly affected ryegrass P uptake per cut (Supplementary table
445 S4). Average ryegrass P uptake per cut decreased with time, from 7.7 mg P after 35
446 days to 5.0 mg P after 110 days. Cumulative P uptakes for residue amended
447 treatments did not significantly differ from the unfertilized control, except for VicV
448 aboveground residues. Amendments with aboveground residues of VicV resulted in a
449 significantly lower cumulative ryegrass P uptake than the unfertilized control by 7.8
450 mg P (Figure 2a). Ryegrass cumulative P uptakes were lower when amended with
451 aboveground or leaf residues than equivalent mineral fertilization, except for FagE
452 and VicF leaf residues (Figure 2 a,b). Mineral fertilization increased ryegrass
453 cumulative P uptake by 5.7 mg P, about a third of the 15 mg P applied.



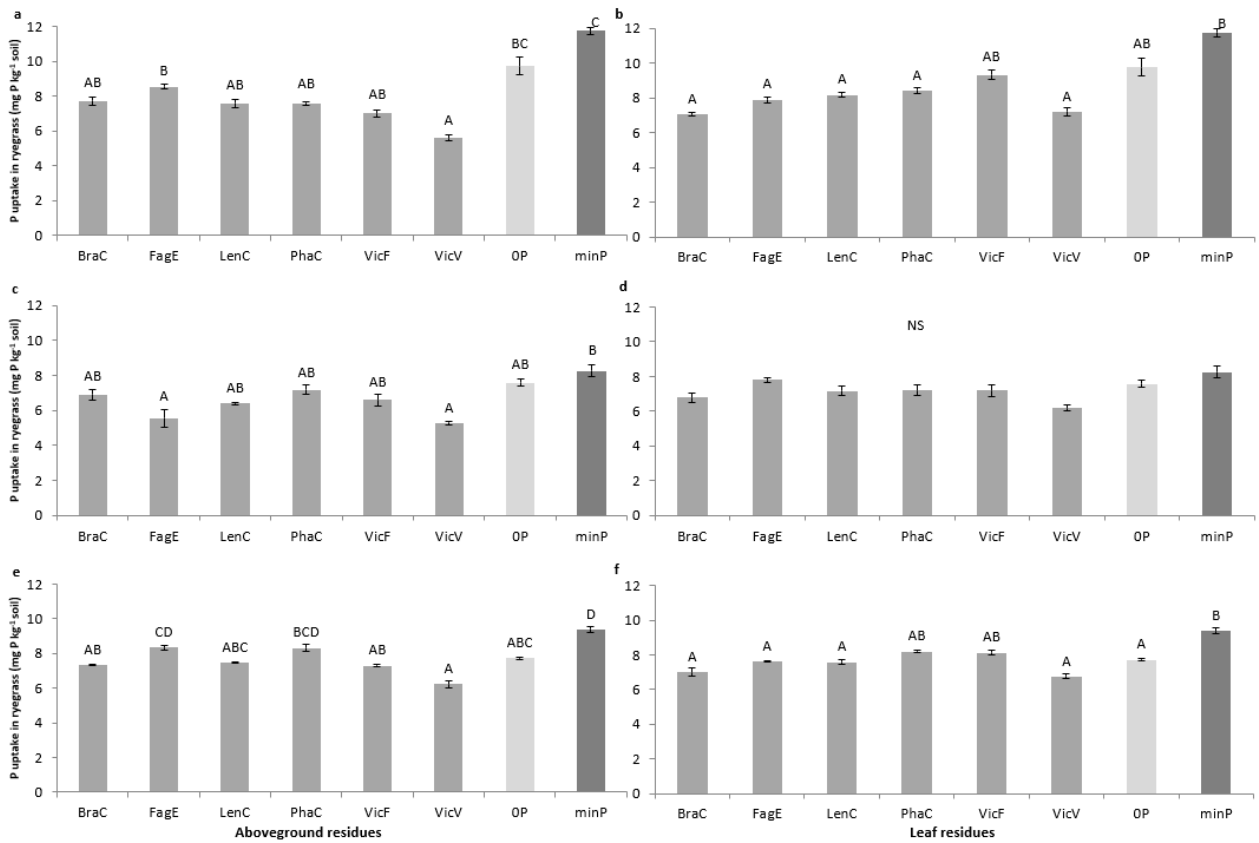
454
455

Fig. 2 Ryegrass cumulative P uptake after amendment with cover crop residues

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457
458

a: Cumulative P uptake over 110 days for aboveground residues; b: Cumulative P uptake over 110 days for leaf residues. \pm standard error. Sum of 5 harvests. Letters above the bars represent statistically significant differences among treatments within the same residue type. BraC: *Brassica carinata*; FagE: *Fagopyrum esculentum*; LenC: *Lens culinaris*; PhaC: *Phacelia tanacetifolia*; VicF: *Vicia faba*; VicV: *Vicia villosa*; OP: Control without P addition; minP: control with 15 mg P kg⁻¹ mineral P

459 Differences in P uptake mostly occurred in early harvests up to 70 days after
460 amendment after which no significant differences were observed (Figure 3). Thirty-
461 five days after amendment most aboveground residues resulted in P uptakes that did
462 not significantly differ from the unfertilized control (Figure 3a). Moreover, most
463 aboveground residues resulted in P uptakes significantly lower than equivalent
464 mineral fertilization (Figure 3a). Aboveground residues of VicV resulted in the lowest
465 P uptake of all aboveground residues, significantly lower than unfertilized control after
466 35 days (Figure 3a). Ryegrass P uptake after VicV aboveground residues
467 amendment was 4.2 mg P lower than for the unfertilized control. After 70 days,
468 ryegrass P uptake was significantly lower than for equivalent mineral fertilization for
469 all aboveground residues except for FagE and PhaC residues (Figure 3e). Significant
470 differences in ryegrass P uptake were observed between residues 35 and 70 days
471 after addition (Figure 3a, 3e). After addition of leaf residues, ryegrass P uptake did
472 not significantly differ from the unfertilized control (Figure 3b, d, f). Ryegrass P uptake
473 after addition of leaf residues was significantly lower than the control with equivalent
474 mineral fertilization, except for VicF and PhaC (Figure 3a, 3c).



475
476

Fig. 3 Phosphorus acquired by ryegrass per harvest after amendment with cover crop residues

477 Ryegrass P uptake, mg P kg⁻¹ soil. a,b: P uptake 35 days after amendment of aboveground residues (left) or leaf
 478 residues (right); c,d: P uptake 47 days after amendment of aboveground residues (left) or leaf residues (right); e,f:
 479 P uptake 70 days after amendment of aboveground residues (left) or leaf residues (right). ± standard error.
 480 Letters above the bars represent statistically significant differences among treatments within the same residue
 481 type. BraC: *Brassica carinata*; FagE: *Fagopyrum esculentum*; LenC: *Lens culinaris*; PhaC: *Phacelia tanacetifolia*;
 482 VicF: *Vicia faba*; VicV: *Vicia villosa*; OP: Control without P addition; minP: control with 15 mg P kg⁻¹ mineral P.

483 3.4 Effect of cover crop residues on soil P pools

484 Pools of soil P differed in their response to the addition of cover crop residues (Table
 485 3). After 10 days, BraC or FagE aboveground residues addition increased P_{res} by 2.7
 486 mg P kg^{-1} (BraC) and 3.2 mg P kg^{-1} (FagE) compared to the unfertilized control.
 487 LenC, PhaC and VicF aboveground residues addition did not significantly change P_{res}
 488 compared to the unfertilized control. Finally, VicV aboveground residues addition
 489 decreased P_{res} by 6.6 mg P kg^{-1} compared to the unfertilized control. Equivalent
 490 mineral fertilization increased P_{res} by 3.7 mg P kg^{-1} compared to the unfertilized
 491 control, about 25 % of the P added.

492 **Table 3: Soil resin extractable P content after amendment with cover crop residues.**

Residues	Time	BraC	FagE	LenC	PhaC	VicF	VicV	0P	minP
Aboveground	10	16.1 ± 0.4 C	16.6 ± 0.7 C	14.2 ± 1.1 BC	15.2 ± 0.6 BC	16 ± 1.1 ABC	6.8 ± 0.8 A	13.4 ± 0.6 B	17.1 ± 1.1 C
	59	11.6 ± 1.1 AB	14.1 ± 1.9 AB	11.2 ± 0.7 AB	14.4 ± 0.4 B	10.4 ± 1.5 AB	9.4 ± 0.4 A	11.9 ± 0.6 AB	14.7 ± 0.8 B
Leaf	10	11.1 ± 1.6 AB	15.7 ± 0.3 C	14.3 ± 0.8 AC	14.6 ± 1.2 BC	16.5 ± 0.5 C	10.2 ± 0.9 A	13.4 ± 0.6 ABC	17.1 ± 1.1 C
	59	12 ± 0.7 A	15.3 ± 0.5 B	14.8 ± 1.1 AB	14.7 ± 0.9 AB	15.2 ± 0.5 AB	13.8 ± 0.3 AB	11.9 ± 0.6 A	14.7 ± 0.8 AB

493 Resin P in mg P kg^{-1} soil (\pm standard error). Time: Time point of extraction in relation to amendment. Letters
 494 represent statistically significant differences among treatments within the same residue type and time since
 495 amendment. P res in mg P kg^{-1} soil. BraC: *Brassica carinata*; FagE: *Fagopyrum esculentum*; LenC: *Lens*
 496 *culinaris*; PhaC: *Phacelia tanacetifolia*; VicF: *Vicia faba*; VicV: *Vicia villosa*; 0P: Control without P addition; minP:
 497 control with 15 mg P kg^{-1} mineral P.

498 Ten days after amendment most leaf residues resulted in similar P_{res} to the
 499 unfertilized control, although significant differences were observed between residues.
 500 FagE and VicF leaf residues resulted in significantly higher soil P_{res} than BraC and
 501 VicV residues. The effect of most leaf residues on P_{res} did not significantly differ from
 502 equivalent mineral fertilization.

503 Fifty-nine days after amendment aboveground residues did not significantly change
 504 P_{res} compared to the unfertilized control (Table 3). Mineral fertilization similarly no

505 longer significantly increased P_{res} compared to the unfertilized control. Significant
 506 differences were nonetheless observed between VicV and PhaC aboveground
 507 residues ($P_{res}= 9.4 \text{ mg P kg}^{-1}$ and $14.4 \text{ mg P kg}^{-1}$ respectively). After 59 days, leaf
 508 residues similarly did not significantly change P_{res} compared to the unfertilized
 509 control, except for FagE leaf residues increasing P_{res} by 3.3 mg P kg^{-1} , 22% of the 15
 510 mg P added. Significant differences between residues were also observed, with a
 511 lower P_{res} after BraC leaf residues ($12.0 \text{ mg P kg}^{-1}$) than after FagE leaf residues
 512 (15.3 mg kg^{-1}).

513 Amendment with aboveground residues of VicV resulted in the highest P_{mic} after 10
 514 days, significantly higher than the unfertilized control and BraC residues and PhaC
 515 residues (Table 4). The increase of P_{mic} after the addition of aboveground residues of
 516 VicV was of 9.2 mg P kg^{-1} compared to the unfertilized control, about two third of the
 517 P added in residues. Microbial P significantly decreased overtime on average for all
 518 residue treatments, from $16.2 \text{ mg P kg}^{-1}$ after 10 days to 8.6 mg kg^{-1} after 59 days.

519 **Table 4: Soil microbial P content after amendment with cover crop residues.**

Residues	Time	BraC	FagE	LenC	PhaC	VicF	VicV	0P	minP
Aboveground	10	12.6 ± 2.1 A	16.2 ± 0.9 AB	14.6 ± 1 AB	13 ± 1.6 A	$14 \pm 2,9$ AB	21.1 ± 0.3 B	11.8 ± 1.8 A	14.2 ± 2.1 AB
	59	10.7 ± 4.5	9.8 ± 1.3	8.3 ± 1	5.5 ± 1.6 NS	7.8 ± 1.2	6.2 ± 1.7	9.3 ± 1.7	10.7 ± 2.1
Leaf	10	19.9 ± 3.5	15 ± 2.2	16.8 ± 3	14.3 ± 2.8 NS	16 ± 1.3	20.8 ± 1	11.8 ± 1.8	14.2 ± 2.1
	59	7.6 ± 4	8.8 ± 1.2	7.1 ± 1.3	8.1 ± 2 NS	11.7 ± 2	8.7 ± 2	9.3 ± 1.7	10.7 ± 2.1

520 Mic P in mg P kg^{-1} soil (\pm standard error). Time: Time point of extraction in relation to amendment. Letters
 521 represent statistically significant differences among treatments within the same residue type and time since
 522 amendment. BraC: *Brassica carinata*; FagE: *Fagopyrum esculentum*; LenC: *Lens culinaris*; PhaC: *Phacelia*
 523 *tanacetifolia*; VicF: *Vicia faba*; VicV: *Vicia villosa*; 0P: Control without P addition; minP: control with 15 mg P kg^{-1}
 524 mineral P.
 525

526 **3.5 Isotopic ^{33}P labelling**

527 No significant SA dilution was observed in ryegrass between the unfertilized control
 528 and soil amended with 15 mg P kg^{-1} mineral fertilizer at any time point, not allowing
 529 us to calculate P derived from fertilizer via indirect labelling (Supplementary figure

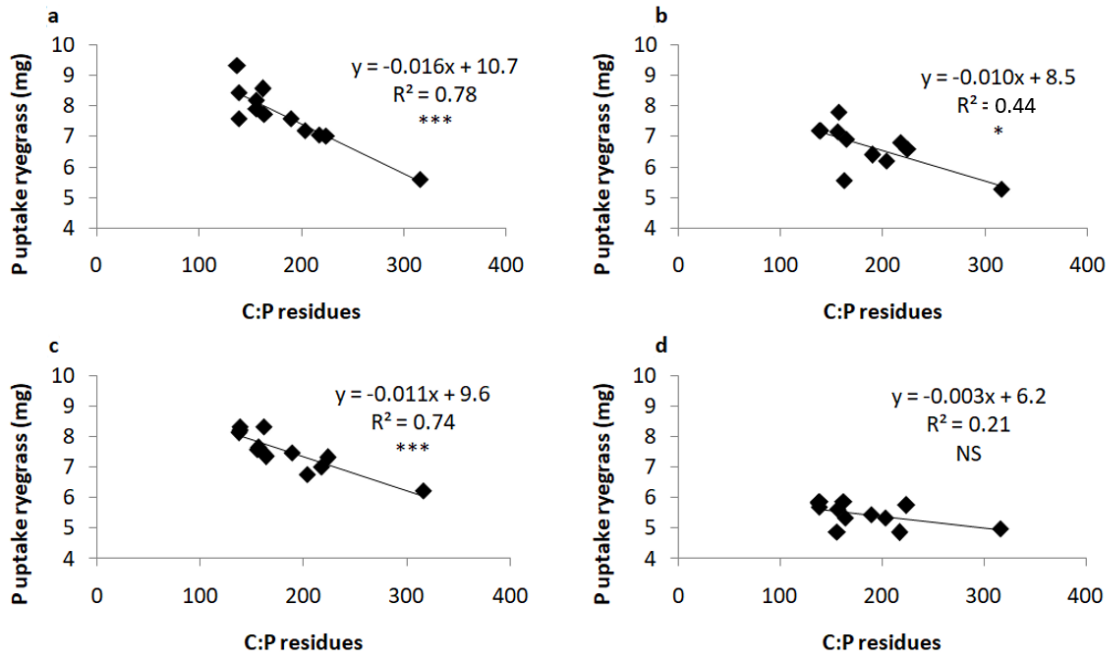
530 S5). Likewise, SA in ryegrass for the unfertilized control did not significantly differ
531 from any residue treatment at any time point (Supplementary figure S6). Similarly, SA
532 in resin extracts and microbial extracts did not significantly differ between the
533 unfertilized control and the control amended with 15 mg P kg⁻¹ mineral fertilizer at any
534 time point.

535 Direct labelling control indicated Pdfd ranging from 1.1 mg P in harvest 1 after 35
536 days to 0.3 mg P in the fifth harvest after 110 days. Cumulative Pdfd in ryegrass
537 shoots was 3.0 mg P, 20 % of the 15 mg P applied (Supplementary table S7).

538 **3.6 Relation between residue traits and P uptake**

539 Cumulative P uptake in ryegrass over the course of the experiment was correlated
540 positively with residue P concentration (Pearson correlation coefficient $r = 0.96$, p
541 $<.001$) and negatively with residue C:P (Pearson correlation coefficient $r = -0.97$, p
542 $<.001$) (Supplementary figure S8). Residues' C:N, N:P and N and C concentrations
543 as well as SLA were not correlated with cumulative P uptake by ryegrass
544 (Supplementary figure S8). Similar positive correlations with residue P concentration
545 and negative correlations with residue C:P were observed for soil P pools
546 (Supplementary figure S9). Residues' C:P was the single best predictor for both
547 cumulative P uptake and per harvest P uptake in ryegrass (Supplementary table
548 S10). Negative relationships between residue C:P and P uptake by ryegrass were
549 observed until 70 days after addition (Figure 4). VicV aboveground residues with a
550 C:P ratio above 300 contributed to overall model fit, while excluding this residue still
551 resulted in significant negative relationships between C:P and P uptake by ryegrass.
552 The slope coefficient of the linear models decreased in absolute value from -0.016 on
553 day 35 to -0.011 on day 70. Incorporating incubation results in the model improved
554 fit. Soil P_{res} was positively correlated with cumulative P uptake by ryegrass

555 (Spearman correlation coefficient $r_s=0.66$, $p<0.024$ after 10 days, Pearson correlation
556 coefficient $r=0.81$, $p=0.001$ after 59 days, supplementary figure S11). Soil P_{mic} 10
557 days after amendment was negatively correlated with cumulative P uptake by
558 ryegrass (Pearson correlation coefficient $r=-0.64$, $p=0.019$). Best model fit was
559 achieved with residue C:P and P_{res} as predictors (Supplementary table S10).



560

561 **Fig. 4 Relationship between P uptake in ryegrass and cover crop residues C:P ratio**

562 a: 35 days after amendment; b: 47 days after amendment; c: 70 days after amendment; d: 91 days after
 563 amendment. No significant model after 91 days onward days after amendment

564 **4. Discussion**

565 **4.1 Soil P availability changed substantially shortly after residue incorporation**

566 The role of cover crop residues on P availability and subsequent crop P uptake
567 remains unclear (Nachimuthu et al., 2009; Noack et al., 2012; Thibaud et al., 1988).
568 Over the course of four months, our experiments highlighted contrasted effects of
569 cover crop residues with diverse traits, converging with time toward mostly neutral
570 effects on subsequent crop P uptake. Shortly after cover crop incorporation, large
571 changes in soil P availability were observed, ranging from + 24 % to - 49 % P_{res}
572 compared to the unfertilized control. The incorporation of most crop residues at first
573 resulted in lower ryegrass P uptakes than equivalent mineral fertilization. Decreased
574 P uptakes were especially pronounced for *Vicia villosa* (VicV) residues, decreasing
575 ryegrass P uptake by 43 % compared to the unfertilized treatment. *Vicia villosa*
576 residues were previously observed to contribute less to P uptake compared to other
577 residues (Maltais-Landry and Frossard, 2015). Alongside other residue properties,
578 *Vicia villosa* phenols and secondary metabolites content have been proposed to
579 possibly slow its decomposition and nutrient release (Gougoulas, 2011; Maltais-
580 Landry and Frossard, 2015). While less pronounced with time, these early dynamics
581 had lasting effects on cumulative P uptakes, likely due to the importance of P
582 availability in early stages of growth (Grant et al., 2001).

583 **4.2 Short term effects on soil P pools faded with time**

584 Early decreases in P availability and ryegrass P uptake rapidly became less
585 pronounced with time, alongside a gradual decrease in P_{mic} for all organic treatments.
586 Coupled with an increase in P_{mic} of 79 % for *Vicia villosa* residues compared to the
587 unfertilized control, our results strongly suggest microbial P immobilization, which is
588 consistent with other studies on crop residues (Alamgir et al., 2012; Noack et al.,

589 2014; Traoré et al., 2020). Decreases in P availability induced by microbial P
590 immobilization are expected to fade with time due to microbial turnover releasing
591 immobilized P in plant available forms (Bünemann et al., 2004; Oehl et al., 2001).
592 However, we did not observe increases in soil P availability (P_{res}) after 59 days
593 despite decreases in microbial P over the same period. As suggested in Alamgir et
594 al. (2012) early neutral effects could have resulted from a balance between residue P
595 release and microbial P immobilization for residue barely supplying enough P to meet
596 microbial requirement during residue degradation. Later release of microbial P in
597 plant available forms could then have been prevented by quick transformation of
598 microbe-derived P to more stable, less available P forms (Alamgir et al., 2012; Ha et
599 al., 2007). Strong sorption of P derived from microbial turnover is unlikely in our soil
600 with an average spike recovery of 58% after 16 h. However, recovery of mineral
601 fertilizer was considerably less, 20 % of applied P based on direct labelling control.
602 The soil used in the experiment presented both a low Olsen P and HCl extracted P in
603 comparison to a significantly higher total P stock, prompting further investigation of
604 the diverse P pools present and their role in sorption dynamics. Further efforts would
605 be needed to investigate the fate of turnover microbial P and its long-term
606 contribution to P availability.

607 **4.3 Residue P and C:P mediated changes in P availability**

608 Diverse chemical and morphological residue traits can offer insight into cover crops
609 uncertain effects on subsequent crop P uptake (Espinosa et al., 2017; Hallama et al.,
610 2019; Maltais-Landry and Frossard, 2015). However, inconsistent and potentially
611 misleading effects are reported for some chemical traits such as residue P
612 concentration or residue C:P ratio (Damon et al., 2014; Kwabiah et al., 2003; de
613 Oliveira et al., 2017; Umrit and Friesen, 1994). Out of the traits examined, we

614 highlighted strong to moderate correlations between residue C:P ratio and ryegrass P
615 uptake up to 70 days after amendment ($R^2=0.8$ after 35 days; $R^2=0.4$ after 47 days,
616 $R^2=0.7$ after 70 days). A strong influence of residue C:P ratio was also observed on
617 soil P availability. In agreement with reports of decreased P uptake by crops
618 amended with residue with a C:P ratio >300 (Tate, 1985), we observed decreases of
619 ryegrass P uptake of up to 43 % compared to the unfertilized control for *Vicia villosa*
620 residues with a C:P of 314. Microbial P immobilization was reported to occur after
621 amendment with residue with C:P ratio >200 in Alamgir et al., (2012), while Prescott
622 (2005) reported a range of critical C:P ratios from 230 to 480. Linear models
623 predicting P uptake by ryegrass showed poor fits for C:P ratios lower than 190 in our
624 experiment, consistent with a C:P threshold for P microbial immobilization of around
625 200. However, increases in P availability were observed after addition of BraC
626 residues (C:P 164, 2.44 g P kg⁻¹) or FagE residues (C:P 162, 2.49 g P kg⁻¹),
627 suggesting a higher critical C:P ratio for quick mineralization and release of residue P
628 than the C:P ratio of 100 suggested in Alamgir et al., (2012) or Hansen et al. (2022).

629 Residues increasing soil P availability in the short term in our experiment nonetheless
630 had a P concentration close to 2.5 g P kg⁻¹, concomitant with suggested thresholds of
631 2.5 to 3 g P kg⁻¹ for fast P release from residues (Damon et al., 2014; Hallama et al.,
632 2019; Maltais-Landry and Frossard, 2015). Overall, despite the transitory nature of
633 C:P ratio influence on P availability via microbial P immobilization, C:P ratio was
634 strongly correlated with the cumulative P uptake in ryegrass over the four months of
635 our experiment. Our results thus strengthen the proxy offered by cover crop residue
636 C:P ratio in understanding subsequent plant P uptake in our moderately P limited
637 soil.

638 Recent efforts similarly highlighted the role of cover crop residues C:P ratio for P
639 uptake by subsequent crops. Although they did not quantify it, previous authors
640 suggested that residue C:P ratio drive P immobilization dynamics (Hansen et al.,
641 2022). Our results reinforce this central role of residue C:P ratios and confirm
642 important microbial P immobilization dynamics. However, different effects of residue
643 C:P ratio were reported according to soil P status in Hansen et al. (2022). This
644 prompts further efforts to investigate the complex impacts of soil P status on the
645 influence of residue C:P on P release from residue via microbial dynamics.

646 **4.4 Neutral effects of residue specific leaf area**

647 Morphological traits and architecture of plant tissues, such as SLA, have also been
648 observed to play an important role in residue decomposition and nutrient dynamics
649 across natural ecosystems (Garnier et al., 2004; Liu et al., 2018; Perez-
650 Harguindeguy et al., 2013; Santiago, 2007; Zuskwert and Prescott, 2017). Litter
651 physical traits, such as SLA, have been proposed to modulate nutrient release and
652 residue decomposition rate (Zuskwert and Prescott, 2017). Reduced surface area per
653 mass, associated with lower SLA, was for instance proposed to explain slower
654 residue decomposition and P release in larger residue pieces (Noack et al., 2014).
655 Recent efforts moreover suggested that different tissue architectures may explain
656 moderate rather than high correlations between C:P and P uptakes in a
657 decomposition experiment (Hansen et al., 2022). Contrary to our hypothesis, no
658 correlation was observed between residues SLA and P uptake by ryegrass or soil P
659 availability. These results contrast with findings from natural ecosystems (Liu et al.,
660 2018; Santiago, 2007). The lack of correlation between SLA and leaf P concentration
661 or other residue traits in our experiment may explain these results. As cover crop
662 species are primarily selected for their fast growing characteristics and easy

663 termination (Hallama et al., 2019), the common cover crop species used might have
664 restricted the range of SLA values compared to more wide variation in natural
665 ecosystems, resulting in no visible effect. Reduced decomposer abundance, due to
666 soil sieving and long soils storage prior to the experiment, likely also reduced
667 potential effects of SLA via modulating decomposer access to residues. Overall,
668 here, residue SLA did not offer a proxy to understand and possibly model the
669 contribution of cover crop residues to P availability.

670 **4.5 Implications for cover crop contribution to subsequent crop P uptake**

671 Potential benefits of cover cropping on P availability have been reviewed across a
672 wide range of contexts with reported increases of up to 50 % in P uptake in
673 subsequent crops (Hallama et al., 2019). However, cover cropping benefits remain
674 very inconsistent with reports of positive but also negative or neutral impacts on
675 subsequent crop P uptake (Hallama et al., 2019). Our results showed similar
676 cumulative P uptake after crop residue amendment as compared to the unfertilized
677 control, with little differences between species except for *Vicia villosa*. Comparable
678 observation of little differences between vegetative stage residues were previously
679 reported by Maltais-Landry and Frossard (2015), while other studies highlighted more
680 pronounced differences (Eichler-Löbermann et al., 2008; El Dessougi et al., 2003).
681 An early decrease or at best maintained P availability in amended soils in our
682 experiment contrasts with reports of increased P availability and uptake after cover
683 crop residues amendment in Maltais-Landry and Frossard (2015), and recent reports
684 of low but positive effects on subsequent P uptake (Hansen et al., 2022). Based on
685 cumulative uptakes over four months, the change in P uptake in ryegrass in our
686 experiment ranged from an increase of +2 % for VicF leaf residues to a decrease of
687 22% for VicV aboveground residues compared to the unfertilized control. However,

688 no significant isotopic dilution was observed between our minP and unfertilized
689 control in ryegrass biomass, as well as in resin extracts. We could thus not calculate
690 P derived from residues based on indirect isotopic labelling but only based on
691 difference in P content in the different components of our system (ryegrass, soil resin
692 extractable P, and microbial P).

693 Our cover crop residues had lower P concentrations (between 1.3 and 3 mg P kg⁻¹)
694 and higher C:P ratio (between 137 and 316) compared to other studies (Hansen et
695 al., 2022; Maltais-Landry and Frossard, 2015), likely because of moderate P
696 limitation during growth. Lower P concentrations and higher C:P ratio for our residues
697 could have resulted in microbial P immobilization and simultaneous P mineralization
698 and release balancing out as proposed in Alamgir et al. (2012). Balanced microbial P
699 immobilization and simultaneous P release would then explain mostly neutral effects
700 of cover crop residues on ryegrass P uptake. Lower contribution of residue P to P
701 uptake by ryegrass in our experiment likely also resulted from our lower application
702 rate of 15 mg P kg⁻¹ soil compared to 50 mg P kg⁻¹ soil in Hansen et al. (2022). Our
703 application rate corresponded to a field productivity of 6.5 t DM ha⁻¹ and a residue P
704 concentration of 3 mg P kg⁻¹ which are representative of what would be expected in
705 the fields sampled. However, cover crop biomass production and P concentrations
706 may vary greatly according to species, growth period, climatic conditions and nutrient
707 status of the soil. Our low but relevant P dose added could have contributed to the
708 lack of significant isotopic dilution. Indeed, other studies using the same indirect
709 isotope method for determining the P uptake by plants applied higher P rates of e.g.,
710 recycling fertilizers (Brod et al. 2016, 30 mg P kg⁻¹ soil; Nanzer et al. 2014 50 mg kg⁻¹
711 soil), or animal manure (Oberson et al. 2010 30 mg P kg⁻¹ soil), or plant residues
712 (Hansen et al., 2022, 50 mg kg⁻¹ soil). The combination of microbial immobilization

713 and slow release of small amounts of remineralized microbial P may have been too
714 low for detection.

715 Co-limitation with N (average PNI = 50 %, average NNI= 91%) might have also
716 amplified the reduced P uptakes as treatments with higher NNI tended to have lower
717 PNI in early harvests, despite important N inputs of 120 mg kg⁻¹ soil supplied after
718 each harvest (600 mg kg⁻¹ soil over the course of the experiment). Moderate P
719 limitation may also have influenced the potential contribution of residue P to P plant
720 uptake. Higher contribution of residue P to P availability is indeed most likely to occur
721 in contexts with high P availability where cover crop accumulate large amount of P
722 (Damon et al., 2014; Thibaud et al., 1988). The contribution of cover crops to P
723 availability was even proposed to be agronomically significant only in contexts where
724 cover crop accumulate large amount of P (Damon et al., 2014; Thibaud et al., 1988).
725 Maintained or decreased subsequent crop P uptake in our soil with moderate P
726 limitation may suggest that benefits observed in similar contexts (Hallama et al.,
727 2019) may be related to cover crops capacity to forage for P unavailable to the main
728 crops, and to increase P availability via mobilization during growth and reduce loss
729 (Hallama et al., 2019). Optimizing cover cropping benefits for P availability in
730 moderately P limited soil may also be ensured via agricultural practices either
731 avoiding the temporary decrease in P availability via carefully managing cover crop
732 C:P ratios via early termination or adapted composition or enhancing P availability
733 during decomposition via mineral fertilization (Baggie et al., 2005).

734 **5. Conclusions**

735 Understanding the factors involved in the fate of residue P in the plant-soil-microbe
736 system is central to manage and improve soil P availability in cropping systems. Our
737 study reinforced the role of residue C:P ratio, strongly underlining the importance of

738 microbial P immobilization dynamics when adding C as part of residues. Residues
739 with high C:P ratios (i.e., >300) resulted in decreased P availability, by up to 49 % for
740 resin P extracts, and decreased cumulative P uptake by up to 22 % compared to the
741 unfertilized control. Contrary to our hypothesis, residue morphology via the proxy of
742 SLA did not appear to affect P release. Our results highlighted mostly neutral effects
743 of cover crop residues grown in a moderately P limited soil on P availability and P
744 uptake by a subsequent crop, which contrasts with previous studies often reporting
745 positive results. Neutral effects of P release from cover crop residues on soil P
746 availability suggested that in context with moderate P availability cover cropping
747 benefits for P availability may be achieved via other pathways such as P mobilization
748 by cover crops during growth, shifts in microbial communities under cover cropping or
749 reduced losses. Exploring the relative contribution of these pathways relative to P
750 release from residue in contexts with varied soil P availability could provide important
751 insights into optimal cover crop composition for enhanced P availability in cropping
752 systems.

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