Tradeoffs among phosphorus-acquisition root traits of crop species for agroecological intensification

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Acknowledgements

The authors thank Vivescia for their financial and technical assistance. We also thank Aurore Coutelier, Matthieu Forster, Philippe Jacolot, Céline Roisin and Erika Samain for their technical assistance. The project received funding from the ANRT (Association Nationale Recherche Technologie).

14 **Abstract**

15 Aims

16 Plant P acquisition strategies are driven by multiple belowground morphological and physiological traits as well
17 as interactions among these traits. This study aimed to characterize the relationships among traits involved in P
18 acquisition to explore tradeoffs and the main P-acquisition strategies and their mediation by soil type.

19 Methods

20 Ten morphological and physiological traits involved in P acquisition were measured across 13 species grown in
21 controlled conditions in two contrasting soils with moderate P limitation.

22 Results

23 Tradeoffs between thicker and thinner roots were observed, with thicker roots exhibiting greater carboxylate
24 release or phosphatase activity in the rhizosheath. Tradeoffs and coordination amongst traits were strongly
25 mediated by soil type. Multivariate analysis of functional traits involved in P acquisition highlighted four main
26 P-acquisition strategies relying primarily on morphological traits, physiological traits or a combination thereof.

27 Conclusions

28 The diversity of strategies demonstrates a potential for functional diversity benefits in cultivated plant
29 communities via preferential access to different P pools leading to complementarities and reduced competition
30 for resource acquisition. Overall, our results underpin functionally-complementary multispecies crop designs,
31 enhancing P availability and cycling efficiency

32 **Key words:** agroecology, cover crops, phosphorus acquisition, root functional trait, tradeoffs

33 **Abbreviations**

34 Δ pH: Change in rhizosheath pH

35 PME: Phosphomonoesterase activity

36 RLD: Root length density

37 SLA: Specific leaf area

38 SRL: Specific root length

Introduction

Phosphorus (P) is a limiting nutrient in many natural and managed ecosystems due to its strong sorption with soil particles which limits its availability for plants. To overcome low P availability and ensure productive agriculture, P fertilisers are applied, albeit often with very low efficiency (Richardson et al. 2011). In highly-productive fertilized systems, there is a significant gap in P exports and inputs, leading to the accumulation of poorly available organic and inorganic P in the soil (Simpson et al. 2011; Bouwman et al. 2017). In these systems, improving P availability can be achieved by selecting for plant traits and strategies that allow access to the legacy P pool (Menezes-Blackburn et al. 2018). Plants have developed a range of morphological, architectural and physiological traits, granting access to the diverse pools of soil P. Morphological traits such as specific root length (SRL) and architectural traits such as root length density (RLD) allow plants to increase their P-foraging capacity (Pang et al. 2010; Haling et al. 2018; Ma et al. 2018). While only inorganic P in solution is taken up by plants, roots can also mobilize both inorganic and organic P by secreting protons (H^+) to dissolve Ca-phosphate, and carboxylate, which compete with P for binding sites, and thus decrease sorption on mineral surfaces (Wang and Lambers 2019). Plants can also hydrolyze organic P through the release of acid phosphatases, both monoesterases and diesterases (Richardson et al. 2011).

Overall, plant P-acquisition strategies are defined by the expression and association of P-acquisition traits. However, as the expression of these traits has a carbon cost, plants tend to rely mainly on one or a few P-acquisition traits (Pearse et al. 2006; Raven et al. 2018). There may thus be interactions among P-acquisition traits such as root morphological traits being negatively correlated with physiological traits (Zhang et al. 2016; Lyu et al. 2016; Wen et al. 2017). This indicates potential tradeoffs among diverse P-acquisition traits. However, trait interactions and tradeoffs that are central in gaining insight into plant P acquisition, are poorly understood, especially for fast-growing plants such as cover crops (Wen et al. 2019). Understanding tradeoffs and trait-combination effects would allow us to unravel the complexity of the P-acquisition strategies of species and bring new knowledge to design cultivated communities (i.e. multi-species crops) such as cover crops or intercrops to improve P acquisition and availability. Furthermore, trait expression and associated processes are strongly influenced by soil conditions, especially P availability (Raven et al. 2018; Wen et al. 2019). Tradeoffs among life history traits and nutrient-acquisition traits are inconsistent across environmental conditions (Sgrò and Hoffmann 2004; Kong et al. 2019), warranting further investigations as for the consistency of tradeoffs involved in P acquisition.

Intermediate crops, often referred to as cover crops, would offer an opportunity to use a high plant species diversity to enhance P recycling in agroecosystems (Hallama et al. 2019). They can accumulate a large amount of nutrients including P during their growing period (Wendling et al. 2016), which is then released at termination to play a major role in maintaining and improving P availability (Dube et al. 2014; Damon et al. 2014). Moreover, through plant traits associated with a high P-foraging capacity and P mobilization, intermediate crops could acquire P from P pools that are unavailable to the cash crop (Nuruzzaman et al. 2005). A promising opportunity to improve soil P availability for crops can thus be developed by enhancing P cycling in intermediate crops on the basis of their potential to acquire P from poorly-available sources (Richardson et al. 2011). Cover crops present a wide range of P-acquisition traits, therefore potentially presenting different P-acquisition strategies exploiting different P pools (Wendling et al. 2016; Lyu et al. 2016). Examining these strategies and the factors conditioning their expression by characterizing root trait relationships in plant species with diverse root traits would result in a better understanding of P acquisition in crop species and insights for the design of more P-efficient systems. In this study, a greenhouse experiment was carried out to measure morphological, architectural and physiological traits in 13 intermediate crops species with diverse phylogenetic lineages in two contrasting soil types, in order to:

- i) Characterize the relationships among traits involved in P acquisition to explore tradeoffs and the main P-acquisition strategies;
- ii) Examine whether P forms and soil type mediate expression of tradeoffs and P-acquisition strategies in intermediate crops.

Material and methods

Greenhouse experiment

Soils used in the greenhouse experiment were collected at 5 to 20 cm depth from two fields from north-eastern France, after topsoil (0-5 cm) removal to further decrease P availability. Fields with a known P deficiency were selected to ensure low P availability. A Retisol (formerly called Albeluvisol) and a Calcaric Cambisol (FAO 2014) were selected for their contrasting soil characteristics, mainly their different P forms, in particular their apatite P concentration (Table 1). Prior to use, the soils were dried at ambient temperature, sieved at 2 mm and then mixed with washed sand (22% mass).

Thirteen (sub)species of diverse phylogenetic lineages (Poaceae: *Avena nuda* L., *Avena strigosa* Schreb; Brassicaceae: *Brassica carinata* A. Braun, *Raphanus sativus* L., *Sinapis alba* L.; Polygonaceae: *Fagopyrum esculentum* Moench.; Fabaceae: *Lens culinaris* Medik., *Pisum sativum* subsp. *arvense* L., *Trifolium alexandrinum* L., *Vicia faba* L., *Vicia sativa* L., and *Vicia villosa* Roth.; Hydrophyllaceae: *Phacelia tanacetifolia* Benth.) were selected for their diverse morphologies, P-acquisition traits and relevance for the local context. The experimental design included two soil types, 13 species and a control (bare soil) with four replicates. Plants were sown mid-January 2018 at two individuals per pot per species in 4.5 L fully filled pots and watered twice a week. Pots were arranged in a random design and greenhouse temperatures were maintained at 22°C during the day (14 hours) and at least 18 °C at night.

Plant traits measurement

At harvest (77 days) plants were manually separated from the bulk soil with special care given to ensure minimum damage. Rhizosheath adhering to the roots up to a maximum of 2 mm after shaking was collected and stored at -20°C for further analysis. Roots were then immersed in 0.20 mM CaCl₂ for 1 hour, after removing any remaining soil particles by quickly rinsing with CaCl₂. The CaCl₂ volume was adjusted to ensure a complete immersion of the root system. The solution was then sampled and stored at -20°C before measuring carboxylic acid exudation by reversed-phase column liquid chromatography (RPLC) (Cawthray 2003; Yacoumas et al. 2020). Briefly, an acid mobile phase (93% 25 mM KH₂PO₄ at pH 2.5 and 7% methanol) allowed a good resolution of five acids (citric, fumaric, maleic, malic, malonic) on a C18 column with a 15 min elution time and a 1 mL min⁻¹ flow rate. Total carboxylate release rate was later calculated as the sum of all previously mentioned acids (see Table 2 for abbreviations).

Morphological traits

Aboveground biomass and roots were separated by cutting the stem 1 cm above the first visible root. Roots were then scanned while being immersed in deionised water using an Epson Scanner perfection V800 (Regent Instruments Inc., Québec, Qc, Canada) to produce a 600 dpi image. The image was analysed using WinRHIZO Regular software V.2016a (Regent Instruments Inc., Québec, Qc, Canada) to determine root traits including root surface area (RSA), the percentage of fine root (FR), defined here as length of roots with a diameter < 0.5 mm, and root length density (RLD). After 48 hours drying at 55°C, scanned roots were weighed to calculate specific root length (SRL). Three young but fully-developed leaves per replicate were scanned at 600 dpi, and then dried at 60°C for 48 hours to determine specific leaf area (SLA). All aboveground biomass was dried at 60 °C for 48 hours and weighed.

Nutrient uptake

Dried leaves and stems were digested via acid digestion and a microwave heating treatment (Lange et al. 2016). Between 0.1 and 0.2 g of biomass was introduced in Teflon vessels with 8 mL of 65% (v/v) HNO₃ and 2 mL of 36% (v/v) HCl and heated to 185°C for one hour. Digests were then filtered and P and manganese (Mn) concentrations (as a proxy for rhizosheath carboxylate concentration) determined by inductively coupled plasma mass spectrometry (ICP-MS) (Thermo Scientific XSERIES2, Beauvais, France). SRM1573, a certified reference material (tomato leaves) was used as a standard.

Rhizosheath properties

After defrosting, acid phosphomonoesterase activity in the rhizosheath (PME) was measured with a modified buffer at pH 6.5 (Tabatabai and Bremner 1969). Briefly, phosphatase activity was assessed via production of *p*-nitrophenol from sodium *p*-nitrophenyl phosphate during a 1 hour incubation at 37°C with 0.5 g dry soil, 0.2 mL toluene, 4 mL modified buffer and 1 mL substrate. *p*-Nitrophenol release was determined spectrophotometrically at 410 nm after stopping the reaction with 4mL 0.5 M NaOH and 1mL 0.5 M CaCl₂ and filtering. Rhizosheath pH was measured on 2 g equivalent dry soil with a 1:10 soil to solution ratio. ΔpH between rhizosheath and bulk soil from unplanted pots post-growth was then calculated.

Data analysis

Linear mixed models (LMM) were used in order to test for differences among plant P uptake and traits among soil types, with species as fixed factors and soil types as random effect. Differences in traits between soils were then investigated with non-parametric tests (Kruskall-Wallis test + post hoc test of Mann Whitney). As multiple differences were observed between soils, further analysis was performed separately for each soil type. To

identify the main covariation in P-acquisition traits and rhizosphere processes, a principal component analysis (PCA) was performed using the “FactomineR” package on log-transformed data (Lê et al. 2008). The number of components was selected to represent more than 75% of the total variability. Tradeoffs between traits were confirmed with Spearman correlation tests as data did not fulfil the condition of normality. Hierarchical classification on principal components (HCPC) was then performed to define groups with similar patterns of P-acquisition traits and influence on the rhizosphere. Species were attached to the group including most of their replicates. A multiresponse permutation procedure (MRPP) confirmed a clear differentiation between clusters in multivariate space. Differences between clusters for each individual factor were then investigated, either with tests of variance (ANOVA and post-hoc test of Tukey) or non-parametric tests (Kruskall-Wallis test + post-hoc test of Mann Whitney).

To investigate the importance of the factors leading to group formation, their influence on P uptake was modelled via generalised linear models (GLM) using the “FactomineR” package. Briefly, all factors were individually tested as predictors of P uptake as well as combinations of the best fitting factors. Models were compared based on second-order Aikake’s information (AICc) with the lowest relative value considered the best fit. Differences between models were tested with ANOVA as well as the criteria $\Delta AICc > 2$. Complementary to GLM regression, partial square path modelling (PLS –PM) was performed to underline the relative ability of trait combinations and type for predicting P uptake. Three clusters of variables, or “latent variables” were defined, respectively, the “root morphology” variables encompassing root surface area, SRL, fine root percentage, root length density, the “root physiology” variables encompassing PME activity, carboxylate release and change in rhizosheath pH and the “aboveground traits” variables encompassing SLA, foliar [P] and [Mn]. Verifications were made to ensure model quality, notably unidimensionality of latent variables and cross-loadings between traits associated with a latent variable and other variables as suggested in Sanchez (2013). To ensure the condition of positively correlated variables in a latent variable, the sign of some variables was changed. Variables and components were selected based on their loading and correlation as suggested in Sanchez (2013). Overall model quality was evaluated with the Goodness of Fit (GoF) index. Analyses were performed with the package “plsrm” version 0.4.9. All tests were performed in R version 3.6.0 with a significance level of 0.05.

Results

Variation in P-acquisition traits and rhizosphere processes

In the Calcaric Cambisol, the PCA summarised 84% of the total variability, with the first two components representing 50.8% of the total variability (Fig.1). In the Retisol 82% of the total variability was summarised by the PCA, with the first two components representing 51.3% of the total variability (Fig.1). Overall, we observed moderate to strong correlations between morphological indicators such as fine root percentage, RLD, SRL and root surface area ($|r|$ between 0.30 and 0.88). We observed similar patterns between physiological indicators such as change in rhizosheath pH, PME activity and carboxylate release, albeit more differentiated by soil type.

In the Retisol, the first component was formed based on all modifications in the rhizosheath properties measured (pH, PME activity) and carboxylate release, while also presenting a gradient of fine root percentage and root surface area. Aboveground, SLA and leaf P concentration were also important contributors to the first component. The component presented a gradient with strong negative correlations between fine root percentage and PME activity ($r=-0.65$) and negative correlation between fine root percentage and rhizosheath acidification ($r=-0.32$). PME activity, rhizosheath acidification and carboxylate release were positively correlated. At the leaf level, SLA was negatively correlated with fine root percentage. The second component was mostly formed based on root physiology and morphology (root length density and surface area). Physiological traits important for this axis were carboxylate release as well as to a lesser extent leaf Mn concentration. The component presented a gradient with a negative correlation between carboxylate release and RLD ($r=-0.36$). Root length density was also positively correlated with root surface area.

In the Calcaric Cambisol, the first component was based on aboveground characteristics such as SLA and foliar Mn concentration. To a lesser extent, the first component was also based on morphological characteristics such as RLD, and rhizosheath modification (rhizosheath acidification). SLA was strongly positively correlated with leaf Mn concentration ($r=0.66$). Root length density and root surface area were positively correlated. The second axis mostly represented morphological traits such as root surface area, fine root percentage and root length density with a smaller influence of leaf traits such as foliar P concentration and marginal modifications to the rhizosheath such as PME activity. Foliar P concentration was positively correlated with fine root percentage ($r=0.33$) and SRL ($r=0.43$), and negatively with root surface area ($r=-0.30$).

Comparison of P-acquisition traits among different clusters

Based on the PCA scores, we identified four groups via HCPC in the Calcaric Cambisol, five in the Retisol (Fig. 1, Table 3). In the Retisol, the first “physiological/exudation” group L1 (Fig. 1) encompassed lentil, common vetch and white mustard. It showed the greatest exudation of carboxylic acids, significant activity of PME in the rhizosheath, as well as the lowest RLD observed in all groups. The second “intermediate/morphological” group L2 encompassed common and naked oat, Indian mustard, buckwheat and forage radish. It presented a low carboxylate release and PME activity in the rhizosheath, while presenting a small increase in rhizosheath pH and a high RLD, fine root percentage and foliar P concentration compared with other groups. The third “physiological/morphological” group L3 had a strong to intermediate expression of all physiological traits as well as SRL, RLD and SLA and a low foliar P concentration. It grouped forage pea, clover and hairy vetch. The fourth “morphological” group L4, encompassing phacelia, presented low expression of P-mining traits, except for an intermediate carboxylate release, a high fine root percentage and the highest RLD and SRL observed in all groups. Finally the “physiological/mining” group L5, encompassing faba bean, had the lowest SRL and fine root percentage associated with a strong expression of all physiological traits with in particular a strong decrease in rhizosheath pH. Overall the different strategies resulted in similar levels of total P uptake.

In the Calcaric Cambisol, the first “morphological” group C1 was mainly characterised by a high root length density and surface area, an intermediate SRL and a low expression of physiological traits. It encompassed naked oat, forage pea and forage radish. The second “morphological/physiological” group C2, encompassing hairy and common vetch had a significantly higher SLA, stronger rhizosheath acidification, intermediate PME activity in the rhizosheath and higher SRL. The third “intermediate” group C3 encompassed common oat, buckwheat, lentil, phacelia, white mustard and clover. It presented the highest percentage of fine roots, intermediate values of SRL, SLA and the highest foliar P. It also presented the highest value of carboxylate release, while not significantly different from the chemical and morphological groups. Finally the fourth “physiological” group C4, encompassing faba bean, presented the highest PME activity in the rhizosheath, and second-highest carboxylate release. It also presented the lowest fine root percentage and lowest SRL. Overall, these different strategies once again resulted in similar levels of total P uptake.

Modelling trait-combination effects on P acquisition

As we observed a similar P uptake among strategies, we investigated overall relationships between P uptake and factors involved in group formation with GLM (Table 4). PLS PM were also used to highlight the combinations of traits and type of trait best predicting P uptake (Fig. 2). In the Retisol, the best model fit was obtained with

fine root percentage, leaf Mn concentration and PME activity as predictors, while a similar fit was also achieved without PME activity. Fine root percentage was the best predictor when used alone, however, it performed worse than models incorporating multiple traits. While offering a lower fit when incorporating multiples traits, SLA was the second-best predictor, being in itself correlated with multiple morphological and physiological traits. The PLS PM approach ($R^2 = 0.5047$) produced similar results, with PME activity in the rhizosheath being the best single predictor in the physiological component, followed by rhizosheath acidification, and fine root percentage being the best predictor in the morphological component, followed by root surface area. Similar weights were associated with the physiological (correlation value =0.37) and morphological (correlation value =0.32) components in this soil with a low predicting ability of the aboveground component leading to its removal.

In the Calcaric Cambisol, the best model fit was achieved with the combination of SLA, root surface area, fine root percentage and pH modification in the rhizosheath. Purely morphological models had a significantly poorer fit than models incorporating pH, while rhizosheath acidification alone was a poor predictor. Excluding correlated traits, the best predictors were SLA and root surface area (while not significantly different from SLA+root surface area+change in rhizosheath pH). SLA was the best predictor for single-trait models. PLS PM ($R^2 = 0.457$) underlined the importance of the morphological component (correlation value =0.31) and aboveground component (correlation value =0.40), while the physiological one was removed due to its poor predicting ability. SLA was the most impactful contributor for the aboveground component. For the morphological component it was root surface area.

Differences among trait variation and tradeoffs per soil type

Trait expressions were significantly different between soil types, with very uneven trait plasticity among species (Table 5). PME activity and carboxylate release were overall significantly lower in Calcaric Cambisol. In contrast, root length density and surface area were higher overall in this soil, especially for Fabaceae and Brassicaceae. Covariation between morphological P-acquisition traits and rhizosphere processes were observed less in Calcaric Cambisol such as the correlation between root surface area and PME and rhizosheath acidification or RLD and carboxylate release observed in Retisol which were not observed in this soil. Positive covariations such as between PME activity in the rhizosheath, carboxylate release and rhizosheath acidification were also not observed in this soil. Similarly, SLA was correlated with change in rhizosheath pH, PME activity and carboxylate release in Retisol, but only with change in rhizosheath pH in Calcaric Cambisol.

Discussion

Tradeoffs in functional traits to understand P acquisition of crop species

Multiple studies have demonstrated the importance of a single trait/few traits for P uptake such as root length density and surface area (Pang et al. 2010; Haling et al. 2018) or PME activity, carboxylate release or rhizosphere acidification (Lambers et al. 2006; Rose et al. 2010; Li et al. 2017; Nobile et al. 2019). However despite increased observations of coordination and tradeoffs among belowground resource-acquisition traits (Roumet et al. 2016; Ma et al. 2018), our understanding of trait interactions and tradeoffs that are central to P acquisition remains limited, especially in crop species (Wen et al. 2019). Our results highlight multiple covariation and tradeoffs between root morphological and physiological traits across a range of fast-growing crop species. Fine root percentage was negatively correlated with PME activity, rhizosheath acidification, and foliar Mn concentration, and marginally with carboxylate release. As foliar Mn can be used as a proxy for rhizosheath carboxylate concentration (Lambers et al. 2015; Pang et al. 2018; Yu et al. 2020), this suggests a greater relevance of physiological strategies associated with P mining for root systems with less fine root percentage. Our results are consistent with recent findings showing that roots with a large diameter present high expression of P-mining traits, while species with thinner fibrous roots express higher levels of morphological traits for P acquisition (Lyu et al. 2016; Wen et al. 2019), extending this observation to a different range of species (intermediate crops species) and context (north-western European soils with moderate P deficiency). Under P stress, plants can modify their root morphology through higher fine root percentage, increased SRL, root hair density and root length density to increase soil foraging at lower cost (Lambers et al. 2006; Shen et al. 2011; Haling et al. 2018). Root physiology can also be modified to increase P availability in the rhizosheath via increased carboxylate, enzyme and proton exudation. Synergistic action of these physiological traits is common, as shown for phytase activity and carboxylate release (Giles et al. 2017) and reinforces the coordination between PME activity in the rhizosheath, carboxylate release and rhizosheath acidification. A possible explanation for this observation is the release of organic P sorbed to soil particles by carboxylates for subsequent mineralisation (Clarholm *et al.*, 2015). While both physiological and morphological strategies should benefit P acquisition, tradeoffs between both are suggested to form along a cost / benefit balance due to the important investment they can represent for the plant (Pearse et al. 2006; Raven et al. 2018). Overall our results confirm and extend previous findings in other systems demonstrating multiple coordination and tradeoffs among morphological and physiological traits involved in P acquisition in crop species (Zhang et al. 2016; Giles et al. 2017; Li et al. 2017). Because physiological traits tend to allow greater access to legacy P pools compared with morphological traits,

which allow access to available P pools (Lyu et al. 2016), this morphological/physiological tradeoff offers insight into how to enhance P acquisition and to increase exploitation of the diverse pools of P. Our results demonstrate a potential to select for species at different ends of the tradeoffs spectrum in multispecies systems to increase P acquisition, while reducing competition for resources. Our results constitute a novel contribution toward understanding P acquisition in crop species, and also underline the need for a better understanding of how these trait combinations and tradeoffs are structured in a multi-traits space to form P-acquisition strategies. Such an understanding would offer the opportunity to better design multispecies cropping systems, notably with the main functions of improving P cycling and availability.

Phosphorus-acquisition strategies to design multispecies crops

Plants present very uneven trait plasticity when exposed to different levels of available P (Pearse et al. 2006; Haling et al. 2018; Wen et al. 2019). Uneven plasticity along tradeoffs and covariations suggests both a convergence toward common resource-acquisition strategies and divergence among strategies (Wendling et al. 2016; Li et al. 2017). Plants under P stress rely on resource-acquisitive strategies, either enhancing expression of root morphological traits associated with soil foraging, or modifying their physiological traits to mobilise poorly-available P (Rose et al. 2010; Teng et al. 2013; Lyu et al. 2016). A more complex association of morphological and physiological traits along a cost-benefit axis has also been suggested (Lynch 2015; Weemstra et al. 2016; Wen et al. 2019), prompting further investigations. A certain dichotomy was indeed observed between P-acquisition strategies relying more on physiological or more on morphological traits, corroborating the tradeoffs we observed. However, multivariate analysis highlighted a diversity of intermediate strategies, rather supporting the hypothesis of a complex association of traits along a cost-benefit continuum for P acquisition. Our results offer important new insights into the complex and diverse range of P-acquisition strategies occupying a different trait space, and thus offering opportunities for complementarities in resource acquisition. In both soils, similar extreme strategies could be identified on both ends of a morphological/physiological spectrum. On the morphological end, a strategy could be identified, presenting a low expression of physiological indicators and high root length density/fine roots percentage, mainly encompassing Brassicaceae and Poaceae. This strategy is probably oriented toward soil scavenging, as an important proportion of fine roots can be a way to forage soil at a low cost, while important root length density similarly denotes an important exploration of a given soil volume (Lynch 2015; Yuan et al. 2016; Ma et al. 2018). Similar groupings of species constituting this group (notably Indian mustard, radish, and oat) have been observed before, based on morphological traits, and proposed to be an intermediate strategy between very resource-acquisitive species such as phacelia, and more conservatives ones

such as faba bean (Wendling et al. 2016). On the other end of the spectrum, the several physiological groups, mainly comprising Fabaceae, presented high expressions of all physiological traits with overall lower fine root percentage and SRL. High rhizosheath phosphatase activity, carboxylate release and rhizosheath acidification indicated strategies potentially increasing P availability via mineralisation of organic P, ligand exchange and dissolution of precipitated phosphates, respectively (Hoffland et al. 1989; Jones et al. 2003). While our results confirm the greater effect of Fabaceae on rhizosphere properties compared with other phylogenetic groups (Maltais-Landry 2015), a diverse spectrum of strategies was observed, also within Fabaceae. Two to three clusters per soil expressed intermediate to high values of physiological indicators, and were comprised mainly, but not only of Fabaceae. These groups differed in their expression of morphological traits, especially RLD, fine roots percentage and SRL. This corroborates the existence of a spectrum of P-acquisition strategies combining scavenging and mining processes in intermediate crops. These contrasting strategies, interestingly, did not differ significantly in their P uptake, indicating a potential for maximising P acquisition in multispecies systems via mixing strategies accessing diverse P pools in soils (Lyu et al. 2016; Li et al. 2017) and as such less competition for resources. Such complementarities in resource acquisition among plant species has been suggested as an explanation for the positive effects of functional diversity (Petchey and Gaston 2006; Faucon et al. 2017). Functionally more diverse systems indeed outperform single species for P uptake (Li et al. 2014; Xue et al. 2016). Overall, our results could lead to enhanced P cycling efficiency and P availability in multispecies cropping systems via better designs exploiting more of the total P stock including the pool of legacy P (Richardson et al. 2011). Functional diversity effects on P availability and uptake are not well known however (Huang et al. 2019), and variable shifts in root functional traits and plant P-acquisition strategy should be expected in multispecies conditions (Li et al. 2014). Hence, there is a need for further studies of functional diversity effects on P availability and P cycling. Perspectives include examining functional diversity effect on P uptake and P availability in systems combining different P-acquisition strategies and in different soil and climate contexts. Other traits potentially involved in P acquisition such as root hair length and density (Haling et al. 2013; Yuan et al. 2016), association with mycorrhizal fungi (Smith and Smith 2011; Campos et al. 2018) or rhizosheath bacteria (Richardson et al. 2011) should also be included in future studies to further refine the strategies identified.

Mediation of tradeoffs and P-acquisition strategies according to P forms in soil

Although expression of both P-mining traits and morphological traits are essential for P acquisition, their costs in a specific context may define how plants express and mix their functional traits (Raven et al. 2018; Zhou et al.

2018). Phosphorus-mining traits in particular have proven to have their efficiency strongly impacted by soil type and soil P forms such as proposed for carboxylates in strongly P-sorbing soils (Wang and Lambers 2019). Indeed, we observed greater relevance and coordination of physiological traits in Retisol, while morphological traits were more expressed in Calcaric Cambisol. The modulation of P-acquisition strategies was further evidenced when modelling P uptake via GLM and PLS PM, providing insight into the relative importance of trait type. Phosphorus uptake was best predicted by root morphological traits and aboveground traits in Calcaric Cambisol, and a mixture of root morphological and physiological traits in Retisol. While several single trait correlations with P uptake were previously observed (Pearse et al. 2006; Lambers et al. 2006; Rose et al. 2010; Wen et al. 2017) our results complement our incomplete knowledge of coordination between physiological and morphological responses as well its mediation by soil type and soil P forms (Lyu et al. 2016). At low concentration, exudates may not be in a range relevant to significantly impact P uptake in Calcaric Cambisol, or they may have their efficiency impacted by soil characteristics. Adverse effects impacting P mobilisation via carboxylate exudation have indeed been observed, because of “Ca-aided co-adsorption” when released at low concentration, with low amounts of carboxylates increasing adsorption of calcium ions, in turn increasing adsorption of P (Duputel et al. 2013). The higher acid buffering capacity of the Calcaric Cambisol might also have impacted the efficiency of rhizosphere acidification as a P-acquisition trait, further decreasing the potential benefits of physiological traits in this soil. Overall, the strong soil mediation observed offers precious insights into P acquisition. As mentioned, morphological and physiological traits benefit P acquisition from different P pools, offering opportunities for enhanced P cycling in multispecies systems, notably by exploiting the pool of legacy P. However, by reinforcing the importance of plant/soil interactions, our results suggest that improved designs for enhanced P benefits should rely on different processes and strategies in different soils. Some processes such as P mobilisation should be less relevant in some contexts (Maltais-Landry et al. 2014), rather suggesting reliance on a mixture of resource-acquisitive strategies (Wendling et al. 2016). To be able to improve P benefits of intermediate crops, further efforts are needed to investigate the stability and relevance of the tradeoffs and strategies involved in P acquisition for a range of soil types and associated P forms and availability.

Conclusions

Enhancing P cycling and availability in cultivated systems via ecological intensification requires a better understanding of tradeoffs and strategies involved in P acquisition. Morphological and physiological traits comprised diverse P-acquisition strategies structured along an axis of trait covariation and tradeoffs. Our results demonstrate tradeoffs between thicker and thinner roots, exhibiting more physiological traits and morphological

377 traits, respectively. Reliance on either morphological or physiological traits and combinations thereof for P
378 acquisition were underlined by model approaches, and strongly mediated by soil P forms. The multiple P-
379 acquisition strategies with similar P uptake observed indicates the potential for positive effects of functional
380 diversity via complementarities in resource acquisition, and thus offers insights into mixture designs for
381 improved P benefits. Finally, varied tradeoffs and strategy plasticity amongst soil with different P forms
382 highlighted the importance of considering soil/plant interactions when attempting to improve our understanding
383 of resource-acquisition strategies. Further studies should investigate trait and strategy plasticity across a gradient
384 of functional diversity and various soil properties to help us select for locally optimized crop services.

385 **Authors' Contributions**

386 Nicolas Honvault carried out the experiment and wrote the manuscript with support from Michel-Pierre Faucon,
387 David Houben and Hans Lambers. Stéphane Firmin and Cécile Nobile helped process the data and perform the
388 analyses. All authors contributed to the final version of the manuscript.

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559 **Table 1** Chemical and physical soil characteristics

	Clay % (<0.002 mm)	Sand % (>0.05 mm)	pH KCl	Ca ^a (g kg ⁻¹)	N tot (%)	CEC (cmol _c kg ⁻¹)	Olsen P ^c (mg kg ⁻¹)	Ca -P ^d (mg kg ⁻¹)
Calcaric	30.7	22.0	7.9	44.7 ^b	0.17	9.3	19.8	542
Cambisol								
Retisol	22.3	5.4	7.4	2.60	0.10	10.5	16.3	76.7

560 ^aExtractant : Ammonium acetate 0.5 M, EDTA 0.02 M pH 4.65

561 ^bCaCO₃ 56.4%

562 ^cAccording to Olsen (1954)

563 ^dApatite phosphorus as defined in García-Albacete et al. (2012)

564 **Table 2** List of abbreviations and associated units

Variable	Abbreviation	Unit
Change in rhizosheath pH	ΔpH	-
Fine root percentage (<0.5 mm $\varnothing$)	FR	-
Phosphomonoesterase activity	PME	$\mu\text{g nitrophenol g}^{-1} \text{ hour}^{-1}$
Root length density	RLD	cm cm^{-3}
Root surface area	RSA	cm^2
Specific leaf area	SLA	$\text{mm}^2 \text{ mg}^{-1}$
Specific root length	SRL	m g^{-1}
Total carboxylate release rate	TCE	$\mu\text{mol g root}^{-1} \text{ hour}^{-1}$

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Table 3 Mean values $\pm$ standard error (n= 4 to 11) and analyses of variance of phosphorus- acquisition traits and rhizosphere processes per cluster

Soil type	Cluster	TCE	PME	Δ pH	RLD	FR	SRL	SLA	Leaf [P]	Leaf [Mn]
Retisol	L1: Physiological/exudation	41.6 $\pm$ 5.3	0.026 $\pm$ 0.004	-0.04 $\pm$ 0.04	0.09 $\pm$ 0.01	0.81 $\pm$ 0.02	29.0 $\pm$ 4.2	46.1 $\pm$ 4.2	2.14 $\pm$ 0.19	47 $\pm$ 5
	L2: Intermediate/morphological	10.8 $\pm$ 1.3	0.017 $\pm$ 0.001	0.11 $\pm$ 0.04	0.20 $\pm$ 0.02	0.85 $\pm$ 0.01	14.4 $\pm$ 1.6	31.5 $\pm$ 2.7	3.20 $\pm$ 0.20	166 $\pm$ 53
	L3: Physiological/morphological	24.1 $\pm$ 4.8	0.036 $\pm$ 0.007	-0.16 $\pm$ 0.05	0.27 $\pm$ 0.03	0.77 $\pm$ 0.02	38.2 $\pm$ 5.4	62.6 $\pm$ 2.6	1.78 $\pm$ 0.17	88 $\pm$ 9
	L4: Morphological	19.5 $\pm$ 2.9	0.020 $\pm$ 0.002	0.03 $\pm$ 0.09	0.33 $\pm$ 0.02	0.87 $\pm$ 0.03	65.4 $\pm$ 8.8	24.6 $\pm$ 4.3	4.17 $\pm$ 0.66	36 $\pm$ 10
	L5 : Physiological/mining	26.5 $\pm$ 5.1	0.038 $\pm$ 0.007	-0.29 $\pm$ 0.05	0.21 $\pm$ 0.02	0.38 $\pm$ 0.03	6.8 $\pm$ 1.4	60.5 $\pm$ 8.8	3.35 $\pm$ 0.23	75 $\pm$ 4
	p value	<.0001	0.0002 ^b	<.0001	<.0001	0.0013 ^b	<.0001	<.0001 ^b	<.0001	0.0053
Calcaric Cambisol	C1 : Morphological	9.6 $\pm$ 2.1	0.011 $\pm$ 0.001	-0.05 $\pm$ 0.01	0.46 $\pm$ 0.02	0.77 $\pm$ 0.02	17.3 $\pm$ 2.4	31.2 $\pm$ 3.9	1.90 $\pm$ 0.22	52 $\pm$ 9
	C2: Morphological/Physiological	17.0 $\pm$ 3.2	0.019 $\pm$ 0.004	-0.22 $\pm$ 0.02	0.29 $\pm$ 0.05	0.72 $\pm$ 0.03	35.4 $\pm$ 3.5	71.4 $\pm$ 7.3	2.16 $\pm$ 0.25	125 $\pm$ 15
	C3: Intermediate	25.0 $\pm$ 7.1	0.010 $\pm$ 0.001	-0.07 $\pm$ 0.01	0.22 $\pm$ 0.02	0.82 $\pm$ 0.01	28.9 $\pm$ 3.9	40.8 $\pm$ 3.9	2.91 $\pm$ 0.22	135 $\pm$ 15
	C4: Physiological	24.8 $\pm$ 13.9	0.022 $\pm$ 0.001	-0.05 $\pm$ 0.03	0.29 $\pm$ 0.05	0.32 $\pm$ 0.02	8.1 $\pm$ 1.1	57.6 $\pm$ 5.1	1.87 $\pm$ 0.34	295 $\pm$ 34
	p value	0.0169	0.0079 ^b	<.0001 ^b	<.0001 ^b	0.0001 ^b	0.0003	0.0002 ^b	0.0161	<.0001

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^b:Kruskall-Wallis test; FR: Fine root percentage (<0.5 mm diameter), Leaf [Mn]: Leaf manganese concentration ($\mu\text{g Mn g}^{-1}$), Leaf [P]: Leaf phosphorus concentration (mg P g^{-1}), PME : Phosphomonoesterase activity ($\mu\text{g nitrophenol g}^{-1} \text{ hour}^{-1}$), RLD: Root length density (cm cm^{-3}), SLA: Specific leaf area ($\text{mm}^2 \text{ mg}^{-1}$), SRL: Specific root length (m g^{-1}), TCE: Total carboxylate release rate ($\mu\text{mol g root}^{-1} \text{ hour}^{-1}$), ΔpH : Change in rhizosheath pH.

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Table 4 Selected models fitted to phosphorus uptake

Soil type	Models	AICc	Δ AICc
Retisol	FR + Leaf [Mn] + PME	-18.8	0.0
	FR + Leaf [Mn]	-17.4	1.4
	FR	-16.5	2.3
	SLA	-14.5	4.3
	PME	-12.5	6.2
	Leaf [Mn]	-8.2	10.6
Calcaric Cambisol	FR + Δ pH + SLA + RSA	-43.4	0.0
	Δ pH + SLA + RSA	-39.5	3.9
	FR + SLA + RSA	-39.5	3.9
	SLA	-35.1	8.4
	RSA	-30.7	12.7
	FR	-25.8	17.6
	Δ pH	-23.4	20.0

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Sorted from best fit to worst. AICc: second order Aikake's information, Δ AICc: Difference between AICc model and lowest AICc observed. FR: Fine root percentage (<0.5

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mm ϕ), Leaf [Mn]: Leaf manganese concentration, PME: Phosphomonoesterase activity, RSA: Root surface area, SLA: Specific leaf area, Δ pH: change in rhizosheath pH

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Table 5 Average trait value $\pm$ standard error and analyses of variance per species and per soil

Soil	Species	FR	Leaf [Mn]	Leaf [P]	PME	RLD	RSA	SLA	SRL	TCE	Δ pH
Retisol	<i>Avena nuda</i>	0.79 $\pm$ 0.02	48 $\pm$ 16	3.58 $\pm$ 0.10	0.020 $\pm$ 0.002	0.14 $\pm$ 0.03	60 $\pm$ 11	32.9 $\pm$ 2.3	10.8 $\pm$ 3.1	24.2 $\pm$ 15.0	0.19 $\pm$ 0.03
	<i>Avena strigosa</i>	0.79 $\pm$ 0.02	144 $\pm$ 31	2.90 $\pm$ 0.17	0.016 $\pm$ 0.001	0.27 $\pm$ 0.09	103 $\pm$ 29	33.0 $\pm$ 2.6	14.7 $\pm$ 1.9	10.4 $\pm$ 2.6	0.01 $\pm$ 0.03
	<i>Brassica carinata</i>	0.83 $\pm$ 0.02	72 $\pm$ 4	2.14 $\pm$ 0.19	0.015 $\pm$ 0.002	0.18 $\pm$ 0.02	70 $\pm$ 9	27.4 $\pm$ 4.9	13.9 $\pm$ 1.4	17.1 $\pm$ 2.4	0.01 $\pm$ 0.05
	<i>Fagopyrum esculentum</i>	0.88 $\pm$ 0.01	456 $\pm$ 121	3.79 $\pm$ 0.50	0.020 $\pm$ 0.001	0.21 $\pm$ 0.04	66 $\pm$ 12	46.3 $\pm$ 5.8	17.2 $\pm$ 7.0	6.8 $\pm$ 2.3	0.10 $\pm$ 0.10
	<i>Lens culinaris</i>	0.78 $\pm$ 0.01	47 $\pm$ 8	2.52 $\pm$ 0.16	0.025 $\pm$ 0.001	0.07 $\pm$ 0.02	38 $\pm$ 11	54.9 $\pm$ 2.8	42.8 $\pm$ 4.5	48.2 $\pm$ 10.1	-0.04 $\pm$ 0.09
	<i>Pisum sativum</i>	0.74 $\pm$ 0.02	45 $\pm$ 10	1.16 $\pm$ 0.07	0.032 $\pm$ 0.005	0.22 $\pm$ 0.07	126 $\pm$ 42	66.2 $\pm$ 3.1	24.9 $\pm$ 7.9	29.5 $\pm$ 12.5	-0.13 $\pm$ 0.03
	<i>Phacelia tanacetifolia</i>	0.87 $\pm$ 0.03	40 $\pm$ 12	4.79 $\pm$ 0.32	0.020 $\pm$ 0.002	0.27 $\pm$ 0.07	96 $\pm$ 29	25.3 $\pm$ 4.0	65.4 $\pm$ 8.9	23.7 $\pm$ 5.0	-0.06 $\pm$ 0.02
	<i>Raphanus sativus</i>	0.68 $\pm$ 0.22	36 $\pm$ 9	3.05 $\pm$ 0.40	0.013 $\pm$ 0.001	0.17 $\pm$ 0.07	66 $\pm$ 15	22.7 $\pm$ 3.6	19.5 $\pm$ 7.5	13.0 $\pm$ 2.4	0.27 $\pm$ 0.04
	<i>Sinapis alba</i>	0.9 $\pm$ 0.020	34 $\pm$ 2	2.04 $\pm$ 0.13	0.018 $\pm$ 0.001	0.11 $\pm$ 0.03	34 $\pm$ 5	32.1 $\pm$ 7.1	17.5 $\pm$ 5.2	25.1 $\pm$ 5.4	-0.08 $\pm$ 0.05
	<i>Trifolium alexandrinum</i>	0.86 $\pm$ 0.02	106 $\pm$ 12	2.13 $\pm$ 0.22	0.027 $\pm$ 0.002	0.23 $\pm$ 0.04	92 $\pm$ 19	59.1 $\pm$ 3.3	48.3 $\pm$ 11.1	22.8 $\pm$ 2.9	-0.29 $\pm$ 0.03
	<i>Vicia faba</i>	0.38 $\pm$ 0.02	75 $\pm$ 4	3.35 $\pm$ 0.23	0.037 $\pm$ 0.005	0.21 $\pm$ 0.01	191 $\pm$ 19	55.2 $\pm$ 8.2	6.5 $\pm$ 1.1	25.2 $\pm$ 3.8	-0.31 $\pm$ 0.04
	<i>Vicia sativa</i>	0.79 $\pm$ 0.01	64 $\pm$ 7	1.82 $\pm$ 0.25	0.053 $\pm$ 0.021	0.12 $\pm$ 0.03	66 $\pm$ 19	54.6 $\pm$ 5.4	34.6 $\pm$ 9.0	33.0 $\pm$ 7.4	-0.04 $\pm$ 0.06
	<i>Vicia villosa</i>	0.72 $\pm$ 0.02	100 $\pm$ 15	1.74 $\pm$ 0.24	0.033 $\pm$ 0.004	0.32 $\pm$ 0.06	183 $\pm$ 45	63.8 $\pm$ 7.3	38.1 $\pm$ 5.3	32.5 $\pm$ 13.9	-0.11 $\pm$ 0.09
	<i>p value</i>	0.0002 ^a	0.0006 ^a	<0.0001	0.0026 ^a	0.0020	<0.0001	0.0004 ^a	<0.0001	0.0126	<0.0001
Calcaric Cambisol	<i>Avena nuda</i>	0.74 $\pm$ 0.02	33 $\pm$ 6	1.63 $\pm$ 0.28	0.013 $\pm$ 0.001	0.47 $\pm$ 0.05	247 $\pm$ 37	29.67 $\pm$ 1.0	9.5 $\pm$ 2.9	7.9 $\pm$ 4.5	-0.03 $\pm$ 0.01
	<i>Avena strigosa</i>	0.82 $\pm$ 0.03	148 $\pm$ 17	2.69 $\pm$ 0.32	0.013 $\pm$ 0.001	0.30 $\pm$ 0.06	127 $\pm$ 35	39.6 $\pm$ 2.1	28.7 $\pm$ 9.3	13.8 $\pm$ 4.6	-0.12 $\pm$ 0.03
	<i>Brassica carinata</i>	0.83 $\pm$ 0.01	92 $\pm$ 31	2.03 $\pm$ 0.18	0.008 $\pm$ 0.001	0.37 $\pm$ 0.03	146 $\pm$ 14	21.8 $\pm$ 3.4	15.4 $\pm$ 1.2	12.0 $\pm$ 2.3	-0.01 $\pm$ 0.01
	<i>Fagopyrum esculentum</i>	0.84 $\pm$ 0.01	67 $\pm$ 3	3.56 $\pm$ 0.27	0.009 $\pm$ 0.001	0.27 $\pm$ 0.09	105 $\pm$ 38	44.4 $\pm$ 8.7	16.1 $\pm$ 3.3	6.2 $\pm$ 1.9	-0.10 $\pm$ 0.01
	<i>Lens culinaris</i>	0.72 $\pm$ 0.01	252 $\pm$ 30	2.91 $\pm$ 0.15	0.013 $\pm$ 0.002	0.22 $\pm$ 0.06	127 $\pm$ 42	58.7 $\pm$ 7.4	34.6 $\pm$ 4.7	23.1 $\pm$ 1.4	-0.09 $\pm$ 0.02
	<i>Pisum sativum</i>	0.66 $\pm$ 0.01	93 $\pm$ 27	0.99 $\pm$ 0.22	0.009 $\pm$ 0.003	0.34 $\pm$ 0.07	223 $\pm$ 46	64.9 $\pm$ 6.2	24.5 $\pm$ 3.1	14.6 $\pm$ 3.8	-0.07 $\pm$ 0.05
	<i>Phacelia tanacetifolia</i>	0.87 $\pm$ 0.01	53 $\pm$ 10	3.71 $\pm$ 0.40	0.012 $\pm$ 0.001	0.19 $\pm$ 0.06	67 $\pm$ 22	18.6 $\pm$ 2.9	53.1 $\pm$ 11.0	78.4 $\pm$ 32.8	-0.03 $\pm$ 0.02
	<i>Raphanus sativus</i>	0.85 $\pm$ 0.02	47 $\pm$ 12	1.99 $\pm$ 0.29	0.012 $\pm$ 0.001	0.44 $\pm$ 0.06	163 $\pm$ 28	17.5 $\pm$ 2.3	27.8 $\pm$ 2.7	9.9 $\pm$ 1.9	-0.07 $\pm$ 0.01
	<i>Sinapis alba</i>	0.86 $\pm$ 0.01	91 $\pm$ 22	1.71 $\pm$ 0.33	0.009 $\pm$ 0.003	0.12 $\pm$ 0.03	44 $\pm$ 9	31.8 $\pm$ 2.8	10.9 $\pm$ 2.1	17.6 $\pm$ 3.3	-0.08 $\pm$ 0.01
	<i>Trifolium alexandrinum</i>	0.84 $\pm$ 0.02	180 $\pm$ 30	4.19 $\pm$ 0.36	0.010 $\pm$ 0.001	0.13 $\pm$ 0.02	57 $\pm$ 11	60.4 $\pm$ 1.8	28.2 $\pm$ 8.8	12.8 $\pm$ 2.1	-0.10 $\pm$ 0.02
	<i>Vicia faba</i>	0.32 $\pm$ 0.02	295 $\pm$ 34	1.87 $\pm$ 0.34	0.022 $\pm$ 0.001	0.29 $\pm$ 0.05	287 $\pm$ 53	57.6 $\pm$ 5.1	8.1 $\pm$ 1.1	24.8 $\pm$ 13.9	-0.05 $\pm$ 0.03
	<i>Vicia sativa</i>	0.67 $\pm$ 0.04	123 $\pm$ 7	2.39 $\pm$ 0.27	0.009 $\pm$ 0.001	0.30 $\pm$ 0.08	198 $\pm$ 57	76.0 $\pm$ 14.3	32.4 $\pm$ 5.7	23.5 $\pm$ 5.0	-0.26 $\pm$ 0.04
	<i>Vicia villosa</i>	0.74 $\pm$ 0.04	141 $\pm$ 27	2.51 $\pm$ 0.23	0.028 $\pm$ 0.008	0.36 $\pm$ 0.08	205 $\pm$ 49	67.2 $\pm$ 10.7	38.8 $\pm$ 4.0	14.0 $\pm$ 3.6	-0.15 $\pm$ 0.02
	<i>p value</i>	<0.0001 ^a	<0.0001	<0.0001	0.0123 ^a	0.0276 ^a	0.0051 ^a	<0.0001	<0.0001	0.0169	0.0012 ^a

^a Kruskal-Wallis test. Analysis performed on log transformed data. FR: Fine root percentage (<0.5 mm diameter), Leaf [Mn]: Leaf manganese concentration ($\mu\text{g Mn g}^{-1}$), Leaf [P]: Leaf phosphorus concentration (mg P g^{-1}), PME : Phosphomonoesterase activity ($\mu\text{g nitrophenol g}^{-1} \text{ hour}^{-1}$), RLD: Root length density (cm cm^{-3}), RSA: Root surface area (cm^2), SLA: Specific leaf area ($\text{mm}^2 \text{ mg}^{-1}$), SRL: Specific root length (m g^{-1}), TCE: Total carboxylate release rate ($\mu\text{mol g root}^{-1} \text{ hour}^{-1}$), ΔpH : Change in rhizosphere pH.

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579 **Fig.1** Principal component analysis (PCA) of functional traits and rhizosphere processes involved in phosphorus acquisition in retisol (a) and Calcaric Cambisol (b)

581 (1) Variable covariation along first two components, (2) clusters formed with Hierarchical Classification on Principal Components (HCPC). Abbreviations: D_pH: change in
582 rhizosphere pH; FR: percentage roots with diameters less than 0.5 mm; Leaf_Mn: foliar manganese concentration; Leaf_P: foliar phosphorus concentration; PME: acid
583 phosphomonoesterase activity; RLD: root length density; RSA: root surface area; SLA: specific leaf area; SRL: specific root area; TCE: total carboxylate release rate.

Fig.2 Partial least square- path models predicting phosphorus uptake

Based on three latent variables, namely root physiology, root morphology and aboveground traits in two soils. Corr is the correlation effect, Rho the Dilon-Golstein coefficient. Variables negatively transformed indicated by -(variable). GoF= Goodness of Fit of the model. ΔpH: change in rhizosheath pH; FR: percentage roots with diameters less than 0.5 mm; Leaf Mn: foliar manganese concentration; PME: acid phosphomonoesterase activity; RLD: root length density; RSA: root surface area; SLA: specific leaf area.