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REVIEW: PART OF A SPECIAL ISSUE ON PLANTS AND CLIMATE CHANGE

The impact of elevated carbon dioxide on the phosphorus nutrition of plants: a review

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• **Background** Increasing attention is being focused on the influence of rapid increases in atmospheric CO_2 concentration on nutrient cycling in ecosystems. An understanding of how elevated CO_2 affects plant utilization and acquisition of phosphorus (P) will be critical for P management to maintain ecosystem sustainability in P-deficient regions.
• **Scope** This review focuses on the impact of elevated CO_2 on plant P demand, utilization in plants and P acquisition from soil. Several knowledge gaps on elevated CO_2-P associations are highlighted.
• **Conclusions** Significant increases in P demand by plants are likely to happen under elevated CO_2 due to the stimulation of photosynthesis, and subsequent growth responses. Elevated CO_2 alters P acquisition through changes in root morphology and increases in rooting depth. Moreover, the quantity and composition of root exudates are likely to change under elevated CO_2, due to the changes in carbon fluxes along the glycolytic pathway and the tricarboxylic acid cycle. As a consequence, these root exudates may lead to P mobilization by the chelation of P from sparingly soluble P complexes, by the alteration of the biochemical environment and by changes to microbial activity in the rhizosphere. Future research on chemical, molecular, microbiological and physiological aspects is needed to improve understanding of how elevated CO_2 might affect the use and acquisition of P by plants.

Key words: Elevated CO_2, climate change, plant nutrition, phosphorous uptake, P transformation, P-use efficiency, root morphology, root exudates, microbial community.

INTRODUCTION

The concentration of CO_2 in the atmosphere continues to rise. It has increased from 270 μL L^{-1} prior to the Industrial Revolution to 384 μL L^{-1} in 2009, and 394 μL L^{-1} in 2013 (Leakey *et al*., 2009; Goufo *et al*., 2014). The rate of change of CO_2 concentration has accelerated with models predicting that the CO_2 concentration will increase to 550 μL L^{-1} by the middle of this century and climb up to 800 μL L^{-1} by the end of this century (Long and Ort, 2010; Feng *et al*., 2014).

Elevated atmospheric CO_2 concentrations can enhance photosynthetic rates in plants. They can therefore act as a carbon 'fertilizer' to induce increases in net ecosystem CO_2 exchange and contribute to increases in net primary productivity (Arnone *et al*., 2000; Kimball *et al*., 2002; Tian *et al*., 2013; Sakurai *et al*., 2014). Thus, elevated CO_2 is likely to stimulate the growth of many plant species (Poorter, 1998; Sakurai *et al*., 2014). However, an increase in the growth of plants will need an increased supply of essential plant nutrients. In fact, limitations in supply of nutrients such as nitrogen (N) may offset the positive effects of elevated CO_2 on photosynthesis, thereby constraining species growth (Drake *et al*., 1997; Ainsworth *et al*., 2003). Decreases in N concentration in the leaf and entire plant have been associated with photosynthetic acclimation (Stitt and Krapp, 1999; Nowak *et al*., 2004; Ainsworth and Long, 2005). The need for extra N supply under elevated CO_2 is indicated by the work of Reich *et al*. (2006) who found that there was a 20–25 % increase in plant biomass by elevated CO_2 with enriched N, in comparison with only 8–12 % with an insufficient N supply. The impact of elevated CO_2 on the N cycle in ecosystems, and on soil N mineralization and immobilization, and organic matter decomposition and turnover have been well studied (Hungate *et al*., 2003; Luo *et al*., 2004; Schneider *et al*., 2004; Wang *et al*., 2013; Xu *et al*., 2013). In comparison, the impact of elevated CO_2 on interactions between soil P supply and plant growth need further interpretation.

Phosphorus is a unique nutrient among the essential plant nutrients with respect to increasing atmospheric CO_2 concentrations, and is the focus of this review. It plays an essential role in plant metabolism as it is involved in conserving and transferring energy in cell metabolism (Raghothama, 1999; Abel *et al*., 2002; Lambers *et al*., 2006), and is an indispensable structural component of nucleic acids, coenzymes, nucleotides, phosphoproteins, phospholiqids and sugar phosphates (Schachtman *et al*., 1998; Veneklaas *et al*., 2012). The growth increases from elevated CO_2 are likely to require more P, which is taken up from the available P pool in soil (Edwards *et al*., 2005; Gentile *et al*., 2012; Jin *et al*., 2012). Several studies have reported that both the magnitude and the direction of the growth response of plants to elevated CO_2 depend on P availability (BassiriRad *et al*., 2001; Jin *et al*., 2013). However, only a small proportion

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of total soil P (generally <1 %) is in the form of labile phosphate ions which are available to plants (Richardson *et al*., 2009). This means that the plant-available P concentrations in soils are small despite the total P in soils being in the range 200–3000 mg P kg^{-1}. This presents challenges to plants in acquiring sufficient P from the soil to meet their needs.

It is not surprising then that some plants have developed special P acquisition strategies to adapt to the small concentrations of available P forms in the soil. The first is the ability of the roots to proliferate, extend and explore the soil. This would include growing root hairs, proteoid roots (some species) and basal roots (Keerthisinghe *et al*., 1998; Hodge, 2004; Ramaekers *et al*., 2010; Haling *et al*., 2013). The second is to develop mycorrhizal associations, where arbuscular mycorrhizal fungi form symbioses with plant roots, with mycorrhizal hyphae increasing the P-absorbing surfaces to increase the spatial availability of P (Facelli *et al*., 2010; Shen *et al*., 2011; Brown *et al*., 2013). The third is to be able to modify the rhizosphere environment to increase P mobilization. This mainly involves proton efflux to acidify the rhizosphere, exudation of carboxylates to mobilize sparingly soluble P via chelation and ligand exchange, and the secretion of phosphatases to mineralize organic P forms in the soil (Po) (Pang *et al*., 2010; Zhang *et al*., 2010; Lynch, 2011; Bayuelo-Jiménez and Ochoa-Cadavid, 2014). For details, readers are referred to recent reviews by Lambers *et al*. (2006) and Richardson *et al*. (2011).

These strategies facilitate the mobilization of P from these non-labile pools, and thereby P availability has been enhanced over a large timescale in weathered soils with the evolution of these strategies (Lambers *et al*., 2008). These evolved strategies induce feedback processes between plants and soils, which are relevant to the photosynthetically fixed C and its allocation (Buendía *et al*., 2014). Increased C fixation and more below-ground investments promote P-enhancing processes in the soil (DeLucia *et al*., 1997; Allen *et al*., 2003).

Thus, an important consideration here is that elevated CO_2 will generally increase the C allocations to roots and the increase in root C will stimulate root growth (Rogers *et al*., 1992, 1994; Li *et al*., 2012) and increase exudate secretions from the roots. This, in turn, will influence conditions in the rhizosphere which is the interface between plant roots and soil (Paterson *et al*., 1997; Haase *et al*., 2008; Drigo *et al*., 2013). The changes in rhizosphere environment are likely to affect P acquisition by plants. Questions therefore arise as to whether plant P demand on the one hand and P acquisition on the other will be affected more by the increase of atmospheric CO_2 concentrations. Understanding this supply–demand balance for labile soil P will be important for developing P management strategies in agricultural systems to cope with increasing atmospheric CO_2 concentrations.

In this review, we examine the current state of knowledge with respect to plant P demand under elevated CO_2 and then focus on the associated mechanisms of P acquisition. This includes changes in root morphology, root exudates and relevant rhizosphere processes that may affect P mobilization and transformations in soils. These possible effects of elevated CO_2 are summarized in Fig. 1, which provides the framework of this review. The need for further research into P functioning in ecosystems in an elevated CO_2 environment is then highlighted.

PLANT P DEMANDS UNDER ELEVATED CO_2

Plant P requirement can be divided into the need for external soil P and the need for internal P within the plant tissues. The external P requirement is the available P in soil that is required to produce 90 % of the maximum plant yield (Sattar *et al*., 2011). Similarly, the internal P requirement is the P concentration in the plant to achieve 90 % of maximum yield (Loneragan and Asher, 1967; Sattar *et al*., 2011). The external and internal P requirements therefore represent the P-acquisition efficiency and P-use efficiency for yield production, respectively (Föhse *et al*., 1988; Veneklaas *et al*., 2012).

The external P requirement is likely to increase with increased plant growth under elevated CO_2 (Table 1). However, the extent of this requirement will depend on the plant species. In general, the growth response to elevated CO_2 is greater in C_3 species than C_4 species, as the CO_2 saturation point in C_3 species (50–150 mg L^{-1} CO_2) is higher than C_4 species (1–10 mg L^{-1} CO_2), and the photosynthetic capability can be greatly enhanced in C_3 species under elevated CO_2 (Wand *et al*., 1999; Lee, 2011). For example, the yield of wheat (C_3) increased by 31 % with elevated CO_2 at 500–700 μL L^{-1} in a Free Air CO_2 Enrichment (FACE) facility (Mauney *et al*., 1994; Amthor, 2001; Jablonski *et al*., 2002), whereas sorghum (C_4) yield was not increased in the same environment (Ottman *et al*., 2001). Within C_3 species, legume species display larger growth responses to elevated CO_2 (600–700 μL L^{-1}) than non-legume species due to the enhanced N_2 fixation (Stöcklin and Körner, 1999; Joel *et al*., 2001; Cernusak *et al*., 2011). Interestingly, a meta-analysis showed that trees had a greater response to elevated CO_2 (475–600 μL L^{-1}) than legumes and C_3 grasses in dry matter production (Ainsworth and Long, 2005). As the plant P demand generally increases along with growth stimulation by elevated CO_2 (Edwards *et al*., 2005; Gentile *et al*., 2012; Zhang *et al*., 2014), this larger growth response by trees than C_3 species and legumes grown under elevated CO_2 suggests that trees would exhibit a higher P demand under elevated CO_2.

The critical levels for the external P requirements have not been established under elevated CO_2. However, several studies with different plant species found that the external P requirements were greater under elevated than under ambient CO_2 (Conroy *et al*., 1990; Barrett and Gifford, 1995; Lewis *et al*., 2010; Jin *et al*., 2012). This can be seen in Table 1 where most species increased P uptake by shoots in response to elevated CO_2 concentrations. This was the case with the growth of cotton wood (*Populus deltoides*) in a sand–gravel root medium with P supplied at six concentrations from 0·004 to 0·5 mM (Lewis *et al*., 2010). A similar situation was reported for chickpea (*Cicer arietinum*) and field pea (*Pisum sativum*) grown in a P-deficient Vertisol with increasing added P from 0 to 16 mg P kg^{-1} soil (Jin *et al*., 2012). In these studies, maximum growth to added P was not achieved. Nevertheless, they showed a similar result that the growth responses to elevated CO_2 (550–700 μL L^{-1}) were more pronounced under P-sufficient than P-deficient conditions.

Elevated CO_2 is likely to affect the internal P requirement of plants because elevated CO_2 alters P utilization within plant tissues (Niu *et al*., 2013*a*). Although the internal P in many species has been investigated under ambient CO_2 environments

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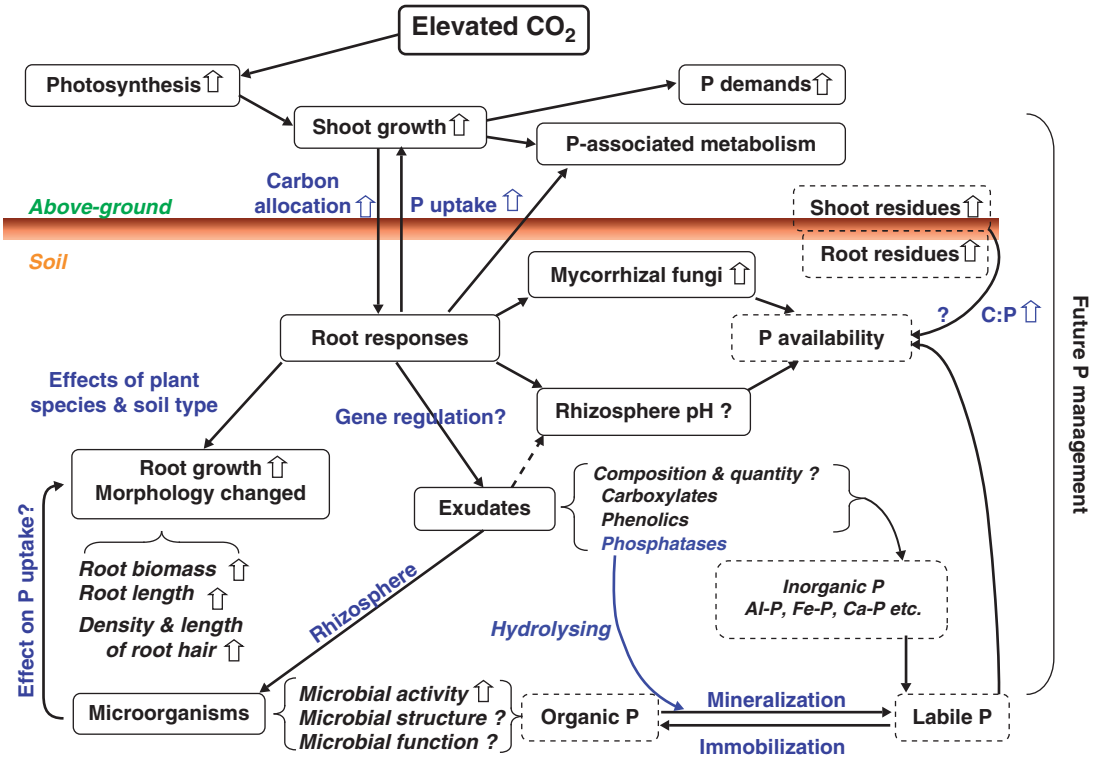

FIG. 1. Proposed mechanisms by which elevated CO_2 impacts plant P nutrition. ⇑ indicates an increase and "?" indicates an unknown effect.

TABLE 1. *Plant P requirement under elevated CO_2*

Plant type	Plant species	Elevated CO_2 (μL L^{-1})	P uptake	Root growth	Reference
Cereal (C_3)	*Oryza sativa*	550	Total P↑ Tissue [P]↑ P-use efficiency↓	–	Yang *et al.* (2007)
Legume (C_3) Legume (C_4)	*Trifolium repens* *Stenotaphrum secundatum*	700	–	Root biomass with P addition↑	Edwards *et al.* (2005)
Legume (C_3)	*Glycine max*	700	P-uptake efficiency↓ Total P↑ Tissue [P]↓	Root d. wt↑	Cure *et al.* (1988), Israel *et al.* (1990)
Legume (C_3)	*Cicer arietinum* *Pisum sativum*	550	Total P↑ Tissue [P]↓	Root d. wt↑ Root length↑	Jin *et al.* (2012)
Cereal (C_3)	*Triticum aestivum*	700	Total P↑ Tissue [P]↓	Root d. wt↑ Root length↑	Jin *et al.* (2013)
Legume	*Medicago sativa*	700		Root d. wt↑ Nodulation↑	Goudriaan and de Ruiter (1983)
Legume	*Vicia faba*	700		Root d. wt↑	Goudriaan and de Ruiter (1983)
Legume	*Lupinus albus*	740 700	P uptake↑	Proteoid roots↑ Onset of cluster rootlets early↑	Campbell and Sage (2002) Watt and Evans (1999)
Wood	*Populus alba* *Populus nigra*	550	–	–	Khan *et al.* (2008)
Wood	*Populus grandidentata* (C_3)	692		Root d. wt↑ Root length↑	Zak *et al.* (1993)
Wood	*Pteridium aquilinum*	539	Tissue [P]		Whitehead *et al.* (1997)
Wood	*Eucalyptus grandis*	660	P contents↑ Leaf [P]↓	Root/shoot↓	Conroy *et al.* (1992)
Grass	*Lolium perenne*	700	–	Root d. wt↑	Goudriaan and de Ruiter (1983)
Grass	*Agrostis capillaris*	700	Shoot [P] P uptake↑	–	Newbery *et al.* (1995)
Grass	*Calluna vulgaris*	539	Tissue [P]		Whitehead *et al.* (1997)

[P], P concentration; ↑, increase; ↓, decrease.

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(e.g. Ankomah and Oseikofi, 1992; Sattar *et al*., 2011), the effects of elevated CO_2 on the internal P requirement remain inconclusive (Table 1). Some studies have found that elevated CO_2 results in a decrease or no change in the P concentration in the shoots of species such as chickpea (Jin *et al*., 2012), wheat (Wolf, 1996; Fangmeier *et al*., 1999), *Hordeum vulgare* (Manderscheid *et al*., 1995), *Eucalyptus grandis* (Conroy *et al*., 1992), *Calluna vulgaris* (Whitehead *et al*., 1997), *Lolium perenne* (Gentile *et al*., 2012) and *Agrostis capillaris* (Newbery *et al*., 1995). In contrast, foliar P concentrations in *Pinus radiata*, *Pinus caribaea* and *Bouteloua eriopoda* increased under 660–700 μL L^{-1} compared with 340–350 μL L^{-1} CO_2 (Conroy *et al*., 1990; BassiriRad *et al*., 1997). However, none of these studies established the internal P requirement under elevated CO_2. Interestingly, Conroy *et al*. (1990) found that the biomass of pine species continued to increase under elevated CO_2 even with a foliar P concentration reaching around 1·5 g kg^{-1} d. wt. In comparison, under ambient CO_2, the biomass did not increase when P concentration exceeded 1·0 g kg^{-1} d. wt.

PLANT P UTILIZATION UNDER ELEVATED CO_2

The two forms in which P exists in plant tissue are the free inorganic orthophosphate form (Pi) and the organic P form (Po). Most of the cellular Pi is stored in the vacuole and acts as a buffer to meet the Pi demands from the cytoplasm (Veneklaas *et al*., 2012). The largest Po pool in plant is the nucleic acid pool, which accounts for 40–60 % of the total Po pool. In this pool, RNA is the dominant component, with ribosomal RNA (rRNA) making up more than 80 % of the total (Kanda *et al*., 1994). The rRNA is required for synthesizing proteins such as the enzyme Rubisco which functions in photosynthesis and so contributes to plant growth (Elser *et al*., 2010; Reef *et al*., 2010).

Elevated CO_2 is likely to affect the transformation of P from inorganic to organic form in plant tissue, thereby mediating P-use efficiency. The increase in photosynthetic rate and plant growth under elevated CO_2 is linked to the concentration of the Rubisco enzyme, because all of the carbon assimilated by autotrophic organisms is metabolized by this enzyme (Ainsworth *et al*., 2003). It is expected that elevated CO_2 increases the Rubisco concentration, and this will require more Pi being transformed into Po for the synthesis of Rubisco because Po is a major component of rRNA involved in the synthesis of the enzyme (Reef *et al*., 2010; Veneklaas *et al*., 2012). Thus, P-use efficiency would increase, as a greater proportion of P in plant tissue is used for photosynthesis-associated metabolisms and assimilation.

Internal redistribution of P within the plant may be altered by elevated CO_2. More than 50 % of P in plants is redistributed to new growing points, especially during later growth stages and under P-deficient conditions (Aerts, 1996). Growth rates decline during the reproductive stage, including root expansion, and so P uptake by root systems decrease. Thus, uptake-dominated P supply is shifted to remobilization-dominated P supply. However, when plants are exposed to elevated CO_2, the growth rate of the shoots increases together with an increase in the carbon allocation to roots, and this generally increases the root-to-shoot C ratio (Ainsworth *et al*., 2003; Jin *et al*., 2012). How these changes affect P redistribution in plants is not known. In addition, the extent of the translocation of P to developing grain is not known. However, it is likely that increasing the grain yield response under elevated CO_2 will result in increased P exports in the grain from the field, given the high content of phytate P in cereal grain (Buddrick *et al*., 2014).

THE EFFECT OF ELEVATED CO_2 ON PLANT STRATEGIES TO ACQUIRE P

Current crop production in P-deficient soils is heavily reliant on the application of P fertilizers. However, more intensive P fertilization is likely to become problematic in the long term, to provide for the increasing P demands of crops under elevated CO_2, because reserves of phosphate ore deposits are finite (Lynch, 2011). There are also concerns about the environmental impact resulting from intensive P fertilization. Thus, it is increasingly important to improve plant P acquisition and P-use efficiency under elevated CO_2.

Elevated CO_2 is likely to affect the P acquisition strategies in several ways. The increase in C assimilation in plants grown under elevated CO_2 is likely to lead to a considerable response in root growth, including changes in root architecture and morphology that will affect P acquisition from soil profiles. Second, the composition and quantity of root exudates are likely to alter under elevated CO_2 and hence these will change rhizosphere properties such as pH, Eh and the capacity for chelation and ligand exchange, which in turn will affect P availability. Third, these root exudates may also modify the association between microorganisms and P transformations. These impacts on P acquisition strategies under elevated CO_2 are addressed in the following sections.

Root morphology traits under elevated CO_2 in relation to P acquisition

As P is an immobile nutrient in soil, increases in root length and root branching under elevated CO_2 may increase the plant's capacity to acquire P from the soil. The effect of a larger root system is shown by the work of Hammond *et al*. (2009). They reported that P uptake in *Oryza sativa* and *Brassica oleracea* genotypes under low P supply was correlated with lateral root growth rate, lateral root length, the number of lateral roots and root surface area. In addition, the root hairs also contributed to P acquisition with direct evidence coming from studies with mutant plants with no root hairs (Bates and Lynch, 2000), and from the comparison of species and genotypes that have contrasting length and density of root hairs (Richardson *et al*., 2011). These changes in root morphology that develop in response to P deficiency are important for P-acquisition efficiency by plants (Lambers *et al*., 2006; Pang *et al*., 2010).

Root morphology will probably change in response to elevated CO_2 and this will alter the P-acquisition efficiency. The increase in photosynthetic C allocation to roots under elevated CO_2 results in stimulation of root growth more than the growth of other plant organs (Norby *et al*., 1992; Benlloch-Gonzalez *et al*., 2014). The elevated CO_2-mediated increase in root growth will bring about increases in root length, root number,

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root diameter and root branching. Yang *et al.* (2007) showed that compared with ambient CO_2 (350 μL L^{-1}), 550 μL L^{-1} increased root biomass by 45 %, root volume by 44 %, number of adventitious roots by 31 % and overall root length by 37 % when rice plants were grown in a Stagnic Anthrosol soil. A greater number of root clusters and a higher percentage of lateral roots were also observed in white lupin (*Lupinus albus*) grown under elevated CO_2 (Watt and Evans, 1999; Campbell and Sage, 2002). Similar trends were found in chickpea, soybean, field pea, wheat, sorghum and cotton (Del Castillo *et al.*, 1989; Rogers *et al.*, 1992, 1994; Jin *et al.*, 2013, 2015). These changes in root morphology result in an increase in the spread of roots through the root zone, which should lead to increases in nutrient uptake (Baker *et al.*, 1990; Idso and Kimball, 1991, 1992; Rogers *et al.*, 1992). A similar result was found by Jin *et al.* (2012), who reported a significant positive relationship between root length and P uptake under both ambient CO_2 and elevated CO_2. The longer roots under elevated CO_2 in that study resulted in greater P acquisition. Thus, it appears that root growth positively responds to elevated CO_2, enabling the roots to explore a larger volume of soil, and this will increase the plant's ability to take up nutrients (Nie *et al.*, 2013), especially immobile phosphate ions.

The response of root morphology to elevated CO_2 and the impact on P acquisition are fundamentally regulated at the genetic level. Ainsworth *et al.* (2006) reported that there were 327 independent genes that were CO_2-responsive when soybean plants were exposed to elevated CO_2, while Raghothama (1999) reported that there were more than 100 genes involved in plant response to P deficiency.

Auxin genes including auxin-responsive promoters (Chandler, 2009) and auxin transport genes (Santelia *et al.*, 2005) are thought to be the most responsive genes to elevated CO_2 and external P status. Auxins are hormonal compounds that regulate plant growth processes, such as the initiation and elongation of root hairs (Pitts *et al.*, 1998; Schiefelbein, 2000). Niu *et al.* (2011) found that elevated CO_2 resulted in the expression of auxin-specific genes, which were likely to enhance the growth of root hairs in *Arabidopsis*. On the other hand, auxin genes that are responsive to P availability are involved in the regulation of the P starvation response in roots (Nacry *et al.*, 2005; Jain *et al.*, 2007). The expression of auxin-responsive genes responds to P deficiency by stimulating pericycle cells to produce lateral roots (López-Bucio *et al.*, 2005). Pérez-Torres *et al.* (2008) further showed that P deficiency increased the expression of the auxin receptor *TRANSPORT INHIBITOR RESPONSE* 1 (*TIR1*), which enhanced the sensitivity of auxins to increase the emergence of lateral roots. Therefore, the expression of these plant genes within a given environment triggers molecular, physiological and cellular processes that modify root architecture (Gilroy and Jones, 2000; Niu *et al.*, 2013*b*). Further investigation of these genetic factors that mediate root development will be required to reveal the molecular mechanisms by which the plant adapts to P deficiency and to elevated CO_2 environments. Specifically, the quantitative relationship between auxins and pericycle cell division leading to the development of new roots, and the elevated CO_2/P supply responsive molecular pathways that regulate the expression of auxin-responsive genes warrant future studies.

Rhizosphere processes in response to elevated CO_2 and their impacts on P availability

The effect of elevated CO_2 on rhizosphere properties is likely to impact on the ability of plants to acquire P from the soil. Elevated CO_2 is likely to increase C flow from plant to soil by increasing the release of root exudates (Lin *et al.*, 2000; Song *et al.*, 2014). These exudates contain functional molecules which facilitate an increase in rhizosphere P solubility, and hence improve P nutrition to plants (Richardson *et al.*, 2009). Furthermore, root exudates are responsible for changes of rhizosphere pH and increases in microbial activity (Shen *et al.*, 2011). These effects of elevated CO_2 can change P availability in the rhizosphere and consequently influence plant P acquisition (Norby *et al.*, 2001; de Graaff *et al.*, 2006).

Root exudates

Exudates released from roots into the rhizosphere can affect the availability of soil P to plants (Randall *et al.*, 2001; Betencourt *et al.*, 2012). Low-molecular-weight carboxylates present in root exudates have been considered to be Pi-mobilizing agents (Johansson *et al.*, 2009). The effectiveness of these carboxylates to mobilize P depends largely on carboxyl (-COOH) and hydroxyl (-OH) functional groups in these molecules. Citrate (tricarboxylic acid, TCA) exhibits the greatest ability to desorb P, followed by oxalate (dicarboxylic acid), while malate, malonate and tartarate are moderately effective (Bolan *et al.*, 1994; Jones, 1998; Jones *et al.*, 2009; Richardson *et al.*, 2009). Citrate is particularly effective at mobilizing P from Fe-phosphates and Al-phosphates in acid soils (Bolan *et al.*, 1994) and Ca-phosphates in calcareous soils, or from rock phosphate fertilizer (Dinkelaker *et al.*, 1989).

The mechanism by which the carboxylates in root exudates affect soil P mobilization under elevated CO_2 is not known. Shen *et al.* (2011) suggested that P is mobilized by desorbing and chelating P from Al–P and Fe–P complexes and from other non-labile pools. However, the extent that elevated CO_2 increases P desorption depends on whether elevated CO_2 stimulates the release of those carboxylates that are effective in mobilizing Pi.

Significant volumes of root exudates have been measured following elevated CO_2 exposure (Cheng and Johnson, 1998; van Ginkel *et al.*, 2000; Allard *et al.*, 2006). For example, after 34 weeks of growth under elevated CO_2, the exudation of soluble C compounds from roots of short-leaf pine increased by 50 % (Norby *et al.*, 1987). Similarly, the release of low-molecular-weight organic compounds increased by 120–160 % and amino acids increased by 250 % when *Pinus sylvestris* was grown for 5 weeks in a nutrient solution under elevated CO_2 (700 μL L^{-1}) in comparison with ambient CO_2 (350 μL L^{-1}) (Johansson *et al.*, 2009). Haase *et al.* (2007) also found that the release of malate, which is the major organic acid in the exudates from *Phaseolus vulgaris*, increased by 177 % after the plants were exposed to elevated CO_2 (800 μL L^{-1}) for 18 d. The increase of these organic compounds is likely to mobilize P in the rhizosphere but to date the mobilization of P in the rhizosphere has not been assessed quantitatively.

There are even fewer studies that have investigated the composition of root exudates in response to elevated CO_2.

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One investigation was carried out by Watt and Evans (1999) to measure the composition of organic acid anions including citrate, oxalate, α-ketoglutarate, malate, succinate, pyruvate and fumarate from white lupins (*Lupinus albus*) grown under elevated CO_2 (700 μL L^{-1}). No significant effect of elevated CO_2 was observed on the composition of these anions during 4 weeks of hydroponic culture. It may be that the release of organic acid anions in response to elevated CO_2 varies with plant species, growth stage and conditions. Further research to screen P-efficient plant species for their efflux of organic acid anions in response to elevated CO_2 is recommended. Such work would improve our understanding of the adaptive mechanism of plant species to P deficiency under elevated CO_2.

How the P-mobilizing carboxylates in root exudates respond to elevated CO_2 needs to be interpreted at the metabolic level. The carboxylates released by roots are thought to be the products from the glycolytic pathway and the TCA cycle, which occur in roots with the involvement of the phosphoenolpyruvate carboxylase (PEPc) enzyme (Johnson *et al*., 1996; Massonneau *et al*., 2001). Malate, for example, is generated from the carboxylation of PEP to produce the glycolytic end-product PEPc (Cramer *et al*., 2005). It has been experimentally shown using ^{14}C labelling that an increase in C supply was accompanied by the increased specific activity of PEPc and exudation of organic acid anions (Johnson *et al*., 1996; Uhde-Stone *et al*., 2003). Interestingly, elevated CO_2 increased the transcription levels of genes encoding enzymes of glycolysis and the TCA cycle. Under elevated CO_2, the TCA cycle accelerated with higher substrate availability (Ainsworth *et al*., 2006). Under P deficiency, PEPc activity was also increased in plants such as chickpea and oilseed rape (Hoffland *et al*., 1992; Moraes and Plaxton, 2000). Thus, the regulation of the synthesis-associated genes for these enzymes is essential for the production of P-mobilizing carboxylates in the glycolytic pathway and TCA cycle under elevated CO_2.

The phenolics are a group of secondary metabolites that mobilize P in soil, and are likely to be influenced by elevated CO_2 as well. A study on the biosynthesis of phenolics showed that the activity of the principal phenolic biosynthetic enzyme in *Senecio vulgaris* increased under elevated CO_2 (Hartley *et al*., 2000). Based on a 2-year field experiment in open-top chambers (375 vs. 550 μL L^{-1}), Goufo *et al*. (2014) reported that the concentration of most phenolic compounds, such as apigenin, sinapicacid, chlorogenic acid, caffeic acid, protocatechuic acid, tricin and apigenin 7-*O*-glucoside, increased significantly in the rhizosphere of mature rice under elevated CO_2. These results indicate that elevated CO_2 enhances the release of phenolics from root systems, and these may in turn increase the P availability in soils. The role of phenolics in mobilizing P has been illustrated in calcareous and acid soils. Hu *et al*. (2005*a*, *b*) showed that phenolics such as caffeic, protocatechuic, *p*-coumaric and vanillic acid exhibit varying capabilities in P mobilization. Their effectiveness depends on the number of phenolic hydroxyl groups that phenolics have and the position of the carboxyl group on the benzoic ring. Furthermore, isoflavonoids are a class of phenolic compounds that are increasingly exuded from white lupin roots under P deficiency. These isoflavonoids include genistein and hydroxygenistein and their corresponding mono- and di-glucoside conjugates (Weisskopf *et al*., 2006). These isoflavonoids are mainly exuded in juvenile and immature cluster roots, and are thought to inhibit the soil microflora from breaking down P-mobilizing citrate in the exudates (Weisskopf *et al*., 2006).

Rhizosphere pH

Soil pH can greatly influence the solubility of P in soils (Shen *et al*., 2011). In acid soils where the concentrations of trivalent Fe and Al are high, labile Pi in soil solution is easily precipitated as Fe- and Al-phosphates or sorbed onto Fe- and Al-(hydr)oxides. In contrast, in alkaline soils where Ca is the major cation, Pi is predominantly precipitated as Ca-phosphates (Richardson *et al*., 2009). Thus, soil pH from 6·0 to 7·0 provides optimal conditions for P solubility (Hinsinger, 2001). Given this relationship between soil pH and P availability, any process that alters soil pH will influence P availability in the soil solution.

There are several ways that elevated CO_2 is able to change P availability by modifying the rhizophere pH. The first is that elevated CO_2 may change the quantity of organic acid anions and associated protons released in exudates from plant roots, leading to pH changes in the rhizosphere (Guo *et al*., 2012). Organic acid anions have often been associated with the release of protons as a source of rhizosphere acidification (Hoffland *et al*., 1989; Hinsinger *et al*., 2003). For example, the release of citrate from cluster roots of white lupin was associated with strong rhizosphere acidification (Neumann and Römheld, 1999), which suggests that H^+ ions released to accompany the efflux of citrate were a major component of the observed acidification of the rhizosphere. As elevated CO_2 is likely to increase the exudation of organic acid anions, the H^+ extrusion accompanying this exudation would lower pH and thereby enhance P mobilization in alkaline soils rather than acidic soils (Lynch, 2011; Bayuelo-Jiménez and Ochoa-Cadavid, 2014).

The second way that elevated CO_2 might impact on rhizosphere pH results from the large amount of CO_2 derived from the respiration of the root and the microbes in the rhizosphere under elevated CO_2. The increased activities of rhizosphere microorganisms (Jin *et al*., 2014) under elevated CO_2 are likely to increase CO_2 concentration in soil (Matamala and Schlesinger, 2000; Carrillo *et al*., 2014) and this CO_2 will dissolve in soil H_2O to form H_2CO_3. As a result, the pH in the rhizosphere is likely to decrease. However, this scenario in terms of rhizospheric pH may be marginal, because gaseous CO_2 diffuses much faster than H_2CO_3 in solution (Anoua *et al*., 1997; Hinsinger *et al*., 2003), and only neutral to alkaline soils can respond to the change in soil CO_2 concentrations because H_2CO_3 with its first *p*K of 6·36 remains undissociated at low pH (Lindsay, 1979).

The third way that elevated CO_2 impacts on rhizosphere pH involves N_2-fixing legumes. When legumes fix N_2, the plants take up more cations than anions and thus extrude H^+ ions from their roots to maintain charge balance (Tang *et al*., 1997). Given that elevated CO_2 stimulates nodulation and N_2-fixation (Prévost *et al*., 2010), legume plants are likely to extrude more H^+ ions and decrease the rhizosphere pH, relative to non-legumes, under elevated CO_2. It would be interesting to determine the pH variation in the rhizosphere of legumes and non-legumes in response to elevated CO_2. Changes in

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rhizosphere pH in response to elevated CO_2 would depend on the balance between the cation–anion exchange across the plasma membranes of the root cells of the plants being compared.

Rhizosphere microorganisms

Elevated CO_2 directly influences the density, diversity and functioning of the rhizosphere microbial communities (Paterson *et al*., 1996; Hodge and Millard, 1998; Haase *et al*., 2008). Drissner *et al*. (2007) found a 48·1 % increase in soil microbial biomass and 12·5 % increase in the Shannon index (species diversity in a community) of bacterial community structure after *Trifolium repens* L. and *Lolium perenne* L. had grown under elevated CO_2 in a FACE facility for 9 years. Similarly, microbial growth rate per unit soil mass in the rhizosphere of *Populus deltoids* was up to 58 % higher under elevated CO_2 than under ambient CO_2 (Blagodatskaya *et al*., 2010). In addition, microbial respiration and the metabolic quotient of microbes in the rhizosphere of wheat increased significantly under elevated CO_2 (Jin *et al*., 2014).

Elevated CO_2 is able to specifically affect the abundance of some microbial genera, which may directly facilitate P solubilization in the rhizosphere. Drigo *et al*. (2009) found that the abundance of *Pseudomonas* bacteria in the rhizosphere increased under elevated CO_2, with active populations of *P. aeruginosa*, *P. fluorescens*, *P. trivialis* and *P. putida* being detected. Both *P. fluorescens* and *P. putida* are considered to be P-solubilizing microorganisms that produce metabolites that solubilize sparingly soluble inorganic P compounds to release phosphate ions (Egamberdiyeva and Höflich, 2003; Krey *et al*., 2013). Similarly, P-solubilizing bacteria associated with proteoid roots of *Telopea speciosissima* are able to release P from calcium phosphate (Wenzel *et al*., 1994). This suggests that elevated CO_2 is likely to benefit these P-solubilizing microorganisms. However, the magnitude of this effect depends on the P compounds in soils, and the plant species, which in turn will determine the abundance of the P-solubilizing microbial species in their rhizospheres (Wenzel *et al*., 1994).

Arbuscular mycorrhizal fungi (AMF) are likely to be stimulated by elevated CO_2, which will assist P acquisition by the host plant. In this symbiotic relationship, AMF provide their host plants with mineral nutrients, such as P, in exchange for carbohydrates supplied to the AMF (Kiers *et al*., 2011). This two-way transfer of resources is certainly affected by elevated CO_2, because elevated CO_2 increases C allocation to the roots of the host plant (Gamper *et al*., 2004). Studies have found that the AMF hyphal network is enlarged by elevated CO_2, resulting in nutrient absorption being significantly increased (Gamper *et al*., 2004; Staddon *et al*., 2004). With a meta-analysis, Treseder (2004) also found that the abundance of AMF increased relative to root length under elevated CO_2. Furthermore, shifts in active AMF species under elevated CO_2 were convincingly confirmed using stable isotope (^{13}C) probing and subsequent real-time PCR techniques (Drigo *et al*., 2010). The increase in symbiotic activity between AMF and plants under elevated CO_2 leads to an expectation that mycorrhizal plant species will adapt better to P-deficient soils compared with non-mycorrhizal species in the elevated CO_2 environment.

On the other hand, it cannot be ignored that elevated CO_2-induced increases in the microbial biomass and activity will mean that these microbes may compete for more P, resulting in P immobilization. The P immobilized by microbes is not negligible, because soil microorganisms constitute a small but significant component of total soil P, typically accounting for around 2–10 % (Achat *et al*., 2010; Richardson and Simpson, 2011). A recent study found that microbial P in the rhizosphere increased by more than 20 % when wheat plants were grown under elevated CO_2, indicating microbes were the main source of P immobilization occurring under elevated CO_2 (Jin *et al*., 2014). The microbial C/P ratio did not change under elevated CO_2 in that study, indicating the increase of microbial P was attributed to the change of microbial biomass C, rather than any change in P composition in microorganisms. This indicates the importance of microbial populations in enhanced P immobilization in the rhizosphere.

Rhizosphere enzymes

The change in rhizosphere enzyme activity in response to elevated CO_2 is likely to affect P mineralization in the rhizosphere. The activities of many enzymes were stimulated by root proliferation under elevated CO_2 (Haase *et al*., 2008) including invertase (48 %), xylanase (23 %), urease (24 %), protease (40 %) and alkaline phosphomonoesterase (54 %) (Drissner *et al*., 2007). Most of these enzymes are involved in nutrient transformation and include phosphatases, which are enzymes that catalyse the transformation of Po to Pi. A study at a tundra site showed that phosphatase activity on the root surface of *Eriophorum vaginatum* was 254 % higher under elevated CO_2 than under ambient CO_2, and this contributed to a more than 40 % increase in the annual P release within tussocks (Moorhead and Linkins, 1997). On the other hand, elevated CO_2 did not alter either the acid phosphatase or the alkaline phosphatase activity in the rhizosphere of chickpea or field pea grown in a P-deficient Vertisol (Jin *et al*., 2012). Furthermore, Haase *et al*. (2008) found that the activity of phosphatases in the rhizosphere of *Phaseolus vulgaris* L. decreased under elevated CO_2. The discrepancy between the studies may be explained by differences in organic matter content of the soils. The P availability in soils with high organic matter (>117 g C kg^{-1} soil) in the arctic tundra ecosystem is likely to depend on phosphatase activity (Moorhead and Linkins, 1997), while the content of organic matter in the soils used in the latter studies were less than 1 g C kg^{-1} soil.

Understanding the mechanisms by which elevated CO_2 affects phosphatase enzymes remains a challenge. Phosphatase enzymes are either of plant or microbial origin. A wide range of plant species secrete phosphatases into their rhizosphere. These plant species include sorghum (*Sorghum bicolor*), cowpea (*Vigna unguiculata*) and mung bean (*Vigna radiata*) (Tarafdar and Claassen, 2001; Lambers *et al*., 2006). Similarly, soil microorganisms such as *Aspergillus* sp. and mycorrhizas produce phosphatases (Tarafdar, 1995). In this respect, the question is raised as to how elevated CO_2 affects (1) the population of phosphatase-producing microbes in the rhizosphere and (2) the activity of phosphatases exuded from the roots of plant species, and (3) what each of these contributes to P

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mineralization. However, it is necessary to quantitatively identify the origin of phosphatases before investigating the elevated CO_2 effect on them.

More recently, the link between phosphatase activity and photosynthate supply has been established. Spohn and Kuzyakov (2013) developed an approach to studying the distribution of phosphatases and photosynthetic C supply using ^{14}C imaging and soil zymography, which provides *in situ* mapping of the two-dimensional distribution of enzyme activity in soil. This approach allows us to understand the relationship between elevated CO_2-driven changes in the allocation of below-ground photosynthates and the spatial distribution of phosphatase activity. The ^{14}C labelling and zymography are achievable under elevated CO_2.

P TRANSFORMATION BETWEEN P POOLS IN THE RHIZOSPHERE UNDER ELEVATED CO_2

Phosphorus transformations in the rhizosphere are continuously occurring, resulting in changes in the P availability to plants (Cross and Schlesinger, 1995). A study on cereals and legumes showed that both Pi and Po fractions ($NaHCO_3$- and NaOH-extractable) were depleted in the rhizosphere and the depletion decreased gradually with distance from the roots (Nuruzzaman *et al*., 2006). This depletion in available P in turn can be replenished by mineralization of Po and dissolution from non-labile Pi pools (Vu *et al*., 2008).

The P fractions in the rhizosphere have been reported to be altered by elevated CO_2. Following 5 years of exposure to elevated CO_2 in a FACE experiment, Khan *et al*. (2008) demonstrated that the NaOH- and HCl-extractable P increased in the rhizosphere, rather than becoming depleted. With chickpea and wheat grown under elevated CO_2 for 6 weeks, Jin *et al*. (2013) found that elevated CO_2 significantly increased $NaHCO_3$- and NaOH-extractable Po in the rhizosphere. This indicated that P immobilization had occurred in the rhizosphere under elevated CO_2.

On a much larger timescale than spans decades or centuries, the mobilization rate of P from soil minerals is likely to increase with increases in atmospheric CO_2 concentration. This view is based on the proposition that the enhancement of P mobilization depends on vegetation processes (Gifford *et al*., 1992, 1996). The vegetation is likely to evolve and develop P-acquisition strategies that enable plants to grow and compete in impoverished low-P soils such as ancient soils in Australia and south-western Africa (Lambers *et al*., 2008). Increased C supply to the roots under elevated CO_2 will be assisting these strategies, and gradually alter them at the genetic level in the plant.

The mechanisms for potential P transformations under elevated CO_2 are thought to be related to the increased below-ground C allocation. The increased input of photosynthates to the roots is likely to stimulate root exudation of organic compounds, which would help to mobilize P from sparingly soluble inorganic P sources (Paterson *et al*., 1997; Wasaki *et al*., 2005). Furthermore, these compounds could putatively affect microbial activities and functions (Richardson, 2001; Richardson *et al*., 2009, 2011), and may accelerate the priming effect, or the turnover of organic matter in the rhizosphere. As a consequence, Po mineralization is likely to be increased. On the other hand, the stimulation of microbial activities may increase microbial demand for P and result in P immobilization. A ^{13}C-labelling study elucidated that the increased photosynthetic C input in the rhizosphere under elevated CO_2 led to a larger amount of P being immobilized by soil microbes (Jin *et al*., 2014). Whether mobilization or depletion of P in the rhizosphere occurs in response to elevated CO_2 depends on the dominant P fluxes that occur at the time.

Appropriate methodologies are available to investigate the biochemical reactions that become dominant in P transformations. Radioisotopes ^{32}P or ^{33}P have been used to investigate the P dynamics in soil (McLaughlin *et al*., 1988; Daroub *et al*., 2000; Vu *et al*., 2010; Noack *et al*., 2014). Studies reported that up to 25 % of added ^{33}P in soil was recovered in soil microorganisms (Oberson *et al*., 2001), and 20–27 % of added ^{33}P in Po fractions (Bühler *et al*., 2003; Bünemann *et al*., 2004), highlighting the importance of biological transformation of P in soil. In addition, a new precipitation approach using ^{31}P nuclear magnetic resonance (NMR) imaging is able to characterize Po molecules in soils (Vestergren *et al*., 2012). The approach would be useful in understanding the P fluxes that occur in the rhizosphere in response to elevated CO_2.

THE IMPACT OF ELEVATED CO_2 ON P MINERALIZATION OF PLANT RESIDUES

The change in quality of plant residues under elevated CO_2 is likely to influence the P cycling in ecosystems. A fundamental change of quality in residues produced in the elevated CO_2 environment will be the reduction in N concentration in the residues, particularly of non-legumes (Butterly *et al*., 2015). Cotrufo *et al*. (2005) provided experimental data showing that N concentrations in plant tissues generated under elevated CO_2 declined by an average of 14 %. Thus, with the increased C/N ratio, the decomposition rate of plant residue may be limited by the lower N concentrations, and lowered further in N-deficient soils (Viswanath *et al*., 2010). Similarly, the increase in C/P ratio may occur under elevated CO_2, as elevated CO_2 leads to a decrease of P concentration in some species such as *Glycine max*, *Eucalyptus grandis* and *Agrostis capillaris* (Conroy *et al*., 1992; Newbery *et al*., 1995; Gifford *et al*., 2000). As a consequence, the high C/P may further inhibit the decomposition process of plant residues, combined with N limitation. The slow decomposition will mean that the residues returned to soil over a longer time scale result in a reduced rate of P transformation from organic to inorganic forms, which will lower the P supply to plants over time. Whether this scenario occurs in the future depends on how P-acquisition strategies evolve on the ability of plant regulating root exudates, altering microbial functions, and thereby favouring P mineralization.

Identifying the magnitude of the P supply from decomposing residues is a challenge. It has been reported that about 40–60 % of P in residues is water-soluble and can be mineralized into soils at initial stages of decomposition (Ha *et al*., 2008). However, if plant residues with a C/P ratio of more than 300 are added to soils, then a net immobilization of P is likely to occur (Iyamuremye *et al*., 1996; Ha *et al*., 2008). Under elevated CO_2, it is not certain whether the water-soluble P composition varies in residues, and whether the increased C/P ratio exceeds

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the threshold. These will be associated with their C chemistry, which determines the form of P incorporated in residues. In addition, the N/P ratio in residues is a significant factor which will determine whether mineralization or immobilization of P will occur when the residue is incorporated into soil (Kwabiah *et al*., 2003). This raises the question of which nutrient (N or P) becomes the dominant factor limiting P supply during the decomposition of residues in the elevated CO_2 environment. This question will require answers from long-term investigations.

FUTURE PERSPECTIVES

Phosphorus nutrition in plants growing in the terrestrial domain is likely to undergo considerable change under elevated CO_2. Although there is limited information on the difference in the impact of elevated CO_2 on P nutrition between agricultural and natural ecosystems, it is likely that differences between these systems will occur. The P acquisition of plants originated from P fertilizer would change considerably in the agricultural ecosystem, while the internal and external P utilization would tend to be intensively improved in the natural ecosystem.

It is likely that increases in P fertilization rates will be required in agricultural systems with increases in the concentrations of atmospheric CO_2. More P would be needed to meet the increased demand for P by crop plants resulting from the 'CO_2 fertilization effect' on crop growth. The required increase in P fertilizer rates will depend on the balance between extra P demand by crop species under elevated CO_2, and the increased capacity of roots to mobilize soil P and to forage for the labile P in soil. Nevertheless, for crop plants in general, the evidence suggests that increased P fertilization will be required to improve the adaptability of cropping systems to increasing atmospheric CO_2 concentrations. This is a concern as the need for more P fertilizer inputs raises questions about long-term sustainability and food security, and environmental impact. Supplies of P rock for manufacturing P fertilizer are finite and we have learnt how the loss of P from agricultural systems can impact negatively on terrestrial water bodies.

Plants in natural systems will continue to adapt to changing environmental conditions. Plants have adapted to low-P soils by developing P acquisition strategies, and this will continue. There will be increasing selection pressure for P-acquisition efficiency, by plants and plant–microbe associations in the high-C environment. They will utilize and exploit the increased C flow to their roots to more efficiently mobilize and/or forage for labile P forms in the soil. The mechanisms for this selection might include the development of longer roots, more lateral roots and root hairs, changes in the quantity and composition of root exudates, and changes in the activities and/or functions of microbes and plant–microbe associations. These adaptation strategies will enable plants to compete for P in the elevated CO_2 environment.

Optimizing P management for crop plants in the future requires a more detailed understanding of plant–soil interactions in response to elevated CO_2 (see Fig. 1). This includes understanding the biochemical processes as to how elevated CO_2 mediates C allocation to root development, root metabolism and the release of root exudates in the rhizosphere. Improved understanding is also needed on how these processes affect microorganisms in the rhizosphere, because these microorganisms can impact significantly on P availability.

A range of experimental approaches are suggested for further research. The first is to undertake geno-to-pheno investigations from the CO_2-induced gene expression in the plants and how this expression influences root architecture formation and root exudate metabolism, as both will affect P acquisition. A second approach would be to use photosynthetic ^{13}C tracing studies to identify soil microbial communities that are responding to elevated CO_2 and are involved in either immobilization or mineralization of P in the rhizosphere. A third approach would be to identify P-containing molecules in the rhizosphere using NMR to determine the quantity and the composition of these molecules during the P transformations under elevated CO_2. These studies need to be undertaken with different plant species in different soils.

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