

## **The impact of elevated carbon dioxide on the phosphorus nutrition of plants — a review**

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### **Abstract**

**Background** Attention is now focusing on the influence of rapid increases in atmospheric CO<sub>2</sub> concentration on nutrient cycling in ecosystems. An understanding how elevated CO<sub>2</sub> affects plant utilization and acquisition of phosphorus (P) will be critical for P management in order to maintain ecosystem sustainability in P-deficient regions.

**Scope** This review focuses on the impact of elevated CO<sub>2</sub> on plant P demand, utilization in plants and P acquisition from soil. A number of knowledge gaps on elevated CO<sub>2</sub>-P associations are highlighted.

**Conclusions** Significant increases in P demand by plants are likely to happen under elevated CO<sub>2</sub> due to the stimulation of photosynthesis, and subsequent growth responses to elevated CO<sub>2</sub>. Elevated CO<sub>2</sub> alters P acquisition through changes of root morphology and increases in rooting depth. Moreover, the quantity and composition of root exudates are likely to change under elevated CO<sub>2</sub>, 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<sub>2</sub> might affect the use and acquisition of P by plants.

**Key words:** elevated CO<sub>2</sub>, P transformation, P-use efficiency, root morphology, root exudates, microbial community

**Abbreviations:** FACE, free air CO<sub>2</sub> enrichment; LMWCs, Low-molecular-weight carboxylates; N, nitrogen; NMR, nuclear magnetic resonance; PEPc, phosphoenolpyruvate carboxylase; Pi, inorganic P; Po, organic P; TCA, tricarboxylic acid cycle.

### **INTRODUCTION**

The concentration of CO<sub>2</sub> in the atmosphere continues to increase. It has increased from 270 μL L<sup>-1</sup> prior to the Industrial Revolution to 384 μL L<sup>-1</sup> in 2009, and 394 μL L<sup>-1</sup> in 2013 (Leakey *et al.*, 2009; Goufo *et al.*, 2014). The rate of change of CO<sub>2</sub> concentration has accelerated with models predicting that the CO<sub>2</sub> concentration will increase to 550 μL L<sup>-1</sup> by the middle of this century and climb up to 800 μL L<sup>-1</sup> by the end of this century (Long and Ort, 2010; Feng *et al.*, 2014).

Elevated atmospheric CO<sub>2</sub> concentrations can enhance photosynthetic rates in plants. They can therefore act as a carbon “fertilizer” to induce increases in net ecosystem CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> with enriched N, in comparison to only 8–12% with at insufficient N supply. The impact of elevated CO<sub>2</sub> 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<sub>2</sub> on interactions between soil P supply and plant growth need further interpretation.

Now P is a unique nutrient among the essential plant nutrients with respect to increasing atmospheric CO<sub>2</sub> concentrations, and is the focus of this review. Phosphorus 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; Jin *et al.*, 2006; Lambers *et al.*, 2006), and is an indispensable structural component of nucleic acids, coenzymes, nucleotides, phosphoproteins, phospholipids and sugar phosphates (Schachtman *et al.*, 1998; Veneklaas *et al.*, 2012). The growth increases from elevated CO<sub>2</sub> 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). A number of studies have reported that both the magnitude and the direction of the growth response of plants to elevated CO<sub>2</sub> depend on the availability of P (BassiriRad *et al.*, 2001; Jin *et al.*, 2011). However, only a small proportion of total soil P (generally < 1%) is in the form of labile phosphate ions which are available to plants (Richardson *et al.*, 2009a). This means that the plant-available P concentrations in soils are small despite the total P in soils being in the range of 200–3000 mg P kg<sup>-1</sup>. This presents challenges to plants in acquiring sufficient P from the soil to meet their needs.

It is not surprising then that 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 symbiotic associations 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, carboxylate exudation 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, 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> concentrations.

In this review, we will examine the current state of knowledge with respect to plant P demand under elevated CO<sub>2</sub> and then focus on the associated mechanisms of P acquisition. These will include changes in root morphology, root exudates and relevant rhizosphere processes that may affect P mobilization and transformations in soils. The need for further research into P functioning in ecosystems in an elevated CO<sub>2</sub> environment will then be highlighted.

## PLANT P DEMANDS UNDER ELEVATED CO<sub>2</sub>

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 eCO<sub>2</sub> (Table 1). However, the extent of this requirement will depend on the plant species. In general, the growth response to elevated CO<sub>2</sub> is greater in C<sub>3</sub> species than C<sub>4</sub> species, since the CO<sub>2</sub> saturation point in C<sub>3</sub> species (50–150 mg L<sup>-1</sup> CO<sub>2</sub>) is higher than C<sub>4</sub> species (1–10 mg L<sup>-1</sup> CO<sub>2</sub>), and the photosynthetic capability can be greatly enhanced in C<sub>3</sub> species under elevated CO<sub>2</sub> (Wand *et al.*, 1999; Lee 2011). For example, the yield of wheat (C<sub>3</sub>) increased by 31% with elevated CO<sub>2</sub> at 500–700 µL L<sup>-1</sup> in a Free Air CO<sub>2</sub> Enrichment (FACE) facility (Mauney *et al.*, 1994; Amthor, 2001; Jablonski *et al.*, 2002), whereas sorghum (C<sub>4</sub>) yield was not increased in the same environment (Ottman *et al.*, 2001). Within C<sub>3</sub> species, legume species display larger growth responses to elevated CO<sub>2</sub> (600–700 µL L<sup>-1</sup>) than non-legume species due to the enhanced N<sub>2</sub> 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<sub>2</sub> (475–600 µL L<sup>-1</sup>) than legumes and C<sub>3</sub> grasses in dry matter production (Ainsworth and Long, 2005). Since the plant P demand generally increases along with growth stimulated by elevated CO<sub>2</sub> (Edwards *et al.*, 2005; Gentile *et al.*, 2012; Zhang *et al.*, 2014), this larger growth response by trees than C<sub>3</sub> species and legumes grown under elevated CO<sub>2</sub> suggests that trees would exhibit a higher P demand under elevated CO<sub>2</sub>.

The critical levels for the external P requirements have not been established under elevated CO<sub>2</sub>. However, a number of studies with different plant species found that the external P requirements were greater under elevated CO<sub>2</sub> than under ambient CO<sub>2</sub> (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<sub>2</sub> concentrations. This was the cases 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* L.) and field pea (*Pisum sativum* L.) grown in a P-deficient Vertisol with increasing added P from 0 to 16 mg P kg<sup>-1</sup> 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<sub>2</sub> (550 to 700 µL L<sup>-1</sup>) were more pronounced under P-sufficient than P-deficient conditions.

Elevated CO<sub>2</sub> is likely to affect the internal P requirement of plants because elevated CO<sub>2</sub> alters P utilization within plant tissues (Niu *et al.*, 2013a). Although the internal P in many species have been investigated under ambient CO<sub>2</sub> environments (e.g. Ankomah and Oseikofi, 1992; Reuter and Robionson, 1997; Sattar *et al.*, 2011), the effects of elevated CO<sub>2</sub> on the internal P requirement remain inconclusive. Some studies have found that elevated CO<sub>2</sub> 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.*, 2011) and *Agrostis capillaries* (Newbery *et al.*, 1995). In contrast, foliar P concentrations in *Pinus radiata*, *Pinus caribaea* and *Bouteloua eriopoda* increased under 660–700 µL L<sup>-1</sup> compared to 340–350 µL L<sup>-1</sup> (Conroy *et al.*, 1990; BassiriRad *et al.*, 1997) (Table 1). However, none of these studies established the internal P requirement under elevated CO<sub>2</sub>. Interestingly, Conroy *et al.* (1990) found that the biomass of pine species continued to increase under elevated CO<sub>2</sub> even with a foliar P concentration reaching around 1.5 g kg<sup>-1</sup> dry weight. In comparison, under ambient CO<sub>2</sub>, the biomass did not increase when P concentration exceeded 1.0 g kg<sup>-1</sup> dry weight.

## PLANT P UTILIZATION UNDER ELEVATED CO<sub>2</sub>

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 this pool (Kanda *et al.*, 1994). The rRNA is required for synthesizing proteins like the enzyme Rubisco which functions in photosynthesis and so contributes to plant growth (Elser *et al.*, 2010; Reef *et al.*, 2010).

Elevated CO<sub>2</sub> is likely to affect the transformation of P from inorganic to organic form in plant tissue, thereby mediating the P-use efficiency. The increase in photosynthetic rate and plant growth under elevated CO<sub>2</sub> 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<sub>2</sub> 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, the P-use efficiency would increase, as 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<sub>2</sub>. 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). The growth rates decline during the reproductive stage, including root expansion and so P uptake by root systems decrease. Thus, there is a shift from uptake-dominated P supply to remobilization-dominated P supply. However, when plants are exposed to elevated CO<sub>2</sub>, both 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.*, 2011). How these changes affect P redistribution in plant 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>, 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<sub>2</sub>.

Elevated CO<sub>2</sub> is likely to affect the P acquisition strategies in a number of ways (Figure 1). The increase in C assimilation in plants grown under elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> are addressed in the following sections.

### *Root morphology traits under elevated CO<sub>2</sub> in relation to P acquisition*

As P is an immobile nutrient in soil, then increases in root length and root branching under elevated CO<sub>2</sub> 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 (Hammond *et al.*, 2009) was correlated with root surface area, lateral root length, lateral root growth rate and the number of lateral roots. 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).

It is likely that there will be changes in root morphology in response to elevated CO<sub>2</sub> and that these will alter the P-acquisition efficiency. The increase in photosynthetic C allocation to roots under elevated CO<sub>2</sub> results in root growth being stimulated more than the growth of other plant organs (Norby *et al.*, 1992; Benlloch-Gonzalez *et al.*, 2014). The elevated CO<sub>2</sub>-mediated increase in root growth will bring about increases in root length, root number, root diameter and root branching. Yang *et al.* (2007) showed that compared to ambient CO<sub>2</sub> (350 μL L<sup>-1</sup>), 550 μL L<sup>-1</sup> increased root biomass by 45%, root volume by 44% and 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* L.) grown under elevated CO<sub>2</sub> (Watt and Evans, 1999; Campbell and Sage, 2002). Similar trends were found in chickpea, soybean, wheat, sorghum and cotton (Del Castillo *et al.*, 1989; Rogers *et al.*, 1992, 1994; Jin *et al.*, 2012, 2013). 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 occurred in the study by Jin *et al.* (2011) who reported a significant positive relationship between root length and P uptake under both ambient CO<sub>2</sub> and elevated CO<sub>2</sub>. The longer roots under elevated CO<sub>2</sub> in that study resulted in greater P acquisition. Thus it appears that root growth positively responds to elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>-responsive when soybean plants were exposed to elevated CO<sub>2</sub>

while Raghothama (1999) reported that there were more than 100 genes were involved in plant response to low-P stress.

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<sub>2</sub> 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<sub>2</sub> 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.*, 2013b). Further investigation of these genetic factors that mediate the root development will be required to reveal the molecular mechanisms whereby the plant adapts to P deficiency and to elevated CO<sub>2</sub> environments. Specifically, the quantitative relationship between auxins and pericycle cell division leading to the development of new roots, and the elevated CO<sub>2</sub>/P supply responsive molecular pathways that regulate the expression of auxin-responsive genes warrant future studies.

#### *Rhizosphere processes in response to elevated CO<sub>2</sub> and their impact on P availability*

The effect of elevated CO<sub>2</sub> on rhizosphere properties is likely to impact on the ability of plants to acquire P from the soil. Elevated CO<sub>2</sub> is likely to increase the 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<sub>2</sub> 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 (LMWCs) present in root exudates have been considered to be Pi-mobilizing agents (Johansson *et al.*, 2009). The effectiveness of these carboxylates to mobilize P largely depends on carboxyl (-COOH) and hydroxyl (-OH) functional groups in these molecules. Citrate (tricarboxylic acid) exhibits the greatest ability to desorb P, followed by oxalate (dicarboxylic acid), with malate, malonate and tartarate being moderately effective (Bolan *et al.*, 1994; Jones, 1998; Jones *et al.*, 2009; Richardson *et al.*, 2009). Citrate is particularly effective at mobilizing P from Al-P and Fe-P complexes in acid soils (Bolan *et al.*, 1994), and Ca-P 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<sub>2</sub> is not known. It is proposed by Shen *et al.* (2011) that P is mobilized by desorbing and chelating P from Al- and Fe-P complexes and from other non-labile pools. However, the extent that elevated CO<sub>2</sub> increases P desorption depends on whether elevated CO<sub>2</sub> stimulates the release of those carboxylates that are effective in mobilizing inorganic P (Pi).

Significant volumes of root exudates have been measured following elevated CO<sub>2</sub> exposure (Cheng and Johnson, 1998; van Ginkel *et al.*, 2000; Allard *et al.*, 2006). For example, after 34 weeks of growth under elevated CO<sub>2</sub>, the exudation of soluble C compounds from roots of short-leaf pine increased by 50% (Norby *et al.*, 1987). Similarly, the exudation of low-molecular-weight organic compounds increased by 120–160% and amino acids increased by 250% when *Pinus sylvestris* L. was grown for 5 weeks in a nutrient solution under elevated CO<sub>2</sub> (700 μL L<sup>-1</sup>) in comparison to ambient CO<sub>2</sub> (350 μL L<sup>-1</sup>) (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* L., increased by 177% after the plants were exposed to elevated CO<sub>2</sub> (800 μL L<sup>-1</sup>) for 18 days. The increase of these organic compounds is likely to mobilize P in the rhizosphere but to date the mobilisation of P in the rhizosphere has not been quantitatively assessed.

There are even fewer studies that have investigated the composition of root exudates in response to elevated CO<sub>2</sub>. 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* L.) grown under elevated CO<sub>2</sub> (700 μL L<sup>-1</sup>). They did not find any significant effect of elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> is recommended. Such work would improve our understanding on the adaptive mechanism of plant species to P deficiency under elevated CO<sub>2</sub>.

How the P-mobilizing carboxylates in root exudates respond to elevated CO<sub>2</sub> need to be interpreted at the metabolic level. The carboxylates released by roots are thought to be the products from the glycolytic pathway and the tricarboxylic acid cycle (TCA), that 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 glycolytic end-product PEPc (Cramer *et al.*, 2005). It has been experimentally shown using <sup>14</sup>C labeling that an increase in C supply was accompanied by the enhanced specific activity of PEPc and exudation of organic acid anions (Johnson *et al.*, 1996; Uhde-Stone *et al.*, 2003). Interestingly, elevated CO<sub>2</sub> increased the transcription levels of genes encoding enzymes of glycolysis and the TCA cycle. Under elevated CO<sub>2</sub>, 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 under elevated CO<sub>2</sub>.

The phenolics are a group of secondary metabolites that mobilize P in soil, and are likely to be influenced by elevated CO<sub>2</sub> as well. A study on the biosynthesis of phenolics showed that the activity of the principle phenolic biosynthetic enzyme in *Senecio vulgaris* increased under elevated CO<sub>2</sub> (Hartley *et al.*, 2000). Based on a two-year field experiment in open-top chambers (375 vs. 550 μL L<sup>-1</sup>), Goufo *et al.* (2014) reported that the concentration of most phenolic compounds, such as apigenin, sinapic acid, chlorogenic acid, caffeic acid, protocatechuic acid, tricetin, and apigenin 7-O-glucoside increased significantly in the rhizosphere of mature rice under elevated CO<sub>2</sub>. These results indicate that elevated CO<sub>2</sub> 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.* (2005a, 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 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). The exudation of these isoflavonoids mainly occur 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 inorganic P (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.*, 2009b). 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, then any process that alters soil pH will influence P availability in the soil solution.

There are a number of ways that elevated CO<sub>2</sub> is able to change P availability by modifying the rhizosphere pH. The first is that elevated CO<sub>2</sub> 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 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<sup>+</sup> ions released to accompany the efflux of citrate were a major component of the observed acidification of the rhizosphere. As elevated CO<sub>2</sub> is likely to increase the exudation of organic acid anions, the H<sup>+</sup> 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<sub>2</sub> might impact on rhizosphere pH results from the large amount of CO<sub>2</sub> derived from the respiration of the root and the microbes in the rhizosphere under elevated CO<sub>2</sub>. The increased activities of rhizosphere microorganisms (Jin *et al.*, 2014) under elevated CO<sub>2</sub> are likely to increase CO<sub>2</sub> concentration in soil (Matamala and Schlesinger, 2000; Carrillo *et al.*, 2014) and this CO<sub>2</sub> will dissolve in soil H<sub>2</sub>O to form H<sub>2</sub>CO<sub>3</sub>. As a result, the pH in the rhizosphere is likely to decrease. However, this scenario in term of rhizospheric pH may be marginal, because gaseous CO<sub>2</sub> diffuses much faster than H<sub>2</sub>CO<sub>3</sub> in solution (Anoua *et al.*, 1997), and only neutral to alkaline soils can respond to the change in soil CO<sub>2</sub> concentrations because H<sub>2</sub>CO<sub>3</sub> with its first *pK* of 6.36 remains undissociated at acidic pH values (Lindsay, 1979).

The third way that elevated CO<sub>2</sub> impacts on rhizosphere pH involves N<sub>2</sub>-fixing legumes. When legumes fix N<sub>2</sub>, the plants take up more cations than anions and thus extrude H<sup>+</sup> ions from their roots to maintain charge balance (Tang *et al.*, 1997). Given that elevated CO<sub>2</sub> stimulates nodulation and N<sub>2</sub>-fixation (Prévost *et al.*, 2010), then legume plants are likely to extrude more H<sup>+</sup> ions and decrease the rhizosphere pH, relative to non-legumes, under elevated CO<sub>2</sub>. It would be interesting to determine the pH variation in the rhizosphere of legumes and non-legumes in response to elevated CO<sub>2</sub>. Changes in rhizosphere pH in response to elevated CO<sub>2</sub> 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<sub>2</sub> 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 that soil microbial biomass increased by 48.1% and the Shannon index (species

diversity in a community) of bacterial community structure increased by 12.5% after *Trifolium repens* L. and *Lolium perenne* L. had grown under elevated CO<sub>2</sub> 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<sub>2</sub> than under ambient CO<sub>2</sub> (Blagodatskaya *et al.*, 2010). In addition, microbial respiration and the metabolic quotient of microbes in the rhizosphere of wheat increased significantly under elevated CO<sub>2</sub> (Jin *et al.*, 2014).

Elevated CO<sub>2</sub> is able to specifically affect the abundance of some microbial genera, which may directly facilitate P solubilisation in the rhizosphere. In one study, Drigo *et al.* (2009) found that the abundance of *Pseudomonas* bacteria in the rhizosphere increased under elevated CO<sub>2</sub>, with active populations of *P. fluorescens*, *P. aeruginosa*, *P. trivialis* and *P. putida* being detected. Both *P. fluorescens* and *P. putida* are considered to be P-solubilizing microorganisms that produce metabolites that release phosphate ions from sparingly soluble inorganic P-bearing compounds (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<sub>2</sub> 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<sub>2</sub>, which will assist P acquisition by the host plant. In this symbiotic relationship, AMF provides 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<sub>2</sub>, because elevated CO<sub>2</sub> 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<sub>2</sub>, resulting in nutrient absorption being significantly increased (Gamper *et al.*, 2004; Staddon *et al.*, 2004). With a meta-analysis, Treseder (2004) also found that mycorrhizal fungal abundance increased relative to root length under elevated CO<sub>2</sub>. Furthermore, shifts in active AMF species under elevated CO<sub>2</sub> conditions were convincingly confirmed using stable isotope (<sup>13</sup>C) probing and subsequent real-time PCR techniques (Drigo *et al.*, 2010). The increase in symbiotic activity between AMF and plants under elevated CO<sub>2</sub> leads to an expectation that mycorrhizal plant species will adapt better to P-deficient soils compared to non-mycorrhizal species in the elevated CO<sub>2</sub> environment.

On the other hand, it cannot be ignored that elevated CO<sub>2</sub>-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% to 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<sub>2</sub>, indicating microbes were the main source of P immobilization occurring under elevated CO<sub>2</sub> (Jin *et al.*, 2014). The microbial C/P ratio did not change under elevated CO<sub>2</sub> 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<sub>2</sub> is likely to affect P mineralization in the rhizosphere. The activities of many enzymes were stimulated by root proliferation under elevated CO<sub>2</sub> (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<sub>2</sub> compared to ambient CO<sub>2</sub>, 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<sub>2</sub> did not alter either the acid 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<sub>2</sub>. 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<sup>-1</sup> soil) in the arctic tundra ecosystem is likely to depend on phosphatase activity (Moorhead and Linkins, 1997), while the content of organic matter the soils used in the latter studies were less than 1 g C kg<sup>-1</sup> soil.

Understanding the mechanisms by which elevated CO<sub>2</sub> affects phosphatase enzymes still 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 like *Aspergillus* sp. and mycorrhizas produce phosphatases (Tarafdar, 1995). In this respect, the question is raised as to how elevated CO<sub>2</sub> affects (i) the population of phosphatase-producing microbes in the rhizosphere, (ii) the activity of phosphatases exuded from the roots of plant species and (iii) what each of these contributes to P mineralization. However, it is necessary to quantitatively identify the origin of phosphatases before investigating the elevated CO<sub>2</sub> 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 <sup>14</sup>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<sub>2</sub>-driven changes in the allocation of below-ground photosynthates and the spatial distribution of phosphatase activity. The <sup>14</sup>C labeling and zymography are achievable under elevated CO<sub>2</sub>.

## **P TRANSFORMATION BETWEEN P POOLS IN THE RHIZOSPHERE UNDER ELEVATED CO<sub>2</sub>**

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<sub>3</sub>- 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<sub>2</sub>. Following 5 years of exposure to elevated CO<sub>2</sub> 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<sub>2</sub> for 6 weeks, Jin *et al.* (2013) found that elevated CO<sub>2</sub> significantly increased NaHCO<sub>3</sub>- and NaOH-extractable Po in the rhizosphere. This indicated that P immobilization had occurred in the rhizosphere under elevated CO<sub>2</sub>.

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<sub>2</sub> concentration. This view is based

on the proposition that the enhancement of P mobilization will depend 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 southwestern Africa (Lambers *et al.*, 2008). Increased C supply to the roots under elevated CO<sub>2</sub> 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<sub>2</sub> are thought to be related to the increased C allocation to underground. 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.*, 2009a, 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 <sup>13</sup>C-labeling study elucidated that the increased photosynthetic C input in the rhizosphere under elevated CO<sub>2</sub> 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<sub>2</sub> 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 <sup>32</sup>P or <sup>33</sup>P has 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 as much as 25% of added <sup>33</sup>P in soil was recovered in soil microorganisms (Oberson *et al.*, 2001), and 20–27% of added <sup>33</sup>P in Po fractions (Bühler *et al.*, 2003; Bünemann *et al.*, 2004), highlighting the importance of biological transformation P in soil. In addition, a new precipitation approach using <sup>31</sup>P NMR (nuclear magnetic resonance) is able to characterize Po molecules in soils (Vestergren *et al.*, 2012). The approach would be useful in understanding these P fluxes that occur in the rhizosphere in response to elevated CO<sub>2</sub>.

## **THE IMPACT OF ELEVATED CO<sub>2</sub> ON P MINERALIZATION OF PLANT RESIDUES**

The change in quality of plant residues under elevated CO<sub>2</sub> is likely to influence the P cycling in ecosystems. A fundamental change of quality in residues produced in the elevated CO<sub>2</sub> environment will be the reduction in N concentration in the residues, particularly of non-legumes (Butterly *et al.* 2015). Cotrofo *et al.* (2005) provide experimental data showing that N concentrations in plant tissues generated under elevated CO<sub>2</sub> declined by an average of 14% based on existing data. 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 the N-deficient soils (Viswanath *et al.*, 2010). Similarly, the increase in C:P ratio may occur under elevated CO<sub>2</sub>, since elevated CO<sub>2</sub> leads to decrease of P concentration in some species such as *Glycine max*, *Eucalyptus grandis* and *Agrostis capillaries* (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 capability of plant regulating root exudates, altering microbial functions, and thereby favoring the 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 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<sub>2</sub>, it is not certain whether the water-soluble P composition varies in residues, and whether the increased C:P ratio exceeds 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 a question as to which nutrient (N or P) becomes the dominant factor limiting P supply during the decomposition of residues in the elevated CO<sub>2</sub> environment. This question will require answers from long-term investigations.

## FUTURE PERSPECTIVES

Phosphorus nutrition in the plants growing in the terrestrial domain is likely to undergo considerable change under elevated CO<sub>2</sub>. Although there is limited information on the difference in the impact of elevated CO<sub>2</sub> on P nutrition between agricultural and natural ecosystems, it is likely that differences between these systems will occur. The P acquisition of plant originated from P fertilizer would considerably change 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<sub>2</sub>. More P would be needed to meet the increased demand for P by crop plants resulting from the 'CO<sub>2</sub> fertilisation effect' on crop growth. The required increase in P fertilizer rates will depend on the balance between extra P demand by crop species under eCO<sub>2</sub>, 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<sub>2</sub> concentrations. This is a concern as the need for more P fertilizer inputs raises 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 in the future. 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 mobilise 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<sub>2</sub> environment.

Optimizing P management for crop plants in the future requires a more detailed understanding of plant-soil interactions in response to elevated CO<sub>2</sub> (Figure 1). This includes understanding the biochemical processes as to how elevated CO<sub>2</sub> 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<sub>2</sub>-induced gene expression in the plants and how this expression influences root architecture formation and the root-exudate metabolism, as both will affect P acquisition. A second approach would be to use photosynthetic <sup>13</sup>C tracing studies to

identify soil microbial communities that are responding to elevated CO<sub>2</sub> 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<sub>2</sub>. These studies need to be undertaken with different plant species in different soils.

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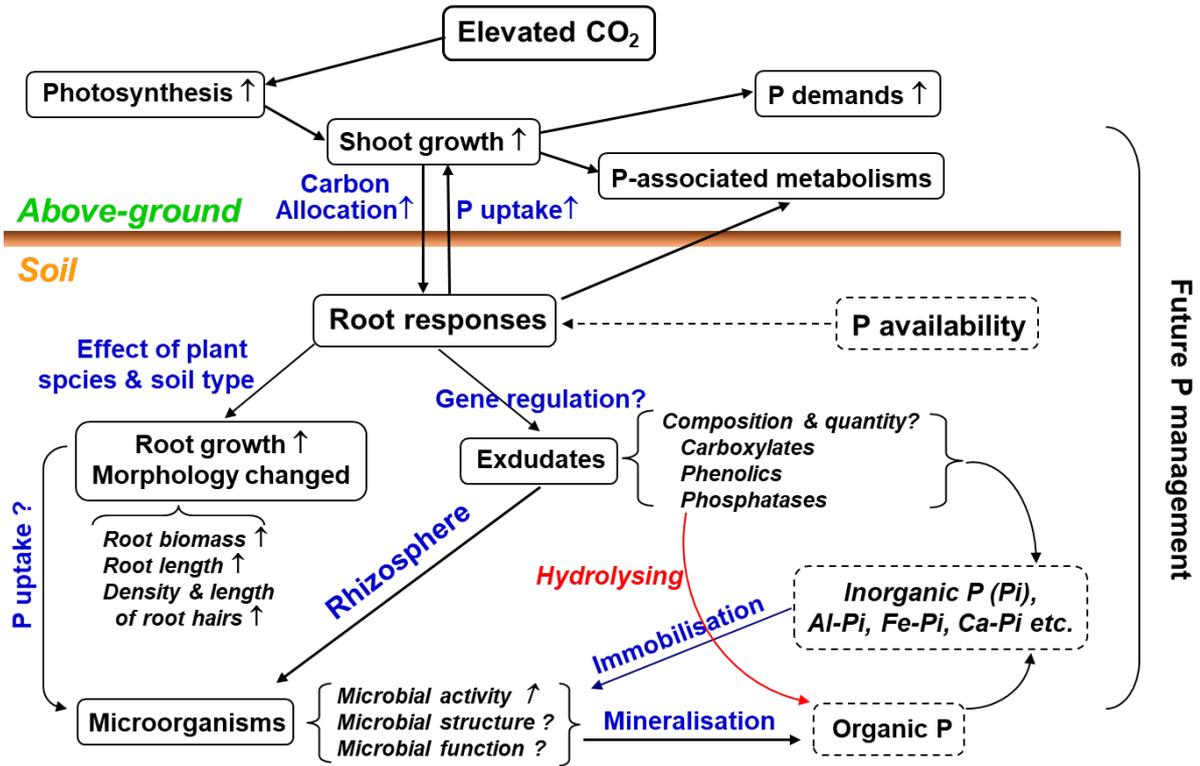


FIG. 1. Proposed mechanisms by which elevated CO<sub>2</sub> impacts plant P nutrition.

**Table 1.** Plant P requirement under elevated CO<sub>2</sub>

Plant gena	Plant species	elevated CO <sub>2</sub> ppm	P uptake	Root growth	References
Cereal (C3)	<i>Oryza sativa</i>	550	Total P↑ Tissue [P] ↑ P-use efficiency↑	-	Yang <i>et al.</i> (2007)
Legume (C3)	<i>Trifolium repens</i>	700	-	Root biomass with P addition ↑	Edwards <i>et al.</i> (2005)
Legume (C4)	<i>Stenotaphrum secundatum</i>			Root dry weight↑	Cure <i>et al.</i> (1988)
Legume (C3)	<i>Glycine max</i>	700	P-uptake efficiency↑ Total P↑ Tissue [P]↓		Israel <i>et al.</i> (1990)
Legume (C3)	<i>Cicer arietinum</i>	550	Total P↑ Tissue [P]↓	Root dry weight↑ Root length↑	Jin <i>et al.</i> (2012)
	<i>Pisum sativum</i>		Tissue [P]↓		
Cereal (C3)	<i>Triticum aestivum</i>	700	Total P↑ Tissue [P]↓	Root dry weight↑ Root length↑	Jin <i>et al.</i> (2013)
Legume	<i>Medicago sativa</i>	700		Root dry weight↑ Nodulation ↑	Goudriaan and de Ruiter (1983)
Legume	<i>Vicia faba</i>	700		Root dry weight↑	Goudriaan and de Ruiter (1983)
Legume	<i>Lupinus albus</i> L.	410 and 740	P uptake↑	Proteoid roots↑	Campbell and Sage (2002)
		700	-	Onset of cluster rootlets early↑	Watt and Evans (1999)
Wood	<i>Populus alba</i> L.	550	-	-	Khan <i>et al.</i> (2008)
	<i>Populus nigra</i> L.				
Wood	<i>Populus grandidentata</i> (C3)	692		Root dry weight↑ Root length↑	Zak <i>et al.</i> (1992)
Wood	<i>Pteridium aquilinum</i>	539	Tissue [P]↑		Whitehead <i>et al.</i> (1997)
Wood	<i>Eucalyptus grandis</i>	660	P contents↑ Leaf [P] ↓	Root/shoot↓	Conroy <i>et al.</i> (1992)
Grass	<i>Lolium perenne</i>	700	-	Root dry weight↑	Goudriaan and de Ruiter (1983)
Grass	<i>Agrostis capillaris</i>	700	Shoot [P] ↑ P uptake↑	-	Newbery <i>et al.</i> (1995)
Grass	<i>Calluna vulgaris</i>	539	Tissue [P] ↑		Whitehead <i>et al.</i> (1997)

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