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Physiological and molecular alterations in plants exposed to high [CO_2] under phosphorus stress

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Abstract

Atmospheric [CO_2] has increased substantially in recent decades and will continue to do so, whereas the availability of phosphorus (P) is limited and unlikely to increase in the future. P is a non-renewable resource, and it is essential to every form of life. P is a key plant nutrient controlling the responsiveness of photosynthesis to [CO_2]. Increases in [CO_2] typically results in increased biomass through stimulation of net photosynthesis, and hence enhance the demand for P uptake. However, most soils contain low concentrations of available P. Therefore, low P is one of the major growth-limiting factors for plants in many agricultural and natural ecosystems. The adaptive responses of plants to [CO_2] and P availability encompass alterations at morphological, physiological, biochemical and molecular levels. In general low P reduces growth, whereas high [CO_2] enhances it particularly in C_3 plants. Photosynthetic capacity is often enhanced under high [CO_2] with sufficient P supply through modulation of enzyme activities involved in carbon fixation such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). However, high [CO_2] with low P availability results in enhanced dry matter partitioning toward roots. Alterations in below-ground processes including root morphology, exudation and mycorrhizal association are influenced by [CO_2] and P availability. Under high P availability, elevated [CO_2] improves the uptake of P from soil. In contrast, under low P availability, high [CO_2] mainly improves the efficiency with which plants produce biomass per unit P. At molecular level, the spatio-temporal regulation of genes involved in plant adaptation to low P and high [CO_2] has been studied individually in various plant species. Genome-wide expression profiling of high [CO_2] grown plants revealed hormonal regulation of biomass accumulation through complex transcriptional networks. Similarly, differential transcriptional regulatory networks are involved in P-limitation responses in plants. Analysis of expression patterns of some typical P-limitation induced genes under high [CO_2] suggests that long-term exposure of

plants to high [CO_2] would have a tendency to stimulate similar transcriptional responses as observed under P-limitation. However, studies on the combined effect of high [CO_2] and low P on gene expression are scarce. Such studies would provide insights into the development of P efficient crops in the context of anticipated increases in atmospheric [CO_2].

Key words: Elevated CO_2, Growth, Mycorrhiza, Phosphorus limitation, Photosynthesis, Root morphology, Root exudation, Transcriptional regulation

Abbreviations: AM, arbuscular mycorrhiza; A_{max}, maximum rate of photosynthesis; APase, acid phosphatase; [CO_2], carbon dioxide concentration; EMH, external mycorrhizal hyphal density; FACE, free air CO_2 enrichment; OTC, open top chambers; P, phosphorus; Pi, inorganic phosphate; PEPCase, phosphoenol pyruvate carboxylase; *rbc*S, Rubisco small subunit; RuBP, ribulose 1,5-bisphosphate; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase

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Introduction

Atmospheric concentrations of carbon dioxide [CO_2] have increased dramatically from approximately 280 ppm in pre-industrial times to 400 ppm (IPCC, 2013), and will continue to rise due to burning of fossil fuels and changing land-use patterns. It is projected that by the middle of this century, [CO_2] would surpass 550 ppm (Meehl et al., 2006). Many experiments have been carried out to study the responses of plants to high [CO_2] at various levels ranging from the ecosystem to the genome (e.g. Ainsworth and Long 2005; Luo et al., 2006; Teng et al., 2006; Niu et al., 2011; Dieleman et al., 2012; AbdElgawad et al., 2014; Zinta et al., 2014). Such studies revealed that elevated [CO_2] increases plant growth and crop yield by the stimulation of carboxylation and suppression of oxygenation activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) particularly in C3 plants, whereas the effects are marginal in C4 plants because Rubisco is already saturated at ambient [CO_2] (reviewed by Bowes 1991; Ghannoum et al., 2003; Feng et al., 2014). However, over longer periods of exposure to high [CO_2], the growth responses of plants depend on water and nutrient availability (Ceulemans and Mousseau 1994; Oren et al., 2001; Li et al., 2007; Norby et al., 2010). The acquisition of mineral nutrients by roots and root symbionts depends primarily on the carbohydrate status of the plant as a whole. The process of root initiation, growth and maintenance and nutrient uptake require a supply of fixed carbon. It is estimated that 10 to 50% of assimilated carbon is respired by the roots, with greater fractions being respired during nutrient shortage (Werf and Nagel, 1996). Vicca et al. (2012) estimated that nutrient-limited forests allocate 20% more of their annual photosynthates to root symbionts than fertile forests possibly favouring the efficient acquisition and uptake of nutrients. Other studies have shown that plant growth rates under sub-optimal nutrient supply are usually enhanced by high [CO_2] during early growth stages (Pal et al., 2005; Pandey et al., 2015), but these enhanced growth rates cannot be sustained

in the long-term unless sufficient nutrients are provided (Drake et al., 1997; Kirschbaum, 2011). Consequently, nutrient availability is clearly a key determinant of plant responses to high [CO_2], yet many issues remain unresolved.

Among mineral nutrients, P is expected to become limited in both natural and agricultural ecosystems (Peñuelas et al., 2013; Obersteiner et al., 2013). P directly controls the responsiveness of photosynthesis to [CO_2], plays a vital role in the formation of high energy bonds and membrane phospholipids, and is an integral component of several metabolic reactions and signal transduction pathways (Duff et al., 1989). Availability of soil P to plants is often limited due to its strong bonding in insoluble forms. In response to persistent P deficiency, many plants develop potential adaptive mechanisms at morphological, physiological, biochemical and molecular levels to overcome P deficiency (reviewed by Lopez-Arredondo et al., 2014). Such adaptive mechanisms include changes in root architecture (Bates and Lynch, 2000), enhanced secretion of organic acids (Singh and Pandey, 2003; Pandey et al., 2013), and increased activity of acid phosphatases (Qiu et al., 2014), ribonucleases (RNase) (Duff et al., 1994), inorganic phosphate (Pi) transporters and phosphoenolpyruvate carboxylases (PEPCase) (Raghothama, 1999). This complex network of mechanisms enhances P uptake in plants under P-limitation. Besides, elevated [CO_2] has been reported to enhance P uptake in plants (Cure et al., 1998; Niu et al., 2013; Pandey et al., 2015). Because the carbon status of plants determines their potential investment in P acquisition, and P status influences plant photosynthesis and growth rate, a multitude of interactions exist between the cycles of these elements. Studying these interactions is important as, globally, plants are increasingly exposed to high [CO_2] and, in many areas, also to decreasing P availability (Peñuelas et al., 2013). In this review, an overview of the interactive effects of high [CO_2] and P is presented at physiological, biochemical and molecular levels.

1. P limitation effects on plants

Phosphorus is an essential macronutrient often limiting plant growth (Peñuelas et al., 2013). In Africa, imbalanced P nutrition has been found to already limit the food production by 10%, with further reductions up to 40% projected by the end of this century in response to the declining soil P stocks (Velde et al., 2014). Reduced photosynthesis is a likely mechanism that may contribute to the reduced growth and yields under P limitation. Reductions in photosynthetic efficiency under P stress have been reported in various crops such as barley and spinach (Foyer and Spencer, 1986), soybean (Lauer et al., 1989), maize (Usuda, 1995), wheat (Rodríguez et al., 1998), pigeon pea (Fujita et al., 2004) and rice (Wissuwa et al., 2005).

During metabolic reactions, large amounts of phosphate (Pi) are regenerated and re-translocated to the stroma within the chloroplast as demonstrated in Fig. 1 A. This maintains Pi homeostasis during carbon fixation via Calvin cycle, as one molecule of Pi is required for every three molecules of CO_2 fixed in the form of triose phosphate (Stitt and Quick, 1989). Several enzymes of 'bypass' reactions are up-regulated under severe P limitation (Palma et al., 2000). These P limitation-induced 'bypass' reactions help in maintaining glycolytic flux and vacuolar pH when the cytosolic levels of adenylates and Pi are very low. These reactions conserve ATP and recycle Pi, and help plants to survive under P stress by circumventing ATP-limited reactions. Lower cytosolic Pi concentration also negatively affects the Calvin cycle, either by altering the levels of phosphorylated intermediates (Duff et al., 1989) or by modulating the activity of enzymes involved in photosynthesis (Theodorou et al., 1992; Theodorou and Plaxton, 1996; Palma et al., 2000).

Leaf Pi concentration affects biomass production through altering photosynthetic rates (Fig. 1 B). However, contrasting views exist on the impact of altered photosynthetic efficiency on biomass accumulation under P deficiency. Low biomass accumulation under P

stress may be due to either reduced photosynthesis (source limitation) (Wissuwa et al., 2005) or accumulation of assimilates that cannot be utilized for growth (sink limitation) (Fredeen et al., 1989). Plénet et al. (2000) confirmed that the growth reduction in maize under P deficiency occurred before the decline in photosynthesis, suggesting that low P availability has a direct effect on growth through sink limitation. Other experimental evidence also suggests that leaf growth of P-deficient plants was not limited by carbohydrate supply to growing tissues (Fredeen et al., 1989; Rodríguez et al., 2000). However, source limitation of growth may not only occur through reduced photosynthesis; plant growth may also be reduced under low P availability because of increased assimilate as well as energy investment in P acquisition systems, thereby imposing a source limitation on plant growth. For example, increased production and exudation of organic acids and increased carbon allocation to mycorrhizal symbionts are well-known plant responses to P limitation (Neumann and Romheld, 1999; Pandey et al., 2005a; Pearse et al., 2006; Pandey et al., 2013; Pandey et al., 2014) that may reduce plant growth even at constant photosynthesis (as summarised in Fig. 1 B).

Limited P supply not only leads to shifts in metabolism and physiology, but it also induces morphological changes in plants. For instance, limited P supply inhibits leaf growth which consequently results in overall plant growth reduction (Fredeen et al., 1989; Jeschke et al., 1996; Nielsen et al., 1998; Rodríguez et al., 1998; Mollier and Pellerin 1999; Chiera et al., 2002). These reductions are the consequence of lower rates of leaf initiation, less dividing cells, as well as reduced leaf expansion (Rodríguez et al., 1998; Rodríguez et al., 2000; Plénet et al., 2000; Chiera et al., 2002; Assuero et al., 2004) (Fig. 1 B). Secondary responses to P stress include change in the hydraulic conductivity of roots, and the resulting lower water potential may be a major reason for the reduced cell expansion in leaves (Radin and Eidenbock, 1984). Other possible reasons for the P limitation-induced growth inhibition could be lower cytokinin contents or decreased cell wall elasticity (Ei-D et al., 1979;

Horgan and Wareing, 1980). These results indicate that P play a key role in the regulation of morphogenetic and leaf expansion processes.

Finally, one of the prominent effects of P limitation is that it favours root growth more than shoot growth. Increasing root-shoot ratio and enhancing the total root surface area favours thorough soil exploration and subsequent P capture. The organic and insoluble P forms present in the soil is converted to soluble by phosphatase enzyme or organic acids respectively exuded into the rhizosphere which is then taken up by Pi transporters (Fig. 2 A). Modification of root system architecture under P limitation, as presented in Fig. 2 C, further enhances soil P uptake, for example, by increased growth of lateral roots and by stimulating secondary root branching at the expense of primary roots (Chevalier et al., 2003; Reymond et al., 2006; Péret et al., 2011). Also the development of 'proteoid' roots, special structures in certain plant families that release large amounts of organic acids, has been attributed to P-deficiency (Adams et al., 2002). Another adaptive strategy in response to P deficiency is increased root hair length and density, which increases total root surface area at minimal carbon cost to improve P uptake (Ma et al., 2001; Lynch and Brown, 2001; Gahoonia and Nielsen, 2003; Gahoonia and Nielsen, 2004). In comparison to the structural adaptations listed above, an even more carbon-efficient strategy to acquire higher amounts of P is to promote mycorrhizal symbioses (Pandey et al., 2005a). The role of mycorrhizae and plant growth promoting rhizobacteria in improving crop productivity under P limitation was reviewed by Nadeem et al. (2014) (Fig. 2 B).

2. High [CO_2] effects on plants

Increases in [CO_2] influence the overall growth, especially of C3 plants, mainly for two reasons. First, the present atmospheric [CO_2] is not enough to saturate the primary carboxylation sites in Rubisco during photosynthesis, while high [CO_2] increases the

velocity of carboxylation. Secondly, [CO_2] competitively inhibits oxygenase reactions, thereby suppressing photorespiration (Laing et al., 1974; Jordan and Ogren, 1981). Consistently, leaf photosynthetic rates were increased under elevated [CO_2] in various C3 and C4 species, however, lesser stimulation was observed in C4 plants (Ainsworth and Rogers, 2007). This little benefit of high [CO_2] in the photosynthesis of C4 plants could be inferred by the fact that C4 plants have less Rubisco protein relative to C3 plants (Wong 1979; Schmitt and Edwards 1981; Ghannoum et al., 1997), and their photosynthesis is almost saturated under current atmospheric [CO_2]. Similarly different functional groups respond differentially to high [CO_2]. For instance, herbaceous dicots shows higher photosynthetic rate (31%) than monocots (12%) (Poorter and Navas, 2003). The influence of high [CO_2] on other enzymes such as ADP-Glucose pyrophosphorylase, sucrose phosphate synthase, rubisco activase and PEPCase, in regulating carbon assimilation has also been studied. Increased activities of these enzymes resulted in higher levels of non-structural carbohydrates including glucose, sucrose, fructose and starch (Makino and Mae, 1999; Davey et al., 2006; Fukayama et al., 2009; Ribeiro et al., 2012; AbdElgawad et al., 2014). The availability of additional photosynthates facilitates plants to grow faster under high [CO_2]. The increased rate of leaf expansion results in higher leaf area, leaf area ratio, relative growth rate and specific leaf area (Uprety et al., 2002; Pandey et al., 2009).

Faster growth necessitates increased uptake rates of water and nutrients explaining why elevated [CO_2] typically stimulates below-ground growth. Increases in root biomass, volume, surface area, fine and extra fine roots and mycorrhizal colonization have been reported in several plant species at high [CO_2] (Ceulemans et al., 1999; Pandey et al., 2009; Reddy et al., 2010). Meta-analysis on mycorrhizal dynamics under nutrient fertilization showed increase in mycorrhizal abundance by 47% under high [CO_2] (Treseder, 2004). A general perception is that high [CO_2] would elicit a shift in carbon allocation in favour of below-ground organs and processes (reviewed by Madhu and Hatfield, 2013), thereby

increasing the root-to-shoot ratio (Ceulemans and Mousseau, 1994; Rogers et al., 1996; Pritchard et al., 1999; Rogers et al., 1999). However, some studies reported decreased root-to-shoot ratio (Salsman et al.,1999; McMaster et al., 1999) in response to high [CO_2] while others did not observe any significant effect (Mo et al., 1992; Ferris and Taylor, 1993; Chaudhuri et al.,1990; Obrist and Arnone, 2003).

Increase in carbon allocation to below-ground growth would also enhance exudation of carbon-containing compounds in the rhizosphere. At molecular level, high [CO_2] enhances the expression of genes encoding enzymes of tricarboxylic acid (TCA) cycle (Ainsworth et al., 2006), which may result in higher exudation rates of organic acids (Johnson et al., 1996). The root-to-shoot partitioning of carbon is hormonally regulated with abscisic acid (Salsman et al., 1999) and gibberellins playing an important role (Ribeiro et al., 2012). To get a mechanistic view on the role of hormones in controlling carbon allocation towards root growth, more detailed experiments are, however, needed.

High [CO_2] not only impacts plant growth through accelerated photosynthesis and altered carbon allocation, but also causes ultra-structural modifications (Hao et al., 2013). Maize leaves exposed to high [CO_2] showed a reduction in the number of epidermal cells, whereas the stomatal index was increased (Driscoll et al., 2006). Increased lengths of stomata and guard cells were observed in rice plants grown at elevated [CO_2] (Uprety et al., 2002). Increases in the number of mitochondria per unit cell area and higher amounts of stroma thylakoid relative to grana membranes were found in the leaves of trees grown at high [CO_2] (Griffin et al., 2001). These cellular and ultra-structural alterations in leaves reflect a major shift in plant metabolism and energy balance that might explain enhanced plant productivity in response to elevated atmospheric [CO_2].

Besides influencing plant growth, high [CO_2] is also found to mitigate the negative impact of various abiotic stresses (e.g. heat and drought), partly by up-regulating the antioxidant defence metabolism, as well as by reducing photorespiration thereby lowering

oxidative pressure (Farfan-Vignolo and Asard, 2012; Naudts et al., 2014; Zinta et al., 2014). Therefore, stress-mitigating effect of high [CO_2] is likely to become increasingly relevant for plant growth in the face of global changes.

3. Interactive effects of P and high [CO_2]

Rising atmospheric [CO_2] is not paralleled by an increase in P inputs (Peñuelas et al., 2013). High [CO_2] typically stimulates growth, whereas P limitation reduces plant productivity. Thus, the fertilizing effect of high [CO_2] is strongly dependent on the availability of P to sustain the accelerated primary metabolic processes. This suggests that plants growing under high [CO_2] would have enhanced P requirements, potentially aggravating P deficiency in already P-depleted plants (Kogawara et al., 2006). Therefore, the interactions between atmospheric [CO_2] and P availability (and requirement) are crucial to comprehend the sensitivity of various plant species to nutrient management under current and future [CO_2] environments. Here, we discuss the interactive effects of P and [CO_2] on the above and below ground processes of plants.

4.1 Photosynthetic responses to high [CO_2] depend on P supply

Phosphorous being a major constituent of nucleic acid (about 40-60% P in the cell), P deficiency affects RNA synthesis and protein synthesis, and thus inhibits metabolism including photosynthesis. Optimum photosynthesis requires 2.0-2.5 mM P is required in the chloroplast. Below this concentration, photosynthesis is totally inhibited (Marschner and Marschner, 2012). Phosphorus limitation inhibits photosynthesis due to reduction in carboxylation activity of Rubisco, regeneration of ribulose-1,5 bisphosphate (RuBP), and [CO_2] diffusion across stomata and mesophyll (Jacob and Lawlor, 1991; Rodríguez et al.,

1998; Fujita et al., 2004; Wissuwa et al., 2005; Singh et al., 2013). P limitation was also found to decrease the efficiency of energy transfer to the photosystem II (PSII) reaction centre and other chlorophyll fluorescence parameters (Singh and Reddy, 2014). The dependence of leaf photosynthetic rate to the leaf nitrogen is influenced by leaf P concentration. A cross biome analysis of 314 species revealed that leaf P limitation constrains the response of leaf photosynthetic rate to leaf nitrogen (Reich et al., 2009). As elevated CO_2 is known to promote photosynthesis, at least in C3 plants, researchers have examined the ability of elevated CO_2 to overcome the P limitation on photosynthesis in different plant species. In most cases, negative effects of P limitation on photosynthesis are often mitigated, to some extent, by high [CO_2] (Imai and Nomura, 1992; Norisada et al., 2006) due to elevated CO_2-mediated reduction in the mesophyll and stomatal resistance to CO_2 diffusion under P limitation as in case of cotton (Singh et al., 2013), and high [CO_2]-mediated enhancement in RuBP regeneration under P limitation as in case of white lupin (Campbell and Sage, 2006). Under conditions of low P supply, net photosynthesis/ photosynthetic capacity (A_{max}) is determined by the pool size of intermediary phosphorylated metabolites which again depends upon P availability. Thus, phosphorylation by ATP constitutes another important mechanism underlying the photosynthetic response under the combination of high [CO_2] and P, because these energy-rich compounds modulate the activity of Rubisco.

From the above discussion, it is evident that even under P limitation elevated CO_2 can enhance photosynthetic rate to some extent. However, the rate of enhancement of photosynthetic rate of plants under elevated CO_2 depends upon P availability. Higher P supply under elevated [CO_2] further enhances the photosynthetic rate (Duchein et al., 1993; Whitehead et al., 1997; Almeida et al., 1999). Thus, plants grown under high [CO_2] require supra-optimal P levels than the plants grown under ambient [CO_2]. In crops such as wheat, long-term exposure of plants to high [CO_2] often leads to acclimation of photosynthesis i.e.,

down-regulation of photosynthesis due to feedback inhibition (Drake et al., 1997; Chen et al., 2005; Pandurangam et al., 2006). Under these conditions, sufficient P supply may help regain the rate of photosynthesis due to increased Rubisco activation and RuBP regeneration (Brooks et al., 1988). High [CO_2] increased the rate of photosynthesis in *Trifolium subterraneum* at higher P concentration (2.0 mM), whereas photosynthesis was inhibited when P supply was lower (Duchein et al., 1993). Similarly, high P level and high [CO_2] stimulated photosynthesis in *T. Repens* under by 88% compared to the low P grown plants, where high [CO_2] increased the rate of photosynthesis by 72% only (Almeida et al., 1999) (Table 1). The increased P demand of high [CO_2] grown plants is, at least partly, because utilization of additional carbon assimilated at high [CO_2] requires more energy and protein turnover.

In summary, photosynthetic inhibition caused by limited P supply could be overcome by high [CO_2] and photosynthetic down-regulation at high [CO_2] could be reversed by increasing P supply. This could be due to the availability of sufficient P for supporting higher protein turnover and metabolic rates at elevated CO_2, improvement in Rubisco activation, RuBP regeneration and overall energy requirement under the combination of high [CO_2] and P. This implies that currently recommended P levels for different crops need to be reassessed. To harvest the benefit of elevated CO_2, the P supply needs to be increased to enhance the yield and quality of crops in the future atmospheric conditions.

4.2 Interactive effects of [CO_2] and P supply on nutrient acquisition and use

It is well known that nutrient availability controls plant growth and development. When mineral nutrients are scarce, plants either evolve strategies for improved nutrient acquisition from soil or utilize their internally available nutrients more efficiently. The

nutrient acquisition (uptake per unit root mass) and utilization (dry matter production per unit nutrient uptake) efficiencies of plants are therefore expected to be modified considerably under altered growth environments.

High [CO_2] and low P availability both stimulate root growth, and it is therefore, expected that their combination would lead to further enhancement of root growth traits (Fig. 2 C). However, there is sole report in *L. albus*, where high [CO_2] and low P resulted in enhanced production of proteoid roots by four- to six-fold and an increase in the average length of lateral roots (Campbell and Sage, 2002) (Table 2). Most studies on plant species (including cotton, cereals, legumes such as *Cicer arietinum*, *Pisum sativum* and *V. radiata*) grown with or without P fertilization exhibited more variability in the response of root system to high [CO_2], and did not show the expected enhancement of root growth (Prior et al., 2003; Jin et al., 2012; Pandey et al., 2015; Pandey, Unpublished). Therefore, interactive effects of [CO_2] and P supply on root system remain inconclusive.

4.2.1 High [CO_2] enhances acid phosphatase activity under limited P supply

Acid phosphatases (APases) are the enzymes responsible for hydrolyzing organically-bound P in the soil (Fig. 2 A). Secretion rates and activity of APases are generally increased under P stress conditions, however, reports on the effect of high [CO_2] on root APases are limited. Additional carbon supply to the plants grown at high [CO_2] is likely to provide energy and carbon necessary for increased synthesis of APase enzymes and their exudation by roots. High [CO_2]-induced changes in APase activity are differentially regulated at various P levels (Fig. 2 C). For example, in wheat roots, increased APase activity at high [CO_2] and P starvation was observed (Barrett et al., 1998; Milan and Pandey, Unpublished). Similarly, *Arabidopsis* plants supplied with low P under high [CO_2] showed enhanced APase activity in both root and shoot, which was confirmed by increased

transcript levels of *AtPAP2* (Niu et al., 2013). This enhanced *AtPAP2* gene expression suggests that high [CO_2] could elicit intracellular P remobilization during P deficiency. At molecular level, APase is transcriptionally regulated by internal Pi levels (Baldwin et al., 2001). Therefore, increased APase activity at high [CO_2] could be due to the reason that the plants growing under low P already have low tissue P concentration (Lefebvre et al., 1990), which is further reduced by increased carbohydrate synthesis at high [CO_2].

On the other hand, there are reports on decrease in APase activity with increasing [CO_2] and P fertilization in plants like *T. repens* (Almeida et al., 1999) and *Ponderosa pine* (Norisada et al., 2006). In contrast, no significant change in APase activity in *L. albus* under high [CO_2] and high P supply was observed (Wasaki et al., 2003). This reduction in activity could be attributed to the higher concentration of P in root tissues. The concentration of P in the root is involved in controlling phosphatase activity (Noat et al., 1980; Dracup et al., 1984). As a consequence, the higher concentration of root P under higher P supply seems to be responsible for the observed decrease in the APase activity. Such a reduction in the APase activity at high P and elevated [CO_2] grown plants may be particularly disadvantageous as they would lack efficiency to uptake P from the soil.

4.2.2 Differential response of organic acid exudation to P and [CO_2]

Root exudates, particularly low molecular weight (LMW) organic acids such as acetic, aconitic, citric, fumaric, gluconic, lactic, malic, oxalic and succinic acids, bring or keep the sparingly soluble P in solution and thus, improve its acquisition by plant roots (Uhde-Stone et al., 2003b) (Fig. 2 A, C). Induction of phosphoenolpyruvate carboxylase (PEPCase) activity in roots under low P leads to enhanced production of organic acids (Johnson et al., 1996). Data on the effect of high [CO_2] at low versus high P level on the exudation of organic acids is inconsistent (Table 2, Fig. 2 C). Campbell and Sage (2002)

reported increased citrate exudation in *L. albus* when grown at high [CO_2] and low P, but enhanced malate exudation when exposed to high [CO_2] with sufficient P. Besides citrate and malate, increased exudation of oxalic acid was also detected in the rhizosphere of *P. ponderosa* in response to [CO_2] enrichment irrespective of P concentrations supplied (Delucia et al., 1997). Similarly, a tendency for greater efflux of citrate per unit dry weight of root tips was reported in *Danthonia richardsonii* under high [CO_2] irrespective of P treatment (Gifford et al., 1995). No consistent effect of high [CO_2] or P supply on total carbon exudation from roots was detected in pine seedlings (Norby et al., 1987; Kogawara et al., 2006).

Enhanced root exudation under high [CO_2] and low P would depend on three factors: (i) increased root growth leading to higher root surface area, (ii) increased internal concentration of organic acids in root tissues due to higher PEPCase activity in roots, and (iii) enhanced expression of efflux-channels or organic anion transporters located at the plasma membrane. The interactive effect of [CO_2] and P nutrition on root system remain inconclusive (discussed previously), on PEPCase activity in proteoid root suggests that high [CO_2] had no effect on total PEPCase activity in either P-deficient or sufficient leaves (Campbell and Sage, 2006), and on organic anion transporters no studies have been carried out. However, a malate transporter (GmALMT1) identified from *Glycine max* was shown to be co-ordinately regulated by P stress, aluminum and low pH (Liang et al., 2013). With limited amount of data available on the interactive effect of [CO_2] and P nutrition, root carbon exudation has fostered a great deal of speculation. It is not possible to conclude that high [CO_2] would increase the rate of carbon exudation per unit root length or mass differently under high versus low P.

4.2.3 Mycorrhizal colonization is enhanced under limited P supply and high [CO_2]

Mycorrhiza is a symbiotic association between plant roots and fungi. The two common types of fungi involved in such association are arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM). Mycorrhizae not only promote plant growth by providing necessary nutrients, but also help plants to cope with stressful environmental conditions (Nadeem et al., 2014). Fig. 2 B depicts that high [CO_2] would indirectly enhance mycorrhizal growth because of increased carbon allocation to the roots due to higher photosynthetic rates, which may favour symbiotic relationships (Hodge 1996; Staddon and Fitter 1998; Treseder, 2004). Study conducted on temperate forest trees under free air CO_2 enrichment (FACE), reported a 14% increase in ECM root colonization (Garcia et al., 2008). Similarly, meta-analysis on mycorrhizal dynamics under nutrient fertilization showed increase in mycorrhizal abundance by 47% under high [CO_2] (Treseder, 2004). Recently, Jina et al. (2014) reported that wheat plants grown in a P sufficient soil under high [CO_2] stimulated microbial biomass, which in turn immobilized more P and resulted in increased C efflux from the root systems.

Since low soil P promotes AM colonization (Pandey et al., 2005a), it is expected that a combination of high [CO_2] and limited P availability would further enhance AM fungus growth. Several studies have been conducted on AM as well as ECM root colonization in response to high [CO_2] with or without P fertilization (Table 2, Fig 2 B, C). For example, in citrus species, colonization by AM fungi increased growth, net CO_2 assimilation rate and nutrient uptake at high [CO_2] and limited P supply (Syvertsen and Graham, 1999). Moreover, high [CO_2] also tends to stimulate the root colonization by ECM fungi (Norby et al., 1987; O'Neill et al., 1987). In *Quercus alba* seedlings, there was 47% increase in ECM colonization when grown in nutrient poor soil with high [CO_2] as compared to ambient [CO_2] (Norby et al., 1987). Similarly, *P. densiflora* seedlings inoculated with ECM fungi, increased P supply and reduced the ratio of extrametrical mycelium to root biomass under ambient [CO_2], but not at high [CO_2] (Kogawara et al., 2006).

Plants grown at high P under elevated [CO_2] resulted in four-fold increase in starch accumulation in leaves, while no significant increase in starch content in roots was noticed as compared to non-mycorrhizal plants (Syvertsen and Graham, 1999). In another study performed in citrus species, high [CO_2] negates the suppressive effect of high P supply on intra-radical colonization and vesicle development in cotton plants, which resulted in larger growth improvement under high [CO_2] than non-mycorrhizal plants (Jifon et al., 2002). In contrast, Fitter et al. (2000) suggested that root colonization with AM fungi is little altered when plants grown at high [CO_2]. Evidence also shows that in *P. sativum*, high [CO_2] had little or no direct effect on external hyphal production and hyphal P uptake capacity indicating that enhanced carbon supply by plant does not alter growth or function of AM fungi (Gavito et al., 2002). Similarly, high [CO_2] greatly reduced the percentage of root length colonized and total length of colonized root in *T. repens* and *Plantago lanceolata* (Staddon et al., 1999).

In general, mycorrhizal growth can be enhanced by limited P supply and elevated [CO_2], which consequently improves plant growth by a number of mechanisms such as regulation of nutrient uptake, production of enzymes (phosphatases). However, effectiveness of these responses also depends on the extent of association between AM and host plant as well as a number of soil and plant factors such as soil volume in pots, which influence root system growth and AM colonization.

4.2.4 Influence of [CO_2] on P uptake and utilization efficiency

High [CO_2] leads to enhanced P uptake to maintain stimulated growth and increased demand for P, but if the P supply is limited then the plant utilizes internal P judiciously to produce biomass thereby improving utilization efficiency. Cure et al. (1988) reported enhanced P uptake and utilization efficiency in the high [CO_2] grown soybean plants, when

compared to the ambient [CO_2] (Fig. 1 B). In another study on soybean, Israel et al. (1990) also observed higher total P content under elevated [CO_2]. While the P uptake efficiency in this study decreased by 28%, and utilization efficiency increased by 159% with high [CO_2] under P stress (Israel et al., 1990). An increase in leaf tissue P concentration and total P uptake was observed in *V. radiata* grown in open top chambers with high [CO_2] and sufficient P application (Pandey, Unpublished). Similarly, in cereal species, total P uptake was enhanced by 70% at sufficient P when grown at high [CO_2] (Pandey et al., 2015). In the same study, P utilization efficiency increased by 26% at low P.

Rice grown under FACE exhibited increased shoot P uptake by 33% in response to high [CO_2], but this stimulation declined gradually with crop development. Imai and Adachi (1996) also found a reduced P utilization efficiency with increasing P levels in rice, but high [CO_2] increased it by 26%. Apart from these reports, Sicher (2005) did not find any effect of [CO_2] or P levels on uptake of P in barley (Fig. 1 B). Similarly, under high [CO_2] the uptake of nitrogen, P and potassium in *Agrostis capillaris* did not increase proportionately with dry mass, irrespective of the level of nutrient supply, but the higher nutrient use efficiencies enabled plants to maintain their accelerated growth at high [CO_2] (Newbery et al., 1995). Efficient utilization is achieved by effective internal P recycling and remobilization (Cruz-Ramirez et al., 2006; Lin et al., 2009; Nilsson et al., 2010), which could be further induced by high [CO_2]. Thus, it can be concluded that high [CO_2] enhances uptake efficiency with sufficient P supply, but improves utilization efficiency under limited P supply. Efforts are needed to unravel the molecular mechanisms involving sensing and responding of plants to low P under [CO_2] enrichment.

4.3 Interactive effects of P and [CO_2] on plant growth

Plant productivity depends on the net balance between photosynthesis and the carbon needs for maintenance and resource acquisition. In more fertile soils, less carbon is invested in root symbionts and in root exudation (Vicca et al., 2012). Consequently, a larger fraction of photosynthesis is used for dry matter production. Plant growth is therefore, likely to be stimulated more by the widespread high [CO_2] induced increase in photosynthesis (see section 4) in sufficient P than under low P conditions (Ceulemans and Mousseau 1994; Oren et al., 2001; Table 1, Fig. 1 B). Together with high concentration of P, [CO_2] enrichment resulted in more than two-fold increase in total dry matter production in *L. albus* (Campbell and Sage, 2002). Similarly, in soybean grown at high P availability, high [CO_2] led to significant increases in root (88%), shoot (84%) and whole plant (85%) dry weight, while at low P concentration the growth stimulation was significantly less (Israel et al., 1990; Sa and Israel, 1998). In cotton and wheat plants, shoot biomass responded more to elevated [CO_2] with higher rates of soil P application (Rogers et al., 1993), although the interactive effect of [CO_2] and P was different in both species. Wheat responded to [CO_2] enrichment already at the lowest P addition rate, while cotton responded only at higher P addition rates with significant interactive effects (Singh et al., 2013). This difference in response between species could be due to differences in the regulation of carbohydrate metabolism by P concentration in the cytoplasm (Pandurangam et al., 2006). But more likely it is attributable to the differences in carbon cost of P acquisition (uptake efficiency and transport costs) between these species. Changes in atmospheric [CO_2] may also increase the critical P concentration i.e., the foliar P concentration required to achieve maximum productivity (Rogers et al., 1993). Therefore, at high [CO_2], more P would be required to support maximum shoot growth, which can either be achieved by enhancing uptake efficiency under sufficient P supply or by improving utilization efficiency under limited P supply.

Studies on *Vigna radiata* (Pandey et al., Unpublished) and cereal species (Pandey et al., 2015) revealed that high [CO_2] enhanced biomass accumulation in plants grown with

sufficient P significantly more than in plants grown at low P indicating that [CO_2] stimulation of biomass accumulation is dependent on P status. In cereal species and *V. radiata*, the increase in total biomass accumulation was more when plants were grown at high [CO_2] as compared to ambient [CO_2] with sufficient P. Similarly, enhanced biomass accumulation was observed in both plant species with high [CO_2] and sufficient P than ambient [CO_2]. However, the relative increase in biomass was 29% in cereal species and 9% in *V. radiata* under sufficient P concentration with high [CO_2]. On the other hand, in rice no significant effect of [CO_2] and P interactions on dry matter accumulation was found (Imai and Adachi, 1996), suggesting that this interaction effect might not be general.

Apart from crop plants, studies on growth response of tree species have also revealed significantly larger increases in dry matter production at high [CO_2] with greater P availability (Table 1). In *Eucalyptus grandis,* high [CO_2] induced the greatest relative increase in growth rate at lowest P fertilizer levels, however, the absolute increase in dry matter in response to CO_2 enrichment was greater with high P levels (Conroy et al., 1992). Contrary to this result, studies on *Pinus radiata* and *P. caribaea* to [CO_2] enrichment showed little growth response at low P supply (Conroy et al., 1988; 1990). But with the increase in P fertilizer rate, maximum growth was attained suggesting that higher foliar P concentrations are required to realise the maximum growth potential of pines at high [CO_2]. Difference in the responses of pines and eucalypts at low P may be due to the fact that eucalypts are adapted to low fertile soils and may therefore be more efficiently responding to high [CO_2] at low P.

Plants adapt to moderate nutrient stress by utilizing the additional assimilates produced by [CO_2] enrichment primarily below ground. Increased root growth in response to nutrient deficiency allows plants to acquire nutrients more efficiently from the soil. Generally, P deficiency causes larger reductions in shoot than in root growth, thereby increasing root-to-shoot ratio (Pandey et al., 2005b; Hu et al., 2010). High [CO_2] further

stimulates this shift by favouring increased biomass partitioning towards root leading to increased root-to-shoot growth as observed in soybean (Israel et al., 1990), *V. radiata* (Pandey, Unpublished) and cereal species (Pandey et al., 2015). On the other hand, in cotton and white lupin, low P and high [CO_2] resulted in reduction of root-to-shoot growth (Campbell and Sage, 2002) while in *Ponderosa pine*, irrespective of soil P concentration a reduction in root-to-shoot ratio at high [CO_2] was observed (Walker et al., 1995) (Table 1). All together it can be concluded that high [CO_2] increases dry matter production under optimum P and enhances partitioning towards root under low P.

4. Effect of P supply and high [CO_2] on transcriptional responses

With a goal to better understand the molecular processes involved in plant adaptation to P deficiency, spatio-temporal regulation of genes has been studied by microarray in shoots and roots of various plant species for short, medium and long-term P deprivation (Wu et al., 2003; Misson et al., 2005; Morcuende et al., 2007; Hammond et al., 2011). Wu et al. (2003) reported differential gene expression patterns in leaves and roots of *Arabidopsis* in response to P starvation suggesting that plants use distinct adaptive strategies to cope with P stress by activating unique sets of genes in these organs. Also, temporal transcriptome analysis of plants to P-limitation revealed the expression of 'early' genes which mostly represent general stress responsive genes followed by the expression of 'late' genes which specifically respond to P deficiency (Fig. 3). Such P-responsive genes belong to various functional categories. For instance, Morcuende et al. (2007) reported that P-limitation induced the expression of phosphate transporters, phosphatases, RNAses, carbohydrate metabolism genes, and caused reprogramming of lipid metabolism where galactolipid and sulfolipid synthesis genes were strongly induced. Such metabolic alterations may help plants acclimatize to P deficiency. Transcriptome analysis of rice roots

under P deficiency (Wasaki et al., 2003) showed up-regulation of genes related to glycolysis, alteration in lipid metabolism, modification of cell wall synthesis and changes in the metal responsive genes. Similarly, some glycolytic pathway related genes were induced in roots of *L. albus* under P starvation (Uhde-Stone et al., 2003a, b). In-depth study on molecular mechanisms defining the phosphate signalling pathway showed that *Pup1*-specific protein kinase gene, *PSTOL1* is involved in regulating root growth and architecture during early stages (Gamuyao et al., 2012). Allele-specific markers for this gene have been reported recently (Pariasca-Tanaka et al., 2014).The systemic response to P starvation is carried through a complex signalling network which involves plant hormones (Nacry et al., 2005; Pérez-Torres et al., 2008; Li et al., 2012), sugars (Karthikeyan et al., 2007) and nitric oxide (Wang et al., 2010), and collectively result in the altered carbohydrate distribution between roots and shoots. Moreover, transcription factors such as PHR1 (OsPHR1, OsPHR2, PvPHR1, ZmPHR1, TaPHR1), PTF1 (OsPTF1, ZmPTF1), MYB2P-1 (OsMYB2P1), MYB62, WRKY (WRKY75, WRKY6), bHLH32 and ZAT6 are involved in the signalling network to regulate plant adaptation to P stress (Yi et al., 2005; Devaiah et al., 2007a, b; Chen et al., 2007; Valdes-Lopez et al., 2008; Zhou et al., 2008; Devaiah et al., 2009; Chen et al., 2009; Li et al., 2011; Dai et al., 2012; Wang et al., 2013). The post-transcriptional regulation as well as long-distance signal is carried out by microRNAs, for instance miR399 maintain P homeostasis by regulating P transporter *PHO2* (Bari et al., 2006; Aung et al., 2006; Lin et al., 2008; Pant et al., 2008). Although the molecular components of P stress signalling in plants has been identified, the overall pathway is still poorly understood and requires further investigation.

Similarly, large number of studies on genome-wide expression profiling of plants grown under high [CO_2] have been carried out (Li et al., 2008; Leakey et al., 2009; Cseke et al., 2009; Wei et al., 2013). Ribeiro et al. (2013) showed that high [CO_2] promote plant growth *via* a complex transcriptional network. It is proposed that high [CO_2] stimulates

biomass accumulation in a GA-independent manner by regulating the expression of growth-related genes (Ribeiro et al., 2012). Few reports involving transcript (Ainsworth et al., 2006; Tallis et al., 2010) and protein (Bokhari et al., 2007; Qiu et al., 2008) profiling of various plants to high [CO_2] showed differential expression of genes and proteins respectively, indicating that the responses of plants to high [CO_2] are species-specific. Molecular and genomic responses of plants to high [CO_2] and interactive effects of [CO_2] with other environmental stresses *viz*. Ozone (Miyazaki et al., 2004; Kontunen-Soppela et al., 2010; Gillespie et al., 2012), salinity (Kanani et al., 2010), drought (Allen et al., 2011; Sicher et al., 2012), high temperature (Madan et al., 2012) and combined heat and drought (Zinta et al., 2014) have been carried out, whereas studies elucidating the interactive effects of P stress and high [CO_2] on gene expression patterns are not available.

A sole study on P-deficient *Arabidopsis* grown under high [CO_2] and fed on nitrate-N showed increased root surface area and root-to-shoot ratio. Molecular dissection of this response revealed that in P-deficient plants, high [CO_2] enhanced the expression of transcription factors as well as P transporter genes including *AtPHO1, AtPHO2, AtPHR1* and *AtPHT1* in roots (Niu et al., 2013). The transcript abundance of *AtPHO1* in roots and *AtPHO2* and *AtPAP2* in shoots under high [CO_2] is indicative of internal P recycling between shoots and roots during the onset of P starvation. Since the data on response of genes to the interactive effects of P starvation and high [CO_2] are scarce, we analysed the expression patterns of typical P-responsive genes of *Arabidopsis* under high [CO_2] using Genevestigator V3 as presented in Fig. 4. Analyses revealed that short-term exposure of plants to high [CO_2] did not show any significant effect on the expression pattern of P stress responsive genes. However, long-term exposure to high [CO_2] resulted in the up-regulation of four out of 22 genes belonging to purple acid phosphatase (*PAP*) family while there was no significant influence on phosphate transporters (*PHT*). Differential regulation of genes involved in carbohydrate metabolism such as amylase (*AMY*), sucrose phosphate synthase

(*SPS*), sucrose phosphatase (*SPP*) and sucrose synthase (*SUSY*) was also observed. Genes belonging to *AMY* (AT4G15210) and *SPS* (AT5G11110 and AT4G10120) families were highly expressed under high [CO_2] and P starvation. Similarly, high [CO_2] is found to induce expression of a few genes involved in P remobilization under P starvation such as mono-galactosyldiacyl glycerol synthase (*MGDS*) and sulfoquinovosyldiacyl glycerol synthase (*SQD*). The induction of genes belonging to *PAP*, *MGDS* and *SQD* families under high [CO_2] is suggestive of an efficient internal scavenging, recycling and remobilization of P resulting in its efficient utilization under P stress. Thus, this data (Fig. 4) indeed shows that long-term exposure to high [CO_2] have a tendency to stimulate similar transcriptional responses as observed under P limitation. To better understand the interactive effects of P limitation and high [CO_2], genome-wide transcriptional studies is a prerequisite. At least, it will be interesting to see how typical P starvation-induced genes respond to a combination of P-limitation and high [CO_2].

5. Conclusions and future perspectives

The high usage of P fertilizers for increasing plant productivity and the continued rise in atmospheric [CO_2] have caused human-induced imbalances in P across the globe (Peñuelas et al., 2013). High [CO_2] enhances plant growth but P limitation causes reduction in growth, particularly in shoot. However, both these environmental factors when applied individually enhance root growth and exudation, and increase mycorrhizal association. Although the individual effects of high [CO_2] or P stress have been widely studied, but their interactive effects on plant growth are still poorly understood. The overall decrease in plant growth due to low P could be partially overcome by high [CO_2], at least during initial growth stage. This is mainly due to the influence of high [CO_2] on Rubisco activation, RuBP regeneration capacity and reduction in resistance to CO_2 diffusion across stomata and

mesophyll. Conversely, the growth stimulation at high [CO_2] further increases the demand for P. Long-term exposure of plants to high [CO_2] resulting in photosynthetic acclimation is overcome by increased supply of P. The reason being assimilation of additional carbon at high [CO_2] requires more energy in the form of ATP, also the energy rich compounds modulates Rubisco activity. Changes in below ground processes under high [CO_2] and P stress include enhanced root growth, increased secretion of APase enzymes and organic acids and increased colonization with mycorrhizal fungi. These adaptations may lead to improved P uptake under high [CO_2], only if sufficient P is available in the soil. Internal P recycling, scavenging and remobilization result in more efficient P utilization under P stress. High [CO_2] may strengthen these processes as several P stress responsive genes like PAPs, RNS, MGDS and SQD, involved in P recycling are up-regulated under high [CO_2]. We believe that future research on the interactive effects of high [CO_2] and P should take following points into account:

1. Different species respond differentially to high [CO_2]. Species-comparisons e.g. C3, C4, monocots and dicots are needed to better understand the interactive effects of high [CO_2] and P-limitation.

2. High [CO_2] ameliorate some of the negative effects of P limitation during early growth stages. However, to sustain growth optimum P is required. The mechanisms underlying this buffering effect of high [CO_2] needs to be explored further. Moreover, ontogenetic effects of plants should also be taken into consideration.

3. P is an important structural constituent of cell membranes in the form of phospholipids. P limitation alters membrane composition, such that non-phosphorus membrane lipids including monogalactosyl diacylglycerol (MGDG*)* and

sulfoquinovosyl diacylglycerol (SQDG) substitute phospholipids. As cell membranes are the first barrier to encounter any kind of abiotic stress, therefore, studies evaluating the membrane lipid compositional changes under different P levels and high [CO_2] are required. Such studies will provide insight into plant responses to future increases in atmospheric [CO_2] and soil P depletion.

4. Although reports on genome-wide transcription profiling of plants under P stress or high [CO_2] are available, but studies to demonstrate their interactive effects at gene, protein or metabolic levels are lacking. More research in the area of 'omics' including transcriptomics, proteomics and metabolomics is warranted to quantify the effects of high [CO_2] under low P availability. Moreover, temporal profiling (short vs long-term) would provide a deeper understanding on the plant stress responses.

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Figure captions:

Fig. 1. Impact of P-limitation and high [CO_2] on above ground processes in plants.

(A) Effect of P-limitation on plant metabolism, and the processes indicated by asterisks depict metabolic adaptions to cope with P-stress (redrawn from Plaxton and Tran, 2011). Abbreviations: ADPGluc (ADP-Glucose); AGPase (ADP-glucose pyrophosphorylase); ATP (Adenosine triphosphate); CS (Citrate synthase); Fru6P (Fructose-6-phosphate); Glu1P (Glucose-1-phosphate); Gluc6P (Glucose-6-phosphate); H^+-ATPase (H^+-pumping ATPase); H^+-PPiase (Inorganic pyrophosphate-dependent H^+-pump); MDH (Malate dehydrogenase); Met-Pi (Mineral bond phosphate); $NADP^+$ (Nicotinamide adenine dinucleotide phosphate); PAP-S (Secreted purple acid phosphatase); PAP-V (Vacuolar purple acid phosphatase); PEP (Phospho*enol*pyruvate); PEPC (Phospho*enol*pyruvate carboxylase); PGI (Phosphoglucose isomerase); PGM (Phosphoglucomutase);Pi (Phosphate); RNase (Ribonuclease); SS (Starch synthase); TPT (Triose phosphate transporter).

B) The effect of P-limitation and its interaction with high [CO_2] on various physiological traits studied on the above ground parts of plants. Upward and downward arrows indicate increase and decrease, respectively in the studied parameter while N.E. means 'no effect'. Direction of arrows in the table is based on the studies of Conroy et al. (1986); Conroy et al. (1990); Lewis et al. (1994); Barrett & Gifford (1995); Walker et al. (1995); Sa and Israel (1998); Stocklin et al. (1998); Almeida et al. (1999); Almeida et al. (2000); Campbell and Sage (2002); Prior et al. (2003); Sicher (2005); Campbell and Sage (2006); Norisada et al. (2006).

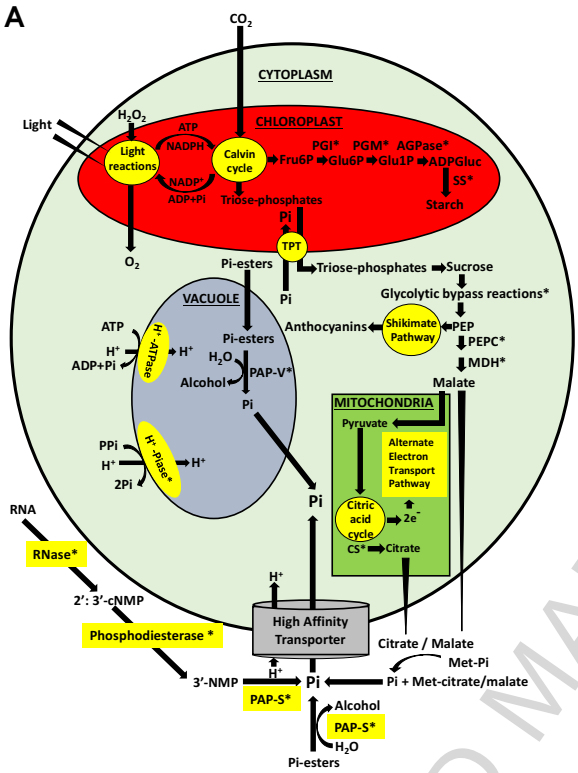
Fig. 2. Influence of P-limitation and high [CO_2] on below ground processes in plants.

(A) Describes the basic mechanism of P uptake by roots. Phosphate (Pi) is transported into the roots by high affinity Pi transporter, whereas carbon (C) is exuded as organic acids (e.g. malate and citrate).

(B) Depicts nutrient exchange occurring in the rhizosphere between plant and fungi by mycorrhizal symbiosis. In this symbiotic association fungus is dependent on the plant for carbohydrates and helps plant to take mineral nutrients. Presence of extra [CO_2] can also modify this exchange process. High [CO_2] leads to increased fixation of C in plant, which in turn alters whole process and ultimately affect plant growth. Upward arrows indicate increase. **(C)** The effect of P-limitation and its interaction with high [CO_2] on various physiological parameters studied on belowground part. Upward and downward arrows indicate increase and decrease, respectively in the studied parameter while N.E. means 'no effect'. Direction of arrows in the table is based on the studies of Imai and Adachi (1996); DeLucia et al. (1997); Almeida et al. (1999); Campbell and Sage (2002); Jifon et al. (2002); Kogawara et al. (2006); Tang et al. (2006); Norisada et al. (2006).

Fig. 3. Early and late responsive genes induced by P-limitation from different functional categories *viz.* (A) Transcription factors, (B) P transport and remobilization, (C) Phospholipids and anthocyanin biosynthesis, (D) Development and root architecture, (E) Stress and Defence and (F) Metabolism. These genes show overlap as well as specificity to short and long-term exposure to P-limitation. Figure was constructed from the data extracted from: Hammond et al.(2003); Uhde-Stone et al. (2003a); Uhde-stone et al. (2003b); Wu et al. (2003); Misson et al. (2005); Bari et al. (2006); Graham et al. (2006); Shin et al. (2006); Chen et al. (2007); Franco-Zorrilla et al. (2007); Hernandez et al. (2007); Muller et al. (2007); Stefanovic et al. (2007); Svistoonoff et al. (2007); Tian et al. (2007); Valdes-Lopez and Hernandez (2008).

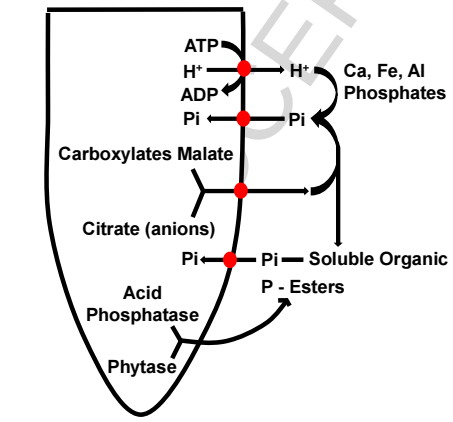
Fig. 4. Heat maps representing expression patterns of typical P-limitation (-P; in root and shoot) induced genes, and their expression patterns under high [CO_2] (+CO_2; at short and long-term exposure) conditions in *Arabidopsis thaliana*. Heat map was constructed from the data obtained from Genevestigator database containing different experiments [Misson et al. (2005); Coupe et al. (2006); Li et al. (2009); Lin et al. (2011); Woo et al. (2012); (Markelz et al. (2014)]. Green and red colour in the heat map depicts down-regulation and up-regulation of genes with respect to control, respectively. Abbreviations: PHT (Phosphate transporter); PAP (Purple acid phosphatase); RNS (Ribonuclease); AMY (Amylase); SPS (Sucrose phosphate synthase); SPP (Sucrose phosphatase); SUSY (Sucrose synthase); MGDS (Mono-galactosyldiacyl glycerol synthase); SQD (Sulfoquinovosyl diacylglycerol synthase).

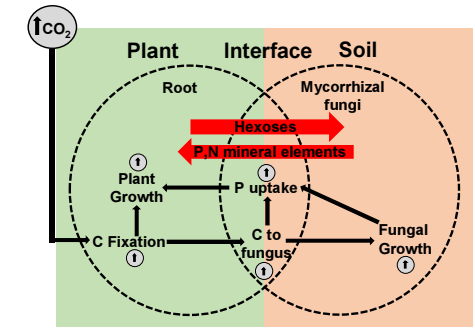


B

Parameter	P limitation	P X Elevated CO_2
Leaf area	↓	↓ or N.E
Dry matter	↓	↑ or N.E
Root to shoot ratio	↑ or N.E	↑
Leaf P content	↓	↑ , ↓ or N.E
P uptake	↑	↑ or N.E
Photosynthesis	↓	↓ or ↑
Rubisco regeneration/ activity	↓	↓ or N.E
PEP carboxylase	↑	N.E
Sugars	↑ or ↓	↑ or N.E

Fig 1





C

Parameter	P limitation	P X Elevated CO_2
Root Hairs	↑	↑
Lateral Roots	↑	↑
Root Biomass	↑	↑
Root exudates (organic acids)	↑	↑ or N.E
Mycorrhizal colonization	↑	↑ or N.E
Acid Phosphatases	↑	↑ or ↓

Fig 2

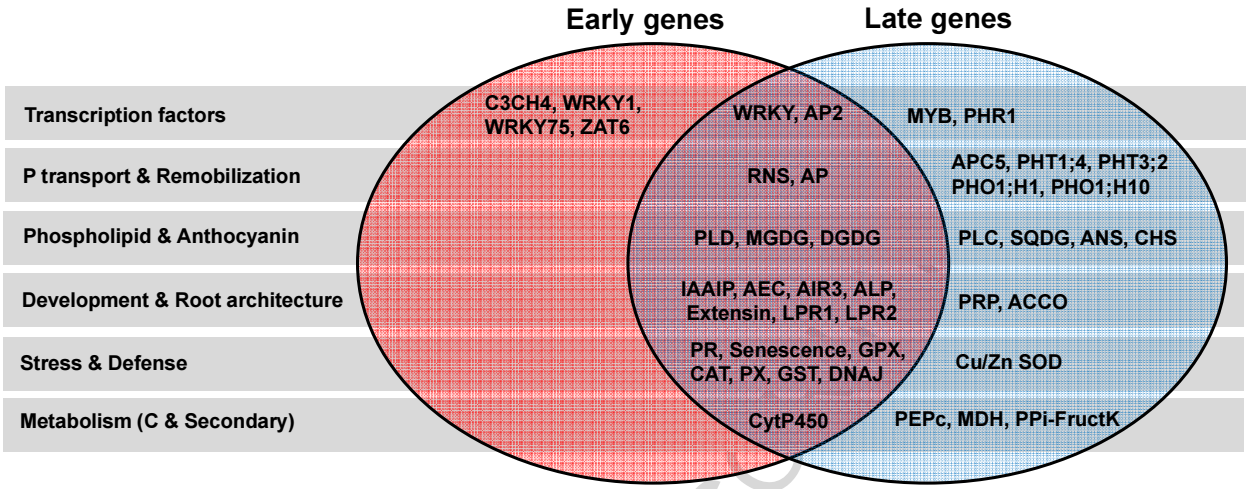


Fig 3

Fig 4

Table 1
Growth response of plants exposed to low and sufficient phosphorus under high [CO_2]. "NE" depicts no effect; "-" depicts not measured

Plant species	Low P	High P	Ambient CO_2	Elevated CO_2	Plant DW/biomass		Photosynthesis		Shoot/root ratio		References
					Low P X CO_2	High P X CO_2	Low P X CO_2	High P X CO_2	Low P X CO_2	High P X CO_2	
Pinus radiata	4.4 mg/pot	40 mg/pot	330 µL/L	660 µL/L	NE	+ 28%	- 30%	+ 150%	-	-	Conroy et al., (1986)
Pinus radiata	600 µg/g	1800 µg/g	340 µL/L	660 µL/L	NE	+ 80%	-	-	-	-	Conroy et al., (1990)
Pinus radiata	600 µg/g	1800 µg/g	340 µL/L	660 µL/L	NE	+ 114%	+ 18%	+ 50%	-	-	
Pinus caribaea	600 µg/g	1600 µg/g	340 µL/L	660 µL/L	NE	+ 140%	-	-	-	-	
Pinus taeda	0.083 mM	0.5 mM	35.5 Pa	71.0 Pa	-	+ 40%	-	-	-	-	Lewis et al., (1994)
Pinus ponderosa	18 µg/g soil	50 µg/g soil	350 µL/L	525 and 700 µL/L	NE and + 60%	+ 28% and 14%	-	-	- 55 and 17.5%	- 40 and 65%	Walker et al., (1995)
Glycine max	0.05 mM	1.0 mM	400 µL/L	800 µL/L	NE	+ 83%	-	-	-	-	Sa and Israel (1998)
Bromus erectus	None	1 g P /m^2 /year	350 µL/L	600 µL/L	- 17%	- 23%	-	-	-	-	Stöcklin et al., (1998)
Mesophytic grasses	None	1 g P /m^2 /year	350 µL/L	600 µL/L	+ 25%	+ 15%	-	-	-	-	
Carex flacca	None	1 g P /m^2 /year	350 µL/L	600 µL/L	+ 230%	+ 178%	-	-	-	-	
Graminoids	None	1 g P /m^2 /year	350 µL/L	600 µL/L	+ 15%	+ 6.4%	-	-	-	-	
Forbs	None	1 g P /m^2 /year	350 µL/L	600 µL/L	+ 25%	+ 25%	-	-	-	-	
Legumes	None	1 g P /m^2 /year	350 µL/L	600 µL/L	+ 370%	NE	-	-	-	-	
Trifolium repens	0.0027 mM	2 mM	35 Pa	70 Pa	NE	+ 30%	+72%	+88%	-	-	Almeida et al., (1999)
Lupinus albus	0·69 µM	0·25 mM	410 µmol/ mol	750 µmol/ mol	NE	+ 100%	-	-	NE	+ 10.4%	Campbell and Sage (2002)
Hordeum vulgare	0.05 mM	1.0 mM	36±1 Pa	100±2 Pa	+ 30%	+ 24%	-	-	-	-	Sicher (2005)
Lupinus albus	0·69 µM	0·25 mM	400 µmol/ mol	750 µmol/ mol	-	-	NE	+ 27%	- 10%	NE	Campbell and Sage (2006)
Pinus densiflora	0	0.6 mM OR 0.1 mM	400 µL/L	700 µL/L	- 17%	- 41% OR NE	- 21.7%	- 13.3% OR NE	-	-	Norisada et al., (2006)

Gossypium hirsutum	150 mg/kg soil	2400 mg / kg soil	360 µmol/ mol	720 µmol/mol	+49%	+51%	-	-	-	-	Prior et al., (2003)
Gossypium hirsutum	2.1 mg P /plant	18.2 mg P /plant	376 µL/L	935 µL/L	NE	+48%	-35%	-45%	-	-	Barrett & Gifford (1995)

Table 2
Root associated parameters of plants exposed to low and sufficient phosphorus under high [CO_2]. "NE" depicts no effect; "-" depicts not measured

Plant species	Low P	High P	Ambient CO_2	Elevated CO_2	Mycorrhizal colonization		Root Exudation		Proteoid roots		Acid Phosphotase		References
					Low P×CO_2	High P×CO_2	Low P×CO_2	High P×CO_2	Low P×CO_2	High P×CO_2	Low P×CO_2	High P×CO_2	
Oryza sativa	3 µM	300 µM	350 µmol/mol	700 µmol/mol	-	-	-	-	-	-	-	Up	Imai and Adachi (1996)
Pinus ponderosa	-	0.34 M OR 64 ppm	350 µmol/mol	700 µmol/mol	-	-	-	NE	-	-	-	-	DeLucia et al., (1997)
Trifolium subterraneum	0.0027, 0.075	0.67, 2 mM	350 µmol/mol	700 µmol/mol	-		-	-	-	-	-	Up	Almeida et al., (1999)
Citrus. sinensis		2 mM P	36 Pa 24 h/ d	70 Pa 24 h/ d	-	Down	-	-	-	-	-	-	Jifon et al., (2002)
Citrus aurantium					-	Down	-	-	-	-	-	-	
Lupinus albus	0.69 µM	0.25 mM	400 µmol/mol	750 µmol/mol	-	-	Up	-	-	-	-	-	Campbell and Sage (2002)
Pinus densiflora	0.02, 0.04, 0.06 mM	0.08, 0.1, 0.2 mM	350 µmol/mol	700 µmol/mol	-	NE	-	-	-	-	-	-	Kogawara et al., (2006)
Lupinus albus	0.69 µM	0.25.mM	400 µmol/mol	750 µmol/mol	-	-	-	-	Up	-	-	-	Campbell and Sage (2002)
Plantago virginica	6.27 µg/g soil		350±30 µmol/mol	700±30 µmol/mol	Up	-	-	-	-	-	-	-	Tang et al., (2006)
Medicago lupulina					Up	-	-	-	-	-	-	-	
Lolium perenne					NE	-	-	-	-	-	-	-	
Veronica didyma					Up	-	-	-	-	-	-	-	
Eleusine indica					Up	-	-	-	-	-	-	-	
Setaria glauca					Up	-	-	-	-	-	-	-	
Poa annua					NE	-	-	-	-	-	-	-	
Kummerowia striata					Up	-	-	-	-	-	-	-	
Gnaphalium					Up	-	-	-	-	-	-	-	

affine													
Avena fatua					NE	-	-		-	-	-	-	
Pinus densiflora	0.02, 0.04, 0.06 mM	0.08, 0.1, 0.2 mM	350 µmol/mol	700 µmol/mol	-	-	-	Up	-	-	-	-	Kogawara et al., (2005)