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Elevated CO_2 Improves Growth and Phosphorus Utilization Efficiency in Cereal Species under Sub-Optimal Phosphorus Supply

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**Elevated CO₂ Improves Growth and Phosphorus Utilization Efficiency in Cereal Species
under Sub-Optimal Phosphorus Supply**

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Running title: Improved growth and PUE under elevated CO₂

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ABSTRACT

Cultivars of *Triticum aestivum*, *T. durum*, and *Secale cereale* were grown at low (2 μM) and sufficient (500 μM) phosphorus (P) under ambient carbon dioxide (380 $\mu\text{mol mol}^{-1}$; aCO₂) and elevated CO₂ (700 $\mu\text{mol mol}^{-1}$, eCO₂) to study responses of cereal species in terms of growth and P utilization efficiency (PUE) under P x CO₂ interaction. Dry matter accumulation increased under eCO₂ with sufficient P. Nevertheless, dry matter accumulated at eCO₂ with low-P was similar to that obtained at aCO₂ with sufficient P. Leaf area was 43% higher under eCO₂ with sufficient P. Significant increase in lateral root density, length and surface area were noted at low-P under eCO₂. Phosphorus use efficiency (PUE) increased by 59% in response to eCO₂ in low-P plants. Thus, eCO₂ can partly compensate effect of low-P supply because of improved utilization efficiency. Among cereals, durum wheat was more suitable in terms of PUE under high CO₂ and limiting P supply.

Keywords: Elevated CO₂, phosphorus nutrition, utilization efficiency, *Secale cereale*, *Triticum aestivum*, *Triticum durum*

INTRODUCTION

Climate change and nutrient availability are the two serious challenges to food security and economic development. During pre-industrial times, the atmospheric carbon dioxide concentration $[\text{CO}_2]$ was approximately $280 \mu\text{mol mol}^{-1}$ which is accumulating in the atmosphere at a very fast pace. At present, the $[\text{CO}_2]$ is $384 \mu\text{mol mol}^{-1}$ which is 40% higher than at any time in the last 20 million years (Pearson and Palmer, 2000). It is projected that by the middle of this century the $[\text{CO}_2]$ would surpass $550 \mu\text{mol mol}^{-1}$ and top $700 \mu\text{mol mol}^{-1}$ by the end of this century (Prentice et al., 2001). Over longer periods, the growth responses of plants to elevated atmospheric CO_2 are directly influenced by other environmental factors, such as water, temperature and nutrient availability (Taub, 2010). The increased growth rates of CO_2 enriched plants are bound to create an enhanced demand for mineral nutrients that make nutrient availability particularly important. Elevated CO_2 plays a major role in plant nutrition and most studies on the effects of elevated CO_2 on plant processes have been done under optimal nutritional conditions (Li et al., 2007). It has been observed that plant growth rates under moderate nutrient insufficiency are usually enhanced by atmospheric CO_2 enrichment, but not to the same extent as under nutrient sufficient conditions (Ziska, 2003) thus, indicating that rising atmospheric CO_2 concentrations can enhance plant growth and change their nutrient demands.

Phosphorus (P) is a vital macronutrient for plant growth that functions in the formation of high-energy bonds, in the structure of certain biomolecules and membranes, and as an integral component of many metabolic reactions and signal transduction pathways (Ticconi et al., 2001),

but its availability to plants is limited. In response to persistent inorganic P deficiency, plants have developed many adaptive morphological, physiological, and molecular mechanisms to cope with Pi insufficiency. These includes changes in root growth and architecture (Pandey et al., 2003), induction of high-affinity P transporters (Ragothama, 1999), increased secretion of acid phosphatase enzyme (Pandey, 2006) and low molecular weight organic acids (Dong et al., 2004), symbiotic associations with mycorrhizal fungi (Pandey et al., 2005) and changes in the activity of several key photosynthetic enzymes (Rao and Terry, 1989). It has been suggested that the Pi requirement of a plant grown under elevated CO₂ would be higher than those grown at ambient CO₂, because photosynthetic rate increases in response to CO₂ especially in C₃ plants. Therefore, this clearly indicates that because of heavy metabolic demand for P acquisition, this limiting nutrient would be responsive to future climatic conditions.

It has been reported that CO₂ influences growth and yield of crop plants markedly under the regimes of P variability through modulating various physiological processes. These physiological processes in plants include photosynthesis (Norisada et al., 2006), dry matter production and partitioning (Imai and Adachi, 1996; Sicher, 2005), growth parameters (Campbell and Sage, 2002), metabolite synthesis, activities of enzymes like acid phosphatase, acid invertase, sucrose synthase, and Rubisco (Sicher, 2005; Norisada et al., 2006), root exudation (Watt and Evans, 1999), nutrient uptake and utilization efficiency (Yang et al., 2007; Khan et al., 2008) and arbuscular-mycorrhizal colonization (Gavito et al., 2002). The interactive effect of CO₂ and P nutrition on response of plants has been reviewed by Pandey et al. (2011).

Cereals remain the world's most important sources of food, both for direct human consumption and indirectly, as inputs to livestock production. In the present experiment, an

attempt was made to study the growth response of cereal species, wheat and rye, to the interactive effects of P nutrition and elevated CO₂. Since P is involved in almost all metabolic processes, it was hypothesized that its demand would be higher under elevated CO₂ through modulation of various growth traits. The wheat varieties PBW-396 and PDW-233 were selected from a previously conducted screening experiment in the field under sufficient and low levels of available soil P (data not presented). These two varieties performed well in terms of above-ground biomass and grain yield. However, rye was included for comparison since it is reported to be efficient in P uptake (Harry and Graham, 1981; Pandey et al., 2005).

MATERIALS AND METHODS

Plant Material and Growth Conditions

Wheat varieties, PBW-396 (*Triticum aestivum* L.) and PDW-233 (*T. durum* L.), and rye, WSP 540-2 (*Secale cereale* L.) were procured from the Division of Genetics, Indian Agricultural Research Institute, New Delhi. These varieties were kept on germination towel after surface sterilization with 0.1% mercury chloride (HgCl₂). Five days after germination, individual seedlings that had a similar plant development were transferred to Hoagland solution with low (2 µM) and sufficient (500 µM) P levels. The plants were supported on Styrofoam sheet (50 mm thickness) with holes made at 5 x 5 cm plant-to-plant and row-to-row distance. The Styrofoam sheet was fitted into plastic containers (30 x 45 x 15 cm) holding 16-L solution. Forty five seedlings were raised in one such container and for each cereal species a separate container was

used. The solution was changed every alternate day and continuously aerated using aquarium pumps and polyvinylchloride (PVC) tubing.

The composition of nutrient solution used was [calcium nitrate $\text{Ca}(\text{NO}_3)_2$] 1.5 mM, potassium nitrate (KNO_3) 5.0, ammonium nitrate (NH_4NO_3) 1.0 mM, magnesium sulfate (MgSO_4) 2.0 mM, boric acid (H_3BO_3) 1.0 μM , manganese chloride tetrahydrate ($\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$) 0.5 μM , zinc sulfate heptahydrate ($\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$) 1.0 μM , copper sulfate pentahydrate ($\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$) 0.2 μM , ammonium molybdate tetrahydrate $[(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}]$ 0.075 μM and iron chloride (FeCl_3) + ethylenediaminetetraacetic acid (EDTA) 3 μM . Phosphorus was supplied in the form of 1.0 M orthophosphoric acid and pH of nutrient solution was maintained at 5.6 during the course of experiment. The level of P (low and sufficient) for wheat was worked out in a preliminary experiment using a series of P concentration ranging from 0 to 700 μM in phytotron under ambient CO_2 condition (data not presented). The tissue P concentration, biomass and visual P deficiency symptoms were taken into account to determine the low and sufficient-P concentration for this experiment. In the whole experiment, plants were sampled on 15th day after germination (excluding 5-d of germination period).

The whole experimental set up was maintained in controlled environment chambers (Model PGW 36, Conviron, Winnipeg, Canada) at National Phytotron Facility, Indian Agricultural Research Institute (IARI), New Delhi. In these chambers, except CO_2 , the growth conditions were maintained as: 22°C/12°C day/night temperature, 10 h photoperiod with photon flux density of 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) and the relative humidity (RH) was 90%. In elevated CO_2 chamber, the $[\text{CO}_2]$ was maintained at 700 $\mu\text{mol mol}^{-1}$ (eCO_2) using automated flow meter and purified CO_2 supply while in the ambient CO_2 chamber (aCO_2), no external CO_2 supply was

given. In aCO₂ chamber, the [CO₂] was measured regularly using portable photosynthetic system LI-6200, (LICOR, Lincoln, NE, USA) which was recorded to be $380 \pm 10 \mu\text{mol mol}^{-1}$.

Growth and Biochemical Analysis

To study root morphology and other growth parameters, 15-d-old plants raised as described above under eCO₂ and aCO₂ with sufficient or low-P were taken. Root morphological parameters such as root length (length of the longest root), measured using a ruler and expressed as cm plant⁻¹ and number of primary and secondary roots were counted on per plant basis. The numbers of lateral roots were counted on 8-d old plants and the lateral root density was calculated and expressed as number of laterals per unit root length.

The root surface area was estimated colorimetrically by the method of Ansari et al. (1995). The method was calibrated with wheat root sections of known surface area (Kalita, 1999). The correlation coefficient was found to be 0.99. From standardization protocol, the factor for calculating surface area was worked out to be $40.36 \mu\text{mol nitrite (NO}_2^-)$ for 100 cm^2 root surface area. The roots of seedlings was immersed in 0.05 M of sodium nitrite (NaNO₂) solution for 10 seconds, and then hung to drain out excess solution present on the root surface. Care was taken to ensure that only roots were in contact with the solution. The roots were then transferred to an Erlenmeyer flask containing 200 ml of distilled water and shaken for 15 min. The nitrite desorbed in the solution was measured by diazotization reaction. Aliquots were pipetted into test tubes and added 1 ml each of 1% sulphanilamide in 1N hydrochloric acid (HCl) and 0.01% N (1-naphthyl) ethylene diammonium dichloride (NEDD). The absorbance of pink

color developed was read at 540 nm using double beam UV-Visible Spectrophotometer (ECIL, Hyderabad, India). The amount of nitrite was calculated from a standard curve prepared with NaNO_2 concentrations ranging from 10 to 100 nmoles. The root surface area was expressed as $\text{cm}^2 \text{ plant}^{-1}$.

Total leaf area was measured using leaf area meter (LI-COR 3000, Lincoln, NE, USA) and expressed as $\text{cm}^2 \text{ plant}^{-1}$. The plants were separated into root and shoot and dried in hot air oven at 65°C until a constant dry weight was reached. Shoot, root, and total plant biomass was obtained and expressed as mg plant^{-1} . Root to shoot ratio was then calculated.

Total sugar was estimated in dried shoot samples by arsenomolybdate method (Nelson, 1944) using improved copper reagent of Somogyi (1952) while starch was measured by anthrone reagent (McCready et al., 1950). P concentration was estimated in root and shoot tissues (Murphy and Riley, 1962) after wet digestion with diacid [nitric acid (HNO_3): perchloric acid (HClO_4)] and measuring the absorbance of blue color phosphomolybdate complex at 660 nm. The P-utilization efficiency (PUE) was calculated by dividing total plant biomass produced by the amount of total P content per plant and expressed as $\text{g dry matter mg}^{-1} \text{ P uptake}$.

Experimental Design and Data Analysis

The experiment consisted of three cereal species, two levels each of CO_2 and P with three replications. The experiment was laid out in completely randomized design with three-factor factorial. In order to truly replicate the CO_2 treatments, three chambers each for ambient and elevated CO_2 treatment with growth conditions as mentioned above were used. A total of six

containers in one growth chamber were kept with three cereal species and two P levels. Data were subjected to analysis of variance (ANOVA) using MSTAT C program (Michigan State University, East Lansing, MI, USA). Statistical significance was determined at 5 and 1% probability level. Means were compared by the critical difference (CD at $P=0.05$, 0.01) following a significant F -test (Chandel, 1997).

RESULTS

Biomass and Leaf Area

A distinct difference was observed in the growth and development of 15-d old plants grown at $a\text{CO}_2$ and $e\text{CO}_2$ with sufficient and low-P (Figure 1). In all three cereal species, plants grown with sufficient P produced more than three leaves compared to those grown with low-P. However, PDW-233 and rye (Figure 1A and 1C) also produced tiller in response to $e\text{CO}_2$ with sufficient P. The root and shoot growth were more in all cereals in response to $e\text{CO}_2$ grown at low-P as compared $a\text{CO}_2$.

Table 1 represents ANOVA for various physiological and biochemical parameters for cereal species in response to elevated CO_2 and P nutrition at $P < 0.05$ and 0.01 level of significance. The shoot, root and total plant dry matter varied significantly ($P < 0.05$ and 0.01) between cereal species, P and CO_2 levels. Shoot dry mass averaged over cereal species was 21% higher in plants raised with sufficient P under $e\text{CO}_2$ compared to $a\text{CO}_2$ (Figure 2A). In plants grown with sufficient P, $e\text{CO}_2$ led to 27, 21, and 14% increase in accumulation of dry matter in

shoots of PDW-233, PBW-396, and rye, respectively, compared to plants raised under aCO₂. However, in plants raised with low-P, the shoot dry matter was 28% higher in response to eCO₂ over aCO₂. The mean root dry matter averaged over CO₂ and P levels was highest in PBW-396 (20.9 mg plant⁻¹) and lowest in rye (13.85 mg plant⁻¹). In plants grown at low-P, a significant increase (52%) in root dry matter was recorded at eCO₂ in comparison to aCO₂ (Figure 2B). Carbon dioxide enrichment had positive effect on total plant dry matter accumulation under sufficient P supply. The total dry matter per plant increased (by 34%) in response to CO₂ enrichment grown with sufficient P (Figure 2C). Interestingly, the total plant dry matter accumulated (averaged over cereals) under low-P at eCO₂ (82.6 mg plant⁻¹) was similar to those grown with sufficient P at aCO₂ (82.1 mg plant⁻¹) indicating that additional carbon is aiding in complete utilization of plant P thereby improving the P-utilization efficiency at low-P with eCO₂. Among cereal species, PDW-233 was found to be most responsive to elevated CO₂ in terms of dry matter accumulation (92.5 mg plant⁻¹) averaged over treatments while rye was least responsive (70.5 mg plant⁻¹). All the cereal species recorded higher root-to-shoot ratio under low-P irrespective of CO₂ levels (Figure 3A). The root-to-shoot ratio averaged over cereal species at low-P recorded a 20% increase in partitioning of dry matter towards roots under eCO₂ in comparison to aCO₂ grown plants.

A significant ($P < 0.05$ and 0.01) increase in whole plant leaf area was found with sufficient P and elevated CO₂ (Table 1). PDW-233 recorded maximum leaf area per plant averaged over CO₂ and P treatments (13.75 cm² plant⁻¹) (Figure 3B). Plants grown with sufficient P, eCO₂ resulted in 43% increase in leaf area as compared to aCO₂. In all cereal species, higher leaf area under sufficient P (12.38 cm² plant⁻¹) was observed compared to low-P

(6.59 cm² plant⁻¹) irrespective of CO₂ level. Among cereal species, percent increase in total leaf area in response to CO₂ enrichment was highest in rye (71%), followed by PBW-396 (59%), and PDW-233 (23%) when grown with sufficient P. However, a marked increase in leaf area was also noted in plants grown at low-P and eCO₂. Percent increase in leaf area in response to eCO₂ in rye and PDW-233 was 39 and 27%, respectively, when grown at low-P.

Root Morphology

Among the root morphological traits, number of lateral root production per plant was significantly ($P < 0.05$) influenced by cereal species, CO₂ and P levels while root length, lateral root density and root surface area showed no significant effect of CO₂ enrichment (Table 1). Rye grown under eCO₂ produced higher number of primary roots irrespective of P treatment (Figure 4A). However, the effect of CO₂ enrichment or P level on number of primary roots per plant was statistically not significant in either PBW-396 or PDW-233. Number of lateral roots per plant averaged over cereal species and P treatment was higher under eCO₂ as compared to aCO₂ (Figure 4B). Lateral root production averaged over CO₂ levels was higher under low-P treatment compared to sufficient P. Among cereals, there was no significant response of rye to CO₂ enrichment, though number of lateral roots was highest under low-P. In PBW-396, about 2-fold increase in lateral root was noted under eCO₂ while it was only 1.2-fold in PDW-233. This indicates that rye was most efficient in lateral root production under low-P.

Root length was significant ($P < 0.05$) only between cereal species and the mean root length averaged over CO₂ and P level was higher in PDW-233 (Figure 5A). Lateral root density,

defined as the number of lateral roots produced per unit length of primary root, varied significantly ($P < 0.05$) only between P levels and cereal species (Table 1, Figure 5B). In general, plants grown at low-P produced higher (13%) lateral root density than those with sufficient P. Rye recorded 2-fold increase in lateral root density at low-P compared to sufficient P irrespective of CO₂ level. Generally, root surface area increases at low-P concentration, which was also noticed in this study in all the cereal species, but there was no significant effect of CO₂ enrichment (Figure 5C). However, the interaction effect between cereal species and CO₂ was significant suggesting that the cereal species responded to CO₂. PDW-233, and rye produced markedly higher root surface area in response to CO₂ levels at low-P, the increase being 50% in rye.

Sugar and Starch Concentration

Total sugar concentration in shoot tissues (on dry weight basis) averaged over all three cereals was maximum in plants grown at low-P, which was 2.0 and 2.3-fold higher than those grown with sufficient P at eCO₂ and aCO₂, respectively (Figure 6A). Among cereal species, sugar concentration averaged over CO₂ and P level was maximum in PBW-396 (19.1 mg g⁻¹ DW) and lowest in PDW-233 (8.25 mg g⁻¹ DW). Nevertheless, PDW-233 responded to CO₂ enrichment by accumulating 3.2-fold higher sugar concentration as against 2.2-fold at ambient CO₂ when grown at low-P over sufficient P. Similarly, in rye, total sugar concentration increased by 2.5-fold and 3.3-fold under eCO₂ and aCO₂, respectively, with low-P as compared to sufficient P. The starch concentration averaged over cereal species showed a significant increase under low-P as

compared to sufficient P while CO₂ treatment had no effect (Figure 6B). The overall increase in starch concentration in shoots at low-P (averaged over CO₂ levels) was 16% as compared to plants grown at sufficient P. Among cereal species, maximum starch concentration was observed in PBW-396 (45.6 mg g⁻¹ DW) while the lowest was recorded in PDW-233 (36.3 mg g⁻¹ DW). Starch accumulation in shoots on per plant basis averaged over cereal species at eCO₂ was 2.41 (low-P) and 3.61 (sufficient P) mg starch plant⁻¹ whereas those grown at aCO₂ accumulated 2.04 (low-P) and 2.79 (sufficient P) mg starch plant⁻¹. Among cereals, PBW-396 accumulated highest starch content (3.25 mg plant⁻¹) (data not presented).

Phosphorus Concentration, Uptake and Utilization Efficiency

Phosphorus concentration in root and shoot tissue was significantly ($P < 0.05$ and 0.01) influenced by CO₂ and P level among the cereal species except, that CO₂ had no significant effect on shoot P concentration (Table 1). Root P concentration averaged over all three cereals increased by 20 and 56% in sufficient and low-P grown plants, respectively in response to elevated CO₂ (Figure 7A). In rye, the root P concentration increased by 11-fold in plants grown with sufficient P at eCO₂ as compared to aCO₂ suggesting higher P demand under elevated CO₂ provided the P supply is not limited. However, even the low-P grown plants showed a 2-fold increase in root P concentration at eCO₂ as compared to aCO₂. The P concentration in shoot tissue was higher at eCO₂ over aCO₂ in sufficient P grown plants though non-significant (Figure 7B). Shoot P concentration averaged over all three cereals increased by 5.5-fold in plants grown at sufficient P as compared to low-P, irrespective of CO₂ level.

The P uptake per plant and PUE were significantly ($P < 0.05$ and 0.01) influenced by CO_2 and P levels among the cereal species (Table 1). The total plant P uptake averaged over all three cereal species grown at eCO_2 increased by 49 and 28% in sufficient and low-P grown plants, respectively as compared to those grown at aCO_2 (Figure 8A). Among cereals, total plant P uptake averaged over CO_2 and P treatments was highest in PDW-233 ($0.195 \text{ mg plant}^{-1}$). The PUE, defined as unit dry matter produced per unit P uptake, was maximum in plants raised under low-P than those raised with sufficient P (Figure 8B). Overall, a 59% increase in PUE was observed in response to eCO_2 as compared to aCO_2 in low-P grown plants. In aCO_2 grown plants, the PUE averaged over cereal species increased by 3-fold at low-P over sufficient P while under eCO_2 , it increased to 6-folds. The PUE averaged over P and CO_2 treatments for PDW-233, PBW-396 and rye were 0.82, 1.11 and $1.22 \text{ g dry matter mg}^{-1} \text{ P uptake}$, respectively. In PBW-396, the PUE was 3.3-fold higher at eCO_2 over aCO_2 when grown with low-P followed by rye which also showed 1.2-fold increase in PUE. However, PDW-233 did not show any increase in PUE due to CO_2 enrichment.

DISCUSSION

Plants respond to elevated $[\text{CO}_2]$ by enhanced production of biomass indicating that an adequate Pi supply for growth in ambient $[\text{CO}_2]$ can limit growth in elevated $[\text{CO}_2]$. Species differ in their ability to overcome nutrient deficiency and the extent to which nutrient requirements change in response to elevated $[\text{CO}_2]$ could also differ among species. Since the bioavailability of soil P to

plants is less, it is pertinent to study the response of cereal species exposed to elevated $[\text{CO}_2]$ under sub-optimum P supply.

In this study, the biomass of all three cereal species was found to be higher at elevated CO_2 grown with sufficient P in the media. However, total plant dry matter accumulated in plants grown with low-P under elevated CO_2 was equivalent to those grown with sufficient P under ambient $[\text{CO}_2]$. This indicates efficient utilization of tissue P under higher $[\text{CO}_2]$. Doubling of CO_2 has been reported to produce largest effect on dry matter accumulation in different plant species provided the nutrient supply is good. Experiments on wheat (Barrett et al., 1998) and barley (Sicher, 2005) under similar conditions confirm these results; however, no such reports are available on rye. Among the cereal species, PDW-233 was found to be more efficient in dry matter accumulation under low-P with eCO_2 as compared to aCO_2 . It has been reported that tetraploid wheat has better drought adaptability than hexaploid and maintain relatively higher dry matter production (Sairam et al., 2001). The present results show that PDW-233 can also adapt to sub-optimal P supply under elevated CO_2 .

Partitioning of dry matter has always been reported to favor root growth under P-limiting conditions as evident from Figure 3A. It is established that under restricted P supply, root growth is enhanced which results in increased root-to-shoot ratio. In this study, root-to-shoot ratio was higher indicating that partitioning of dry matter favors root growth under P limitation which was further enhanced by 20% under elevated CO_2 . Similar reports on rice plants were found with different levels of P and eCO_2 , in which both low-P and high CO_2 increased dry matter partitioning towards the roots (Imai and Adachi, 1996). The reason for increase in root-to-shoot ratio might be the restricted accumulation of shoot dry matter to a much greater extent than the

root dry matter relative to control nutritional treatments (Israel et al., 1990). These reports suggest that plants have the capacity to acclimate to moderate nutrient stress and to utilize the additional assimilates produced by CO₂ enrichment to manufacture dry matter, particularly below ground. Increased root growth in response to sub-optimal nutrient supply is advantageous and allows plants to obtain and utilize the available mineral supply efficiently.

A significant increase in whole plant leaf area was observed with sufficient P and elevated CO₂, which was 43% as compared to those grown at aCO₂. Among cereal species, PDW-233 produced maximum leaf area in all the treatments compared to PBW-396 and rye. This result is in accordance with Israel et al. (1990) who also reported a similar increase in whole plant leaf area in soybean plants with elevated CO₂ (700 $\mu\text{mol mol}^{-1}$) averaged over nutritional treatments. An increase in leaf area and rate of leaf elongation by 18 and 32%, respectively, in wheat due to CO₂ enrichment have been reported (Seneweera and Conroy, 2005). However, sufficient P supply is crucial for leaf expansion since it is known that P deficiency restricts leaf expansion leading to reduced leaf area (Plenet et al., 2000). This restricted leaf expansion is caused by reduction in the rate of cell division and cell expansion under limited P supply (Assuero et al., 2004).

Root morphological characters such as architecture (spatial arrangement) and branching, size, density, and length of root hairs have profound effect on acquisition of nutrients from soil. Any change in the rooting environment such as deficiency of a nutrient element or changed [CO₂], alters root growth and development by enhancing rooting density, thereby, producing more number of lateral roots. The wheat and rye plants grown at eCO₂ with low-P produced higher number of lateral roots per plant, root length and root surface area compared to those

grown at aCO₂ with low-P. Increase in root surface area, volume and root hair length in wheat under P stress has been reported earlier (Pandey et al., 2003). The increase in root surface area under P deficiency is because of the production of finer root hairs and root hair density, which are actively engaged in P mobilization and uptake (Gahoonia and Nielsen, 2004). In cotton plants grown in soil with or without P fertilization, Prior et al. (2003) observed a higher root mass ranging between 55 and 122% in P unfertilized soil due to CO₂ enrichment but the lateral root density did not show any significant effect of CO₂ and P interaction. However, in the present study, rye responded to low-P by producing more than two-fold lateral roots per unit length of primary root. More research is needed along this line to establish the architectural changes in root and its influence on P uptake under elevated CO₂.

Total sugar concentration in shoots increased in plants grown with low-P as compared to sufficient P under both CO₂ levels. Among cereal species, though the maximum total sugar concentration was recorded in PBW-396, but other two cereals also showed a sharp increase in sugar concentration at low-P compared to sufficient P, which was more than 2.5-fold. The present results are consistent with earlier works on barley (Sicher and Kremer, 1988), wheat (Rogers et al., 1993), and rice (Wissuwa et al., 2005; Li et al., 2006) where it was observed that both sugars and starch concentration increases under P deficient condition. However, the soluble carbohydrate and starch content in shoot on per plant basis was not affected by low-P or CO₂ level. The possible reason for enhanced soluble carbohydrate concentration in shoot tissue under low-P might be due to a lower export from shoot to root as a result of limitations in ATP for sucrose-proton co-transport in phloem loading and lower demand at the sink sites. However, the plants were 15-d old and actively growing, so the possibility of lower demand at the sink site

could be ruled out. Rao et al. (1990) suggested that under low-P treatment, activities of some of the key enzymes related to sucrose synthesis pathway, such as sucrose phosphate synthase, cytosolic fructose-1,6-bisphosphatase (FBPase) and uridine-5-diphosphoglucose (UDPG) pyrophosphorylase, increased resulting in higher concentration of soluble carbohydrates. This may be one of the possible reasons for higher total sugars in low-P grown plants though we did not measure the activities of these enzymes. These results warrant additional research on CO₂ x P interaction at biochemical and molecular level. It is speculated that under elevated CO₂, nonstructural carbohydrate levels in plant tissues exposed to nutrient insufficiency would stimulate lateral root formation and thereby improve nutrient acquisition.

It is expected that nutrient uptake (uptake per unit root mass) and utilization (dry matter per unit nutrient uptake) efficiencies may change considerably when the growth environment is altered. Plants grown under non-limiting P supply and elevated CO₂ exhibited higher P concentration in both root and shoot tissues. However, in response to elevated CO₂, the P concentration in shoot decreased by 31% while it increased by 55% in root in comparison to ambient CO₂ grown plants. This decrease in shoot P concentration might be due to dilution effect caused by higher photosynthetic rate at eCO₂ as observed in the case of nitrogen nutrition (Taub and Wang, 2008). Conversely, on a per plant basis, total P content increased by 49% in plants grown with sufficient P under elevated CO₂. Conroy et al. (1992) also reported enhanced P uptake in *Eucalyptus grandis* seedling in response to elevated CO₂ with increasing levels of P supply. At elevated CO₂, the critical concentration of P increased while that of nitrogen decreased in wheat (Rogers et al., 1993). This indicates that more P would be required to support the maximum shoot growth to enable increased flux of carbon through photosynthetic carbon

reduction cycle. These results suggest that critical foliar P concentration currently used to define nutritional status and phosphatic fertilizer management may need to be reassessed as the atmospheric [CO₂] rises.

Generally, the PUE was higher under sub-optimal P supply in all the cereal species. But in response to eCO₂, it increased by 59% in comparison to aCO₂ grown plants at low-P. Increase in PUE is associated with decrease in shoot P concentration due to dilution effect as is evident from the results at elevated CO₂. Imai and Adachi (1996) found a decrease in PUE with increasing P levels in rice while elevated CO₂ increased it by 26%. Amongst cereal species, PDW-233 accumulated highest amount of total dry matter (92.5 mg plant⁻¹) and P content (0.194 mg P plant⁻¹) averaged over P x CO₂ level resulting in lowest PUE. However, the increase in PUE in PBW-396 was 3.3-fold at eCO₂ over aCO₂ when grown with low-P. Upreti et al. (2009) showed that wheat cultivar of different ploidy level responds to elevated CO₂ differentially. The modern wheat cultivar (*Triticum aestivum*) was found to be largely sink-limited. It was demonstrated that hexaploid wheat had less photosynthetic rate per unit leaf area as compared to tetraploid and diploid wheat in spite of having larger leaf size (Upreti et al., 2009). Yet another study provides evidence that tetraploid wheat responds to elevated CO₂ by increasing starch concentration and least decrease in grain protein indicating its suitability in terms of carbon (C): nitrogen (N) ratio (Sinha et al., 2009).

Thus, these findings suggest that the overall decrease in growth due to P insufficiency could be partially ameliorated by CO₂ enrichment. The present study has lead to a better understanding of how cereal crops might be expected to respond to CO₂ enrichment and provides a view on the responsiveness of cereals to P availability under rising CO₂ conditions. The

tetraploid wheat (PDW-233) proves to be more suitable in terms of P utilization efficiency under future conditions of high CO₂ and limiting P supply though hexaploid wheat (PBW-396) also has the potential to perform better by improving PUE.

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Table 1 Analysis of variance (ANOVA) on physiological and biochemical traits of cereal species grown under elevated CO₂ and phosphorus stress

Sources of variation Traits	Species (2) [#]	CO ₂ level (1)	Phosphorus (1)	S x CO ₂ (2)	S x P (2)	CO ₂ x P (1)	S x CO ₂ x P (2)
Shoot dry weight	**	**	**	n.s.	*	*	*
Root dry weight	**	**	**	n.s.	**	n.s.	n.s.
Total plant dry weight	**	**	**	n.s.	**	n.s.	n.s.
Root-shoot ratio	**	**	**	**	n.s.	**	**
Total leaf area	**	**	**	n.s.	n.s.	**	n.s.
No. of primary roots	**	*	n.s.	*	n.s.	n.s.	n.s.
No. of lateral roots	*	**	*	n.s.	**	n.s.	n.s.
Root length	*	n.s.	n.s.	n.s.	**	n.s.	n.s.
Lateral root density	*	n.s.	*	n.s.	**	n.s.	n.s.
Root surface area	**	n.s.	**	**	**	n.s.	n.s.
Total sugar concentration	**	**	**	**	**	n.s.	**
Starch concentration	**	n.s.	**	**	**	**	**
P concentration in shoot	**	n.s.	**	**	**	**	**
P concentration in root	**	**	**	**	**	n.s.	**
Total plant P uptake	**	**	**	**	**	**	**
P utilization efficiency	**	**	**	**	**	**	**

[#]Values in parenthesis denotes degrees of freedom; *, ** and n.s. significant at $P = 0.05$, 0.01 and non-significant, respectively

A

B

C

Figure 1. Interactive effect of elevated CO₂ and phosphorus nutrition on growth and morphological changes in three cereal species (A) PDW-233 (*Triticum durum* L.) (B) PBW-396 (*Triticum aestivum* L.) and (C) WSP-540-2, rye (*Secale cereale* L.). Seedlings were grown in nutrient solution with two levels of P (Low-P; 2 μ M and sufficient P; 500 μ M) and ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Sampling was done at 15-d after transferring seedlings to nutrient solution.

Figure 2. Interactive effect of elevated CO₂ and phosphorus nutrition on (A) shoot dry weight (B) root dry weight, and (C) total plant dry weight of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μ M and sufficient (+P) 500 μ M]; ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Error bars represent SEM values; *values averaged over cereal species for P x CO₂ treatment.

Figure 3. Interactive effect of elevated CO₂ and phosphorus nutrition on (A) root to shoot ratio, and (B) total leaf area per plant of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μ M and sufficient (+P) 500 μ M]; ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Error bars represent SEM values; *values averaged over cereal species for each P x CO₂ treatment.

Figure 4. Interactive effect of elevated CO₂ and phosphorus nutrition on (A) number of primary roots per plant, and (B) number of lateral roots per plant of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μ M and sufficient (+P) 500 μ M]; ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Error bars represent SEM values; * values averaged over cereal species for each P x CO₂ treatment.

Figure 5. Interactive effect of elevated CO₂ and phosphorus nutrition on (A) root length per plant (B) lateral root density, and (C) root surface area per plant of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μ M and sufficient (+P) 500 μ M]; ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Error bars represent SEM values; * values averaged over cereal species for each P x CO₂ treatment.

Figure 6. Interactive effect of elevated CO₂ and phosphorus nutrition on (A) total sugar, and (B) starch concentration in leaves of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μ M and sufficient (+P) 500 μ M]; ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Error bars represent SEM values; * values averaged over cereal species for each P x CO₂ treatment.

Figure 7. Interactive effect of elevated CO_2 and phosphorus nutrition on (A) root phosphorus concentration, and (B) shoot phosphorus concentration of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μM and sufficient (+P) 500 μM]; ambient (aCO_2 380 $\mu\text{mol mol}^{-1}$) and elevated CO_2 (eCO_2 700 $\mu\text{mol mol}^{-1}$). Error bars represent SE_m values; * values averaged over cereal species for each P x CO_2 treatment.

Figure 8. Interactive effect of elevated CO₂ and phosphorus nutrition on (A) total plant phosphorus uptake, and (B) phosphorus utilization efficiency of 15-d old cereal species. Plants were grown in nutrient solution with two levels of P [low (-P) 2 μ M and sufficient (+P) 500 μ M]; ambient (aCO₂ 380 μ mol mol⁻¹) and elevated CO₂ (eCO₂ 700 μ mol mol⁻¹). Error bars represent SEM values; * values averaged over cereal species for each P x CO₂ treatment.