

Original Research Article

<https://doi.org/10.20546/ijcmas.2017.611.347>

Interactive Effect of Elevated (CO₂) on Biomass and Carbohydrate Partitioning under Phosphorus Stress

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ABSTRACT

We investigated the interaction of elevated (CO₂) on partitioning of carbohydrate from shoot to root under phosphorus (P) stress. Experiment was conducted on wheat varieties (*Triticum durum* (PDW-233) and *Triticum aestivum* (PBW-396) to study the interactive effects of P (5 μM and 500 μM) and (CO₂) (400 and 700 μL L⁻¹) was taken. In P-starved plants higher growth was observed at elevated (CO₂). Under nutrient deficiency and/or elevated (CO₂) higher root-to-shoot ratio was observed and increasing nutrient uptake by providing more root surface. P levels or (CO₂) did not cause significant changes to the leaf soluble sugar content, whereas starch concentration increased at low P, irrespective of the CO₂ treatment. The chl_a and total chlorophyll varied significantly only due to nutrient treatment while chl_b was also influenced by (CO₂). The root protein averaged over nutrient treatment increased by 16% in PDW-233 whereas it reduced by 30% in PBW-396 as compared to ambient (CO₂). PDW-233 recorded higher shoot and root protein averaged over (CO₂) and nutrient treatments. The root dry weight was almost doubled in both varieties at e(CO₂) while the total biomass accumulation increased by 54 to 70%. PBW-396 responded to e(CO₂) in terms of biomass accumulation under low P compared to PDW-233 the sugar concentration was more than doubled in PBW-396 as compared to PDW-233. The increase in reducing, non-reducing and total sugars at low P was 40, 122 and 93%, respectively as compared to control. This experiment shows that extra CO₂ help to ameliorate the effect of P deficiency. The severe effects of P deficiency on growth and development of wheat plant was mitigated to some extent by elevated (CO₂).

Keywords

Phosphorus stress,
Biomass, Climate
change.

Article Info

Accepted:
24 September 2017
Available Online:
10 November 2017

Introduction

The increment in the population, urbanization and change in the land use practice tremendously increases in the fossil fuel consumption and results in increase in atmospheric CO₂ concentration (CO₂). The IPCC predicts a wide range of future (CO₂) scenarios, from 540 to 970 ppm by the year 2100 and found that atmospheric CO₂ concentration (CO₂) has increased from 280 ppm during the pre-industrial times to almost

400 ppm at present (IPCC, 2013). Elevated (CO₂) would have profound effects on plant growth like increased rate of carbohydrate synthesis and net photosynthesis coupled with inhibition of photorespiration, ultimately increasing biomass and yield. The basic source of carbon for plant is atmospheric CO₂ which is used to synthesize the metabolites. Increase in atmospheric (CO₂) can modify the root architecture and also the increase the

amount of the exudation of carbon containing compounds (Xu *et al.*, 2016).

P is a non-renewable resource and is projected its depletion by the year 2050 from the major sink of the world due to its intensive use in agriculture (Vance *et al.*, 2003). Being such a vital macronutrient, P nutrition profoundly influences plant growth and development, ultimately affecting crop yield. Most of the soil P remains absorbed onto soil colloids, making it unavailable for plant uptake. P is implicated in essential functions including formation of high-energy bonds, biomolecules and membranes. It is also an integral component of metabolic pathways and signalling cascades (Ticconi *et al.*, 2001). Yet another environmental factor affecting global crop production is the alarming rise in atmospheric CO₂ concentration (hereafter referred as (CO₂)). In spite of public attention focused on the deleterious effects of increasing levels of (CO₂) on global climate, it also exerts direct effects on plant growth and development (Ziska, 2008). These effects result from the central role of CO₂ in plant metabolism. During photosynthesis, plants chemically reduce CO₂ using solar energy. Apart from gaining energy, photosynthesis also provides biomolecules that make up plant structure. Approximately 96% of total dry mass of a plant is made up of carbon, hydrogen and oxygen assimilated as organic compounds during photosynthesis (Marschner, 1995). Therefore, photosynthesis is at the heart of the nutritional metabolism of plants, and increasing the availability of (CO₂) for photosynthesis can have profound effects on plant growth and physiology.

The enhanced availability of (CO₂) particularly in C3 plants would lead to an increased demand of mineral nutrients. Favourable responses of plants to elevated (CO₂) in terms of a rise in photosynthesis and higher biomass may be compromised under

nutrient deficient conditions. Although P deficiency reduces photosynthetic rate, reason for the growth inhibition in P-starved plants arises from a lesser ability to use the available carbohydrates, rather than decline in carbohydrate availability. P deficiency triggers starch accumulation in immature leaves, roots and stem (Jia *et al.*, 2017). Previous report suggests that elevated (CO₂) grown plants require more P than those grown at ambient (CO₂) owing to the increment in photosynthetic rate especially in C3 plants. Despite poor soil fertility, legumes accumulated higher biomass when exposed to elevated rather than ambient (CO₂) (Poorter and Navas 2003). Similarly, wheat plants raised under P deficiency with elevated (CO₂) exhibited higher biomass as compared to those grown under ambient (CO₂) (Pandey *et al.*, 2015a). It is therefore, imperative to understand the interactive effects of CO₂ enrichment and availability of other limiting nutrients on plant growth and development.

P deficiency decreased soybean growth to the extent of 68 and 74% lower biomass and seed yield, attributable to its negative influence on leaf area and net photosynthesis. Increased biomass partitioning toward roots under P deficiency is a consequence of the crops' ability to adjust above- and below-growth growth to enhance nutrient acquisition (Lenka and Lal, 2012). Higher root-to-shoot ratio observed under nutrient deficiency and/or elevated (CO₂) aids in increasing nutrient uptake by providing more root surface. Soil exploration by enhanced root surface area is a preferred adaptation to changing climatic scenarios wherein elevated (CO₂) would increase carbon supply for the production of finer roots (Singh *et al.*, 2013). In contrast, Maestre and Reynolds (2006) reported that root proliferation of a *Brachypodium* increased with nutrient availability and was not influenced by atmospheric (CO₂). It was suggested that belowground biomass

increased with elevated (CO₂) only when sufficient nutrient requirement of the plant was met. In P-starved plants higher growth was observed at elevated (CO₂) without significant increase in nutrient uptake. Higher root dry weight coupled with increased root surface area also improved nutrient acquisition at elevated (CO₂). P deficiency reduced tissue P concentration to a greater extent as compared to plant biomass, leading markedly higher P use efficiency. A higher ratio of N to P was a characteristic phenomenon in P-starved plants, irrespective of (CO₂) treatment. Increased tissue N status of P-starved plants suggests the altered assimilation pathways and N mobility inside the plant (Rufty *et al.*, 1993).

Wheat cultivars with different ploidy levels respond variably to elevated (CO₂), particularly the modern bread wheat (*Triticumaestivum*) was largely sink limited (Uprety *et al.*, 2009). Hexaploid wheat exhibited lesser net photosynthesis per unit leaf area compared to tetraploid and diploid cultivars. Tetraploid wheat responds to elevated (CO₂) though increased starch concentration and least reduction in grain proteins (Sinha *et al.*, 2009). These results suggest that decrease in plant growth due to P deficiency may be partially restored by (CO₂) enrichment. P deprivation inhibits photosynthesis attributed to reduction in the maximum carboxylation efficiency of Rubisco, regeneration of ribulose-1,5-bisphosphate (RuBP) and diffusion of CO₂ across stomata and mesophyll (Singh *et al.*, 2013). The negative effects of P deficiency on photosynthesis may be mitigated to some extent by elevated (CO₂) (Campbell and Sage, 2006).

Irrespective of (CO₂), the total sugar and starch content in shoots increased in low P grown plants compared to sufficient P. However, soluble carbohydrates and starch on

per plant basis remained unaffected by either low P or (CO₂). This may be attributed to lower export from shoots to root as a result of limited ATP for sucrose-proton co transport during phloem loading and a lower demand at the sink sites. Higher activity of enzymes such as sucrose phosphate synthase, cytosolic fructose-1,6-bisphosphatase and uridine-5-diphosphoglucose pyrophosphorylase resulted in increased production of soluble carbohydrates at low P availability. Elevated (CO₂) increases non-structural carbohydrate synthesis that in turn stimulates lateral root formation and improves nutrient acquisition. Such a trend of enhancement in the amount of non-structural carbohydrates was observed in P deficient barley grown under elevated (CO₂) (Sicher, 2005). P levels or (CO₂) did not cause significant changes to the leaf soluble sugar content (Campbell and Sage, 2002), whereas starch concentration increased at low P, irrespective of the CO₂ treatment (Kogawara *et al.*, 2006). P starved plants exhibited more than double starch content irrespective of (CO₂), and when averaged over P levels, elevated (CO₂) caused a three-fold increment in starch content compared to ambient (CO₂).

Barley roots were unable to utilize the available assimilates under both elevated (CO₂) and low P treatments. P deficiency increased sucrose and starch by seven- and 11-fold respectively in soybean. P starved barley exhibited slight increase in transitory starch (Schenck, 2017). In cotton, higher starch concentration was observed at sufficient P and elevated (CO₂), with concomitant reduction in soluble carbohydrates at ambient (CO₂) and sufficient P (Barrett and Gifford, 1995). Higher starch was noted at high P supply under elevated (CO₂) in white clover (*Trifolium*). While, neither (CO₂) nor P nutrition affected carbohydrate concentration of proteoid roots (Denton *et al.*, 2007).

Materials and Methods

Plant material

Two wheat varieties i.e. PBW-396; *Triticum aestivum* (2n=42) and PDW-233; *Triticum durum* (2n=28) were taken for this study. We surface-sterilized wheat two wheat varieties, PBW-396 (*Triticum aestivum* L.) hexaploid and PDW-233 (*T. durum* L.) tetraploid for 1 min in 0.1% mercuric chloride (HgCl₂) washed them thoroughly with water, and germinated them on germination towel for 5-6 days. This was then transferred to Hoagland solution with different nutrient combinations low P (5 µM), low S (10 µM), low P/S (5 µM P + 10 µM S) and control. Eighty seedlings were transplanted to 10-liter opaque plastic containers filled with an aerated nutrient solution containing (Ca(NO₃)₂) 1.5 mM, (KNO₃) 5.0, (NH₄NO₃) 1.0 mM, (MgCl₂) 2.0 mM, (K₂SO₄), (FeCl₃) and micronutrients. Phosphorus was supplied in the form of 1.0 M orthophosphoric acid and sulphur was supplied as K₂SO₄. pH of nutrient solution was maintained at 5.6 during the course of experiment the whole set up was maintained in controlled environment chambers with two CO₂ levels at National Phytotron Facility (NPF), New Delhi (Pandey *et al.*, 2015). The experimental setup was maintained in controlled environment chambers (Model PGW 36, Conviron, Winnipeg, Canada) at National Phytotron Facility, Indian Agricultural Research Institute (IARI), New Delhi. The growth conditions were maintained as: 22°C/12°C day/night temperature, 10 h photoperiod with photon flux density of 450 µmol m⁻² s⁻¹ (PAR) and the relative humidity (RH) was 90%. In elevated CO₂ chamber, the (CO₂) was maintained at 700 µmol mol⁻¹ e(CO₂) using automated flow meter and purified CO₂ supply while in the ambient CO₂ chamber a(CO₂), no external CO₂ 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 ± 10 µmol mol⁻¹.

Estimation of chlorophyll and carotenoid concentration in leaf tissue

Chlorophyll (CHL) and carotenoid contents were estimated by nonmaceration method (Hiscox and Israelstom 1978). Absorbance was recorded at 645 and 663 nm for chlorophylls and 470 nm for total carotenoid contents.

Sugars and Protein

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 (HNO₃:HClO₄) and measuring the absorbance of blue colour phosphomolybdate complex at 660 nm. Total soluble proteins were estimated by Bradford (1976).

Experimental design and data analysis

The experiment consisted of three cereal species, two levels each of CO₂ and P with three replications. The experiment was laid out in completely randomized design with three-factor factorial. Data were subjected to analysis of variance (ANOVA) using MSTAT C programme (Michigan State University, East Lansing, MI, USA).

Result and Discussion

The major pigments involved in photosynthetic activity, i.e., Chlorophyll and carotenoid concentration were estimated in leaf tissue. The *chl a* and total chlorophyll

varied significantly only due to nutrient treatment while *chl_b* was also influenced by (CO₂). There was only marginal increase in chlorophyll concentration under low P (Fig. 1a - c). The photosynthetic pigments were estimated in leaf tissues. The *chl_a* and total chlorophyll varied significantly only due to nutrient treatment while *chl_b* was also influenced by (CO₂). However, there was only marginal increase in chlorophyll and carotenoid concentration in leaf tissues under low P. Similar increase in chlorophyll and carotenoid concentrations were reported earlier under low P in different wheat genotypes (Pandey, 2001). Averaged over variety and nutrients, there was a reduction in *chl_b* concentration in response to e(CO₂). Similar trend for total carotenoid concentration in leaf tissue as chlorophyll was observed except that it was influenced significantly (P<0.01) by variety also (Fig. 1d). Although no effect of e(CO₂) was observed in this experiment, however a recent study showed significant positive effect of interaction between CO₂ and low P on chlorophyll and carotenoid accumulation in wheat species (Pandey *et al.*, 2015a). Under P starvation, the increase in chlorophyll concentration is a well-known P deficiency symptom which is due to accumulation of starch in the chloroplasts (Marschner, 1995). This is also evident from the data on leaf starch concentration in wheat seedlings grown under low P treatment. Among varieties, the carotenoid concentration was higher in leaf tissue of PDW-233 as compared to PBW-396.

Protein concentration in leaf and root tissue were significantly (P<0.01) influenced by variety and nutrient treatment while root protein was also affected by (CO₂) levels (Fig. 2a, b). Among varieties, PDW-233 recorded higher shoot and root protein averaged over (CO₂) and nutrient which were 21% and 19%, respectively as compared to PBW-396. The protein concentration in roots

was not much affected due to low nutrient treatment, particularly in PDW-233 (Fig. 2b). Under e(CO₂), the root protein averaged over nutrient treatment increased by 16% in PDW-233 whereas it reduced by 30% in PBW-396 as compared to a(CO₂). Data on leaf and root protein concentration showed significant effect of variety and nutrient treatment while (CO₂) levels also influenced root protein. PDW-233 recorded higher shoot and root protein averaged over (CO₂) and nutrient treatments. This result is in agreement with earlier reports (Kastori *et al.*, 2000; Tewari *et al.*, 2010). The protein concentration in roots was not affected due to nutrient deprivation treatments, particularly in PDW-233. In response to e(CO₂), the root protein increased in PDW-233 but decreased in PBW-396 which may be due to ploidy level.

The shoot, root and total plant biomass were significantly affected by (CO₂) level, nutrient treatment and between the varieties. There was marked increase in biomass accumulation in response to e(CO₂) in both varieties, PDW-233 and PBW-396, as compared to a(CO₂). In response to e(CO₂), the shoot dry weight averaged over nutrients increased by 64 and 88% in PDW-233 and PBW-396, respectively as compared to a(CO₂) (Fig. 4a). The root dry weight was almost doubled in both varieties at e(CO₂) while the total biomass accumulation increased by 54 to 70%. PBW-396 responded to e(CO₂) in terms of biomass accumulation under low P compared to PDW-233 as reported earlier (Pandey *et al.*, 2015a). Similarly, the root dry weight was almost doubled in both varieties at e(CO₂) (Fig. 4b). The total biomass accumulation in both variety also increased by 70% in PDW-233 and 54% in PBW-396 at e(CO₂) in comparison to a(CO₂) (Fig. 4c). Among varieties, PBW-396 was observed to be more responsive to e(CO₂) in terms of biomass accumulation. Our results are in agreement with earlier reports on different plant species.

Earlier studies also reported increases in biomass accumulation in the range between 10-143% in many C_3 crops (Kimball, 1983). Root-to-shoot ratio was significantly influenced by nutrients ($P < 0.05$) but no effect of (CO_2) and variety was observed (Fig. 4d). However, the root-to-shoot ratio was significantly ($P < 0.01$) influenced by the interactive effects between (CO_2) x N and (CO_2) x N x V. The root-to-shoot ratio averaged over (CO_2) and variety increased under low P (41%). In our previous study, we reported enhanced dry matter accumulation at $e(CO_2)$ with sufficient P supply in cereal species (Pandey *et al.*, 2015a). Goudriaan and

Ruiter, (1983) found that doubling of CO_2 had the largest effect on dry matter production provided nutrient supply is good. Similar results were reported on rice plants when grown under different levels of P and $e(CO_2)$ because 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 was restricted shoot biomass accumulation to a much greater extent than root dry weight relative to the control nutritional treatments (Israel *et al.*, 1990).

Fig.1 Interactive effect of (CO_2), nutrient and variety on photosynthetic pigments in two wheat varieties grown for 26 days after transferring to hydroponics medium. (A) Chlorophyll a (B) chlorophyll b (C) total chlorophyll (D) total carotenoids

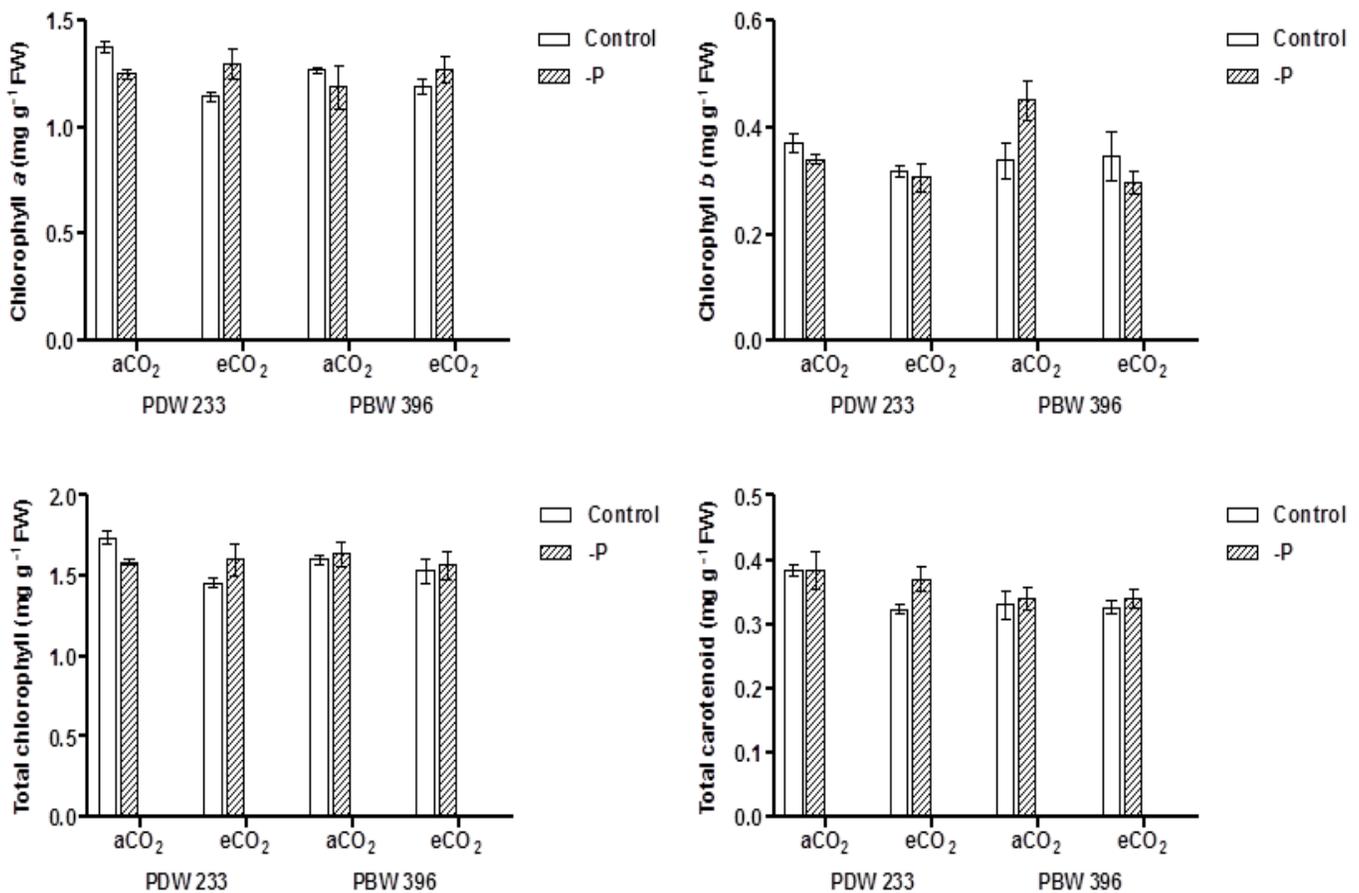


Fig.2 Interactive effect of (CO₂), nutrient and variety on soluble protein concentration in two wheat varieties grown for 26 days after transferring to hydroponics medium. (A) Shoot protein (B) root protein

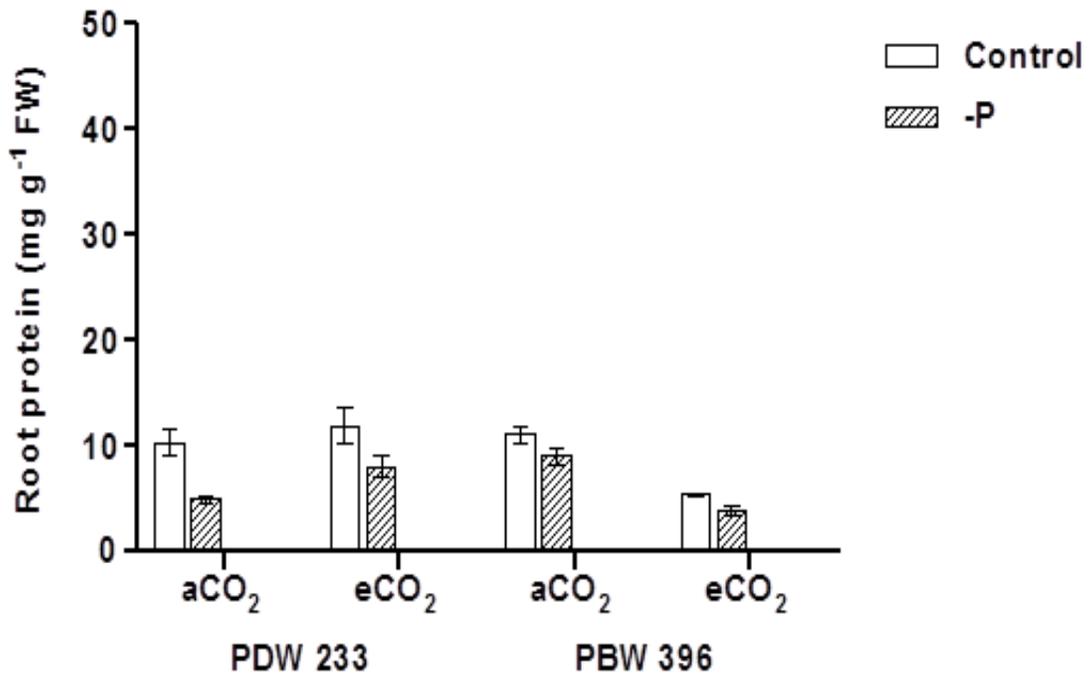
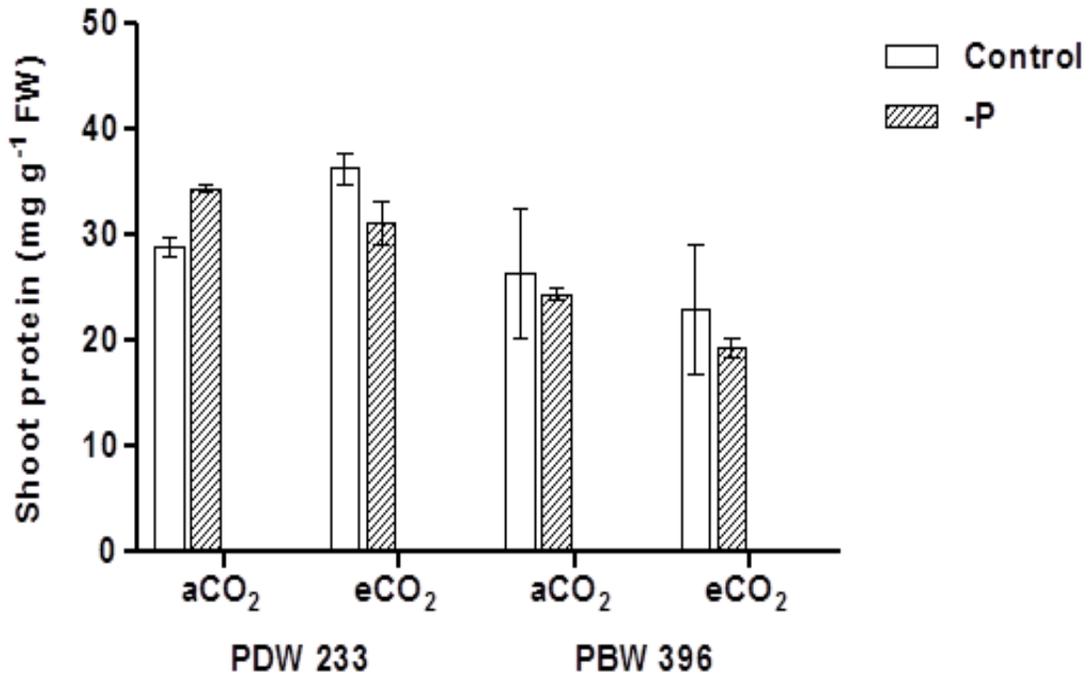


Fig.3 Interactive effect of (CO₂), nutrient and variety on carbohydrate concentration in shoot in two wheat varieties grown for 26 days after transferring to hydroponics medium. (A) Total reducing sugars (B) reducing sugars (C) non-reducing sugars (D) starch

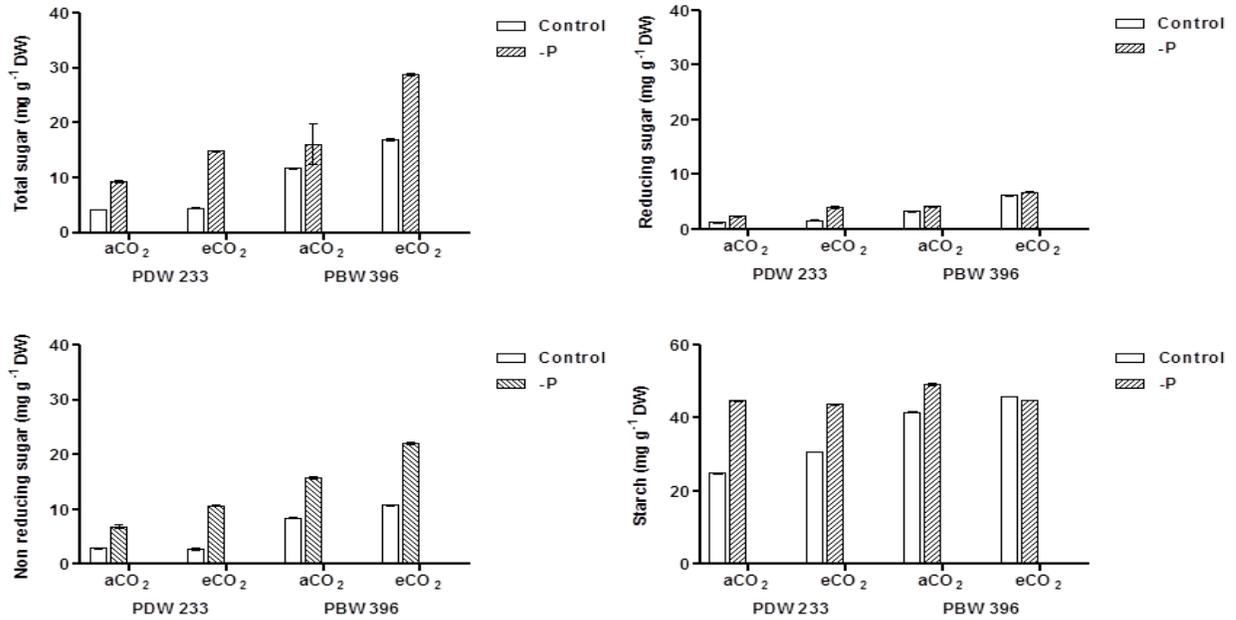


Fig.4 Interactive effect of (CO₂), nutrient and variety on biomass accumulation in two wheat varieties grown for 26 days after transferring to hydroponics medium. (A) Shoot dry weight (B) root dry weight (C) total plant dry weight (D) root-to-shoot ratio

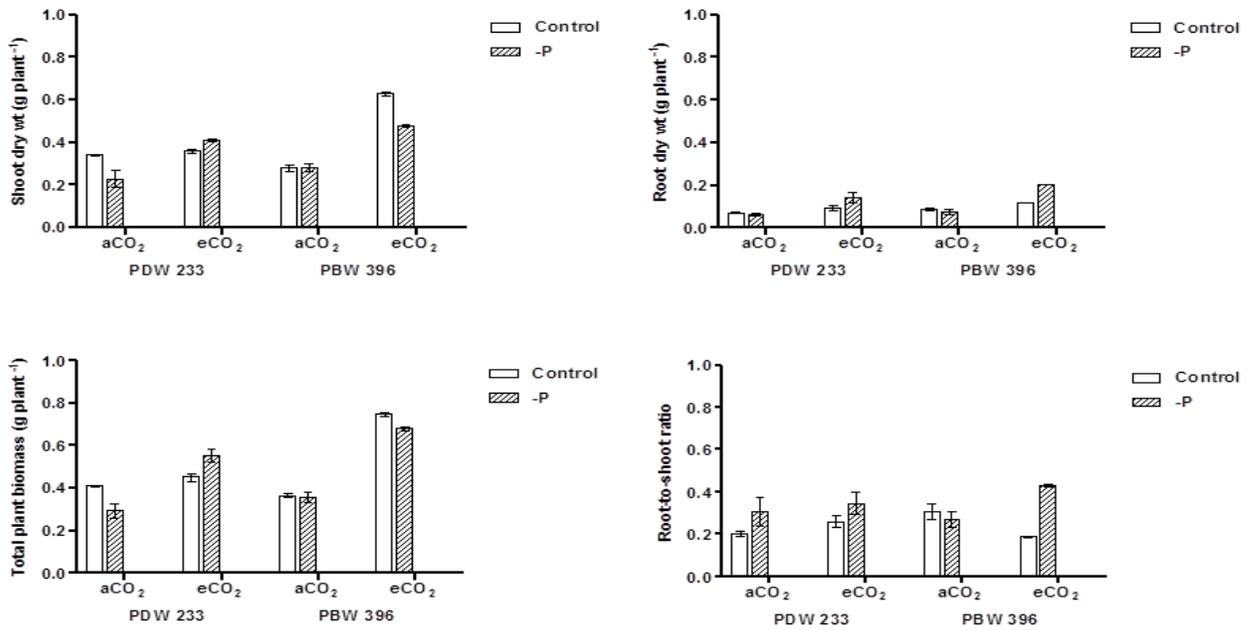
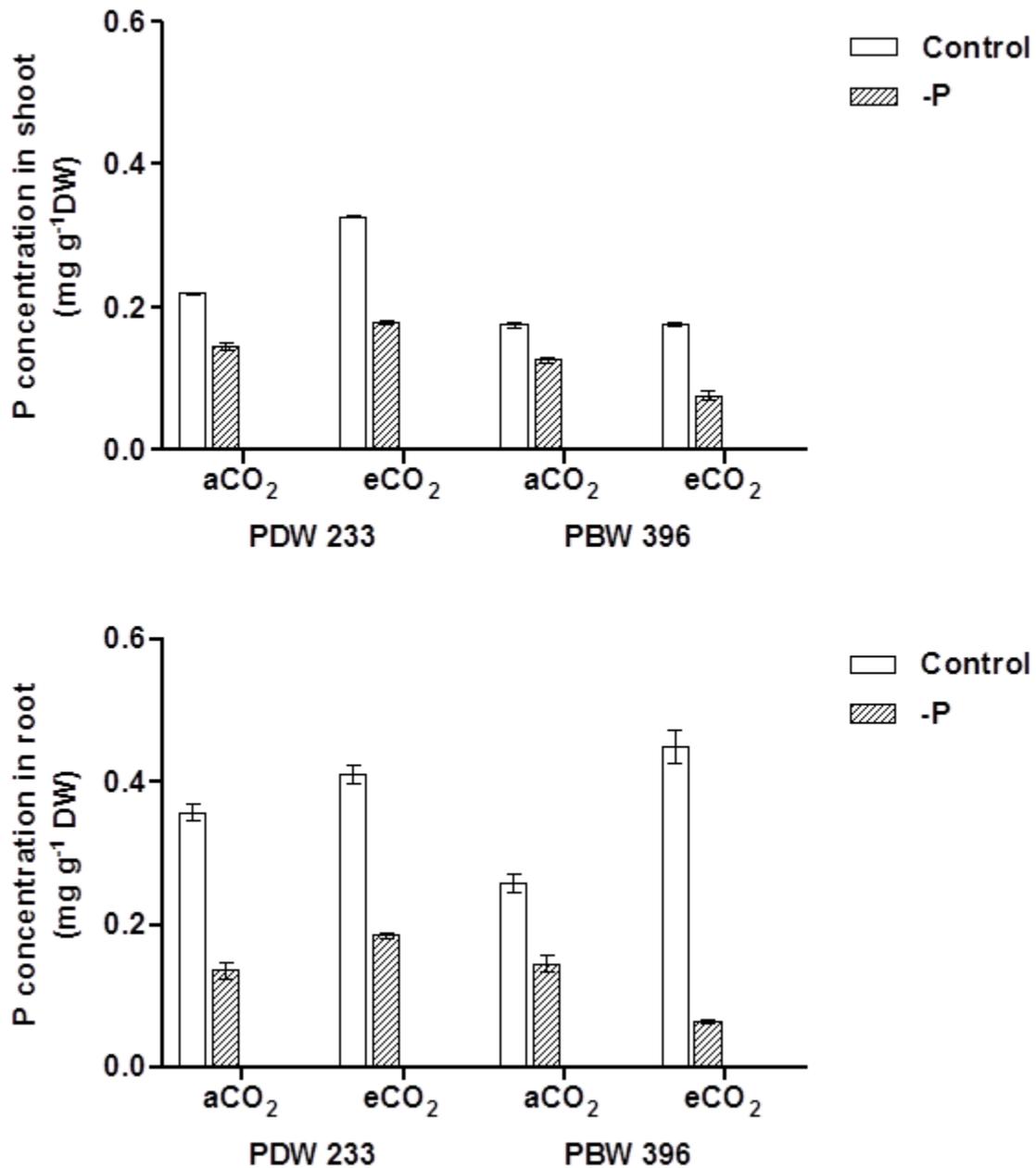


Fig.5 Interactive effect of (CO₂), nutrient and variety on tissue phosphorus concentration in two wheat varieties grown for 26 days after transferring to hydroponics medium. (A) Shoot P concentration (B) root P concentration



The total sugars, reducing and non-reducing sugars in leaf tissue were significantly ($P < 0.01$) influenced by (CO₂), nutrient and variety. Moreover, the interaction between all

these factors also significantly affected the sugars and starch components. Total sugars averaged over nutrient treatments increased by 44% in both varieties in response to

e(CO₂) as compared to a(CO₂) (Fig. 6a). Similarly, reducing and non-reducing sugars also showed marked increase in response to e(CO₂) in both varieties (Fig. 3b,c). The carbohydrate concentration in leaf was significantly affected by (CO₂), nutrient and variety. Reducing and non-reducing sugars and total sugar increased in both varieties in response to e(CO₂). The sugar and starch concentration were higher in PBW-396 compared to PDW-233. Accumulation of sugar and starch were markedly higher at low P. Among varieties, averaged over nutrients and (CO₂), the sugar concentration was more than doubled in PBW-396 as compared to PDW-233. The increase in reducing, non-reducing and total sugars at low P was 40, 122 and 93%, respectively as compared to control (Fig. 3 b,c).

The leaf starch concentration varied significantly due to nutrient and variety while effect of (CO₂) was non-significant (Fig. 3d). Similar to sugar concentration, PBW-396 also accumulated higher (27%) starch as compared to PDW-233. In both varieties, the low P resulted in higher starch as compared to control. The overall increase in leaf starch concentration noted was 28% at low P as compared to control (Fig. 3d). The interactive effect of CO₂ and low P on sugar and starch concentration is in confirmation with other studies in cereal species (Pandey *et al.*, 2015a), barley (Sicher and Kremer, 1988), and rice (Wissuwa *et al.*, 2005) in which both sugars and starch concentration increased under P deficient condition. The role of P in starch synthesis is very well understood. The ratio of Pi to triosephosphates strongly affects the rate of starch synthesis in chloroplast (Marschner, 1995). The accumulation of starch and sugars in leaves of P deficient plants may be because of many reasons. The low Pi concentrations in the cytosol resulting in low export of trioses from the chloroplast, and the increase in activity of ADPG

pyrophosphorylase (Rao *et al.*, 1990) due to low Pi concentrations in the stroma. Accumulation of starch and sugars in leaves can also be indirectly the result of lower export due to limitations in ATP for sucrose-proton co-transport in phloem loading and lower demand at the sink sites.

The P concentration in shoot and root tissues were significantly influenced by (CO₂), nutrient and variety along with their interactive effects. In shoot tissue, there was an overall 30% increase in P concentration at e(CO₂) compared to a(CO₂). There is a synergistic relationship of elevated CO₂ and P with all nutrients interacting which influences the uptake and use efficiency of each nutrient by plants. Varietal response to e(CO₂) showed a higher shoot P concentration in PDW-233 (42%) as compared to PBW-396 (17%) in over a(CO₂). It was obvious to find a marked reduction in shoot P concentration at low P (41%) and low P/S (37%) treatment but a higher value at low S (40%) in comparison to control (Fig. 5a). It is expected that nutrient uptake (uptake per unit root mass) and utilization (dry matter per unit nutrient uptake) efficiencies will be modified considerably when the growth environment is altered. The P concentration in shoot and root tissues and P uptake were significantly influenced by (CO₂), nutrient and variety. An overall 40% increase in P concentration in root tissue was recorded at e(CO₂) compared to a(CO₂) (Fig. 5b). Among varieties, averaged over nutrient treatment, PBW-396 (57%) showed a higher root P concentration than PDW-233 (27%) in response to e(CO₂) over a(CO₂). The increase in P concentration in shoot and root was 30% and 40%, respectively at e(CO₂) as compared to a(CO₂). Similarly, the P uptake in shoot, root and total plant increased 21%, 39% and 25%, respectively in response to e(CO₂). At low P and low P/S treatment more than 60% reduction in root P concentration was

observed in comparison to control. When compared between nutrient treatments, it was obvious that P concentration in shoot and root tissue and P uptake were less at low P.

There was marginal increase in total chlorophyll at low P condition, but $e(\text{CO}_2)$ increased it further in both the varieties. Total carotenoid content also showed similar trend but $e(\text{CO}_2)$ led to 11% higher total carotenoid content. Shoot (21%) and root (19%) protein concentration was higher in PDW-233 under $e(\text{CO}_2)$ and nutrient deprived condition as compared to PBW-396. Total sugar concentration increased by 44% in both varieties in response to $e(\text{CO}_2)$ as compared to $a(\text{CO}_2)$. Similar trends were observed for reducing and non-reducing sugars in response to $e(\text{CO}_2)$ in both varieties. Starch content increased at low P condition under $e(\text{CO}_2)$. This shows the $e(\text{CO}_2)$ provide extra carbon to plant and thus there is more accumulation of dry matter.

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How to cite this article:

Milan Kumar Lal and Renu Pandey. 2017. Interactive Effect of Elevated (CO₂) on Biomass and Carbohydrate Partitioning under Phosphorus Stress. *Int.J.Curr.Microbiol.App.Sci*. 6(11): 2966-2977. doi: <https://doi.org/10.20546/ijemas.2017.611.347>