

# Effect of elevated CO<sub>2</sub> and temperature on phosphorus efficiency of wheat grown in an Inceptisol of subtropical India

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## ABSTRACT

In a phytotron experiment, wheat was grown under two levels of atmospheric CO<sub>2</sub> [ambient (385 ppm) vs. elevated (650 ppm)], two levels of temperature (ambient vs. ambient +3°C) superimposed with three levels of phosphorus (P) fertilization: 0, 100, and 200% of recommended dose. Various measures of P acquisition and utilization efficiency were estimated at crop maturity. In general, dry matter yields of all plant parts increased under elevated CO<sub>2</sub> (EC) and decreased under elevated temperature (ET); however, under concurrently elevated CO<sub>2</sub> and temperature (ECT), root (+36%) and leaf (+14.7%) dry weight increased while stem (-12.3%) and grain yield (-17.3%) decreased, leading to a non-significant effect on total biomass yield. Similarly, total P uptake increased under EC and decreased under ET, with an overall increase of 17.4% under ECT, signifying higher P requirements by plants grown thereunder. Although recovery efficiency of applied P fertilizer increased by 27%, any possible benefit of this increase was negated by the reduced physiological P efficiency (PPE) and P utilization efficiency (PUtE) under ECT. Overall, there was ~17% decline in P use efficiency (PUE) (i.e. grain yield/applied P) of wheat under ECT.

**Keywords:** climate change; wheat yield; <sup>32</sup>P tracer; Indo-Gangetic plains; P nutrition

Rising concentration of atmospheric CO<sub>2</sub> is expected to increase the growth and productivity of C<sub>3</sub> crops like rice and wheat (Kimball et al. 2002, Sujatha et al. 2008). Conversely, associated rise in air temperature may reduce the crop yield, particularly in tropical and subtropical countries like India (Manoj-Kumar et al. 2011b). Thus, to counter the yield reducing effect of atmospheric warming, benefits of carbon fertilisation under rising CO<sub>2</sub> must be realized in Indian agriculture. Elevated CO<sub>2</sub> (EC) studies, however, suggest that EC-induced growth stimulation cannot sustain on nutrient deficient soil (Campbell and Sage 2006), implying that nutrients' application may have to be increased in future to materialize the carbon fertilisation effect of higher CO<sub>2</sub> on crop productivity (Manoj-Kumar et al. 2011a). Given the already existing widespread deficiency of available phosphorus (P) in Indian soils, it is expected to become a critical nutrient to regulate the responses of crop plants under rising CO<sub>2</sub> (Manoj-Kumar

et al. 2011b). Meeting the EC-induced increase in plant P requirement will, therefore, be important for sustaining crop productivity under the future elevation of atmospheric CO<sub>2</sub> and temperature in India.

There could be broadly two possible ways to meet the enhanced P requirement by crops; first, by increasing the doses of P fertilization, and second, by plant's adaptation in terms of its ability to extract P from soil (i.e. P acquisition efficiency), and to convert the absorbed P into grain/biomass yield (i.e. P utilization efficiency) (Raghothama 1999). As P fertilisation involves considerable economic and environmental cost (Vance et al. 2003), it is pertinent to investigate the use efficiency of applied fertilizer-P in a changing climate. Assessment of P uptake- and utilization efficiency is also required to predict the possibility of plants adaptation in response to enhanced P requirement under the future scenario of atmospheric CO<sub>2</sub> and temperature, particularly in the soil and

climatic conditions of India. The current study, therefore, investigates the possible changes in P acquisition and utilization efficiency by wheat under the projected elevation of atmospheric CO<sub>2</sub> and temperature in subtropical India.

## MATERIAL AND METHODS

**Experimental conditions and treatment details.** In a factorial CRD experiment in phytotron growth chambers, wheat (*Triticum aestivum* L. cv. HD-2687) was grown in 1.5 kg capacity pots (3 plants/pot) under two levels of atmospheric CO<sub>2</sub> [ambient (385 ppm) vs. elevated (650 ± 10 ppm)] and two levels of temperature (ambient vs. ambient +3°C) superimposed with three levels of P fertilization: control (no P), 100% (30 mg P/pot) and 200% (60 mg P/pot) of recommended P applied through <sup>32</sup>P-tagged DAP. Each of the treatment combinations (2 CO<sub>2</sub> × 2 temperature × 3 P) were replicated thrice. The experimental soil was a Typic Haplustept of subtropical India (New Delhi) with sandy-loam texture and pH of 8.15. It contained 0.48% organic carbon, 203, 31.2 and 221 kg/ha of available N, P and K, respectively. Further details can be seen elsewhere (Manoj-Kumar et al. 2011b). Considering the current (Figure 1) and the projected CO<sub>2</sub> and temperature levels in subtropical India, the ambient day/night temperatures (AT) during vegetative and grain filling period were set at 23/9°C and 27/12°C, respectively; ET in the respective growth phases were 26/12°C and 30/15°C, respectively, with a variation of ±0.3°C. 12-h photoperiod and photon flux density of 600 μmol/m<sup>2</sup>/s were maintained inside the chambers. Pots were

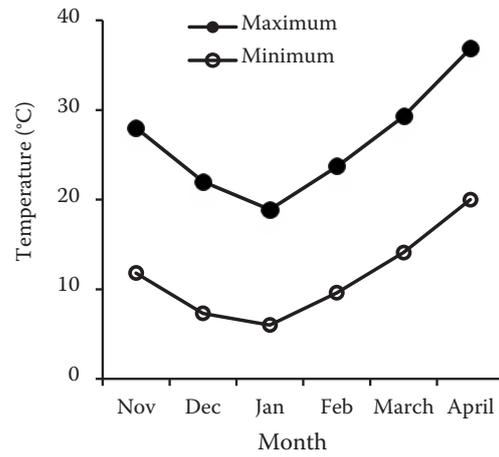


Figure 1. Mean maximum and minimum temperature of wheat-growing months in New Delhi (average of 2001 to 2007) as recorded by meteorological observatory of IARI, New Delhi

regularly watered to avoid moisture stress. They were regularly transferred from one chamber to another, with the required changes in the growth conditions therein. Pots were frequently rotated within the chambers too.

**Measurements, calculations and data analysis.** Plants were harvested (3 plants/pot from 3 replicated pots) at maturity, and separated into root, leaf, stem and grains. Dry weight of plant parts was recorded after drying them in a hot-air oven till constant weight. Samples were digested in a 2:1 mixture of HNO<sub>3</sub> and HClO<sub>4</sub> and P concentration was determined by molybdo-phosphoric acid method. Radio-assay for <sup>32</sup>P activity was carried out using liquid scintillation counter. Percent P derived from fertilizer (%Pdff) was calculated as ratio of the specific activities of plant material and the fertilizer standard. Various measures of P

Table 1. Significance of phosphorus (P), temperature (T) and CO<sub>2</sub> (C) effects on various parameters under study

Parameters	P	T	C	P × T	P × C	C × T	P × T × C
Total biomass yield (g/pot)	**	**	**	**	**	**	*
Total P uptake (mg/pot)	**	**	**	ns	ns (0.06)	ns	ns
%Pdff	**	ns	*	ns	*	ns	ns
Fertilizer-P uptake (mg/pot)	**	*	**	ns	*	ns	ns
SPUE [P uptake (mg)/root (g)]	**	*	**	ns	ns	*	ns
PPE [biomass yield (g)/P uptake (mg)]	**	ns	**	ns	ns	*	ns
PUtE [grain yield (g)/P uptake (mg)]	**	**	ns	ns	ns	ns	ns
PRE (%)	**	**	**	ns	ns	ns	ns
PUE [grain yield (g)/applied P (mg)]	**	**	**	*	*	ns	ns

ns – not significant; \**P* < 0.05; \*\**P* < 0.01; PRE – P recovery efficiency; SPUE – specific P uptake efficiency; PPE – physiological P efficiency; PUtE – P utilization efficiency; PUE – P use efficiency

Table 2. Effects of atmospheric CO<sub>2</sub> (385 vs. 650 ppm), temperature and phosphorus levels on dry weight, P concentration and P uptake of wheat plant parts

	CO <sub>2</sub> levels		Temp. levels		Phosphorus levels		
	ambient	elevated	ambient	ambient +3°C	control P	100% P	200% P
<b>Root</b>							
Dry weight (g/pot)	0.75 <sup>b</sup>	0.98 <sup>a</sup>	0.86 <sup>c</sup>	0.88 <sup>c</sup>	0.73 <sup>b</sup>	0.89 <sup>a</sup>	0.99 <sup>a</sup>
P conc. (%)	0.11 <sup>c</sup>	0.12 <sup>c</sup>	0.09 <sup>b</sup>	0.14 <sup>a</sup>	0.10 <sup>b</sup>	0.12 <sup>ab</sup>	0.13 <sup>a</sup>
P uptake (mg/pot)	0.88 <sup>b</sup>	1.17 <sup>a</sup>	0.80 <sup>b</sup>	1.25 <sup>a</sup>	0.74 <sup>b</sup>	1.08 <sup>a</sup>	1.25 <sup>a</sup>
%Pdff	39.1 <sup>c</sup>	40.2 <sup>c</sup>	39.2 <sup>f</sup>	40.1 <sup>f</sup>	–	35.2 <sup>b</sup>	44.1 <sup>a</sup>
Fertilizer-P uptake (mg/pot)	0.40 <sup>c</sup>	0.54 <sup>b</sup>	0.39 <sup>b</sup>	0.55 <sup>a</sup>	–	0.38 <sup>b</sup>	0.56 <sup>a</sup>
<b>Leaf</b>							
Dry weight (g/pot)	2.60 <sup>b</sup>	3.67 <sup>a</sup>	3.48 <sup>a</sup>	2.80 <sup>b</sup>	2.86 <sup>b</sup>	3.20 <sup>a</sup>	3.36 <sup>a</sup>
P conc. (%)	0.08 <sup>c</sup>	0.09 <sup>c</sup>	0.07 <sup>b</sup>	0.10 <sup>a</sup>	0.07 <sup>c</sup>	0.09 <sup>b</sup>	0.10 <sup>a</sup>
P uptake (mg/pot)	2.15 <sup>b</sup>	3.12 <sup>a</sup>	2.51 <sup>b</sup>	2.76 <sup>b</sup>	1.86 <sup>c</sup>	2.69 <sup>b</sup>	3.34 <sup>a</sup>
%Pdff	30.5 <sup>c</sup>	34.0 <sup>c</sup>	31.2 <sup>d</sup>	33.3 <sup>d</sup>	–	28.2 <sup>b</sup>	36.3 <sup>a</sup>
Fertilizer-P uptake (mg/pot)	0.76 <sup>b</sup>	1.25 <sup>a</sup>	0.96 <sup>c</sup>	1.05 <sup>c</sup>	–	0.77 <sup>b</sup>	1.24 <sup>a</sup>
<b>Stem</b>							
Dry weight (g/pot)	3.58 <sup>b</sup>	4.14 <sup>a</sup>	4.38 <sup>a</sup>	3.34 <sup>b</sup>	3.61 <sup>b</sup>	3.94 <sup>a</sup>	4.03 <sup>a</sup>
P conc. (%)	0.05 <sup>d</sup>	0.05 <sup>d</sup>	0.04 <sup>b</sup>	0.05 <sup>a</sup>	0.04 <sup>b</sup>	0.04 <sup>b</sup>	0.07 <sup>a</sup>
P uptake (mg/pot)	1.69 <sup>b</sup>	2.03 <sup>a</sup>	1.98 <sup>b</sup>	1.73 <sup>b</sup>	1.26 <sup>b</sup>	1.43 <sup>b</sup>	2.88 <sup>a</sup>
%Pdff	32.0 <sup>d</sup>	34.3 <sup>d</sup>	32.1 <sup>d</sup>	34.1 <sup>d</sup>	–	29.5 <sup>b</sup>	36.8 <sup>a</sup>
Fertilizer-P uptake (mg/pot)	0.65 <sup>b</sup>	0.83 <sup>a</sup>	0.77 <sup>d</sup>	0.71 <sup>d</sup>	–	0.42 <sup>b</sup>	1.06 <sup>a</sup>
<b>Grain</b>							
Dry weight (g/pot)	3.54 <sup>b</sup>	5.15 <sup>a</sup>	5.55 <sup>a</sup>	3.13 <sup>b</sup>	3.22 <sup>c</sup>	4.69 <sup>b</sup>	5.11 <sup>a</sup>
P conc. (%)	0.35 <sup>b</sup>	0.40 <sup>a</sup>	0.35 <sup>b</sup>	0.40 <sup>a</sup>	0.32 <sup>b</sup>	0.39 <sup>a</sup>	0.42 <sup>a</sup>
P uptake (mg/pot)	12.3 <sup>b</sup>	20.6 <sup>a</sup>	20.0 <sup>a</sup>	13.0 <sup>b</sup>	10.2 <sup>c</sup>	17.8 <sup>b</sup>	21.5 <sup>a</sup>
%Pdff	47.9 <sup>d</sup>	50.7 <sup>d</sup>	48.8 <sup>e</sup>	49.8 <sup>e</sup>	–	44.6 <sup>b</sup>	54.0 <sup>a</sup>
Fertilizer-P uptake (mg/pot)	6.98 <sup>b</sup>	12.6 <sup>a</sup>	11.7 <sup>a</sup>	7.91 <sup>b</sup>	–	7.99 <sup>b</sup>	11.6 <sup>a</sup>

Values followed by different letters within the same parameter under different levels of the same growth factor are significantly different ( $P < 0.05$ ) by the Duncan's Multiple Range Test. Results pertaining to the main effect of any particular growth factor are averaged over all the levels of remaining two factors. I.e. mean values reported under each level of CO<sub>2</sub> and temperature are derived from 18 observations ( $n = 18$ ) comprising of six treatments, each with three replications. And the mean values reported under each level of P are derived from 12 observations ( $n = 12$ ) comprising of 4 treatments each with three replications. 100% P (30 mg P/pot) and 200% P (60 mg P/pot) roughly correspond to the recommended and twice recommended dose of P to wheat

efficiency were calculated as follows (Doberman 2005):

$$\text{SPUE} = \frac{\text{total P uptake in plant (mg P/pot)}}{\text{root dry weight (g/pot)}}$$

$$\text{PPE} = \frac{\text{total plant biomass (g/pot)}}{\text{total P uptake in plant (mg P/pot)}}$$

$$\text{PUtE} = \frac{\text{total grain yield (mg P/pot)}}{\text{total P uptake in plant (mg P/pot)}}$$

$$\text{PRE} = \frac{\text{total P uptake from fertilizer (mg P/pot)}}{\text{fertilizer applied (mg P/pot)}} \times 100$$

$$\text{PUE} = \frac{\text{total grain yield (g/pot)}}{\text{fertilizer applied (g/pot)}}$$

Experimental data were analyzed following standard statistical methods of Gomez and Gomez (1984). Analysis of variance was carried out using statistical software MSTATC (version 1.41, Crop and Soil Sciences Department, Michigan, USA). The Duncan's Multiple Range Test was used to segregate significance of difference among the mean values.

## RESULTS AND DISCUSSION

**Dry matter yields of wheat.** Dry matter yields of all the plant parts increased under EC (root:

+30.7%, leaf: +41.2%, stem: +15.6%, grain: +45.5%, and total plant biomass: +32.4%) (Tables 1, 2 and 3), but decreased (except root) under ET (leaf: -19.5%, stem: -23.7%, grain: -43.6% and total plant biomass: -28.7%). While EC-induced yield enhancement can be attributed to carbon-fertilisation effect (Kimball et al. 2002), yield reduction under ET might have been caused by the thermal stress particularly during grain-filling period of wheat. Interestingly, plant parts responded differently under the concurrently elevated CO<sub>2</sub> and temperature (ECT). Particularly noticeable were the 36.2% increase in root mass and 17.3% decline in grain yield under ECT. While grain yield reduction under ECT can be ascribed to shortening of grain filling period by 8 days, the higher root mass could be a compensatory response of plant to meet the increased P requirement under high-CO<sub>2</sub> atmosphere (BassiriRad et al. 2001).

**Phosphorus uptake by wheat.** P content in plant parts was unaffected under EC (except in grains) but increased under ET (Table 2); as also under ECT. Total P uptake by plant increased by 58% and decreased by 26% under EC and ET respectively, with 17.4% increase under ECT relative to ACT. Increased grain P content (14%) under EC is not in line with the frequently observed reduction in elemental concentration in plant tissues under CO<sub>2</sub>-enriched atmosphere (Loladze 2002) which is usually ascribed to the 'biomass dilution effect'. In our study, however, P uptake increased along with the increased biomass under EC, which might have checked the dilution of P in plant tissues. EC-induced increase in critical P concentration of wheat under EC (Rogers et al. 1993) also supports our observation.

**Percent (%) Pdff and total P uptake from fertilizer.** There was a slight increase in %Pdff by whole plant at EC but was unaffected at ET (Table 3). The %Pdff was always higher at 200% P than at 100% P level. Increases in %Pdff under ECT compared

to ACT were non-significant. A massive increase (~74%) in total fertilizer-P uptake under EC was the combined effect of increased P uptake and slightly increased proportion of fertilizer-derived P. Fertilizer-P uptake by plant was ~45% higher at 200% P than at 100% P due to higher %Pdff at 200% P supply. Similarly, there was a substantial increase in fertilizer-P uptake (26.7%) under ECT compared to ACT.

**Specific P uptake efficiency (SPUE).** Alteration in SPUE is an adaptation mechanism to cope with the conditions of P deficiency. A moderate increase in SPUE of wheat (~21%) under EC (Table 4) might have been induced by the higher P requirement of plant grown thereunder. Unlike our observation, Cure et al. (1988) reported a 22% decline in P uptake efficiency of soybean under doubled CO<sub>2</sub> concentration; the finding, however, came out of a solution culture experiment with relatively higher levels of P supply. Contrary to the positive effect of EC, the SPUE of wheat was reduced by ET and ECT compared to their respective ambient treatments.

**Physiological P efficiency (PPE) and P utilization efficiency (PUtE).** PPE and PUtE are the measures of plant's ability to convert the absorbed P into total biomass yield and grain yield, respectively. PPE of wheat was reduced by 15% under EC (Table 4). However, increased harvest index under EC restricted the decline in PUtE to a non-significant 9.5% ( $P = 0.35$ ). This does not corroborate the findings of Conroy (1992) and Niklaus et al. (1998), who reported increased P use efficiency by plants under high-CO<sub>2</sub> atmosphere. These studies, however, were not representative of the soil and climatic conditions in India. ET caused a non-significant decline in PPE but a significant decline of 23% in PUtE of wheat. The decline was mediated mainly through the adverse effects of higher temperature on total biomass and grain yield coupled with the less pronounced effects

Table 3. Effects of atmospheric CO<sub>2</sub> (385 vs. 650 ppm), temperature and phosphorus levels on dry weight, P concentration and P uptake of whole plant

	CO <sub>2</sub> levels		Temperature levels		Phosphorus levels		
	ambient	elevated	ambient	ambient +3°C	control P	100% P	200% P
Dry weight (g/pot)	10.5 <sup>b</sup>	13.9 <sup>a</sup>	14.3 <sup>a</sup>	10.2 <sup>b</sup>	10.4 <sup>c</sup>	12.7 <sup>b</sup>	13.5 <sup>a</sup>
P uptake (mg/pot)	17.1 <sup>b</sup>	27.0 <sup>a</sup>	25.3 <sup>a</sup>	18.7 <sup>b</sup>	14.0 <sup>c</sup>	23.0 <sup>b</sup>	29.0 <sup>a</sup>
%Pdff	50.9 <sup>d</sup>	55.9 <sup>c</sup>	54.2 <sup>d</sup>	54.0 <sup>d</sup>	–	42.2 <sup>b</sup>	48.6 <sup>a</sup>
Fertilizer-P uptake (mg/pot)	8.70 <sup>c</sup>	15.1 <sup>b</sup>	13.7 <sup>c</sup>	10.1 <sup>d</sup>	–	9.71 <sup>d</sup>	14.1 <sup>c</sup>

Treatments description and statistical analyses are the same as described in the legend of Table 2

Table 4. Effects of atmospheric CO<sub>2</sub> (385 vs. 650 ppm), temperature and phosphorus levels on phosphorus efficiency in wheat

	CO <sub>2</sub> levels		Temperature levels		Phosphorus levels		
	ambient	elevated	ambient	ambient +3°C	control P	100% P	200% P
SPUE [P uptake (mg)/root mass (g)]	22.8 <sup>b</sup>	27.6 <sup>a</sup>	29.4 <sup>c</sup>	21.3 <sup>d</sup>	19.2 <sup>c</sup>	25.8 <sup>b</sup>	29.3 <sup>a</sup>
PPE [biomass yield (g)/P uptake (mg)]	0.66 <sup>a</sup>	0.56 <sup>b</sup>	0.62 <sup>d</sup>	0.60 <sup>d</sup>	0.77 <sup>a</sup>	0.57 <sup>b</sup>	0.48 <sup>c</sup>
PUtE [grain yield (g)/P uptake (mg)]	0.21 <sup>b</sup>	0.19 <sup>b</sup>	0.22 <sup>a</sup>	0.17 <sup>b</sup>	0.23 <sup>a</sup>	0.20 <sup>b</sup>	0.17 <sup>c</sup>
PRE (%)	20.5 <sup>b</sup>	35.3 <sup>a</sup>	32.1 <sup>a</sup>	23.8 <sup>b</sup>	–	32.4 <sup>a</sup>	23.4 <sup>b</sup>
PUE [grain yield (g)/applied P (mg)]	98.3 <sup>b</sup>	143 <sup>a</sup>	154 <sup>a</sup>	87.7 <sup>b</sup>	–	156 <sup>a</sup>	85.2 <sup>b</sup>

Treatments description and statistical analyses are the same as described in the legend of Table 2. PRE – P recovery efficiency; SPUE – specific P uptake efficiency; PPE – physiological P efficiency; PUtE – P utilization efficiency; PUE – P use efficiency

on total P uptake by plant. Increasing doses of P fertilization also showed suppressive effect on both the measures of P efficiency. Particularly noteworthy was the substantial decline in both PPE (–17.5%) and PUtE (–30.4%) under ECT compared to ACT. The reduced P efficiencies in combination with the increased P uptake under ECT imply that plant will absorb more P from soil to meet its higher P requirement, but the conversion efficiency of absorbed P into grain and total biomass yield will be poor under the future scenario of high CO<sub>2</sub> and temperature.

**P recovery efficiency (PRE) and P use efficiency (PUE).** PRE (% recovery of applied fertilizer) by wheat increased significantly under EC relative to AC (Table 4). This increase was the combined effect of higher %Pdff and the higher total P uptake by plant under EC. PUE (grain yield per unit P application) was also improved by 45.5% at EC owing to the similar increase in grain yield. ET caused 26% decline in PRE and 43% in PUE of wheat (Table 4). The results reinforce the prediction of Aggarwal (2007) who, based on a simulation study, expressed the possibility of reduced fertilizer use efficiency in Indian agriculture under the changing scenario of global warming. As expected, PRE and PUE at 200% P level were always lower than at 100% P. Notwithstanding the reduction in PRE under ET, it was increased by 27% under ECT. A 17% decline in PUE caused by a similar decline in grain yield under ECT is not an encouraging observation for future wheat production under a changing climate in India.

Overall, our study suggests that plant's P requirement may increase under the rising atmospheric CO<sub>2</sub> and temperature as indicated by the significantly higher uptake of P despite the reduced yield of wheat under ECT. Although certain compensatory responses by plants, in terms of better root

growth and higher recovery efficiency of applied P, may be elicited in response to higher P requirement, the benefits of such responses may get offset by the reduction in P utilization efficiency and overall P use efficiency under ECT. Our study, therefore, underlines the need of P-efficient crop cultivars and the nutrient management practices for sustaining crop productivity in a changing climate.

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