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BRIEF COMMUNICATION

# Effects of phosphorus and chilling under low irradiance on photosynthesis and growth of tomato plants

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## Abstract

To determine the effects of phosphorus nutrition on chilling tolerance of photosynthetic apparatus, tomato (*Lycopersicon esculentum* Mill. cv. Kenfengxin 2002) plants were raised under different P contents and subjected to 7 d of chilling at 9/7 °C. After chilling (2 h or 7 d) plant growth, P content in tissue, gas exchange and chlorophyll fluorescence were measured. Decreasing P concentration [P] in the nutrient solution markedly reduced plant growth and the chilled plants exhibiting higher optimum [P] than the unchilled plants. Decreasing [P] significantly decreased light saturated net photosynthetic rate ($P_{Nsat}$), maximum carboxylation velocity of Rubisco ($V_{cmax}$), maximum potential rate of electron transport contributed to Rubisco regeneration ($J_{max}$), quantum efficiency of photosystem (PS) 2 ($\Phi_{PS2}$) and $O_2$ sensitivity of $P_{Nsat}$ ($PS_{O2}$) and this trend was especially apparent in chilled plants.

*Additional key words*: chlorophyll fluorescence, inorganic phosphate limitation, net photosynthetic rate, Rubisco, *Lycopersicon esculentum*

Plants are frequently exposed to stresses such as nutrient deficiency, salinity, chilling, pathogens, *etc.* (Zhou *et al*. 2004a,b, Stępień and Kłobus 2006, Bertamini *et al.* 2007, Weng *et al*. 2008). Phosphorus deficiency is very common since the combination of P with aluminum and iron in soil makes it difficult to be absorbed by plants. There are many reports about the effects of P deficiency on plant physiology (Shinano *et al*. 2005, Wissuwa *et al*. 2005, Weng *et al*. 2008). Low P may affect photosynthesis by modifying the contents of phosphorylated intermediates within the chloroplast, activation of Calvin-cycle enzymes, and RuBP regeneration (Sawada *et al*. 1992, Rao and Terry 1995). In severely P-deficient leaves the regeneration of ATP is slow and the rate of photosynthesis and the export of photosynthates is decreased (Jacob and Lawlor 1992, Rao and Terry 1995). Recently, it has been suggested that the production, rather than the utilization of photosynthates for tomato plants is limited when P supply is decreased (De Groot *et al*. 2001).

Crops frequently encounter long episodes of unfavourable conditions such as low temperature in combination with low irradiance (Zhou *et al*. 2004b, 2006, Hu *et al*. 2006). Besides inhibition of ion uptake, chilling directly disrupts all major components of the photosynthetic apparatus (Allen and Ort 2001). Although P is known to be involved in the regulation of several photosynthetic processes, relatively little is known about the relationship between chilling, P concentration [P] and photosynthesis. Low [P] increases chilling sensitivity and retards recovery after a chilling period. It has been argued that [P], which is

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*Abbreviations*: $c_i$ - intercellular $CO_2$ concentration; $F_v/F_m$ - maximum photochemical efficiency of PS 2; $F_v'/F_m'$ - efficiency of excitation capture by open PS 2 centers; $g_s$ - stomatal conductance; $J_{max}$ - maximum potential rate of electron transport contributed to Rubisco regeneration; [P] - phosphorus concentration; $P_{Nsat}$ - light saturated net photosynthetic rate; $PS_{O2}$ - $O_2$ sensitivity of photosynthesis; $q_p$ - photochemical quenching coefficient; S/R - shoot to root ratio; TPDM - total plant dry mass; $V_{cmax}$ - maximum carboxylation velocity of Rubisco; $\Phi_{PS2}$ - quantum efficiency of PS 2.
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sufficient under optimal temperature, may not be sufficient during chilling (Starck *et al*. 2000). Farmers are known to apply more P fertilizer on crops during the cool season than during the optimal growth season, for the purpose of enhancing chill tolerance. However, there is not yet enough evidence to justify this practice.

To examine the relationship between [P] and the chill tolerance of the photosynthetic apparatus, tomato plants were raised under different [P] in nutrient solutions and subjected to a period of chilling under low irradiance.

The experiments were conducted at Huajiachi Campus, Zhejiang University from March to June in 2006. Tomato (*Lycopersicon esculentum* Mill. cv. Kenfengxin 2002) plants were grown in plastic pots in a greenhouse. The pots were filled with a mixture of soil: *Perlite* (1:1, v/v). The plants were watered and fertilized daily with a half-strength Enshi nutrient solution comprising the following nutrients [mM]: $Ca(NO_3)_2 \cdot 4\ H_2O$ 1.5, $KNO_3$ 4.0, $MgSO_4 \cdot 7\ H_2O$ 1.0, $NH_4H_2PO_4$ 0.6, $H_3BO_3$ $46\times10^{-3}$, $FeSO_4$ $18\times10^{-3}$, $Na_2EDTA$ $16\times10^{-3}$, $MnCl_2$ $14\times10^{-3}$, $ZnSO_4$ $0.7\times10^{-3}$, $Na_2MoO_4$ $0.5\times10^{-3}$, $CuSO_4$ $0.3\times10^{-3}$. Groups of six seedlings at the 4-leaf stage were transplanted into 15 $dm^3$ containers filled with the same Enshi solution. The conditions in the greenhouse were as follows: a 12-h photoperiod, day/night temperature of 25/17 °C, average photosynthetic photon flux density (PPFD) of 600 µmol $m^{-2}\ s^{-1}$ and air relative humidity 80 %.

After 5 d pre-culture, plants were transported into nutrient solutions with different [P]: *1*) 0 mM, *2*) 0.15 mM, *3*) 0.60 mM, *4*) 2.40 mM. To grow plants under different [P], $PO_4^{3-}$ was replaced by $SO_4^{2-}$ at an equivalent $Na^+$ concentration, or $KNO_3$ was replaced by $KH_2PO_4$ and $NaNO_3$. The nutrient solutions were changed every 5 d. Fourteen days later, half of the plants were exposed to 9/7 °C (day/night) at 100 µmol $m^{-2}\ s^{-1}$ PPFD as the chilling treatment. The other half of the plants was maintained in the greenhouse at 25/17 °C at 600 µmol $m^{-2}\ s^{-1}$ PPFD as unchilled plants. After 7 d, the chilled plants were returned back to the greenhouse and grown together with unchilled plants for further 7 d.

Dry mass of shoots and roots was measured after drying in oven at 80 °C till constant mass. Leaf samples (300 mg) were digested using concentrated sulphuric acid at 250 °C. The total P concentration was analyzed using the ammonium molybdate colorimetric method (Jackson 1958). During plant growth, light saturated photosynthetic rate ($P_{Nsat}$), stomatal conductance ($g_s$) and intercellular $CO_2$ concentration ($c_i$) were measured with an infrared gas analyser (*Ciras-1*, *PP System*, Hitchin, UK). The air temperature was maintained at 25 °C, air humidity at 80 %, PPFD at 1000 µmol $m^{-2}\ s^{-1}$, and $CO_2$ concentration at 380 µmol $mol^{-1}$. Measurement and estimation of the maximum carboxylation velocity of Rubisco ($V_{cmax}$) and the maximum potential rate of electron transport contributed to RuBP regeneration ($J_{max}$) were made according to Zhou *et al*. (2004b) and Ethier and Livingston (2004).

Modulated chlorophyll fluorescence was measured with a pulse amplitude fluorimeter (*Hansatech Instruments*, Norfolk, UK) on the same leaves previously used for gas exchange measurements. Leaves were maintained in darkness for 20 min prior to measurement of the maximum quantum efficiency of PS 2 ($F_v/F_m$). An actinic light source (600 µmol $m^{-2}s^{-1}$) was applied to achieve steady state fluorescence yield, *i.e*. the quantum efficiency of PS 2 ($\Phi_{PS2}$), the efficiency of excitation capture by open PS 2 centers ($F_v'/F_m'$), and the photochemical quenching coefficient ($q_p$) (Zhou *et al*. 2004a,b).

To estimate deficiency in inorganic phosphate (Pi) in chloroplasts, $P_{Nsat}$ was determined under both photo-respiratory (21 % $O_2$) and non-photorespiratory (2 % $O_2$) conditions. $O_2$ sensitivity of photosynthesis ($PS_{O2}$) was calculated as follows: $PS_{O2}$ = ($P_{Nsat}$ at 2 % $O_2$ - $P_{Nsat}$ at 21 % $O_2$) /$P_{Nsat}$ at 21 % $O_2$. Pi limitation is characterized by reduced sensitivity to $O_2$ (Leegood and Furbank 1986).

The measurements were performed on randomly selected samples from four replicates and Duncan's multiple range test at $P \leq 0.05$ was used to compare the significance of differences among treatments.

The unchilled plants had their highest P contents in leaves at 0.60 mM [P] while chilled plants had their highest P contents in leaves at 2.40 mM [P]. Chilling resulted in reductions in P contents in leaves except that P contents in chilled leaves supplied with 2.40 mM [P] was not significantly different from that in unchilled leaves. For unchilled plants, roots and shoots showed greatest biomass accumulation at 0.15 mM and 0.60 mM [P], respectively. Other concentrations decreased root and shoot biomass accumulation. Chilling significantly decreased plant dry matter and a larger effect on shoots than on roots was observed. However, an increase in root biomass accumulation was observed in chilled plants at 0 and 2.40 mM [P]. In comparison to unchilled plants showing the highest total plant dry mass (TPDM) at 0.60 mM [P], chilled plants showed highest TPDM at 2.40 mM [P]. It is apparent that plants need higher [P] under low temperature than under optimum conditions (Table 1). In agreement with this, previous studies showed that increased P supply increased plant growth at high salinity (Kaya *et al*. 2001, Shibli *et al*. 2001). Here we also found that R/S increased with the decrease in P supply, and this trend is especially apparent in chilled plants. In agreement with our observation, Starck *et al.* (2000) observed that chilling had greater negative effects on shoots than on roots in tomato plants. Results from other studies also support that plants allocate a greater proportion of their biomass to the root system when mineral elements are scarce (Hermans *et al*. 2006).

Unchilled plants showed their highest $P_{Nsat}$ and $g_s$ at 0.60 mM [P] with only slight difference among 0.15, 0.60 and 2.40 mM [P] treatments (Table 2). As observed in our previous studies (Hu *et al*. 2006), chilling resulted in significant decreases in $P_{Nsat}$ and $g_s$ and the reductions were most significant at 0.15 mM [P] in which $P_{Nsat}$ and $g_s$ were only 36.7 and 24.2 % of the unchilled plants at 2 h of recovery after chilling, respectively. $P_{Nsat}$ and $g_s$ were very low at 0 mM [P]. In addition to the decreases in $P_{Nsat}$ and $g_s$,

Table1. Changes of phosphorus contents in leaves, root and shoot dry matter, total plant dry matter (TPDM) and root/shoot ratio (R/S) as influenced by phosphorus concentration ( 0 - 2.40 mM) in the nutrient solution and chilling (7/9 °C). Means ($n$ = 4) within a row followed by different letters are significantly different at $P \leq 0.05$.

| Parameters | Recovery | 0 mM | | 0.15 mM | | 0.60 mM | | 2.40 mM | |
|---|---|---|---|---|---|---|---|---|---|
| | | unchilled | chilled | unchilled | chilled | unchilled | chilled | unchilled | chilled |
| P content [mg $g^{-1}$ (d.m.)] | 2 h | 4.00d | 3.10e | 5.70c | 4.40d | 8.10a | 5.50c | 7.40ab | 7.30b |
| Root d.m. [g $plant^{-1}$] | 7 d | 0.19e | 0.37d | 0.71a | 0.57c | 0.55c | 0.65b | 0.38d | 0.63b |
| Shoot d.m. [g $plant^{-1}$] | 7 d | 0.62e | 0.99e | 5.55b | 2.87d | 8.45a | 4.48c | 7.38a | 4.80bc |
| TPDM [g $plant^{-1}$] | 7 d | 0.81g | 1.36f | 6.26c | 3.44e | 9.00a | 5.13d | 7.76b | 5.43d |
| R/S | 7 d | 0.31a | 0.37a | 0.13c | 0.20b | 0.07d | 0.15c | 0.05d | 0.13c |

Table 2. Changes of light saturated photosynthetic rate ($P_{Nsat}$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($c_i$), maximum carboxylation velocity by Rubisco ($V_{cmax}$), maximum potential rate of electron transport contributed to RuBP regeneration ($J_{max}$), maximum photochemical efficiency of PS 2 ($F_v/F_m$), quantum efficiency of PS 2 ($\Phi_{PS2}$), photochemical quenching coefficient ($q_p$), efficiency of excitation capture by open PS 2 centers ($F_v'/F_m'$) and $O_2$ sensitivity of photosynthesis ($PS_{O2}$) as influenced by phosphorus concentration in the nutrient solution and chilling. Means ($n$ = 4) within a row followed by different letters are significantly different at $P \leq 0.05$.

| Parameters | Recovery | 0 mM | | 0.15 mM | | 0.60 mM | | 2.40 mM | |
|---|---|---|---|---|---|---|---|---|---|
| | | unchilled | chilled | unchilled | chilled | unchilled | chilled | unchilled | chilled |
| $P_{Nsat}$ [µmol $m^{-2}$ $s^{-1}$] | 2 h | 0.35e | 0.73d | 10.59ab | 3.43d | 12.95a | 8.17bc | 11.71a | 6.70c |
| | 7 d | 0.41d | 3.62c | 5.24c | 7.13b | 8.47a | 9.17a | 8.23ab | 9.41a |
| $g_s$ [mmol $m^{-2}$ $s^{-1}$] | 2 h | 52.3 c | 12.7 e | 135.5 a | 31.4 d | 161.7 a | 91.5 b | 149.6 a | 63.3 c |
| | 7 d | 74.3 c | 84.1 c | 79.3 c | 144.2 ab | 144.1 ab | 159.3 a | 122.7 b | 129.8 b |
| $c_i$ [µmol $mol^{-1}$] | 2 h | 323.7 a | 231.3 b | 189.2 c | 161.1 d | 206.7 bc | 183.3 cd | 211.5 bc | 198.3 c |
| | 7 d | 328.3 a | 283.3 b | 267.7 b | 241.3 c | 234.3 c | 239.2 c | 216.7 c | 228.3 c |
| $V_{cmax}$ [µmol $m^{-2}$ $s^{-1}$] | 2 h | 7.9 e | 16.5 d | 66.3 a | 29.0 c | 67.8 a | 43.6 b | 78.6 a | 49.6 b |
| | 7 d | 12.9 f | 22.5 e | 35.9 d | 58.8 bc | 74.6 a | 78.9 a | 71.3 ab | 67.4 b |
| $J_{max}$ [µmol $m^{-2}$ $s^{-1}$] | 2 h | 25.8 d | 38.3 d | 221.8 a | 116.7 c | 246.8 a | 136.8 b | 215.0 a | 159.6 b |
| | 7 d | 32.7 e | 71.7 d | 111.3 c | 146.2 b | 209.3 a | 213.1 a | 214.9 a | 194.1 a |
| $F_v/F_m$ | 2 h | 0.31c | 0.47b | 0.84a | 0.83a | 0.84a | 0.83a | 0.83a | 0.83a |
| | 7 d | 0.28d | 0.67c | 0.78b | 0.71b | 0.85a | 0.84a | 0.84a | 0.84a |
| $\Phi_{PS2}$ | 2 h | 0.08d | 0.09d | 0.36b | 0.21c | 0.47a | 0.24c | 0.44a | 0.28c |
| | 7 d | 0.04d | 0.16d | 0.23c | 0.30ab | 0.26bc | 0.36a | 0.32a | 0.37a |
| $q_p$ | 2 h | 0.46c | 0.27d | 0.58b | 0.61ab | 0.69a | 0.56b | 0.65a | 0.58b |
| | 7 d | 0.19e | 0.29d | 0.41c | 0.46c | 0.51bc | 0.65a | 0.59ab | 0.68a |
| $F_v'/F_m'$ | 2 h | 0.17e | 0.32d | 0.62a | 0.34d | 0.68a | 0.43c | 0.68a | 0.47b |
| | 7 d | 0.21c | 0.54b | 0.57b | 0.66a | 0.51b | 0.56b | 0.54b | 0.55b |
| $PS_{O2}$ | 2 h | 0.21c | 0.13d | 0.29b | 0.22c | 0.37a | 0.33b | 0.38a | 0.43a |
| | 7 d | 0.19c | 0.22bc | 0.29b | 0.27b | 0.40a | 0.38a | 0.41a | 0.38a |

chilling also lowered $c_i$ values. There was a general decrease in $P_{Nsat}$ and $g_s$ for unchilled plants due to leaf senescence while $P_{Nsat}$ and $g_s$ for chilled plants were little changed and increased after 7 d of recovery at optimal growth conditions. Starck *et al.* (2000) found that mineral starvation combined with chilling reduced the rate of photosynthesis and stomatal conductance to a greater extent than in plants grown in a full nutrient solution. Therefore, plants need higher [P] for the proper operation of the photosynthetic apparatus at low temperature than at optimum temperature.

Although chilling and P supply had significant influence on $g_s$, reduction in $CO_2$ assimilation could not be solely attributed to stomatal factor alone. For example, P starvation resulted in a reduction in $g_s$ while $c_i$ was increased (Table 1). In fact, $V_{cmax}$ and $J_{max}$ were not different at 0.15 - 2.40 mM [P] in unchilled plants at time corresponding to 2-h recovery of chilled plants but they were significantly lower in plants treated with 0.15 mM [P] after 7 d. $V_{cmax}$ and $J_{max}$ for chilled plants mostly increased with the increases in [P] in the nutrient solution. At 7 d, chilled leaves had similar to or slightly higher $V_{cmax}$ and $J_{max}$ values than the unchilled leaves especially under P deficient conditions. The significant correlation between $P_{Nsat}$ and $V_{cmax}$ ($r^2$ = 0.99, $P$ < 0.05) suggest that non-stomatal factors were mainly responsible for the changes in $P_{Nsat}$ induced by P supply, irrespective of chilling. $V_{cmax}$ may decrease owing to the inactivation or loss of Rubisco, while the reduction in $J_{max}$ is associated with a diminution in other enzymes of Calvin cycle

(Woodrow and Berry 1988, Harrison *et al*. 1998). Indeed, the inactivation of Rubisco can be induced by inhibition of cytokinin synthesis under low P supply and chilling (Schmülling *et al*. 1997). Moreover, the decrease in RuBP regeneration could have resulted from limited ATP supply, either because low [P] treatment diminishes photosynthetic electron transport capacity, or because there is insufficient Pi available for the phosphorylation of ADP to ATP.

Significant declines in $F_v/F_m$ were observed only in P deficient plants, suggesting that photoinhibition is responsible, at least partly, for the reduction in $CO_2$ assimilation for P-deficient plants. At 2 h of recovery after chilling, unchilled plants showed higher $\Phi_{PS2}$, $q_p$ and $F_v'/F_m'$ than the chilled plants. Meanwhile, unchilled plants had the highest $\Phi_{PS2}$, $q_p$ and $F_v'/F_m'$ at 0.60 mM [P] while chilled plants had the highest $\Phi_{PS2}$ and $F_v'/F_m'$ at 2.40 mM [P], respectively, although the difference was not significant in some cases. Similar to those changes previously seen in $P_{Nsat}$ and $g_s$, there were significant decreases in $\Phi_{PS2}$, $q_p$ and $F_v'/F_m'$ in unchilled plants and increases in $\Phi_{PS2}$, $q_p$ and $F_v'/F_m'$ in chilled plants at 7 d although there were some exceptions. Accordingly, chilled plants showed higher $\Phi_{PS2}$, $q_p$ and $F_v'/F_m'$ than unchilled plants (Table 2). Both $\Phi_{PS2}$ and $q_p$ increased with the increase in [P] in the nutrient solution while $F_v'/F_m'$ was highest at 0.15 mM [P] at 7 d. Since photoinhibition occurred only in 0 mM [P] treated plants, the reductions in $\Phi_{PS2}$ in other treatments could be attributed to the reduced demand for energy in the form of ATP and NADPH. This is indicated by the decreases of $V_{cmax}$ and $J_{max}$, a down-stream regulation mechanism for the photosynthetic electron transport under stress conditions (Zhou *et al*. 2004b, Hu *et al*. 2006). Meanwhile, the reduction in $\Phi_{PS2}$ can be attributed to a decrease in the number of open PS 2 reaction centres as well as reduced efficiency of PS 2 reaction centres since both $q_P$ and $F_v'/F_m'$ changed with the change in $\Phi_{PS2}$. In agreement with our results, Campbell and Sage (2006) also showed that photosynthesis in low-P plants appeared limited by the rate of RuBP regeneration, probably through inhibition of the Calvin cycle.

To determine whether the change of [P] or chilling was associated with the changes in limitations in Pi supply to the chloroplasts, $PS_{O2}$ was determined in unchilled plants and chilled plants at 2 h and 7 d of recovery after chilling. $PS_{O2}$ increased with the increase in [P] in the nutrient solution both in chilled and unchilled plants. Chilling significantly decreased $PS_{O2}$ within 0 - 0.60 mM [P] range especially in P-deficient plants. There was significant increase in $PS_{O2}$ for P-deficient plants when they were moved to optimum growth conditions. The decrease of $PS_{O2}$ indicated that low [P] led to the limitation of thylakoid ATP synthase activity arising from insufficient return of Pi to the chloroplast caused by the accumulation of triose phosphates (Allen and Ort 2001). All these results indicate that Pi limitation was the cause of a reduction in the RuBP regeneration capacity in low [P] conditions. In other word, limitations in P supply to the chloroplasts were partly responsible for the decreased photosynthesis (Paul *et al*. 1992).

In conclusion, our results provide clear evidence for the P-dependent difference in the susceptibility of tomato plants to chill-induced inhibition of photosynthesis and plant growth. It is apparent that plants need higher P supply at low temperature than at optimal growth temperature. P deficiency has diverse effects on many photosynthetic processes and reduction in photosynthetic capacity induced by P deficit is mostly attributed to the dysfunction of Calvin cycle and limitations in Pi supply to the chloroplasts, leading to a down-regulation photochemical activity in PS 2.

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