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Title

P-starvation Induced Solubilization and Acquisition of P from Sparingly Soluble P-sources by Brassica Cultivars

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Authors

Akhtar, M. Shahbaz

Oki, Yoko

Tadashi, Adachi

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Introduction

Phosphorus (P) rapidly forms insoluble complexes with Fe and Al under acidic and Ca and Mg under alkaline conditions. Replenishment of soil P reserves through fertilization is a common practice, but the economic sustainability of this practice is in question, as economically recoverable P reserves are estimated to be 50% depleted by the middle of this century (Abelson 1999). There is an urgent need to explore and deploy alternative strategies enhancing P-acquisition and use efficiency in both low and high input sustainable agricultural systems. The adaptation of plants to low P availability is therefore of considerable interest in both basic and applied plant biology. The cultivars efficient in solubilizing Ca-P complexes may help to cope with the problem of unavailability of applied fertilizers as the major portion (88-99%) of total P in alkaline calcareous soils exist as Ca phosphates of varying solubilities. Under Pi deprivation, plant roots can alter solution Pi availability by rhizosphere acidification through H⁺-efflux and OAs exudation. In calcareous soils, rhizosphere acidification by H⁺ extrusion causes dissolution of poorly available Ca-P minerals. Plant species such as buckwheat, oilseed rape and legumes are quite efficient in utilizing rock P by releasing OAs due to changes in cellular metabolism as a Pi starvation response. Anion channels such as Cl⁻ channels and MATE (Multidrug and Toxin Extrusion) proteins have been suggested as potential candidates for OAs excretion (Vance et al. 2003). OAs can diffuse into the rhizosphere due to the high electrochemical potential gradient existing between the cytoplasm of root cells and the soil solution, and can release P from unavailable bound soil P-reserves. P-starvation also favors lateral root growth over primary root growth. The reason for this is that the cortical cells in both the elongation and mature zones of the primary roots remain shorter when P-supply is low (Williamson et al. 2001). All these changes improve the capacity of the plant root system to better explore and mine the soil for P.

Materials and Methods

To investigate the role of P-starvation induced root mediated rhizospheric acidification in P-solubilization and acquisition from sparingly soluble P-sources and remodeled root architecture under P-stress, diverse *Brassica* cultivars (P-tolerant class-I and P-sensitive class-II) in terms of P-acquisition and P-use efficiency were used. Experiments were conducted in a cultivation chamber (CFH-405; Tomy Seiko Co., Tokyo, Japan) at a cycle of 14 h/20°C night and 10 h/25°C day and a light intensity of 40 μmol m⁻² s⁻¹ (3800 lx). The relative humidity of the chamber was adjusted to 60%. Modified Hoffland's solutions were renovated at 3-d intervals, and sparingly soluble P sources were stirred mechanically twice a day. P-stress induced root mediated *in situ* rhizospheric pH changes were observed using agar media. Solution pH changes were monitored regularly in all pots on 0, 3, 6, 9, 12, 15, and 21th day after transplanting (DAT). Phosphorus was applied to individual pots as KH₂PO₄ as a control treatment (KP) at 200 μM P, and rock-P (RP) at 2 g L⁻¹ and Ca₃(PO₄)₂ (TCP) at 0.2 g L⁻¹, respectively as sparingly soluble P-sources. Using rhizobox cropping technique, length of the primary roots and the length of the branched zone of primary roots were measured on 12 and 21 DAT as described by Mollier and Pellerin (1999). After 7 days in a complete nutrient solution, the seedlings were transferred to an aerated nutrient solution containing 200 μM P (+P) using KH₂PO₄, without P (-P), RP (2 g L⁻¹), and Ca₃(PO₄)₂ at 0.2 g L⁻¹, respectively in 3.5-L pots for additional 12 days. Plant roots were submerged in 300 ml of aerated solution with 0.5 mM CaCl₂ (pH = 5.5) for 4 h and 8 h, respectively and root exudates

were collected for carboxylates. The solution was evaporated to about 5 ml under reduced pressure at 45° C on a rotary evaporator. Solution containing root exudates was allowed to pass first through a cation exchange column (16 mm x14 cm) filled with 5 g Dowex 50 W x 8 (100-200, H⁺ form) resin and then through an anion exchange column filled with 2 g Dowex 1 x 8 resin (0.15-0.06 mm, Cl⁻ form) without adjusting the pH. Carboxylates (citrate, malate and succinate) retained in the anion exchange resin were eluted with 8N formic acid. The eluent was concentrated to dryness and the residue was re-dissolved in 1 ml ultra pure water adjusted to pH 2.1 with HClO₄ and filtered with 0.45 μM filter and carboxylates were detected by HPLC.

Results and Discussion

Dissolution of sparingly soluble Ca-phosphate around plant roots due to the acidification of rhizosphere by root exuded protons was observed when plants were fed with NH₄⁺ as N source. In NO₃⁻ medium, root growth was faster than in the NH₄⁺-medium but no dissolution of Ca-P was observed. *In situ* root mediated pH changes (appearance of typical patterns in the root vicinity) was more prominent under P-stress environment. Class-I (P-efficient) cultivars showed a more decrease in solution media pH than class-II (P-inefficient) cultivars (Figure 1A-B). Cultivars accumulating higher amount of total P in plants had a lower pH in the rooting media and vice versa (Figure 1C). Total amount of OAs exuded from the roots of P-stressed plants differed from those of plants grown under adequate P-supply (Figure 1D). Apparently, when plants were supplied with sufficient P, OAs were released in low amounts by all cultivars. On the other hand, OAs were released in higher amounts, when plants were re-cultured for 12 days under P-starvation. Class-I cultivars exuded 2-3 fold higher OAs than class-II cultivars. Nevertheless, the amounts of extruded OAs appeared to be cultivar and time specific. However, the exudation rate of cultivars of both classes decreased with time. The highest exudation rate was found after the first 4 h collection and then tended to decrease (Figure 1D).

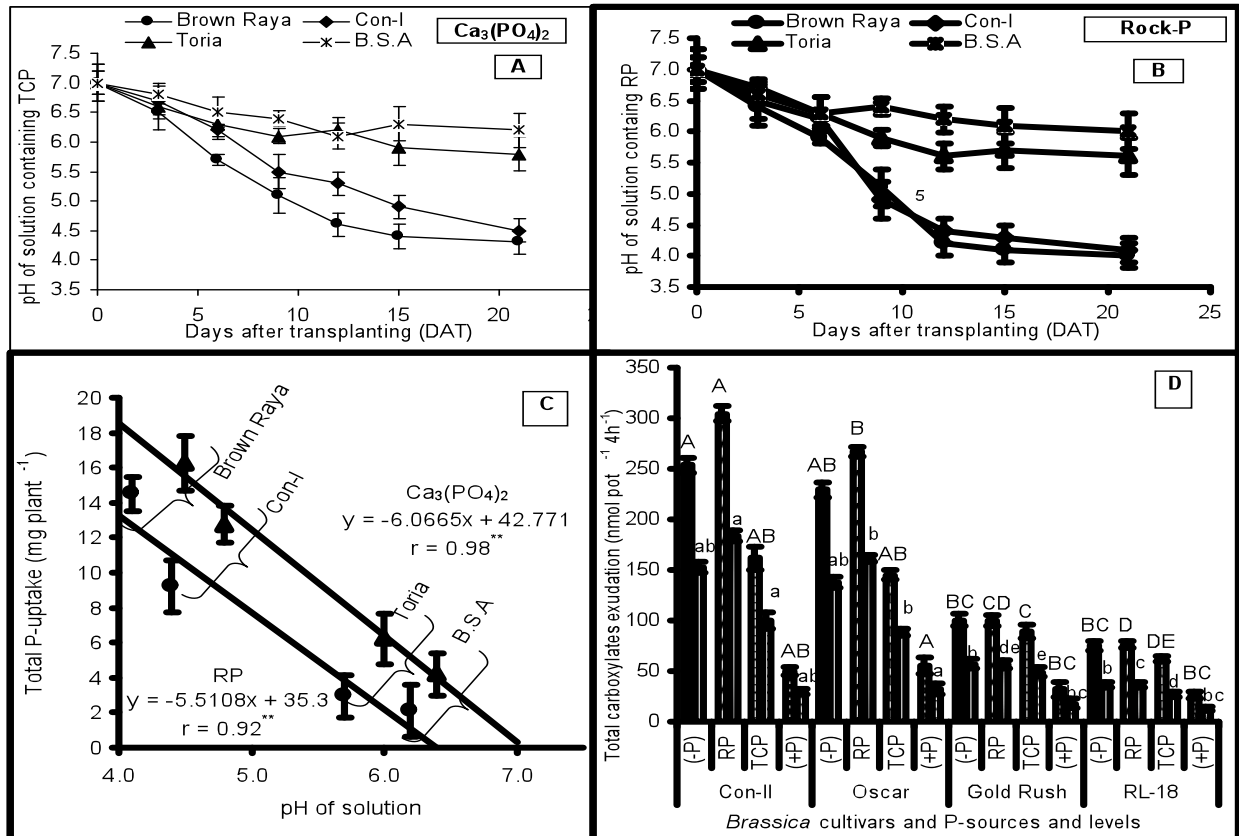


Figure 1. Changes in solution pH measured at 0, 3, 6, 9, 12, 15, and 21 DAT (A-B), total P-uptake in relation to solution pH at 21 DAT (C) and carboxylates exuded (D) by diverse cultivars grown with $\text{Ca}_3(\text{PO}_4)_2$ (TCP) and rock-P (RP); error bars show \pm SE; ** = significant at $P < 0.01$.

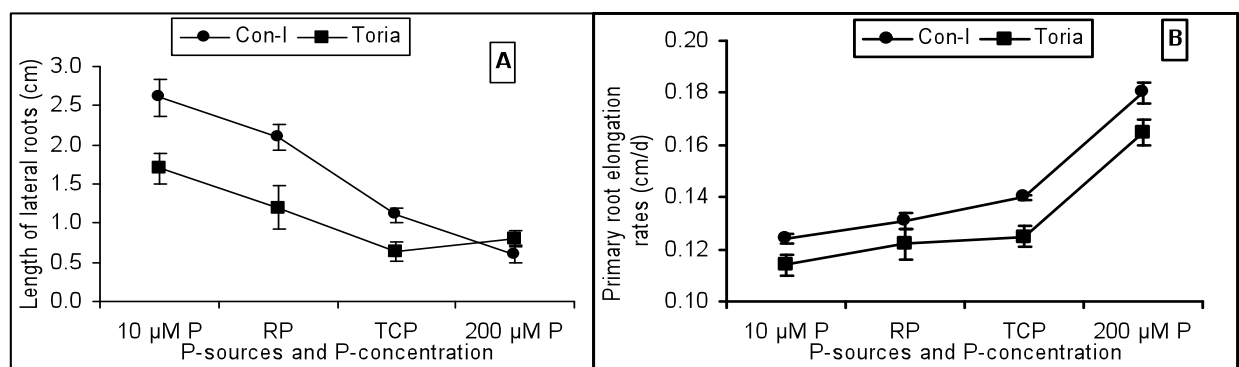


Figure 2. Changes in the length of lateral roots (A) and the primary root elongation rate (B) by two cultivars grown in rhizobox containing sand media with KP(+P) (200 μM P) and KP(-P) (10 μM P) using KH_2PO_4 , and $\text{Ca}_3(\text{PO}_4)_2$ (TCP) and rock-P (RP). error bars show \pm SE.

Most RPs are made of apatite like Ca-phosphates and thus exhibit an increasing solubility with decreasing pH. H^+ released by ATPase pumps located in plasmalemma during nutrient uptake attack RP to solublize P for meeting plant growth requirements. OAs exudation charge balanced by H^+ -efflux may additionally contribute to rhizosphere acidification. Exuded OAs are

able to mobilize inorganic P into the soil solution, by competing with phosphate groups for the same binding/ adsorption sites in soil and forming stronger complexes with Al^{3+} , Fe^{3+} and Ca^{2+} than phosphate does. Phosphorus can be liberated from Ca-P minerals as the OAs complex with Ca or block the sorption of P to other charged or through Ligand exchange process.

Significant differences were observed between cultivars grown with RP, TCP and AP in rhizoboxes. The length of lateral roots increased (Figure 2A), where as the elongation rates of primary roots decreased (Figure 2B) under P-stress induced with RP and TCP. This phenomenon was more prominent in class-I cultivars than class-II cultivars to scavenge P more efficiently from sparingly soluble P-sources. Faster elongation rate of the primary roots under high P-supply and the lateral roots under P-stress means that photosynthate allocation to both primary and lateral roots is different under different conditions of P-availability, and reflects different strategies to acquire enough nutrients; especially P under different conditions of P-availability.

Conclusions

Tested cultivars showed differential growth potential and diversity in accessing, mobilization and acquisition of P from sparingly soluble RP and TCP. Remodeling in root architectural systems are important rescue traits for maximizing P-acquisition under P-starvation, because root systems that have higher ratios of surface area to volume will effectively exploit larger volume of soil. P-stress induced rhizospheric acidification due to copious H^+ -efflux and carboxylates exudation by P-efficient/tolerant cultivars were important adaptive traits for mobilization and acquisition of Pi from extra cellular sparingly soluble P-forms such as RP and TCP or bound soil P-forms.

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