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Table 2. Effect of soil texture on RA of apple trees after 1 year of pot growth.

| Treatment | | Primary root | | Lateral root | | | No. of fine root groups |
|---|---|---|---|---|---|---|---|
| | | Length (cm) | Thickness (cm) | Length (cm) | Thickness (cm) | No. | |
| Sandy soil | Control | 54.9 a | 0.445 bc | 38.9 a | 0.163 b | 4.7 a | 88.5 a |
| | Organic manuring | 53.3 a | 0.465 b | 24.5 bc | 0.166 a | 3.8 b | 66.3 b |
| Clay soil | | 53.6 a | 0.528 a | 32.0 b | 0.167 a | 5.7 a | 84.4 a |

Means with the same letter are not significantly different at $p<0.05$.



Table 3. Effect of soil texture on RA of apple trees after [illegible] years of pot growth.

| Treatment | | Primary root | | Lateral root | | | No. of fine root groups |
|---|---|---|---|---|---|---|---|
| | | Length (cm) | Thickness (cm) | Length (cm) | Thickness (cm) | No. | |
| Sandy soil | Control | 60.9 b | 0.597 b | 30.7 a | 0.236 a | 4.3 bc | 116.0 a |
| | Organic manuring | 73.6 a | 0.659 a | 26.2 b | 0.194 bc | 8.2 a | 103.7 ab |
| Clay soil | | 53.1 c | 0.568 bc | 30.1 a | 0.214 ab | 6.0 ab | 75.7 b |

Means with the same letter are not significantly different at $p<0.05$.

Table 4. Effect of soil particle size on RA of seedling apple (sampled at 30 days).

| Soil grain sizes (mm) | Length of primary root (cm) | First order lateral root | | | Second order lateral root | | Total no. of lateral root |
|---|---|---|---|---|---|---|---|
| | | No. | Length (cm) | Density (no./cm$^3$) | No. | Length (cm) | |
| <0.25 | 3.21 de | 11.07 d | 0.20 e | 3.45 abc | 0.27 d | 0.11 d | 11.33 d |
| 0.5-1.0 | 3.99 d | 17.00 c | 0.45 d | 4.26 a | 9.18 a | 0.17 d | 26.18 abc |
| 1.0-2.0 | 6.29 bc | 21.83 ab | 0.68 abc | 3.47 ab | 5.36 abc | 0.28 abc | 27.19 ab |
| 5.0-7.0 | 7.23 b | 15.00 cd | 0.60 abc | 2.07 e | 1.78 cd | 0.39 a | 16.78 d |
| 7.0-10.0 | 8.52 a | 25.42 a | 0.75 a | 2.98 bcd | 6.87 ab | 0.29 ab | 32.29 a |

Means with the same letter are not significantly different at $p<0.05$.



# Effects of Phosphate Uptake on Root Architecture of Apple Seedlings in Water Culture

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**Keywords:** *Malus hupehensis* Rehd., fertilizer, nutrient uptake, phosphorus, root

**Abstract**

**Phosphate uptake and root architecture of apple (*Malus hupehensis* Rehd.) seedlings at the 25 leaf stage were studied under five phosphate concentrations (0 to 10 mM phosphate) in hydroponic culture for 30 days. The length of the first order lateral roots, the number of lateral roots and phosphate absorption decreased consistently with increasing phosphate concentration. Under phosphate starvation, the number of lateral roots and the length of the first order lateral roots increased, while the proportion of thin roots was 73%. Roots of apple stock quickly reached their greatest phosphate uptake rates in 30 min. The total number of lateral roots was similar, and lower than that in P deficiency of 0.01 mM and 1.0 mM phosphate. But the length of the first order lateral roots were closer than that in phosphorus deficiency, and the portion of thin roots also increased (63%) in 0.01 mM phosphate. The length of the first order lateral root was reduced, but the proportion of thin roots also increased (64%). Apple roots reached their greatest phosphate uptake rates in 1h in 0.01 mM and 0.1 mM P. First order lateral roots became shorter and thicker in 1 mM and 10 mM P, and the roots reached their greatest phosphate uptake rates in 2h, but their overall phosphate uptake rates were lower. The results demonstrate that the capacity of phosphate uptake is improved by forming the root architecture in P-deficiency, and reached its greatest phosphate uptake rates in 30 min. While the phosphate availability changes, root architectures are altered and caused relative changes of P-uptake rates in apple seedlings. This is an adaptation to the changes of rhizosphere phosphate availability in apple trees.**

## INTRODUCTION

Root architecture refers to the spatial configuration and distribution of roots in the growing medium. Manipulating apple aerial architecture by pruning is a means to utilize light more efficiently and to obtain regular yields of good fruit quality. Manipulating the root architecture in certain ways is a means to utilize soil nutrients more efficiently and to improve water and mineral nutrient absorption (Yang et al., 2002; Bates and Lynch, 2001; Ma et al., 2001; Forde and Lorenzo, 2001). Root architecture has received little attention in research. The spatial distribution and concentration of nutrients in soil solution have an obvious influence on root architecture, and the plants may also alter root architecture (Lopez-Bucio et al., 2003; Birgit et al., 2002; Linkohr et al., 2002) and adapt to phosphate stress (Forde and Lorenzo, 2001; Williamson et al., 2001). These changes are important to the soil mineral nutrient absorption, especially to calcium (Ca), phosphorus (P), iron (Fe) and zinc (Zn) that are difficult to dissolve; in proper soil, mycorrhizae may aid phosphorus uptake under low phosphorus supply conditions.

The objective of the present work was to study the relationship between root architecture and phosphate uptake of apple seedlings, and model the relation among phosphorus, apple root architecture and phosphorus uptake. We attempt to study the mechanism of apple trees adapting to phosphorus nutrient stress by causing changes of root architecture under hydroponic culture and to take the relevant steps to raise the efficiency of phosphate uptake.

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## MATERIALS AND METHODS

This experiment was carried out using a hydroponic system to maintain apple (*Malus hupehensis* Rehd.) seedlings with 12 to 15 leaves in the following five phosphate concentrations: 0, 0.01, 0.1, 1.0 and 10 mM·L$^{-1}$ (Zhang and Qu, 2003).

Phosphate uptake and root architecture parameters of apple seedlings were measured after 30 days of treatment with one of the five phosphate concentrations, as previously described by Han et al. (1995), except for the original phosphate uptake solution of 0.8 mM. Samples of the nutrient solution were analyzed for phosphate concentration by a vanadate-molybdate colorimetric method after 0.5, 1, 2, 3, 4, 6, 9, 12, 15 and 25h, respectively.

## RESULTS

### Effects of Phosphate Concentration on Root Architecture Parameters

The number, length and the thickness of the lateral root are important parameters used to describe the root architecture of apple seedlings. The length and number of the first order lateral roots, the number of the second order lateral roots and the total number of lateral roots decreased consistently with increasing phosphate concentration (Table 1).

Under phosphate starvation (0 mM·L$^{-1}$), the number of lateral roots and the length of the first order lateral roots obviously increased, and the incidence of thin roots (roots with a diameter less than 0.3 mm) was 73%. The total lateral root number in phosphorus concentrations ranging from 0.01 mM to 1.0 mM was similar to but lower than that in the solution containing no phosphorus. The length of the first order lateral roots was longer than that in the 0 mM·L$^{-1}$ phosphorus solution and the proportion of thin roots was also higher (63%) at 0.01 mM phosphate. At a low phosphate concentration of 0.1 mM, the length of the first order lateral roots was reduced, but the percentage of thin roots increased to 64%. When the phosphorus concentration reached 1.0 mM·L$^{-1}$, first order lateral roots became shorter and thicker with a percentage of thin roots of only 12%. The length of the first order lateral roots and the number of lateral roots decreased in the 10.0 mM phosphate solution (Table 1). The results demonstrated that the apple trees continuously altered their root architectures as the phosphate availability changed. The numbers of lateral roots and the length of the first order lateral roots increased, and lateral roots became thinner at the lower (0.01 mM·L$^{-1}$) phosphate concentration; The growth rates and initiative of lateral roots were reduced when the phosphate concentrations ranged from 0.01 mM·L$^{-1}$ to 10.0 mM·L$^{-1}$. At the higher phosphate concentration of 10.0 mM phosphate, the growth rates and initiation of the lateral roots were inhibited in apple trees.

### Effect of Phosphate Availability on Changes of Phosphate Uptake

Over time, it was observed that P uptake was variable and tended to decrease, while P-uptake rates were similar and varied little in all treatments after 6h (Fig. 1).

The rates of phosphate absorption of apple roots decreased with increasing phosphate concentration. The roots reached their greatest phosphate uptake rates in 30 min under phosphate starvation (0 mM·L$^{-1}$). Then, phosphate uptake rates were reduced, but remained higher in treatments with phosphate starvation than in others. When the phosphate concentration ranged from 0.01 mM·L$^{-1}$ to 0.1 mM·L$^{-1}$, the roots reached their greatest phosphate uptake rates in 1h, but the phosphate uptake rates were higher at 0.01 mM phosphate than that at 0.1 mM concentration. When phosphate concentrations ranged from 1.0 mM to 10.0 mM, the roots reached their greatest phosphate uptake rates in 2h, but their overall phosphate uptake rates were lower. The phosphate uptake rate was higher and longer when the phosphate concentration was lower than 0.1 mM, and P-uptake rates were also higher at 3h and close to the greatest phosphate uptake rates at 1.0 mM and 10.0 mM phosphate. When the phosphate concentration was higher than 1.0 mM, the phosphate uptake rates quickly decreased to the lower level after 2h (Fig. 1). These results demonstrate that the capacity of rhizosphere P-uptake rises under lower phosphate concentration, and the plant quickly adapts to the lower phosphate concentration stress, and the plant's roots reach their greatest P-uptake rates in a short time. With the increase of phosphate availability, the capacities of rhizosphere P-uptake are reduced, and the sensitivities of apple roots to rhizosphere phosphate availability decrease. This is an adaptation to the changes of the rhizosphere phosphate availability in apple trees.

## DISCUSSION

The root architecture has effects on the rates of nutrient uptake (Lopez-Bucio et al., 2002; Wang et al., 2003). Liao and Yan (2000) used molecular mapping of QTLs to determine that root architecture of plants is closely related to P-uptake efficiency under field conditions. Our results indicate that root architecture parameters of apple stocks (the lengths, numbers and diameter of lateral roots, etc.) are closely related to the rhizosphere phosphate availability. Root architectures are altered and cause relative changes in P-uptake rates. Phosphate uptake rates, or the capacity of the new roots to capture the available rhizosphere phosphate, are higher in shorter times with the decrease of available phosphate concentration in apple trees. Under the natural selection of phosphate stress of long times, the apple trees alter root architecture by increasing of the number and length of lateral roots, and this causes relative changes in P-uptake rates, and the capacities of the rhizosphere P-uptake are improved in soil.

Under the conditions of P-deficiency, the number of lateral roots and the length of first order lateral roots increase quickly, and it is also observed that roots become thinner in diameter, lengths differ and the percentage of these roots increases. The rates of long roots also increase, so the new root architecture is formed to adapt to the rhizosphere P-deficiency conditions. In the meantime, the apple trees respond quickly to the rhizosphere P availability with the increase of P uptake, the roots quickly reach their greatest phosphate uptake rates in 30 min. With P concentrations ranging from 0.01 mM to 1.0 mM, the lateral root numbers are similar, but are lower than that in P-deficiency. The lengths of the first order lateral root are closer than that in P-deficiency, and the percentage of the thin roots is also higher at 0.01 mM phosphate. The lengths of the first order lateral roots become short and uniform, but the percentage of the thin roots is also higher at 0.1 mM phosphate. Roots reached their greatest phosphate uptake rates in 1h at 0.01 mM and 0.1 mM P. First order lateral roots became shorter and thicker at 1.0 mM P, and the roots reached their greatest phosphate uptake rates in 2h, with lower rates of P-uptake overall. At the highest phosphate concentration (10.0 mM), the length of the first order lateral roots and the number of lateral roots obviously decreased, and P-uptake rates reduced quickly after 2h. This suggests that the changes of root architecture cause relative changes in the continuous absorption rate of phosphate, which may be an adaptation to the available rhizosphere phosphate by apple trees.

These results may be related to high affinity phosphate transporter genes induced under phosphate deficiency conditions (Chang et al., 2004; Ming et al., 2004) which have now been isolated from *Arabidopsis*, wheat and rice. The expression of the phosphate transporter genes may only be found in roots, and it is quickly induced by the P-deficiency conditions, and it is reversed by re-supplying phosphate. Under phosphate starvation, the phosphate uptake efficiency has been improved by the increase of the high affinity of phosphate in soil. The high affinity phosphate transporter protein may play a role during the process of transporting phosphate from the external lower phosphate concentration conditions into the cytoplasm that has higher phosphate concentration (Wang and Cheng, 2004). The proteins are induced and produced by lower phosphate condition, and their concentrations get the highest in the phosphate-deficiency condition. The high affinity phosphate transporter proteins are highly sensitive to phosphate concentration, and have changes with the changes of the external phosphate concentration. When the roots of apple trees growing in the conditions of phosphate lower or starvation shift or meet the phosphate-rich environment, the instantaneous value of the phosphate uptake rates is higher, but these proteins concentration reduce quickly during the short times (30 min to 1.5h) with the increase of the internal phosphate concentration of roots, then the phosphate uptake rates of apple tree roots gradually recover the normal.

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**Tables**

Table 1. The effects of five different phosphate concentrations in water culture on parameters of root architecture of *Malus hupehensis* Rehd. (±SD).

| P concentration ($mM \cdot L^{-1}$) | First order lateral roots No. | First order lateral roots Length (cm) | No. of second order lateral roots | No. of third order lateral roots | Total no. of lateral roots |
|---|---|---|---|---|---|
| 0 | 44.8±16.21 | 3.09±1.69 | 88.4±15.39 | 7.28±3.96 | 140.5±34.39 |
| 0.01 | 25.43±6.24 | 3.07±0.88 | 75.7±21.18 | 3.44±3.09 | 104.5±29.20 |
| 0.10 | 29.78±4.45 | 2.05±0.56 | 66.5±13.83 | 0.54±1.13 | 96.8±19.4 |
| 1.00 | 29.50±2.65 | 1.96±0.75 | 73.7±27.9 | 1.13±1.11 | 104.3±33.2 |
| 10.0 | 9.11±1.38 | 1.83±0.33 | 12.6±2.57 | 0.89±0.49 | 22.6±7.63 |

**Figures**

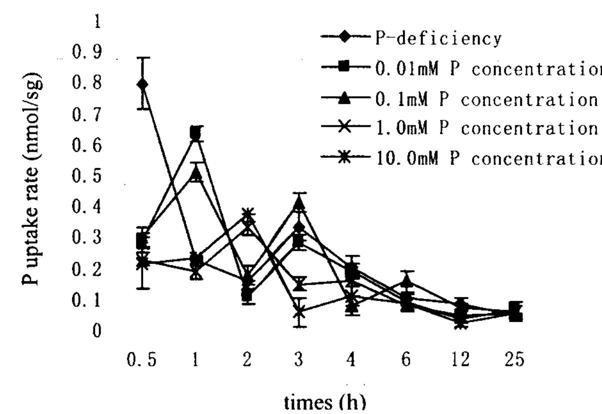


Fig. 1. Changes of phosphate uptake in *Malus hupehensis* Rehd. under different P concentrations.

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