Phosphorus efficiency of ornamental plants in peat substrates

Azizollah Khandan-Mirkohi1,2* and Manfred K. Schenk2

1 Horticultural Department, Agricultural Faculty, Urmia University, Urmia, Iran
2 Institute of Plant Nutrition, Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Germany

Abstract
A pot experiment was conducted to investigate factors contributing to phosphorous (P) efficiency of ornamental plants. Marigold (Tagetes patula) and poinsettia (Euphorbia pulcherrima) were cultivated in a peat substrate (black peat 80% + mineral component 20% on a volume basis), treated with P rates of 0, 10, 35, 100, and 170 mg (L substrate)⁻¹. During the cultivation period, plants were fertigated with a complete nutrient solution (including 18 mg P L⁻¹) every 2 d. Both poinsettia and marigold attained their optimum yield at the rate of 35 mg P (L substrate)⁻¹ and the critical level of P in shoot dry matter of both crops was 5–6 mg g⁻¹. After planting, plant-available P increased at lower P rates to a higher level for poinsettia than for marigold, but no significant change was observed at higher P rates. Balance sheet calculations indicated that at lower P rates more P was fertigated than was taken up by the plants. Root-length density, root-to-shoot ratio, and root-hair length of marigold were doubled compared to that of poinsettia. Root-length density increased with crop growth, and 10 d after planting the mean half distance between roots exceeded the P-depletion zone around roots by a factor of 3 and 1.5 for poinsettia and marigold, respectively. Thus, at this early stage poinsettia exploited only 10% of the substrate volume whereas marigold utilized 43%. Later in the cultivation period, the depletion zones around roots overlapped for both crops. Taking into account P uptake via root hairs, the simulation revealed that this was more important for marigold compared to poinsettia especially at low P-supply levels. However, increase of P uptake due to root hairs was only 10%–20% at optimum P supply. For the two lower P levels, the P-depletion profile around roots calculated for 10 d after planting showed that after 2 d of depletion the concentration at the root surface was below the assumed Km value (5 μM) and the concentration gradient was insufficient to fit the demand. A higher content of plant-available P in the substrate was observed for poinsettia compared to marigold in the treatment with P application adequate for optimum growth, because more fertigated P was accumulated during early stages of cultivation due to lower root-length density of poinsettia. The observed difference of root morphological parameters did not contribute significantly to P-uptake efficiency, since P mobility in the peat substrate was high.

Key words: marigold / model / poinsettia / P uptake / P supply / root hairs

Accepted February 27, 2009

1 Introduction
Plant species as well as genotypes of a given species differ in phosphorus (P) efficiency, which is the ability of the plant to grow well under low P availability in the soil (Loneragen and Asher, 1967; Dechassa et al., 2003). This may be due to utilization efficiency, which is the ability of plants to utilize P in the shoot for dry-matter production, or due to uptake efficiency, which is the ability to acquire P from the soil (Loneragen and Asher, 1967). Uptake efficiency may arise from favorable root morphological characteristics, mobilization of P by releasing root exudates into the rhizosphere, or association of roots with mycorrhiza (Raghothama, 1999).

Claassen and Steingrobe (1999) have described nutrient acquisition of plants by the mechanistic simulation model "NST 3.0", which considers transport of nutrients to the root surface by mass flow and diffusion and inflow into the root following Michaelis-Menten kinetics. This model also considers root morphological traits such as root radius, root hairs as well as the competition between roots. Also, the contribution of mycorrhiza to P uptake can be described (Deressa and Schenk, 2008). However, the mobilization of P by root exudation is not considered in the model.

Long root hairs, high root-to-shoot ratio, and small root radius were observed for some crops cultivated in mineral soils as significant morphological root characteristics contributing to P-uptake efficiency (Föhse and Jungk, 1983; Barber, 1995). Additionally, preferential root distribution in the top soil was identified for bean as root morphological trait of P efficiency (Lynch and Brown, 2001). Furthermore, P may be mobilized in the soil by exudation of organic anions such as citrate (Dechassa and Schenk, 2004) which form complexes with Ca, Al, and Fe and thus dissolve P bound to these elements. Organic anions can desorb P from sesqui-oxide surfaces by anion exchange (Bolan et al., 1994). Phosphatase exudation was also reported to hydrolyze and solubilize inorganic P.
from soil organic phosphates, which are estimated to account for about 30%–80% of total P in mineral soils (Gilbert et al., 1999).

The physiological characteristics of P-uptake kinetics are not considered as significant for P efficiency of plants cultivated in mineral soil, since P transport in the soil limits P uptake (Barber, 1995). However, investigation of P dynamics in peat substrates revealed that the mobility of P was high in the substrate due to its low buffer power (1–17; Khandan-Mirkohi and Schenk, 2008), whereas in mineral soils, these values are in the range of 100–2000 (Jungk and Claassen, 1997). In a preliminary experiment, a lower level of plant-available P in the substrate was observed at optimum growth of marigold compared to that of poinsettia.

Therefore, the present study aimed (1) to assess the reason for the observed difference in plant-available P in substrate at optimum growth for poinsettia and marigold, (2) to investigate factors contributing to the P efficiency of the plants cultivated in substrate, and (3) to quantify their significance by using the mechanistic simulation model “NST 3.0”.

2 Material and methods

2.1 The growth medium

The growth medium was prepared by mixing 80% of black peat that passed through a 2 mm sieve and 20% of mineral component (consisted of 33% sand, 43% silt, and 24% clay) on volume basis. Phosphorus was applied to the substrate in the form of Ca(H2PO4)2 at the rates of 0, 10, 35, 100, and 170 mg P (L substrate)−1. Nitrogen (N) and potassium (K) were applied at a rate of 150 mg (L substrate)−1 in the form of NH4NO3 and K2SO4, respectively. Additionally, Flory® 10 (EUFLOR GmbH, Munich, Germany; www.euflur.de), which contains Mg and micronutrients (10% magnesium oxide, 3.5% Fe-HEDTA, 2% Cu-EDTA, 0.8% Mo, 0.5% Mn, 0.5% B, 0.3% Zn, and 0.02% Co), was applied at the rate of 50 mg product (L substrate)−1. The substrate pH was increased to 0.3% Zn, and 0.02% Co), was applied at the rate of 50 mg L−1 of Flory® 10 were used. Poinsettia plants were pinched above seven leaf buds. Two harvests were conducted for each crop: 53 and 67 d after planting for poinsettia and 27 and 41 d after planting for marigold, respectively.

2.3 Analytical procedures

The volume weight of substrates was determined according to the standard method of VDLUFA (1991). Pots without plants were used to estimate water loss through evaporation. Transpiration was calculated as the difference between the amount of water lost from pots with plants and evaporation from pots without plants. The substrate pH was measured in 0.01 M CaCl2 suspension using a substrate-to-solution ratio of 1:2.5. Available P in the substrate (C2) was measured using CAT extraction (0.01 M CaCl2 + 0.002 M DTPA) according to Alt and Peters (1992). Substrate solution was collected by centrifugation at 1000 g for 20 min, and P concentration in the substrate solution (C2) was determined according to Murphy and Riley (1962). Buffer power (b) was calculated as the ratio C1/C2 (Tab. 1). The Freundlich function was used to describe the relationship between C2 and Cb (Barber, 1995). Plant material was dried at 70°C for 5 d, and shoot dry weight was recorded. Dry-matter P content was determined after dry-ashing according to Gericke and Kurmies (1952).

2.4 Root morphological and physiological parameters

Roots were separated from substrate by washing over sieves (0.5 mm). In order to check if roots were infected with arbuscular mycorrhiza (AM), root samples were stained and examined microscopically according to Vierheilig et al. (1998). However, no mycorrhiza colonization was observed in both crops. Total root fresh weight (RFW; g plant−1) was determined according to Schenk and Barber (1979). Root length (L; cm plant−1) was measured according to the line intersect method of Tennant (1975), and root growth rate constant (k; cm d−1) was calculated assuming linear growth as follows:

\[ k = \frac{(L_2 - L_1)}{t_2 - t_1}, \tag{1} \]

where \( t \) is the time after planting and the subscripts 1 and 2 refer to the first and second harvest, respectively.

Mean root radius (\( r_0; \text{cm} \)) was calculated as:

\[ r_0 = \sqrt[3]{\frac{RFW}{\pi \times L}}, \tag{2} \]

Mean half distance between neighboring roots (\( r_1; \text{cm} \)) was calculated as:

\[ r_1 = \sqrt[3]{\frac{V}{\pi \times L}}, \tag{3} \]

where \( V \) is the volume of substrate in the pot (cm³).
Surface area per cm root cylinder \((\text{SAC}\,\text{cm}^2)\) was calculated as:

\[
\text{SAC} = 2\pi \times r_0 \times h,
\]

where \(h\) is the length of root cylinder (1 cm).

For quantification of root hairs, an undisturbed substrate sample was cut carefully and placed into tap water in a shallow tray and soaked for about 1 h. The substrate was completely separated from roots, which were collected and cut into 1 cm pieces. Root hairs were counted as described by Dechassa et al. (2003), and root-hair parameters were calculated according to Brewster et al. (1976).

Phosphorus-uptake rate related to the root-cylinder surface area \((I_{\text{nab}}\, \mu\text{mol cm}^{-2} \text{s}^{-1})\) was calculated as:

\[
I_{\text{nab}} = \frac{I}{\text{SAC}}.
\]

The uptake rate was modified to calculate effective uptake rate \((I_n\, \mu\text{mol cm}^{-2} \text{s}^{-1})\) considering both surface areas of root cylinders and root hairs:

\[
I_n = \frac{I}{\text{SAC} + \text{SAH}}.
\]

Where \(\text{SAH}\) is the surface area of root hairs per 1 cm root length (cm²).

Water-uptake rate of root cylinder \((V_0\,\text{cm}^3 \text{cm}^{-2} \text{s}^{-1})\) was computed as:

\[
V_0 = \frac{W_2 - W_1}{(SA_2 + SA_1)/2} \times \frac{1}{t_2 - t_1},
\]

Where \(W\) is the transpired water by the plant (cm³), \(SA\) is the total root surface area of root cylinder (cm² plant⁻¹), and \(t\) is the time (s).

Table 1: Specific model parameters of poinsettia and marigold used for simulation of P uptake at first harvest. Root-hair distribution was computed for all P rates. Half distance between root hairs is given exemplary for optimum P level of poinsettia: 9.9, 18, 46, 144, and 490 \((\times 10^{-3}\text{cm})\) and of marigold: 6.7, 10.2, 17, 33.7, 81.6, 194, and 361 \((\times 10^{-3}\text{cm})\) in the compartments with 0–0.0167, 0.0167–0.0334, 0.0334–0.05, 0.05–0.067, 0.067–0.0835, 0.0835–0.1, and 0.1–0.117 cm distance from root surface, respectively. \(b\) = buffer power; \(C_l\) = substrate-solution P concentration; \(r_0\) = root radius; \(r_1\) = mean half distance between roots; \(L_0\) = initial root length; \(k\) = growth rate of roots; \(I_{\text{max}}\) = maximum uptake rate; \(V_0\) = water-uptake rate of root cylinder.
2.5 Phosphorus supply to the root

Total P uptake from substrate into the plant root was calculated as the sum of mass flow and diffusion.

Mass flow ($MF; \mu mol \text{ cm}^{-2} \text{ s}^{-1}$) was calculated as:

$$MF = V_0 \times C_i,$$

where $V_0$ is the uptake rate of water into root cylinder (cm$^3$ cm$^{-2}$ s$^{-1}$) and $C_i$ is the concentration of nutrient in the solution ($\mu mol$ cm$^{-3}$).

The effective diffusion coefficient ($D_e; \text{ cm}^2 \text{ s}^{-1}$) of P in the substrate was calculated according to Nye (1966):

$$D_e = D_L \theta f b,$$

where for $D_L$ (the diffusion coefficient of H$_2$PO$_4^-$ in water at 25$^\circ$C) the value of 8.9 x 10$^{-6}$ cm$^2$ s$^{-1}$ was used (Edwards and Huffman, 1959), for $\theta$ (the volumetric water content) the value of 0.5 cm$^3$ cm$^{-3}$, and as impedance factor ($f$) the value of 0.09 was taken (Khandan-Mirkohi and Schenk, 2008), and $b$ is the buffer power, which was calculated as the ratio $C_b/C_i$.

The extension of depletion zone around a root was calculated according to Syring and Claassen (1995):

$$\Delta x = \sqrt{\pi D_e t},$$

where $\Delta x$ is the distance from the root surface at which the decrease of concentration is 21% of the maximum decrease at the root surface and $t$ is the time (s). The extended depletion zone was calculated after 2 d, because plants were fertigated in 2 d intervals.

2.6 Velocity of phosphorus replenishment

Equilibrated substrate of 3rd P level having a volumetric water content of 27% was adjusted to the volumetric water content of 50% by adding distilled water and also by adding the fertigation solution, respectively. The substrate solution was collected immediately after adjusting water content and after 1 h, 2 h, 4 h, 8 h, 12 h, and 48 h by centrifugation at 1000 g for 20 min. Within 4 h, a new equilibrium was nearly reached indicating a fast sorption and desorption of P in the substrate (Fig. 1).

2.7 Modeling phosphorus uptake

The mechanistic simulation model “NST 3.0” described by Claassen and Steingrobe (1999) was used to predict plant P uptake. This model considers delivery of nutrients to the root surface by mass flow and diffusion and uptake by the root following Michaelis-Menten kinetics. Phosphorus uptake was predicted assuming linear root-growth rate, homogenous root distribution in the pot, and competition between roots for 2 d of depletion. The relevance of root hairs to P uptake was estimated as the difference between prediction with root cylinder and root cylinder plus root hairs. Specific input data are summarized in Tab. 1.

2.8 Statistical analysis

Treatments were replicated four times (each replicate consisted of two plants) in a completely randomized block design, and data were evaluated using analysis of variance (SAS, 1996). Differences between the treatments were compared using the Tukey test at $\alpha = 0.05$.

3 Results

3.1 Phosphorus dynamics in the substrate

CAT-soluble P ($C_s$) reflected the increase of P supply in both poinsettia and marigold (Fig. 2A, B). Due to P fertigation, $C_s$ increased at 1st harvest at lower P levels, whereas no change occurred with the two highest P levels for both crops. All $C_s$ levels remained almost constant between 1st and 2nd

---

Figure 1: Phosphorus concentration in substrate solution ($C_i$) after addition of water (desorption) or fertilizer solution (sorption) to peat substrate (black peat 80% + mineral component 20%, v/v; application rate of 35 mg P [L substrate]$^{-1}$).

Figure 2: CAT-soluble P content of the substrate ($C_s$) during cultivation of poinsettia (A) and marigold (B) at various P levels.
Phosphorus efficiency of ornamental plants

3.2 Plant growth

The increase in P supply resulted in a significant increase of shoot-dry-matter yield of both crops (Fig. 4). The increase of shoot dry matter during growth of both crops was in the same range for the three higher P levels and clearly above the lower P levels. This differentiation was already visible at 1st harvest. Maximum growth of both crops was already obtained at a P level of 35 mg (L substrate)\(^{-1}\). Dry-matter yield of poinsettia was 2-fold higher than that of marigold. However, considering the pot volume both crops produced almost the same amount of dry matter per L of substrate.

Relative shoot-dry-matter yield increased with increasing shoot P concentration (Fig. 5A, B) and both crops attained their optimum yield (90% of maximum yield; Ulrich, 1952) with the same P concentration at the 2nd harvest (Fig. 5B). The critical P level was slightly higher for both crops at the 1st harvest.

Table 2: Substrate characteristics at planting (CAT-soluble P, \(C_s\); P concentration in substrate solution, \(C_{Li}\); buffer power, \(b\)) for poinsettia and marigold at different P-application rates.

<table>
<thead>
<tr>
<th>P-application rate (a)</th>
<th>Poinsettia</th>
<th>Marigold</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(P (C_s)^a)</td>
<td>(P (C_s)^b)</td>
</tr>
<tr>
<td>0</td>
<td>2</td>
<td>0.1</td>
</tr>
<tr>
<td>10</td>
<td>3</td>
<td>0.3</td>
</tr>
<tr>
<td>35</td>
<td>11</td>
<td>1.5</td>
</tr>
<tr>
<td>100</td>
<td>42</td>
<td>22</td>
</tr>
<tr>
<td>170</td>
<td>84</td>
<td>45</td>
</tr>
</tbody>
</table>

\(a\) mg P (L substrate\(^{-1}\)); \(b\) mg P (L solution\(^{-1}\))

Table 3: Comparison of P applied via fertigation to P uptake by poinsettia and marigold at various P-application rates during the cultivation period (data normalized per liter substrate to allow comparison between crops).

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Amount of P (mg [L substrate(^{-1})]</th>
<th>Up to 1st harvest</th>
<th>1st to 2nd harvest</th>
<th>Fertilization uptake</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Applied</td>
<td>Fertilization(^a)</td>
<td>Uptake</td>
<td>Fertigation(^a)</td>
</tr>
<tr>
<td>Poinsettia</td>
<td>0</td>
<td>53</td>
<td>13</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>53</td>
<td>17</td>
<td>19</td>
</tr>
<tr>
<td>Marigold</td>
<td>35</td>
<td>57</td>
<td>42</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>57</td>
<td>46</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>170</td>
<td>57</td>
<td>52</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>24</td>
<td>2</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>25</td>
<td>7</td>
<td>25</td>
</tr>
<tr>
<td>Marigold</td>
<td>35</td>
<td>28</td>
<td>18</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>29</td>
<td>28</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>170</td>
<td>29</td>
<td>31</td>
<td>34</td>
</tr>
</tbody>
</table>

\(a\) Differences in the amount of applied P via fertigation are due to variation in crop transpiration.
Root morphological parameters of both crops were also significantly affected by P supply (Fig. 6). Root-length density increased with P supply up to optimum P level at 1st and 2nd harvest of marigold, but for poinsettia no change of root-length density was observed at both harvests (Fig. 6A). Root-length density of marigold was 2-fold higher than that for poinsettia. However, root hairs of both crops were longer at low P supply compared to high P (Fig. 6B). Marigold had 2-fold longer root hairs than poinsettia at all P levels. In addition, marigold had smaller root radius \( (r_0 = 0.02 \text{ cm}) \), compared to poinsettia \( (r_0 = 0.04 \text{ cm}) \). Total root length per gram shoot dry matter of marigold \( (20–40 \text{ m} [\text{g shoot dry matter}]^{-1}) \) was also double that of poinsettia \( (10–20 \text{ m} [\text{g shoot dry matter}]^{-1}) \) at all P levels.

The mean half distance between roots \( (r_1) \) decreased with plant age and was about half for marigold compared to poinsettia throughout cultivation (Fig. 7). Extension of depletion
zone ($\Delta x$) was calculated for a 2 d depletion period, because the plants were fertigated every 2 d. At 10 d after planting, $\Delta x$ for marigold was 2/3 of $r_1$, but was only 1/3 in the case of poinsettia. Later during cultivation, $\Delta x$ extended beyond $r_1$. Thus, at the very early stages (10 DAP) marigold exploited about 43% of substrate volume, whereas only 10% were exhausted by poinsettia.

3.3 Phosphorus uptake

The simulated P uptake taking into account root cylinder plus root hairs agreed well with the experimentally observed values for both crops (Fig. 8A), although at lower P levels a slight overestimation was observed. The enhancement of predicted P uptake by root hairs was higher at lower P levels for both crops (Fig. 8B). However, at optimum P supply, the increase of P uptake by root hairs was only 10%–20% compared to root cylinder. Root hairs enhanced predicted P uptake significantly, more for marigold than for poinsettia.

The simulated P-depletion profiles with root cylinder plus root hairs at root surface indicated a steep concentration gradient (Fig. 9). The depletion zone extended with increase of P supply and reached approx. 2 mm at optimum P level, a value similar to that given in Fig. 7 for $\Delta x$. The concentration at root surface was 0.81 $\mu$M and 0.96 $\mu$M for treatment 10 mg P (L substrate)$^{-1}$ and 10.4 and 12.4 $\mu$M for the treatment 35 mg P (L substrate)$^{-1}$ for poinsettia and marigold, respectively.

4 Discussion

4.1 Phosphorus dynamics in the substrate

The increase of P-application rate resulted in enhancement of CAT-soluble P ($Cs$) and substrate-solution P ($Cli$) for both poinsettia and marigold (Fig. 2A, B and Tab. 2). The close correlation ($r^2 = 0.96$) between the $Cs$ and $Cli$ was exponential, thus the buffer power ($b$) decreased with increasing P level (Tab. 2) as has been reported for mineral soils (Hendriks et al., 1981). Phosphorus sorption and desorption in the substrate was fast (Fig. 1). The concentration of P in the substrate solution ($Cli$) at optimum P level was 1.5 mg L$^{-1}$ for both crops. This value was at least 5 times higher than the value of 0.3 mg L$^{-1}$, which has been reported for most mineral soils (Barber, 1995). This high $Cli$ was necessary to meet the demand of plant roots, since $b$ was very low (Tab. 2) compared to mineral soils (Jungk and Claassen, 1997). However, it was in the range as reported for horticultural substrates (Khandan-Mirkohi and Schenk, 2008). The low $b$ values show that the mineral component used had a small P-sorption capacity and P in the substrate was more mobile compared to mineral soil.

Supplementary P application through fertigation increased the level of $Cs$ for both crops from planting until 1st harvest at low P levels, but not at high P levels (Fig. 2A, B). Although the amount of fertigated P exceeded P uptake at the two lower P levels (Tab. 3), plants suffered from P deficiency. This indicates that rather the transport of P to the root surface than the amount of P limited growth at this stage. This was confirmed by calculation of P-depletion profiles at root surface (Fig. 9). After 2 d of depletion, the concentration at root

---

Figure 8: Ratio of predicted vs. observed P uptake of poinsettia and marigold taking into account root cylinder plus root hairs for the calculation (A) and enhancement of P uptake calculated from the difference between simulations with and without P uptake via root hairs (B), as affected by P application (simulation for 2 d uptake after 1st harvest; observed uptake was calculated assuming linear growth between first and the second harvest).

Figure 9: Calculated depletion profile in substrate solution ($C_h$) for poinsettia and marigold 10 d after planting (simulated for 2 d taking into account P uptake via root cylinder plus root hairs) at three P-application levels.
surface was below the assumed $K_p$ value (5 μM) and the concentration gradient was insufficient to fit the demand. Obviously, the plants needed a concentration gradient of about 30–40 μM to drive the necessary flux. This gradient could not be established at the two lower P levels.

The increase of $C_r$ at the lower P levels from planting up to the 1st harvest was more pronounced for poinsettia than for marigold. This may be explained by the larger mean half distance between poinsettia roots and the comparatively small extension of the P-depletion zone (Fig. 7). Poinsettia roots exhausted about 10% of the substrate volume, but marigold exploited about 43% at 10 d after planting. Thus, more of the fertigated P was accumulated in the nonexploited substrate with poinsettia leading to a more pronounced increase of $C_r$. Later during cultivation, the mean half distance between roots decreased and the whole substrate volume could be exploited so that no further increase of $C_r$ occurred. This is completely different from the open-field situation, where plants acquire P from only a small part (less than 20%) of the soil volume (Jungk and Claassen, 1997; Claassen and Steingrobe, 1999).

4.2 Plant growth

The optimum P level of both poinsettia and marigold was 35 mg (L substrate)$^{-1}$ (Fig. 4), which resulted in about the same P concentration of shoot dry matter (Fig. 5), suggesting that the utilization efficiency of both crops was the same. The critical P level of both crops was in the range as reported for other horticultural crops (Sanchez, 2007). Root-length density of poinsettia at both harvests was in the range as known for field-grown crops in the upper soil layer (Schenk and Barber, 1980), whereas RLD for marigold was clearly higher. However, even the lower RLD of poinsettia was enough to exploit the whole pot volume, since the depletion zones of roots overlapped because of the low buffer power (Fig. 7).

Root hairs were longer at low P supply for both crops (Fig. 6B). Similarly, increased root-hair length under P deficiency was observed for tomato, rape, and spinach grown in nutrient solution or in soil (Föhse and Jungk, 1983). The length of root hairs varies greatly within and among plant species (Hofer, 1996) and depends on the supply of P, NO$_3$, and Fe (Hoffmann and Jungk, 1995; Föhse and Jungk, 1983). However, not all plant species respond to nutrient deficiency with increased root-hair length. Dechassa et al. (2003) observed no difference in root-hair length in cabbage, carrot, and potato cultivated in mineral soil at different P-supply levels. Furthermore, it was reported that in mineral soil increased root-hair growth may also be induced by water shortage (Reid and Bowen, 1979). The average root-hair length was 0.23 and 0.38 mm for poinsettia and marigold, respectively. These values were in the range reported for other crops (the shortest being for onion [0.05 mm] and the longest [0.62 mm] for spinach; Föhse et al., 1991).

Simulation of P uptake showed that the importance of root hairs for the predicted P uptake was higher at the low P levels for both crops (Fig. 8B). At the optimum P level, root hairs increased predicted P uptake over that of the root cylinder only by 10%–20%, since P buffering in the substrate was low. Long root hairs are highly efficient in acquiring P from mineral soil by extending the depletion zone (Föhse et al., 1991), since $b$ for P is high. The low $b$ of P in the peat substrate led to a high effective diffusion coefficient ($D_{eff}$). Therefore in contrast to soil, P was considerably mobile in the peat substrate (Khandan-Mirkohi and Schenk, 2008) and longer root hairs of marigold were less important to extend the depletion zone for P acquisition. The effective diffusion coefficient of P in the substrate was comparable with $D_{eff}$ of K in mineral soils (10$^{-7}$ to 10$^{-8}$ cm$^2$ s$^{-1}$, Khandan-Mirkohi and Schenk, 2008). Therefore, the situation of P in the substrate is comparable with the situation of K in mineral soil, where longer root hairs are not relevant for its depletion (Claassen and Steingrobe, 1999).

4.3 Modeling of plant and substrate parameters

The predicted P uptake by root cylinder plus root hairs reflected the observed P fairly well indicating that plant and substrate parameters involved in P uptake were well determined (Fig. 8A; Tab. 1) and that no additional mechanism of P mobilization was involved. However, a slight overestimation was observed at lower P levels for both crops. Sensitivity analysis revealed that changing of $I_{max}$ and $C_{min}$ did not change the prediction, but increasing $K_m$ from 5 μM to 6 μM and to 10 μM reduced the overestimation close to 1:1 line at low P levels for marigold and poinsettia, respectively. This indicates that for both crops, a higher $K_m$ value has to be assumed. The values 6 and 10 μM are in the range as known from other crops (e.g., for onion the value of 10.3 μM was determined; Deressa and Schenk, 2008).

5 Conclusions

The observed higher content of plant-available P in the substrate for optimum growth of poinsettia compared to marigold was attributed neither to the utilization efficiency nor to the uptake efficiency. The observed higher P level for optimum growth of poinsettia was an artifact of the lower root-length density after planting.

Acknowledgments

We thank General Office of Scholarship and Overseas students (MSRT, IRAN) for granting the first author and the anonymous referees and associate editor for the useful suggestions given to this paper.

References


Brewster, J. L., Bhat, K. K. S., Nye, P. H. (1976): The possibility of predicting solute uptake and plant growth response from indepen-
Phosphorus efficiency of ornamental plants 377


