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Characteristics of phosphorus uptake kinetics of poinsettia and marigold

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ABSTRACT

In a previous experiment it has been found that maximum uptake rate (I max), Michaelis constant (K m), and minimum nutrient concentration (C min) as plant physiological characteristics may be important for phosphorus (P) uptake in peat-substrate. Thus, variation of P uptake parameters was evaluated with a series of depletion studies for poinsettia (Euphorbia pulcherrima) and marigold (Tagetes patula) under fluctuating climatic conditions and different developmental stages.

Relative growth rate (RGR) of marigold was higher than that of poinsettia and declined for both crops with plant age. Lower air temperature reduced the RGR of poinsettia, but not of marigold. However, the lower light intensity reduced the RGR of marigold while it had no effect on the RGR of poinsettia. A short photoperiod reduced the RGR of poinsettia. Maximum uptake rate also decreased with plant age and with decrease of air temperature for both poinsettia and marigold; however, it was independent of light intensity. Maximum uptake rate of poinsettia was lower during short photoperiod than that of longer photoperiod. A close correlation between RGR and I max was observed with both poinsettia and marigold throughout all treatments. The K m and C min were affected neither by plant age, air temperature, light intensity nor by day length. However, higher I max, but lower K m and C min values were observed for marigold than for poinsettia during all treatments. The required P availability in the substrate was not much affected by short term fluctuations of growing conditions and photoperiod. However, it was clearly reduced with plant age for both crops which should be considered for fertilization.

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1. Introduction

The uptake of nutrients by plants follows the saturation kinetics of Michaelis–Menten, which can be described mathematically by (1) I max which occurs under saturating nutrient concentration where all the available binding sites are loaded, (2) K m which is nutrient concentration where the actual uptake equals half the I max and (3) C min which is the minimum nutrient concentration below which no net uptake can occur (Barber, 1995).

Different values of I max, K m, and C min have been reported among brassica (Akhtar et al., 2007) and maize cultivars (Schenk and Barber, 1980). These parameters may also vary with plant age (Edwards and Barber, 1976; Bhadoria et al., 2004; Sharifi and Zeharh, 2006), and environmental conditions (Brewster et al., 1976; Hallmark and Huffaker, 1978; Steingrobe and Schenk, 1994). Maximum uptake rate decreases with plant age, since more roots are available to meet the nutrient demand for new growth (Barber, 1995). The demand depends on nutrient concentration in new growth, change of nutrient concentration in the whole plant as well as the quantity of new growth. The new growth can be related to plant weight by the RGR and a close correlation between the RGR and I max has been observed (Steingrobe and Schenk, 1994; Cheaib et al., 2005; Rodgers and Barmeix, 1988). Steingrobe and Schenk (1994) found that the RGR was affected by growing conditions such as temperature and radiation.

Root physiological properties are significant for K + and NO3– acquisition in mineral soil, but not for P (Claassen and Steingrobe, 1999). However, the mobility of P in peat-substrates (which are generally used for pot plant production) is an order of magnitude higher than in mineral soils, i.e. similar to mobility of K + in mineral soil (Khandan-Mirkohi and Schenk, 2008; Claassen and Steingrobe, 1999). Thus, root morphological characteristics are of minor importance for exhaustion of the substrate volume whereas physiological P uptake characteristics of plants may be significant for adaptation of nutrient supply to demand of crops as well as for environmental conditions affecting the plant growth rate. The uptake rate can be used to roughly estimate the concentration difference between bulk substrate solution and concentration at...
root surface which could meet the P demand assuming that P is transported to root surface only by diffusion (Barralough, 1986). Thus, this study aimed at investigating the effect of short term variable environmental conditions on P uptake kinetics of poinsettia and marigold at different developmental stages and to evaluate the need for adaptation of P supply.

2. Material and methods

2.1. Propagation and growth

Poinsettia (Euphorbia pulcherrima cv. ‘Premium Red’) cuttings were taken from mother plants 8 cm long and 7–8 nods. Except for three fully developed upper leaves all others were removed. The cuttings were rooted in nutrient solution under plastic covers for 25 days. Marigold (Tagetes patula cv. ‘Nana Orange Jacket’) seeds were germinated in fine sand and grown for 7 days. Both crops were transferred to 1.8 L ceramic pots. Later, 45 Jacket’ seeds were germinated in fine sand and grown for 7 days. The uptake of P was measured through its depletion from solution based on the Michaelis–Menten function.

2.2. Treatments

Characteristics of P uptake kinetics were determined 20, 40, 70, and 95 days and 15, 25, 31, and 40 days after planting (DAP) for poinsettia cuttings and marigold seedlings, respectively. Additional day/night temperature treatments were 15/11 and 25/21 °C at 30 and 25 DAP for poinsettia and marigold, respectively. Light intensity variations were 100 and 300 μmol m−2 s−1 PAR at 40 DAP (poinsettia) and 31 DAP (marigold). The plants were subjected to these conditions 2 days prior to determination of P uptake characteristics. For poinsettia, also the day/night photoperiod was varied to 8/16 h beginning from 40 DAP.

2.3. Determination of P uptake kinetics

Parameters of P uptake kinetics were determined by a series of depletion experiments as described by Claassen and Barber (1974). The uptake of P was measured through its depletion from solution in a series of time intervals (Fig. 1). The measured uptake was used to calculate the uptake rate of the crop knowing the existing root length. The data of the depletion curve was used to describe the relation between actual solution concentration and uptake rate based on the Michaelis–Menten function.

The initial P concentration was 20 μM, whereas for the other nutrients the nutrient solution mentioned above was used. Two millilitres of solution samples were taken at first every 10 min and later every 40 min and the sampled solution was replaced by distilled water. The experiment was continued until no further depletion was observed (Cmin was reached). Phosphorus concentration in nutrient solution was monitored twice per day and the pot was generally depleted faster with marigold compared to poinsettia. An exemplary depletion curve is given in Fig. 1.

The RGR (g g−1 day−1) of plants was obtained by weighing the plants just before turning off the light on the day before running the depletion study and 24 h later. The surface water of roots was removed by dripping for 2 min. The RGR was calculated according to Hunt (1982):

\[
RGR = \frac{\ln(FW_2) - \ln(FW_1)}{t_2 - t_1}
\]

where FW describes plant fresh weight (g plant−1), t is time (day); subscripts 1 and 2 refer to the first and the second measurement, respectively.

The fresh weight of roots (RFW, g plant−1) was determined according to Schenk and Barber (1979) and root length (L, cm plant−1) was determined by means of photo-analysis software (WinRHIZO, Canada, Regent Instruments Inc.; www.regentinstruments.com) based on the line intersect method of Tennant (1975).

Mean root radius (r0, cm) was calculated as:

\[
r_0 = \sqrt{\frac{RFW}{\pi \times L}}
\]

2.5. Theoretical estimation of concentration gradient

The significance of the measured uptake rates were evaluated theoretically for pot plants grown in peat-substrate by estimation...
of the concentration difference between bulk substrate solution and concentration at root surface ($\Delta C$, mmol cm$^{-3}$) according to Barraclough (1986):

$$\Delta C = C_l - C_l^0 = -\left(\frac{I_{\text{max}}}{4\pi D_L u_f}\right)
\left(1 - \frac{1}{\pi r_0^2 \text{RLD}} \ln \frac{1}{\pi r_0^2 \text{RLD}}\right)$$

(3)

where $C_l$ is the average bulk substrate solution concentration (mmol cm$^{-3}$), $C_l^0$ is the concentration at the root surface (mmol cm$^{-3}$), $I_{\text{max}}$ is the maximum uptake rate (mmol cm$^{-1}$ root s$^{-1}$), $D_L$ is the diffusion coefficient of H$_2$PO$_4^-$ in water at 25 °C for which the value of $8.9 \times 10^{-6}$ cm$^2$ s$^{-1}$ was used (Edwards and Huffman, 1959), for the volumetric water content ($\theta$) the value of 0.5 cm$^3$ cm$^{-3}$, for the impedance factor ($f$) the value of 0.09, and for RLD which is root length density (cm cm$^{-3}$) the values of 6.9, 11.5, 14.3, and 18.4 at 15, 25, 31, and 40 DAP and 2, 4, 7.1, and 9.6 at 20, 40, 70, and 95 DAP for marigold and poinsettia, respectively, were taken from Khandan-Mirkohi and Schenk (2008, 2009). For $r_0$ the calculated values of 0.025 and 0.06 cm were used for marigold and poinsettia, respectively.

2.6. Statistical analysis

Experiments were run in a randomized block design with completely separate experiments for poinsettia and marigold and replicated five times. Data were analyzed using analysis of variance of SAS (SAS, 1996). The treatments were handled as a single factor in the analysis. Means were compared between the treatments at $\alpha = 0.05$ using Tukey-test and at $\alpha = 0.001$ for multiple regression analysis.

3. Results

3.1. Plant growth

Shoot dry matter (SDM) of poinsettia and marigold increased with plant age (Fig. 2). Marigold flowered 40 DAP, whereas poinsettia required 100 DAP for reaching a marketable size. Shoot dry matter of both crops did not significantly change under different air temperature and light intensity, since variation was applied only for 2 days (data not shown). The short photoperiod induced flowering and consequently reduced SDM of poinsettia compared to plants which continued vegetative growth at long photoperiod. Significant reduction for SDM was found after 95 DAP (55 days after transferring to short photoperiod), but this reduction was not yet significant 70 DAP.

The relative growth rate of both poinsettia and marigold declined with plant age (Fig. 3A). This decline was faster in case of marigold compared to that of poinsettia. The RGR of marigold was several times higher than that of poinsettia, especially at early stages. Lower air temperature reduced the RGR of poinsettia, but not of marigold (Fig. 3B). In contrast, the lower light intensity induced flowering and consequently reduced SDM of poinsettia compared to plants which continued vegetative growth at long photoperiod. Significant reduction for SDM was found after 95 DAP (55 days after transferring to short photoperiod), but this reduction was not yet significant 70 DAP.

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negatively affected the RGR of marigold, but had no effect on the RGR of poinsettia (Fig. 3C). Poinsettia plants grown at short photoperiod had a lower RGR compared to those grown at long photoperiod at 95 DAP, but not at 70 DAP (Fig. 3D).

Root surface/shoot d.m. ratio (RSR) of marigold was four times higher than that of poinsettia (Fig. 4). This parameter increased with plant age for marigold up to flowering stage and then declined. However, in case of poinsettia it increased up to 40 DAP after which it remained almost constant. The short day length decreased RSR of poinsettia at both 70 and 95 DAP (Fig. 4).

Phosphorus concentration in shoot and root dry matter of marigold declined with plant age (Fig. 5B), whereas with poinsettia shoot P concentration increased and no significant change was observed for its root P concentration (Fig. 5A). Root and shoot P concentration of poinsettia was higher than shoot P concentration. During short photoperiod the shoot P concentration of poinsettia was enhanced compared to longer photoperiod (Fig. 5C). Light intensity and air temperature did not affect P concentration in plant dry matter (data not shown).

3.2. Physiological P uptake parameters

Maximum P uptake rate decreased with plant age for both poinsettia and marigold (Fig. 6A). Marigold had higher \( I_{\text{max}} \) than poinsettia at all growth stages. At high air temperature, \( I_{\text{max}} \) was enhanced for both poinsettia and marigold (Fig. 6B). However, \( I_{\text{max}} \) was independent of light intensity for both poinsettia and marigold (Fig. 6C). The \( I_{\text{max}} \) was lower for poinsettia grown during short photoperiod than that of long photoperiod for both 70 and 95 DAP (Fig. 6D). The \( I_{\text{max}} \) was closely related to the RGR of both poinsettia and marigold over all treatments, whereas it was not correlated to RSR of both crops (Table 1). Thus, inclusion of RSR into the multiple regression analysis did not improve the correlation coefficient.

Michaelis constant and \( C_{\text{min}} \) were affected neither by plant age nor by both air temperature and light intensity for both poinsettia and marigold (Fig. 7A–C). Also, no change was observed for \( K_{\text{m}} \) and \( C_{\text{min}} \) values of poinsettia under different photoperiod (Fig. 7D). However, \( K_{\text{m}} \) and \( C_{\text{min}} \) values were higher for poinsettia compared to marigold. As a mean of all treatments, \( K_{\text{m}} \) was 10.47 and 5.27 and \( C_{\text{min}} \) was 0.42 and 0.21 \( \mu M \) for poinsettia and marigold, respectively.

3.3. Theoretical evaluation of P demand for peat grown pot plants

The P uptake rate of poinsettia and marigold plants was used to estimate the concentration gradient necessary to meet the P demand during growth in peat-substrate using Eq. (3). This estimated concentration was 290 \( \mu M \) for marigold and 320 \( \mu M \) for poinsettia at planting (Fig. 8). However, at later stages it declined to 140 and 71 \( \mu M \) for marigold (40 DAP) and poinsettia (95 DAP), respectively. The variation of \( I_{\text{max}} \) by short term fluctuations of growing conditions did not result in a significant change of concentration gradient (data not shown).

4. Discussion

4.1. Plant growth parameters

Relative growth rate declined with plant age for both crops (Fig. 3A) as generally recognized (Hunt, 1982). The change of the RGR for marigold was faster compared to poinsettia. This might be due to the much smaller weight of marigold seedlings (0.48 g d.m. plant\(^{-1}\)) than of poinsettia cuttings (4.26 g d.m. plant\(^{-1}\)), since the RGR declines faster in early stages of growth when the plant weight is lower. Shoot dry matter and RSR of both crops were not significantly affected by air temperature and light intensity, since
variation was applied only for 2 days (data not shown). However, effect was observed for the RGR (Fig. 3B and C), because the RGR was measured based on an increase of fresh matter weight during 24 h for each plant separately. Higher air temperature increased the RGR of poinsettia, but not for marigold (Fig. 3B). This was due to lower temperature requirement for optimum growth of marigold. The air temperature of 15°C was clearly below the optimum temperature of poinsettia, but not for marigold (Dole and Wilkins, 1999).


<table>
<thead>
<tr>
<th>Parameters</th>
<th>y = a₀ + a₁x₁ + a₂x₂</th>
<th>y = a₀ + a₁x₁</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poinsettia</td>
<td>0.69***</td>
<td>0.77***</td>
</tr>
<tr>
<td>Marigold</td>
<td>0.55***</td>
<td>0.57***</td>
</tr>
<tr>
<td>Poinsettia</td>
<td>0.65</td>
<td>1.62</td>
</tr>
<tr>
<td>Marigold</td>
<td>1.62***</td>
<td>1.60</td>
</tr>
<tr>
<td>a₁</td>
<td>20.62***</td>
<td>24.00***</td>
</tr>
<tr>
<td>a₂</td>
<td>8.0 × 10⁻⁸ ns</td>
<td>8.0 × 10⁻⁸ ns</td>
</tr>
</tbody>
</table>

ns, non-significant (n = 50 and 60 for marigold and poinsettia, respectively).


Table 1

*Multiple regression, y = a₀ + a₁x₁ + a₂x₂ *Simple regression, y = a₀ + a₁x₁

Fig. 6. (A) The influence of plant age (days after planting, DAP), (B) air temperature, and (C) light intensity on maximum P uptake rate (I_max) of poinsettia and marigold and (D) the effect of photoperiod on I_max of poinsettia. Different letters (for A–C between different DAP and for D between different photoperiods) indicate significant differences at p < 0.05.

Fig. 7. (A) The influence of plant age (days after planting, DAP), (B) air temperature, and (C) light intensity on Michaelis–Menten constant (K_m) and minimum P concentration (C_min) of poinsettia and marigold and (D) the effect of photoperiod on K_m and C_min of poinsettia. No significant change of K_m and C_min was observed for both crops over all treatments at p < 0.05.
Light intensity increased the RGR of marigold, but not for poinsettia (Fig. 3C). The reason might be that marigold requires a greater light intensity for saturation of photosynthesis. Different light saturation for photosynthesis has been reported for some plant species (Dennison and Alberte, 1982). Increased growth and number of flowers with enhanced light intensity was observed with marigold (Dole and Wilkins, 1999). It was reported that the light intensity over 200 μmol m\(^{-2}\) s\(^{-1}\) decreased the time span towards the flowering of marigold (Pramuk and Runkle, 2003). Short photoperiod reduced both the SDM and the RGR of poinsettia, since flower induction retarded the growth (Figs. 2 and 3D). Plants during long photoperiod continued vegetative growth, and no flower induction was observed.

After the flowering of marigold, the RSR declined as it is well documented for many crops after anthesis (Barber, 1995). Under short photoperiod the RSR of poinsettia declined (Fig. 4), which was due to shortage of light. This effect already occurred at 70 DAP, since the partitioning of assimilates in favor of the shoot under light shortage retarded the root growth, and SDM was not affected yet (Fig. 2).

The P concentration in mature shoot dry matter of poinsettia and marigold was about 4 mg [g d.m.]\(^{-1}\) at 40 DAP, which was about the critical P level of both crops (Khandan-Mirkohi and Schenk, 2009). Root P concentration was higher than shoot P concentration of poinsettia, but for marigold almost no difference was observed between shoot and root P concentration. Higher and also lower P concentration in the root dry matter in comparison to the shoot dry matter was reported in the literature (Asher and Loneragan, 1967; Shane et al., 2004; Akhtar et al., 2007).

4.2. Uptake kinetic parameters

Maximum P uptake rate declined with plant age for both poinsettia and marigold (Fig. 6A). Similarly, a decrease of uptake rate with plant age was reported for other crops (Edwards and Barber, 1976; Bhadoria et al., 2004; Sharifi and Zebarth, 2006). Maximum P uptake rate decreases with plant age, since P demand is met by a continuously growing root leading to a lower demand per unit root length (Barber, 1995). The larger root system compensates for the lower uptake rate and the P demand is satisfied by the smaller \(I_{\text{max}}\). Thus, decrease of \(I_{\text{max}}\) follows the same pattern as the RGR and both are positively related to each other (Table 1). Reason for this close correlation is that \(I_{\text{max}}\) as well as the RGR are related to the existing plant material. However, for calculation of the RGR the new growth is considered in relation to the plant weight whereas for \(I_{\text{max}}\) the nutrient demand induced by new growth is related to the existing root surface. Therefore, the correlation must be close as long as demand increases linearly with new growth while the RSR remains constant. Similarly, a linear relationship between \(I_{\text{max}}\) and RGR for pine seedlings (Cheaib et al., 2005) and between \(I_{\text{max}}\) for NO\(_3\)\(^-\) and RGR of wheat and lettuce (Rodgers and Barnmeix, 1988; Steingrobe and Schenk, 1994) has been reported.

Some discrepancy was observed in the relationship between \(I_{\text{max}}\) and the RGR. At high light intensity marigold displayed a higher RGR (Fig. 3C), but without any change of uptake rate (Fig. 6C). This might be due to a dilution of P in shoot dry matter with growth of marigold (Fig. 5B) leading to a delayed response of the uptake rate, thus uptake physiology was stepping behind the growth rate. Marigold had higher \(I_{\text{max}}\) than poinsettia at all growth stages and under various climate conditions (Fig. 6A–C), since the RGR of marigold was higher. The observed values for \(I_{\text{max}}\) were in the same range that is documented for other crops (Brewster et al., 1976; Schenk and Barber, 1980; Bhadoria et al., 2004).

All the environmental conditions and also plant age affected \(I_{\text{max}}\), but not \(K_m\) and \(C_{\text{lim}}\) (Fig. 7), indicating that definitely the number of transporters had been changed, but not the characteristics of the uptake system (Raghothama, 1999). The \(K_m\) value (mean of all treatments) was twice as high (10.47 μM) for poinsettia compared to marigold (5.27 μM). The value of 5 μM had been reported as common \(K_m\) for most crops (Barber, 1995). However, a \(K_m\) value of 10.3 μM for onion has also been observed (Deressa and Schenk, 2008). The mean \(C_{\text{lim}}\) value for poinsettia (0.42 μM) was twice as high as compared to marigold (Fig. 7). These values are in the range reported for many crops (Brewster et al., 1976; Schenk and Barber, 1980; Bhadoria et al., 2004; Deressa and Schenk, 2008).

4.3. Theoretical evaluation of P demand for peat grown pot plants

The concentration gradient necessary to meet the P demand of poinsettia and marigold plants grown in peat-substrate was evaluated theoretically by means of Eq. (3) using data for peat grown plants taken from Khandan-Mirkohi and Schenk (2009). This approach assumes that P is transported to the root surface only by diffusion and strong competition between roots and hence extension of depletion zone over mean half distance between roots should not occur (Barraclough, 1986). These conditions were met at early stages, but for two later stages an overlapping of depletion zones was observed. However, decreasing of RLD to exceed the mean half distance did not affect the results significantly. Furthermore, the equation describes a steady state situation, whereas in reality a dynamic situation exists for P in the peat-substrate solution, since buffer power is low (Khandan-Mirkohi and Schenk, 2008) and P is continuously top dressed via fertigation. Despite these shortcomings the approach allows to evaluate the significance of \(I_{\text{max}}\) variation for plants grown in peat.

The higher \(I_{\text{max}}\) of marigold could be satisfied by a lower concentration gradient in substrate solution compared to poinsettia (Fig. 8). This was due to a higher RLD of marigold compared to that of poinsettia (see Eq. (3)). However, assuming a Freundlich-function relationship between \(C_i\) (mg P L\(^{-1}\)) and concentration of plant available P in peat-substrates (\(C_p\), mg P [L substrate]\(^{-1}\)) (\(C_i = 7.62 C_p^{0.56}\)) as described by Khandan-Mirkohi and Schenk (2009), \(C_i\) values of 26 and 27.5 mg P [L substrate]\(^{-1}\) at planting and 17.3 and 12 mg P [L substrate]\(^{-1}\) at last harvest would be required to meet the demand of marigold and poinsettia, respectively. Obviously, the difference between species was too
small to be taken into account for fertilization. Also, with both crops short term fluctuations of growing conditions as well as short photoperiod for poinsettia were of minor significance for the required P availability in the substrate, since the uptake rate was not changed immensely (Fig. 6B–D). However, for both crops declined considerably with plant age which should be considered for top dressing by fertigation and evaluation of substrate P status. The C values of 26–27.5 mg P [L substrate]–1 presented here were in the range as recommended for high fertilized substrate (22–131 mg P [L substrate]–1) at planting (Röber and Schacht, 2008).

5. Conclusions

Marigold had clearly lower $K_m$ and $C_{min}$ but higher $I_{max}$ compared to poinsettia. However, the amount of $C_t$ to meet the demand of both crops was not much different. Also, short term fluctuations of growing conditions and short photoperiod were of minor significance for the required P availability in the substrate and have not to be considered in fertilization. However, the need for $C_t$ was clearly reduced with developmental stage of both crops which has to be taken into consideration for fertilization.

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References


