PHOSPHATE DYNAMICS IN PEAT-BASED SUBSTRATES AND P EFFICIENCY OF ORNAMENTAL PLANTS

Von der Naturwissenschaftlichen Fakultät

der Gottfried Wilhelm Leibniz Universität Hannover

zur Erlangung des Grades

Doktor der Gartenbauwissenschaften

Dr. rer. hort.

genehmigte Dissertation

von

M.Sc. Azizollah Khandan-Mirkohi

geboren am 30.04.1973 in Sarab-Iran

2009

Referent: **Prof. Dr. Manfred K. Schenk**
Korreferent: **Dr. Bernd Steingrobe**
Tag der Promotion: **24. 04. 2009**

Dedicated to my parents and my family

Especially my Father who passed away during my PhD study

Erklärung zur Dissertation

Hierdurch erkläre ich, dass die Dissertation:

Phosphate Dynamics in Peat-Substrate and P Efficiency of Ornamental Plants

selbstständig verfasst und alle benutzten Hilfsmittel sowie evlt. Zur Hilfeleistung herangezogene Institutionen vollständig angegeben wurden.

Die Dissetation wurde nicht schon als Diplom- oder ähnliche Prüfungsarbeit verwendet.

Hannover, den

_____

Unterschrift

Name: **Azizollah Khandan-Mirkohi**

ABSTRACT

Plant species and genotypes may differ in phosphorus (P) efficiency through uptake efficiency and/or utilization efficiency. However, nothing is known for P efficiency of ornamental plants grown on peat-substrates.

It was found that the mobility of P in peat-substrate was considerably higher compared to that in mineral soils, since the effective diffusion coefficient (D_e) was higher. The high value for D_e was attributed mostly to the low buffer power (b) rather than to the impedance factor. Buffer power was two orders of magnitude lower in peat-substrate compared to mineral soil. The b in peat-substrate depended on the used mineral component. It was positively correlated with oxalate-soluble Fe and Al content in the substrate.

Investigation on physiological uptake parameters showed that maximum P uptake rate (I_{max}) decreased with plant age and with decrease of air temperature for both poinsettia and marigold, but it was independent of light intensity. I_{max} was lower in induced plants of poinsettia than in vegetatively growing plants. Michaelis constant (K_m) and minimum nutrient concentration (C_{min}) were not affected by all treatments. However, clearly lower K_m and C_{min}, but higher I_{max} were observed for marigold compared to that for poinsettia.

Marigold had higher root length density (*RLD*) and root: shoot ratio, longer root hairs, and smaller root radius compared to that of poinsettia. However, the favorable root morphological parameters of marigold compared to that of poinsettia were of minor importance for exhaustion of the substrate volume, since P was highly mobile in peat-substrates. Additionally, the optimum yield and quality of both crops were attained at 12 mg P (CAT-soluble) [L substrate]$^{-1}$ and the critical level of P in shoot dry matter of both crops was the same indicating that both crops had also similar utilization efficiency.

Key words: impedance factor, buffer power, uptake rate, root hairs

KURZFASSUNG

Pflanzenarten und Genotypen können sich in ihrer P-Effizienz unterscheiden, die auf einer hohen Verwertungseffizienz und/oder einer hohen Aufnahmeeffizienz beruhen. Untersuchungen zur P Effizienz von Zierpflanzen in Torfsubstraten sind jedoch nicht bekannt.

Es konnte gezeigt werden, dass die Mobilität von P in Torfsubstraten aufgrund des höheren effektiven Diffusionskoeffizienten (D_e) deutlich höher war als in Mineralböden. Der hohe Wert für D_e war vor allem durch die geringere Pufferung (b) und weniger durch den Impedanzfaktor bedingt. Die Pufferung war im Torfsubstrat um zwei Größenordnungen niedriger als im Mineralboden und abhängig von der eingesetzten mineralischen Komponente. Die Pufferung war positiv korreliert mit dem Oxalat-löslichem Fe und Al-Gehalt im Substrat

Untersuchungen der physiologischen Aufnahmeparameter an Poinsettien und Tagetes zeigten, dass die maximale Aufnahmerate (I_{max}) von P mit dem Pflanzenalter und der Lufttemperatur abnahm und es keinen Zusammenhang mit der Lichtintensität gab. Bei Poinsettien war I_{max} geringer bei induzierten als bei vegetativ wachsenden Pflanzen. Michaelis Konstante (K_m) und die minimale Nährstoffkonzentration (C_{min}) waren unbeeinflusst von allen Behandlungen. Deutlich geringere K_m und C_{min}-Werte aber ein höherer I_{max} Wert waren bei Tagetes im Vergleich zu Poinsettien zu beobachten.

Tagetes hatte eine höhere Wurzellängendichte (*RLD*), ein größeres Wurzel/Spross-Verhältnis, längere Wurzelhaare und einen geringeren Wurzelradius verglichen mit Poinsettien. Die günstigeren morphologischen Wurzelparameter von Tagetes waren jedoch für die Ausschöpfung des Bodenvolumens von geringerer Bedeutung, da P in Torfsubstraten sehr mobil war. Optimales Wachstum und beste Qualität beider Zierpflanzen wurden bei 12 mg P (CAT-löslich) [L Substrat]$^{-1}$ erreicht; der Ertragsgrenzwert für P in der Sprosstrockenmasse war für Tagetes und Poinsettien identisch, d.h. die Verwertungseffizienz war gleich.

Schlagwörter: Impedanzfaktor, Pufferung, Aufnahmerate, Wurzelhaare

GENERAL INTRODUCTION

The international trade of ornamental plants is a big business in the global economy (*Videa*, 2002). However, the quantity and quality of the flowers for sale all reflect the consumer satisfaction and changing demands of the world market. These crops are usually grown with high phosphorus (P) fertilization on peat-substrates. Thus, optimization of plant quality by formation of plants by mild P stress and prevention of P toxicity by optimum nutrition of the plant and adaptation of fertilizer program may enable the growers to produce high quality crops and to control the production cost.

1. Phosphorus as a nutrient

Phosphorus (P) plays a fundamental role in photosynthesis, respiration, and regulation of a number of enzymes (*Raghothama*, 1999; *Abel* et al., 2002). However, orthophosphate as the preferred form for assimilation is not easily accessible to most plants, because plants can only take up P from the soil solution and the level of P in soil solution is regulated mainly by its interaction with organic or inorganic surfaces in the soil. The greater proportion of P is adsorbed at minerals and the adsorption capacity varies greatly among the mineral soils (*Nye*, 1979). It is adsorbed to iron and aluminum oxide content as well as surfaces of calcium and magnesium carbonates, converted to organically bound forms, or insolubly precipitated with common cations like iron, aluminum, and calcium (*Holford*, 1997; *Rausch* and *Bucher*, 2002).

Plant species differ greatly in the uptake, accumulation and use of P (*Clark*, 1983; *Adu-Gyamfi* et al., 1989). It was reported that the uptake patterns of various plant species enhances the solubilization of alkaline rock phosphates (*Hoffland* et al., 1989). Also, the organic form of P is a considerable fraction in soils (30-80%) which has to be mineralized before it becomes available to plants (*Raghothama*, 1999).

Phosphorus deficiency has many effects that result in quantitative decreases in the rate of growth, and ultimately yield. More efficient utilization of P reserves by crops depends on the supply by the medium and the capacity of plant root system for

uptake (*Fried* and *Shapiro*, 1961). In order to overcome P deficiency, its supply to plant roots must somehow be increased or plant must fit to the supply capacity of the soil.

2. Phosphorus supply to the root

Interactions between P availability in the soil and its acquisition by the plant determine the P supply of the plant. Its availability depends on present quantity, replenishment capacity and its mobility in the soil (*Jungk* and *Claassen*, 1989). The available P for plants is only the present quantity in soil solution or the amount in equilibrium with that (*Hoffmann* and *Jungk*, 1995). Thus, low P concentration in the soil solution might be a major factor limiting plant growth in many ecosystems where its concentration is commonly less than 1 µM and in most soils it seldom exceeds 10 µM (*Barber*, 1995; *Raghothama*, 1999). In fact the total transport of nutrients in the soil towards the root is assumed as the sum of mass-flow and diffusion. It was observed that only a small fraction of taken up P by plants (< 4%) reaches the root by mass-flow in mineral soil, and diffusion has a main role on movement of this ion (*Claassen* and *Steingrobe*, 1999).

2.1. Mass flow and diffusion

The rate at which P and water are taken up is important to generate the driving force for movement of P through the soil by mass-flow of soil solution. Also, the nutrient will move from the zone of higher concentration to the lower concentration by diffusion if the concentration of the nutrient at the root surface is different from that in the bulk soil solution (*Barber*, 1995).

2.1.1. Mass flow

The amount of nutrient being transported by mass flow (*MF*, µmol cm^{-2} s^{-1}), is given by the product of the volume of water absorbed (V_0, cm^3 cm^{-2} s^{-1}) and the concentration of the nutrient in the soil solution (C_{li}, µmol cm^{-3}):

$$MF = V_0 \times C_{li}, \quad (1)$$

2.1.2. Diffusion

In principle diffusion in water follows Fick's first law which states that diffusion is proportional to the concentration gradient (*Barber*, 1995; *Jungk* and *Claassen*, 1997).

$$FD = -D \times (\Delta c / \Delta x), \quad (2)$$

Where, D ($cm^2\ s^{-1}$), is the diffusion coefficient in uniform medium, $\Delta c / \Delta x$ ($\mu mol\ cm^{-3}\ cm^{-1}$) is the concentration gradient. The minus sign indicates that movement is from higher to the lower concentration. In the Fick's first law the diffusion coefficient, D, replaced with effective diffusion coefficient (D_e, $cm^2\ s^{-1}$) to consider the effective soil parameters on diffusion coefficient (*Nye*, 1979):

$$D_e = D_L \theta f \times (1/b), \quad (3)$$

where, D_L, is the diffusion coefficient of $H_2PO_4^-$ in water at 25 °C; θ is the volumetric water content; f is the impedance factor and b is the buffer power which was calculated as the ratio between available P in the solid phase (C_s) and soil solution P (C_{li}) (*Nye*, 1979). The buffer power is often defined by dC_s/dC_{li} which can be simplified as $\Delta C_s/\Delta C_{li}$ (*Claassen* and *Steingrobe*, 1999). Volumetric water content (θ) is important for normalizing of b and also for the value of f. For un-buffered nutrients which are not adsorbed by the soil, e.g., NO_3^-, Cl^-, and Br^-, the value for $\theta \times 1/b$ is constant and equal to 1, hence for these nutrients:

$$D_e = D_L f, \quad (4)$$

Thus, in this case D_e is only influenced by f (*Nye*, 1979). The value of f is equal to 1 for free solutions such as water. Therefore, the variation in water content in the soil affects the range of pore sizes that remain water-filled and increasing soil moisture decreases the tortuosity of the diffusion path and hence increases the f. Consequently, the effective diffusion coefficient (D_e) is less than that in the free solution (D).

2.2. Impedance factor and buffer power

Pore volume and P sorption capacity of peat-substrates are the main factors, which may have an important role affecting *f* and *b* (*Brückner*, 1997). Considerable research has been conducted regarding the development of media with optimal physical and chemical properties (*Di Benedetto* and *Klasman*, 2004). For many years, various ornamental plants are grown in peat-substrates containing clay (is called afterwards mineral component), since the pore volume, water holding capacity, cation exchange capacity and P sorption capacity are influenced as physical and chemical properties of peat-substrates by addition of fine fraction of mineral components (*Verhagen*, 2004). The volume of pores which filled with water, may affect the dynamics of ions in the substrate through changing the pathway, since the cross-section available for diffusion is affected. Additionally, increasing solids per unit volume by adding fine mineral components may also be expected to restrict physically the diffusion path (*Warncke* and *Barber*, 1972a).

Buffer power of soils depends on the change of the P concentration in the soil solution and the rate of replenishment from the solid phase (*Barber*, 1995; *Marschner*, 1995). It was demonstrated that mineral components have a stronger affinity for P ions than for most other anions such as sulphate and bicarbonate (*Hinsinger*, 2001). *Linquist* et al. (1997) showed that P sorption is higher for smaller soil aggregates. Furthermore, P strongly interacts with surface-active sesqui-oxides and hydrates of mineral components (*Marschner*, 1995). Thus, its adsorption is influenced by properties such as the types of mineral component as well as the Fe and Al oxide content in the soil (*Lima* et al., 2000; *Zhang* et al., 2005).

However, for peat-substrates which are commonly used in large scale for horticultural production, nothing is known about D_e and the mobility of P, since *b* and *f* were not yet determined.

3. P efficiency

Nutrient efficiency can be defined as the ability of plant species or varieties to obtain high yield at low nutrient supply. Plant species differ extensively in the uptake and use of mineral elements (*Clark*, 1983). This ability is often formed by uptake efficiency which is the superior ability of plants to acquire P from the soil through alterations in root morphology, exudation of P mobilizing compounds, and adaptation of P transporters (*Raghothama*, 1999). Additionally enhanced P use efficiency could be involved in this ability through lower cellular P requirements or more efficient remobilization of P within the plant (*Kochian* et al., 2004). Therefore, the genetically based variation in the ability of plants to tolerate P deficiency stress is a trait which is termed P efficiency.

3.1. P uptake efficiency

Because of the low availability of P in the soil, plants have evolved numerous adaptive mechanisms to acquire P from the soil such as increase in root proliferation in a large volume of soil, specialized root structures, root-mediated changes in rhizosphere chemistry, association of roots with vesicular-arbuscular mycorrhizae (VAM), and adaptation of root physiological parameters. Long root hairs and high root: shoot ratio was observed for some crops cultivated in mineral soils as significant morphological root characteristics contributing to the P uptake efficiency (*Föhse* and *Jungk*, 1983; *Föhse* et al., 1988; *Itoh* and *Barber*, 1983; *Gahoonia* and *Nielsen*, 1996 and 1997; *Eticha* and *Schenk*, 2001; *Bhadoria* et al., 2004).

3.1.1. Root hairs

Root hairs emerge and elongate in a zone several millimeters behind the root tip in most species and its length varies greatly within and between species (*Clarkson*, 1985; *Hofer*, 1996) and depends on supply of P, NO_3 and Fe (*Hoffmann* and *Jungk*, 1995; *Bates* and *Lynch*, 1996; *Föhse* and *Jungk*, 1983; *Schmidt* et al., 1999). Furthermore, it was also reported that root hair growth is as well induced by water

shortage in mineral soil (*Reid* and *Bowen*, 1979). 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 (*Brassica oleraceae* L. cv. Farao), carrot and potato cultivated in mineral soil at different P supply. Long root hairs are highly efficient to acquire immobile nutrients from mineral soil such as phosphate by extending the depletion zone (*Föhse* et al., 1991; *Bates* and *Lynch*, 2001). However, for mobile nutrients such as potassium longer root hairs are insignificant for its depletion (*Claassen* and *Steingrobe,* 1999).

3.1.2. Root/shoot ratio

Reduced shoot growth and increased root: shoot ratio was frequently reported for P deficient plants (*Parks* et al., 2000; *Whiteaker* et al., 1976). Reduction of leaf expansion and reduced leaf initiation are reported as a direct explanation for the decrease of shoot growth under P deficiency (*Lynch* et al., 1991). Decreased root hydraulic conductance and reduced transport of cytokinins from root to the shoot were also expected to be the reasons for reduced leaf expansion and initiation (*Salama* and *Wareing*, 1979). High root: shoot ratio was reported to be the reason for P uptake efficiency of wheat, ryegrass (*Föhse* et al., 1988), and maize (*Bhadoria* et al., 2004). Also, preferential root distribution in the top soil was identified for bean as root morphological trait of P efficiency (*Lynch* and *Brown*, 2001). If a plant species has a higher root: shoot ratio the P demand per unit length of root will be lower than for a species having a lower root: shoot ratio.

3.1.3. Specialized roots

Plants with specialized root structures (e.g., cluster roots) are also efficient in P uptake (*Neumann* and *Martinoia*, 2002). This type of roots develops on root systems of a range of species belonging to a number of different families (e.g., *Proteaceae*, *Casuarinaceae*, *Fabaceae* and *Myricaceae*). Their morphology is variable but typically, large numbers of determinate branch roots develop over very short distances of main root axes (*Shane* and *Lambers*, 2005). Cluster roots are an

adaptation for nutrient acquisition from low fertility soils. *Proteaceae* are famous for their root modifications (proteoid roots) that enhance P uptake (*Handreck*, 1997). These plants are adapted to grow well under low P availability.

3.1.4. Mycorrhizal symbiosis

In addition, a large volume of soil could be explored by mycorrhizal symbiosis to enhance the quantity of immobile ions and their availability to plants, which can be accounted for an increase in P uptake at low concentration in the soil (*Bolan*, 1991). The effect of mycorrhizal symbiosis is primarily based on improved uptake of nutrients, especially for P under low fertility conditions (*Marschner*, 1995). The carbohydrate requirement of fungal association may depress the growth of mycorrhizal plants (*Pfeffer* et al., 1999). However, the effects of mycorrhizae on P uptake and ultimately plant growth are higher than the carbon costs (*Grandcourt* et al., 2004). Roots of most vascular plants except for a few families mainly belonging to the *Chenopodiaceae*, *Crucifereae*, *Cyperaceae*, *Juncaceae* and *Proteaceae* are associated with Vesicular-arbuscular mycorrhizae (VAM) under natural conditions, in nearly all soils (*Bolan*, 1991). It was reported that number of flowers and shoot and root fresh weights of marigold, which were planted in the soil significantly increased when inoculated with VAM (*Aboul-Nasr*, 1996). A high correlation was also found between P uptake by marigold and VAM hyphae length at limited P supply in the soil (*Abou El Seoud*, 2008).

3.1.5. Rhizosphere chemistry

The excretion of root exudates such as malate and citrate (*Dechassa* and *Schenk*, 2004; *Hinsinger*, 2001) or protons into the rhizosphere (*Neumann* and *Römheld*, 1999; *Ryan* et al., 2001) are some root-mediated changes in the rhizosphere chemistry aimed at increasing P availability. Root exudation is largely dependent on the nutritional status of the plant and e.g. occurs in response to P deficiency. Organic anions excreted from root form complexes with Ca, Al and Fe and thus dissolve P bound to these nutrients and release it for uptake by plant (*Marschner*, 1995).

Additionally, organic anions can desorb P from sesqui-oxide surfaces by anion exchange (*Bolan* et al., 1994; *Hinsinger*, 2001; *Dakora* and *Phillips*, 2002). 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).

3.1.6. Physiological uptake kinetics

Plants may also adapt its root physiological uptake parameters under nutrient starvation. The uptake of nutrients by plants follows the saturation kinetics of Michaelis-Menten, the same that define enzyme activity (*Marschner*, 1995), which can be described by three parameters, a) maximum uptake rate (I_{max}), which occurs under saturating nutrient concentration where all the available binding sites are loaded, b) Michaelis constant (K_m), which is nutrient concentration where the actual uptake equals half the I_{max} and c) minimum nutrient concentration (C_{min}) below which no net uptake can occur (*Barber*, 1995). The higher I_{max} means the high availability of transporters and the lower K_m means the higher affinity between the transporters and ions. I_{max} and C_{min} differ considerably among plant species (*Schenk* and *Barber*, 1980; *Brewster* et al., 1976a; *Bhadoria* et al., 2004; *Deressa* and *Schenk*, 2008). As a common value for many crops the K_m of 5 µM for P was reported by *Barber* (1995); however, the higher and lower K_m value was also reported for other crops (*Jungk* et al., 1990; *Föhse* et al., 1991; *Schenk* and *Barber*, 1980; *Bhadoria* et al., 2004; *Deressa* and *Schenk*, 2008). Roots are able to alter the uptake kinetics in response to low P availability based on their demand, particularly by increasing I_{max} (*Nielsen* and *Barber*, 1978; *Schenk* and *Barber*, 1980; *Jungk* et al., 1990), whereas changes in K_m and C_{min} are of minor importance in this process (*Raghothama*, 1999). It was implied that the I_{max} is related to nutrient demand (*Nye* and *Tinker*, 1977), and the nutrient demand is also related to the plant growth rate.

3.1.7. Relationship between relative growth and uptake rates

The relative growth rate (*RGR*) generally declines with plant age (*Hunt*, 1982) and is highly affected by environmental conditions, e.g. temperature, light intensity and photoperiod. Plant species may have different photosynthetic capacities as either a strong or weak light intensity response (*Hodges* and *Barber*, 1983). The integrated control of light intensity, photoperiod and day/night temperature may also affect the quality of some ornamental crops (*Bodson* and *Verhoyen*, 2000; *Vogelezang*, 2000).
The change in *RGR* under fluctuating environmental conditions may influence the P uptake rate. A linear relationship between I_{max} for P and *RGR* of pine seedlings (*Cheaib* et al., 2005) and between I_{max} for NO_3 and *RGR* of wheat and lettuce (*Rodgers* and *Barneix*, 1988; *Steingrobe* and *Schenk*, 1994) was reported. Similarly, decrease of uptake rate by plant age was reported for cotton (*Nayakekorala* and *Taylor*, 1990), wheat and rice (*Bhattacharyya* and *Datta*, 2005), maize and groundnut (*Bhadoria* et al., 2004), corn (*Edwards* and *Barber*, 1976), and potato cultivars (*Sharifi* and *Zebarth*, 2006). Plant species with a larger root system may also compensate the lower uptake rate, and thus the P demand may be satisfied by the smaller I_{max} (*Barber*, 1995).

In mineral soil, however the improved root morphology such as higher root length density, smaller root radius, longer root hairs, and higher root growth rate are relatively more important than kinetic parameters in P acquisition to explore more P from a large volume, since P in soil is immobile and its concentration in soil solution is considerably low (*Bieleski*, 1973; *Nye*, 1977; *Jungk* and *Claassen*, 1997). Thus, the diffusion to the root surface is mostly the rate limiting step in P acquisition by plants and not the rate of transport across the membrane (*Nye*, 1977; *Chapin*, 1980; *Barber*, 1995). However, significance of uptake kinetics is not yet evaluated for peat-substrates.

3.2. P utilization efficiency

Plants can obtain high yield and produce more biomass with a low P concentration in their dry matter, through lower cellular P requirements or more efficient remobilization

of P within the plant (*Claassen* and *Steingrobe*, 1999; *Kochian* et al., 2004). The mechanism of internal P utilization efficiency is not yet clarified. However, the ability of plant to recycle P in the plant is dependent on the activity of enzymes such as *acid phosphatase* and *ribonuclease*, where an increase in the activity of both enzymes was reported (*Shinano* et al., 2005). These enzymes may be involved in hydrolyzing of organic compounds to mobilize and recycle P in the plant (*Duff* et al., 1994). Therefore, some plants are considered as use efficient plants generally through their lower cellular P requirements to maintain normal metabolic activities or developing of strategies to more efficient internal remobilization of P so that all organs receive adequate amounts of phosphorus, especially new growing organs.

4. Modeling of plant and substrate parameters

Mechanistic models of nutrient uptake have been developed over the last three decades in order to evaluate the parameters involved in nutrient transport to the root surface and uptake by the plant. *Nye* and *Spiers* (1964) constructed the first steady-state model of mass flow and diffusion of nutrients to the root surface. Further developments included Michaelis-Menten uptake kinetics (*Barber* and *Cushman*, 1981; *Claassen* and *Barber*, 1976; *Cushman*, 1979; *Nye* and *Marriott*, 1969). Then, the model was modified with including the effects of new root growth to allow development of the depletion zone over time (*Smethurst* and *Comerford*, 1993). Later, the mechanistic simulation model (NST 3.0) described by *Claassen* and *Steingrobe* (1999) additionally 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 yet considered in the model.

5. Phosphorus demand for optimum yield

The critical concentration is usually defined as the nutrient concentration that is just sufficient for maximum growth (usually 90% of maximum yield) (*Ulrich*, 1952). This range as determined experimentally, is a narrow range of nutrient concentrations,

above which the plant is amply supplied with nutrients (luxury consumption), and below which the plant is deficient. However, for ornamental crops not only the optimum yield production, but also the plant performance and maintenance quality is also important to be considered for determining of critical P level.

One of the more important quality parameters is the control of plant height which may improve the aspect and facilitate the handling and marketing. This parameter is most traditionally regulated by application of growth retardants such as *Cycocel*, *B-Nine*, and *Bonzi* (paclobutrazol) (*Armitage*, 1993; *Dole* and *Wilkins*, 1999). However, tighter restrictions have recently been placed on chemical use in agriculture, so non-chemical alternatives have received a great deal of attention to regulate plant growth in recent years (*Cox*, 2001). The height of ornamentals particularly poinsettia can also be controlled more 'naturally' using a negative DIF (difference between day and night temperature) (*Dole* and *Wilkins*, 1999; *Vogelezang*, 2000). However, in recent years, P starvation is also considered as an effort to control the height of some ornamental bedding plants (*Borch* et al., 2003). According to the numerous reports low P availability restricted growth of shoot and strengthened root activity for many crops (*Föhse* et al., 1988; *Bhadoria* et al., 2004; *Nielsen* et al., 2001). Restricted P availability with a buffer technique is called a new method to regulate growth of ornamental plants (*Hansen* and *Nielsen*, 2001). But, leaf area and shoot dry matter of marigold were both reduced under limited P availability (*Borch* et al., 2003).

Low P fertility is risky strategy that may cause unacceptable reductions in plant quality. Also, excessive P application in greenhouse may induce toxicity symptoms and reduce the growth and quality for a number of plant species (*Nichols* and *Beardsell*, 1981; *Parks* et al., 2000). The physiology of P toxicity is not well understood (*Shane* et al., 2004), however, the growth inhibition, early leaf senescence, inhibition of starch synthesis, and chlorotic and/or necrotic regions on leaves are generally symptoms of P toxicity (*Asher* and *Loneragan*, 1967; *Marschner*, 1995; *Parks* et al., 2000; *Lambers* et al., 2002).

Thus, limiting the concentration of available P (C_s) to a level that fit the demand of crops for optimum growth may be important for horticultural crops in the greenhouse, since they are normally fertilized heavily.

Therefore, in this study two representative ornamental plant species were selected in order to evaluate the P efficiency of ornamental plants.

6. Representative ornamental plants

Marigold (*Tagetes patula* cv. 'Nana Orange Jacket') is propagated by seeds and is grown as bedding plant, basket flower, cut flower and pot crop in the most parts of the world. Its petals are also used as coloring agents that contain high levels of xanthophylls (*Dole* and *Wilkins*, 1999; *Chi-Manzanero* et al. 2000). Marigold is a genus of *Asteraceae* family and an herbaceous crop with aromatic divided leaves. Its seeds germinate quite rapidly within 2-3 days at 25 ℃. Marigold flowers under all photoperiod in the temperature range of 17 to 18 ℃, however, in the temperature range of 21 to 24 ℃ it flowers only under short photoperiod (*Dole* and *Wilkins*, 1999). Different responses for photoperiod between marigold cultivars, hybrids, and species were reported and long days delayed the flowering of most cultivars (*Dole* and *Wilkins*, 1999).

Poinsettia (*Euphorbia pulcherima* cv. 'Premium Red') is commercially propagated by terminal stem cuttings taken from mother plants (*Dole* and *Wilkins*, 1999). It is grown as a major ornamental pot crop in the world, especially in the west countries. Its late-season growth habit and vibrant bract colors have strongly influenced its importance as ornamental decorate for the Christmas season, hanging basket plant and occasionally as a cut flower and landscape shrub. Poinsettia is a genus of *Euphorbiaceae* which were divided into free-branching and restricted branching patterns (*Dole* and *Wilkins*, 1999). For production of vegetative cuttings and multi-flowered pot plants, the free-branching characteristic is important. Thus, most commercial cultivars are free-branching. Poinsettia is an obligate short day plant and its flower induction is mostly affected by photoperiod and temperature (*Wang* et al,

2003). Differences between cultivars for the number of days from initiation to the first bract color in response to photoperiod were also reported (*Wieland* et al., 2000).

7. Significance and scope of the study

Based on the literature and presented knowledge, this research was aimed at investigating the dynamics of phosphorus (P) as well as the parameters involved in P transport to plant roots in peat-substrates, efficiency of selected ornamental plants grown in the greenhouse on these substrates under specific environmental conditions, and characteristics of P uptake kinetics of these crops grown in nutrient solution under varied environmental conditions at different developmental stages. The plant and substrate parameters will also be evaluated using mechanistic simulation model (NST 3.0) described by *Claassen* and *Steingrobe* (1999).

The mobility of P in peat-substrates is discussed in chapter 1, characteristics of phosphorus uptake kinetics of ornamental plants are discussed in chapter 2, and finally phosphorus efficiency of ornamental plants in peat-substrates and plant quality aspect are discussed in chapter 3.

CHAPTER 1

PHOSPHORUS DYNAMICS IN PEAT-BASED SUBSTRATES

This is the pre-peer reviewed version of the following article:

(With kind permission of Wiley-VCH Verlag GmbH & Co. KGaA)

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2008): Phosphorus dynamics in peat-based substrates. *J*. *Plant Nut*. *Soil Sci*. 171, 804–809.

Abstract

The mobility of nutrients in soils is well characterized, whereas little information is available for common horticultural substrates based on peat. Aim of the current study was to investigate the mobility and dynamics of phosphorus (P) as well as the parameters involved in P transport to plant roots in peat-substrates. A series of experiments was run to determine the impedance factor (*f*) and the buffer power (*b*). The impedance factor was determined for black peat, and black peat mixed with 20% and 40% (v/v) of mineral component at volumetric water content (θ) of 40, 50, 60, and 70% and at different diffusion time. Buffer power was calculated for black peat and black peat mixed with 20% (v/v) of seven different mineral components. Phosphorus was applied at rates of 0, 35, and 100 mg L^{-1} substrate, respectively. The impedance factor was not affected by addition of the mineral component to peat. However, *f* increased from 0.03 to 0.2, by increasing θ from 40 to 60%, indicating that water content has a significant effect on this parameter. Substrate solution P ranged from 0.3 - 27 and 1 - 95 mg P L^{-1} solution for the P application rate of 35 and 100 mg P L^{-1} substrate, respectively. Buffer power of the substrates ranged from 1 to 17.25 depending on the mineral component and it was positively correlated with oxalate-soluble Fe and Al in the substrate. The calculated effective diffusion coefficient for P in the substrate was in the range of 10^{-7} to 10^{-8} cm^2 s^{-1}. This high value could be attributed mostly to the low buffer power rather than to the high impedance factor.

Key words: Impedance factor/ buffer power/ substrate solution P/ mineral component

1. Introduction

The availability of nutrients to plants depends on their mobility in the soil, where transport towards the root occurs via mass flow and diffusive flux (*Barber*, 1995). The amount of nutrients transported to the root surface via mass flow depends on the nutrient concentration in the soil solution and the amount of water transpired by the plant. Diffusive flux, the movement of nutrients towards a root surface caused by a concentration gradient, is affected by the effective diffusion coefficient, D_e (*Nye*, 1966):

$$D_e = D_L \theta f \times (1/b), \quad (1)$$

where, D_L is the diffusion coefficient of solute in water ($cm^2\ s^{-1}$), θ is volumetric water content ($cm^3\ cm^{-3}$), f is the impedance factor and b is the buffer power of the soil. Extension of the depletion zone around roots increases with D_e and this may lead to inter-root competition for mobile nutrients such as nitrate and potassium. However, for P root competition in mineral soils is unlikely, because the buffer power for P is generally high (*Jungk* and *Claassen*, 1997). The range of D_e for NO_3, K, and P in mineral soils is 10^{-6} to 10^{-7}, 10^{-7} to 10^{-9}, and 10^{-8} to 10^{-11} $cm^2\ s^{-1}$, respectively (*Barber*, 1995). High buffer power leads to small D_e, which limits the diffusion of P to the root surface (*Nye*, 1979; *Barber*, 1995). Buffer power of soils depends on the change of the P concentration in the soil solution and the rate of replenishment from the solid phase (*Barber*, 1995; *Marschner*, 1995). Furthermore, P strongly interacts with surface-active sesqui-oxides and hydrates of mineral components (*Marschner*, 1995). Thus, its adsorption is influenced by properties such as the types of mineral component as well as the Fe and Al oxide content in the soil (*Zhang* et al., 2005).

The impedance factor (f), which describes the tortuosity of the diffusive pathway, is also an important factor affecting nutrient mobility in the soil (*Warncke* and *Barber*, 1972a). A high impedance factor causes a larger D_e and increases the diffusion of P to the root surface (*Nye*, 1979; *Barber*, 1995). An increase of f with an increase of θ was reported for mineral soils (*Barraclough* and *Tinker*, 1981; *Bhadoria* et al., 1991a). However, reports on the influence of bulk density on f are not consistent. *So* and *Nye*

(1989) observed little effect of bulk density on *f*, whereas *Barraclough* and *Tinker* (1981), and *Bhadoria* et al. (1991b) found a decrease in *f* with an increase of bulk density. On the other hand, *Warncke* and *Barber* (1972b) reported an initial increase and then a decrease of *f* with further increase of bulk density.

However, for peat-substrates that are commonly used for horticultural production, nothing is known about D_e and the mobility of nutrients, since *b* and *f* were not yet determined. The current study was aimed at evaluating the influence of *b* and *f* on the effective diffusion coefficient of P in substrates mixed with mineral components, as these are commonly used in the substrate industry.

2. Materials and methods

2.1. Impedance factor (*f*)

The anion exchange membrane method described by *Barraclough* and *Tinker* (1981) was modified and used to determine the effective diffusion coefficient (D_e) in order to calculate *f* of the substrate. PVC cells (VITLAB, Landgraf Laborsysteme HLL GmbH, Langenhagen, Germany; www.vitlab.de) having 28 mm diameter, 49 mm height and a volume of 30 cm^3 were used. An anion exchange membrane (BDHA551642S, VWR International Ltd., Poole, BH151TD, England) was immersed in double-distilled water for 24 h, and then bathed 3 times for 30 min in 1 M $CaCl_2$ solution to completely saturate the membrane with Cl^-.

The following substrates were prepared on the basis of volume weight from black peat, which was passed through a 2 mm sieve, and ground mineral component (Tab. 1, F): 100% black peat, 80% black peat + 20% mineral component, and 60% black peat + 40% mineral component. Substrates were mixed with $CaBr_2$ solution, so that the target volumetric water content and as initial concentration 1.66 µmol Br^- cm^{-3} substrate were achieved.

Table 1: Physical and chemical properties of substrate components

Substrate components	**Texture** (%)			**Amorphous Al and Fe oxides** (g L^{-1})		
	Sand	Silt	Clay	Al	Fe	Sum (Al + Fe)
Black peat(BP)	-	-	-	0.054	0.093	0.15
Mineral component A	4.9	29	66.1	0.386	0.445	0.83
Mineral component B	22.1	16.7	61.2	1.149	17.244	18.39
Mineral component C	7.2	43.1	49.7	1.921	6.950	8.87
Mineral component D	9.8	51.7	38.5	1.157	3.639	4.80
Mineral component E	37.3	36.7	26.0	0.459	0.632	1.09
Mineral component F	33.0	43.3	23.7	1.263	1.749	3.01
Mineral component G	19.0	61.6	19.4	0.409	2.961	3.37

The prepared substrates were packed into the PVC cells, covered with a lid and stored for 24 h in a water vapor-saturated vessel at room temperature. Then chloride-saturated membrane discs were carefully pressed on the substrate surface in the cells, a PVC disc was put on the membrane and covered by a piece of foam enveloped with polyethylene. Finally, the cell was closed with a lid and placed in a water vapor-saturated vessel at room temperature. After termination of measurement, membrane discs were removed and washed free of substrate particles with distilled water. The Br^- on the membrane was eluted by bathing three times for 5 min in 10 mL 0.5 M HNO_3 solution. The extracts were combined, the volume was made up to 30 mL, and Br^- was measured by ICP-MS.

The effective diffusion coefficient was calculated using the following equation (*Warncke* and *Barber*, 1972a):

$$D_e = \frac{M_t^{\,2}\pi}{4C_0^{\,2}t}, \qquad (2)$$

where, D_e (cm^2 s^{-1}) is the effective diffusion coefficient, M_t (µmol cm^{-2}) is the total amount of Br^- that has diffused into the anion exchange membrane in time (t, s), and

C_0 (µmol cm^{-3}) is the initial uniform concentration of Br^- in the substrate. For non-buffered systems holds $\theta/b = 1$, hence f was calculated (*Nye*, 1979):

$$f = D_e/D_L, \quad (3)$$

where, D_L is the diffusion coefficient of solute in water ($cm^2\ s^{-1}$). For Br^- in water at 25 °C, the value of 2.08×10^{-5} $cm^2\ s^{-1}$ was used (*Parsons*, 1959).

To determinate the optimum diffusion period the substrate 80% black peat + 20% (v/v) mineral component was packed into the PVC cells with a bulk density of 0.4 g cm^{-3} determined according to *VDLUFA* (1991). The volumetric water content was kept at 50% and diffusion was run for 2, 4, 6, 12, and 24 h, respectively. To evaluate the influence of water content the volumetric water content of black peat substrate (100%), 80% black peat + 20% mineral component, and 60% black peat + 40% mineral component (bulk density of 0.16, 0.4, and 0.6 g cm^{-3}, respectively, as determined according to *VDLUFA*, 1991) was adjusted to 40, 50, 60, and 70%, respectively.

2.2. Buffer power (*b*)

Black peat (BP) which was passed through a 2 mm sieve was mixed with seven different ground mineral components (A to G; Tab. 1) in a proportion of 80% BP, and 20% mineral component (v/v). Phosphorus was applied to each substrate at rates of 0, 35, and 100 mg P L^{-1} substrate in the form of $Ca(H_2PO_4)_2$. The substrate pH was adjusted to 5.7 ± 0.2 by adding calcium carbonate at a rate of 4-8 g L^{-1} substrate (Fig. 1). Volumetric water content was maintained at 50%. The substrates were equilibrated in an oven at 50 °C for 24 h, then at room temperature for 3 d prior to determining the amount of P adsorbed to the solid phase which is potentially participating in the diffusion (C_s), and prior to measuring the concentration of P in the substrate solution (C_{li}). Our previous work showed that incubation of substrate at a temperature of 50 °C for 24 h was closely correlated with CAT-soluble P after 9 weeks of storage. CAT (0.01 M $CaCl_2$ + 0.002 M DTPA) was reported to be a suitable

solution to extract potentially plant-available P (C_s) in horticultural substrates (*Alt* and *Peters*, 1992).

Buffer power (b) was calculated as the ratio C_s/C_{li} and the value obtained was used to calculate D_e of P in the substrate using equation 1. For the calculations the following values were used: diffusion coefficient of solute in water (D_L) 8.9 × 10^{-6} cm^2 s^{-1} at 25 °C (*Edwards* and *Huffman*, 1959), volumetric water content (θ) 0.5 cm^3 cm^{-3}, impedance factor (f) 0.083 and 0.09 for 100% black peat and 80% black peat + 20% mineral component, respectively.

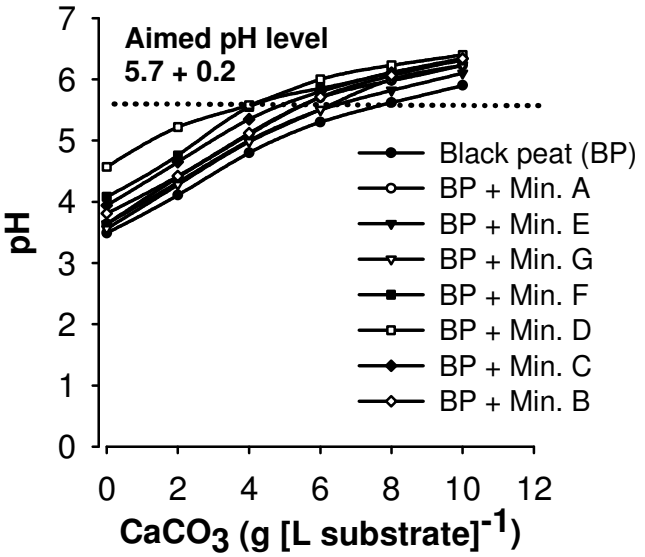

Figure 1: Calibration of pH with calcium carbonate ($CaCO_3$) for black peat and for black peat mixed with different mineral components (Min. A – Min. G); 80% black peat + 20% mineral component (v/v).

2.3. Extension of the depletion zone (Δx)

The extension of the depletion zone around a root can be calculated using the value of D_e (which is a measure of ion mobility in the soil) according to *Syring* and *Claassen* (1995):

$$\Delta x = \sqrt{\pi D_e t}\,, \qquad (4)$$

where, Δx 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).

2.4. Mean half distance between neighboring roots (r_1)

By assuming homogeneous distribution of roots in the substrate the mean half distance between neighboring roots (r_1) was calculated as (*Claassen* and *Steingrobe*, 1999):

$$r_1 = \sqrt{v/\pi \times L}\,, \qquad (5)$$

where, v is substrate volume in the pot (cm^3), and L is root length (cm $plant^{-1}$).

2.5. Soil analysis

The pH was measured in 0.01 M $CaCl_2$ suspension using a substrate: solution ratio of 1: 2.5. The total diffusible P in the substrate (C_s) was determined according to *Alt* and *Peters* (1992) using the CAT extraction procedure (20 g fresh substrate in 160 mL CAT-solution, 1 h extraction time). Furthermore, substrate solution was collected by centrifugation at 1000 *g* for 20 min. P concentration in substrate solutions was determined according to *Murphy* and *Riley* (1962). Amorphous iron (Fe) and aluminum (Al) were extracted using 0.2 M oxalate solution (*Blakemore* et al., 1987) and measured by ICP-MS. Particle-size distribution in each mineral component was determined using the sedimentation technique (*Dewis* and *Freitas*, 1970). The volume weight of substrates was determined according to *VDLUFA* (1991).

2.6. Statistics

For each experiment, the treatments were replicated three times. Data were analyzed using analysis of variance in SAS (*SAS* institute Inc., Cary, USA, 1996). Means separation was conducted at the 0.05 probability level using the Tukey-Test.

3. Results and discussion

3.1. Impedance factor

The method used for determination of the impedance factor is based on the assumption that the Br^- anion is adsorbed immediately upon reaching the anion exchange membrane (zero sink assumption). This depends on the loading time of the anion exchange membrane and is essentially true for a short loading time. Fig. 2 shows that running the diffusion up to 6 h resulted in the same *f* value. However, for longer diffusion periods, *f* decreased significantly. This indicates that the zero sink assumption at the substrate-membrane interface was valid only for a short-term diffusion period up to 6 h. *Barraclough* and *Tinker* (1981) did not observe significant differences in the diffusion coefficients of Br^- over 24, 48, and 96 h. The shorter loading time in the present study may be due to less capacity of the exchange membrane as Br^- sink. Thus, the *f* value of 0.09 (i.e. the mean value after 2, 4, and 6 h of diffusion time at a volumetric water content of 0.5 cm^3 cm^{-3}) was used to calculate D_e of P in the substrate. This value is low compared to values observed by *Barraclough* and *Tinker* (1981) in mineral soils at water content of 0.4 cm^3 cm^{-3}. At this water content, most of the micro and macro pores in mineral soils are filled with water and water tension is close to zero (*Brady* and *Weil*, 1999), but in a peat-substrate at the same water content, only micro pores are filled with water and water tension is stronger than -10 kPa (*Naasz* et al., 2005). Thus, the ions have to move through the tortuous pore system, which results in reduction of their diffusion in the substrate.

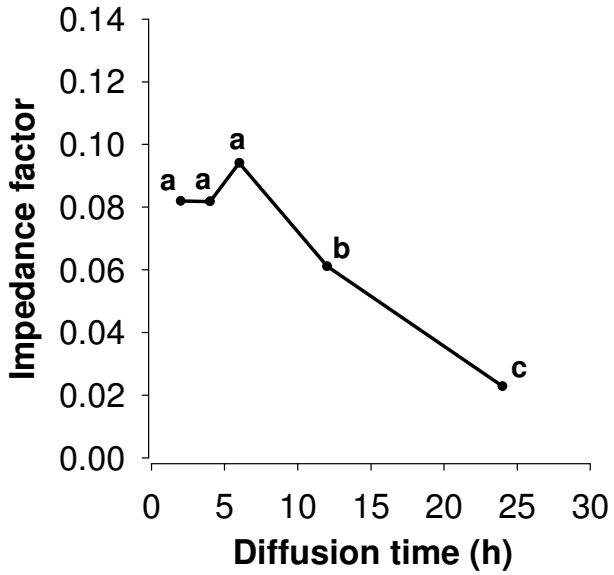

Figure 2: Impedance factor of peat-based substrate (80% Black peat + 20% mineral component, v/v) as affected by diffusion time (different letters indicate significant differences at p<0.05).

Tortuosity of the pathway strongly depends on volumetric water content since the cross-section available for diffusion is affected. Additionally, increasing solids per unit volume may also be expected to restrict physically the diffusion path (*Warncke* and *Barber*, 1972a). The results presented in Fig. 3 confirm that *f* increased similarly with increasing θ up to 60% for all substrates regardless of the portion of mineral component. A further increase in water content did not affect the impedance factor in the substrates with mineral component, resulting in a significantly higher *f* value for the 100% black peat at a θ of 70%. This is because the liquid phase becomes more continuous and the diffusion path less tortuous when the volumetric water content is increased (*Warncke* and *Barber*, 1972a). The increase of *f* with θ has been reported by several authors (*Barraclough* and *Tinker*, 1981; *So* and *Nye*, 1989; *Bhadoria* et al., 1991a, 1991b; *Jungk* and *Claassen*, 1997). For the substrates with mineral components it can be assumed that the additional water did not significantly increase the water-filled pore volume (and thus reduced the length of diffusion path) since in

these treatments water saturation was observed (i.e. a water film at the substrate surface was visible), which indicated that more water was supplied than necessary to fill the pore space.

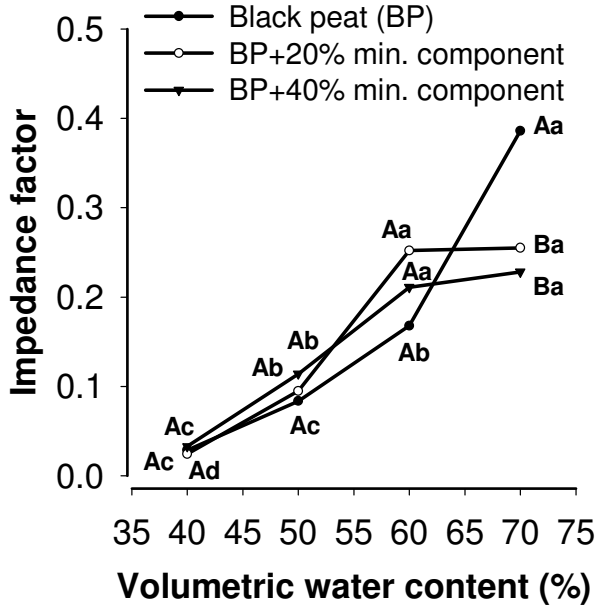

Figure 3: Influence of volumetric water content and mineral component proportion in peat-based substrate on impedance factor (different upper case letters indicate significant difference at a given volumetric water content and different lower case letters indicate significant differences for a given substrate, respectively, at p<0.05).

Increasing solids per unit volume by adding mineral component to the black peat led to increased bulk density of the substrates from 0.16 to 0.6 g cm^{-3}. This did not significantly affect the impedance factor (Fig. 3). This is in accordance with results from *So* and *Nye* (1989), who investigated the effect of water content and soil bulk density on chloride diffusion in two soils. They observed that soil water had a large effect while soil bulk density had a small effect. However, *Bhadoria* et al. (1991b) reported that at the same θ, the impedance factor decreased with increase of bulk density. Also, *Barraclough* and *Tinker* (1981) found a strong negative effect of bulk density on *f*, which is in contrast to the results presented here. They assumed more

fine pores at a higher bulk density, which increased the tortuosity. However, adding mineral component to the black peat caused a 10-15% decrease in total pore space to 75% (v/v) in the present study. Investigations of *Bohne* and *Wrede* (2005) demonstrated that in white peat/clay mixtures water capacity was more than 70% (v/v). This explains that the increase of bulk density of substrates by adding mineral component did not significantly affect the impedance factor. On the other hand, *Warncke* and *Barber* (1972b) reported that *f* initially increased with increase of bulk density from 1.1 to 1.3 g cm^{-3} and then decreased with further increase of bulk density to 1.6 g cm^{-3}. However, this investigation was done at constant water content on weight basis (w/w), leading to variation in water content on the volumetric basis that biased the results.

3.2. Buffer power

In mineral soils, the greater proportion of P is adsorbed at minerals and the adsorption capacity varies greatly among the soils (*Nye*, 1979). The mobility of P in soil depends on the amount of P in the soil solution and its replenishment from the solid phase (*Barber*, 1995). Phosphorus adsorption characteristics are influenced by one or a combination of properties such as Fe and Al oxide content as well as type and content of mineral components (*Zhang* et al., 2005). Thus, the effect of mineral components, which are commonly used to prepare substrates, on P dynamics was investigated. Applying P to different substrates increased CAT-soluble P (C_s) in the same pattern as substrate solution P (C_{li}) (Fig. 4).

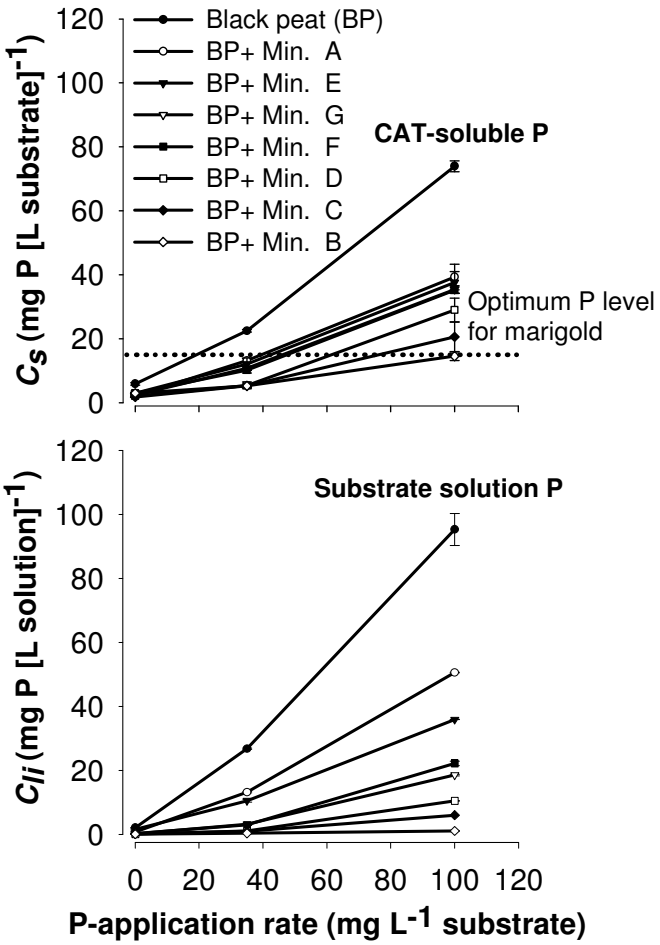

Figure 4: Effect of P application rate on CAT-soluble P (C_s) and substrate solution P (C_{li}) in black peat and in peat based substrates mixed with different mineral components (Min. A - Min. G); 80% black peat + 20% mineral component (v/v).

The highest C_s as well as C_{li} were observed in black peat (100%) and the lowest in the substrate based on black peat + mineral component B. Fig. 4 shows that the amount of P necessary to obtain 16 mg C_s at the optimum P level of marigold (unpublished data) ranged between 19-100 mg P L^{-1} substrate depending on mineral component mixed with black peat. The concentration of P in substrate solution ranged from 0.3-27 and 1-95 mg L^{-1} solution at P application rates of 35 and 100 mg L^{-1} substrate, respectively. For each of the substrates, there was a linear positive relationship between C_s and C_{li} (Fig. 5). However, the slope differed significantly

being the highest for black peat (100%) and the lowest for 80% black peat + 20% mineral component B. Phosphorus concentration in substrate solution (C_{li}) at optimum C_s varied from 1-17 mg P L^{-1} solution. These values were considerably higher than those reported for agricultural soils (*Barber*, 1995; *Jungk* and *Claassen*, 1997), which are in the range of 0.03 to 0.5 mg P L^{-1} solution. This may be due to the specific situation in pots where the whole substrate volume is exhausted by roots and where not the mobility of P but rather the amount of plant-available P (C_s) is limits growth.

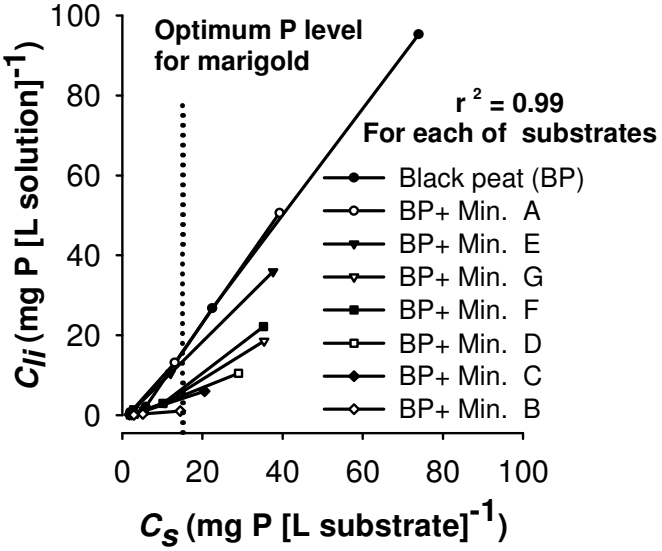

Figure 5: Relationship between CAT-soluble (C_s) and substrate solution P (C_{li}) in black peat and in peat-based substrates mixed with different mineral components (Min. A – Min. G); 80% black peat + 20% mineral component (v/v).

As illustrated in Fig. 6, the calculated buffer power (*b*) resulting from the ratio of C_s and C_{li} decreased with increasing P application rate. The *b* was highest for 80% black peat + 20% mineral component B and lowest for black peat (100%). The highest *b* (17.25) in the fertilized substrates was much lower than reported for mineral soils (100-2000; *Jungk* and *Claassen*, 1997). Buffer power for black peat was 1-3, indicating that there was nearly no P adsorption. Such a low *b* indicates that P in the substrate was more mobile and available for plants than in the soil. However, also for

some substrate mixtures with mineral components, such as mineral component A and E, a very low *b* was observed. On the other hand, variation of *b* of substrate mixtures with mineral components was not related to their clay content since mineral component A and B had the same clay content (Tab. 1), but a completely different *b* value. Variation between mineral components was related to the content of amorphous Fe and Al (Fig. 7).

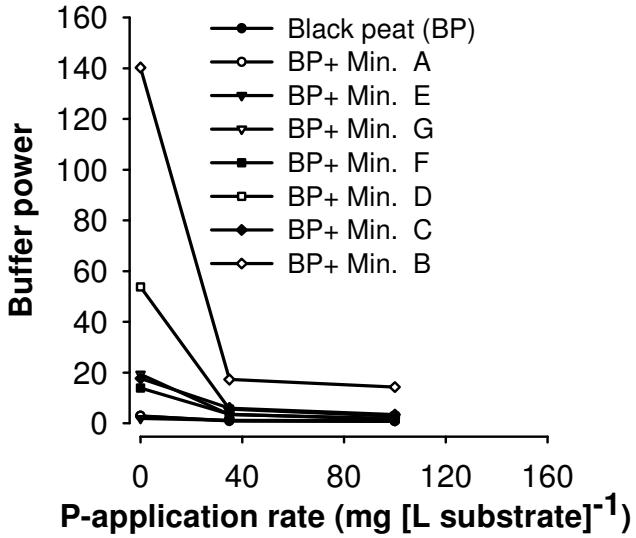

Figure 6: Effect of P application rate on P buffer power in black peat and in peat based substrates mixed with different mineral components (Min. A – Min. G); 80% black peat + 20% mineral component (v/v).

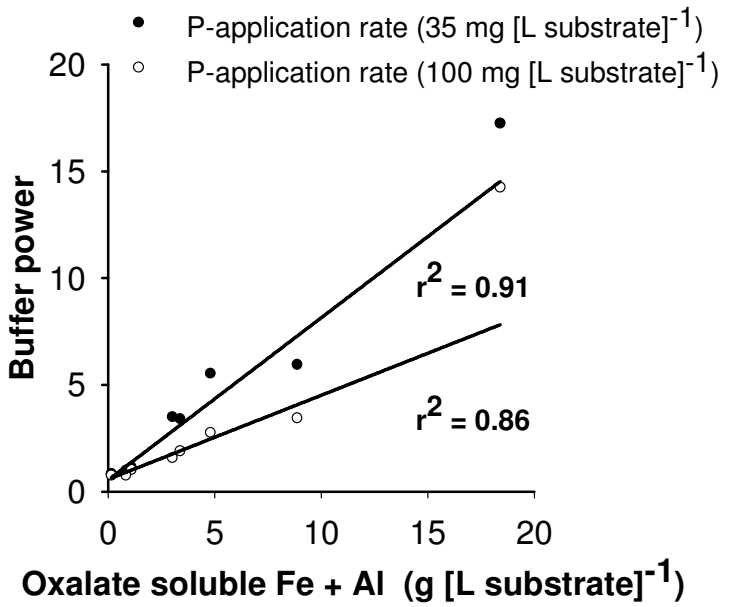

Figure 7: Buffer power as a function of oxalate-soluble Fe and Al in substrates fertilized with 35 and 100 mg P L^{-1} substrate, respectively.

Buffer power increased with increasing in Fe and Al contents of the substrate mixtures. The sum of Al and Fe oxides gave a better correlation than Fe and Al alone indicating that both influenced P sorption. The results are in agreement with *Börling* et al. (2001) who reported a high correlation between oxalate-extractable Fe and Al with P sorption capacity in Swedish soils. The amount of Al and Fe in the mineral components was independent of clay content (r^2 = 0.23). Thus, it can be pointed out that extraction of Fe and Al with ammonium oxalate can be used as a suitable approach for estimating P sorption capacity of mineral components used for substrate production.

3.3. Effective diffusion coefficients (D_e)

The values for *f* and *b* determined in this study were used to calculate the effective diffusion coefficient (D_e) for peat-substrates. D_e was in the range of 10^{-7} to 10^{-8} cm^2 s^{-1}, which is at least 10 times higher than D_e in mineral soils (Tab. 2). This can be attributed mostly to a lower buffer power of the substrate rather than to a higher

impedance factor, which was in the range as known for mineral soils or even lower. The higher value of D_e in the substrate indicates that P in the substrate should be more available for plants than in mineral soils. This would allow roots to extend the depletion zone about 10 times more than in mineral soil (Tab. 2). On the other hand, this leads to an overlapping of depletion zones of roots, particularly the mean half distance between roots (r_1) was just half of that generally observed in mineral soils. This means that plants grown in pots use the whole substrate volume for P nutrition whereas plants grown in mineral soils acquire P from less than 20% of the soil volume and only a small part of total soil volume between neighboring roots is highly depleted (*Jungk* and *Claassen*, 1997; *Claassen* and *Steingrobe*, 1999).

Table 2: Parameters describing P mobility in mineral soils and peat-based substrates

Substrate	Parameter					
	Solution P (C_{li}) [mg L^{-1}]	Impedance factor [a] (f)	Buffer power (b)	Effective diffusion coefficient (D_e) [cm^2 s^{-1}]	Extension of the depletion zone [a] [cm]	r_1 [b] [cm]
Mineral soil [c]	0.1 - 0.5	0.15 - 0.30	100 - 2000	10^{-8} - 10^{-11}	0.002 - 0.02	0.2 - 0.5
Black peat (BP)	25 - 95	0.08 - 0.17	1 - 3	10^{-7}	0.23	0.1 - 0.2
BP + min. component	0.5 - 50	0.09 - 0.20	1 - 17	10^{-7} - 10^{-8}	0.1 - 0.23	0.1 - 0.2

[a] Volumetric water content of 0.2 - 0.3 cm^3 cm^{-3} for mineral soil, and 0.5 - 0.6 cm^3 cm^{-3} for both BP and BP + mineral component was used. Extension of the depletion zone was calculated for 2 d.

[b] r_1 = Mean half distance between neighboring roots; Root length density (*RLD*) in the substrate was 5 - 24 cm cm^{-3} (unpublished data) and for mineral soil the values of 1.4 -8.2 cm cm^{-3} were taken from *Claassen* and *Steingrobe* (1999).

[c] Based on data from *Nye* and *Tinker* (1977), *Barber* (1995), *Jungk* and *Claassen* (1997), and *Claassen* and *Steingrobe* (1999).

CHAPTER 2

CHARACTERISTICS OF PHOSPHORUS UPTAKE KINETICS OF ORNAMENTAL PLANTS

This is the pre-peer reviewed version of the following article:

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2009): Characteristics of phosphorus uptake kinetics of poinsettia and marigold. *Scientia Horticulturae* (submitted)

Abstract

Maximum uptake rate (I_{max}), Michaelis constant (K_m), and minimum nutrient concentration (C_{min}) as plant physiological characteristics may be important for P uptake in peat-substrate. Thus, variation of these parameters was evaluated with a series of depletion studies for marigold (*Tagetes patula*) and poinsettia (*Euphorbia pulcherrima*) as representative ornamental plants 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 *RGR* of marigold while it had no effect on *RGR* of poinsettia. The short photoperiod reduced *RGR* of poinsettia. I_{max} also decreased with plant age and with decrease of air temperature for both poinsettia and marigold; however it was independent of light intensity. I_{max} of poinsettia was lower at short photoperiod than that at long photoperiod. A close correlation between *RGR* and I_{max} was observed with both poinsettia and marigold over all treatments. The K_m and C_{min} was affected neither by plant age nor by air temperature, light intensity and day length. However, higher I_{max}, but lower K_m and C_{min} values were observed for marigold than for poinsettia at 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 to be considered for fertilization.

Key words: Uptake rate, relative growth rate, plant age, temperature, light intensity, photoperiod

1. Introduction

Nutrient uptake rate depends on its concentration at root surface and follows Michaelis-Menten kinetics, which can be described mathematically by maximum uptake rate (I_{max}) which occurs under saturating nutrient concentration where all the available binding sites are loaded, Michaelis constant (K_m) which is nutrient concentration where the actual uptake equals half the I_{max} and 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; *Kuhlmann* and *Barraclough*, 1987; *Nayakekorala* and *Taylor*, 1990; *Bhattacharyya* and *Datta*, 2005; *Bhadoria* et al., 2004; *Sharifi* and *Zebarth*, 2006), and environmental conditions (*Brewster* et al., 1976a; *Hallmark* and *Huffaker*, 1978; *Steingrobe* and *Schenk*, 1994; *Baligar* et al., 2006). I_{max} decreases with plant age since more roots are available to meet the demand for new growth (*Kuhlmann* and *Barraclough*, 1987; *Barber*, 1995). The demand depends on nutrient concentration in new growth, change of nutrient concentration in the whole plant and the amount of new growth. The new growth can be related to plant weight by the relative growth rate (*RGR*) where a close correlation between *RGR* and uptake rate was observed (*Steingrobe* and *Schenk*, 1994; *Cheaib* et al., 2005; *Rodgers* and *Barneix*, 1988). *Steingrobe* and *Schenk* (1994) found that the relative growth rate was affected by growing conditions such as temperature and radiation.

Root physiological properties are significant for K and NO_3 acquisition in mineral soil, but not for phosphorus (P) (*Claassen* and *Steingrobe*, 1999). However, the mobility of P in peat-substrates (as they are generally used for pot plant production) is in magnitude higher than in mineral soil similar to mobility of K in mineral soil (*Khandan-Mirkohi* and *Schenk*, 2008; *Claassen* and *Steingrobe*, 1999; Chapter 1). 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 plant growth rate. The concentration difference between bulk substrate solution and at root surface can be calculated from the uptake rate to meet the demand assuming that P is transported to root surface only by diffusion (*Barraclough*, 1986). Thus, this study aimed at investigating the effect of short term variable environmental conditions on P uptake kinetics of representative ornamental plants 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 having 8 cm of length and 7-8 nods. Except for three upper fully developed leaves all others were removed. The cuttings were rooted under plastic in nutrient solution during 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 days after transplanting 4 L plastic pots were used for poinsettia. Poinsettia was trained to a single stem. The nutrient solution contained in mM: 2.5 N as $Ca(NO_3)_2$ and $(NH_4)_2SO_4$, 0.1 P as KH_2PO_4, 0.75 K as KH_2PO_4 and KCl, 2 Ca as $Ca(NO_3)_2$ and $CaCl_2$, 1 Mg as $MgSO_4$, 1.25 S as $MgSO_4$ and $(NH_4)_2SO_4$. The composition for micronutrients was in µM: 40 Fe as Fe-EDTA, 25 B as H_3BO_3, 1.5 Mn as $MnSO_4$, 1.5 Zn as $ZnSO_4$, 0.5 Cu as $CuSO_4$, and 0.1 Mo as $NaMoO_4$. The pH of nutrient solution was 5.8 ± 0.1. The nutrient solution was aerated and changed when the concentration of P had dropped to 5 µM. Plants were grown in a growth chamber under day/night temperature of 20/16 °C, light intensity of 200 µmol m^{-2} s^{-1} PAR, and day/night photoperiod of 16/8 h. Relative humidity of growth chamber was 65% during the day time.

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). Plants were subjected to these conditions two 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 depletion experiments as described by *Claassen* and *Barber* (1974). The initial P concentration was 20 µM whereas for the other nutrients the abovementioned nutrient solution was used. Two mL of solution samples were taken at first every 10 minutes and later every 40 minutes and the sampled solution was replaced by distilled water. The experiment was continued until no further depletion was observed (C_{min} was reached). Phosphorus concentration in nutrient solution was measured according to *Murphy* and *Riley* (1962). The product of ion concentration in the solution (c, µM) and the volume of solution (v, mL) was calculated as total amount of P in the solution (Q):

$$Q = cv, \quad (1)$$

Phosphorus concentration in the pot was depleted with marigold after about 3 h, whereas for poinsettia it took more than 10 h (Fig. 1).

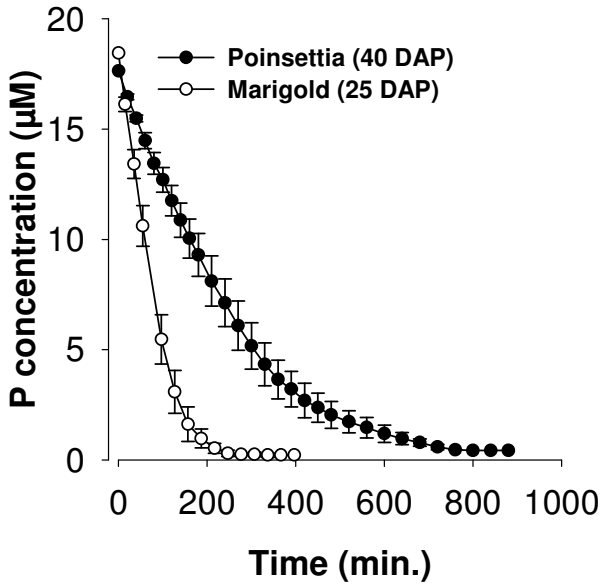

Figure 1: Depletion of P in nutrient solution with poinsettia and marigold.

For estimation of I_{max} (µmol cm^{-2} s^{-1}) and K_m (µ*M*) the numeric iteration procedure SAS NLPLM based on the Levenberg-Marquardt procedure (*Seidel D.*, and *Hothorn*, *L.*, person. Comm., 2003) was run. Details are described by *Deressa* and *Schenk* (2008). For calculation of root surface, root hairs were not considered, since poinsettia had none at all and with marigold only few were visible.

2.4. Determination of plant parameters

The relative growth rate (*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):

$$RGR = ln(FW_2) - ln(FW_1)/t_2 - t_1, \quad (2)$$

where, *FW* is 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 (r_0, cm) was calculated as:

$$r_0 = \sqrt{RFW/\pi \times L}\,, \qquad (3)$$

Plant shoot and root was dried at 70 °C for 5 days. Phosphorus concentration of shoot and root dry matter was determined after milling and dry ashing according to *Gericke* and *Kurmies* (1952).

2.5. Estimation of concentration gradient

The concentration difference between bulk substrate and root surface (Δc, µmol cm^{-3}) was estimated according to *Barraclough* (1986):

$$\Delta C = C_l - C_{l0} = -\left(\frac{I_{max}}{4\pi D_L \theta f}\right)\left(1 - \frac{1}{1-\pi r_0^{\,2} RLD} \ln \frac{1}{\pi r_0^{\,2} RLD}\right), \qquad (4)$$

where, C_l is the average bulk substrate solution concentration (µmol cm^{-3}), C_{l0} is the concentration at the root surface (µmol cm^{-3}), I_{max} is the maximum uptake rate (µmol cm^{-1} root s^{-1}), D_L is the diffusion coefficient of $H_2PO_4^-$ in water at 25 °C for which the value of 8.9 × 10^{-6} cm^2 s^{-1} was used (*Edwards* and *Huffman*, 1959), for the volumetric water content (θ) 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 and 2009). For r_0 which is the root radius 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 and replicated five times. Data were analyzed using analysis of variance of SAS (*SAS*, 1996). Means were

compared between the treatments at α = 0.05 using Tukey-Test and at α = 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 days after planting (DAP) whereas poinsettia required 95 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 two 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. This reduction was not yet significant 70 DAP, but after 95 DAP which was 55 days after transferring to short photoperiod significant reduction for *SDM* was found. The relative growth rate (*RGR*) of both poinsettia and marigold declined with plant age (Fig. 3A). This decline was faster in case of marigold compared to that of poinsettia.

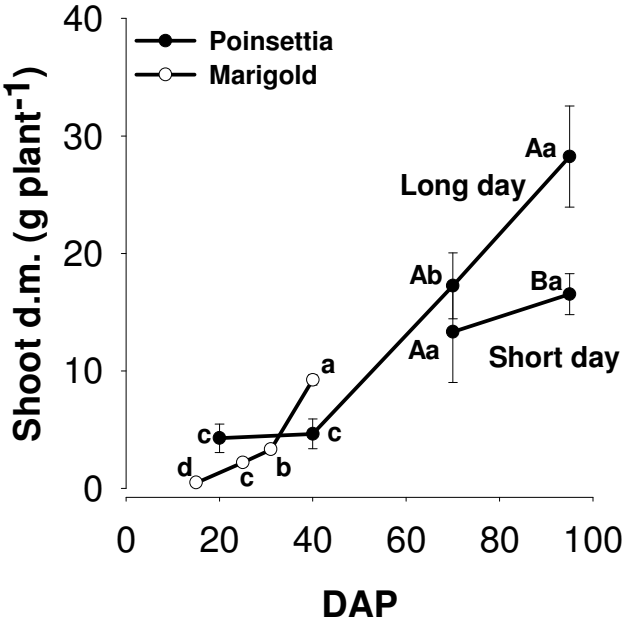

Figure 2: The influence of plant age (days after planting, DAP) on shoot dry matter of poinsettia and marigold and the effect of photoperiod on shoot d.m. of poinsettia. Different lower case letters indicate significant difference between different DAP for each plant species and different upper case letters indicate significant differences between photoperiods for a given DAP, respectively at p<0.05.

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 negatively affected the *RGR* of marigold, but had no effect on *RGR* of poinsettia (Fig. 3C). Poinsettia plants grown at short photoperiod had lower *RGR* at 95 DAP compared to plants grown at long photoperiod, 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, then remained almost constant. The short day length decreased *RSR* of poinsettia at both 70 and 95 DAP (Fig. 4).

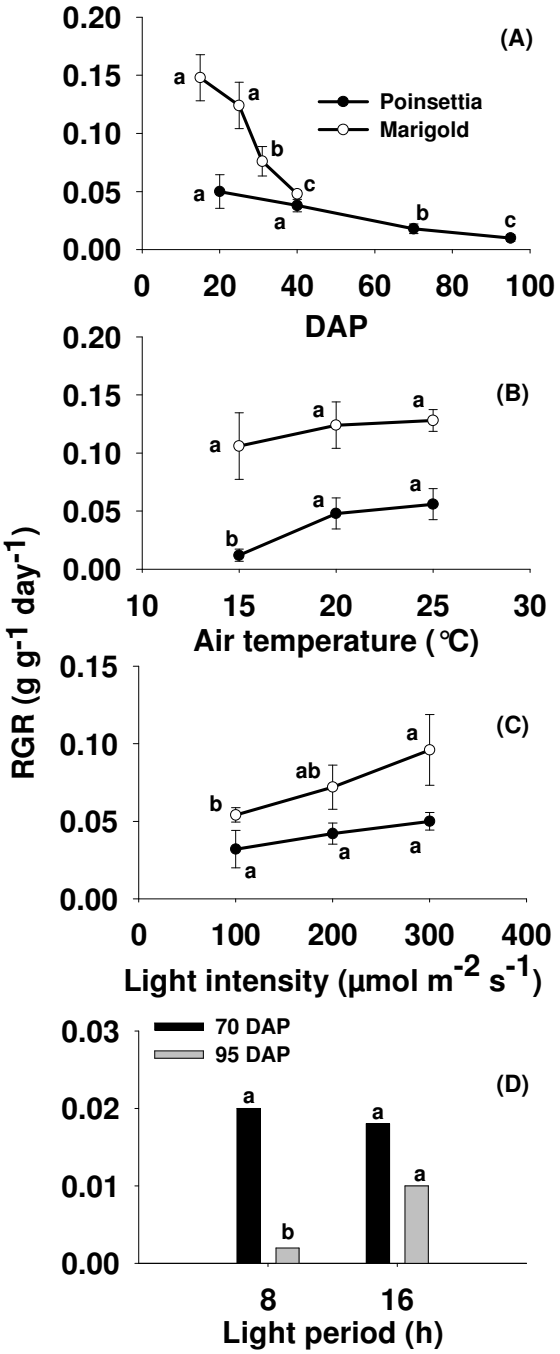

Figure 3: (A) The influence of plant age (days after planting, DAP), (B) Air temperature, and (C) Light intensity on relative growth rate (RGR) of poinsettia and marigold; and (D) the effect of photoperiod on RGR of poinsettia. Different letters (for A, B, and C within each crop and for D between different photoperiods) indicate significant differences at $p<0.05$.

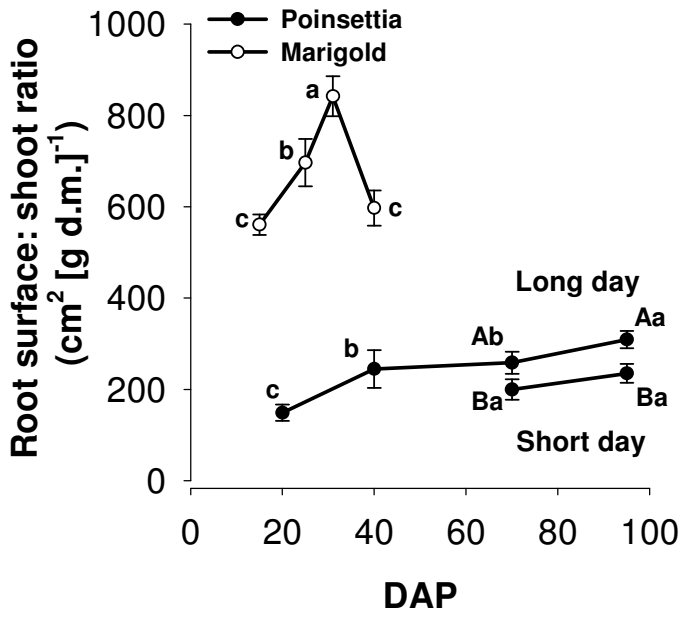

Figure 4: The effect of plant age (days after planting, DAP) on root surface: shoot d.m. ratio of marigold and poinsettia, and the effect of photoperiod on root surface: shoot d.m. ratio of poinsettia. Different lower case letters indicate significant difference between different DAP at a given plant species and different upper case letters indicate significant differences between photoperiods for a given DAP, respectively at $p<0.05$.

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

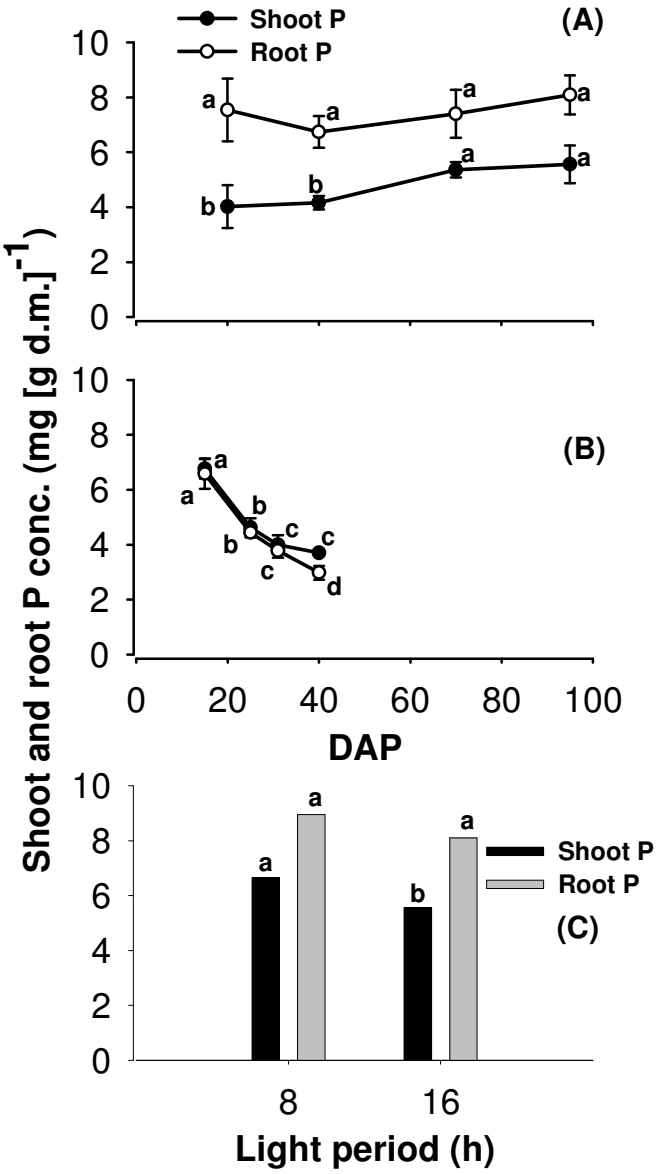

Figure 5: The influence of plant age (days after planting, DAP) on shoot and root P concentration of (A) poinsettia and (B) marigold; and (C) the effect of photoperiod on shoot and root P concentration of poinsettia at 95 DAP. Different letters (for A, and B between different DAP for each plant species and for C between different photoperiods for shoot or root P indicate significant differences at p<0.05.

3.2. Physiological P uptake parameters

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

Table 1: Multiple and simple linear regression analysis of plant factors affecting I_{max}

	Multiple regression [a] $y = a_0 + a_1x_1 + a_2x_2$		Simple regression [b] $y = a_0 + a_1x_1$	
Parameters	Poinsettia	Marigold	Poinsettia	Marigold
r^2	0.69 ***	0.55 ***	0.77***	0.57***
a_0	0.65	1.62	0.17	1.60
a_1	20.62 ***	06.67 ***	24.00***	6.60***
a_2	-9.4×10^{-4} ns	8.0×10^{-5} ns	-	-

[a,b], y is I_{max}; a_0 is intercept for I_{max}; a_1 is slope for relative growth rate (*RGR*, g g^{-1} day^{-1}); a_2 is slope for root surface: shoot ratio (*RSR*, cm^2 root [g d.m. shoot]$^{-1}$).

***, significant at $P < 0.001$; ns, non-significant (n = 50 and 60 for marigold and poinsettia, respectively).

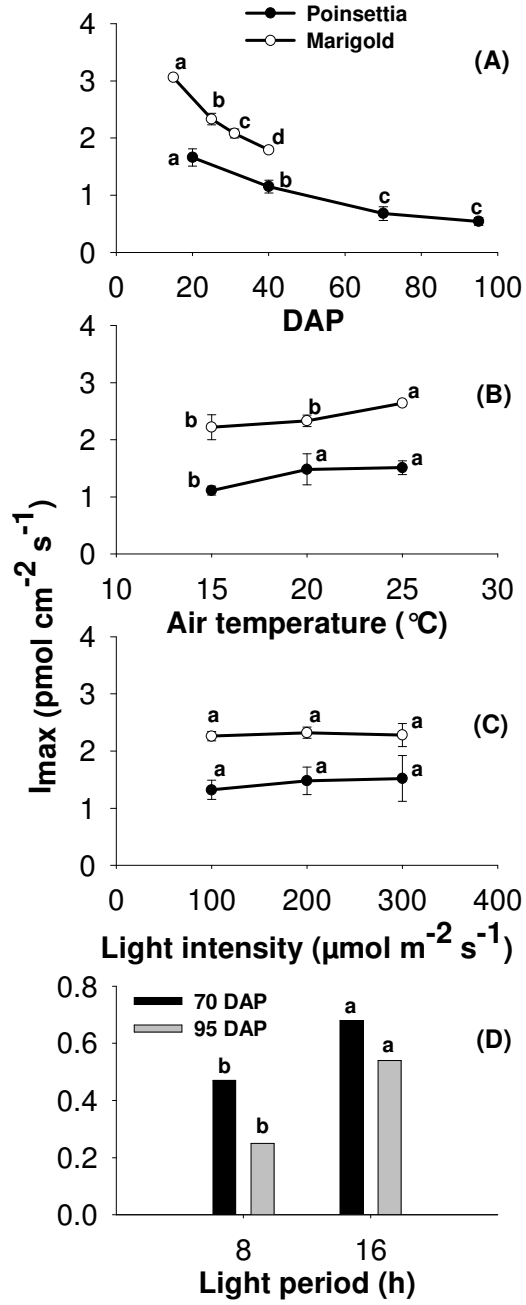

Figure 6: (A) The influence of plant age (days after planting, DAP), (B) Air temperature, and (C) Light intensity on maximum P uptake rate (I_{max}) of poinsettia and marigold; and (D) the effect of photoperiod on I_{max} of poinsettia. Different letters (for A, B and C between different DAP at a given plant species and for D between different photoperiods at a given DAP) indicate significant differences at $p<0.05$.

Michaelis constant (K_m) and minimum P concentration (C_{min}) was affected neither by plant age nor by air temperature and light intensity for both poinsettia and marigold (Fig. 7A, B, and C). Also, no change was observed for K_m and C_{min} values of poinsettia under different photoperiods (Fig. 7D). However, K_m and C_{min} values were higher for poinsettia compared to marigold. As mean of all treatments, K_m was 10.47 and 5.27 and C_{min} was 0.42 and 0.21 µM for poinsettia and marigold, respectively. The roughly estimated concentration difference between bulk substrate solution concentration and concentration at root surface necessary to meet the uptake rate (equation 4) was 290 and 320 µM for marigold and poinsettia at planting, respectively (Fig. 8). However, at later stages it declined to 140 and 71 µM for marigold (40 DAP) and poinsettia (95 DAP), respectively.

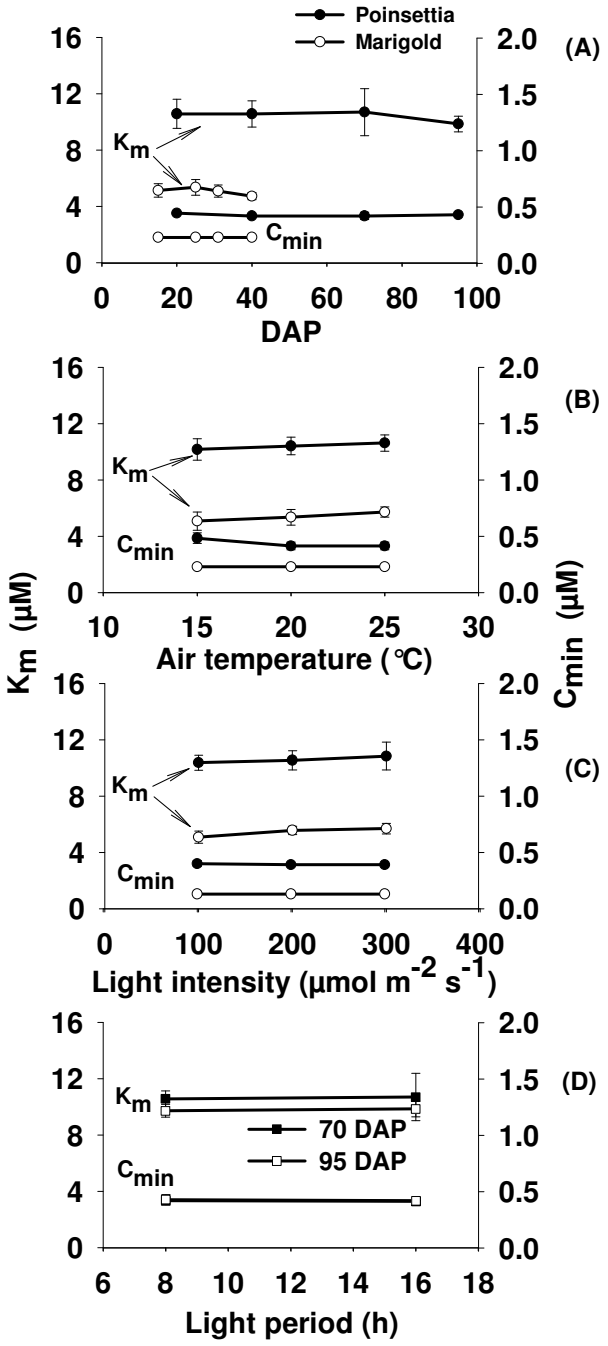

Figure 7: (A) The influence of plant age (days after planting, DAP), (B) Air temperature, and (C) Light intensity on Michaelis constant (K_m) and minimum P concentration (C_{min}) of poinsettia and marigold; and (D) the effect of photoperiod on K_m and C_{min} of poinsettia. No significant change of K_m and C_{min} was observed for both crops over all treatments at $p<0.05$.

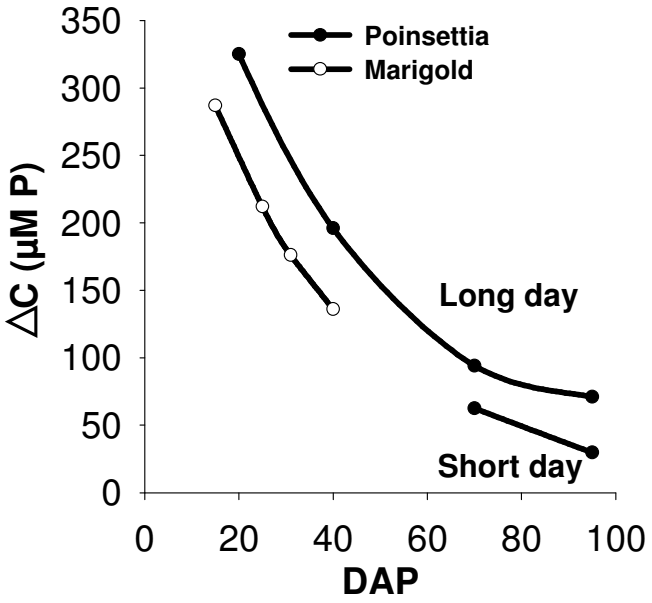

Figure 8: The concentration difference in solution between the bulk substrate and at root surface (∆c) of marigold and poinsettia at different plant age (days after planting, DAP) and under different photoperiod for poinsettia.

4. Discussion

4.1. Plant growth parameters

Relative growth rate (*RGR*) declined with plant age for both crops (Fig. 3A) as it is generally known (*Hunt*, 1982). The change of *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 that of poinsettia cuttings (4.26 g d.m. plant^{-1}), since *RGR* declines faster in early growth stages when plant weight is lower. Shoot dry matter (*SDM*) and root surface: shoot d.m. ratio (*RSR*) of both crops were not significantly affected by air temperature and light intensity, since variation was applied only for two days (data not shown). However, effect was observed for *RGR* (Fig. 3B, C), because the *RGR* was measured based on increase of fresh matter weight during 24 h for each plant separately. 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).

Light intensity increased the *RGR* of marigold, but not for poinsettia (Fig. 3C). Reason might be that marigold requires a higher 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; *Tsukamoto* et al., 1971). It was reported that the light intensity over 200 µmol m^{-2} s^{-1} decreased the time to flowering of marigold (*Pramuk* and *Runkle*, 2003). Short photoperiod reduced both *SDM* and *RGR* of poinsettia, since flower induction retarded the growth (Fig. 2 and 3D). Plants at long photoperiod continued vegetative growth, and no flower induction was observed.

Root surface: shoot d.m. ratio (*RSR*) increased with plant age for both poinsettia and marigold (Fig. 4) as it is reported for some other crops (*Lambers* and *Poorter*, 1992; *Dusek* and *Kvet*, 2006). After flowering of marigold, *RSR* declined as it is well known for many crops after anthesis (*Barber*, 1995). Under short photoperiod *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 shoot dry matter was not yet affected (Fig. 2). Similarly, for *Pinus sylvestris* L. reduced partitioning of assimilates to the root was observed under light shortage which led to the reduction of *RSR* (*Hees* and *Clerkx*, 2003).

Shoot and root P concentration declined with plant age for marigold, but it was almost constant for poinsettia (Fig. 5A and B). This was due to the fact that poinsettia was propagated by cuttings taken from mother plants, whereas marigold was grown from seedlings where the composition of dry matter changes in favor of carbohydrates with plant growth. Decrease of shoot P concentration with plant age was reported for some crops (*Bhadoria* et al., 2004; *Akhtar* et al., 2007). 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 root than in shoot d.m. was reported in literature (*Asher* and *Loneragan*, 1967; *Jungk* et al., 1990; *Gaume* et al., 2001; *Shane* et al., 2004; *Akhtar* et al., 2007).

4.2. Uptake kinetic parameters

Maximum P uptake rate (I_{max}) declined with plant age for both poinsettia and marigold (Fig. 6A). Similarly, decrease of uptake rate with plant age was reported for other crops (*Edwards* and *Barber*, 1976; *Bhadoria* et al., 2004; *Sharifi* and *Zebarth*, 2006). I_{max} 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_{max}. Thus, decrease of I_{max} follows the same pattern as *RGR* and both are positively related to each other (Tab. 1). Reason for this close correlation is that I_{max} as well as *RGR* are related to the existing plant matter. However, for calculation of *RGR* the new growth is considered in relation to the plant weight, whereas for I_{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 *RSR* remains constant. Similarly, a linear relationship between I_{max} for P and *RGR* of pine seedlings (*Cheaib* et al., 2005) and between I_{max} for NO_3 and *RGR* of wheat and lettuce (*Rodgers* and *Barneix*, 1988; *Steingrobe* and *Schenk*, 1994) was reported.

Some discrepancy was observed in the relationship between I_{max} and *RGR*. At high light intensity marigold had higher *RGR* (Fig. 3C), but without any change of uptake rate (Fig. 6C). This might be due to dilution of P in shoot d.m. with growth of marigold (Fig. 5B) leading to a delayed response of uptake rate. Marigold had higher I_{max} than poinsettia at all growth stages and under various climate conditions (Fig. 6A, B, and

C), since *RGR* of marigold was higher. The observed values for I_{max} were in the range as reported for other crops (*Brewster* et al., 1975 and 1976a; *Schenk* and *Barber*, 1980; *Jungk* et al., 1990; *Singh* et al., 2003; *Bhadoria* et al., 2004).

All the environmental conditions and also plant age affected I_{max}, but not K_m and C_{min} (Fig. 7), indicating that definitely the number of transporters had been changed, but not the characteristics of uptake system (*Raghothama*, 1999). The K_m value (mean of all treatments) was double 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 was also observed (*Deressa* and *Schenk*, 2008). The mean C_{min} value for poinsettia (0.42 µM) was twice as high compared to marigold (Fig. 7). These values are in the range reported for many crops (*Brewster* et al., 1976a; *Schenk* and *Barber*, 1980; *Bhadoria* et al., 2004; *Deressa* and *Schenk*, 2008). The higher I_{max} of marigold could be satisfied by a lower concentration gradient in substrate solution compared to poinsettia (Fig. 8). However, assuming a Freundlich-function relationship between C_{li} (mg P L^{-1}) and concentration of plant available P in peat-substrates (C_s, mg P [L substrate]$^{-1}$) ($C_s = 7.62\ C_{li}^{0.56}$) as described by *Khandan-Mirkohi* and *Schenk* (2009), C_s 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 (Fig. 9). 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 uptake rate was not changed very much (Fig. 6B, C, and D). However, C_s requirement of both crops declined considerably with plant age, which should be considered for top dressing by fertigation and evaluation of substrate P status (Fig. 9). The C_s values of 26-27.5 mg P [L substrate]$^{-1}$), which presented here were in the range as recommended for high fertigated substrate (22-131 mg P [L substrate]$^{-1}$) at planting (*Röber* and *Schacht*, 2008).

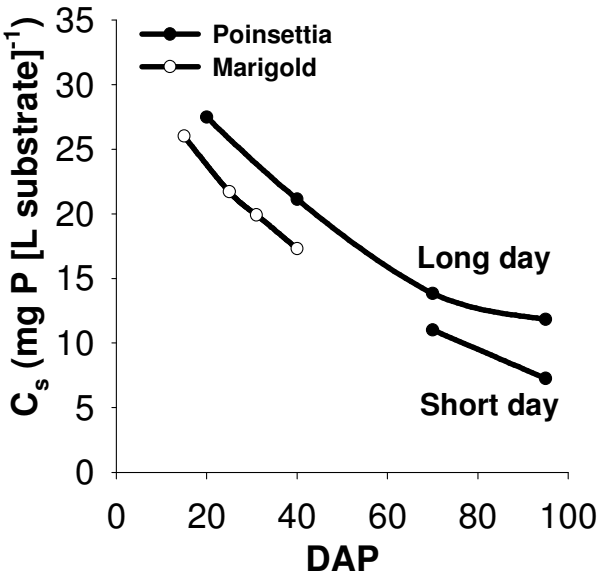

Figure 9: Theoretically estimated plant available P demand (C_s) of marigold and poinsettia at different plant age (days after planting, DAP) and under different photoperiod for poinsettia.

5. Conclusions

Marigold had clearly lower K_m and C_{min}, but higher I_{max} than poinsettia. However, the concentration of plant available P in the substrate (C_s) 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_s was clearly reduced with developmental stage of both crops, which has to be taken into consideration for fertilization.

CHAPTER 3

PHOSPHORUS EFFICIENCY OF ORNAMENTAL PLANTS IN PEAT-SUBSTRATES

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2009): Phosphorus efficiency of ornamental plants in peat-substrates. *J. Plant Nut. Soil Sci*. "DOI: 10.1002/jpln.200700360"

Abstract

Previously it was observed that marigold had a lower level of plant available P (C_s) than that of poinsettia at optimum growth. Thus, this study aimed at investigating the factors contributing to phosphorous (P) efficiency of ornamental plants and to quantify their significance. Accordingly, marigold (*Tagetes patula*) and poinsettia (*Euphorbia pulcherima*) were cultivated in peat-substrate, black peat 80% + mineral component 20% (v/v), treated with P rates of 0, 10, 35, 100, and 170 mg [L substrate]$^{-1}$. During cultivation plants were fertigated with a complete nutrient solution (18 mg P L^{-1}) every two days.

Both poinsettia and marigold attained their optimum yield and quality at the rate 35 mg P [L substrate]$^{-1}$ and the critical level of P in shoot dry matter of both crops was 5-6 mg [g d.m.]$^{-1}$. Plant available P (C_s) increased after planting 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 for this cultivation period indicated that at lower P rates more P was fertigated than was taken up by the plants. Root length density (*RLD*), root: shoot ratio and root hair length of marigold was doubled compared to that of poinsettia. Root length density increased with crop growth and ten days after planting (DAP) the mean half distance between roots (r_1) 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 exhausted 43%. Later during cultivation, the depletion zones around roots overlapped for both crops.

Root hairs increased predicted P uptake significantly more for marigold compared to that of poinsettia. However, at optimum P supply root hairs enhanced P uptake compared to that of root cylinder only by 10-20%. For the two lower P levels, the P depletion profile around root calculated for 10 DAP showed that after two days of depletion, the concentration at root surface was below the assumed K_m value (5 µM) and the concentration gradient was insufficient to match the demand.

Results indicate that poinsettia had a higher content of plant available P in the substrate at optimum growth compared to that of marigold, since more fertigated P accumulated during early stages of cultivation due to lower *RLD*. 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, substrate

1. Introduction

Plant species and genotypes of a given species may differ in 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 trait may occur through utilization efficiency, which is the ability of plants to utilize P in the shoot for dry matter production, or through uptake efficiency, which is the ability to acquire P from the soil (*Loneragan* and *Asher*, 1967). The uptake efficiency may arise due to favorable root morphological characteristics, mobilization of P by exuding chemical components from root to the rhizosphere, or association of roots with mycorrhiza (*Raghothama*, 1999).

Nutrient acquisition of plants can be described by a mechanistic simulation model (NST 3.0) (*Claassen* and *Steingrobe*, 1999), 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: shoot ratio and small root radius were observed for some crops cultivated in the mineral soils as significant morphological root characteristics contributing to the 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) or protons (*Neumann* and *Römheld*, 1999). Organic anions form complexes with Ca, Al and Fe and thus dissolve P bound to calcium, iron and aluminum. These 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 is limiting P uptake (*Barber*, 1995). However, investigation of P dynamics in peat-substrates (*Khandan-Mirkohi* and *Schenk*, 2008) revealed that the mobility of P was high in the substrate due to its low buffer power (*b*). Buffer power was in the range of 1-17, whereas mineral soils normally have *b* in the range of 100-2000 (*Jungk* and *Claassen*, 1997). In a previous experiment, it was observed that marigold had a lower level of plant available P (C_s) in the substrate during cultivation at optimum growth compared to poinsettia.

Therefore, the present study aimed at assessing the background for difference in plant available P in the substrate at optimum growth for poinsettia and marigold; to investigate factors contributing to the P efficiency of the plants cultivated in substrate, and to quantify their significance by using the mechanistic simulation model (NST 3.0).

2. Material and methods

2.1. The growing medium

The growing medium was prepared by mixing 80% of black peat (*BP*) that passed through a 2 mm sieve and 20% of mineral component on volume basis. Phosphorus was applied to the substrate in the form of $Ca(H_2PO_4)_2$ 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 NH_4NO_3 and K_2SO_4, 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 5.7 ± 0.2 by liming with calcium carbonate at a rate of 4 g [L substrate]$^{-1}$. Finally, the substrate was equilibrated in an oven at a temperature of 50 °C for 24 h, and then at a room temperature for 3 days. It was previously shown that incubation of substrate at a

temperature of 50 °C for 24 h was closely correlated to the CAT-soluble P after 9 weeks storage.

2.2. Cultivation and harvesting

The prepared substrate was packed into plastic pots at a bulk density of 0.4 g cm^{-3}. Marigold seedlings (*Tagetes patula* cv. 'Nana Orange Jacket') and rooted poinsettia cuttings (*Euphorbia pulcherrima* cv. 'Premium Red') were transplanted into the plastic pots having a volume of 320 and 620 cm^3 on 3rd of June and 20th of July, respectively. Plants were grown in a greenhouse at day/night heating temperatures of 25 °C/ 18 °C.

Natural radiation was supplemented with 80 µmol m^{-2} s^{-1} photosynthetic photon-flux density (*PAR*) for poinsettia when the radiation was lower than 100 µmol m^{-2} s^{-1} to extend the photoperiod to 16 h, in order to keep a constant vegetative growth up to 67 days after planting (DAP). Then, darkness was applied at 70 DAP by means of black cloth to shorten the day length to 8 h up to 130 DAP, when plants reached the marketable size. Marigold was grown under natural radiation. The substrate moisture was maintained at 50% (v/v) by weighing and fertigating the pots every second day. The fertigation solution was prepared from NH_4NO_3, KH_2PO_4, K_2SO_4, and $MgSO_4$ and contained N, P, K, and Mg at concentrations of 160, 18, 133, and 10 mg L^{-1}, respectively. Additionally, 250 mg L^{-1} of Flory® 10 was used.

Poinsettia plants were pinched above 7 leaf buds. Marigold and poinsettia were harvested three times at 27, 41, and 54 DAP and 53, 67, and 130 DAP, as first, second and final harvest, respectively. Final harvest was done after measuring of plant quality parameters such as plant height and diameter, number of branches for poinsettia, and number of flower buds and flowers for marigold. Plant height was measured from substrate surface as shown on photo 1.

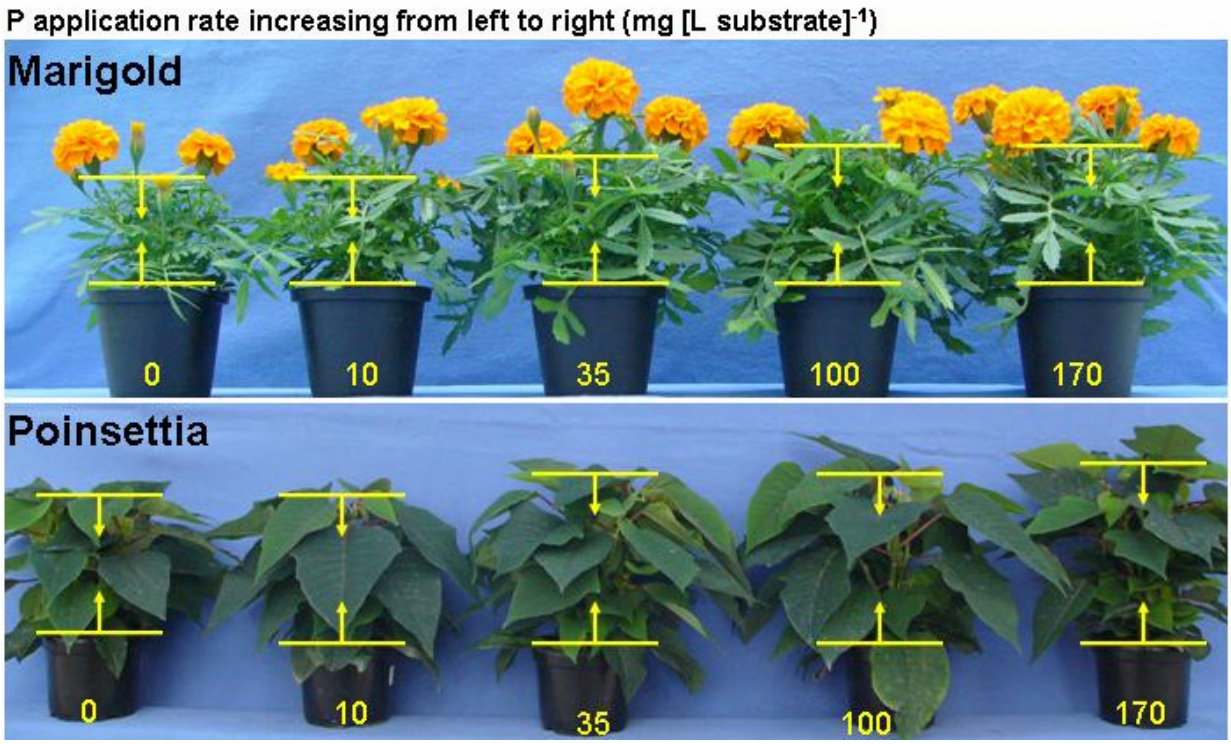

Photo 1: An exemplary photo of representative plant of marigold and poinsettia under different P levels (increasing from left to right). The colored lines and arrows show the approximate points of measurement for plant height.

2. 3. Analytical procedures

2. 3.1. Physical and chemical properties

The volume weight of substrates was determined according to standard method of *VDLUFA* (1991). Pots without plant 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 $CaCl_2$ suspension using a substrate: solution ratio of 1:2.5. Available P in the substrate (C_s) was measured using CAT extraction (0.01 M $CaCl_2$ + 0.002 M DTPA) according to *Alt* and *Peters* (1992). Substrate solution was collected by centrifugation at 1000 g for 20 minutes and

phosphorus concentration in the substrate solution (C_{li}) was determined according to *Murphy* and *Riley* (1962). Buffer power (*b*) was calculated as the ratio C_s/C_{li} (Tab. 1).

Table 1: Substrate characteristics at planting (CAT-soluble P, C_s; Phosphorus concentration in substrate solution, C_{li}; Buffer power, b) with poinsettia and marigold at different P-application rate.

P-application rate [a]	Poinsettia			Marigold		
	P (C_s)[a]	P (C_{li})[b]	*b*	P (C_s)[a]	P (C_{li})[b]	*b*
0	2	0.1	26	3	0.1	32
10	3	0.3	11	5	0.2	24
35	11	1.5	7	12	1.5	8
100	42	22	2	33	17	2
170	84	45	2	63	43	1.5

[a] mg P [L substrate]$^{-1}$; [b] mg P [L solution]$^{-1}$

Freundlich-function was used to describe the relationship between C_s and C_{li} (*Barber*, 1995). Plant material was dried at 70 °C for 5 days and shoot dry weight was recorded. Dry matter P content was determined after dry ashing according to *Gericke* and *Kurmies* (1952).

2. 3.2. Root morphological parameters

Roots were separated from substrate by washing over sieves (0.5-2 mm). In order to check if roots were infected with arbuscular mycorrhiza (*AM*), root samples were stained and observed under microscope according to *Vierheilig* et al. (1998). However, no mycorrhiza colonization was observed in both poinsettia and marigold.
Total fresh weight of roots (*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 day^{-1}) was calculated assuming linear growth as follows:

$$k = (L_2 - L_1)/(t_2 - t_1), \quad (1)$$

where, t is the time (day).

Mean root radius (r_0, cm) was calculated as:

$$r_0 = \sqrt{RFW/\pi \times L}, \quad (2)$$

where, RFW is the root fresh weight (g plant^{-1}).

Mean half distance between neighboring roots (r_1, cm) was calculated as:

$$r_1 = \sqrt{v/\pi \times L}, \quad (3)$$

where, v is the volume of substrate in the pot (cm^3).

Surface area (SAC, cm^2) per cm root cylinder was calculated as:

$$SAC = 2\pi \times r_0 \times h, \quad (4)$$

where, h is the length of root cylinder (one cm).

Subscripts 1 and 2 refer to the first and the second harvest, respectively.

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 hour. The substrate completely separated from roots which were gathered and cut into pieces of 1 cm. Sixty root pieces per replicate were collected in glass vials half-filled with water and dyed with 1 mL of 1% acid fuchsine solution. The root pieces were scored using a microscope with magnification of 50× for high, medium, and low root hair density. Root hair length and density of five pieces of each category was determined using eyepiece with inscribed square grids. Length of one side of a grid unit (r) was 0.016667 cm. The first horizontal line was adjusted parallel to the root axis at the point of emerging root hairs, then root hairs crossing horizontal and vertical grid lines were counted separately for each line and computation was done for root hair parameters according to *Brewster* et al. (1976b).

2. 3.3. Root physiological parameters

For the concentration of P in substrate solution where uptake equals zero (C_{min}) the value which is common for many crops (0.4 µM) was taken from *Barber* (1995). For Michaelis constant (K_m), which is the concentration of P in the substrate solution at which uptake is half the maximum rate (I_{max}), the value of 5 µM was assumed (*Barber*, 1995). The rate of P uptake at highest P supply of each plant was taken as maximum uptake rate (I_{max}).

For calculation of P uptake rate (I, µmol cm^{-1} root length s^{-1}) linear root growth was assumed:

$$I = \frac{U_2 - U_1}{(L_2 + L_1)/2} \times \frac{1}{t_2 - t_1}, \quad (5)$$

where, U is total P uptake (µmol plant^{-1}), t is the time (s).

Phosphorus uptake rate related to the root cylinder surface area (I_{na}, µmol cm^{-2} root s^{-1}) was calculated as:

$$I_{na} = \frac{I}{SAC}, \quad (6)$$

The uptake rate was modified to calculate effective uptake rate (I_n, µmol cm^{-2} root s^{-1}) considering both root and root hairs surface area:

$$I_n = \frac{I}{(SAC + SAH)}, \quad (7)$$

where, SAH is the surface area of root hairs per one cm root length (cm^2) which was calculated as:

$$SAH = 2\pi \times r_{0h} \times RHL, \quad (8)$$

where, r_{0h} is root hair radius (value of 5×10^{-4} cm, which is common for most crops was taken from *Föhse* et al. (1991); RHL is root hair length per cm root cylinder (cm).

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

$$V_0 = \frac{W_2 - W_1}{(SA_2 + SA_1)/2} \times \frac{1}{t_2 - t_1}, \quad (9)$$

where, W is the transpired water by the plant (cm^3), SA is the total surface area of root cylinder (cm^2 $plant^{-1}$), and t is the time (s).

Subscripts 1 and 2 refer to the first and the second harvest, respectively.

2. 3.4. Phosphorus dynamics in the substrate

Mass-flow (MF, µmol cm^{-2} s^{-1}) was calculated as:

$$MF = V_0 \times C_{li}, \quad (10)$$

where, V_0 is the uptake rate of water into root cylinder (cm^3 cm^{-2} s^{-1}), and C_{li} is the concentration of nutrient in the solution (µmol cm^{-3}).

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

$$D_e = D_L \theta f \times (1/b), \quad (11)$$

where, for D_L, the diffusion coefficient of $H_2PO_4^-$ in water at 25 °C, the value of 8.9 × 10^{-6} cm^2 s^{-1} was used (*Edwards* and *Huffman*, 1959), for θ, 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 from *Khandan-Mirkohi* and *Schenk* (2008) and b is the buffer power which was calculated as the ratio C_s/C_{li}.

2.3.5. Extension of the depletion zone (Δx)

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

$$\Delta x = \sqrt{\pi D_e t}, \quad (12)$$

where, Δx 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 two days, since in two days interval the plants were fertigated.

2.3.6. Velocity of P replenishment

Equilibrated substrate of the 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 1h, 2h, 4h, 8h, 12h, and 48h by centrifugation at 1000 g for 20 minutes. Within 4 hours nearly a new equilibrium was reached indicating a fast sorption and desorption of P in the substrate (Fig. 1).

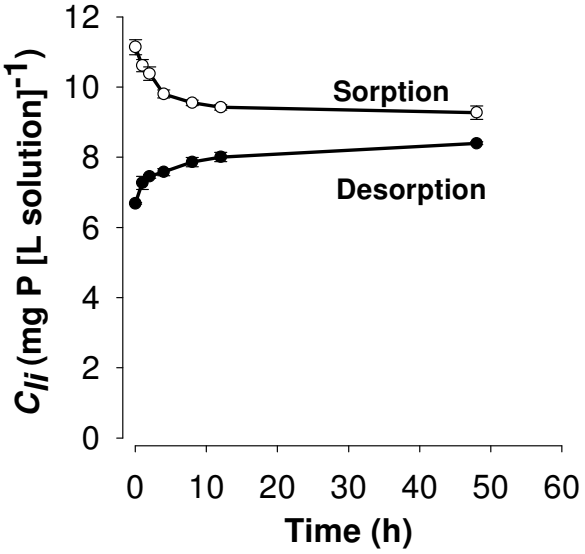

Figure 1: Phosphorus concentration in substrate solution (C_{li}) after addition of water (desorption) or fertilizer solution (sorption) to peat-substrate (black peat 80% + mineral component 20%, v/v; application rate of 35 mg P [L substrate]$^{-1}$).

2. 4. Modeling P 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 two days 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 table 2 and 3.

Table 2: Specific model parameters of poinsettia and marigold used for simulation of P uptake at first harvest

Plant species	**Poinsettia**					**Marigold**				
P-application rate (mg [L substrate]$^{-1}$)	**0**	**10**	**35**	**100**	**170**	**0**	**10**	**35**	**100**	**170**
Substrate parameters										
b	3.6	3.3	2.8	1.9	1.5	17.8	12	4.8	2.5	1.7
C_{li} (µmol cm^{-3}) × 10^{-2}	14	17	27	79	173	2	3	10	45	120
Plant morphological parameters										
r_0 (cm) ×10^{-2}	4	4	4	4	4	2	2	2	2	2
r_1 (cm) ×10^{-2}	27	26	24	24	24	23	20	16	16	16
L_0 (cm plant^{-1}) ×10^{2}	27.2	28.8	33.1	33.9	34.0	20.1	26.4	39.8	40.5	40.6
k (cm day^{-1})	159	157	133	129	129	314	304	272	268	267
Plant physiological parameters										
I_{max} (µmol cm^{-2} s^{-1}) ×10^{-7} (root hairs neglected)	5.3	5.3	5.3	5.3	5.3	5.8	5.8	5.8	5.8	5.8
I_{max} (µmol cm^{-2} s^{-1}) ×10^{-7} (root hairs included)	4.2	4.2	4.2	4.2	4.2	2.9	2.9	2.9	2.9	2.9
V_0 (cm^3 cm^{-2} s^{-1}) ×10^{-7}	7.5	7.4	11.9	12.1	12.6	7.1	7.2	8.6	9.8	10.5

b = buffer power; C_{li} = 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_{max} = maximum uptake rate; V_0 = water uptake rate of root cylinder.

Root hairs 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 (×10^{-3} cm) and of marigold: 6.7, 10.2, 17, 33.7, 81.6, 194, and 361 (×10^{-3} 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.

Table 3: Specific model parameters of poinsettia and marigold used for simulation of P uptake at planting (10 DAP)

Plant species	**Poinsettia**					**Marigold**				
P-application rate (mg [L substrate]$^{-1}$)	**0**	**10**	**35**	**100**	**170**	**0**	**10**	**35**	**100**	**170**
Substrate parameters										
b	26	11	7	2	2	26	11	7	2	2
C_{li} (µmol cm^{-3})× 10^{-2}	0.3	0.8	4.8	72	145	0.3	0.8	4.8	72	145
Plant morphological parameters										
r_0 (cm) ×10^{-2}	4	4	4	4	4	2	2	2	2	2
r_1 (cm) ×10^{-2}	62	60	56	56	56	37	32	26	26	26
L_0 (cm plant^{-1}) ×10^2	5.1	5.4	6.2	6.4	6.4	7.4	9.8	14.8	15	15
k (cm day^{-1})	51	54	62	64	64	74	98	148	150	150

b = buffer power; C_{li} = 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.

The parameters for root hairs and plant physiology were the same as indicated in table 2.

2. 5. Statistical analysis

Treatments were replicated four times (each replicate consisted of two plants) in a completely randomized block design and data were analyzed using analysis of variance of SAS (*SAS*, 1996). Means were compared between the treatments at α = 0.05 using Tukey-Test.

3. Results

3.1. Phosphorus dynamics in the substrate

The 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 harvest. At the same P level, increase of C_s was higher with poinsettia than with marigold. The plant available P (C_s) was closely related to P concentration in the substrate solution (C_{li}) (Fig. 2C). Buffer power (b) decreased with increasing P level (Tab. 1). The amount of fertigated P almost matched the P uptake of both crops at the higher P levels, but exceeded the P taken up considerably at the two lower P levels. This was much more pronounced for the period from planting to the first harvest than between first and second harvest (Tab. 4).

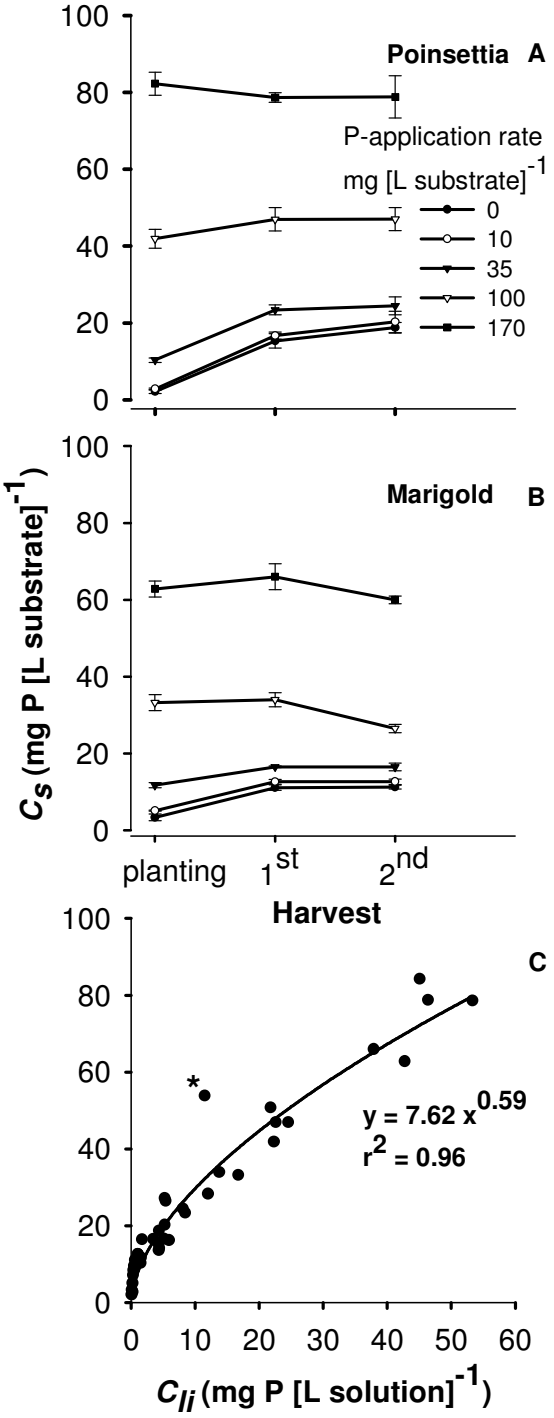

*Figure 2: CAT soluble P content of the substrate (C_s) during cultivation of poinsettia (A) and marigold (B) at different P levels; The relation between substrate solution P (C_{li}) and C_s at different time of measurement during cultivation of poinsettia and marigold (C), * Outlier, not included in the regression.*

Table 4: Comparison of fertigated and taken up P during cultivation of poinsettia and marigold at different P-application rates (Data normalized per L substrate to allow comparison between crops)

Plant species	Amount of P (mg [L substrate]$^{-1}$)						
		Up to 1st Harvest		1st to 2nd Harvest		Fertigation-Uptake	
	Applied	Fertigation	Uptake	Fertigation	Uptake	Up to 1st Harvest	1st to 2nd Harvest
Poinsettia	0	53	13	19	18	40	1
	10	53	17	19	18	36	1
	35	57	42	20	22	15	-2
	100	57	46	20	30	11	-10
	170	57	52	20	31	5	-11
Marigold	0	24	2	21	14	22	7
	10	25	7	25	18	18	7
	35	28	18	34	27	10	7
	100	29	28	34	43	1	-9
	170	29	31	34	50	-2	-16

3.2. Plant growth and quality

Increase in P supply resulted in a significant increase of shoot dry matter yield, and also improved the quality of both poinsettia and marigold (Fig. 3, Tab. 5 and 6). The increase of shoot dry matter and improvement of quality parameters of both crops were in the same range for three higher P levels during growth and clearly above the lower P levels. The maximum growth and quality of both crops was obtained at applied P level of 35 mg [L substrate]$^{-1}$. This differentiation was already visible at 1st harvest. Dry matter yield of poinsettia was two-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.

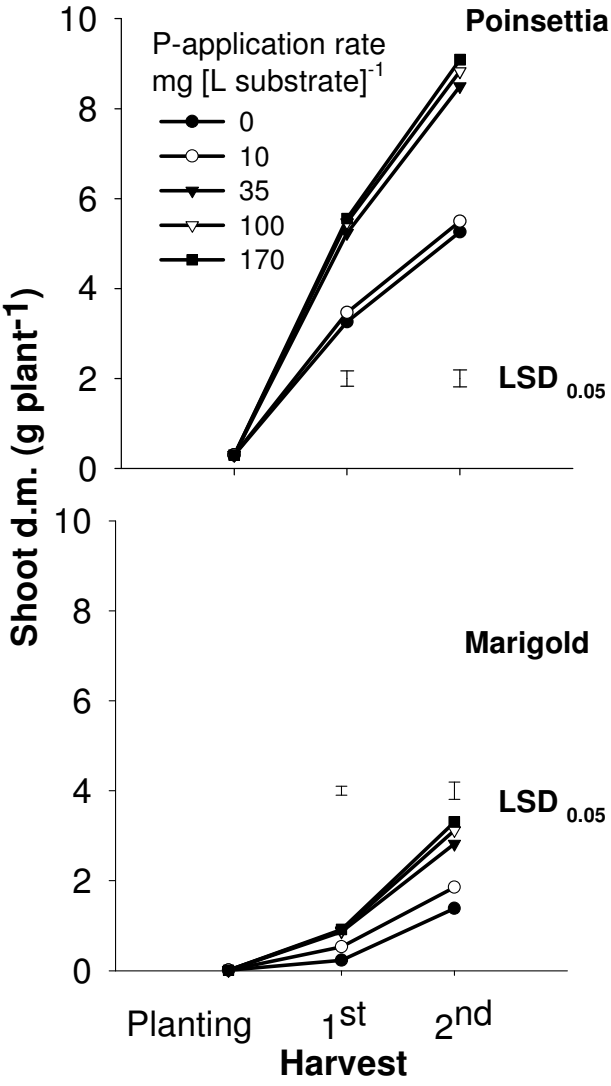

Figure 3: Absolute shoot dry matter of poinsettia and marigold during crop growth at different P levels.

Table 5: Quality parameters of poinsettia as affected by P-application rate [a]

P-application rate (mg [L substrate]$^{-1}$)	Plant dry matter (g plant^{-1})	Plant height (cm)	Plant diameter (cm)	Number of branches (# plant^{-1})
0	18.0 b	28.2 b	30 b	6.6 b
10	18.5 b	28.5 b	30 b	6.6 b
35	22.7 a	32.2 a	40 a	7.7 a
100	22.7 a	32.5 a	40 a	7.8 a
170	22.9 a	32.8 a	40 a	7.8 a

[a] Different letters indicate significant differences at $p<0.05$

Table 6: Quality parameters of marigold as affected by P-application rate [a]

P-application rate (mg [L substrate]$^{-1}$)	Plant dry matter (g plant^{-1})	Plant height (cm)	Plant diameter (cm)	Number of flowers (# plant^{-1})
0	2.40 c	8 b	16 b	3.2 c
10	3.44 b	9 b	17 b	4.1 b
35	4.45 a	13 a	28 a	5.1 a
100	4.76 a	13 a	28 a	5.1 a
170	4.85 a	13 a	28 a	5.3 a

[a] Different letters indicate significant differences at $p<0.05$

Relative shoot dry matter yield increased with increasing shoot P concentration (Fig. 4A, B) and both crops attained their optimum yield (90% of maximum yield) with the same P concentration at the second harvest (Fig. 4B). The critical P level was slightly higher for both crops at the first harvest.

Root morphological parameters of both poinsettia and marigold were also significantly affected by P supply (Fig. 5). Root length density increased with P supply up to

optimum P level at the first and the second harvest of marigold, but for poinsettia almost no change of root length density was observed at both harvests (Fig. 5A).

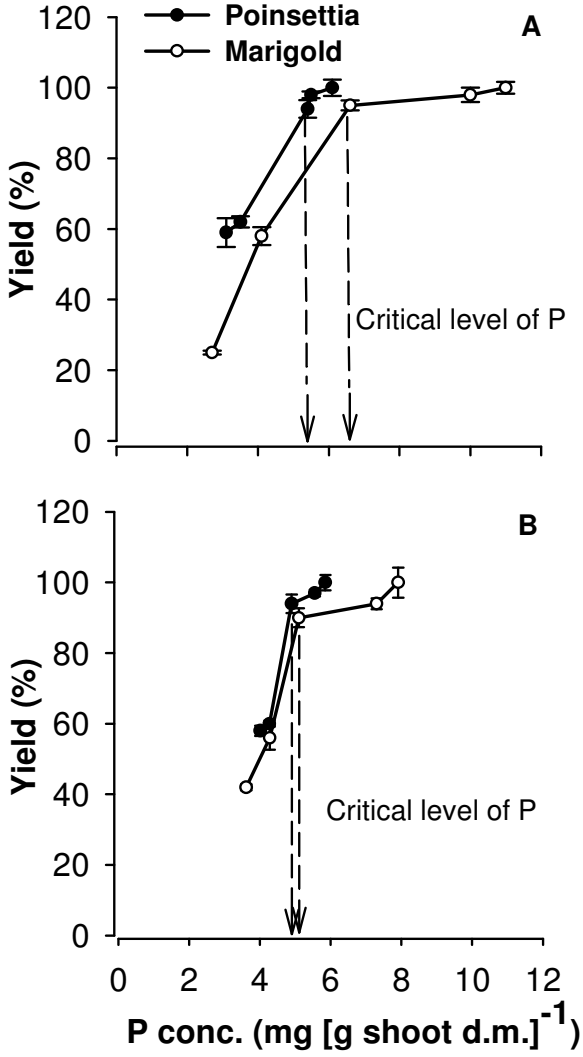

Figure 4: Relative yield of poinsettia and marigold as affected by plant P concentration in shoot dry matter at 1st (A) and 2nd harvest (B) (maximum yield = 100%).

Root length density of marigold was two fold higher than that for poinsettia. However, root hairs of both crops were longer at low P supply compared to high P (Fig. 5B). Marigold had two fold longer root hairs than poinsettia at all P levels. In addition, marigold had smaller root radius (r_0= 0.02 cm), compared to poinsettia (r_0= 0.04 cm).

Root/ shoot ratio of marigold (20-40 m [g shoot dry matter]$^{-1}$) was also double that of poinsettia (10-20 m [g shoot dry matter]$^{-1}$) at all P levels.

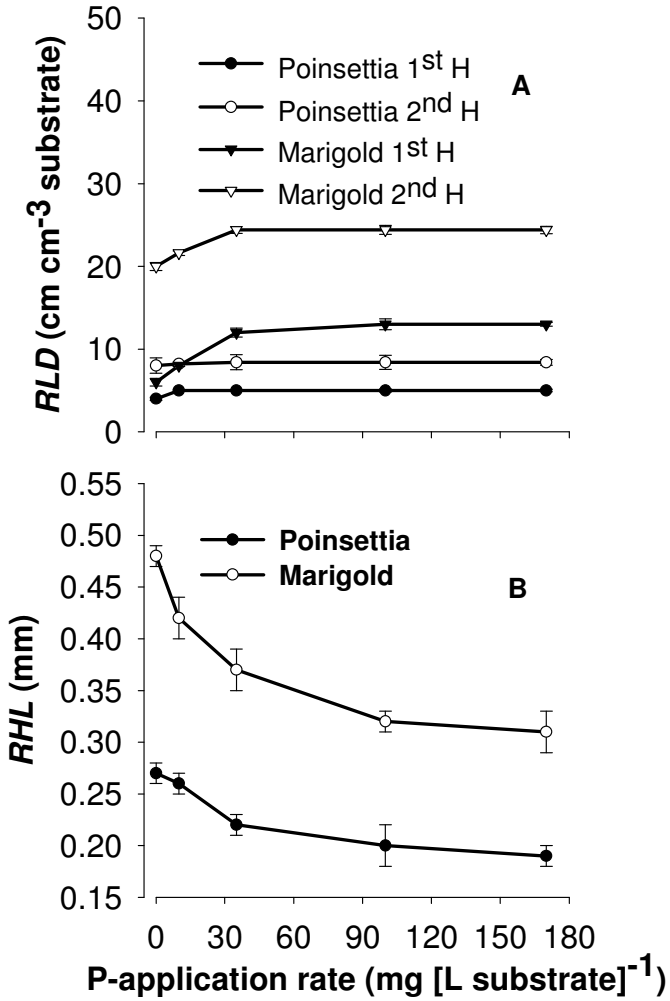

Figure 5: The effect of P supply on root length density (RLD) (A) and mean root hair length (RHL) (B) of poinsettia and marigold.

The mean half distance between roots (r_1) decreased with plant age and was about half for marigold compared to poinsettia throughout cultivation (Fig. 6). Extension of depletion zone (Δx) was also calculated after two days of depletion, since the plants were fertigated every two days. At ten days after planting, Δx for marigold was two-third of r_1, but was only one-third in the case of poinsettia. Later during cultivation, Δx

extended beyond the r_1. Thus, at the very early stages (10 DAP) marigold exploited about 43% of substrate volume, whereas only 10% was exhausted by poinsettia.

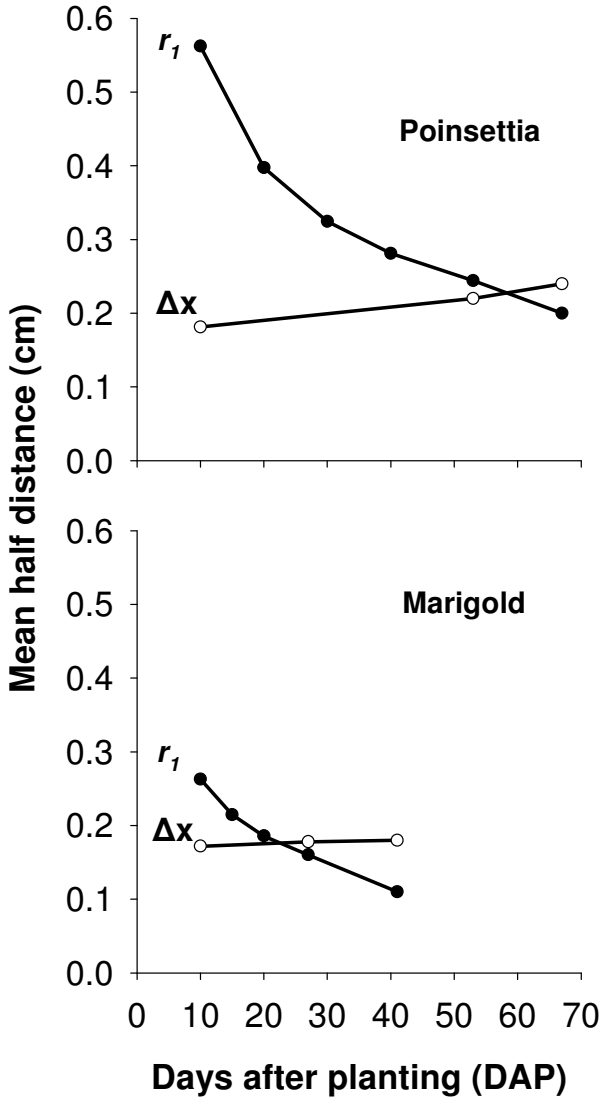

Figure 6: Mean half distance (r_1) during cultivation of poinsettia and marigold compared with estimated distance of depletion zone (Δx) after 2 days for the optimum P level (35 mg [L substrate]$^{-1}$). Plant data between planting and first harvest were calculated assuming linear growth.

3.3. Phosphorus uptake

The simulated P uptake with root cylinder plus root hairs agreed well with the experimentally observed values for both poinsettia and marigold (Fig. 7A). However, at lower P levels, a slight over prediction was observed. Root hairs enhanced predicted P uptake significantly more for marigold compared to poinsettia (Fig. 7B).

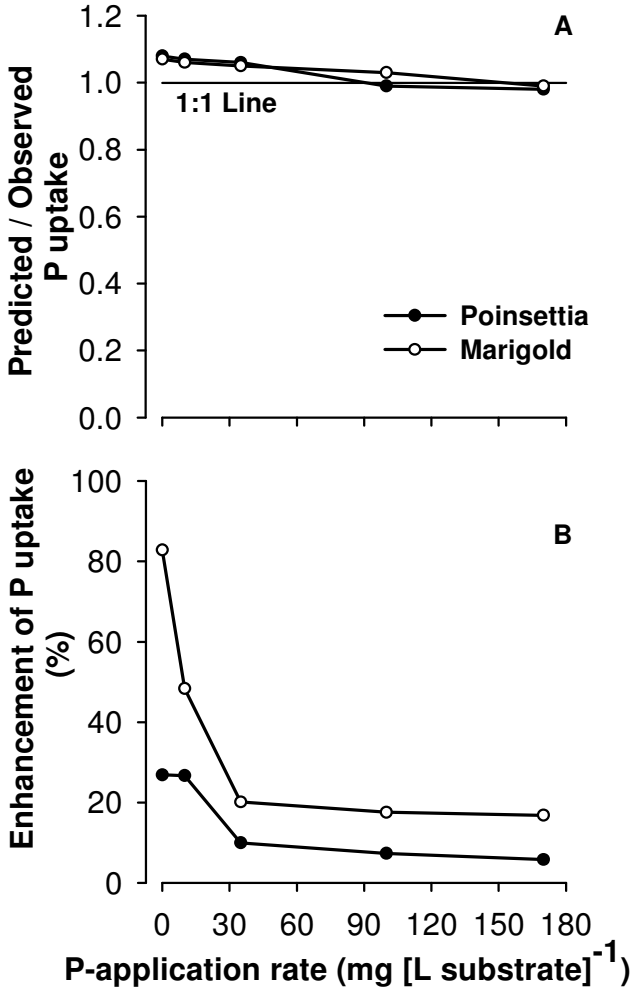

Figure 7: Predicted/observed P uptake of poinsettia and marigold simulated for root cylinder plus root hairs (A) and enhancement of P uptake by root hairs compared to root cylinder (B), as affected by P application (simulation for two days uptake after first harvest; observed uptake was calculated assuming linear growth between first and the second harvest).

At optimum P supply, the increase of P uptake by root hairs was only 10-20% compared to root cylinder.

The simulated P depletion profiles with root cylinder plus root hairs at root surface indicated a steep concentration gradient (Fig. 8). The depletion zone extended with increase of P supply and reached at optimum P level a value similar to that given in figure 6. The concentration at root surface was 0.8 and 0.96 µM for treatment 10 mg P [L substrate]$^{-1}$ and 10 and 12.4 µM for the treatment 35 mg P [L substrate]$^{-1}$ for poinsettia and marigold, respectively.

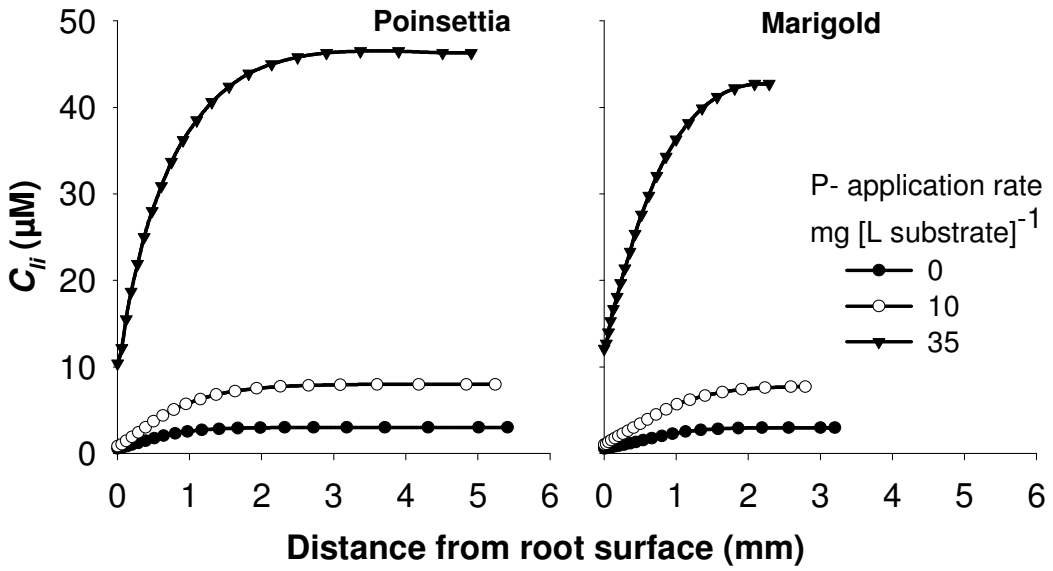

Figure 8: Depletion profile in substrate solution (C_{li}) at low, sub-optimum and optimum P level of poinsettia and marigold 10 DAP (simulated for two days for root cylinder plus root hairs).

4. Discussion

4.1. Phosphorus dynamics in the substrate

The increase of P application rate resulted in increase of CAT-soluble P (C_s) and substrate solution P (C_{li}) for both poinsettia and marigold (Fig. 2A, B and Tab. 1). The close correlation ($r^2 = 0.96$) between the C_s and C_{li} was exponential in the low range of C_s up to 20 mg P [L substrate]$^{-1}$, thus the buffer power (b) decreased with increasing P level (Tab. 1) as it is well known for mineral soils (*Hendriks* et al., 1981). About 30% of the applied P was extracted by CAT and 4% of that was contained in the substrate solution at optimum P level, although the substrates contained 20% (v/v) of mineral component. Phosphorus sorption and desorption in the substrate was fast (Fig. 1). The concentration of P in the substrate solution (C_{li}) at optimum P level was 1.5 mg L^{-1} for both poinsettia and marigold, which was at least 5 times higher than the value (0.3 mg L^{-1}) generally observed in most mineral soils (*Barber*, 1995). This high C_{li} was necessary to meet the demand of plant roots, since the b of 7-8 was very low (Tab. 1) compared to mineral soils, which normally have b in the range of 100-2000 (*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 used mineral component had small P sorption capacity and P in the substrate was more mobile.

Supplementary P application through fertigation increased the level of C_s with both poinsettia and marigold from planting until first harvest at low P levels, but not at high P levels (Fig. 2A, B). This reflected the balance sheet of fertigated P and P taken up (Tab. 4). Thus, the amount of fertigated P exceeded P uptake at two lower P levels, but plants suffered from P deficiency indicating that rather than the amount of P, the transport of P to the root surface limited growth at this stage. This was confirmed by simulated P depletion profiles at root surface (Fig. 8) where after two days of depletion, the concentration at root surface was below the assumed K_m value (5 µM) and the concentration gradient was insufficient to match the demand. Obviously, the

well supplied plants needed a concentration gradient of about 30-40 µM to drive the necessary flux. This gradient could not be established at two lower P levels.

The increase of C_s at the lower P levels from planting up to the first harvest was more pronounced with poinsettia than with marigold. This may be explained by the larger mean half distance between poinsettia roots and the comparatively small extension of P depletion zone (Fig. 6). Poinsettia roots exhausted about 10% of the substrate volume, but marigold exploited about 43% at 10 DAP. Thus, more of the fertigated P was accumulated in the non-exploited substrate with poinsettia leading to a more pronounced increase of C_s. Later during cultivation, mean half distance between roots decreased and the whole substrate volume could be exploited, so that no further increase of C_s could occur. This is completely different from the situation in the field, 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 and quality

Optimum P level of both poinsettia and marigold was 35 mg [L substrate]$^{-1}$ (Fig. 3; Tab. 5 and 6), which resulted in about the same P concentration in shoot dry matter (Fig. 4) 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). Obviously, limiting P application rate to the optimum level did not reduce the growth and quality of both marigold and poinsettia. However, below the optimum P level the dry matter yield and whole plant quality and performance e.g. plant height of both crops was negatively affected (Tab. 5 and 6, photo 1). The reduced height of plant is a desirable quality aspect for ornamental crops (*Borch* et al., 2003). However, not only the plant height, but also all other quality parameters including plant diameter of the both crops reduced at low P availability. Thus, restricted P availability may not be recommended as a tool for the control of plant height.

Root length density (*RLD*) 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 with marigold *RLD* 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. 6).

Root hairs were longer at low P supply with both poinsettia and marigold (Fig. 5B). Similarly, increased root hair length under P deficiency was observed with plants grown in both nutrient solution and soil for tomato, rape and spinach (*Föhse* and *Jungk*, 1983). The length of root hairs varies greatly within and between plant species (*Hofer*, 1996) and depends on 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 (*Brassica oleraceae* L. cv. Farao), carrot and potato cultivated in mineral soil at different P supply. Furthermore, it was reported that in mineral soil 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 many 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. 7B). At the optimum P level root hairs increased predicted P uptake only by 10-20% over that of the root cylinder, since P buffering in the substrate was low (b= 8). Long root hairs are highly efficient to acquire P from mineral soil by extending the depletion zone (*Föhse* et al., 1991), since P is immobile due to high b. The low b of P in the peat-substrate led to a high effective diffusion coefficient (D_e). Therefore, P was considerably mobile in the peat-substrate compared to mineral soil (*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 (D_e) of P in the substrate was comparable with D_e 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 insignificant for its depletion (*Claassen* and *Steingrobe*, 1999).

4.3. Modeling of plant and substrate parameters

The predicted P uptake with root cylinder plus root hairs reflected the observed P uptake fairly well (Fig. 7A); indicating that plant and substrate parameters involved in P uptake were well determined (Tab. 2), and that no additional mechanism of P mobilization was involved. However, a slight over prediction was observed at lower P levels for both poinsettia and marigold. Sensitivity analysis revealed that changing of I_{max} and C_{min} did not change the prediction, but increasing K_m by a factor of 1.2 (6 µM) and 2 (10 µM) reduced the overestimation close to 1:1 line at low P levels for both marigold and poinsettia, respectively. This indicates that both crops might have a higher K_m value than 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 (C_s) in the substrate at optimum growth of poinsettia compared to marigold was attributed neither to the utilization efficiency nor to the uptake efficiency. Similar utilization efficiency was found for both crops at optimum P supply (Fig. 4) and the observed different root morphological parameters (higher *RLD*, longer root hairs, smaller root radius, and higher root: shoot ratio in case of marigold compared to poinsettia) did not contribute significantly to P uptake efficiency, since P mobility in the peat-substrate was high. However, after planting the low root length density (*RLD*) of poinsettia caused a larger mean half distance between roots (r_1), which resulted in the accumulation of fertigated P to a higher level compared to that of marigold. Therefore, these two crops are not different in P efficiency. The observed higher P level for poinsettia at optimum growth was an artifact of the lower *RLD* after planting.

GENERAL DISCUSSION

The mobility of P in peat-substrates compared to mineral soil, plant characteristics affecting P uptake, yield and quality production including adaptation of fertilization program are generally discussed in this section.

1. Phosphorus mobility in the substrate

The results revealed that P in peat-substrate was more mobile than that in mineral soil. Among two main driving forces for the movement of P through mineral soil (mass-flow and diffusion), diffusion has a key role for movement of this ion (*Claassen* and *Steingrobe*, 1999). In mineral soil less than 4% of P taken up by plants reaches the root by mass-flow. However, the contribution of mass-flow to P transport to root surface in the substrate was 20-60% at optimum P level of poinsettia and marigold (Fig. 1). This high contribution of mass-flow was mainly due to the higher substrate solution P concentration (C_{li}) which was observed in the peat-substrate (Tab. 1, page 61).

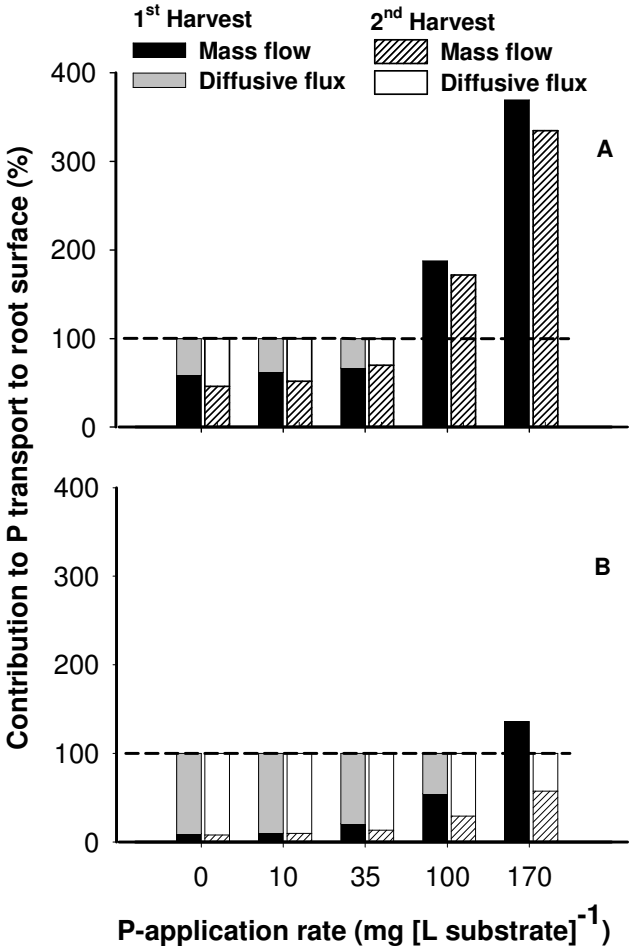

Figure 1: Contribution of mass-flow and diffusion to P transport to root surface of (A) poinsettia and (B) marigold at first and second harvest

1.1. Buffer power (*b*)

The observed buffer power (*b*) in the peat-substrates was much lower than reported for mineral soils (*Jungk* and *Claassen*, 1997). Buffer power is an indicator of P adsorption characteristics of soil which was influenced mainly by Fe and Al oxide content of mineral components, but not by their clay content (Fig. 6, page 30; Fig. 7, page 31).

Buffer power was calculated as the ratio between available P in the substrate (C_s) and phosphorus concentration in the substrate solution (C_{li}) and a close relationship between C_s and C_{li} was observed in peat-substrate (Fig. 5, page 29; Fig. 2, page 69).

The observed C_{li} for optimum growth of poinsettia and marigold (48 µM) was almost 5 times higher than the highest value (10 µM) commonly reported for mineral soils (*Barber*, 1995; *Jungk* and *Claassen*, 1997). Surprisingly, the C_{li} of 10 µM was not sufficient for optimum growth of poinsettia and marigold in the substrate (Fig. 8, page 77), since the concentration gradient was not sufficient to meet the demand at this level of C_{li}. It was observed that the well supplied plants cultivated in peat-substrates needed a concentration gradient of around 40 µM to drive the necessary flux. The simulation approach revealed that such a high concentration gradient in the peat-substrate was necessary because of very low *b* (=7) compared to that in mineral soil (*b* = 1000, *Barber*, 1995) (Tab. 1, page 61).

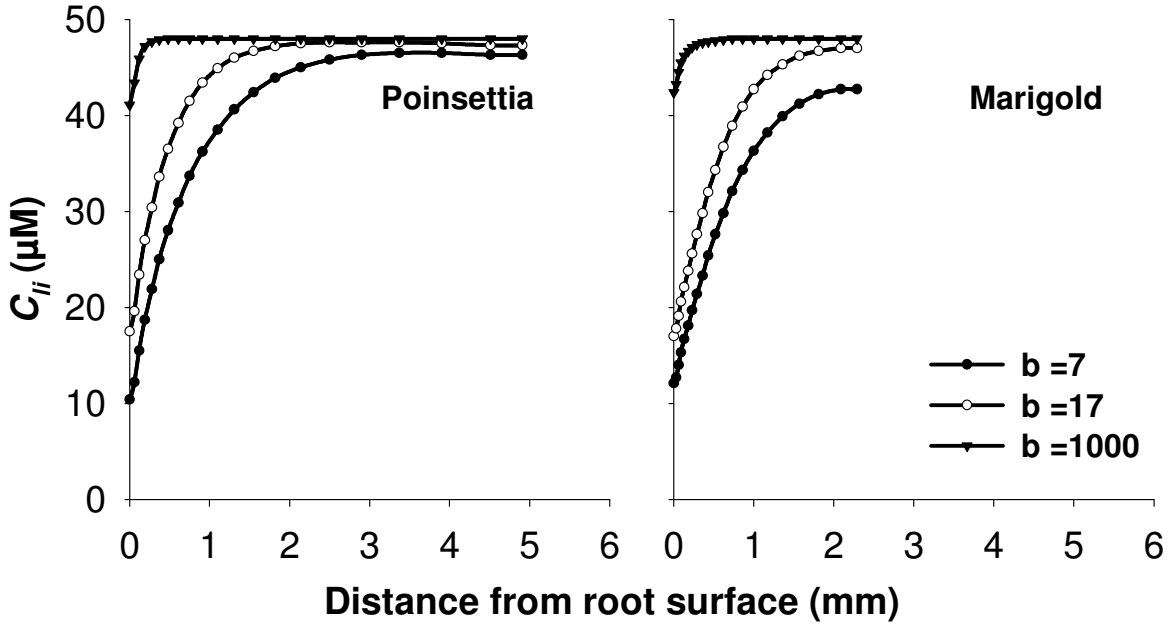

Figure 2: The change of depletion profile for P at root surface of poinsettia and marigold at optimum growth as affected by different buffer power (chosen data were taken from Tab. 3, page 67; simulation for two days uptake 10 DAP).

The highest *b* of 17 which was observed at optimum P in peat-substrate mixed with mineral components (Fig. 6, page 30) slightly changed the depletion profile and decreased the concentration gradient (30 µM), but still a huge difference was observed between peat-substrate and mineral soil. However, the depletion profile changed dramatically using *b* of 1000 which is generally observed in mineral soil and the concentration gradient (5-8 µM) became close to that normally expected for mineral soil (*Barraclough*, 1989; *Barber*, 1995).

1.2. Impedance factor (*f*)

1.2.1. Volumetric water content (*θ*)

The observed impedance factor (*f*) for peat-substrate at volumetric water content (*θ*) of 0.4 cm^3 cm^{-3} was significantly lower than that which was reported for mineral soil at the same *θ* (*Barraclough* and *Tinker*, 1981). At this level of *θ*, mineral soil is already saturated and most of the micro and macro pores are filled with water (*Brady* and *Weil*, 1999). The *θ* of 0.4 cm^3 cm^{-3} is generally higher than the field capacity of 0.2-0.3 cm^3 cm^{-3} for sandy loam soil and clay loam soil, respectively (*Jabro* et al., 2008). On the other hand, it is noticeably lower than water capacity for peat-substrates (0.6-0.8 cm^3 cm^{-3}; *Bohne* and *Wrede*, 2005). Peat-substrates are normally dry at *θ* of 0.4 cm^3 cm^{-3} and only small portion of macro pores are still filled with water (*Naasz* et al., 2005) which also may not be assumed in the normal condition. Thus, for usual water content a similar *f* value of 0.2-0.3 could be assumed for soil/peat-substrate (Fig. 3, page 26; *Barraclough* and *Tinker*, 1981).

The impedance factor increases, when *θ* is increased, since the liquid phase becomes more continuous and the diffusion path less tortuous (*Warncke* and *Barber*, 1972a; *Barraclough* and *Tinker*, 1981; *Bhadoria* et al., 1991a). Similarly, for peat-substrate without mineral component *f* increased with increasing of *θ* till 0.7 cm^3 cm^{-3}, however, a further increase of *f* with *θ* over 60% was not expected in the substrates mixed with mineral component, since it was already saturated at this level of water content.

1.2.2. Bulk density

Adding mineral component to the black peat causes an increase of solids per unit volume and hence was expected to restrict physically the diffusion path. However, impedance factor (*f*) was not significantly affected by adding grind mineral component (Fig. 3, page 26). Macro and medium pores are the main portion of the pore space in peat-substrate which contains plant-available water (*Bohne* and *Wrede*, 2005) and this portion of pore space may not be affected with grind mineral components, and hence did not considerably change the total pore space of the substrate. Thus, the change of *f* by adding grind mineral components was not noticeable. Medium pores may be affected by granulated mineral components, which are the main commercial form used in the substrate industry. However, granulated mineral components could not be used for determination of *f*, due to some practical limitation e.g. well leveling of the soil/substrate surface (page 20) to avoid trapped air pockets in between exchange membrane and soil or substrate surface (*Barraclough* and *Tinker*, 1981).

Similarly, small effect of bulk density on *f* was observed by *So* and *Nye* (1989), whereas decrease of *f* by increase of bulk density was reported by *Bhadoria* et al. (1991b) and *Barraclough* and *Tinker* (1981). They assumed more fine pores at the higher bulk density which led to a more tortuous pathway. On the other hand, an initial increase of *f* with increase of bulk density and then decrease of that with further increase of bulk density was reported at constant water content on weight basis (w/w) (*Warncke* and *Barber*, 1972b) which may be biased, since water content on weight basis leads to a variation in water content on the volumetric basis.

1.3. Diffusion coefficient (D_e)

Buffer power (*b*), impedance factor (*f*), and volumetric water content (θ) are the main factors affecting the effective diffusion coefficient (D_e) (*Nye*, 1979). The calculated D_e for P was considerably higher in peat-substrate than in mineral soil and it was comparable with D_e of K in mineral soil (*Barber*, 1995; *Claassen* and *Steingrobe*, 1999). For the high D_e value, low *b* and high *f*, both are the main factors (*Nye*, 1979;

Barber, 1995). However, as already was discussed the *f* value was almost similar (0.2-0.3) in peat-substrates and mineral soil at normal conditions. Thus, the high D_e for P in peat-substrates was attributed mostly to the low *b*.

The calculation of D_e for P, K and NO_3 in peat-substrate and mineral soil revealed that obviously, D_e was increased in the same order in both mineral soil and peat-substrate for P< K< NO_3 (Tab. 1). For K and NO_3 almost the same D_e was observed for both media. Obviously, D_e for P in peat-substrate was higher than that in mineral soil. This was because, the *b* for P was considerably lower in peat-substrate compared to mineral soil, whereas the *b* for K and NO_3 was almost the same for both media.

Table 1: The diffusion coefficient of P, K, and NO_3 in peat-substrate compared to mineral soil [a]

Nutrient	D_L [b]	Buffer power (b) [b]		D_e [b]	
		Mineral soil	Peat-substrate	Mineral soil	Peat-substrate
P	08.9	100-2000	1-17	10^{-8}-10^{-11}	10^{-7}-10^{-8}
K	19.8	2-8	2-6	10^{-7}-10^{-9}	10^{-7}
NO_3	19.2	0.2	0.5	10^{-6}-10^{-7}	10^{-6}

[a] Equation 1 (page 18) was used for calculation of D_e ($cm^2\ s^{-1}$)

[b] D_L ($\times 10^{-6}$,$cm^2\ s^{-1}$), is diffusion coefficient of nutrients in water at 25 °C (*Barber*, 1995); D_e ($cm^2\ s^{-1}$), is effective diffusion coefficient; For volumetric water content (θ) the values of 0.5 and 0.2 $cm^3\ cm^{-3}$, and for *f* the values of 0.09 and 0.2 in peat-substrate and mineral soil was used for computations, respectively. For mineral soil *f* and θ was taken from *Barraclough* and *Tinker* (1981) and *b* was taken from *Barber* (1995) and *Claassen* and *Steingrobe* (1999).

2. P efficiency

The variation in the ability of plants to tolerate P deficiency stress is a genetically based trait which often is termed P efficiency and can be distinguished in uptake and utilization efficiency.

2.1. Uptake efficiency

2.1.1. Root traits

Clear differences in root morphological parameters were observed between poinsettia and marigold. Marigold had favorable root morphological parameters such as higher *RLD*, longer root hairs, higher root: shoot ratio, and smaller root radius compared to poinsettia. The favorable root morphology is important for efficient acquisition of P from soil. The *RLD* for marigold was higher compared to the range as known for field grown crops in the upper soil layer (*Heins* and *Schenk*, 1987; *Schenk* and *Barber*, 1980), whereas with poinsettia *RLD* was in the range.

The favorable root morphology is important in mineral soil to exploit more volume of soil, but in peat-substrate the whole volume of pot could be depleted after a given period due to high mobility of P in the substrate (Tab. 1). The depletion zones for P in peat-substrate were overlapping 50 and 20 days after planting (DAP) for poinsettia and marigold, respectively (Fig. 6, page 75). Even poinsettia which had a lower *RLD* was able to exploit the whole pot volume. In addition, the length of root hairs was not significant for extension of depletion zone for P in peat-substrate, since it was highly mobile; in contrast to mineral soil, where long root hairs are highly efficient to extend the depletion zone of P (*Föhse* et al., 1991; *Bates* and *Lynch*, 2001). For the same reason, mycorrhizae would not effectively contribute to P uptake from peat-substrate. However, the contribution of mycorrhizae to P uptake in mineral soil is generally reported. Additionally, mobilization of P was also insignificant in peat-substrate again due to its high mobility, in contrast to mineral soil where some root-mediated changes in the rhizosphere chemistry such as excretion of organic acids or protons could

increase the mobility and availability of P (*Ryan* et al., 2001; *Dechassa* and *Schenk*, 2004). The mechanistic simulation model also confirmed that additional mechanisms of P mobilization and acquisition were not involved in P uptake, since P transport in peat-substrate and P uptake were well described without considering these processes (Fig. 7, page 76).

2.1.2. Physiological uptake kinetics

Root physiological properties are significant for K and NO_3 acquisition in mineral soil, but not for phosphorus (P) (*Claassen* and *Steingrobe*, 1999). However, the mobility of P in peat-substrates is similar to the 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. Maximum P uptake rate (I_{max}) was higher at early stages for both marigold and poinsettia than at later stages (Fig. 6, page 44). Because of this higher uptake rate at early stages a higher plant available P (C_s) was needed to match the demand of crops compared to the later stages. The calculated C_s values at early stages were 26 and 27.5 mg P [L substrate]$^{-1}$ and 17.3 and 12 mg P [L substrate]$^{-1}$ at later stages for marigold and poinsettia, respectively (page 53).

However, the experimentally observed C_s (11-12 mg [L substrate]$^{-1}$) at planting for optimum growth and quality of marigold and poinsettia (Tab. 1, page 61) was lower than the theoretically calculated values of C_s at early stages (26 and 27.5 mg [L substrate]$^{-1}$) (page 53). This was because the computed I_{max} for nutrient solution experiment was higher (Fig.6, page 46) than the highest uptake rate in peat-substrate (Tab. 2, page 66). Secondly, the observed uptake rate at optimum growth (3.1 and 3.7 [µmol cm^{-2} s^{-1}] $\times 10^{-7}$ for marigold and poinsettia, respectively) was just half the uptake rate at the highest P level.

2.2. Utilization efficiency

At optimum P level the dry matter yield production per unit of P was similar for both poinsettia and marigold, since the P concentration in dry matter was about the same and in the range as reported for other horticultural crops (*Sanchez*, 2007). Thus, similar utilization efficiency was expected for these crops in peat-substrate. However, higher utilization efficiency was reported for some plant species and cultivars in mineral soil at low and sufficient P supply (*Clark*, 1983; *Kochian* et al., 2004; *Akhtar* et al., 2007). The higher ability of efficient plant to release the inorganic P from vacuole to the cytoplasm or low requirement for metabolic activities at cellular level were speculated as the reason for efficient utilization of P (*Duff* et al., 1994; *Raghothama*, 1999). However, the mechanism for internal utilization efficiency is not yet clearly known.

3. Available P concentrations for optimum growth and quality

The optimum growth and quality of both representative ornamental crops (marigold and poinsettia) was observed at the same plant available P (C_s) of 11-12 mg [L substrate]$^{-1}$ at planting (Tab. 1, page 61). This level of C_s was increased to 16 and 24 mg [L substrate]$^{-1}$ at later stages for marigold and poinsettia, respectively. The increase occurred, since more P was fertigated than was taken up by the plant and the volume of unexploited substrate was larger at early stages (57% and 90% for marigold and poinsettia, respectively) (Fig. 6, page 75). During early growth stage, the concentration gradient was only little decreased after 6 days of depletion (Fig. 3). However, during later growth stages the concentration gradient was reduced by half and even more within 6 days, since mean half distance between roots (r_1) was decreased (Fig. 6, page 75) and hence the amount of C_s was limiting. Thus, to ensure a sufficiently high concentration gradient, P had to be supplemented by frequent fertigation at later stages but not in the early growing stage.

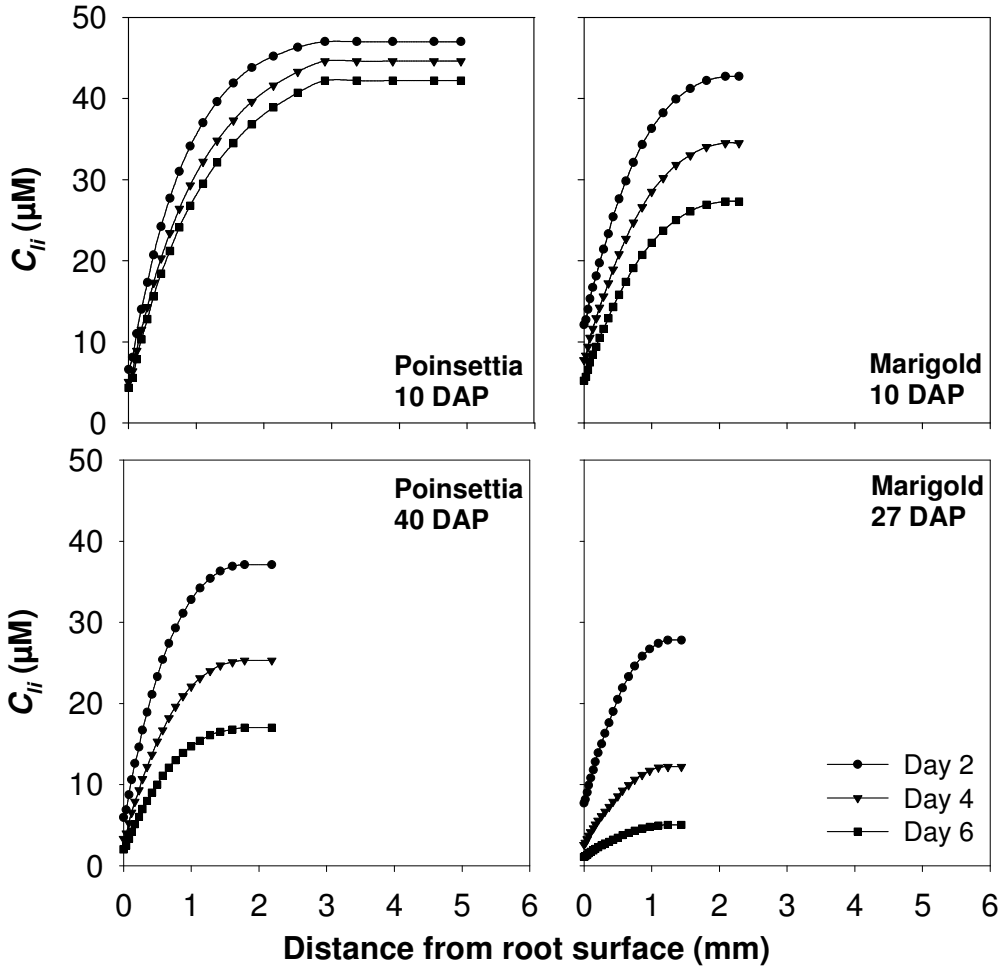

Figure 3: Depletion profile of P at optimum P application rate (35 mg [L substrate]$^{-1}$) for poinsettia and marigold 10 DAP, and at first harvest (27 and 40 DAP for marigold and poinsettia, respectively); simulated for different depletion time; Data for modeling are given in table 2, page 66 and table 3, page 67).

4. The effect of mineral component on plant available P (C_s)

A completely different substrate solution P (C_{li}) and buffer power (b) was found in the substrates mixed with different mineral components at the same plant available P (C_s) (Fig. 5, page 29). To investigate the mobility of P at the same C_s (16 mg [L substrate]$^{-1}$, extracted by CAT) P transport to plant was calculated by means of simulation model (NST 3.0) using the plant data given in table 2, page 66. In mineral component B, taken up P was considerably lower compared to the other mineral components,

which had lower *b* and higher C_{li} (Tab. 2). However, using the C_s of 40 which reflect about three-fold higher C_{li} and a relatively lower *b* led to the same amount of taken up P as was observed with other mineral components. This indicates that in the substrate with a high *b* value (min. component B), CAT-solution dissolves more P than that is really available for the plants compared to the other substrates with a low *b* and high C_{li}.

Table 2: The change of P uptake for poinsettia and marigold as related to different substrate solution P (C_{li}) and buffer power (b) which reflected the same CAT-soluble P (16 mg [L substrate]$^{-1}$) in the substrate with different mineral component

Substrate components	Substrate parameters		Taken up P (µmol plant^{-1})	
	C_{li} (µM)	*b*	Poinsettia	Marigold
BP+Min. component B	35	17.00	61.1	44.7
BP+Min. component B [a]	100	13.25	81.1	60.2
BP+Min. component C	150	3.55	82.8	60.5
BP+Min. component D	170	3.02	83.5	61.0
BP+Min. component F	230	2.24	84.7	62.5
BP+Min. component G	270	1.93	85.2	63.2
BP+Min. component E	470	1.11	86.4	64.7
BP+Min. component A	540	0.96	86.6	64.9
Black peat (BP)	600	0.86	86.7	65.1

[a] CAT-soluble P of 40 mg (L substrate)$^{-1}$

Consequently, an extraction procedure which could reflect more closely the C_{li} rather than *b* is recommended for a better description of P availability in the substrate, especially when a mineral component with a high P sorption capacity is used. Since CAT is already a weak extraction solution, in fact water with regard to P, it might be useful to examine the decrease of the ratio between fresh peat-substrate to CAT-solution rather than looking for the other extraction procedure. Generally, the ratio of 1: 8 is used nowadays, but the ratio of 1: 4 or 1: 2 could be potentially examined for this purpose.

SUMMARY

The mobility of nutrients in peat- substrates were investigated, since little information was available. Also, little information was available for P efficiency of ornamental crops cultivated on peat-substrates. Thus, a series of studies aimed at a) investigating the dynamics of P in peat-substrates as well as the parameters involved in P transport to plant roots, b) characterizing the uptake kinetics of P at different plant ages and fluctuating environmental conditions, c) evaluating factors contributing to P efficiency of marigold (*Tagetes patula*) and poinsettia (*Euphorbia pulcherima*) as representative ornamental plants in peat-substrate.

a) The impedance factor (f) and buffer power are the main parameters affecting effective diffusion coefficient (D_e) and thus the mobility of P in mineral soil and peat-substrate.

- Similar impedance factor (f) was observed at water holding capacity of peat-substrate and at field capacity of mineral soil
- Impedance factor increased with volumetric water content (θ), but bulk density had no effect on that
- Solution P concentration (C_{li}) at optimum P level was in magnitude higher in peat-substrate compared to mineral soil.
- Buffer power (b) was two orders of magnitude lower in peat-substrate compared to mineral soil.
- The b in peat-substrate depended on the used mineral component. It was positively correlated with oxalate-soluble Fe and Al in the substrate rather than the clay content.
- Thus, the calculated D_e for P in peat-substrate was at least 10 times higher than D_e in mineral soils.
- The higher value of D_e in the substrate indicates that P in the substrate was more available for plants than in mineral soils.

b) Due to high mobility of P in peat-substrate, the modification in root morphology and exudation of P mobilizing compounds were not expected to be significant on mobilizing and enhancement of P solubilization. However, adjustment of uptake physiology (maximum uptake rate, I_{max}; Michaelis constant, K_m; and minimum nutrient concentration, C_{min}) might be an important factor affecting P uptake in these substrates.

- A close correlation between relative growth rate (*RGR*) and I_{max} was observed with both poinsettia and marigold over all treatments.
- Marigold had higher *RGR* compared to poinsettia. *RGR* declined with plant age for both crops. Lower air temperature reduced the *RGR* of poinsettia, but not of marigold. However, the lower light intensity reduced *RGR* of marigold while it had no effect on *RGR* of poinsettia. The short photoperiod reduced *RGR* of poinsettia.
- I_{max} decreased with plant age and with decrease of air temperature for both poinsettia and marigold; however it was independent of light intensity.
- I_{max} of poinsettia was lower at short photoperiod than that at long photoperiod.
- The K_m and C_{min} was affected neither by plant age nor by air temperature, light intensity and day length.
- Marigold had clearly lower K_m and C_{min}, but higher I_{max} than poinsettia at all treatments.
- The calculated C_s to meet the demand of both crops was not much different and did not change under fluctuating environmental conditions, but it was clearly reduced with developmental stage of both crops.
- Thus, the need for C_s at early stage was higher than that at later stages for both crops, since the uptake rate of P was significantly higher at early stages compared to the later stages.

c) Marigold and poinsettia as representative ornamental crops had different P uptake rate, thus their response to different P availability in peat-substrate was evaluated.

- The optimum yield and quality of both crops were attained at P application rate of 35 mg [L substrate]$^{-1}$.
- Marigold had almost double root length density (*RLD*), root: shoot ratio and root hair length compared to that of poinsettia. Thus, marigold exhausted 43% of the substrate volume at early stage, whereas poinsettia exploited only 10% of that. However, the depletion zones around roots overlapped for both crops later during cultivation.
- Balance sheet calculations for early stage of growth indicated that below optimum fertigated P met P uptake of both crops fairly well in these treatments whereas the P level more P was supplied than was taken up by plants.
- Thus, the C_s increased to a higher level for poinsettia compared to marigold due to its lower *RLD*, which led to accumulation of more fertigated P during early stages of cultivation.
- The critical level of P in shoot dry matter of both marigold and poinsettia was the same indicating that both crops had similar utilization efficiency.
- The observed difference of root morphological parameters did not contribute significantly to P uptake efficiency, since P mobility in the peat-substrate was high.

REFERENCES

Abel, *S*., *Ticconi*, *C.A*., and *Delatorre*, *C.A*. (2002): Phosphate sensing in higher plants. *Phys*. *Plant*. 115, 1–8.

Abou El Seoud, *I.I.A*. (2008): Phosphorus efficiency of tagetes plant inoculated with two arbuscular mycorrhizal fungi strains. *Aus*. *J*. *Basic* and *App*. *Sci*. 2, 234–242.

Aboul-Nasr, *A*. (1996): Effects of vesicular-arbuscular mycorrhiza on *Tagetes erecta* and *Zinnia elegans*. *Mycorrhiza*, 6, 61–64.

Adu-Gyamfi, *J.J*., Fujita, *K*., and *Ogata*, *S*. (1989): Phosphorus absorption and utilization efficiency of pigeon pea (*Cajanus cajan* (L) Millsp.) in relation to dry matter production and dinitrogen fixation. *Plant Soil* 119, 315–324.

Akhtar, *M.S*, *Oki*, *Y*., *Adachi*, *T*., *Murata*, *Y*., and *Khan*, *H.R*. (2007): Relative phosphorus utilization efficiency, growth response, and phosphorus uptake kinetics of brassica cultivars under a phosphorus stress environment. *Comm*. *Soil Sci*. *Plant Anal*. 38, 1061–1085.

Alt, *D*., and *Peters*, *I*. (1992): Die $CaCl_2$/DTPA-Methode zur Untersuchung gärtnerischer Erden auf Mengen- und Spurenelemente. *Agribiol. Res*. 45, 204–214.

Armitage, *A.M*. (1993): Bedding plants. Prolonging shelf performance. Ball Publishing, Batavia, III.

Asher, *C.J*., and *Loneragan*, *J.F*. (1967): Response of plants to phosphate concentration in solution culture: I. Growth and phosphorus content. *Soil Sci.* 103, 225–233.

Baligar, *V.C*., and *Fageria*, *N.K*. (2006): Light intensity effects on growth and micronutrient uptake by tropical legume cover crops. *J. Plant Nut*. 29, 1959–1974.

Barber, *S.A.,* and *Cushman*, *J.H.* (1981): Nitrogen uptake model for agronomic crops. In: *Iskandar, I.K.* (Eds.): Modeling Waste Water Renovation-Land Treatment. Wiley-Interscience, New York, pp 382–409.

Barber, *S. A*. (1995): Soil Nutrient Bioavailability: A Mechanistic Approach. Wiley, New York, pp. 85–110.

Barraclough, *P.B*., and *Tinker*, *P.B*. (1981): The determination of ionic diffusion coefficients in field soils. I. Diffusion coefficients in sieved soils in relation to water content and bulk density. *J. Soil Sci*. 32, 225–236.

Barraclough, *P.B*. (1986): The growth and activity of winter wheat roots in the field: Nutrient inflows of high yielding crops. *J. Agric. Sci*. 106, 53–59.

Barraclough, *P.B*. (1989): Root growth, macro-nutrient uptake dynamics and soil fertility requirements of a high-yielding winter oilseed rape crop. *Plant Soil* 119, 59–70.

Bates, *T.R*., and *Lynch*, *J.P.* (1996): Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. *Plant Cell Environ*. 19, 529–538.

Bates, *T.R*., and *Lynch*, *J.P.* (2001): Root hairs confer a competitive advantage under low phosphorus availability. *Plant* and *Soil* 236, 243–250.

Bhadoria, *P.B.S*., *Kaselowsky*, *J*., *Claassen*, *N*., and *Jungk*, *A*. (1991a): Phosphate diffusion coefficients in soil as affected by bulk density and water content. *Z. Pflanzenernähr. Bodenkd.* 154, 53–57.

Bhadoria, *P.B.S*., *Kaselowsky*, *J*., *Claassen*, *N*., and *Jungk*, *A*. (1991b): Impedance factor for chloride diffusion in soil as affected by bulk density and water content. *Z. Pflanzenernähr. Bodenkd.* 154, 69–72.

Bhadoria, *P.B.S*., *Dessougi*, *H.E.I*., *Liebersbach*, *H*., and *Claassen*, *N*. (2004): Phosphorus uptake kinetics, size of root system and growth of maize and groundnut in solution culture*. Plant Soil* 262, 327–336.

Bhattacharyya, *P.*, and *Datta*, *S.C.* (2005): Modification of phosphate uptake model considering changing buffering capacity of soil and release threshold limit of phosphorus in soil due to rhizosphere effect. *Comm. Soil Sci. Plant Anal.* 35, 1773–1792.

Bieleski, *R.L.* (1973): Phosphate pools, phosphate transport, and phosphate availability. *Ann. Rev. Plant Phys.* 24, 225–252.

Blakemore, *L.C.*, *Searle*, *P.L.*, and *Daly*, *B.K.* (1987): Extractable iron, aluminum and silicon. In: Methods for Chemical Analysis of Soils. New Zealand Bureau Scientific Report 80, Dep. Sci. Indus. Res., Lower Hutt. pp. 71–76.

Bodson, *M.*, and *Verhoyen*, *M.N.J.* (2000): Culture techniques with special emphasis on environmental implications chemical, physical and biological means of regulating crop growth in ornamentals and other crops. *Acta Hort.* 515, 1–304.

Bohne, *H.*, and *Wrede*, *A.* (2005): Investigations of physical properties of substrates. *Eur. J. Hort. Sci.* 70, 1–6.

Bolan, *N.S.* (1991): A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant* and *Soil*, 134, 189–207.

Bolan, *N.S.*, *Naidu*, *R.*, *Mahimairaja*, *S.*, and *Baskaran*, *S.* (1994): Influence of low-molecular-weight organic acids on the solubilization of phosphates. *Biol. Fert. Soils* 18, 311–319.

Borch, *K.*, *Miller*, *C.*, *Brown, K.M.*, and *Lynch*, *J.P.* (2003): Improved drought tolerance in marigold by manipulation of root growth with buffered-phosphorus nutrition. *HortScience* 38, 212–216.

Börling, *K.*, *Ottabong*, *E.*, and *Barberis*, *E.* (2001): Phosphorus sorption in relation to soil properties in some cultivated Swedish soils. *Nutr. Cycl. Agroecosyst.* 59, 39-46.

Brady, *N.C.*, and *Weil*, *R.R*. (1999): The nature and properties of soils. Upper Saddle River, NJ: Prentice Hall. p. 881.

Brewster, *K.K., Bhat*, *S.*, and *Nye*, *P.H*. (1975): The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. II. The growth and uptake of onions in solutions of constant phosphate concentration. *Plant Soil* 42, 171–195.

Brewster, *K.K.*, *Bhat*, *S.*, and *Nye, P.H*. (1976a): The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. IV. The growth and uptake of rape in solutions of different phosphorus concentration. *Plant Soil* 44, 279–293.

Brewster, *J.L.*, *Bhat*, *S.*, and *Nye*, *P.H.* (1976b): The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. V. The growth and phosphorus uptake of rape in soil at a range of phosphorus concentrations and a comparison of the results with the predictions of a simulation model. *Plant* and *Soil* 44, 295–328.

Brückner, *U.* (1997): Physical properties of different potting media and substrate mixtures-Especially air-and water capacity. *Acta Hort*. 450, 263–270.

Chapin, *F.S.* (1980): The mineral nutrition of wild plants. *Annul. Rev. Ecol. Sys*. 11, 233–260.

Cheaib, A., *Mollier*, *A.*, *Thunot*, *S.*, *Lambrot*, *C.*, *Pellerin*, *S.*, and *Loustau*, *D*. (2005): Interactive effects of phosphorus and light availability on early growth of maritime pine seedlings. *Ann. For. Sci*. 62, 575–583.

Chi-Manzanero, *B.*, *Robert*, *M.L.*, and *Rivera-Madrid*, *R*. (2000): Extraction of total RNA from a high pigment content plant marigold (*Tagetes erecta*). *Molecular Biotechnology*. 16, 17–21.

Claassen, *N.*, and *Barber*, *S.A.* (1974): A method for characterizing the relation between nutrient concentration and flux into roots of intact plants. *Plant Phys*. 54, 564–568.

Claassen, *N.*, and *Barber*, *S.A.* (1976): Simulation model for nutrient uptake from soil by a growing plant root system. *Agron. J*. 68, 961–964.

Claassen, *N.*, and *Steingrobe*, *B.* (1999): Mechanistic simulation models for a better understanding of nutrient uptake from soil. In: *Rengel, Z.* (Eds.): Mineral Nutrition of Crops: Fundamental Mechanisms and Implications. The Haworth Press Inc., New York, pp. 327–367.

Clark, *R.B.* (1983): Plant genotype differences in the uptake, translocation, accumulation, and use of mineral elements required for plant growth. *Plant* and *Soil*, 72, 175–196.

Clarkson, *D.T*. (1985): Factors affecting mineral nutrient acquisition by plants. *Ann. Rev. Plant Phys.* 36, 77–115.

Cox, *D.*, (2001): Using phosphorus starvation to regulate growth. *Greenhouse Product News*, 11, 22–25.

Cushman, *J.H*. (1979): An analytical solution to solute transport near root surfaces for low initial concentration. I. Equation's development. *Soil Sci. Soc. Am. J*. 43, 1087–1090.

Dakora, F.D., and *Phillips*, *D.A.* (2002): Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant* and *Soil* 245, 35–47.

Dechassa, *N.*, *Schenk*, *M.K.*, *Claassen*, *N.*, and *Steingrobe*, *B.* (2003): Phosphorus efficiency of Cabbage (*Brassica oleraceae* L. var. capitata), Carrot (*Daucus carota* L.), and Potato (*Solanum tuberosum* L.). *Plant* and *Soil* 250, 215–224.

Dechassa, *N.*, and *Schenk*, *M.K.* (2004): Exudation of organic anions by roots of cabbage, carrot, and potato as influenced by environmental factors and plant age. *J. Plant Nutr. Soil Sci.* 167, 623–629.

Dennison, *W.C.*, and *Alberte*, *R.S.* (1982): Photosynthetic responses of *zostera marina* L. (Eelgrass) to in situ Manipulations of Light Intensity. *Oecologia* 55, 137–144.

Deressa, *T.G.*, and *Schenk*, *M.K*. (2008): Contribution of roots and hyphae to P uptake of mycorrhizal onion (*Allium cepa* L.): a mechanistic modeling approach. *J. Plant Nut. Soil Sci*. 171, 810–820.

Dewis, *J.*, and *Freitas*, *F.C.R*. (1970): Physical and chemical methods of soil and water analysis. Soil Bull. No 10. FAO. Rome.

Di Benedetto, A.H., and Klasman, R. (2004): The Effect of Plug Cell Volume on the Post-transplant Growth for *Impatiens walleriana* Pot Plant. *Europ. J. Hort. Sci*., 69, 82–86.

Dole, *J.M.*, and *Wilkins*, *H.F*. (1999): Floriculture: Principles and Species. Pearson, Prentice Hall, USA, pp. 304–613.

Duff, *S.M.G.*, *Sarath*, *G.*, *and Plaxton*, *W.C*. (1994): The role of acid phosphatase in plant phosphorus metabolism. *Physiol. Plant*. 90, 791–800.

Dusek, *J.*, and *Kvet*, *J*. (2006): Seasonal dynamics of dry weight, growth rate and root/shoot ratio in different aged seedlings of *Salix caprea. Biologia* 61, 441–447.

Edwards, *J.H.*, and *Barber*, *S.A*. (1976): Nitrogen flux into corn roots as influenced by shoot requirement. *Agron. J.* 68, 471–473.

Edwards, *O. W.*, and *Huffman*, *E.O*. (1959): Diffusion of aqueous solutions of phosphoric acid at 25°. *J. Phys. Chem.* 63, 1830–1833.

Eticha, *D.*, *and Schenk*, *M.K.* (2001): Phosphorus efficiency of cabbage varieties. In: *Horst*, et al. (Eds.): Plant Nutrition - Food Security and sustainability of agro-ecosystems through basic and applied research. Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 542–543.

Föhse, *D.*, and *Jungk*, *A.* (1983): Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. *Plant* and *Soil* 74, 359–368.

Föhse, *D.*, *Claassen*, *N.*, and *Jungk*, *A.* (1988): Phosphorous efficiency of plants. I. External and internal P requirement and P uptake efficiency of different plant species. *Plant* and *Soil* 110, 101–109.

Föhse, *D.*, *Claassen*, *N.*, and *Jungk*, *A.* (1991): Phosphorous efficiency of plants. II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species. *Plant* and *Soil* 132, 261–272.

Fried, *M.*, and *Shapiro*, *R.E*. (1961): Soil-plant relationships in ion uptake*. Ann. Rev*. *Plant*. *Phys*. 12, 91–112.

Gahoonia, *T.S.*, and *Nielsen*, *N.E.* (1996): Variation in acquisition of soil phosphorus among wheat and barley genotypes. *Plant* and *Soil* 178, 223–230.

Gahoonia, *T.S.*, and *Nielsen*, *N.E.* (1997): Variation in root hairs of barley cultivars doubled soil phosphorus uptake. *Euphytica* 98, 177–182.

Gaume, *A., Mächler*, *F.*, *De Leon*, *C.*, *Narro*, *L.*, and *Frossard*, *E*. (2001): Low-P tolerance by maize (*Zea mays* L.) genotypes: Significance of root growth, and organic acids and acid phosphatase root exudation. *Plant Soil* 228, 253–264.

Gericke, *V.S.*, and *Kurmies*, *B.* (1952): Die Kolorimetrische Phosphors-äurebestimmung mit Ammonium-Vanadat-Molybdat und ihre Anwendung in der Pflanzenanalyse. *Z. Pflanzenernähr. Bodenk.* 59, 235–245.

Gilbert, *G.A.*, *Knight*, *J.D.*, *Allan*, *D.L.*, and *Vance*, *C.P.* (1999): Acid phosphatase activity in phosphorus-deficient white lupin roots. *Plant Cell Environ*. 22, 801–810.

Grandcourt, *A.D.*, *Epron*, *D.*, *Montpied*, *P.*, *Louisanna*, *E.*, *Bereau*, *M.*, *Garbaye*, *J.*, *and Guehl*, *J.M*. (2004): Contrasting responses to mycorrhizal inoculation and phosphorus

availability in seedlings of two tropical rainforest tree species. *New Phytologist* 161, 865–875.

Hallmark, *W.B.*, and *Huffaker*, *R.C.* (1978): The influence of ambient nitrate, temperature, and light on nitrate assimilation in sudangrass seedlings. Phys. *Plant* 44, 147–152.

Handreck, *K.A.* (1997): Phosphorus requirements of Australian native plants. *Aus. J. Soil Res.* 35, 241–289.

Hansen, *C.W.*, *and Nielsen*, *K.L.* (2001): Reduced phosphorus availability as a method to reduce chemical growth regulation and to improve plant quality. In: *Horst* et al. (Eds.): Plant Nutrition - Food Security and sustainability of agro-ecosystems through basic and applied research. Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 314–315.

Hees, *A.F.M.*, and *Clerkx*, *A.P.P.M.* (2003): Shading and root-shoot relations in saplings of silver birch, pedunculate oak and beech. *Fore. Ecol. Man.* 176, 439–448.

Heins, *B.*, *and Schenk*, *M.* (1987): Root growth and nitrate uptake of vegetable crops. *J. Plant Nut.* 10, 9–16.

Hendriks, *L.*, *Claassen*, *N.*, and *Jungk*, *A.* (1981): Phosphatverarmung des wurzelnahen Bodens und Phosphataufnahme von Mais und Raps. *Z. Pflanzenernähr. Bodenk.* 144, 486–499.

Hinsinger, H. (2001): Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant* and *Soil* 237, 173–195.

Hodges, *M.*, *and Barber*, *J.* (1983): Photosynthetic adaptation of pea plants grown at different light intensities: State 1 - State 2 transitions and associated chlorophyll fluorescence changes. *Planta* 157, 166–173.

Hofer, *R.M.* (1996): Root hairs. In: *Waisel* et al. (Eds.): Plant Roots - The Hidden Half. Marcel Dekker Inc., New York, pp. 111–126.

Hoffland, *E.*, *Findenegg*, *G.R.*, *Nelemans*, *J.A*. (1989): Solubilization of rock phosphate by rape. *Plant Soil* 113, 155–160.

Hoffmann, *C.*, and *Jungk*, *A.* (1995): Growth and phosphorus supply of sugar beet as affected by soil compaction and water tension. *Plant* and *Soil* 176, 15–25.

Holford, *I.C.R*. (1997): Soil phosphorus: its measurement and its uptake by plants. *Aust. J. Soil Res*. 35, 227–239.

Hunt, *R*. (1982): Plant Growth Curves: The Functional Approach to Plant Analysis. Edward Arnold Ltd, London.

Itoh, *S*., *and Barber*, *S.A*. (1983): Phosphorus uptake by six plant species as related to root hairs. *Agron*. *J*. 75, 457–461.

Jabro, *J.D*., *Evans*, *R.G*., *Kim*, *Y*., and *Iversen*, *W.M*. (2008): Estimating in situ soil–water retention and field water capacity in two contrasting soil textures. *Irrig*. *Sci*. DOI 10.1007/s00271-008-0137-9

Jungk, *A*., and *Claassen*, *N.* (1989): Availability in soil and acquisition by plants as the basis for phosphorus and potassium supply to plants. *Z*. *Pflanzenernähr*. *Bodenk*. 152,151–l57.

Jungk, *A*., and *Claassen*, *N.* (1997): Ion diffusion in the soil-root system. *Adv. Agron.* 61, 53–110.

Jungk, *A*., *Asher*, *C.J*., *Edwards*, *D.G*., and *Meyer*, *D*. (1990): Influence of phosphate status on phosphate uptake kinetics of maize (*Zea mays*) and soybean (*Glycine max*). *Plant Soil* 124, 175–182.

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2008): Phosphorus dynamics in peat-based substrates. *J. Plant Nut. Soil Sci*. 171, 804–809.

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2009): Phosphorus efficiency of ornamental plants in peat-substrates. *J. Plant Nut. Soil Sci*. "DOI: 10.1002/jpln.200700360".

Kochian, *L.V*., *Hoekenga*, *O.A*., and *Pineros*, *M.A*. (2004): How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorus efficiency. *Ann. Rev. Plant Biol*. 55, 459–493.

Kuhlmann, *H*., and *Barraclough*, *P.B*. (1987): Comparison between the seminal and nodal root systems of winter wheat in their activity for N and K uptake. *Z*. *Pflanzenernaehr*. *Bodenkd.* 150, 24–30.

Lambers, *H*., and *Poorter*, *H*. (1992): Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23, 187–261.

Lambers, *H*., *Juniper*, *D*., *Cawthray*, *G.R*., *Veneklaas*, *E.J*., and *Martinez-Ferri*, *E*. (2002): The pattern of carboxylate exudation in *Banksia grandis* (*Proteaceae*) is affected by the form of phosphate added to the soil. *Plant* and *Soil* 238, 111–122.

Lima, *J.M*., *Anderson*, *S.J*., and *Curi*, *N*. (2000): Phosphate-Induced clay dispersion as related to aggregate size and composition in hapludoxs. *Soil Sci. Soc. Am. J*. 64, 892–897.

Linquist, *B.A*., *Singleton*, *P.W*, *Yost*, *R.S*., and *Cassman*, *K.G*. (1997): Aggregate size effects on the sorption and release of phosphate in an ultisol. *Soil Sci. Soc. Am. J*. 61, 160–166.

Loneragan, *J.F*., and *Asher*, *C.J.* (1967): Response of plants to phosphate concentration in solution culture. II. Rate of phosphate absorption and its relation to growth. *Soil Sci.* 103, 311–317.

Lynch, *J.P*., and *Brown*, *K.M.* (2001): Topsoil foraging – an architectural adaptation of plants to low phosphorus availability. *Plant* and *Soil* 237, 225–237.

Lynch, *J.*, *Lauchli*, *A.*, and *Epstein*, *E.* (1991): Vegetative growth of the common bean in response to P nutrition. *Crop Sci.* 31, 380–387.

Marschner, *H.* (1995): Mineral Nutrition of Higher Plants. Academic Press, London. pp. 411–446.

Murphy, *J.*, and *Riley*, *J. P.* (1962): A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 27, 31–36.

Naasz, *R.*, *Michel*, *J.C.*, and *Charpentier, S.* (2005): Measuring hysteretic hydraulic properties of peat and pine bark using a transient method. *Soil Sci. Soc. Am. J.* 69, 13–22.

Nayakekorala, *H.*, and *Taylor*, *H.M.* (1990): Phosphorus uptake rates of cotton roots at different growth stages from different soil layers. *Plant Soil* 122, 105–110.

Neumann, *G.*, and *Martinoia*, *E.* (2002): Cluster roots-an underground adaptation for survival in extreme environments. *Trends in Plant Science* 7, 162–167.

Neumann, *G.*, and *Römheld*, *V.* (1999): Root excretion of carboxylic acids and protons in phosphorus-deficient plants. *Plant Soil* 211, 121–130.

Nichols, *D.G.*, and *Beardsell*, *D.V.* (1981): Interactions of calcium, nitrogen and potassium with phosphorus on the symptoms of toxicity in *Grevillea* cv. 'Poorinda Firebiro'. *Plant* and *Soil* 61, 437–445.

Nielsen, *N.E.*, and *Barber*, *S.A.* (1978): Differences among genotypes of corn in the kinetics of P uptake. *Agron. J.* 70, 695–699.

Nielsen, *K.L.*, *Eshel*, *A.*, and *Lynch*, *J.P.* (2001): The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. *J. Exp. Bot.* 52, 329–339.

Nye, *P.H.*, and *Marriott*, *F.C.H.* (1969): A theoretical study of the distribution of substances around roots resulting from simultaneous diffusion and mass flow. *Plant Soil* 30, 459–472.

Nye, *P.H.*, and *Spiers*, *J.A.* (1964): Simultaneous diffusion and mass flow to plant roots. *Trans. Int. Cong. Soil Sci. 8th*. Rompresfilatelia, Bucharest, Hungary. pp 535–541.

Nye, *P.H.*, and *Tinker*, *P.B.* (1977): Solute movement in the soil-root system. Studies in Ecology. Blackwell Scientific Publications, Oxford. p. 342.

Nye, *P.H.* (1966): The measurement and mechanism of ion diffusion in soils. 1. The relation between self diffusion and bulk diffusion. *J. Soil Sci.* 17, 16–23.

Nye, *P.H.* (1977): The rate limiting step in plant-nutrient absorption from soil. *Soil Sci.* 123, 292–297.

Nye, *P.H.* (1979): Diffusion of ions and uncharged solutes in soils clays. *Adv. Agron.* 31, 225–273.

Parks, *S.E.*, *Haigh*, *A.M.*, and *Creswell*, *G.C.* (2000): Stem tissue phosphorus as an index of the phosphorus status of *Banksia ericifolia* L. *Plant* and *Soil* 227, 59–65.

Parsons, *R.* (1959): Handbook of Electrochemical Constants. Academic Press Inc., New York. p. 79.

Pfeffer, *P.*, *Doubs*, *J.D.*, *Becard*, *G.*, *Shachar-Hill*, *Y.* (1999): Carbon uptake and metabolism and transport of lipids in an arbuscular mycorrhiza. *Plant Physiology* 120, 587–598.

Pramuk, *L.A.*, and *Runkle*, *E.* (2003): Temperature and Light on Bedding Plants. *Greenhouse Product News* 3, 32–41.

Raghothama, *K.G.* (1999): Phosphate acquisition. *Annul. Rev. Plant Phys. Plant Mol. Biol.* 50, 665–693.

Rausch, *C*, and *Bucher*, *M*. (2002): Molecular mechanisms of phosphate transport in plants. *Planta* 216, 23–37.

Reid, *C.P.P.*, and *Bowen*, *G.D.* (1979): Effects of soil moisture on V/A mycorrhiza formation and root development in Medicago. In: *Harley*, *J.L.*, and *Scott-Russell*, *R*. (Eds.): The soil-root-interface., Academic Press, London, pp. 211–219.

Röber, *R.*, and *Schacht*, *H*. (2008): Pflanzenernährung im Gartenbau. Eugen, Ulmer, KG, Sttutgart, pp.93.

Rodgers, *C.O.*, and *Barnneix*, *A.J*. (1988): Cultivar differences in the rate of nitrate uptake by intact wheat plants as related to growth rate. *Phys. Plant* 72, 121–126.

Ryan, *P.R.*, and *Delhaize*, *E*. (2001): Function and mechanism of organic anion exudation from plant roots. *Annul. Rev. Plant Phys. Plant Mol. Biol*. 52, 527–560.

Salama, *A.M.S.*, and *Wareing*, *P.F*. (1979): Effects of mineral nutrition on endogenous cytokinins in plants of sunflower (*Helianthus annuus* L.). *J. Exp. Botany*. 30, 971–981.

Sanchez, *A.C*. (2007): Phosphorus. In: *Barker*, *A.V.*, and *Pilbeam*, *D.J*. (Eds.): Plant Nutrition, CRC Press, Taylor and Francis Group, Boca Raton, pp. 51–90.

SAS, Institute Inc. (1996): SAS/STAT Software. Cary, NC, USA.

Schenk, *M.K.*, and *Barber*, *S.A*. (1979): Phosphate uptake by corn as affected by soil characteristics and root morphology. *Soil Sci. Soc. Am. J*. 43, 880–883.

Schenk, *M.K.*, and *Barber*, *S.A*. (1980): Potassium and phosphorus uptake by corn genotypes grown in the field as influenced by root characteristics. *Plant Soil* 54, 65–76.

Schmidt, *J.S.*, *Harper*, *J.E.*, *Hoffman*, *T.K.*, and *Bent*, *A.F.* (1999): Regulation of soybean nodulation independent of ethylene signaling. *Plant Physiol*. 119, 951–959.

Shane, *M.W.*, and *Lambers*, *H.* (2005): Cluster roots: A curiosity in context. *Plant* and *Soil* 274, 101–125.

Shane, *M.W.*, *Margaret*, *E.M.*, and *Lambers*, *H.* (2004): Tissue and cellular phosphorus storage during development of phosphorus toxicity in *Hakea prostrate* (*Proteaceae*). *J. Exp. Botany* 55, 1033–1044.

Sharifi, *M.*, and *Zebarth*, *B.J.* (2006): Nitrate influx kinetic parameters of five potato cultivars during vegetative growth. *Plant Soil* 288, 91–99.

Shinano, *T.*, *Nanamori*, *M.*, *Dohi*, *M.*, *Wasaki*, *J.*, and *Osaki*, *M.* (2005): Evaluation of phosphorus starvation inducible genes relating to efficient phosphorus utilization in rice. *Plant* and *Soil* 269, 81–87.

Singh, *S.*, *Bhadoria*, *P.B.S.*, and *Rakshit*, *A.* (2003): Simulation of phosphorus uptake by peanut in low phosphorus supplying soil. *Ital. J. Agro.* 7, 65–71.

Smethurst, *P.J.*, *Comerford*, *N.B.* and *Neary*, *D.G.* (1993): Predicting the effects of weeds on K and P uptake by young slash pine on a Spodosol. *For. Ecol. Manage.* 60, 27–39.

So, *H.B.*, and *Nye*, *P.H.* (1989): The effect of bulk density, water content and soil type on the diffusion of chloride in soil. *J. Soil Sci.* 40, 743–749.

Steingrobe, *B.*, and *Schenk*, *M.K.* (1994): A model relating the maximum nitrate inflow of lettuce to the growth of roots and shoots. *Plant Soil* 162, 249–257.

Syring, *K.M.*, and *Claassen*, *N.* (1995): Estimation of the influx and the radius of the depletion zone developing around a root during nutrient uptake. *Plant Soil* 175, 115–123.

Tennant, *D.* (1975): A test of a modified line intersect method of estimating root length. *J. Ecol.* 63, 995–1001.

Tsuksmoto, *Y.*, *Imanishi*, *H.*, and *Yahara*, *H.* (1971): Studies on the flowering of marigold: II. Interactions among day-length, temperature, light intensity and plant regulators. *J. Japan. Soc. Hort. Sci.* 40, 65–69.

Ulrich, *A.* (1952): Physiological bases for assessing the nutritional requirements of plants. *Annul. Rev. Plant Phys*. 3, 207–228.

VDLUFA (1991): Bestimmung der Rohdichte (Volumengewicht) von gärtnerischen Erden und Substraten ohne sperrige Komponenten. VDLUFA Methodenbuch, Band I. Die Untersuchung von Böden. 4. Auflage, VDLUFA Verlag, Darmstadt.

Verhagen, *J.B.G.M.* (2004): Effectiveness of clay in peat based growing media. *Acta Hort*. 644, 115–118.

Videa (2002): Deceptive Beauty (A Look at the Global Flower Industry). *Global citizens for global era* 1, 1–16.

Vierheilig, *H.*, *Coughlan*, *A.P.*, *Wyss*, *U.*, and *Piche*, *Y.* (1998): Ink and vinegar, a simple staining technique for Arbuscular-Mycorrhizal fungi. *Applied* and *Environ*. *Microbiol*. 64, 5004–5007.

Vogelezang, *J.V.M.* (2000): Improvement of plant quality by integrated control of light, temperature and DIF-Strategy. *Acta Hort*. 515, 83–90.

Wang, *N.*, *Barrett*, *J.E.*, *Bartuska*, *C.*, *Nell*, *T.A.*, *Schoellhorn*, *R.K.*, and *Hamilton*, *P.E.* (2003): effects of low light levels during the dark period on flower development in *Euphorbia pulcherrima*. *Acta Hort*. 624, 185–190.

Warncke, *D.D.*, and *Barber*, *S.A.* (1972a): Diffusion of zinc in soil: I. The influence of soil moisture. *Soil Sci. Soc. Am. Proc.* 36, 39–42.

Warncke, *D.D.*, and *Barber*, *S.A.* (1972b): Diffusion of zinc in soil: II. The influence of soil bulk density and its interaction with soil moisture. *Soil Sci. Soc. Am. Proc.* 36, 42–46.

Whiteaker, *G.*, *Gerloff*, *G.C.*, *Gabelman*, *W.H.*, and *Lindgren*, D. (1976): Interaspecific differences in growth of beans at stress levels of phosphorus. *J. Amer. Soc. Hort. Sci.* 101, 472–475.

Wieland, *C.E.*, *Barrett*, *J.E.*, *Nell*, *T.A.* and *Clark*, *D.G.* (2000): Floral initiation in *Euphorbia pulcherima* at high temperatures. *Acta Hort.* 515, 213–218.

Zhang, *H.*, *Schroder*, *J.L.*, *Fuhrman*, *J.K.*, *Basta*, *N.T.*, *Storm*, *D.E.*, and *Payton*, *M.E.* (2005): Path and multiple regression analyses of phosphorus sorption capacity. *Soil Sci. Soc. Am. J.* 69, 96–106.

ACKNOWLEDGEMENTS

Firstly, I would like to express my great deal of gratitude to my supervisor Prof. Dr. Manfred K. Schenk whose critical advice, stimulating suggestions and encouragement throughout my study made me to successfully complete my PhD work.

I want to thank Dr. Bernd Steingrobe from institute of agricultural chemistry, University of Goettingen for his kindness to be my co-supervisor, Prof. Dr. Heike Bohne from institute of Floriculture and Tree Sciences, Leibniz University of Hannover, and Prof. Dr. Besslar from Geschäftsbereich Gartenbau for their willingness to be my external examiners.

I highly acknowledge the General Office of Scholarship and Overseas students (MSRT, IRAN) for granting me the funding for this PhD work.

I express my deepest thanks to Mss. Anne Herwig, Mrs. Iris Wienkemeir, Mrs. Birgit Stedeler, Mr. Andre Specht and Dr. Dejene Eticha for their technical assistance, Frau Ingrid Dusy for her administrative support, and of course Tesfaye Balemi, Tesfaye Gashaw, Mr. Kefyalew Negisho, Dr. Katja Bogdan, Dr. Hendrik Führs, Mr. Benjamin Klug, Mss. Melanie Bremer for their friendly support in several occasions.

I would also like to be grateful to Mr. Herbert Geyer, Mr. Alexsander Klein and Mss. Gerlinde Geisler for their help and assistance during plant production in the greenhouse.

Finally, I would like to express my especial thank to my mother, sisters, brothers, my wife and my children whose love and patience enabled me to complete my study. I also pray that my God rest the soul of my lovely father in peace, since I wouldn't have reached to the current success of my educational career without his endeavor.

CURRICULUM VITAE

Personal Data

Full Name:	Azizollah Khandan-Mirkohi
Marital status:	Married
Date and place of birth:	30 April 1973, Sarab, Iran

Tertiary Education

01/2005-Present	Ph.D. student in Horticulture, Hannover University, Germany
09/1999-11/2001	M.Sc. in Horticulture Tehran University, Iran
02/1996-02/1998	B.Sc. in Plant Products Engineering (Horticulture) Tehran University, Iran
09/1993-02/1996	A.Sc. in Plant Products Technology (Horticulture) Tabriz University, Iran

High Education

09/1987-06/1991	Emam Khomeini High School, Sarab, Iran

Secondary Education

09/1984-06/1987	Shirajin village Secondary school, Sarab, Iran

Elementary Education

09/1979-06/1984	Mirakooh-Haji village Elementary school, Sarab, Iran

Career after Graduation

06/2002-01/2005	Executer expert Bureau of flower and ornamental plants, Deputy of Horticulture Ministry of Jehad-Agriculture, Tehran, Iran

Scientific Publications

Khandan, *A*., *Babalar*, *M*., *Naderi*, *R*., and *Asgari*, *M.A*. (2007): The influence of different ratios of NH_4 and NO_3 on cut flower production of roses (*Rosa hybrida* cv. 'Varlon'). *Iranian J. Hort. Sci*. Tech. 8, 139–148.

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2008): Phosphorus dynamics in peat-based substrates. *J. Plant Nut. Soil Sci*. 171, 804–809.

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2009): Phosphorus efficiency of ornamental plants in peat-substrates. *J. Plant Nut. Soil Sci*. "DOI: 10.1002/jpln.200700360"

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*. (2009): Characteristics of phosphorus uptake kinetics of ornamental plants. *Scientia Horticulturae* (submitted)

Conference reports

Khandan, *A*., *Babalar*, *M*., and *Naderi*, *R*.: Effect of different nutrient solutions on the quantitative and qualitative yield of cut flower in rose plants (*Rosa hybrida* cv. 'Varlon'). A scientific poster presented at *the 26th International Horticultural Congress* held from 11–17 August, 2002, Toronto, Canada.

Khandan, *A*., *Babalar*, *M*., and *Naderi*, *R*.: The effect of different source and ratios of nitrogen on production of rose cut flower in hydroponic system. A scientific report presented at *the 3rd Iranian national symposium on application of bio-material and proper use of fertilizers and pesticides in agriculture* held from 18–20 February, 2004, Karaj, Iran.

Khandan-Mirkohi, *A*., and *Schenk*, *M.K*.: Phosphorus efficiency of ornamental plants. A scientific poster presented at *the 1st international conference 'Plant Nutrition meets plant Breeding'* held from 26–28 September, 2006, Uni. Hohenheim, Stuttgart, Germany.