Effects of Phosphorus on Shoot and Root Growth, Partitioning, and Phosphorus Utilization Efficiency in *Lantana*

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Abstract. This study was undertaken to critically analyze the effects of reduced phosphorus (P) on shoot and root growth, partitioning, and phosphorus utilization efficiency (PUE) in *Lantana* (*Lantana camara* ‘New Gold’). Plants were grown in a 1:1 mixture of perlite and vermiculite with complete nutrient solutions containing a range of P concentrations considered to be deficient (1 mg·L⁻¹), low (3 and 5 mg·L⁻¹), adequate (10 mg·L⁻¹), and high (20 and 30 mg·L⁻¹). Higher P supply had most dramatic effect on increasing the number of leaves and leaf surface area, subsequently leading to a disproportionate increase in shoot biomass than root biomass. Increasing P from 1 to 30 mg·L⁻¹ linearly ($P < 0.0001$) increased shoot dry weight (DW) during vegetative growth, and logarithmically ($P < 0.0001$) during reproductive growth. Regardless of plant growth stage, biomass of roots and flowers (inflorescences) logarithmically increased ($P < 0.0001$) with increasing P concentrations. Plants grown with lower P allocated more biomass to roots than shoots, resulting in a higher root-to-shoot ratio. Increasing P concentration to 20 mg·L⁻¹ increased the accumulation of P in all plant parts, but predominantly in shoots, whereas further increasing the concentration increased the accumulation primarily in roots and flowers. Higher P accumulation in plant tissues did not strongly contribute to the biomass production. Phosphorus utilization efficiency was higher with lower P supply in all plant tissues. P-deficient roots had the highest PUE and specific root length (SRL), and retained higher proportion of P compared with nondeficient roots. Our results indicate that P concentration at 20 mg·L⁻¹ is sufficient to maintain optimal vegetative growth while reproductive growth does not require P concentrations over 10 mg·L⁻¹ as it stimulates greater level of P accumulation in plant parts with little or no effect on growth and flowering, and biomass accumulation in *lantana*.

Phosphorus is an essential nutrient for plant growth and reproduction. Intensive use of P fertilizers for crop production has led to

eutrophication and deterioration of water quality, causing serious environmental concerns. P used in fertilizers is obtained from global phosphate rock reserves, and is a non-renewable resource that could be depleted in 50–100 years (Marschner, 2012), and therefore, increasing the efficiency with which these reserves are used to produce crops is vital to maintain or increase crop productivity in current crop production systems (Cordell et al., 2009).

The major environmental impacts caused by horticulture operations include runoff that carries pollutants including P, which can be driven by overfertilization of P, excessive irrigation, or the use of soilless potting media with less ability to retain P than mineral soils (Whitcher et al., 2005; Yeager and Wright, 1982). Particularly, overfertilization of P has been a long-standing problem causing economic losses to farmers and negatively impacting environments. Conversely, insufficient P can lead to a loss of crop productivity and yield, and therefore, it is critical to

precisely determine the P requirements of crops to ensure crop production and meet the growing environmental challenges.

A large number of studies have shown that early season P supply is critical for optimum crop yield of many field-grown crops (Grant et al., 2001), which might have led to the practice of providing P starter fertilizers for greenhouse and nursery crop production, and this practice is still common. Superphosphate is routinely incorporated into potting media followed by regular fertilization with either liquid fertilizer or controlled-release fertilizer containing P (Wright and Niemiera, 1987). Excessive concentrations of P have been applied for crop production during this practice, exaggerating the risk of P runoff to the environment. Little is known about optimum P rates for most greenhouse and nursery crop production (Bailey and Nelson, 2004; Warncke and Krauskopf, 1983), and therefore, P fertilizer has been applied far in excess of what is required to achieve high crop productivity. For example, in conventional horticultural production systems, plants are often grown with P concentrations ranging from 90 to 150 mg·L⁻¹ to compensate for the lack of buffering capacity of soilless media (Bjerregård and Hansen, 1983; Williams and Nelson, 1996). Current application rates of P largely depend on nitrogen fertilizer recommendations. Due to a general perception that P stimulates root growth and helps the transplants to obtain a quick establishment, the application of fertilizers with low N:P ratios is still common (Broschat and Klock-Moore, 2000; Hansen and Lynch, 1998; Williams and Nelson, 1996). Alternatively, the fertilizers with a ratio of 2:1:2 are often recommended for commercial greenhouse crops (Nelson, 1996; Whitcher et al., 2005).

A few studies have been conducted to determine an optimum P concentration for container crop production (Wright and Niemiera, 1987). P applications of ≈ 10 mg·L⁻¹ in the irrigation water have resulted in maximum growth of *Ilex crenata* (Yeager and Wright, 1982) and *Chamaecyparis lawsoniana* (Van der Boon, 1981), which was also true for the rooted cuttings of *Rhododendron* and *Cotoneaster adpressus praecox* (Havis and Baker, 1985). Meanwhile, maximum growth was achieved in *Vinca* and new guinea impatiens grown at P concentration around 20 mg·L⁻¹ (Whitcher et al., 2005). Plant growth, biomass accumulation, and P dynamics can be affected during the transition from vegetative to reproductive growth as demonstrated in chrysanthemum (Hansen and Lynch, 1998). Therefore, plant growth stage should be considered when determining P requirement of a crop. Many additional factors can affect P requirement of the crop including growing media, and irrigation method and frequency (Majsztrik et al., 2011); however, it is important to define a baseline P concentration required for an optimum plant growth and the implications of such a baseline without interference with other factors.

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The effects of P on root growth and root-to-shoot ratio present conflicting results among the studies on container crops. According to Harris (1992), authors of several publications state or imply that P fertilizations primarily stimulate root growth, while other studies reported that increasing P supply increased root growth but decreased root-to-shoot ratio (Hansen and Lynch, 1998; Kim et al., 2008; Lynch et al., 1991), or it had no effect on root growth or root-to-shoot ratio (Broschat and Klock-Moore, 2000; Dufault and Schultheis, 1994; Ristvey et al., 2007). Little is known about the P accumulation patterns and PUE in container crops, and there are only a few reports on the effects of P fertilization on partitioning in relation to their productivity. Such information is critical as it will help design more efficient management strategies for P fertilizer by better aligning the P requirements of crops and the application amount and timing of the nutrient. An understanding of such relationships is important to determine sustainable management practices for P fertilization. The objective of this experiment was to critically analyze the effects of P on shoot and root growth, P partitioning, and PUE in lantana (*L. camara* 'New Gold'). Our results will aid in refining the effects of P on plant growth and flowering in ornamental crops, and establishing the best P management practices.

Materials and Methods

Plant growth and culture methods. Rooted cuttings of *L. camara* 'New Gold' were obtained from Leilani Nursery in Waimanalo, HI, and uniform cuttings were chosen and transplanted into 15-cm-diameter pots filled with 1:1 (v/v) perlite and vermiculite. The plants were grown at Magoon Greenhouse Facility, University of Hawaii at Manoa, without supplemental irradiance. Day and night temperatures in the greenhouse during the experimental periods averaged 24.4 ± 2.4 °C and 20.9 ± 0.5 °C and 28 ± 4 °C and 23 ± 2 °C, respectively. Relative humidity was $55\% \pm 5$ and $64\% \pm 5$ (day/night). Photosynthetically active radiation varied throughout the day with a maximum of $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants were completely randomized for two harvest times. Each harvest consisted of six plants. The first six plants were randomly chosen and harvested after 3 weeks and the remaining six after 7 weeks. The experiment was conducted twice.

P treatment. Plants were fertigated at each irrigation with half-strength modified Hoagland's nutrient solution (Epstein and Bloom, 2005; Hoagland and Arnon, 1950) containing $2500 \mu\text{M}$ KNO_3 , $2500 \mu\text{M}$ $\text{Ca}(\text{NO}_3)_2\cdot 4\text{H}_2\text{O}$, $250 \mu\text{M}$ K_2SO_4 , $1000 \mu\text{M}$ $\text{MgSO}_4\cdot 7\text{H}_2\text{O}$, $80 \mu\text{M}$ Fe-EDTA, $4.5 \mu\text{M}$ $\text{MnCl}_2\cdot 4\text{H}_2\text{O}$, $0.3 \mu\text{M}$ $\text{ZnSO}_4\cdot 7\text{H}_2\text{O}$, $0.16 \mu\text{M}$ $\text{CuSO}_4\cdot 5\text{H}_2\text{O}$, $0.16 \mu\text{M}$ $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}\cdot 4\text{H}_2\text{O}$, and $20 \mu\text{M}$ H_3BO_3 , which was adjusted to provide a nitrogen concentration of 7.5 mM ($105 \text{ mg}\cdot\text{L}^{-1}$). An aqueous solution of $500 \mu\text{M}$ KH_2PO_4 was applied to provide P at the rate of 35, 100,

200, 335, 665, or $1000 \mu\text{M}$ (1, 3, 6, 10, 20, or $30 \text{ mg}\cdot\text{L}^{-1}$) as final concentration. These concentrations were considered to be deficient ($1 \text{ mg}\cdot\text{L}^{-1}$), low (3 and $5 \text{ mg}\cdot\text{L}^{-1}$), sufficient ($10 \text{ mg}\cdot\text{L}^{-1}$), and high (20 and $30 \text{ mg}\cdot\text{L}^{-1}$), respectively. Fertigation was done every other day during the first 3 weeks, and every day for the rest of the weeks as plants grew bigger. The nutrient solution was adjusted to the pH 5.9 to 6.1 before fertigation.

Data collections. Plants grown were harvested at 3 and 7 weeks after transplanting. Plant height, branch number (longer than 5 cm), and leaf number (longer than 3 cm) were recorded weekly. Plant width was calculated as an average of values from two perpendicular measurements. The number of flowers (inflorescences) was counted by the number of open flowers twice every week from 4 weeks after transplanting when plants started to bloom. Flower diameter was calculated as an average of values from two perpendicular measurements. At the time of harvest, plant height, width, branch number, leaf number, and flower number were recorded again. Individual leaves longer than 1 cm were destructively harvested to measure leaf area with Epson Expression 10000XL (Epson America, Inc., Long Beach, CA) scanner, and leaf area was analyzed using the WinRHIZO Pro software (Regent Instrument Inc. Quebec City, QC, Canada). Fresh weight of open flowers was measured and the number of individual florets was counted.

Measurements of plant DW and plant P content. Shoots (leaves and stems), roots, and flowers were separated to dry in an oven set at 105 °C for 30 min, and then kept at 75 °C until the samples were completely dry. The biomass was measured as DW. All plant materials were ground to a particle size of 10 mesh with a Wiley mill (Thomas Scientific, Philadelphia, PA) and $\approx 0.07 \text{ g}$ samples for each treatment were used for acid digestion, and P content of shoots, roots, and flowers was determined using the P-molybdate blue color reaction (Murphy and Riley, 1962). The total P content was calculated as the sum of the content of all tissue components.

P utilization efficiency. P utilization efficiency was defined as the total biomass produced per unit P accumulated in tissue (g tissue DW/mg P) based on the definition by Rose and Wissuwa (2012). The PUE of the shoots, roots, and flowers was calculated as the DW of the tissue divided by the total P content in the tissue. Similarly, the PUE of the whole plant was determined as the sum of DWs of all plant parts divided by the total P content in plant tissues (g DW/mg P).

Root parameter analysis. Roots were carefully harvested and rinsed before being scanned using the Epson Expression 10000XL scanner. A representative root subsample was collected when the root system was too large to be scanned for the analysis of total root length. Root length, root average diameter, volume, and surface area were estimated using WinRHIZO Pro software. The total root length was estimated by multiplying the subsample length by the DW ratio of the scanned

subsample and the total DW of the roots. Specific root length [root length per unit root dry mass ($\text{m}\cdot\text{g}^{-1}$)] was calculated by dividing the total root length by the root DW.

Allometric analysis. Shoot and root dry matter of plants harvested at 3 or 7 weeks after transplanting were used to analyze the allometric relationship of roots and shoots. The allometric relationship of the log scale DW values was fitted by linear regression and the allometric coefficient (K) was obtained from the slope of the linear regression line (Hunt, 1990).

Statistical analysis. Plants were arranged in a completely randomized block design with six replicates. Data were analyzed with analysis of variance general linear model using Minitab (Minitab Inc., State College, PA). When the data were not normally distributed, the data were transformed with Box-Cox transformation, allowing data to be normally distributed. Pairwise comparisons between treatments were conducted using Tukey's honestly significant difference test when P concentration had significant effects. The whole experiment was repeated twice. Block effect was not included in the data output since we observed consistent results from the two experiments. Therefore, the data were pooled and P effects were tested at $P < 0.05$. Best-fitting lines were determined by linear or nonlinear regression analysis using SigmaPlot 12.5 (Systat Software, Inc., Chicago, IL).

Results

Plant growth responses to P availability. Lower P significantly decreased overall plant growth in lantana (Fig. 1). P-deficient plants produced considerably fewer number of leaves and branches from the first week after transplanting and remained lower throughout the growth period. The growth differences among different P treatment become greater over time. Despite the semitrailing growth habit of lantana, P availability had significant effect on plant height, which was reduced by more than 35% in P-deficient plants compared with high P plants.

The first flower opened in the 4th week after transplanting regardless of P concentrations, and the number of flowers rapidly increased from the following week (Fig. 1). Increasing P from 1 to $30 \text{ mg}\cdot\text{L}^{-1}$ increased the number of flowers about five times; however, there were no differences when P concentrations were higher than $10 \text{ mg}\cdot\text{L}^{-1}$ (Table 2).

Leaf characteristics, such as total leaf area and leaf number, were the parameters most affected by P availability (Tables 1 and 2). It was exponentially reduced by lower P, especially at the concentrations lower than $10 \text{ mg}\cdot\text{L}^{-1}$. When P concentration was reduced from 30 to $10 \text{ mg}\cdot\text{L}^{-1}$, leaf area decreased by 35% and 32% at 3 and 7 weeks, respectively. With the further reduction to $1 \text{ mg}\cdot\text{L}^{-1}$, leaf area decreased by more than 55% and 70% at 3 and 7 weeks, respectively (Tables 1 and 2).

Fig. 1. Effects of P supply on plant growth of lantana. Plants were grown for 7 weeks with P concentrations at 1, 3, 5, 10, 20, or 30 mg·L⁻¹. (A) Pictures showing differential growth of lantana at 3 weeks and at 7 weeks after transplanting. (B) Changes in vegetative and reproductive parameters over the course of production. Data shown are means of at least six plants.

The total root length, root surface area, and root volume decreased by reduced P at both harvests (Tables 1 and 2), while specific root length (m·g⁻¹), the ratio of root length to dry mass of fine roots, was significantly higher with reduced P. Root diameter was not different among the treatment groups at 3 weeks but tended to increase at 7 weeks as P concentration was raised or lowered to the adequate level.

Biomass partitioning in response to P availability. Reducing P concentrations from 30 to 1 mg·L⁻¹ decreased the total plant biomass, and more evidently in shoot than root biomass, resulting in a proportional increase in the root-to-shoot ratio (Tables 1 and 2). However, reducing P from 30 to 20 mg·L⁻¹ did not affect the biomass of each plant part at 7 weeks after transplanting (Table 2).

Biomass accumulation and partitioning were highly influenced by P availability and plant growth phase. The biomass of shoots, roots, and

flowers increased dramatically with increasing P concentrations in both vegetative and reproductive growth phases, and biomass accumulation was highest in shoots, followed by roots and flowers (Fig. 2). During vegetative growth, shoot biomass production was linearly ($P < 0.0001$) related to the increasing P concentrations, but root biomass production was logarithmically ($P < 0.0001$) related to P concentrations (Fig. 2A). During reproductive growth, however, increasing P concentrations logarithmically ($P < 0.0001$) increased biomass production of all plant parts (Fig. 2B). Total plant biomass production was heavily affected by shoot biomass accumulation pattern in both growth phases (Fig. 2).

Root-to-shoot ratios were markedly higher at deficient P regardless of growth phases, and gradually declined as P concentrations increased (Tables 1 and 2). There were no significant differences in root-to-shoot ratios

between different growth stages, and the similar patterns of exponential decay were observed in both growth phases. Allometric coefficient is an index of the balanced growth between root and shoot components integrated at two different harvest times. The allometric analysis based on log-scale root dry mass vs. shoot dry mass for 3- and 7-week-old plants indicated that P concentrations had great effect on carbon allocation to roots, and plants allocated higher proportion of carbon to roots than shoots when P was reduced from 30 to 1 mg·L⁻¹ (Table 3; Fig. 3).

Flower biomass production decreased with reduced P due to the decrease in flower number, diameter, and area (Table 2). Although the numbers of flowers, leaves, and branches per plant were higher with increasing P concentrations (Table 2), these variables did not differ significantly among P concentrations when the results were expressed as per unit area (100 sq. cm⁻²) (Fig. 4). Similarly, the average biomass of individual flower head was not significantly different in nondeficient plants (Fig. 4A). Deficient P reduced the number of florets and the size of individual florets (data not shown).

P accumulation in plant tissues. P contents in shoots, roots, and flowers increased with increasing P concentrations (Table 4; Fig. 5). However, plants accumulated a similar proportion of P in shoots ($\approx 70\%$) regardless of P availability. Total P content was four and five times higher in shoots than in roots and flowers, respectively. P-deficient plants accumulated a higher proportion of P in roots (22%) and a lower proportion of P in flowers (6%) than the roots and flowers of nondeficient plants (averagely 15% and 14%, respectively) (Table 4). Although increase in P content in plant tissues was closely related to biomass increase, biomass accumulation occurred when P supply increased from deficient to adequate level (Fig. 5). Higher P content in plant tissues did not strongly affect biomass accumulation as evidenced by gradual slopes (Fig. 5). Increasing P concentration from 10 to 20 mg·L⁻¹ sharply increased P accumulation in all plant parts, particularly in shoots, while further increasing P concentration from 20 to 30 mg·L⁻¹ accelerated P accumulation in roots and flowers without affecting P content in shoots (Table 4; Fig. 5).

When expressed on a tissue dry matter basis (mg P per g DW), flower P concentration was higher than the ones in shoots or roots from all P treatments (Table 4). PUE was the highest in P-deficient plants. Plant tissues varied with PUE, but P-deficient roots had the highest PUE, whereas the lowest PUE was observed in flowers, particularly in plants with sufficient P.

Discussion

P is critical during vegetative stage of growth. P is as an essential macronutrient that plays a vital role in plant growth, development, and reproduction. Our results show that

Table 1. The effect of P supply on growth and development of lantana at 3 weeks after transplanting.

Variables	P concn (mg·L ⁻¹)						F value	P
	1	3	5	10	20	30		
Plant height (cm)	15.4 d ^z	17.0 d	18.8 c	19.2 c	21.6 b	23.9 a	55.5	***
Plant width (cm)	8.5 d	14.5 cd	19.0 bc	23.8 b	31.5 a	34.3 a	32.1	***
Branch number	5.8 d	8.0 c	8.4 bc	10.1 ab	10.9 a	11.1 a	18.1	***
Leaf number	45.8 e	56.6 d	63.0 c	75.2 b	98.3 a	94.6 a	392.8	***
Leaf area (cm ²)	144.5 e	231.4 d	314.6 c	348.4 bc	435.9 b	537.9 a	70.4	***
Shoot dry mass (g)	1.32 d	1.93 cd	2.53 bc	2.54 bc	3.26 b	4.87 a	40.4	***
Root dry mass (g)	0.50 c	0.75 bc	0.81 abc	0.84 abc	0.95 ab	1.23 a	5.4	**
Total plant biomass (g)	1.81 d	2.67 cd	3.34 bc	3.38 bc	4.22 b	6.09 a	29.0	***
Root-to-shoot ratio	0.38 a	0.38 a	0.32 ab	0.33 ab	0.29 ab	0.25 b	3.5	*
Total root length (m)	37.9 d	45.5 cd	50.5 bcd	56.2 abc	64.0 ab	71.6 a	8.6	***
Total root surface area (cm ²)	431 c	545 bc	621 bc	681 b	750 ab	903 a	10.1	***
Total root volume (cm ³)	3.9 c	5.3 bc	6.1 bc	6.6 b	7.0 ab	9.1 a	10.4	***
Average root diameter (cm)	0.36 a	0.39 a	0.39 a	0.38 a	0.37 a	0.40 a	1.6	NS
Specific root length (m·g ⁻¹)	80.4 a	71.5 ab	65.0 ab	65.0 ab	67.0 ab	52.3 b	3.2	*

^zWithin-row means followed by different letters are significantly different by Tukey's honestly significant difference test at $P \leq 0.05$.

Each value in the table is the mean of 6 to 12 replicates.

Two blocks were pooled for statistical analysis. Block effects were not shown.

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 2. The effect of P supply on growth and development of lantana at 7 weeks after transplanting.

Variables	P concn (mg·L ⁻¹)						F value	P
	1	3	5	10	20	30		
Plant height (cm)	26.0 c	36.5 b	34.7 ab	32.7 ab	40.2 a	39.5 a	13.26	***
Plant width (cm)	23.3 d	36.8 c	43.0 bc	47.9 ab	53.3 a	54.4 a	24.7	***
Branch number	11.2 d	17.5 d	24.2 c	27.7 bc	33.5 ab	35.2 a	36.5	***
Leaf number	91.2 e	181.0 d	209.3 d	267.0 c	371.3 b	537.3 a	186.9	***
Leaf area (cm ²)	234.9 f	497.1 e	644.8 d	865.1 c	1,026.1 b	1,269.7 a	290.9	***
Flower number	7.5 d	14.5 c	24.0 b	26.2 b	34.7 a	34.7 a	48.3	***
Flower diameter (cm)	3.1 c	3.6 b	4.0 a	4.1 a	4.1 a	4.1 a	58.9	***
Flower area (cm ²)	7.5 c	14.5 b	22.0 a	26.2 a	32.5 a	34.7 a	56.3	***
Shoot dry mass (g)	2.202 d	4.562 c	5.399 c	7.425 b	9.623 a	10.774 a	88.6	***
Root dry mass (g)	0.758 c	1.569 b	1.525 b	2.061 b	2.674 a	2.730 a	30.8	***
Flower dry mass (g)	0.095 e	0.453 d	0.776 c	0.922 bc	1.149 ab	1.385 a	43.8	***
Total plant biomass (g)	3.06 e	6.58 d	7.83 d	10.23 c	13.17 b	15.04 a	117.3	***
Root-to-shoot ratio	0.35 a	0.34 a	0.28 ab	0.28 ab	0.28 ab	0.24 b	3.8	***
Total root length (m)	59.1 d	73.6 d	77.5 cd	101.2 bc	124.1 b	149.0 a	38.7	***
Total root surface area (cm ²)	690 d	948 c	1,025 c	1,393 b	1,620 ab	1,867 a	45.9	***
Total root volume (cm ³)	6.4 d	9.8 c	10.8 c	15.3 b	16.9 ab	18.7 a	40.2	***
Average root diameter (cm)	0.37 c	0.41 ab	0.42 ab	0.44 a	0.43 ab	0.40 bc	6.6	***
Specific root length (m·g ⁻¹)	78.0 a	57.6 b	52.7 b	51.2 b	46.8 b	47.0 b	10.9	***

^zWithin-row means followed by different letters are significantly different by Tukey's honestly significant difference test at $P \leq 0.05$.

Each value in the table is the mean of 6 to 12 replicates.

Two blocks were pooled for statistical analysis. Block effects were not shown.

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

reduced P restricts plant growth during both vegetative and reproductive growth, but more dramatically at the earlier stage of growth. However, P deficiency amplifies over time, leading to deficiency symptoms being more evident in the later stage of growth. This is particularly true for P-deficient plant, in which the total plant biomass of vegetative plant was $\approx 30\%$ of the high P plant, but that of reproductive plant was only $\approx 20\%$ (Tables 1 and 2). Similarly, P restrictions during the first 4 to 6 weeks of growth led to large reductions in tillering and head formation in wheat and barley (Grant et al., 2001), supporting our results.

It is apparent that plant growth phase plays an important role in crop biomass accumulation in response to P availability. Shoot biomass linearly increased with increasing concentration of P during vegetative growth, while it gradually increased during reproductive growth (Fig. 2). As reported in the early finding that P supply is critical for many field-grown crops during early season

(Grant et al., 2001), our results indicate that higher P supply is important for lantana during its early growth.

Reduced P had a much smaller impact on reproductive plants than it does on vegetative plants. Increasing P concentration did not lead to a linear rapid increase in plant biomass production of reproductive plants, and flower biomass gradually increased with concomitant biomass accumulation of shoots. Reduced biomass production in reproductive nondeficient plant may be due to the decline of root growth rates compared with vegetative plant (Hansen and Lynch, 1998). P may not be actively used for root biomass production during reproductive growth due to the competition with developing flowers that may act as a stronger sink than roots for P. Therefore, it is critical to apply P fertilizer based on their growth phase: high P during vegetative growth and sufficient P during reproductive growth, which is consistent with the early studies in field crops (Grant et al., 2001).

Although P supply during early development has a dominant effect on crop yield potential, P concentration at 20 mg·L⁻¹ is considered to be sufficient to maximize vegetative growth of lantana. It implies that the P supply using superphosphate or an external supply of P fertilizer over this concentration does not have a positive impact on crop productivity potential. During reproductive growth, P accumulation in flowers is largely due to redistribution from the leaf and stem tissue (Hansen and Lynch, 1998). P supply at 10 mg·L⁻¹ appears to be sufficient in lantana during reproductive stage, allowing carbohydrate translocation mechanisms to function for maximum productivity (Grant et al., 2001). It should be noted that these concentrations were determined based on a perlite and vermiculite mixture in which native P is considered to be negligible. Optimum P concentrations for crop production could vary considerably by the type of the growing medium used, and could be even lower

Fig. 2. The effects of P supply on the dry biomass of whole plant, shoots, roots, and flowers, and root-to-shoot ratio of *lantana* at (A) 3 weeks (vegetative stage) and (B) 7 weeks (reproductive stage) after transplanting. Linear or logarithmic regression analysis was used to response correlations. The regression line was fitted through the data for 3 weeks (A) in whole plant [$y = 0.12x + 2.20$, $P < 0.0001$]; shoots [$y = 0.10x + 1.53$, $P < 0.0001$]; and roots [$y = 0.18\ln(x) + 0.50$, $P < 0.0001$], and for 7 weeks (B) in whole plant [$y = 3.49\ln(x) + 2.69$, $P < 0.0001$]; shoots [$y = 2.55\ln(x) + 1.82$, $P < 0.0001$]; roots [$y = 0.59\ln(x) + 0.76$, $P < 0.0001$]; and flowers [$y = 0.40\ln(x) + 0.08$, $P < 0.0001$].

Table 3. Allometric coefficients (K) of root-to-shoot ratio of *lantana* grown under different P concentrations.

P concn	Root-to-shoot ratio	
	K	r^2
1	1.99 a ^z	0.83
3	1.51 ab	0.87
5	1.24 b	0.80
10	1.23 b	0.78
20	1.13 b	0.86
30	1.03 b	0.85
F value from ANOVA		
P concentration	6.38	***

ANOVA = analysis of variance.

^zWithin-column means followed by different letters are significantly different by Tukey's honestly significant difference test at $P \leq 0.05$.

Each value is derived from paired measurements of root dry weight (DW) and shoot DW (Hunt, 1990) measured at 3 and 7 weeks after transplanting.

ns, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

than 10 mg·L⁻¹ if P sources are incorporated into the medium.

Excess P does not increase the number of flowers. Our observation that flower buds began to develop at 4 weeks and anthesis occurred in the same week regardless of P supply indicates that high P is not needed to promote flower initiation in *lantana*. Plants grown with reduced P produced a lower

number of flowers, presumably due to a slightly delayed flower development in association with a decreasing number of individual florets (Fig. 4). Such phenological delay may represent a temporal redistribution of resources to increase reproductive success in response to limited resources (Lynch and Brown, 2006). Fertilizers containing excess P have been considered as bloom boosters and often recommended to be used as starter fertilizers to enhance flowering as well as root growth (Bost, 2014; Bouquet, 1943). We did not observe any differences in the number of flowers and P content per unit DW between two high P levels (20 and 30 mg·L⁻¹) applied *lantana*. A surplus of P, however, accumulated in flowers. Similarly, there was no difference in biomass production between adequate P (3 mg·L⁻¹) and excess P (150 mg·L⁻¹) applied *chrysanthemum* (*Dendranthema × grandiflorum*) except a higher number of colored flower buds at anthesis by the application of excess P (Hansen and Lynch, 1998). Interestingly, when plant productivity was expressed on a unit area basis, DW of individual flower not differ in nondeficient plants and the numbers of flowers, leaves, and branches were the same regardless of P concentration. Such parameters can be important morphological criteria of yield (Caradus et al., 1991). These results indicate

Fig. 3. The effects of P on allometric coefficient (K) of root-to-shoot ratio. The plants were fertigated with a half-strength Hoagland's nutrient solution containing 1, 3, 5, 10, 20, or 30 mg·L⁻¹ P on a regular basis. Data were collected at 3 and 7 weeks after transplanting. Mean values with different letters are significantly different ($P < 0.05$). The regression lines were fitted through the data for 1 mg·L⁻¹ ($y = 0.32x + 0.06$) as shown in dotted line; 10 mg·L⁻¹ ($y = 0.23x + 0.30$) in dashed line; and 30 mg·L⁻¹ ($y = 0.21x + 0.43$) in solid line.

that reduced P decreased the size of plants without affecting productivity. These features may be used to control plant size in replacement of growth retardants that are known to reduce plant size in commercial ornamental crop production.

The effect of P on root-to-shoot ratio is largely concentration dependent. Reducing P concentration had the most significant effect on leaf characteristics during both vegetative and reproductive stages. Reduction in leaf area and the number of leaves is characterized as the most obvious effects in P-deficient plants due to the reduced rates of cell division and expansion (Chiera et al., 2001). This is in contrast to the root growth of P-deficient plants, which was less inhibited by reduced P, leading to a typical increase in root-to-shoot ratio. It is well documented that low P availability increases the allocation of dry matter to roots while suppressing shoot growth, resulting in increased root-to-shoot ratios, which has been demonstrated in herbaceous species, such as *chrysanthemum* (*Dendranthema × grandiflorum*) (Hansen and Lynch, 1998), *petunia* (*Petunia × hybrida*), tomato (*Lycopersicon esculentum* Mill.) (Kim et al., 2008), and common bean (*Phaseolus vulgaris* L.) (Lynch et al., 1991). Meanwhile, some studies have shown that P had no effect on either root growth or root-to-shoot ratio in a wide range of plant species (Broschat and Klock-Moore, 2000; Dufault and Schultheis, 1994; Melton and Dufault, 1991; Weston and Zandstra, 1989; Yeager and Wright, 1982), in which P concentrations were excessively high compared with the range evaluated in our study. Our results showed that increasing P from 1 to 30 mg·L⁻¹ promotes both shoot and root growth; however, disproportionate

growth of shoots over roots sharply decreases the root-to-shoot ratio when P concentration changes from deficient to low, and slightly decreases it when P concentration changes

from low to high. It is clear that the effect of P on root-to-shoot ratio is largely concentration dependent. When plants experience P deficiency, growth reduction is generally greater

in the shoots than in the roots, allowing the plant to maintain root growth and encounter and extract P from the belowground environment (Grant et al., 2001). Discrepancy over the effect of P on root growth or root-to-shoot ratio observed in the aforementioned studies may be accounted for by the differences in P concentrations or the additional P available in the potting medium (Ristvey et al., 2007). It is obvious that reducing P gradually increases root-to-shoot ratio, although the significant difference can be manifested only at the extreme P concentrations: deficient and excess P supplies. Even in the studies that reported no effect of P on root-to-shoot ratio, it appears that the deficient to low P increased the root-to-shoot ratio in a wide range of container-grown plants (Broschat and Klock-Moore, 2000) and in bell pepper (*Capsicum annuum* L.) (Dufault and Schultheis, 1994). Our allometric analysis clearly shows that reduced P preferentially stimulates root growth over shoot growth in lantana. It appears that allocation to root dry mass in vegetative P-deficient plants was achieved at the expense of shoot dry mass, whereas it was gained at the expense of flower dry mass in reproductive plants. The practical implication of these results is that deficient P supply during vegetative growth enhances root growth; however, it significantly limits plant productivity from which plant may not recover, and therefore, supplying sufficient P for the 3- to 4-week vegetative growth is important because it allows maximum plant growth while maintaining a balanced root-to-shoot ratio for plants to optimize resource acquisition.

P requirement of lantana based on P accumulation and partitioning. In this study, we used a perlite and vermiculite mixture to avoid overestimate of P utilization efficiencies under reduced P and to better quantify P requirements of the plant. P accumulation in plant tissues was highly associated with P supply, sharply increasing at high P concentrations (Fig. 5). Interestingly, increasing P concentration from 10 to 20 mg·L⁻¹ coincided with the accumulation of P in all plant parts, with a particularly sharp increase in shoots. Further increasing to 30 mg·L⁻¹ did not affect concentration in shoots but accelerated P accumulation in roots and flowers (Table 4; Fig. 5). These results indicate that P concentration at 10 mg·L⁻¹ is adequate to encourage normal plant growth and reproduction of

Fig. 4. The effects of P supply on (A) the average biomass of individual flower head, (B) the number of flowers per unit area, (C) the number of branches per unit area, and (D) the number of leaves per unit area in lantana. The top panel shows the size of flower (inflorescence) and the size and number of individual florets (left to right: 22, 25, 25, 29, 29, and 28). The plants were fertigated with a half-strength Hoagland's nutrient solution containing 1, 3, 5, 10, 20, or 30 mg·L⁻¹ P on a regular basis. Data were collected at 7 weeks after transplanting. Data shown are means $\pm$ SE of at least six plants. Mean values with different letters are significantly different ($P < 0.05$).

Table 4. The effects of P supply on P content and P utilization efficiency (PUE) of whole plant, shoots, roots, and flowers of lantana at 7 weeks after transplanting.

P concn (mg·L ⁻¹)	P content (mg/plant)				P concn (mg P/g dry weight)				PUE (g dry weight/mg P)			
	Whole plant	Shoots	Roots	Flowers	Whole plant	Shoots	Roots	Flowers	Whole plant	Shoots	Roots	Flowers
1	1.82 d ²	1.3 d	0.4 d	0.11 d	0.64 b	0.59 d	0.53 d	1.20 c	1.75 a	1.72 a	1.91 a	0.84 a
3	6.05 cd	4.22 cd	1.06 cd	0.76 cd	0.98 b	0.93 cd	0.70 cd	1.55 bc	1.14 b	1.15 b	1.52 b	0.64 b
5	9.38 bc	6.34 bc	1.32 cd	1.79 bcd	1.25 b	1.18 cd	0.88 cd	2.03 bc	0.87 bc	0.86 bc	1.17 bc	0.49 c
10	14.02 b	9.66 b	2.35 bc	2.06 bc	1.43 b	1.30 c	1.14 bc	2.23 b	0.76 c	0.77 c	0.88 c	0.43 c
20	42.89 a	36.15 a	3.58 b	3.55 b	2.72 a	3.82 a	1.34 b	3.59 a	0.32 d	0.27 d	0.80 c	0.24 d
30	47.33 a	32.3 a	8.57 a	6.73 a	2.93 a	3.01 ab	3.12 a	3.98 a	0.32 d	0.33 d	0.32 d	0.27 d
F value	286.76	185.06 b	55.84 b	27.35	25.52	63.80	84.45	26.08	53.91	49.75	39.76	77.63
P	***	***	***	***	***	***	***	***	***	***	***	***

²Within-column means followed by different letters are significantly different by Tukey's honestly significant difference test at $P \leq 0.05$.

Each value in the table is the mean of six replicates.

Two blocks were pooled for statistical analysis. Block effects were not shown.

ns, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Fig. 5. The effects of P supply on P allocation (left column) and dry biomass accumulation (right column) in whole plant, shoots, roots, and flower of lantana. The plants were fertigated with a half-strength Hoagland's nutrient solution containing 1, 3, 5, 10, 20, or 30 mg·L⁻¹ P on a regular basis and harvested at 7 weeks after transplanting. Solid lines indicate logarithmic fits to the respective data ($P < 0.05$).

lantana during reproductive stage, and concentrations over this range appear to be superfluous as P accumulation has little or no influence on biomass gain of plant parts. When P content was expressed on a dry mass basis, P was favorably accumulated in flowers compared with shoots and roots regardless of the concentration of P applied. This might be because P in flowers was diluted by its higher water content in the

tissue (averagely 82.5%) compared with shoot (71.7%) and root (78.9%) tissues. P accumulated in lantana flowers might be derived from internal redistribution and remobilization of P originated from the leaves and/or roots accumulated during the earlier growth period and/or in part directly from the P applied to the media. The P-deficient roots of common bean retain P within the tissue without mobilizing it, while

P in leaves and stems is remobilized to the grain regardless of P concentrations (Snapp and Lynch, 1996). In perennial species, roots can be an important storage site for nutrients during low growth periods, and the main source of remobilized P during high growth demand or reproductive periods (Cote and Dawson, 1990).

Thus, the productivity of plants may not be affected even if higher P concentration is applied, increasing potential risks of P losses to the environment. Similar results were reported in azaleas (*Rhododendron* L. 'Karen') grown with excess P (25 mg per week) in which P was mainly stored in leaf and root tissues without increasing plant DW (Ristvey et al., 2007). In their study, it was also reported that higher P fertilization rates increased P leaching from the substrate. Because azaleas have low nutritional requirements, an N:P ratio of 20:1 was sufficient for azaleas grown in a commercial potting mix. The fertilization rates of 100 mg N and 5 mg P per week in their study can be translated into 20 mg·L⁻¹ N and 1 mg P per day. Although a direct comparison may not be possible due to the differences in many production components, our results indicate that the N:P ratios of 5:1 and 10:1 are sufficient to maintain the growth of lantana even when inert media are used. If lantana is grown in a commercial mix, a fertilizer with a higher N:P ratio may be suitable due to the native N and P sources in the media.

The P requirement is well documented in wheat, in which postanthesis growth is governed by two competing processes: the P requirements of vegetative tissues to continue normal cellular function and the P demand of the developing grain (Rose et al., 2007). In our study, P concentration at 10 mg·L⁻¹ appears to meet the needs for the growth and flowering of lantana, which is evidenced by the rapid P accumulation in shoots over this range (Fig. 5). P concentrations over 10 mg·L⁻¹ strongly stimulated the accumulation of P in roots and flowers by a magnitude of two to three times without concomitant increase in dry biomass. These results suggest that P concentration over 10 mg·L⁻¹ is superfluous during the reproductive phase and that DW accumulation of plant parts does not coincide with the amount of P in these tissues. P contents could be well above the P concentrations required for normal cellular function (Veneklaas et al., 2012), and most P contained in plant parts can be released to the environment in the form of waste streams (Raboy, 2009). Thus, careful consideration is needed when applying P for crop production to reduce the environmental impact and sustainably produce crops.

The PUE is the amount of biomass produced per unit of acquired P, and is one of the major components of plant P use efficiency under P limiting conditions (Good et al., 2004; Huang et al., 2011). A higher PUE of some white clover genotypes was related to a better use of stored P (Caradus and Snaydon, 1987). P supply to plants is often fluctuating, and therefore, P remobilization

within the plant is critical for plant survival (Huang et al., 2008; Vance et al., 2003). The PUE in shoots, roots, and flowers was negatively correlated with biomass production, and the highest PUE was observed in P-deficient roots. Plants develop adaptive mechanisms in response to low P, such as changes in morphological or physiological characteristics in roots that may affect P acquisition (Lynch and Brown, 2006; Raghothama and Karthikeyan, 2005). It was suggested that a higher root-to-shoot ratio may help improve PUE of plants, especially under P deficiency (Föhse et al., 1988). Such adaptive responses are critical for plants to ensure a satisfactory dry matter production. In our study, we demonstrated that root morphological characteristics of lantana were altered by P availability. Decreasing P supply led to an increased specific root length and a higher root-to-shoot ratio, and such changes were positively correlated with a higher PUE ($r^2 = 0.54$ and 0.12 , respectively; $P < 0.05$). These characteristics may be associated with a greater exploitation of P from the rhizosphere and help plants better adapted to P limitation.

There is no doubt that P is essential for plant growth and reproduction. Plants require a relatively high P during the early stages of growth to promote vegetative growth, and sufficient P supply during reproductive growth to optimize plant productivity. It is important to recognize the roles of P as a major nutrient element and to properly manage production systems to ensure appropriate concentrations of P are provided to the developing crop. It entails recognition of P requirement of a crop, and such changes on P demand over ontogenetic phases. Our results indicate that minimal rates necessary to support the optimal growth of lantana is $20 \text{ mg} \cdot \text{L}^{-1}$ during vegetative stage and $10 \text{ mg} \cdot \text{L}^{-1}$ during reproductive stage. Since P requirements could be varied by crops and substrates used for crop production, P requirements of various horticulture crops should be determined to better manage production systems and to mitigate the environmental concerns.

In summary, our study refines the effects of P fertilization on plant growth, and provides critical information on the biomass accumulation during vegetative and reproductive growths, in relation to P accumulation and partitioning in lantana. To obtain high productivity, plants must receive an adequate amount of P as it is directly related to dry matter accumulation, and the growth stage of a plant needs to be considered when determining an optimum concentration of P. Improved cultural practices will help growers to stay in business while complying with federal and state regulations, which are likely to become more stringent with time.

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