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Response to Phosphorus Availability during Vegetative and Reproductive Growth of Chrysanthemum: II. Biomass and Phosphorus Dynamics

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Abstract. **Whole-plant biomass accumulation, P dynamics, and root–shoot interactions during transition from vegetative to reproductive growth of 'Coral Charm' chrysanthemum (*Dendranthema ×grandiflorum* Ramat.) (Zander, 1993) were investigated over a range of P concentrations considered to be deficient (1 μM), adequate (100 μM), and high (5 mM). In nondeficient plants, transition from vegetative to reproductive growth resulted in reduced relative growth rate and root and shoot biomass accumulation. Reproductive plants showed a higher commitment of the whole plant to the production of developing flowers than to leaves and roots, whereas, in vegetative plants, the highest component production rate was in leaves. This indicates changes in the source–sink relationships during transition from vegetative growth making developing flowers stronger sinks for photoassimilates than roots. Phosphorus allocated to developing flowers was predominantly lost from leaves. Phosphorus-deficient plants showed characteristic P-deficiency symptoms and favored root growth over shoot growth regardless of growth stage. Phosphorus availability in nondeficient plants affected root growth more than shoot growth. No substantial differences in shoot biomass production, relative growth rate, and CO_2 assimilation rates were observed in adequate-P and high-P plants. However, the root component production rate, root to shoot ratio, root length ratio, specific root length, specific root area, root mass to leaf area ratio, and root respiration increased in adequate-P plants compared with high-P plants, which indicates that high root activity was maintained without affecting shoot biomass in buffered P conditions. Our results suggest that the high P concentrations used in many horticultural systems may have no benefit in terms of shoot growth and may actually be detrimental to root growth.**

Cultivated flowering plants are often exposed to stress conditions during production, especially in the postproduction phase. Even in crops grown under glass, where water and nutrients are rarely limiting, it may be necessary to consider root relative to shoot growth, not only in relation to growth during production but also in relation to a future period with less-favorable postharvest growth conditions when light intensity, water, and nutrient availability are often low. Transition from vegetative to reproductive growth may lead to changes in source–sink relationships; the root is a less competitive sink than developing flowers (Amthor, 1989; Hood et al., 1993; Kallerackal and Milburn, 1985) and may adversely affect stress tolerance.

Phosphorus concentrations of 3 μM have been shown to be sufficient for maximum growth rate for different species (First and Edwards, 1987; Lynch et al., 1991). In conventional horticultural production systems, however, plants are often grown with high concentrations of P, often ranging from 3 to 5 mM (Bjerregård and Hansen, 1983; Williams and Nelson, 1996). 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 (Gutschick and Kay, 1995; Lynch et al., 1991; Rao et al., 1993). Erickson (1990) found that, when the P supply reduced growth by 50% in birch seedlings, roots accounted for 40% of the total plant biomass.

We hypothesized that the high levels of P fertilizer used in conventional horticultural production may reduce root growth, which may in turn increase plant sensitivity to postproduction stress. If so, reduced P fertilization might improve plant quality and cause less environmental pollution. The objective of this study was to test this hypothesis by analyzing whole-plant CO_2 exchange, biomass, and P dynamics in chrysanthemum as affected by P supply, with particular attention to the transition from vegetative to reproductive growth. This paper only includes the biomass and P dynamics results, whereas gas-exchange results are discussed in Hansen et al. (1997, 1998).

Materials and Methods

Plant culture. Vegetative cuttings of 'Coral Charm' chrysanthemum (*Dendranthema ×grandiflorum*) (Zander, 1993) were propagated in a nutrient solution at 25% of the concentration of the P-free solution used during the experiment (see below). In the nutrient solution used for propagation the P concentration was 1 μM. Cuttings were kept under long-day conditions to ensure vegetative growth. Four-week-old rooted cuttings were transplanted into a nonrecirculating, aerated hydroponic system as described by Hansen et al. (1997); assigned randomly to three P treatments, two daylength treatments, and three blocks; and grown until anthesis.

Phosphorus treatment. Three P treatments were used: 1, 100, and 5 mM. These were considered to be low, adequate, and high P, respectively. To maintain low and stable P concentrations, a solid-

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phase alumina-P buffer (Al_2O_3-P) technique as described by Lynch et al. (1990) was used in the two lower P treatments. Bags containing alumina-P buffer were placed directly in a P-free nutrient solution, so that the total amount of P taken up by the plants experiencing low-P and adequate-P conditions was provided from the alumina-P buffer. The P concentration in the high-P treatment was not substantially depleted and so was unbuffered; i.e., 5 mM KH_2PO_4 was added directly to the nutrient solution. The composition of the P-free nutrient solution was (in μM): 420 K_2SO_4, 1720 KNO_3, 1350 $Ca(NO_3)_2$, 320 $MgSO_4$, 830 NH_4NO_3, 500 $Mg(NO_3)_2$, 110 NaCl, 40 Fe-EDTA, 5 $MnSO_4$, 2 $ZnSO_4$, 0.6 $CuSO_4$, 8 H_3BO_3, and 0.008 $NH_4Mo_7O_{24}$.

Solution samples were collected periodically, and P content was analyzed as described by Murphy and Riley (1962). When the desorption P concentration began to decrease, the depleted buffer bag was replaced with a new one providing the desired P concentration. Solution electrical conductivity (EC) and pH were monitored three times a week and pH was adjusted with either 1.0 M KOH or 0.5 M HCl if necessary to maintain pH at 5.5 to 6.0. The nutrient solution was replaced at 4 weeks after transplanting (WAT) and an EC of 1.5 to 2.0 $mS \cdot cm^{-1}$ was maintained during the experiment.

Photoperiod treatment. Flower induction was controlled by modifying the natural photoperiod. All plants were covered with dark cloth after a 9-h (0800 to 1700 HR) photoperiod in naturally lit greenhouse conditions in State College, Pa. (lat. 41° N). Night-break lighting for 3.5 h (from midnight to 0330 HR) was given to one-half of the plants to maintain vegetative growth for comparison with reproductive plants. Incandescent light (1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) used to prolong the photoperiod was installed underneath the dark cloth. The reason for covering all the plants from both daylength treatments was to ensure similar temperature and photosynthetic photon flux density (PPFD) in all treatments.

Growth conditions. Environmental data were monitored with 1-min intervals and averaged over 10 min during April to July 1994. Average day/night air temperature during the growth period was 22.1/20.1 °C, minimum and maximum day/night air temperature was 18.5/18 °C and 28.8/22.5 °C, respectively. Only minor variations in solution temperature were seen diurnally and during the growth period. Average day/night solution temperature during the growth period was 21.6/20.6 °C. Average daytime relative humidity (RH) was 24%, and average nighttime RH was 67%.

PPFD varied during the photoperiod; it was typically ≈600 to 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during midmorning measurements and 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during midafternoon CO_2 exchange measurements.

Data collection. Successive destructive harvests followed whole-plant photosynthesis and respiration measurements (described by Hansen et al., 1997, 1998). Leaf area, plant height, and biomass were determined representing one plant per treatment per harvest repeated three times a week at an interval of 2 d. Plants from different replications had the same physiological age. Measurements started 3 weeks after the plants were transplanted into the hydroponic tanks, providing a sufficient period for adapting to the new growth conditions, and continued until anthesis, when the number of flower buds showing color was recorded.

Root length and area were estimated from scanned images. Root subsamples were stained in 10% isopropanol with 1% methyl violet and images obtained by using a flat-bed scanner (HP Scanjet IIc; Hewlett-Packard, San Jose, Calif.) and Deskscan II scanning software. The Delta-T Scan program was used for estimating root length and area. The dry mass of subsamples used to determine length and area was used to calculate specific root length [SRL, root length per unit root dry mass ($m \cdot g^{-1}$)] and specific root area [SRA, root area per unit root dry mass ($m^2 \cdot g^{-1}$)], from which the length and area of the total root system was estimated. Tissue samples separated into roots, leaves, stems, and flower buds (if

Table 1. Weekly growth parameters for chrysanthemum as influenced by P availability in different growth phases. Each value is the mean of 15 plants measured at five harvests through time. Standard error in parentheses.

	Growth parameter[z] ($mg \cdot g^{-1}$)						
	RGR_{tot}	RGR_{root}	RGR_{shoot}[y]	CPR_{root}	CPR_{leaf}	CPR_{stem}[x]	df
Low P							
Vegetative	–8	231	–101	71	38	–102	
Reproductive	13	280	–89	69	30	–86	
Adequate P							
Vegetative	435	464	427	62	242	115	
Reproductive	246	261	238	48	37	170	
High P							
Vegetative	444	479	420	59	255	150	
Reproductive	307	318	305	46	64	197	
F value							
P treatment (P)	255^{***}	9^{**}	177^{***}	1^{NS}	6^{**}	22^{***}	2
Daylength (DL)	43^{***}	12^{**}	23^{***}	1^{NS}	18^{***}	1^{NS}	1
WAT[w]	---[v]	---	---	13^{***}	2^{*}	14^{***}	3
P × DL	16^{**}	7^{*}	8^{**}	0^{NS}	4^{*}	0^{NS}	2
P × WAT	---	---	---	4^{**}	2^{NS}	3^{NS}	6
DL × WAT	---	---	---	1^{NS}	0^{NS}	1^{NS}	3
P × DL × WAT	---	---	---	1^{NS}	1^{NS}	0^{NS}	6

[z]RGR = relative growth rate (leaves, stem, flower buds); CPR = component production rate.
[y]Includes leaves, stems, and flower buds (if present).
[x]Includes stems and flower buds (if present).
[w]WAT = weeks after transplanting.
[v]Not included in the analysis.
[NS,*,**,***]Nonsignificant or significant at $p = 0.05$, 0.01, and 0.001, respectively.

present) were dry ashed in a muffle furnace at 500 °C for 12 h, dissolved in 0.1 M HCl, and analyzed for total P content after Murphy and Riley (1962).

Data analysis. From the harvest data, root to shoot ratio (RSR), relative growth rate (RGR), and component production rate (CPR) were calculated as described by Hunt (1990). The root length ratio [RLR, root length per unit plant dry mass ($m \cdot g^{-1}$)] and SRL and SRA of the total root system were calculated.

Numerical differentiation of the dry matter accumulation and the P content data were performed as described by Lynch and White (1992) to obtain values of biomass and P flux over time. Numerical differentiation formulas based on least-squares fitting of second-degree polynomials to three points for evenly spaced x values was used as described by Erickson (1976).

Results were analyzed statistically in SAS (SAS Institute, Cary, N.C.) as a fully randomized design. The following data were logarithmically transformed, allowing data to be normally distributed before analysis of variance by GLM procedure: RSR, RLR, root mass to leaf area ratio, Total P, Leaf P, and root P to shoot P ratio. The statistical models were reduced by stepwise discarding nonsignificant variables ($p > 0.05$). Least square means and standard errors of means are presented in the figures and tables.

Results

Transition to reproductive growth. Transition from vegetative to reproductive growth resulted in reduced relative growth rates of shoots and roots and biomass accumulation in adequate-P and high-P plants. The leaf biomass accumulation was affected to a much larger extent than root biomass (Table 1). Since stem samples included flowers and flower buds, a high CPR_{stem} in reproductive compared with vegetative plants shows a greater commitment of the whole plant to produce developing flowers than roots and leaves. Increasing stem biomass flux in reproductive nondeficient plants coincided with decreasing leaf and root biomass flux (Fig. 1 B and C), whereas in vegetative plants biomass flux increased for all tissue categories (Fig. 1 E and F).

Reproductive and vegetative P-deficient plants were quite similar with regard to shoot and root biomass accumulation (Table 1).

Reproductive, nondeficient plants were 22% shorter than vegetative plants (19.3 ± 0.4 cm vs. 24.8 ± 0.4 cm). SRL was lower in reproductive than in vegetative plants (Table 2), whereas root dry mass per unit leaf area was highest in reproductive plants (Table 2). RLR (see F and p values in Fig. 2B) and SRA (Table 2) were not significantly affected by transition to reproductive growth. Only minor differences, although significant at $p < 0.003$, were seen in the RSR between vegetative and reproductive plants and interacted with P treatment (see F and p values in Fig. 2A). Phosphorus-deficient, vegetative plants showed a slightly higher RSR than reproductive plants, whereas the opposite was observed in plants grown with the two highest P concentrations.

Total leaf P content was slightly higher in vegetative than reproductive plants (Fig. 3), whereas the opposite was seen in P concentrations [mmol(g tissue dry mass)$^{-1}$] (Table 3). Stem P (including flower and flower buds) was highest in reproductive plants. Root P was not significantly affected by transition to reproductive growth (Table 3). Leaf P content increased over time only in vegetative plants grown with the two highest P concentrations, and declined over time in reproductive and in vegetative P-deficient plants (Fig. 3). Phosphorus was lost predominantly from leaves of reproductive plants (Fig. 4). Increasing stem P flux in reproductive plants coincided with decreasing leaf P flux, and to a lesser extent decreasing root P flux (Fig. 4). Negative leaf and root P flux may have been due to allocation of P to developing flowers. The maximum rate of loss occurred at 4 to 5 WAT for high-P plants and from 5 to 7 WAT for adequate-P plants (Fig. 4). At anthesis (first open flower) an average of 34 ± 5 and 54 ± 5 colored flower buds ($p < 0.05$) were present in adequate-P and high-P plants, respectively, whereas there were only 4 ± 1 colored buds in low-P plants.

Effects of P availability. Characteristic P deficiency symptoms such as small, dark green leaves and a reddish coloration on the basal stem were seen in low-P plants from 2 to 3 WAT. Plant height was reduced by 50% from 26 ± 0.4 to 13 ± 0.4 cm and leaf area by 85% (Hansen et al., 1997, 1998) compared with plants receiving adequate P and high P. The early and persistent suppression of shoot biomass resulted in very low relative growth rates of shoots (Table 1) and wilting of basal leaves.

Plants grown with the two highest P concentrations showed no visual symptoms of nutrient deficiency or toxicity. Besides the lower number of colored flower buds at anthesis in adequate-P plants, there were no substantial differences in shoot and root biomass production (Table 1) and plant height was similar (26 ± 0.4). Leaf area only slightly increased in high-P plants. The highest shoot RGR was seen in vegetative plants experiencing adequate-P conditions, although total RGR was similar in adequate-P and high-P plants (Table 1).

Dry matter partitioning between roots and shoots was highly influenced by P availability. High values of CPR_{leaf} and CPR_{stem} compared with CPR_{root}, especially in vegetative adequate-P and high-P plants (Table 1), showed a higher commitment of the whole plant shoot biomass rather than root biomass production. Conversely, P-deficient plants favored root growth over shoot growth, as shown by high CPR_{root} in Table 1, and a positive biomass flux

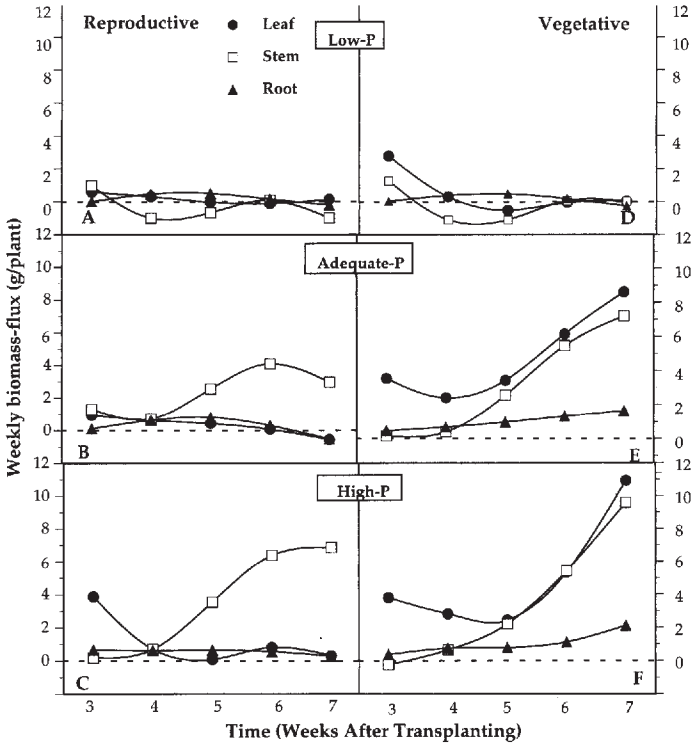


Fig. 1. Biomass flux in leaves, stems, and roots of reproductive (**A–C**) and vegetative (**D–F**) plants at three P treatments. Each point represents the differentiated value of the mean of three replications.

Table 2. Root growth parameters (dry mass basis) for chrysanthemum as influenced by P availability in different growth phases. Each value is the mean of three 15 plants (three replicates × five harvests). Standard error in parentheses.

	Growth parameter[z]			
Phosphorus availability	SRL ($m \cdot g^{-1}$)	SRA ($m^2 \cdot g^{-1}$)	Root mass: leaf area ratio ($g \cdot m^{-2}$)	df
Low P				
Vegetative	44 (3.7)	0.04 (0.003)	81 (1.7)	
Reproductive	41 (3.5)	0.04 (0.003)	82 (1.9)	
Adequate P				
Vegetative	86 (3.9)	0.06 (0.003)	17 (1.6)	
Reproductive	73 (3.7)	0.06 (0.003)	29 (1.6)	
High P				
Vegetative	73 (3.9)	0.05 (0.003)	16 (1.6)	
Reproductive	65 (3.9)	0.05 (0.003)	25 (1.6)	
F values				
P treatment (P)	67^{***}	39^{***}	860^{***}	2
Daylength (DL)	7^{**}	0^{NS}	129^{***}	1
WAT[y]	2^{NS}	2^{NS}	53^{***}	4
P × DL	1^{NS}	0^{NS}	29^{***}	2
P × WAT	0^{NS}	1^{NS}	9^{***}	8
DL × WAT	1^{NS}	1^{NS}	10^{***}	4
P × DL × WAT	0^{NS}	1^{NS}	1^{NS}	8

[z]SRL = specific root length; SRA = specific root area; SRM = specific root mass.
[y]WAT = weeks after transplanting.
^{NS,*,**,***}Nonsignificant or significant at $p = 0.05$, 0.01, and 0.001, respectively.

into roots coinciding with negative leaf and stem biomass flux, regardless of growth stage (Fig. 1 A and D), shows that plants were actually losing tissue to support root growth. The highest RSR was found in P-deficient plants. RSRs were quite similar for plants grown with the two highest P levels (Fig. 2A).

Specific root respiration decreased with P availability (Hansen et al., 1997, 1998). High P availability likewise caused a decrease in the RLR 5 weeks after the treatments began compared with plants grown with adequate and low P (Fig. 2B). The highest SRL and SRA was seen in adequate-P plants (Table 2), whereas RLR (Fig. 2B) and root mass to leaf area ratio increased with decreasing P availability (Table 2).

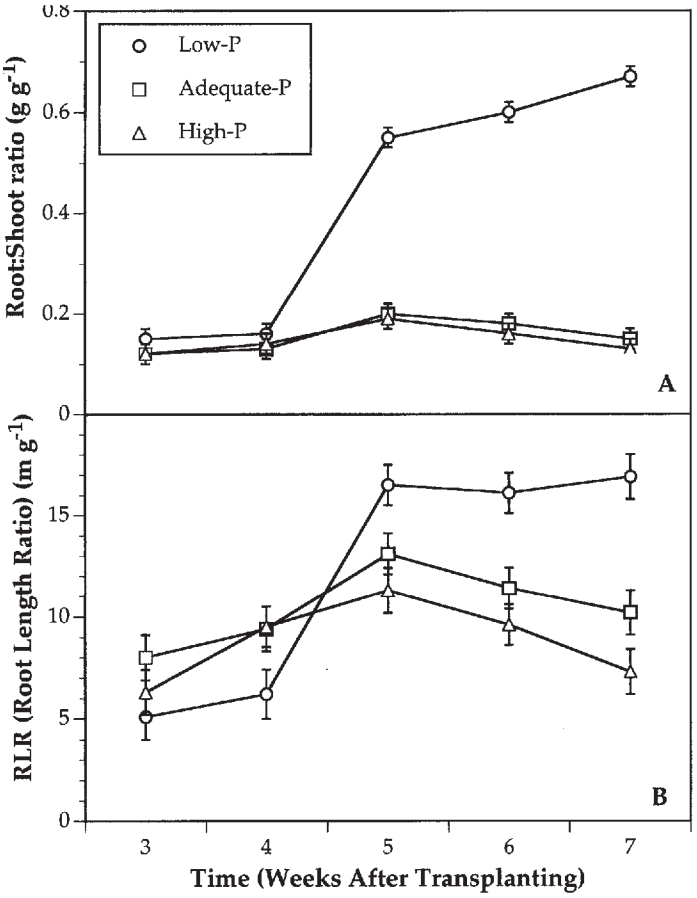
Phosphorus accumulation increased with P availability (Fig. 3, Table 3). Phosphorus-deficient plants accumulated a relatively higher proportion of P in roots than nondeficient plants (Fig. 3). When expressed on a tissue dry matter basis, root P content either exceeded or was similar to leaf P in plants from all P treatments; the lowest P content was seen in stems (Table 3). The root to shoot P ratio increased by almost 2-fold in P-deficient plants and was not significantly affected by growth stage (Table 3).

Fig. 2. (**A**) Effect of P availability on the root:shoot ratio. (**B**) Changes in root length ratio defined as root length per unit plant dry mass over time. Each point represents the mean of six plants (three replications × two daylength treatments). The following F values were obtained from the analyses of variance (GLM) from successive models reduced by stepwise discarding of NS variables.

Parameter	RSR	RLR
P treatment (P)	350^{***}	8^{***}
Daylength (DL)	10^{**}	0^{NS}
Weeks after transplanting (WAT)	105^{***}	32^{***}
P × DL	11^{***}	2^{NS}
P × WAT	38^{***}	9^{***}
DL × WAT	1^{NS}	1^{NS}
P × DL × WAT	1^{NS}	1^{NS}

^{NS,***,***}Nonsignificant or significant at $p = 0.05$, 0.01, or 0.001, respectively; df shown in Table 2.

Leaf P flux was highest in high-P plants with a high positive P flux from 6 to 7 WAT regardless of growth stage (Fig. 4).



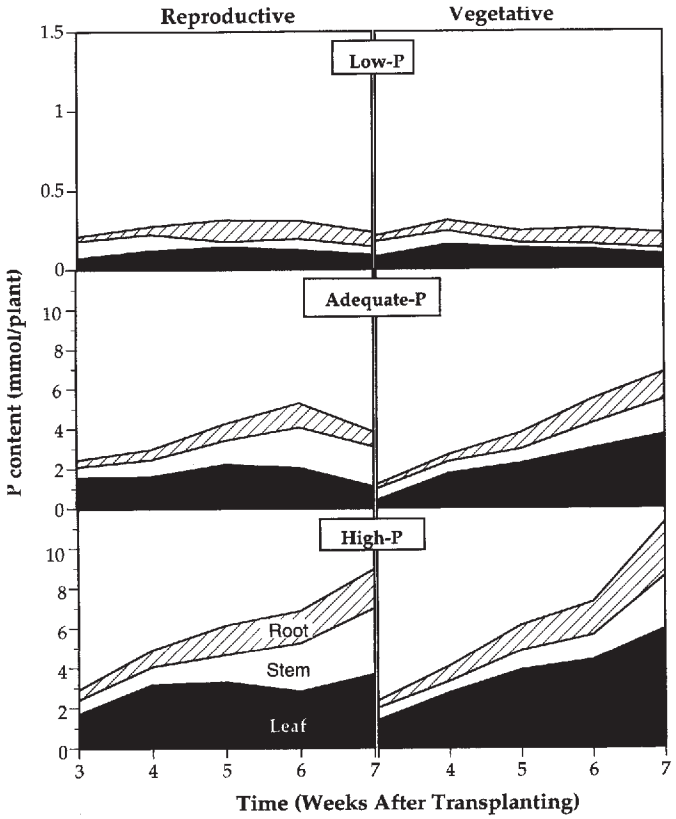


Fig. 3. Phosphorus partitioning in reproductive and vegetative plants grown with three P levels. Patterns from bottom to top of each panel represent leaf, stem (including flower buds in reproductive plants), and root. Each panel is the mean of three replications. F values from the analyses of variance (GLM) from successive models reduced by stepwise discarding of ns variables.

Parameter	Leaf	Stem	Root
P treatment (P)	705^{***}	851^{***}	398^{***}
Daylength (DL)	4^{*}	19^{***}	0^{NS}
Weeks after transplanting (WAT)	14^{***}	17^{***}	63^{***}
P × DL	0^{NS}	0^{NS}	0^{NS}
P × WAT	2^{NS}	22^{***}	1^{NS}
DL × WAT	4^{**}	1^{NS}	2^{NS}
P × DL × WAT	2^{*}	0^{NS}	2^{NS}

^{NS,***,***}Nonsignificant or significant at $p = 0.05$, 0.01, or 0.001, respectively; df shown in Table 2.

Discussion

When studying the effects of P availability on plant growth under controlled conditions, it is difficult to maintain sufficiently low and stable P concentrations. Most prior P-deficiency studies used P starvation or unbuffered P conditions, which may lead to stress conditions of undesired severity. Phosphorus concentrations of 0.4 μM (Elliott et al., 1983), <2 μM (Lynch et al., 1990), and 3 μM (Coltman et al., 1982) have been used as low-P treatments. Gutschick and Kay (1995) included 0.1 to 1.0 μM P in their low-P treatments and considered 3 μM as luxury-P treatment. Such very low P concentrations may be depleted within a very short time after addition to the solution (Lynch et al., 1990), and, if appropriate equipment is not used to monitor and regulate P supply frequently, some kind of P-buffer system is needed to maintain sufficiently low and stable P concentrations in the media. The method used in our study was a simple, inexpensive, and reproducible way of preparing alumina-P buffers. For a larger scale use of alumina-P buffers, an automated system for Al preparation could be developed. Gourley et al. (1993) found that P adsorption onto alumina was rapid (66% to 77% of total P within the first 24 h), indicating that the preparation period of alumina-P buffers might be reduced by reducing the loading time.

The high and positive stem biomass flux in reproductive nondeficient plants continuing until anthesis and coinciding with decreased leaf and root biomass flux (Fig. 1) provide evidence of C allocation to developing flowers. Positive and increasing biomass flux in all tissue categories of vegetative nondeficient plants

Table 3. Phosphorus concentration (dry mass basis) in vegetative and reproductive chrysanthemum plants grown with three P levels. Each value is the mean of 15 plants (three replications × five harvests) with standard error in parentheses measured at five harvests through time.

	P (mmol·g^{-1})				Total root P:	
	Total	Leaf	Stem[z]	Root	total shoot P[y]	df
Low P (P1)						
Vegetative	0.05 (0.01)	0.07 (0.01)	0.03 (0.03)	0.06 (0.02)	0.44 (0.01)	
Reproductive	0.06 (0.01)	0.08 (0.01)	0.04 (0.03)	0.06 (0.02)	0.45 (0.01)	
Medium P (P2)						
Vegetative	0.24 (0.01)	0.29 (0.01)	0.15 (0.03)	0.34 (0.02)	0.20 (0.01)	
Reproductive	0.29 (0.01)	0.40 (0.01)	0.20 (0.03)	0.37 (0.02)	0.17 (0.01)	
High P (P3)						
Vegetative	0.34 (0.01)	0.43 (0.01)	0.17 (0.03)	0.56 (0.02)	0.24 (0.01)	
Reproductive	0.38 (0.01)	0.54 (0.01)	0.22 (0.03)	0.58 (0.02)	0.25 (0.01)	
F value						
P treatment (P)	1318^{***}	796^{***}	679^{***}	509^{***}	63^{***}	2
Daylength (DL)	20^{***}	24^{*}	85^{***}	2^{NS}	0^{NS}	1
WAT[x]	13^{***}	7^{***}	12^{***}	0^{NS}	38^{***}	4
P × DL	1^{NS}	5^{**}	13^{***}	2^{NS}	1^{NS}	2
P × WAT	3^{**}	2^{NS}	3^{**}	1^{NS}	6^{***}	8
DL × WAT	2^{NS}	2^{NS}	5^{**}	1^{NS}	1^{NS}	4
P × DL × WAT	2^{NS}	1^{NS}	4^{**}	1^{NS}	1^{*}	8

[z]Includes stems and flower buds (if present).
[y]Includes leaves, stems, and flower buds (if present).
[x]WAT = weeks after transplanting.
^{NS,*,**,***}Nonsignificant or significant at $p = 0.05$, 0.01, or 0.001, respectively.

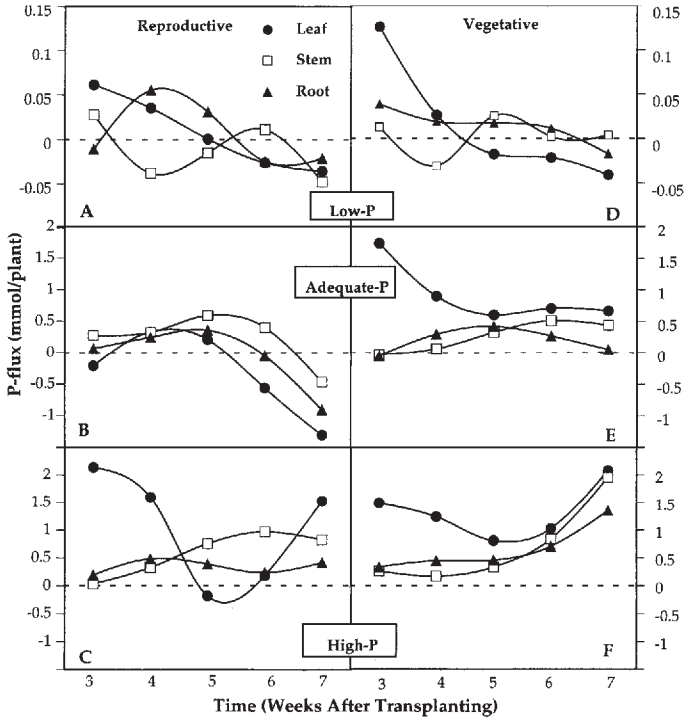


Fig. 4. Weekly phosphorus flux in leaves, stems, and roots of reproductive (**A–C**) and vegetative (**D–F**) plants at three P treatments. Each point represents the differentiated value of the mean of three replications.

supports the suggestion of changes in the source–sink relationships during transition to reproductive growth, indicating that the root may become a less competitive sink than the developing flowers. However, the significant decline in the CPR_{leaf} and the slight decline in CPR_{root} in reproductive compared with vegetative plants showed that leaves were affected to a much larger extent than roots during transition to reproductive growth.

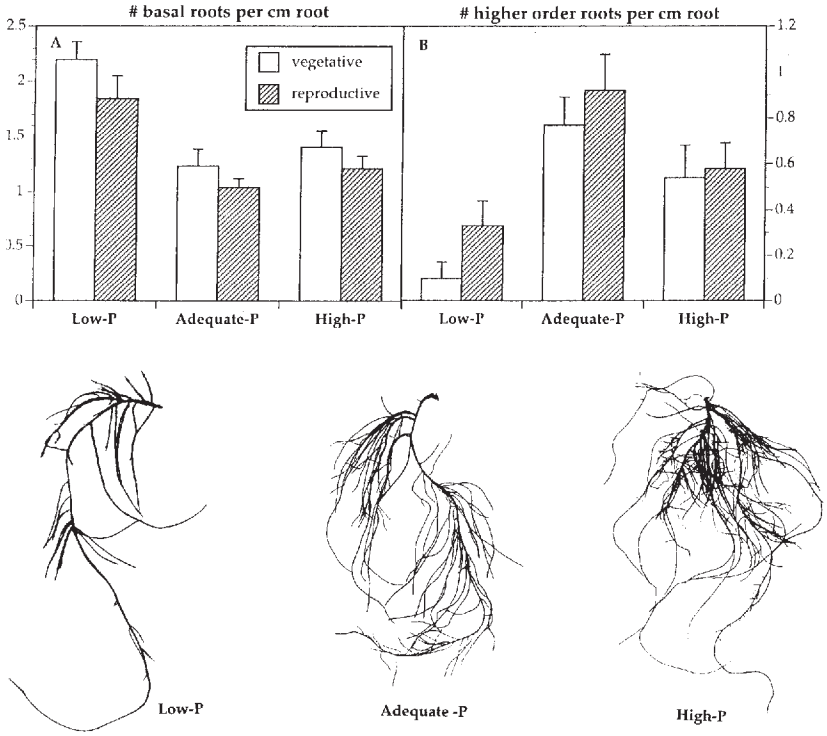
The decline in root growth rates in nondeficient, reproductive plants compared with vegetative plants, but not in P-deficient plants, reflects a higher sink strength by developing flowers due to a higher number of flower buds present in adequate-P and high-P plants.

Plant P content increased to a lesser extent in leaves and roots than in stems of reproductive compared to vegetative plants (Table 3), indicating that remobilization of P from leaves and roots to developing flowers took place and may account for the negative P flux predominantly seen in leaves and roots of reproductive, adequate-P plants. The significantly higher RGR, leaf dry matter accumulation (Table 1), and leaf area (Hansen et al., 1997, 1998) in vegetative compared with reproductive plants suggest that the decline in leaf P in vegetative plants when expressed on a dry mass basis (Table 3) may be explained by the P content's being "diluted" in more tissue.

Similar biomass production (Table 1) in adequate-P and high-P plants showed that there were no growth benefits other than a higher number of colored flower buds at anthesis from applying the extra available P in the high-P treatment. Kageyama and Konishi (1992) found that high-P reduced time to flowering in chrysanthemum. The total number of flower buds rather than the number of colored flower buds is needed to give a precise picture of the impact of high-P on flower bud production. Although anthesis occurred within the same week the lower number of colored buds in adequate-P plants might have been due to a slightly delayed flower development. Even if the number of flower buds might have been reduced, the flower bud production in adequate-P plants is considered to be very high and therefore shows that high-P is not needed for a sufficient flower production. Lynch et al. (1991) found that leaf CO_2 exchange rate (CER) was linearly correlated with leaf P concentration (dry mass basis) up to 70 $\mu mol \cdot g^{-1}$ in common bean, and further increments in P concentration did not increase CER further. Similar CO_2 assimilation rates in adequate-P and high-P plants measured on a whole-plant level in this study (Hansen et al., 1997, 1998) support this finding.

The decrease in RLR (Fig. 1B) and SRL (Table 2) in high-P compared with adequate-P plants may indicate some differences in root topology between plants from the two highest P treatments. Analysis of the number of basal and higher order roots in scanned images of root subsamples supported this assumption by showing significantly fewer higher order roots per unit root length in high-P plants (Fig. 5B). This is consistent with the findings of Han (1995) that root branching was significantly reduced in different bean species when grown with high-P (1 mM) compared with P-starvation resulting in a lower number of lateral meristems per cm root. The significantly lower number of growing points in high-P plants may account for the reduced root respiration compared with adequate-P plants (Hansen et al., 1997, 1998). Phosphorus deficient plants showed a high frequency of basal roots but a low number of higher order roots (Fig. 5A) resulting in a more herringbone topology compared with nondeficient plants (Fig. 5C).

Fig. 5. Number of basal roots (**A**) and higher order roots (**B**) in vegetative and reproductive plants at three P treatments. Each bar is the mean of three replications, with SE. Effects of P treatment and growth stage on the number of basal roots were significant at $p = 0.001$ and 0.05, respectively, and at $p = 0.001$ and 0.01, respectively, for the number of higher order roots. (**C**) Images of root subsamples.



If water and nutrient uptake are based more upon root length than mass as suggested by Eissenstat (1992) the increased SRL in adequate-P compared with high-P plants (Table 2) may indicate that plants grown with reduced P invest their root biomass more efficiently than high-P plants.

The reduction of RGR of low-P plants was not only attributable to a decrease in photosynthetic rate. SLM increasing by 30% compared to plants grown with the highest P concentrations and starch accumulation in young leaves (Hansen et al., 1997, 1998) may indicate that growth was inhibited more than photosynthesis. However, the high root mass to leaf area ratio implies that P-deficient plants had to sustain more root mass per unit photosynthesizing area and is consistent with findings of Lynch and Beebe (1995). The significantly higher RSR in P-deficient plants compared with nondeficient plants (Fig. 2A) was achieved by early and persistent suppression of shoot growth but not root growth. This is similar to findings reported for other species (e.g., Rao et al., 1993 (soybean, *Glycine max*; and sugar beet, *Beta vulgaris*); Lynch et al., 1991 (common bean, *Phaseolus vulgaris*); Gutschick and Kay, 1995 (sunflowers, *Helianthus annuus*)).

Fredeen et al. (1989) found that low-P plants accumulated more P in roots than in shoots. Even though we found a nearly 2-fold higher root to shoot P ratio in P-deficient plants (Table 3) the P content in roots did not exceed the shoot content. Changes in the root to shoot P ratio reflects that roots undergo adaptive changes in response to P deficiency such as shifting biomass partitioning by limiting shoot growth more than root growth (Fig. 1A and Table 1) and thereby affecting the balance between roots acquiring P and the shoots using it to support the photosynthetic rate and flower development. The increased root to shoot P ratio in P-deficient plants (Table 3) showed that a higher proportion was either retained in the roots or reallocated from the leaves to the roots. Decreasing P content over time in leaves of P-deficient plants coincided with wilting of basal leaves and increasing root P content (Fig. 3 and 4) suggesting that reallocation of P from senescing leaves to the roots took place due to a high demand for P for root growth.

Our observation that P-uptake increased with increasing P availability, as indicated by continued increases in plant P content, even though biomass production and RGR were quite similar in plants receiving adequate-P and high-P is consistent with findings of Crafts-Brandner (1992) and Kageyama and Konishi (1992). This may indicate a luxury or storage pool of P not active in or needed for CO_2 assimilation and suggests a low efficiency of P utilization. In reproductive plants, however, the increased P-uptake is most likely due to supporting the higher number of developing flowers in high-P plants. Of the two highest P levels employed in our study, the high-P level most closely corresponds to the levels used in conventional horticultural production systems. Our data suggest that besides the higher number of colored flower buds at anthesis, there were no growth benefits from employing high P availability, whereas high P availability reduced root growth. The impact of improved root growth on postproduction stress tolerance will be assessed in future studies.

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