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Influence of phosphorus on gas exchange and plant growth of two morphologically distinct types of *Capsicum annuum*

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Abstract

Tolerance to phosphorus stress was studied in *Capsicum annuum* L. Chile ancho cv. San Luis and bell pepper cv. Jupiter plants. Plants were fertilized weekly with Long-Ashton nutrient solution (LANS) modified to supply 0, 11, 22, 44, 66, or 88 g(P) m^{-3} (P0, P11, P22, P44, P66, P88). Phosphorus stress occurred in both cultivars at P0 and P11, with reduced plant growth and development. At P0, the lowest percentage of total biomass was directed toward reproductive growth. The root/shoot ratio was greatest at P0, reflecting greater dry matter partitioning to the root system. Growth of 'San Luis' was more sensitive to phosphorus stress than 'Jupiter'. A greater percentage of total biomass was directed towards reproductive growth in 'Jupiter' than 'San Luis'. Increasing P nutrition elevated leaf tissue P in both cultivars with highest leaf tissue P at P88. There were no differences in tissue P between P0 and P11 'San Luis' plants, whereas P0 'Jupiter' plants had the lowest tissue P. Low P-plants generally had the highest tissue N and lowest S, Mn, and B. In both cultivars, gas exchange was lowest at P0, as indicated by reduced stomatal conductance (g_s) and net photosynthetic rate (P_N). Internal CO_2 concentration and leaf-to-air vapor pressure difference (VPD) were generally highest with P-stressed plants. Phosphorus use efficiency, as indicated by P_N per unit of leaf tissue P concentration (P_N/P), was highest at P11. Generally, no P treatments exceeded the gas exchange levels obtained by P44 (full strength LANS) plants. Both P_N and g_s declined during reproductive growth in 'San Luis', which fruits more rapidly than 'Jupiter', whereas no reduction in gas exchange occurred with 'Jupiter'.

Introduction

The limitation of P deficiency to agricultural production is an enormous worldwide problem, including pepper production areas in the US and Mexico. P deficiency reduces P_N (Dietz and Foyer 1986). Bell pepper is highly responsive to P nutrition and dependent on mycorrhizae for P uptake (Haas *et al.* 1987, Davies and Linderman

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1991). Pepper is the principal export crop of Mexico to the US and Canada during November to May and has an estimated economic value of >$500 million. Chile ancho pepper is an important source of vitamin C in the Mexican diet, and has gained international popularity with the increased consumption of Mexican foods (Bosland 1992).

The objectives of this study were to characterize the effect of P nutrition on growth and gas exchange of two *C. annuum* cultivars: a bell pepper type and a chile ancho pepper, which differ in morphology and growth habit. Do these two types differ in sensitivity to P-stress? Long-term goals of this research include the selection of mycorrhizal symbionts that enhance P-stress tolerance of these two cultivars.

Materials and methods

Seeds of the *C. annuum* Chile ancho pepper cv. 'San Luis' and bell pepper cv. 'Jupiter' were planted in 1 peat: 1 perlite (v/v) on August 4, 1993 and transplanted 2 weeks later (at the 2-leaf stage) into 1 700 cm^3 containers containing 1 coarse sand: 1 low-P soil (v/v) with a nutrient analysis [g m^{-3}] of 0.9 NO_3-N, 2.1 NH_4-N, 1.5 P, and 10.7 K, pH of 7.7, EC of 0.17, and textural analysis of 85 % sand, 10 % clay, and 5 % silt.

Plants were established in a glasshouse with average day and night temperatures of 21.4 and 20.0 °C, respectively. Relative humidity ranged from 55 to 98 % and maximum photosynthetic photon flux (PPF) was from 1000 to 1200 μmol m^{-2} s^{-1} at plant height. Plants were grown under long-day conditions by using supplemental incandescent lighting with a 2-h night interruption. Prior to transplanting, seedlings were fertilized using full strength Long-Ashton nutrient solution (LANS; Hewitt 1966) containing 44 g(P) m^{-3}. After transplanting, plants were fertilized weekly using 250 cm^3 of modified LANS containing 0, 11, 22, 44, 66, or 88 g(P) m^{-3} (P0, P11, P22, P44, P66, P88).

Gas exchange was measured 50 and 76 d after transplanting on chile ancho peppers and 65 and 94 d after transplanting on bell peppers. P_N, g_s, intercellular CO_2 concentration (C_i), and air-to-leaf vapor pressure differences (VPD) were measured on two newly matured leaves of five plants per treatment ($n = 10$) with a portable photosynthesis unit (*LI-6200*, *Li-Cor*, Lincoln, NE, USA) using the *Li-Cor* 250 cm^3 chamber. Measurements were made on newly matured leaves from 09:00-11:00 h and 13:30-15:30 h in the glasshouse where plants were grown. Only the afternoon values are presented, since treatment effects were the same. All P_N and g_s measurements were made with the initial CO_2 concentration at about 360 cm^3 m^{-3} under 1000 μmol m^{-2} s^{-1} of PPF from a 400 W high pressure sodium vapor lamp filtered through 5 cm of water enclosed in a *Plexiglas* box. Phosphorus use efficiency (P_N/P) was calculated by dividing afternoon P_N on the final day for gas exchange measurement by leaf P concentration at the end of the experiment.

Fifteen plants per treatment ($n = 15$) were harvested on day 77 for 'San Luis' and day 95 for 'Jupiter', respectively. The experiments were arranged in a completely randomized block design. Treatment effects were determined by using ANOVA

(SAS Institute 1988). Each cultivar was treated as a separate experiment. 'San Luis' grows and fruits more quickly than 'Jupiter'. The decision to harvest at different chronological dates was based on both cultivars having achieved similar morphological (reproductive) stages of development. Plants were measured for leaf number, as well as leaf area, fruit number, fruit, leaf, and stem fresh and dry masses. Total plant dry mass, root/shoot ratio, and leaf area ratio were determined. Leaf tissue elements were determined with an inductively coupled plasma atomic emission spectrophotometer (*3510ICP, W.R. Grace & Co*, Fogelsville, PA, USA). Newly matured leaves were harvested from 15 plants, and 5 plants were pooled per replication ($n = 3$).

Results

Phosphorus stress was observed in 'San Luis' and 'Jupiter' at P0 and P11 in the form of reduced plant growth and development: leaf number and area, fruit, leaf, and stem dry mass, root, shoot and total plant dry masses (Table 1). Greatest P-stress occurred at P0 with 84 and 80 % reductions in San Luis and Jupiter, respectively, in total plant

Table 1. Influence of phosphorus (P) on plant growth and development of *Capsicum annuum* Chile ancho 'San Luis' and bell pepper 'Jupiter' (values represents a mean of 15 plants ±SE). *Values analyzed with ANOVA, using GLM procedures (SAS Institute, Cary, North Carolina). dm = dry mass.

P	Leaf No.	Leaf area [cm^2]	Fruit No.	Fruit dm [g]	Leaf dm [g]	Stem dm [g]	Root dm [g]	Total plant dm [g]	Root/ shoot ratio [kg kg^{-1}]
'San Luis'									
P0	33.8±2.7	188±15	0.1±0.1	0.1±0.1	0.7±0.1	1.0±0.1	0.8±0.1	2.6±0.2	0.44±0
P11	59.7±3.3	560±24	2.0±0.2	2.8±0.4	3.1±0.2	3.1±0.2	1.6±0.1	10.6±0.4	0.17±0
P22	71.3±3.2	748±24	2.4±0.3	4.9±0.4	4.0±0.2	4.1±0.2	2.1±0.1	15.1±0.6	0.16±0
P44	75.9±4.2	761±21	2.0±0.2	5.7±0.2	4.2±0.2	4.5±0.2	2.3±0.1	16.7±0.6	0.16±0
P66	76.3±3.6	829±26	2.9±0.4	5.8±0.4	4.3±0.2	4.7±0.2	2.4±0.1	17.2±0.6	0.16±0
P88	74.6±2.9	814±11	2.4±0.2	6.3±0.3	4.3±0.1	4.6±0.2	2.5±0.1	17.7±0.5	0.16±0
$P>F^*$	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
'Jupiter'									
P0	24.8±2.1	335±29	0.5±0.1	0.5±0.1	1.5±0.1	0.9±0.1	1.1±0.1	4.0±0.2	0.38±0
P11	35.3±1.9	668±29	1.9±0.2	8.7±0.5	3.4±0.1	2.2±0.1	2.1±0.1	16.4±0.8	0.15±0
22	41.4±1.9	756±19	2.4±0.3	10.7±0.4	3.7±0.1	2.3±0.1	2.4±0.1	19.1±0.8	0.14±0
44	43.2±1.8	840±17	2.7±0.3	10.8±0.6	3.8±0.1	2.7±0.2	2.5±0.2	19.8±1.5	0.14±0
66	40.5±1.5	787±20	2.7±0.3	12.5±0.3	3.7±0.1	2.2±0.1	2.1±0.1	20.5±1.3	0.11±0
88	40.8±1.6	798±27	3.1±0.3	12.4±0.6	3.6±0.1	2.5±0.1	2.5±0.1	21.0±0.9	0.14±0
$P>F^*$	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

dry mass compared to the full strength LANS (P44) treatment. At P0, the lowest percentage of total biomass was directed toward reproductive growth, *e.g.*, 4 and 13 % for 'San Luis' and 'Jupiter', respectively. The root/shoot ratio was greatest at P0, reflecting greater dry matter partitioning to the root system. Generally, maximum growth was observed at P44; however, at P66 and P88 leaf area was greatest in 'San Luis', and fruit dry mass greatest in 'Jupiter'. A greater percentage of total biomass was directed towards reproductive growth in 'Jupiter' than 'San Luis' (*e.g.*, 13 *vs.* 4 % at P0, and 55 *vs.* 34 % at P44). 'San Luis' was more sensitive to P-stress at P11 than 'Jupiter' with a 37 *vs.* 17 % reduction in total plant dry mass, respectively, when compared to plants receiving full strength LANS (P44).

With increasing P supply, leaf tissue P increased in both cultivars with maximum leaf tissue P at P88 (Table 2). In 'San Luis', there were no differences in tissue P between P0 and P11 plants, whereas P0 'Jupiter' plants had the lowest tissue P. Low-P plants generally had the highest tissue N and lowest S, Mn, and B. Low-P 'San Luis' had higher K, while low P 'Jupiter' had lower K than higher P plants.

Table 2. Influence of phosphorus (P) on leaf elemental content of *Capsicum annuum* Chile ancho 'San Luis' and bell pepper 'Jupiter'. Means of all leaves of five plants that were pooled for a single measurement with 3 pooled samples per treatment ($n = 3$). *Values analyzed with ANOVA, using GLM procedures (SAS Institute, Cary, North Carolina, USA). NS = not significant.

Cultivar	P	N [%]	P [%]	K [%]	S [%]	Mn [mg kg^{-1}]	Cu [mg kg^{-1}]	B [mg kg^{-1}]
'San Luis'	P0	5.47±0.09	0.09±0.01	2.65±0.14	0.34±0.03	46.1±3.2	8.5±0.5	35.8±3.0
	P11	3.20±0.00	0.11±0.01	2.55±0.23	0.51±0.05	56.9±0.7	11.0±0.2	49.0±1.8
	P22	2.43±0.09	0.17±0.01	1.97±0.06	0.47±0.02	59.3±3.2	11.5±0.2	52.8±1.0
	P44	1.97±0.20	0.22±0.01	1.85±0.12	0.42±0.01	55.6±3.2	11.1±0.0	54.1±0.9
	P66	2.20±0.15	0.28±0.02	1.73±0.17	0.45±0.02	57.6±2.2	11.3±0.1	51.9±0.9
	P88	2.17±0.09	0.36±0.01	1.96±0.08	0.46±0.02	60.7±1.4	12.6±0.6	60.7±3.9
*P>F**		0.0001	0.0001	0.0031	0.0079	0.0343	0.0001	0.0003
'Jupiter'	P0	5.73±0.12	0.03±0.01	1.35±0.11	0.17±0.00	30.0	5.4±0.2	20.0±1.3
	P11	4.03±0.03	0.07±0.02	1.88±0.31	0.36±0.10	47.0	6.1±0.4	37.3±13.6
	P22	3.43±0.12	0.13±0.00	2.37±0.11	0.41±0.01	47.7	7.7±0.2	42.0±3.4
	P44	2.93±0.20	0.23±0.02	2.40±0.11	0.38±0.02	56.3	8.1±0.5	50.0±1.9
	P66	3.27±0.07	0.29±0.03	2.38±0.12	0.44±0.01	65.2	10.0±1.2	64.8±9.6
	P88	3.40±0.12	0.36±0.01	2.22±0.09	0.40±0.03	49.3	8.5±0.7	53.7±5.6
*P>F**		0.0001	0.0001	0.0055	0.0217	NS	0.0073	0.0318

In both cultivars, gas exchange was lowest at P0, as indicated by low g_s and P_N (Table 3). At P0, C_i was generally highest indicating that CO_2 was accumulating in mesophyll tissues with lower g_s and P_N in P-stressed plants; the leaf-to-air VPD was also generally highest at the maximum P-stress. Both cultivars had greatest phosphorus use efficiency (P_N/P) at P11 (Fig. 1). Generally, no P treatments exceeded the gas exchanges obtained in P44 plants.

Table 3. Influence of phosphorus (P) on gas exchange of *Capsicum annuum* 'San Luis' at 50 and 76 d and 'Jupiter' at 65 and 94 d after transplanting. Net photosynthetic rate (P_N), stomatal conductance (g_s), internal CO_2 concentration (C_i), and vapor pressure difference (VPD). Measurements on 2 leaves per plant and five plants per treatment ($n = 3$). *Values analyzed with ANOVA, using GLM procedures (*SAS Institute*, Cary, North Carolina, USA).

Day	P	P_N [µmol m^{-2} s^{-1}]	g_s [mol m^{-2} s^{-1}]	C_i [cm^3 m^{-3}]	VPD [kPa]
'San Luis'					
50	P0	1.98±0.42	0.14±0.02	302.0±3.9	19.93±0.52
	P11	9.52±0.45	0.34±0.04	263.6±3.4	17.66±0.63
	P22	8.66±1.23	0.36±0.06	274.7±3.9	17.38±1.09
	P44	9.00±0.55	0.31±0.03	267.3±1.9	17.43±0.40
	P66	9.24±0.80	0.35±0.05	269.7±3.9	15.68±1.06
	P88	11.13±1.15	0.59±0.09	274.6±2.3	15.35±0.48
*P>F**		0.0001	0.0001	0.0001	0.0001
76	P0	1.15±0.29	0.03±0.01	308.9±7.3	18.25±0.36
	P11	4.74±1.04	0.14±0.03	294.5±7.5	18.16±0.97
	P22	4.54±0.50	0.10±0.02	283.3±4.6	19.66±1.03
	P44	4.96±0.57	0.12±0.01	288.6±5.9	17.75±0.62
	P66	5.57±0.41	0.14±0.01	283.3±4.4	16.78±0.34
	P88	7.76±1.13	0.26±0.05	296.7±5.5	15.54±0.71
*P>F**		0.0001	0.0001	0.0455	0.0049
'Jupiter'					
65	P0	2.96±0.25	0.09±0.01	273.3	20.18±0.78
	P11	8.49±0.91	0.35±0.08	272.9	18.80±0.95
	P22	10.85±0.60	0.69±0.09	288.0	15.03±0.66
	P44	12.38±0.75	0.78±0.19	277.8	15.46±0.95
	P66	9.51±0.92	0.60±0.18	276.3	16.68±0.80
	P88	11.65±0.82	0.69±0.13	276.5	16.70±0.64
P>F*		0.0001	0.0029	NS	0.0002
94	0	1.88±0.21	0.08±0.01	316.8±3.5	21.83±0.64
	11	12.54±0.71	0.44±0.06	285.0±3.2	17.13±0.72
	22	14.54±1.46	0.98±0.03	297.6±2.7	15.25±0.68
	44	15.14±0.57	0.99±0.06	306.8±3.7	13.71±0.37
	66	15.59±1.38	1.06±0.16	298.7±3.1	14.46±0.82
	88	15.69±0.99	1.06±0.13	300.5±4.0	13.34±0.61
*P>F**		0.0001	0.0001	0.0001	0.0001

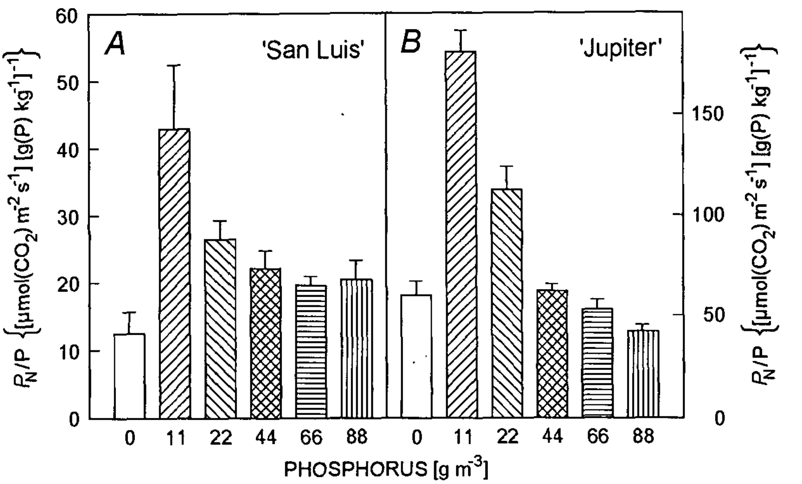

Fig. 1. Phosphorus use efficiency of 'San Luis' and 'Jupiter' peppers. Phosphorus use efficiency (P_N/P) was calculated by dividing afternoon P_N on the final day for gas exchange measurement by leaf elemental P concentration at the end of the experiment (n = 10).

Discussion

This work characterizes the role of P nutrition on gas exchange and plant growth and development of two morphologically different *C. annuum* cultivars. 'San Luis' had smaller individual leaves and a reduced leaf area than 'Jupiter' bell pepper—characteristics that can allow greater tolerance to drought (Kramer and Boyer 1995). Other traits included a higher percentage of plant biomass directed towards vegetative than reproduction growth in 'San Luis', which also had a greater root/shoot ratio than 'Jupiter' (0.44±0 and 0.38±0 kg kg^{-1}, respectively). 'Jupiter' peppers must receive supplemental irrigation during commercial production, while production of 'San Luis' in Mexico is not always on irrigated land (Andrews 1995). 'San Luis' fruits more quickly than 'Jupiter'.

Greatest P-stress occurred at P0 with dramatic reductions in P_N and g_s, vegetative and reproductive growth. While growth of P11-treated plants was greatly reduced, gas exchange was comparable to higher-P-treated plants. In part, this may be explained by the greater efficiency of photosynthesis per unit of leaf P concentration (P_N/P) in the P11-treated plants. P_N/P is relevant to studies of this nature because P_N is a key growth parameter, and P deficiency limits crop productivity. None of these plants were inoculated with mycorrhizae in these experiments; however, a long-term goal of this research is to select mycorrhizal symbionts that enhance P-stress tolerance of *C. annuum*. Phosphorus nutrition is considered to be central to mycorrhizal enhancement of plant growth and its subsequent application in low input sustainable agricultural systems. High P_N/P values were found in mycorrhizal plants (Brown and Bethlenfalvay 1988, Davies *et al.* 1993). Plants with optimum P concentration should be more vigorous with higher P_N and g_s than plants with limiting P (Radin 1984, Dietz and Foyer 1986, Radin and Eidenbock 1986, Hansen *et* *al.* 1998). Low P can also reduce the concentration and activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) and slow the regeneration of intermediate substances in the Calvin cycle (Lauer *et al.* 1989, Rao and Terry 1994). In our study, the higher value of P_N/P at P11 was due both to a low P concentration and a high P_N relative to P0 plants. Apparently there is a threshold of 0.11 and 0.07 % leaf tissue P that must be obtained for 'San Luis' and 'Jupiter', respectively, to significantly enhance gas exchange. Above P22, there was generally no further increase in P_N in both cultivars while tissue P concentration tended to increase and thus, P use efficiency decreased. Commercially produced peppers are nutrient deficient at 0.15 % and nutrient sufficient at 0.25 % P (Maynard and Hochmuth 1997), which corresponds with our growth and gas exchange results.

'San Luis' was more sensitive to P stress than 'Jupiter'. At P11, phosphorus stress was greater for 'San Luis' than 'Jupiter' as indicated by a 37 *vs.* 17 % reduction, respectively, in total plant dry mass when compared to plants receiving full strength LANS (P44). 'San Luis' had a 45 % reduction in individual leaf area (5.6 *vs.* 10 cm^2, respectively, at P0 and P44 treatments), while 'Jupiter' had a 30 % reduction (13.4 *vs.* 19.4 cm^2, respectively). At P11 there was a 51 and 19 % reduction in reproductive growth, respectively, for 'San Luis' and 'Jupiter' when compared to full strength LANS. At P0, P11, and P22, P levels were lower ($p < 0.0001$) in 'Jupiter' than Chile ancho, yet phosphorus use efficiency (P_N/P) was also greater in 'Jupiter' than 'San Luis' due to lower tissue P and higher P_N. Phosphorus use efficiency was also 493 to 200 % greater in 'Jupiter' than 'San Luis' from P0 and P88. Although each cultivar was treated as a separate experiment, gas exchange measurements were made when both cultivars achieved similar morphological (reproductive) stages of development, because 'San Luis' fruits more quickly than 'Jupiter'. The decision to terminate the 'San Luis' experiment was in part that P_N and g_s declined between days 50 and 76, while 'Jupiter' did not decrease in these parameters between sampling dates. The transition from vegetative to reproductive growth can result in reduced photosynthetic production (Hansen *et al.* 1998); this occurred with 'San Luis', but was not a factor with 'Jupiter'.

While leaf tissue P increased with increasing P application, growth generally plateaued at P44. Low-P plants generally had the highest tissue N and lowest S, Mn, and B, which agrees with other reports on P (Hewitt and Smith 1974). Low-P 'San Luis' plants had a higher K, while low P 'Jupiter' had the lowest K. P44 decreased leaf tissue N and K of bell pepper Early Bountiful (Davies and Linderman 1991). The values suggest that luxury consumption of P occurred above P44 (both cultivars had 0.36 % P at P88), but total plant dry mass did not increase. While P_N was highest in 'San Luis' at P88, there was no difference in P_N of 'Jupiter' among P44 to P88 treated plants.

In summary, P-stress reduced plant growth and development and gas exchange of Chile ancho 'San Luis' and 'Jupiter' bell pepper. 'San Luis' was more sensitive to P-stress than 'Jupiter'. A greater percentage of total biomass was directed towards reproductive growth in 'Jupiter' than 'San Luis'. The smaller leaves of 'San Luis' which are apparently beneficial under water stress do not provide a benefit under P-deficiency. Selection of cultivars adapted to water stress may result in below average yields at P-deficiency. C_i and VPD deficit were generally highest with P-stressed plants, due to low g_s. The potential for low P to limit RuBPCO regeneration and affect P_N should have significant effects on g_s as stomata are sensitive to C_i (Radin 1984, Radin and Eidenbock 1986). The subsequent reduction in carbon uptake adversely affected the ontogeny of both pepper cultivars. Phosphorus use efficiency (P_N/P), was highest at P11. Apparently there is a threshold of 0.11 and 0.07 % leaf tissue P that must be obtained for 'San Luis' and 'Jupiter', respectively, to significantly enhance gas exchange.

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