Calcium-activated Root Growth and Mineral Nutrient Accumulation of *Lupinus havardii*: Ecophysiological and Horticultural Significance

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ABSTRACT. *Lupinus havardii* Wats. (Big Bend bluebonnet) has received considerable attention as a new specialty cut flower crop. We studied the consequences of Ca fertigation on growth, water use, and mineral nutrient uptake of *L. havardii* ('Texas Sapphire') for 88 days in a greenhouse. Four Ca concentrations were included (as CaCl₂) in the fertigation solution at concentrations of 0, 2.5, 5.0, or 10.0 mM. Calcium supply did not affect the number of racemes produced per plant or total dry matter accumulation per plant. However, root dry matter accumulation, root : shoot ratio, net root mineral nutrient accumulation (milligrams P, K, Ca, Mg, and Fe per plant; micrograms Mn, B, and Cu per plant), and the preferential allocation of mineral nutrients to roots were influenced quadratically by CaCl₂ supply, increasing up to 5.0 mM CaCl₂ and then decreasing at 10.0 mM CaCl₂. Lack of root sink response by plants exposed to 10.0 mM CaCl₂ was associated with lowest daily rate of pot evapotranspiration, probably resulting from osmotic or Cl toxicity stress. Increased root sink strength for dry matter and mineral nutrients in response to CaCl₂ supply up to 5.0 mM Ca is consistent with calcicole-like behavior and the native distribution of *L. havardii* on xeric, calcareous soils, where root growth and expansion favoring water and mineral nutrient acquisition may be of significant adaptive value for survival. The Ca-related increase in root growth was reflected in up to a 5% to 20% increase in fertilizer P and K recovery per plant. Results indicate that Ca fertilization may be an effective horticultural strategy in greenhouse production of *L. havardii*, particularly for matching the natural edaphic habitat of the species and thus increasing efficiency of water and mineral nutrient management.

The fragrant and attractive blue raceme of the winter annual *Lupinus havardii* has considerable potential as a new greenhouse specialty cut flower in the southwestern United States (Davis et al., 1994). Since *L. havardii* is indigenous to a narrow geographic band extending ~500 to 600 km along the Texas–Mexico border, which surrounds Big Bend National Park (see map in Davis et al., 1994), the species is commonly known as Big Bend bluebonnet. This semiarid region is located in the Chihuahuan Desert and is characterized by xerophytic vegetation, low annual rainfall (15 to 30 cm per year), high annual mean temperature (19 to 20 °C), long frost-free growing season (230 to 290 d), 65% to 80% mean annual possible sunshine, and high surface evaporation potential (180 to 230 cm per year) with a significant precipitation deficit every month of the year (Arbingast et al., 1973; Levings et al., 1998). The harsh climate is accompanied by calcareous soils, often underlain by indurated CaCO₃ layers, and the cationic composition of its intermittent surface waters is dominated by Ca and Mg (Arbingast et al., 1973; Soil Conservation Service, 1974, 1985).

Calcium improves the productivity and postproduction quality of floricultural crops (Harbaugh and Woltz, 1989; Huett, 1994; Lawton et al., 1989; Mikesell, 1992; Starkey and Pedersen, 1997;

Torre et al., 1999; Volpin and Elad, 1991; Woltz and Harbaugh, 1986), including *L. havardii*, as we have observed in a preliminary study (Valenzuela-Vazquez and Picchioni, 1999). However, the consequences of Ca fertilization on *L. havardii* growth and mineral nutrient uptake are not known. The most commercially important *Lupinus* sp. (*L. albus* L., *L. angustifolius* L., and *L. luteus* L.) are reported to possess calcifuge-like behavior, and for a myriad of postulated reasons, typically exhibit a growth reduction on Ca-supplemented root media or on naturally calcareous soils (Jessop et al., 1990; Loneragan and Snowball, 1969a, 1969b; Peiter et al., 2000; Tang et al., 1993a; White and Robson, 1989a, 1989b). Russell hybrid lupins are the only known *Lupinus* taxa to have received broad use as ornamentals (hardy herbaceous flowering perennial), and they, too, are thought to grow best under acidic soil conditions (Still, 1994).

It has long been established that growth of plants, in response to Ca-containing greenhouse culture solutions, occurs in a manner that closely correlates with the Ca status in soils of their native habitats (Clarkson, 1965; Snaydon and Bradshaw, 1961). In the recent floricultural literature, however, ecophysiological characteristics of crop species under study, in particular their native soil preferences, have received little attention. Thus, in artificial environments, the response of a floral crop to applied Ca may be positive (as discussed above), or it may be indifferent (Frett et al., 1985; Smith et al., 1998). No quantitative data are available on greenhouse culture and management of *L. havardii*, particularly in regard to mineral nutrient requirements and response to Ca fertilization.

In view of the indigenous distribution of *L. havardii*, we hypothesized that growth would respond positively to Ca in greenhouse culture solutions. Therefore, the objective of this research was to study the consequences of Ca fertilization (as CaCl₂) on growth, dry matter partitioning, water use (as inferred by evapotranspiration), net mineral nutrient uptake, and mineral nutrient allocation patterns among organs of *L. havardii*.

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Materials and Methods

PLANT MATERIAL, CULTURE, AND WATER USE. Seeds of 'Texas Sapphire' *L. havardii* were obtained in Winter 1997, originating from the third generation of recurrent phenotypic selection completed by Mackay and Davis (1998). To overcome physical dormancy, seeds were scarified in concentrated H_2SO_4 for 2 h (Mackay et al., 1996). On 27 Jan. 1998, 250 scarified seeds were sown individually into cell pack trays (individual cell volume of 170 mL; T.O. Plastics, Inc., Minneapolis, Minn.), containing Metromix 200 (50% to 60% vermiculite, 22% to 32% sphagnum moss, and 12% to 20% perlite, by volume; Scotts Co., Marysville, Ohio). Trays were taken to a greenhouse to await germination and for the duration of the experiment (described below), with temperature minima of $16 \pm 3^\circ C$ and maxima of $30 \pm 5^\circ C$. Maximum and minimum greenhouse irradiance at plant level was measured using a quantum sensor (LI-89; LI-COR, Inc., Lincoln, Nebr.). Natural photosynthetic photon flux [PPF (400 to 700 nm)] varied between 550 and $1250 \mu mol \cdot m^{-2} \cdot s^{-1}$.

Two weeks after sowing, germinated seedlings were 6 to 8 cm in height, and 68 seedlings were selected for uniformity and transplanted individually into 12-L plastic pots containing Metromix 200. From this stage through the end of the study, pots were fertigated with tap water containing (in $mg \cdot L^{-1}$) 100N–44P–83K supplied by Peters 20N–8.8P–16.6K water soluble fertilizer (J.R. Peters, Inc., Allentown, Pa.). Pots were irrigated by hand when an average of 50% of the total water storage had been depleted (total water storage measured 4 h after an irrigation). Water depletion was monitored gravimetrically on four single-plant pot replicates per treatment (described below), and the irrigation volume (3.4 L/pot) resulted in a leaching fraction of 6% to 14%. Fertigation frequency ranged between 4 and 9 d, depending on treatment, greenhouse air temperature, natural irradiance, and plant age. Gravimetric data were used to estimate evapotranspiration (ET, $mL \cdot d^{-1}$ per pot) by dividing total pot water depletion by number of days since the previous irrigation. Pot ET was monitored from 1 to 75 d past initiation of $CaCl_2$ treatment (described below), which comprised most of the 88-d treatment duration.

At first visible appearance of terminal reproductive buds (9 Apr.), $CaCl_2$ was added to the fertigation solution at concentrations of 0, 2.5, 5.0, or 10.0 mM. The tap water contained 1.2 mM Ca; hereafter, the four $CaCl_2$ treatment concentrations will be referred to as 0, 2.5, 5.0, and 10.0 mM $CaCl_2$. On 8 Apr. (1 d before initiation of $CaCl_2$ treatment), four representative plants were harvested. Roots

were washed free of growing medium then rinsed with deionized water. Shoots (combined leaves, petioles, and lateral and main stems) and roots were then dried at $60^\circ C$ for 10 d, and the tissues were saved for dry matter determination and mineral nutrient analysis as described below. The remaining crop (64 potted seedlings) was grown to maturity for dry matter and mineral nutrient analyses.

RACEME SAMPLING AND MINERAL NUTRIENT ANALYSES. Mature racemes were 40 to 55 cm in length and supported 25 to 30 fully opened flowers as stipulated in the cultivar guidelines published by Mackay and Davis (1998). Two racemes per treatment for each of four replications (blocks described below) were harvested 23 May, 10 June, and 16 June. Racemes were dried at $60^\circ C$ for 14 d, weighed, and saved for mineral nutrient analyses. Because of raceme variability (asynchronous raceme development within and between plants) and a minority of plant dry matter and mineral nutrient accumulation in racemes (<20% of plant totals), we did not determine total raceme dry matter and total raceme mineral nutrient accumulation per plant, rather only the raceme mineral nutrient concentrations expressed as an average of the three raceme harvest dates.

MEDIUM ANALYSES AND PLANT DRY MATTER ACCUMULATION, MINERAL NUTRIENT ACCUMULATION, AND NET MINERAL NUTRIENT UPTAKE PER UNIT OF ROOT WEIGHT. At the end of 88 d $CaCl_2$ treatment (6 July), the 5-month-old plants were harvested and divided into shoots (combined leaves, petioles, and lateral and main stems; racemes excluded) and roots. At this time, a 2-cm-wide $\times$ 10-cm-deep core of growing medium was removed from each pot. The pH and electrical conductivity (EC) were determined in the medium saturation extract. Roots were washed free of growing medium and rinsed with deionized water. Shoots and roots were then dried at $60^\circ C$ for 10 d, followed by dry weight determination. Dry matter accumulation was determined as the difference in dry matter obtained between final measurement (6 July) and the average measurement taken at the initiation of $CaCl_2$ treatment (8 Apr.).

Dried shoots, roots, and racemes were ground to pass a 40-mesh (0.635-mm) screen, and 100 to 200-mg subsamples were subjected to acid block digestion (Parkinson and Allen, 1975). Concentrations of P, K, Ca, Mg, S, Fe, Mn, B, Cu, and Zn were determined by a plasma emission spectrometer (JY70+, Instruments J.A., Edison, N.J.). Net mineral nutrient accumulation during $CaCl_2$ treatment per shoot or root system was determined as the product of mineral nutrient concentration and the corresponding organ DW, minus the average mineral nutrient content at the beginning of $CaCl_2$ treatment (8 Apr.). Percentage mineral nutrient distribution in shoots and

Table 1. Dry matter accumulation and root : shoot dry weight ratio of *Lupinus havardii* 'Texas Sapphire' during fertigation for 88 d with $CaCl_2$ solutions of varying concentrations.^z

CaCl ₂ solution concn (mM)	Dry matter accumulation (g/plant) ^y			Root : shoot ratio ^x
	Shoots	Roots	Total	
0	51.9	4.2	56.0	0.080
2.5	66.2	6.8	73.1	0.098
5.0	68.4	9.6	78.0	0.137
10.0	60.3	4.4	64.7	0.072
Significance				
L	NS	NS	NS	NS
Q	NS	**	NS	**

^zEach value is the mean of four, single-plant replications.

^yNet dry matter accumulation from initiation to termination of $CaCl_2$ treatment.

^xCalculated using final root and shoot dry matter at termination of $CaCl_2$ treatments.

NS,** Nonsignificant or significant main effects at $P \leq 0.01$ for $CaCl_2$ treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts.

Fig. 1. Evapotranspiration (ET) of *Lupinus havardii* 'Texas Sapphire' during fertigation for 88 d with CaCl_2 solutions of varying concentrations. Each symbol is the mean of four, single-plant replications obtained gravimetrically just before a fertigation. Time indicates days from initiation of CaCl_2 fertigation.

roots (as a function of total plant mineral nutrient accumulation, minus racemes) was also calculated.

The rate of net mineral nutrient uptake per unit of root weight (J), expressed weekly as $\mu\text{mol}\cdot\text{g}^{-1}\text{DW}$, was determined using the equation outlined by Pitman (1975) as follows:

$$J = (M_2 - M_1) / [W_R(T_2 - T_1)] \quad [1]$$

Values of M_2 and M_1 are the respective mineral nutrient contents of the whole plant (minus racemes) at time T_2 , the end of the study (6 July), and at T_1 , the beginning of CaCl_2 treatment (8

Apr.). The value of W_R is the root DW average between T_2 and T_1 .

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS. The experimental design was a randomized complete block with four blocks. Each block consisted of four plants per CaCl_2 treatment, and all data were subjected to analysis of variance (ANOVA) procedures. Sums of squares for CaCl_2 fertigation solution concentration main effects were partitioned into single degree of freedom linear and quadratic orthogonal contrasts. Pot ET, medium pH and EC, plant DW determinations, and plant mineral nutrient analyses included one randomly selected plant per block. Pot ET was analyzed factorially as $\text{CaCl}_2 \times \text{time}$ (4 CaCl_2 treatments $\times$ 12 pot weight dates). Plant dry matter accumulation, root : shoot DW ratio, mineral nutrient concentrations, net mineral nutrient accumulation, mineral nutrient percentage distribution, and the net uptake of mineral nutrients per unit of root weight were treated as a one-way ANOVA with the four CaCl_2 treatments.

Results

GROWING MEDIUM ANALYSES. EC of both fertigation solution (0.90 to $2.63\text{ dS}\cdot\text{m}^{-1}$) and its resulting growing medium saturation extract (1.66 to $2.65\text{ dS}\cdot\text{m}^{-1}$) were well correlated with CaCl_2 concentration of the fertigation solution ($r = 1.0$ and 0.99 , respectively; data not presented). Saturation extract medium pH (6.3 to 6.4) was slightly more acidic than that of the irrigation solution (6.7 to 6.9) and did not differ between the CaCl_2 treatments.

PLANT DRY MATTER ACCUMULATION AND PARTITIONING. Total dry

Table 2. Mineral nutrient concentrations in shoots, roots, and racemes of *Lupinus havardii* 'Texas Sapphire' following fertigation for 88 d with CaCl_2 solutions of varying concentrations.^z

CaCl_2 solution concn (mM)	Mineral nutrient					
	P	K	Ca	Mg	Mn	B
	(% dry wt)				$(\mu\text{g}\cdot\text{g}^{-1}\text{ dry wt})$	
Shoots						
0	0.41	1.95	1.46	0.68	---	---
2.5	0.37	1.82	1.63	0.60	---	---
5.0	0.38	2.36	1.92	0.68	---	---
10.0	0.31	2.06	2.57	0.76	---	---
Significance						
L	**	NS	**	NS	---	---
Q	NS	*	NS	NS	---	---
Roots						
0	0.35	0.63	0.87	0.61	76	14
2.5	0.37	1.05	1.09	0.82	116	13
5.0	0.52	1.52	1.74	1.43	211	19
10.0	0.63	1.11	1.97	0.86	186	20
Significance						
L	NS	NS	**	NS	**	*
Q	NS	**	NS	*	NS	NS
Racemes						
0	0.43	1.66	0.61	0.39	---	---
2.5	0.41	1.64	0.58	0.35	---	---
5.0	0.41	1.57	0.77	0.34	---	---
10.0	0.38	1.60	0.75	0.28	---	---
Significance						
L	**	NS	*	**	---	---
Q	NS	NS	NS	NS	---	---

^zEach value is the mean of four, single-plant replications.

NS,*,** Nonsignificant or significant main effects at $P \leq 0.05$ or 0.01 , respectively, for CaCl_2 treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts.

matter accumulation per plant in combined shoots and roots was unaffected by CaCl_2 treatment (Table 1). Total shoot dry matter accumulation, which comprised 88% to 93% of the dried vegetative biomass gains, was also unaffected by CaCl_2 treatment. Root dry matter accumulation per plant and the root : shoot ratio increased with increasing CaCl_2 supply up to 5.0 mM CaCl_2 . Roots of plants treated with 5.0 mM CaCl_2 accumulated over double the amount of dry matter than those of control plants, and this was reflected in a 71% increase in the root : shoot ratio. A decrease in root growth at 10.0 mM CaCl_2 caused an overall quadratic effect of CaCl_2 concentration, and presumably resulted from osmotic or Cl toxicity stress. We did not determine whether osmotic or specific Cl toxicity was the chief cause of root growth reduction at 10.0 mM CaCl_2 .

High plant to plant variability in number of marketable racemes available for harvest on a given day was observed. Other than the three raceme harvest dates of 23 May, 10 June, and 16 June, there were no other dates on which all treatment $\times$ block combinations had a minimum of two marketable racemes. However, no influence of CaCl_2 treatment on total raceme numbers produced per plant over the course of 88 days treatment was observed. Plants produced raceme numbers consistent with those earlier reported (20 to 25 per plant; Mackay and Davis, 1998). Average dry matter per harvested raceme on all sampling dates ranged between 0.60 and 0.65 g and was not affected by CaCl_2 treatment. Total raceme dry matter accumulation per plant and total raceme mineral nutrient accumulation per plant represented <20% of the plant totals. That is, roots plus shoots accumulated over 80% of total plant dry matter and mineral nutrients.

EVAPOTRANSPIRATION (ET). Daily ET, expressed per pot as $\text{mL}\cdot\text{d}^{-1}$, increased with time from 8 d following CaCl_2 treatment initiation (17 Apr.) through 75 d following treatment initiation (23 June) (Fig. 1). The general increase in ET with time resulted from gradual increases in greenhouse air temperature, natural photoperiod and

irradiance, and plant size as the season and growth stages progressed from early spring to early summer. On four of the 9 d between days 55 and 64 (3 to 12 June), overcast skies reduced overall ET by 40%, and the CaCl_2 treatment concentration had little influence on water use when measured at 64 d, just following the cloudy weather. Observations indicated that <20% of ET was attributable to evaporation of water from the medium surface (data not presented), thus ET values were largely representative of transpiration.

Pot ET was generally the lowest with plants irrigated with 10.0 mM supplemental CaCl_2 . The ET values averaged over all measurement dates per pot were 657, 606, 606, and 524 $\text{mL}\cdot\text{d}^{-1}$ for the 0, 2.5, 5.0, and 10.0 mM CaCl_2 solutions, respectively (linear contrast for CaCl_2 main effect significant at $P \leq 0.01$). The inverse relationship between CaCl_2 treatment concentration and average ET per pot was reflected in the total volume of irrigation solution applied to meet our growing medium water depletion and leaching fraction guidelines during the 75-d ET observation period (53.9, 49.5, 48.7, and 47.8 L/pot for the 0, 2.5, 5.0, and 10.0 mM CaCl_2 treatments, respectively). After accounting for the leaching fraction, these values were within $\pm 5\%$ of the total accumulated ET per pot estimated as the product of average ET in $\text{mL}\cdot\text{d}^{-1}$ and 75 d.

PLANT MINERAL NUTRIENT CONCENTRATIONS. The CaCl_2 treatments affected P, K, and Ca concentrations in shoots, which included the combined leaf, petiole, and lateral and main stem tissues (Table 2). Shoot P concentration decreased linearly with CaCl_2 concentration, whereas shoot, root, and raceme Ca concentration increased with the CaCl_2 level. Shoot K concentration also increased in response to CaCl_2 concentration, but quadratically instead of linearly, due to a decrease in the K concentration at 10.0 mM CaCl_2 . A similar quadratic influence of CaCl_2 treatment was observed for root K and Mg concentrations. Raceme P and Mg concentrations decreased with CaCl_2 treatment concentration in a linear fashion. Sulfur concentrations in shoots, roots, and racemes

Fig. 2. Net (A) Ca and (B) Mn accumulation in shoots of *Lupinus havardii* 'Texas Sapphire' during fertigation for 88 d with CaCl_2 solutions of varying concentrations. Each symbol is the mean of four, single-plant replications. Nonsignificant (ns) or significant main effects for CaCl_2 treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts at $P \leq 0.05$ (*) or 0.01 (**).

Fig. 3. Net mineral nutrient accumulation in roots of *Lupinus havardii* 'Texas Sapphire' during fertigation for 88 d with CaCl_2 solutions of varying concentrations. Each symbol is the mean of four, single-plant replications. Nonsignificant (ns) or significant main effects for CaCl_2 treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts at $P \leq 0.05$ (*) or 0.01 (**).

Table 3. Mineral nutrient accumulation in roots (from Fig. 3) expressed as a percentage of root plus shoot total mineral nutrient accumulation in *Lupinus havardii* ‘Texas Sapphire’ during fertigation for 88 d with CaCl₂ solutions of varying concentrations.^z

CaCl ₂ solution concn (mM)	Root mineral nutrient accumulation (% of root + shoot total)						
	P	K	Ca	Mg	Fe	Mn	B
0	6.2	2.4	4.6	6.8	61.3	15.4	5.8
2.5	8.6	5.8	6.2	12.9	82.2	23.1	7.1
5.0	16.3	8.5	11.5	22.9	93.2	34.6	11.4
10.0	13.3	3.8	5.5	7.8	72.2	17.3	6.2
Significance							
L	*	NS	NS	NS	NS	NS	NS
Q	*	**	**	**	**	**	**

^zEach value is the mean of four, single-plant replications.

NS,*,** Nonsignificant or significant main effects at $P \leq 0.05$ or 0.01, respectively, for CaCl₂ treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts.

were unaffected by CaCl₂ treatment, and the pooled treatment averages were 0.46%, 0.84%, and 0.23% of dry matter, respectively (data not presented).

Among the micronutrients, only root Mn and B were affected by CaCl₂ treatment, increasing linearly with CaCl₂ concentration (Table 2). Shoot Mn and B concentrations averaged 49 and 20 $\mu\text{g}\cdot\text{g}^{-1}$ DW, respectively, and raceme Mn and B concentrations averaged 30 and 27 $\mu\text{g}\cdot\text{g}^{-1}$ DW, respectively (data not presented). In shoots, roots, and racemes, the respective Fe, Cu, and Zn concentrations (data not presented), averaged across treatments and expressed as $\mu\text{g}\cdot\text{g}^{-1}$ DW were: Fe (144, 7758, and 109); Cu (3, 18, and 8); and Zn (22, 85, and 41).

PLANT MINERAL NUTRIENT ACCUMULATION, DISTRIBUTION, AND NET UPTAKE PER UNIT OF ROOT WEIGHT. In shoots, net accumulation of P, K, Mg, and S was unaffected by CaCl₂ treatment and averaged 223, 1200, 415, and 286 mg/plant, respectively (data not presented). Also, net accumulation of Fe, B, Cu, and Zn in shoots did not differ between CaCl₂ treatments, averaging 8900, 1195, 177, and 1286 μg /plant, respectively (data not presented). However, shoot Ca and Mn accumulation increased linearly with CaCl₂ concentration (Fig. 2A and B, respectively).

A pronounced quadratic influence of CaCl₂ concentration occurred on mineral nutrient accumulation in roots. Root P, K, Ca, Mg, Fe, Mn, B, and Cu accumulation increased by 3 to 7 times above the control treatment up to 5.0 mM CaCl₂, and then decreased at 10.0 mM CaCl₂ (Fig. 3). A similar but nonsignificant trend was observed for root S and Zn accumulation, averaging 55 mg and 561 μg /plant, respectively (data not presented).

With increasing CaCl₂ treatment concentration, plants exposed to up to 5.0 mM supplemental CaCl₂ exhibited an increasing ten-

dency to distribute their vegetative allotments of P, K, Ca, Mg, Fe, Mn, and B to roots (Table 3). Preferential mineral nutrient allocation to roots decreased at 10.0 mM CaCl₂, as indicated by a quadratic effect of the CaCl₂ concentration. Most of the S, Cu, and Zn was distributed to shoots (56% to 88% of combined root plus shoot total), and while the pattern of S, Cu, and Zn allocation followed the same trend with CaCl₂ concentration as the above elements, it did not change significantly with CaCl₂ concentration (data not presented).

Net uptake of P, K, Mg, S, and B per unit of root DW per week (J, from Eq. 1) decreased by 15% to 35% below the control as CaCl₂ concentration was increased to 5.0 mM, then increased with the 10.0 mM treatment (Table 4). The J value for Ca increased linearly and quadratically with CaCl₂ treatment concentration (Table 4), and the J values for Fe, Mn, Cu, and Zn were unaffected by CaCl₂ treatment concentration (data not presented).

Discussion

Results draw attention to the relationship between and natural distribution of *L. havardii* and growth in a greenhouse. Unlike the *Lupinus* sp. of significant commercial importance (*L. albus*, *L. angustifolius*, and *L. luteus*), *L. havardii* appears to be adapted to Ca-rich soils owing to the nature of its indigenous range in the southwest United States. In the present study, Ca addition up to 5.0 mM more than doubled total dry matter accumulation in roots, increased net accumulation of P, K, Ca, Mg, Fe, Mn, B, and Cu in roots by 3 to 7 times, and resulted in a preferential allocation of dry matter and P, K, Ca, Mg, Fe, Mn, and B to roots without affecting shoot growth (Tables 1 and 3, Fig. 3). In calcicole grasses, a similar alteration in photosynthate allocation (increase in root : shoot ratio) in response

Table 4. Weekly net mineral nutrient uptake (J, from Eq. 1) by *Lupinus havardii* ‘Texas Sapphire’ during fertigation for 88 d with CaCl₂ solutions of varying concentrations.^z

CaCl ₂ solution concn (mM)	J ($\mu\text{mol}\cdot\text{g}^{-1}$ root dry wt)					
	P	K	Ca	Mg	S	B
0	247	834	672	530	302	3.3
2.5	197	720	677	455	233	2.8
5.0	160	707	611	406	219	2.3
10.0	216	1019	1384	673	300	4.2
Significance						
L	NS	NS	**	NS	NS	NS
Q	**	**	**	**	**	**

^zEach value is the mean of four, single-plant replications.

NS, ** Nonsignificant or significant main effects at $P \leq 0.05$, respectively, for CaCl₂ treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts.

Fig. 4. Recovery of fertilizer K and P in roots plus shoots of *Lupinus havardii* 'Texas Sapphire' following fertigation for 88 d with CaCl₂ solutions of varying concentrations. Each value is the mean of four, single-plant replications. Nonsignificant (ns) or significant main effects for CaCl₂ treatments partitioned into linear (L) and quadratic (Q) orthogonal contrasts at $P \leq 0.05$ (*).

to addition of Ca(NO₃)₂ at 2.5 to 5.0 mM in greenhouse culture solutions has been reported (Bradshaw et al., 1958; Snaydon and Bradshaw, 1961).

Root : shoot ratios of annual crops (including *Lupinus* sp.) typically decline following seedling establishment and decrease to a minimum during the reproductive stage (Dracup and Kirby, 1996; Klepper, 1991). With *L. havardii*, there was a slight reduction in root : shoot ratio in controls between the initiation of flowering (beginning of CaCl₂ treatment) and the end of the study [0.084 ± 0.012 to the study termination value of $0.080 (\pm 0.010)$ shown in Table 1]. Up to the 5.0 mM solution concentration, however, root : shoot ratio and the absolute and relative mineral nutrient accumulation in roots of the CaCl₂-treated seedlings increased markedly.

Calcium is directly essential for root growth (Emanuelsson, 1984; Hanson, 1984; Kirkby and Pilbeam, 1984; Marschner, 1995; Poovaiah and Reddy, 1991; Rios and Pearson, 1964). Its role is thought to involve development of lateral and primary root meristems (Howard and Adams, 1965; Jackson, 1967), and the number of growing meristems ultimately determines relative sink strength of the root system (Klepper, 1991). Two other lupins, *L. atlanticus* Gladst. and *L. pilosus* Murr., are more adapted to calcareous soils and develop more extensive secondary and tertiary lateral root systems in greenhouse conditions than the calcifuges *L. angustifolius* and *L. albus* (Clements et al., 1993; Kerley et al., 2000; Tang et al., 1993b, 1995). Thus, an increase in root sink strength in response to Ca may be an important resource allocation strategy expressed by calcicole-behaving *Lupinus* sp., which contrasts with the edaphic preference of their counterpart calcifuge species (e.g., *L. albus*, *L. angustifolius*, and *L. luteus*).

Calcareous soils are often associated with semiarid, xeric climates (Bohn et al., 1985), and soluble Ca concentrations in calcareous mineral soil solutions of the southwest United States (e.g., Picchioni et al., 1990) are similar to the fertigation solution Ca concentrations applied to the soilless medium in the current study. The preferential carbon and mineral nutrient allocation to roots is suggestive of increasing root sink strength in response to applied Ca, which presumably represents an adaptive trait for maintaining rates of water and mineral nutrient acquisition in a semiarid environment where both water and the transport of minerals to the root surface are limited. Therefore, differences in growth among *Lupinus* sp. in Ca-rich environments (Tang et al., 1993a, 1993b, 1995) may relate to differential capacity for root growth in response to Ca, in addition to the often-postulated differential susceptibilities to excess Ca or

HCO₃ (Jessop et al., 1990; Peiter et al., 2000), to high pH (Tang et al., 1995), or to Fe, Mg, and P deficiency (Islam et al., 1987; Tyler et al., 1992; White and Robson, 1989a, 1989b).

Further ecophysiological ramifications emerge from the increase in root growth and root : shoot ratio resulting from CaCl₂ treatment (up to 5.0 mM) that we observed in *L. havardii*. Total mineral nutrient accumulation (net uptake) per plant was unaffected by CaCl₂ solution treatment in our experimental conditions. For a given level of mineral nutrient demand per plant, a larger root mass would require a lower rate of mineral nutrient uptake per unit of root mass to sustain growth (Gutschick, 1993; Tables 1 and 4). The time for mineral nutrient depletion zones (e.g., K and P) to develop around absorbing root surfaces increases with decreasing mineral nutrient uptake per unit of root mass; this trait is thought to extend duration of return on carbon investment in roots (Gutschick, 1993; Gutschick and Kay, 1995). Thus, increased root growth in response to Ca observed in our study supports an ecophysiological basis for Ca-dependent adaptation of *L. havardii* to xeric, calcareous sites.

Increased root growth from Ca treatment may also be of practical importance to greenhouse cultivation of *L. havardii*. The quantity of mineral nutrients absorbed by a plant is a function of size of the root mass and rate of mineral nutrient uptake for each unit of root mass (Loneragan et al., 1969b). In our greenhouse conditions, the pronounced increase in root dry matter production by the CaCl₂-treated plants (up to 5.0 mM CaCl₂) more than offset the reduction in K uptake per unit of root weight (Table 4) in determining recovery of applied K fertilizer. The CaCl₂ treatment concentration exerted a quadratic influence on recovery of the applied fertilizer K (3967 to 4473 mg/pot, depending on total volume of irrigation per treatment), such that the 5.0 mM solution increased K recovery by $\approx 20\%$ over the control treatment (Fig. 4). A similar trend in recovery of applied fertilizer P (2103 to 2372 mg/pot) was observed (Fig. 4), although the magnitude of that increase was smaller ($\approx 5\%$) and it was not statistically significant because of the limited number of plant replicates.

The increase in fertilizer nutrient recovery by Ca-treated plants is important for developing fertilizer management practices for *L. havardii*, especially in view of increasing environmental concerns over losses of applied greenhouse chemicals to ground and surface water supplies (Birnbaum, 1992; Latimer et al., 1996). Further work is necessary to study fertilizer N recovery patterns of *L. havardii* exposed to Ca irrigation solutions in greenhouse conditions, and to determine if irrigation inputs can be reduced with Ca-treated *L. havardii*, which again would be consistent with the natural tendencies and indigenous habitat of the species.

In conclusion, *L. havardii* appears to be naturally suited for greenhouse cultivation with Ca fertilization. Calcium supplementation to greenhouse fertilization solutions is compatible with the evolved nutrient requirements of this species and may have significant bearing on water and fertilizer use efficiency in a greenhouse environment. An appreciation for the natural climatic and edaphic habitat of *L. havardii* also supports an ecophysiological basis for the shifting of carbon and mineral nutrient allocation to roots in response to increasing Ca supply. As we show here, this Ca-dependent resource allocation strategy is altogether different from that of the commercially existing and widely cultivated lupins.

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