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A novel interaction of magnesium translocation with the supply of phosphorus to roots of grapevine (*Vitis vinifera* L.)*

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Abstract. The role of phosphorus (P) in leaf magnesium (Mg) concentrations and photosynthesis was investigated in field and glasshouse experiments with grapevine (*Vitis vinifera* L., cvs. Chenin blanc, Chardonnay, and Carignane). In the field, leaves of vines growing on soil with low available P exhibited symptoms of Mg deficiency and had low P and Mg concentrations. The rate of photosynthesis for leaves of untreated control vines was approximately 0.7 nmol CO_2 cm^{-2} s^{-1}. When P fertilizer was applied to the soil, Mg deficiency symptoms were eliminated, and leaf P and Mg concentrations increased to above critical levels. When Mg was applied as a foliar spray, leaf Mg increased to above critical levels, but leaf P did not change significantly. In both experiments, the rate of photosynthesis increased to greater than 1.0 nmol CO_2 cm^{-2} s^{-1} after nutrient applications. Thus, under low soil P conditions, leaf photosynthesis was limited by leaf Mg concentrations. In glasshouse experiments in which vines were grown with and without P for three seasons, Mg accumulated in large roots of −P vines to approximately twice the concentration found in roots of +P vines. Analysis of the xylem exudate from detopped plants showed that Mg concentration in xylem sap of +P vines was twice as great as that in −P vines. When P was supplied to −P vines, the concentration of Mg increased to the concentration of +P vines within 2 days. The results show that the translocation of Mg from roots to shoots of grapevine is dependent upon P supply to the roots and suggest that Mg translocation is more sensitive than uptake to P supply.

Key-words: Vitaceae; mineral nutrition; ion translocation; xylem sap; photosynthesis; potassium; woody perennial.

Introduction

Recently, grapevines with magnesium deficiency symptoms were observed on low P and low pH soils in California (Skinner, Cook & Matthews, 1988). In Germany, grapevines growing on acid soils exhibited leaf symptoms that are similar to both P and Mg deficiencies, and tissue analyses confirmed that leaves with such symptoms had less than half the normal amount of P and Mg (Gärtel, 1965). Mineral nutrient interactions are common and occur in both the soil solution and within the plant (Robson & Pitman, 1983). The uptake of Mg can be strongly depressed by other cations, particularly K^+ (Kurvits & Kirkby, 1980). Rufty, MacKown & Israel (1989) recently presented evidence that nitrate uptake was dependent upon P status. However, there is no direct evidence of an interaction between P and Mg on the concentration of Mg in soil solutions, Mg transport to the root surface (Wilkinson, 1972), Mg uptake (Gerloff & Gabelman, 1983), or Mg translocation (Mengel & Kirkby, 1987).

The field observations suggested that such an interaction may play a role in grapevine responses to low P supply. Vegetative growth, the initiation, development, and maintenance of flower primordia, and yield in grape are sensitive to P status (Skinner, Matthews & Carlson, 1987; Skinner *et al.*, 1988; Skinner & Matthews, 1989), but the physiological mechanisms which determine these responses are unknown. Therefore, this study was conducted to determine if an interaction between P and Mg uptake and translocation was occurring in grapevines subjected to low P supply.

Materials and methods

Field experiments

Commercial vineyards of *Vitis vinifera* L., cvs. 'Chenin blanc' ('St George' rootstock) and 'Chardonnay' (own roots) in Napa Valley, California, U.S.A., were selected for experimentation on the bases of preliminary analyses indicating low soil or plant P and of visual observation of Mg deficiency symptoms. Soils were identified and classified according to U.S. Department of Agriculture Soil Conservation Service Soil Survey of Napa County (1978). Phosphorus (triple super phosphate or phosphoric acid) was applied to some vines in a rando-

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mized complete block design consisting of three replicates and ten vines per replicate as previously described (Skinner *et al.*, 1988). Fertilizer applications were made in 1982 and 1986 for the Chenin blanc (0.14 kg P $vine^{-1}$) and in 1985 for the Chardonnay (0.27 kg P $vine^{-1}$) by incorporating the material beneath the emitter of the drip irrigated vines. Two weeks prior to bloom in 1987, 40 mol m^{-3} $MgSO_4$ was applied as a foliar spray to half of the previously untreated Chenin blanc vines (approximately 50 g Mg $vine^{-1}$).

Greenhouse experiments

Two-year-old grapevines (cv. Carignane) were grown in a glasshouse in 12-dm^3 pots in a soil : sand : peat (1 : 1 : 1) mixture for three growing seasons of approximately 25 weeks each under conditions previously described (Matthews, Cheng & Weinbaum, 1987; Skinner & Matthews, 1989). At the end of each growing season, vines were pruned to three two-bud spurs and stored at approximately 2 °C for 4–5 months. Nutrients (Hoagland & Arnon, 1950) were supplied ($\pm$P in 1/4 × Hoagland's solution; 0.5 mol m^{-3} Mg; +P = 0.25 mol m^{-3} phosphate) to runoff three or four times per week. Treatments consisted of five vines with individual vines serving as replicates.

Soil and plant chemical analysis

Five samples (approximately 100 g each) were collected from the surface (0–30 cm) soil of each replicate at both field sites. Replicate samples were composited, air-dried, and passed through a 2-mm-mesh sieve. Determinations were made of available P using a modified Bray-1 procedure (Olsen & Sommers, 1982), pH using a saturated paste (McLean, 1982), EC using a saturation extract (Rhodes, 1982b), CEC using Ba saturation and Ca replacement (Rhodes, 1982a), and exchangeable K, Ca and Mg using NH_4OAc equilibration and flame photometry or atomic absorption spectrophotometry (Doll & Lucas, 1973).

Leaf samples consisting of 10 leaves per replicate were taken opposite the basal cluster at bloom and veraison (the onset of fruit ripening indicated by colour change and softening of the fruit) unless otherwise indicated. In the greenhouse experiments, root samples were collected at the end of the third season. Soil was gently washed from the root mass and roots separated into two size classes (greater or less than 1.5 mm root diameter). All tissues were oven-dried at 70 °C for 48 h, ground to pass a 1 mm mesh screen, and stored at room temperature until analysed. For some experiments, the shoots of potted vines were excised, the cut surface was washed repeatedly with distilled water, and xylem exudate collected for 30–100 min in silicone tubing that was attached to the cut end of the stem base.

Extractable phosphorus (EP) of plant tissue was determined spectrophotometrically using a 2% acetic acid extraction procedure with colour development resulting from the antimony-catalysed ascorbic acid reduction of the phosphomolybdate complex (Skinner *et al.*, 1987). Total phosphorus (TP) was determined from HCl extracts of dry-ashed samples using the same colour development procedure as EP. Mg and K were determined using atomic absorption spectroscopy from the same extracts as TP.

Leaf gas exchange

The rate of net photosynthesis was determined for mid-cane leaves of Chenin blanc vines that had and had not received foliar applications of Mg. Measurements were conducted with a custom portable gas exchange system based on an ADC Mark III infra red gas analyser as previously described (Williams & Smith, 1985). Measurements were conducted from 1300 to 1500 on a clear day (air temp approx. 30 °C), 15 August 1987.

Results

Leaves in the Chenin blanc and Chardonnay vineyards that exhibited the characteristic interveinal chlorosis indicative of Mg deficiency (Christensen, Kasimatis & Jensen, 1978) had lower Mg, EP and TP concentrations than symptomless leaves (Table 1). In chlorotic leaves, both TP and Mg were below concentrations recognized as adequate for grape (Christensen *et al.*, 1978). The soils of both vineyards were low in P, but sufficient in Mg, Ca and K to support normal plant growth (Table 2). Given these concentrations of cations, soil pH and CEC (Table 2) should not have limited Mg availability (Mengel & Kirkby, 1987). These observations were the basis for pursuing a possible interaction of P and Mg in grape.

Although petioles are a standard tissue utilized for nutrient analysis in many dicot crops, Skinner *et al.* (1987) showed that the sensitivity of lamina EP concentration to variations in P supply was greater in laminae than in petioles. Similarly with Mg, basal lamina responded more quickly to treatments and exhibited greater differences among treatments than

Table 1. Concentrations (g kg^{-1} d wt) of extractable phosphorus (EP), total phosphorus (TP), and total magnesium (Mg) of healthy and chlorotic lamina taken from hillside Chenin blanc and Chardonnay vineyards in California in June 1986

Variety	EP	TP	Mg
Chenin blanc:			
Chlorotic	0.31	1.1	1.1
Healthy	0.77	1.8	3.6
Chardonnay:			
Chlorotic	0.86	1.7	1.4
Healthy	1.60	2.6	3.0

Table 2. Chemical analysis of a Sobrante and a Forward soil (Napa Valley, California) from which the healthy and chlorotic leaves of Table 1 were obtained

Soil	pH	P (mg kg^{-1})	CEC	K (mmol 100 g^{-1})	Ca	Mg
Sobrante[1]	5.9	3.0	24.0	0.46	11.1	1.79
Forward[2]	5.3	4.0	13.0	0.33	3.9	1.47

[1]Fine-loamy, mixed, thermic Mollic Haploxeralfs.
[2]Gravelly loam, medial, mesic Typic Vitrandepts.

Table 3. Concentration of Mg in petioles of Chenin blanc grapevines for six sample dates after vines had (+P) and had not (−P) received 0.14 k P·vine^{-1} in 1982*

	Petiole Mg (g kg^{-1} d wt)					
	1983		1984		1985	
	−P	+P	−P	+P	−P	+P
Bloom	6.33 a	7.26 a	3.43 a	4.99 b	3.38 a	6.04 b
Veraison	7.34 a	8.52 a	6.42 a	7.29 a	4.59 a	7.04 b

*Means within a sampling date followed with diferent letters are significantly different at $P < 0.05$ by Fisher's PLSD test.

petioles. In the second and third seasons after P application, the concentration of Mg in bloomtime petioles of the Chenin blanc leaves was significantly greater in P-treated vines than in untreated control vines (Table 3). Similar differences were apparent at veraison each season but did not become significant until the third season following P applications.

Lamina Mg concentrations were significantly greater in P-treated vines than in controls in the first season after treatment (Fig. 1). In laminae, the differences between treated and untreated vines diminished in subsequent seasons as the leaf Mg concentrations of P-treated vines declined (Fig. 1).

The concentration of Mg in basal lamina was highly dependent upon lamina P status, exhibiting a maxima of 3.25 g kg^{-1} d wt at an EP concentration of approximately 1.2 g kg^{-1} d wt (Fig. 2). Lamina Mg concentrations decreased at EP concentrations above and below this (Fig. 2). Similar responses to low lamina EP concentrations were observed for yield and clusters shoot^{-1} (Skinner *et al.*, 1988).

In 1987, half of the untreated control vines received Mg as a foliar application two weeks before bloom (approximately 15 June). Lamina Mg concentrations increased following foliar application but was still less than in P-treated vines (Fig. 3). The foliar treatment (+Mg) had no effect on lamina TP concentration (Fig. 3). The response of photosynthesis to altered Mg concentration was determined during fruit ripening. The rate of photosynthesis in the +Mg, −P leaves was similar to that of leaves of the −Mg, +P vines and both were significantly greater than in the −Mg, −P leaves of untreated control vines (Fig. 3).

In order to pursue the mechanism of the P−Mg interaction, potted vines were cultured with or without P in the nutrient solution. The TP concentration in roots was two- to four-fold greater in P-treated vines than in untreated vines (Table 4). In −P vines, the concentration of Mg was slightly and approximately two-fold greater in fine and large roots, respectively, than in +P vines. There was no corresponding accumulation of Ca in large roots.

Since Mg in roots of −P plants accumulated to a concentration greater than in +P plants but was deficient in leaves, experiments were conducted to determine the effect of P supply on the concentration of Mg in stem xylem sap. Initial Mg concentrations in the xylem exudate of −P plants were approximately 50% of that in +P plants (Fig. 4A, day 0).

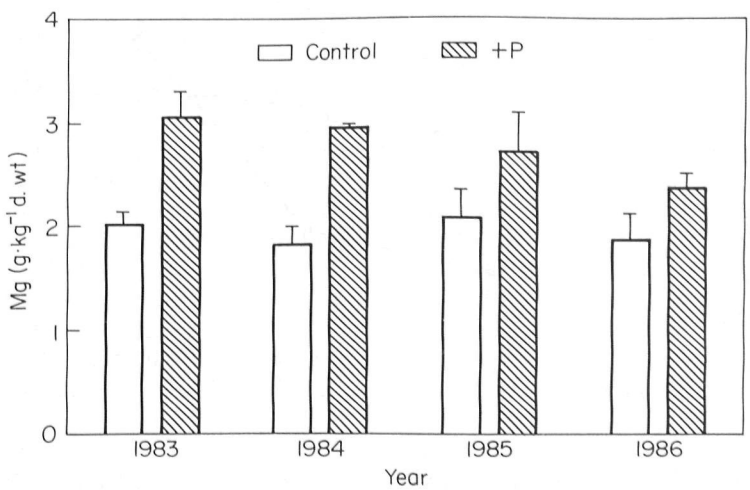

Figure 1. Concentration of magnesium (Mg) in leaf lamina of grapevine cv. Chenin blanc sampled at bloom of several seasons for vines which received phosphorus fertilizer (+P) in 1982 and for untreated controls. Vertical bars represent 0.5 s.e.m. ($n = 3$).

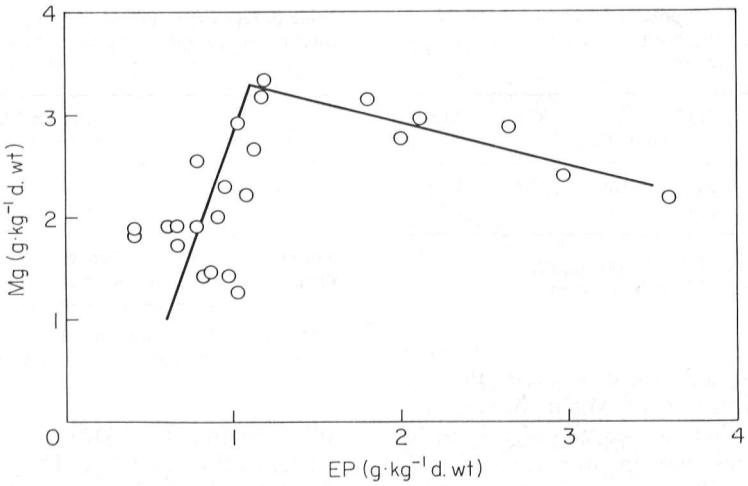

Figure 2. Concentration of Mg in leaf lamina of grapevine cv. Chenin blanc having various extractable phosphorus (EP) concentrations. Each datum represents a ten-leaf sample taken at bloom of several seasons for untreated control vines and vines which received P fertilizer treatments.

When P was then supplied to −P plants, the concentration of Mg increased more than twice within 2 d and decreased only slightly over the next 2 weeks (Fig. 4A). When P was eliminated from the nutrient supply of +P plants, Mg concentrations increased initially and then gradually decreased to a level similar to that of −P plants at day 0 (Fig. 4A).

In contrast to Mg, the concentration of K in xylem exudate was greater in −P plants than in +P controls (Fig. 4B, day 0). After P was supplied to −P plants, K concentration of the exudate increased transiently then decreased over several days to a stable value similar to that of vines which continually received P (Fig. 4B). Conversely, removal of the P supply from +P plants resulted in an increase in K to a stable concentration 50% greater than initially present at day 0 and similar to the K concentration in the sap of −P plants at day 0 (Fig. 4B).

Discussion

The results demonstrate a novel interaction of P and Mg in plant nutrition in which the concentration of Mg in leaves of grape was responsive to the supply of P to the roots. The P−Mg interaction was of sufficient magnitude to result in Mg-deficiency symptoms and Mg-limited photosynthesis in vines on Mg-sufficient but P-deficient soils in the field.

Low leaf Mg concentrations could not be attributed to a low concentration of Mg or to low Mg

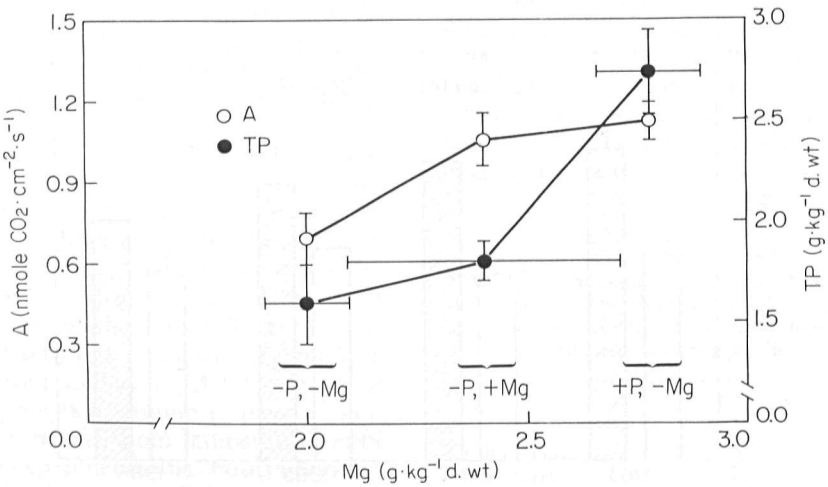

Figure 3. Rate of net photosynthesis (left axis) and concentration of total phosphorus (TP) (right axis) of leaves of grapevine cv. Chenin blanc at different leaf Mg concentrations. Leaf Mg concentration was established by P fertilizer treatments (+P, −Mg), foliar Mg treatments (+P, +Mg), or untreated controls (−P, −Mg). Mineral analysis was conducted on the leaf lamina used for measurements of photosynthesis. Error bars indicate 0.5 s.e m. ($n = 5$).

Table 4. Concentrations (g kg^{-1} d wt) of total phosphorus (TP) and Mg in fine (<1.5 mm) roots and of TP, Mg and Ca in large (>1.5 mm) roots of Carignane grapevines which were grown for three seasons with and without P. Data are means and standard errors of five replications

Root diameter	−P	+P
< 1.5 mm:		
TP	0.50±0.02	1.3±0.008
Mg	2.91±0.25	2.4±0.12
> 1.5 mm:		
TP	0.50±0.02	2.2±0.08
Mg	3.2 ±0.30	1.7±0.08
Ca	6.3 ±0.02	5.9±0.03

availability due to limiting CEC or pH of the bulk soil. The pH in the rhizosphere of P-deficient plants may have been lower than in the bulk soil (e.g. Grinsted *et al.*, 1982), and this could lead to diminished cation uptake in general (Marschner, 1986). However, several lines of evidence argue that altered rhizosphere pH did not play a primary role. First, because the supply of Mg to roots is primarily by mass flow (Barber, 1984; Kirkby & Mengel, 1976) and because the rate of Mg uptake is low compared to the concentrations in the soil solution (Kirkby & Mengel, 1976), depletion of Mg in the rhizosphere is unlikely. Second, there was no evidence that cation uptake in general was diminished. The concentrations of K and Ca in leaves (Skinner *et al.*, 1988) and of K in xylem sap and Ca and Mg in roots (present study) were not low. Only for Mg in P-deficient plants were low concentrations observed in leaves and xylem sap. Third, recent (and independent) studies with (*Pistacia vera*), grown in solution culture showed that when P was withheld for two seasons, leaf Mg concentrations decreased similar to grape (Gonzales-Reyna, 1987). Thus, the interaction occurs in the plant and is not dependent upon the presence of soil.

The interaction involves a P stimulation of Mg translocation from roots to leaves. This was evidenced by the accumulation of Mg in the roots of P-deficient plants, the increase in leaf Mg concentrations when P was supplied to P-deficient plants, the low concentrations of Mg in stem xylem sap of P-deficient plants, and the reversible changes in sap concentrations of Mg in response to changing P supply. The changes of Mg concentration in the xylem sap were stochiometrically compensated by changes in the concentration of K. In −P plants, K and Mg in xylem sap were approximately 0.7 mol m^{-3} greater and less, respectively, than in +P controls. In similar experiments with kiwifruit (*Actinidia chinensis*, also a vine of perhaps similar physiology), the ionic composition of the xylem exudate was initially fairly stable but changed significantly after several hours of bleeding (Ferguson, 1980). Since in grapes the rate of exudation was slower in −P vines, there may have been larger

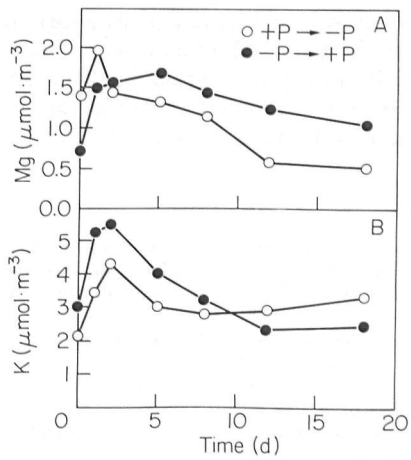

Figure 4. Concentration of Mg (A) and K (B) in xylem exudate of grapevines cv. Carignane that were detopped at various times after the nutrient supply was switched from +P to −P and from −P to +P.

changes sap concentration during sap collection in −P vines compared to +P vines. However, this does not confound the interpretation because the Mg concentration in the sap of −P vines (which were then supplied P) increased rather than decreased. Impaired translocation of Mg under adequate Mg supply is not unprecedented. Examples include a stem immobilization of Mg in a unique maize hybrid (Gerloff & Gableman, 1983), and a K inhibition of labelled Mg translocation from roots to shoots in sunflower (Schimansky, 1981).

It is not clear whether Mg absorption was also inhibited by low P supply. When translocation of Mg was inhibited by withholding P, Mg accumulated slightly in fine roots and to about 200% of controls in structural roots. A similar pattern of basal accumulation and leaf deficiencies was observed in pistachio, where Mg accumulated in fine roots, large roots, rootstock wood and leaves of −P plants to 125, 137, 214 and 54% of the P-sufficient control concentrations (Gonzales-Reyna, 1987). In contrast to Mg, the concentration of P in fine and large roots of −P grape plants, in which the uptake of P was clearly inhibited by its low availability, was 38 and 23% of control values, respectively. Although ion influx rates may not be inferred from external and root concentrations only (Drew *et al.*, 1984), these observations suggest that Mg uptake was less inhibited than long distance translocation.

Significant ion uptake can occur basipetal to the root apex (Atkinson & Wilson, 1979), but the decline in uptake with suberization of the endodermis may be greater for Ca and Mg (Ferguson & Clarkson, 1976) than for K or P (Marschner, 1986). Presumably uptake was greater in the fine apical roots than in the more basipetal structural roots. Thus, Mg was probably absorbed and then transported axially to the large roots (in grape) and trunk (in pistachio) where it accumulated. Crystals that stained heavily for Mg

were observed in fresh sections of structural roots but resolving treatment differences was difficult. The supply of P may play a role in maintaining the solubility of Mg for radial transport or to prevent reabsorption from vessel lumen.

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