Mycorrhizal Colonization in Dryland Vineyards of the Willamette Valley, Oregon

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ABSTRACT. Arbuscular mycorrhizal fungi (AMF) enhance the growth of numerous plants, including grapevines, by increasing the absorptive surface area between roots and soil. A survey of commercial vineyards in Oregon was conducted to assess the levels of root colonization by AMF at two times during the growing season. Grapevines sampled, ranged in age from 2 to 29 years old and were growing in 10 different soil types from 3 soil orders. AMF colonization of fine (feeder) roots of vines was generally high, averaging 73% and 69% of root length colonized at bloom and veraison, respectively. Vine age, soil type, cultivar, trellis type and vine row aspect did not influence colonization of roots by AMF. In-row cultivation reduced AMF colonization at bloom, and foliar application of soluble phosphorus fertilizers reduced arbuscules (the site of nutrient transfer in mycorrhizas) in roots at veraison. The proportion of roots colonized by AMF at bloom was negatively correlated to leaf N concentrations and positively correlated to soil and leaf K concentrations. The proportion of roots containing arbuscules at bloom was positively correlated to soil pH and leaf K concentrations, but negatively correlated to leaf P and N concentrations. AMF colonization of roots was negatively correlated to soil moisture at veraison. Root colonization by AMF in Oregon's dryland vineyards appears to be reduced by culti-

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The authors thank Thomas McGeary and Keiko Mihara for technical assistance and Carolyn Scagel for advice on statistics and editorial suggestions.

vation and foliar P application, but may be enhanced by increasing soil pH.

KEYWORDS. Arbuscular mycorrhizal fungi, foliar P fertilizer, glomalean fungi, nutrients, soil moisture, soil pH, *Vitis vinifera*

INTRODUCTION

The Willamette Valley in Oregon, is a cool climate viticultural region, known for producing high quality Pinot noir (*Vitis vinifera* L.) wines. Soils traditionally believed to produce the best wine quality in this region are the red-hill soils (Ultisols of Jory, Bellpine, and Nekia series), which are highly weathered, acid soils of low fertility (Brown, 1992). The extractable phosphorus (Bray-1) in red-hill soils is very low, often below 10 ppm. Vineyards also have been planted on moderately fertile soils (Mollisols and Alfisols) located close to the valley floor and on lower hillsides around the region. However, many of these soils have restrictive clay layers and/or low subsoil pH that may limit plant production without irrigation.

Grapevines form mycorrhizas with arbuscular mycorrhizal fungi (AMF) which are known to enhance their growth and nutrient uptake, especially uptake of phosphorous (Karagiannidis et al., 1995; Biricolti et al., 1997; Petgen et al., 1998). AMF may also confer added drought tolerance to grapevines, as documented with many annual plants (Augé, 2001). We suspected that grapevines grown in the dryland vineyards of Oregon would be dependent on AMF to obtain nutrients and water. We also thought that vines planted in red-hill soils would have a greater dependency on AMF than vines grown in the higher fertility soils near the valley floor.

Work in Australia and New York has shown that grapevines of many cultivars and rootstocks from commercial vineyards are colonized by AMF (Possingham and Obbink, 1971; Deal et al., 1972). More recently, AMF colonization levels of grapevines were found to be negatively correlated to the soil extractable P levels in vineyards of Italy and Greece (Schubert and Cravero, 1985; Karagiannidis and Nikolaou, 1999). Root colonization by AMF is often reduced when soil P levels are high (Smith and Read, 1997). A survey of vineyards in the Willamette Valley

was conducted to document the levels of AMF colonization in grape roots in an effort to understand factors that influence mycorrhiza development. The primary goal was to examine AMF colonization in vineyards of Oregon with known differences in soil type, vine age, and management practices to determine if these factors influenced the extent of AMF development in roots. We also measured soil and plant nutrient status of vineyards at bloom in order to understand how AMF colonization may be related to these factors under current production conditions.

MATERIALS AND METHODS

Site Selection and Sampling

The selection of vineyards included in our survey was based on comparing soils (Ultisols versus Mollisols and Alfisols) and obtaining similar numbers of vineyards with respect to vine age. Only self-rooted Pinot noir and Chardonnay vines were included in our survey to avoid potential effects of rootstocks on AMF colonization (Schreiner, 2003). After selecting sites, interviews with growers were conducted to obtain soil, cultivar, and planting information, as well as the management practices used over the past 3 years. Soil series present in each vineyard was confirmed by checking the latest NRCS county surveys. The plant, soil and management factors used in our analysis are shown in Table 1. Soils were grouped as red-hill soils (Ultisols) or other soils, henceforth referred to as valley soils. Trellis types encountered in this study were vertical shoot positioning (VSP), single wire (SW), or Geneva double curtain (GDC).

Soil and root samples were collected from 31 vineyards near the time of bloom (June 28-July 2, 1999), using a 3 cm (diameter) soil corer taken to a depth of 50 cm. Four replicate samples were collected in each vineyard along a transect that ran diagonally across the vineyard. Each replicate sample consisted of 5 soil cores taken from 5 adjacent vines, which were combined. Cores were taken from within the vine row area that was kept weed-free with herbicides or by in-row cultivation at a distance of 20-30 cm from the trunk of each vine. The location of each replicate sampling site was noted, so that we could re-sample the same sites later in the season. Leaf samples were collected from the same 5 vines at each replicate sampling location, by removing a most recently fully expanded leaf and a leaf opposite to the developing clusters from each

TABLE 1. Vineyards sampled for colonization by AMF at bloom or veraison, 1999 in various groups.

Factor	Level	Vineyards sampled at bloom (n = 31)	Vineyards sampled at veraison (n = 21)
Cultivar	Chardonnay	12	6
	Pinot noir	19	15
Soil type	Red-hill (Ultisols)	13	12
	Valley (Mollisols, Alfisols)	18	9
Vine age class	1 (< 10 yr)	6	4
	2 (10-15 yr)	8	3
	3 (16-20 yr)	12	10
	4 (> 20 yr)	6	4
Trellis type	VSP	19	12
	SW	7	6
	GDC	5	3
Vine row aspect	N-S	21	14
	E-W	10	7
Cultivation in row	Yes	2	2
	No	29	19
Foliar P application	Yes	5	4
	No	26	17

vine. Care was taken to select typical leaves for each plant sampled. Petioles were removed from the leaves and discarded. The average length of fruiting canes was measured for each of the 5 vines.

Root and soil samples were collected again shortly after veraison (onset of ripening, Sept. 13-17, 1999) using cores as above, or by hand-digging to a depth of 50 cm and removing roots and soil when roots were encountered. We could not core all sites at veraison due to the high soil strength in the dry vineyards. The number of vineyards sampled at veraison was reduced to 21, because of additional time needed to collect soil samples. Soil and leaf samples were stored on ice for transport and kept at 4°C prior to processing.

Soil and Plant Analysis

Leaf samples were washed with distilled water and oven dried at 70°C for 5 d. Leaf nutrient concentrations were determined using only two of the four replicate samples per vineyard to reduce costs. Dry leaves were ground to pass through a 40 mesh (850 μm) screen and dry-ashed. Nitrogen was determined via CNS analyzer (Leco CNS-2000 Macro

Analyzer, St. Joseph, MI) and P, K, Ca, Mg, Fe, Mn, Cu, B, and Zn were measured by ICP-OES (Perkin Elmer Optima 3000DV, Wellesley, MA) at the Oregon State University Central Analytical Laboratory.

Soil samples were thoroughly mixed and a 75-100 g subsample was removed to determine soil moisture gravimetrically (Gardner, 1986). Soil was dried at 110°C for 5 d to obtain dry mass. A second soil subsample was air-dried at ambient temperature for analysis of soil pH and available nutrient concentrations for the bloom sampling date. Four replicate samples from each vineyard were pooled for soil nutrient analysis. Soil analysis was conducted by the Oregon State University Central Analytical Laboratory using standard procedures. Soil pH and B were determined in water extracts; NO_3 and NH_4 by KCl extraction; P by Bray 1 method; K, Ca, and Mg by ammonium acetate extraction; and Fe, Zn, Mn, and Cu by DTPA extraction.

Grapevine roots were handpicked from soil, washed over a 500 μm sieve, and separated into woody and fine root fractions. Fine roots used in our analysis were primary roots with an intact cortex, varying in color from white to brown (class A and B roots as defined by Mohr, 1996). Fine roots were blotted dry, weighed, and transferred to vials containing FAA (formaldehyde:acetic acid:alcohol, 5%:10%:50% v/v) for storage. Roots were cleared and stained to reveal AMF using the procedure outlined by Schreiner (2003). Fine root length was determined using the grid-line intercept method of Newman (1966) under a stereoscope. The proportion of fine root length that was colonized by AMF (non-septate hyphae, vesicles or arbuscules) and the proportion containing only arbuscules were determined using the method of McGonigle et al. (1990) as modified by Schreiner (2003) for grape roots. Arbuscules are specialized, ephemeral structures produced within individual root cortical cells that are believed to be the site of nutrient transfer between AMF and plants (Blee and Anderson, 1998; Ezawa et al., 2002). The proportion of root length containing arbuscules will henceforth be referred to as arbuscular colonization. The proportion of root length colonized by any AMF structure will be referred to as mycorrhizal colonization.

Statistical Analysis

All data were subjected to ANOVA procedures to examine the impact of factors shown in Table 1 on plant and soil variables. Soil types were grouped into the red-hill soils (Ultisols) and valley soils (Mollisols and Alfisols), after finding no significant effects due to individual soil series. Vine age classes were grouped into 4 categories in order to have

comparable numbers of vineyards in each category. Only 1 vineyard younger than 5 years was sampled, so all vines under ten years were grouped together. Interactions between factors were included where appropriate. Homogeneity of variance was ensured using Cochran's test, and means were compared using Tukey's HSD for unequal sample size at 95% confidence. Effects of categorical factors on AMF colonization were compared in matching replicate samples from the 21 vineyards sampled at both dates. Each factor was independently tested and those factors with significant effects on either measure of AMF colonization at 90% confidence were further tested by multifactor ANOVA. Only those factors and interactions that were significant at 95% confidence were kept in the final model. Correlations (Pearson Product Moment Correlation Coefficient) between AMF colonization and soil and plant variables at bloom were investigated using the mean values for each vineyard. All statistical analysis was conducted using Statistica version 6.1 (Statsoft, 2001).

RESULTS AND DISCUSSION

The average values and associated ranges for all variables measured in this study are shown in Table 2. Mycorrhizal colonization of grape roots ranged from 36% to 94% of root length colonized (average of 70%). AMF colonization levels were slightly higher than previous reports from Italy of 60% and 58% (Nappi et al., 1985; Schubert and Cravero, 1985), and considerably higher than a survey of 45 vineyards in Greece that averaged only 40% mycorrhizal colonization (Karagiannidis and Nikolaou, 1999). Mycorrhizal colonization was negatively correlated to available soil P levels in vineyards from Greece, but we found no relationship between soil P availability and mycorrhizal colonization in Oregon. The range of available soil P in our study (8-69 ppm) was similar to the study in Greece (7-64 ppm). However, soil pH was much lower in our study (average 5.9), compared to the vineyards examined in Greece (average 7.5).

Mycorrhizal colonization did not significantly change from bloom to veraison, which was confirmed by ANOVA on matching samples from both sample dates (Table 3). Arbuscular colonization ranged from 7% to 65% and increased from bloom to veraison (Table 2). Greater arbuscular colonization at veraison was confirmed by ANOVA on matching samples (Table 3). There is only scant information in the literature regarding arbuscules in grape roots and those data are not quantitative.

TABLE 2. Mean values and ranges for plant and soil variables measured in Oregon vineyards at bloom or veraison, 1999.

Variable *	Bloom (n = 31) Mean	Bloom (n = 31) Range	Veraison (n = 21) Mean	Veraison (n = 21) Range
% Mycorrhizal Root Length	72.9	36-94	68.7	50-88
% Arbuscular Root Length	31.3	7-60	48.1	18-65
Soil Moisture (% gravimetric)	20.6	12.5-30.9	16.1	8.9-20.7
Fine Root Length (mm/g dry soil)	0.383	0.18-0.87		
Leaf N (g/kg)	31.3	25-43		
Leaf P (g/kg)	3.50	2.3-5.2		
Leaf K (g/kg)	12.5	9.2-14.8		
Leaf Ca (g/kg)	13.5	7.7-21.5		
Leaf Mg (g/kg)	2.60	2.1-3.6		
Leaf Fe (mg/kg)	99	53-158		
Leaf Mn (mg/kg)	181	118-288		
Leaf Cu (mg/kg)	19	13-26		
Leaf B (mg/kg)	72	17-216		
Leaf Zn (mg/kg)	39	15-130		
Soil pH	5.91	5.3-6.4		
Soil NO_3 (mg/kg)	4.98	1.5-13.1		
Soil NH_4 (mg/kg)	5.16	2.5-12.5		
Soil P–Bray 1 (mg/kg)	21	8-69		
Soil K (mg/kg)	163	14-484		
Soil Ca (mg/kg)	1615	260-3680		
Soil Mg (mg/kg)	328	49-1154		
Soil Fe (mg/kg)	42	9-141		
Soil Mn (mg/kg)	21	5-60		
Soil Cu (mg/kg)	1.1	0.5-5.0		
Soil B (mg/kg)	0.4	0.1-0.8		
Soil Zn (mg/kg)	1.3	0.2-9.1		

* Roots and soil collected from 0-50 cm depth.

TABLE 3. Impact of sampling data and management practices on AMF colonization of grape roots in matching replicate samples at bloom and veraison, 1999.

ANOVA Factor	df	% Mycorrhizal Colonization MS	F	P	% Arbuscular Colonization MS	F	P
Sample Date (S)	1	45	0.16	0.687	1998	8.96	0.003
In Row Cultivation (C)	1	9004	32.08	< 0.001	3022	13.56	< 0.001
Foliar P Fertilizer (P)	1	1271	4.53	0.035	4129	18.52	< 0.001
S * C	1	1843	6.57	0.012	958	4.30	0.040
S * P	1	461	1.64	0.202	2878	12.91	< 0.001
Error	132	281			223		

Arbuscular colonization ranging from 22% to 52% of fine root length was found in an experimental rootstock vineyard sampled at veraison, during the same year as this study (Schreiner, 2003). The average level of arbuscular colonization found here at veraison is higher than the few reports of arbuscular colonization in other perennials (Plenchette et al., 1981; Schultz et al., 1981; Cooke et al., 1992), which may suggest a greater reliance of grapevines grown in this region on AMF compared to other woody crops. More arbuscules found in roots at veraison, as compared to bloom, suggests that enhanced functioning of the symbiosis occurred (in terms of either nutrient of water uptake) during the latter part of the summer when soils are drier. Neither measure of AMF colonization of roots was influenced by variety, soil type, vine age, or trellis type (data not shown).

Soil moisture was quite variable across the vineyards surveyed, ranging from 12.5% to 30.9% at bloom. Soil moisture declined over the season and was reduced by ~5% (5 g water per 100 g dry soil) on average in individual vineyards from bloom to veraison. Since the majority of soils in our survey were silt loams or silty clay loams, the average water content of 16% at veraison, was approaching the wilting point in the topsoil (Brady and Weil, 1999). Soil moisture was not affected by soil type, but was affected by in-row cultivation (higher water content in tilled soils) as tested by ANOVA ($p = 0.05$, data not shown). The reason for this is unclear, but the higher water content of soil in tilled vine rows may have resulted from a reduction in surface runoff during rainfall events.

Leaf and soil nutrient concentrations showed large variation across the vineyards surveyed (Table 2). Much to our surprise, the nutrient status in soil and leaf samples were generally unaffected by soil type. Only leaf Fe, soil Fe, soil B, and soil Mg were significantly affected by soil type ($p = 0.05$, data not shown). However, there was a trend for valley soils to have higher nutrient levels in both leaves and soils for most minerals, except N, K, B and Zn, which were slightly higher in the red-hill soils. Even though soil pH was not significantly different between soils, the level of soil Ca was 30% higher and soil Mg was 95% higher in the valley soils, compared to the red-hill soils. Soil pH was significantly correlated to leaf K concentrations ($r = 0.68$), and to available soil Ca ($r = 0.54$), soil K ($r = 0.51$), soil Mn ($r = 0.44$) and soil Mg ($r = 0.42$).

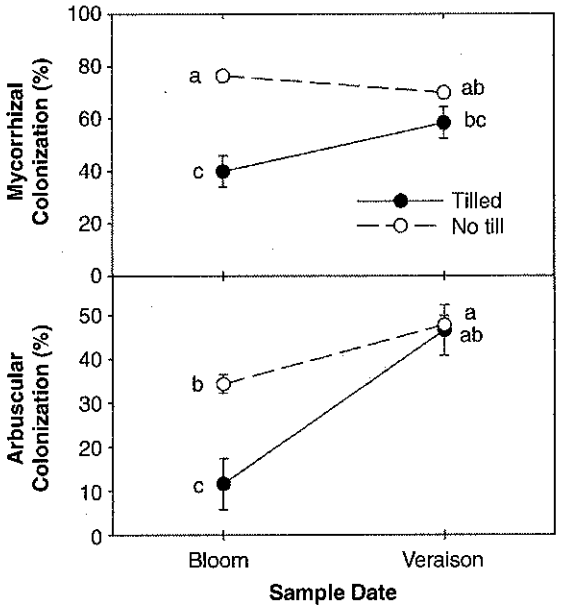
Relationships between individual soil and leaf nutrient tests were not significant. For example, leaf P was not correlated to soil P. Although, leaf N concentrations showed the closest such relationship with soil NO_3 concentrations ($r = 0.35$, $p = 0.067$). The lack of significant correlations between soil test values and leaf nutrient concentrations in our

survey is consistent with much of the early work in vineyard nutrition. As Cook (1966) states "soil analyses usually have not proved reliable . . . due in part to difficulties in getting soil samples truly representative of the root distribution and to the difficulty in establishing laboratory techniques to extract elements from the samples to the same degree in a few minutes that the grapevine does over a period of up to six months activity." In addition, the re-allocation of mineral nutrients stored in permanent vine tissues can supply a large proportion of demand in a given season's growth, so that uptake of nutrients from soil may not be coupled with demand of the developing canopy (Mullins et al., 1992).

The salient finding from our study was that in-row cultivation and foliar P application were the only categorical factors that impacted AMF colonization (Table 3). Both in-row tillage and foliar P application reduced root colonization by AMF in an interaction with sample date. In-row cultivation suppressed both mycorrhizal and arbuscular colonization at bloom compared to those vineyards that did not till in the vine row (Figure 1). However, AMF colonization recovered to the same level as the untilled vineyards by veraison. This is the first report of tillage effects on AMF in vineyards, but cultivation is well known to reduce AMF colonization in many crops (Smith and Read, 1997; Miller, 2000), primarily through the disruption of the external mycelium of AMF.

Foliar P applications reduced arbuscular colonization of roots by 2-fold at the time of veraison, but had only a small impact on overall mycorrhizal colonization (Figure 2). Higher plant P status resulting from foliar P applications in Oregon vineyards appeared to have a specific effect on arbuscules in roots with relatively little impact on other AMF structures. AMF colonization of roots was unaffected by foliar P applications at bloom. AMF colonization in higher plants is regulated by plant P status, such that development of the fungi in roots is reduced as plant P concentrations rise above a suboptimal level (Smith and Read, 1997). In most cases overall mycorrhizal colonization (hyphae, vesicles and arbuscules) is reduced by increasing plant P status, but some studies have shown a preferential reduction in arbuscular colonization, similar to our findings, as plant P status increased (Braunberger et al., 1991; Duke et al., 1994). A negative correlation between leaf P concentrations at bloom and arbuscular colonization, but a lack of such correlation with overall mycorrhizal colonization (Table 4) supports the notion that arbuscules are more quickly down-regulated by plant P status than other fungal structures. Since the arbuscule is also the likely site of carbon supply to the fungus (Blee and Anderson, 1998; Ferrol et al., 2002), growth of the external AMF hyphae should also have been re-

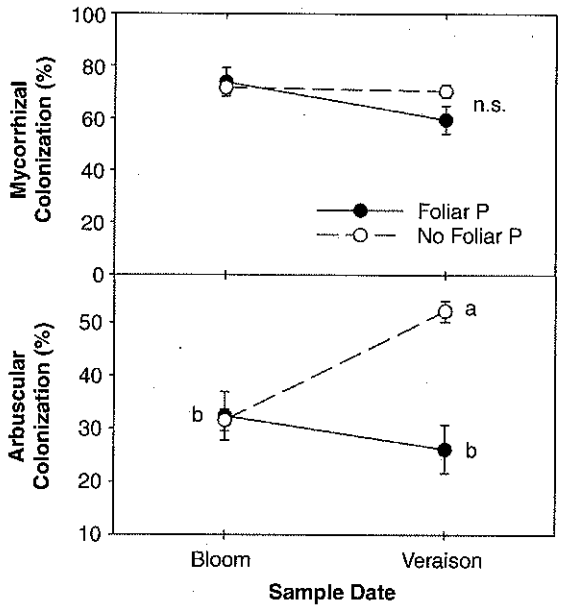
FIGURE 1. Effect of in-row cultivation on root length colonized by AMF in Oregon vineyards, 1999. Data represent LS means with standard errors. Tukey's HSD groups are indicated.



duced as a consequence of foliar P use, thereby decreasing the extent of soil exploration by MF hyphae. This in turn may reduce the nutrient and water uptake via AMF at a time in the season when vines are under the greatest stress. The negative effect of foliar P application on AMF is probably more detrimental to vines in dryland vineyards than in-row cultivation, since AMF colonization levels had recovered in the tilled sites to the control level by veraison. Research is ongoing to understand the impact of foliar P use on AMF and vine water relations in controlled studies in Oregon. It is noteworthy that two vineyards that had applied soft-rock phosphate (insoluble P) to the foliage did not show depressed levels of AMF colonization. Apparently, only soluble forms of P applied to the foliage caused the reduction in AMF colonization. The vineyards that applied rock phosphate were placed in the non-foliar P group for our analysis.

Relationships between AMF colonization and the other plant and soil variables measured at bloom are shown in Table 4. Mycorrhizal colonization was most closely related to the inverse of leaf N, followed by soil

FIGURE 2. Effect of foliar P application on root length colonized by AMF in Oregon vineyards, 1999. Data represent LS means with standard errors. Tukey's HSD groups are indicated.



and leaf K concentrations. Arbuscular colonization was most closely related to soil pH, followed by cane length, leaf K concentrations and the inverse of leaf P concentrations. These relationships show that vineyards with more acid soils and reduced K status had lower levels of AMF colonization. Decreasing soil pH has not always been linked to reduced colonization by AMF (Wang et al., 1993), but a trial conducted in a tropical Ultisol with maize also showed a decline in AMF colonization over a similar pH range as this study (Nurlaeny et al., 1996).

Vineyards that had higher N and P concentrations in plant tissues had reduced colonization by AMF, which is well known (Smith and Read, 1997). While leaf N was negatively correlated to both measures of AMF colonization, arbuscules were negatively correlated only to leaf P, supporting the belief that arbuscules are the site of P transfer in arbuscular mycorrhizas (Ezawa et al., 2002). Higher leaf and soil K concentrations were associated with increased AMF colonization in Oregon vineyards. This finding is not in agreement with Karagiannidis and Nikolaou

TABLE 4. Significant correlations between plant and soil variables and AMF colonization of roots from Oregon vineyards at bloom, 1999. Mean values were used (n = 31).

AMF Variable	Correlated Variable	Correlation Coef. (R)	P
% Mycorrhizal Root Length	Leaf [N]	−0.556	0.002
	Soil [K]	0.435	0.021
	Leaf [K]	0.419	0.026
	Fine Root Length	−0.403	0.033
	Soil Moisture	−0.401	0.035
	Soil pH	0.395	0.038
% Arbuscular Root Length	Soil pH	0.615	< 0.001
	Cane Length*	0.550*	0.034*
	Leaf [K]	0.516	0.005
	Leaf [P]	−0.461	0.014
	Soil [K]	0.459	0.014
	Leaf [N]	−0.436	0.021
	Fine Root Length	−0.421	0.026

* Correlations to Cane length were based on 19 vineyards with VSP trellis type.

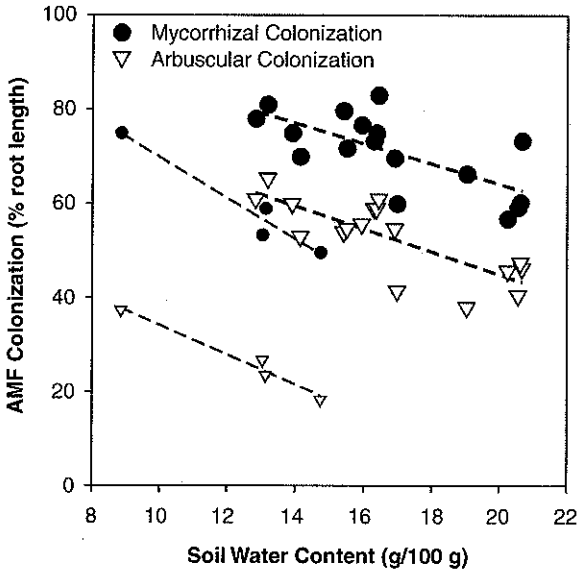
(1999) who found lower colonization by AMF associated with high leaf and soil K concentrations. However, our soil K concentrations were about 50% of the values reported by Karagiannidis and Nikolaou (1999).

Soil moisture was an important determinant of AMF colonization at version. Total mycorrhizal colonization and arbuscular colonization were negatively correlated to soil moisture at veraison (Figure 3). This relationship was statistically significant ($p < 0.05$) in those vineyards that had applied foliar P ($n = 4$), and in those vineyards that had not applied foliar P ($n = 17$), when analyzed separately. Colonization by AMF was enhanced in the drier vineyards whether or not foliar P was used, even though AMF colonization was reduced (offset) by foliar P application. This finding confirms earlier work in an experimental rootstock vineyard where AMF colonization was also negatively correlated to soil moisture (Schreiner, 2003). Apparently, mycorrhizal colonization of roots is stimulated in grapevines as soil moisture declines. These results imply that AMF are important in grapevine water relations in the field, and support findings of greater drought tolerance due to mycorrhizal colonization in grafted Cabernet Sauvignon vines grown under controlled conditions (Nikolaou et al., 2003).

CONCLUSIONS

Our survey of commercial vineyards in Oregon showed that soil type, vine age, trellis type, and aspect had little impact on the coloniza-

FIGURE 3. Relationship between soil moisture and AMF colonization in Oregon Vineyards at veraison, 1999. Small symbols represent vineyards receiving foliar phosphorus (n = 4). Means are shown.



tion of *Vitis vinifera* roots by AMF. However, management factors of in-row cultivation and foliar P fertilization reduced colonization by AMF. While cultivation primarily reduced AMF colonization near the time of bloom, foliar P application reduced arbuscular colonization at veraison when soils were drier and vines appeared to be more reliant on AMF. Soil moisture and soil pH were also important determinants of AMF colonization. Raising soil pH, if soils are below a pH of 5.5, and minimizing the use of foliar P fertilizers appear to be the best management strategies to enhance colonization by AMF in Oregon vineyards.

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