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Mycorrhizas and Mineral Acquisition in Grapevines

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Abstract: Grapevines (*Vitis* spp.) form mycorrhizal associations in fine roots with arbuscular mycorrhizal fungi (AMF) from the order *Glomales*. AMF enhance the growth and mineral uptake of many plants by producing an absorptive, mycelial network in soil that helps roots capture water and nutrients required for plant growth. Numerous studies have shown that grapevines are dependent on AMF for normal growth and development, although few reports have focused on the role of AMF in grapevine nutrient uptake. As with many crops, AMF have been shown to increase phosphorus (P) uptake by grapevines. Much less is known about the role of AMF in the uptake of other plant nutrients by grapevines. While AMF have been reported to increase nitrogen, potassium, and zinc uptake in a few studies, it is unclear how universal these findings are. Enhanced uptake of nutrients by AMF in vineyards is dependent on a variety of soil properties and management inputs. AMF may also enhance the drought resistance of grapevines, which is likely related to improved plant nutrient status as found with other crops. Mycorrhizas are expected to play an increasingly important role in vineyard production systems as more vineyards receive less water to enhance fruit quality and as more vineyards are planted on less fertile soils.

Key words: arbuscular mycorrhizal fungi, drought tolerance, nutrient uptake, *Vitis*

It has been known for over a century that grapevines (*Vitis* spp.) form symbiotic associations in their roots with arbuscular mycorrhizal fungi (AMF) (see Possingham and Obbink 1971). AMF coevolved with higher plants approximately 400 million years ago and may be responsible for the movement of plants to the terrestrial environment (Pirozynski and Malloch 1975, Simon et al. 1993, Redecker et al. 2000). AMF are found in nearly all soils, although propagules of AMF and subsequent root colonization can be suppressed in some soil environments, including high-input agricultural systems (Sieverding 1991, Kabir et al. 1997). Even so, more than 20 species of AMF have been identified in intensively managed agricultural soils (Ellis et al. 1992, An et al. 1993). Thirty-seven different species of AMF, representing a considerable proportion (~25%) of the total AMF diversity known (Morton and Benny 1990, Walker and Trappe 1993), have been identified from a single, abandoned agricultural field (Bever et al. 2001). While AMF are generally regarded as nonspecific symbionts (a single fungus species can form mycorrhizas with numerous host plant species), preferred associations between specific fungi and plant species occur in various ecosystems (Johnson et al. 1992, Bever et al. 1996), including vineyards (Schreiner, unpublished data).

Different species of AMF have different responses (or tolerance) to agricultural practices such as tillage (Douds et al. 1995), fertilization (Hayman et al. 1975, Johnson and Pfleger 1992), and pesticide use (Schreiner and Bethlenfalvay 1997). Different species of AMF (and even isolates within a species) also differ in their ability to promote plant growth and nutrient uptake (Wilson 1988, Bethlenfalvay et al. 1989). Differential responses among species of AMF to management practices (Douds et al. 1993, Galvez et al. 1995, Jacquot et al. 2000) may alter the benefit derived by the host plant because of shifts in the fungal species inhabiting its roots. Indeed, the enrichment of less effective species of AMF (in terms of plant growth promotion) has been observed in corn and soybean fields that were successively monocropped (Johnson et al. 1992). Whether or not a buildup of less effective isolates of AMF will occur in vineyards over time is unknown, but the potential may be even greater than in annual cropping systems, since grapevine roots are continually present. The vegetation between the grapevine rows, including cover crops and weeds, could play an important role in maintaining an effective, highly diverse community of AMF in vineyards (Baumgartner et al. 2004).

AMF are best known for their contribution to mineral uptake by plants, particularly those minerals that have limited mobility in soil, such as phosphorus (P), zinc (Zn), and copper (Cu) (Marschner 1995, Smith and Read 1997). AMF have been shown to enhance the uptake of nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and iron (Fe) in some circumstances (Clark and Zeto 2000), but many researchers still consider AMF primarily in regard to enhanced P uptake (Koide 1991, Smith and Read 1997). Nutrient uptake is enhanced by AMF primarily because of greater exploration of soil by the external hyphal network of these fungi. As a result, mycorrhizal roots are often more efficient than nonmycorrhizal roots in obtaining soil nutrients (Smith and Read 1997). Mineral nutrients absorbed by the external hyphae of AMF are rapidly translocated to fungal structures within roots (Bago et al. 2002), where they are exchanged for host-derived photosynthate (hexoses).

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Although some transfer of metabolites between plant and fungus can occur across intercellular hyphae (Ryan et al. 2003), the exchange of phosphate (and possibly other ions) and sugar between roots and AMF occurs to the greatest extent in root cortical cells containing arbuscules (see Koide and Mosse 2004). Arbuscules are short-lived, dendritic (treelike) structures that develop within individual root cells, vastly increasing the surface area contact between plant and fungus. The presence or extent of arbuscules in roots is therefore a good indicator of a functional mycorrhiza relationship (that is host and fungus actively exchange metabolites) (Ferrol et al. 2002). AMF are completely dependent on plant-derived carbon for their growth and reproduction. Plants can benefit from AMF by acquiring greater quantities of soil nutrients at the cost of supporting the carbon requirements of the fungi.

Under conditions of high soil nutrient supply, common in many horticultural cropping systems, the cost of supporting AMF can sometimes exceed the benefit derived in terms of nutrient uptake (Eissenstat et al. 1993, Ryan and Graham 2002). Winegrape production is a unique horticultural cropping system in which high nutrient supply is undesirable, as excessive canopy growth is often associated with reduced fruit quality. It is unlikely that fertilizer inputs (particularly P) in vineyards will exceed the point at which mycorrhizal roots are less efficient than roots without AMF. In fact, there are only rare occasions when P fertilizer has been shown to enhance growth or productivity of grapevines (Cook 1966, Cook et al. 1983, Skinner et al. 1988), even though P has long been recognized as a key limiting soil nutrient in agriculture (Ozanne 1980, Brady and Weil 1999). This contradiction suggests that either grapevines heavily rely on AMF to supply P needs or they use alternative P-gathering mechanisms similar to those found in plant species that are incapable of forming mycorrhizas (such as the production of very small diameter roots, prolific root hair development, production of proteoid roots, or high rhizosphere phosphatase activity) (Koide and Schreiner 1992). There is no indication in the current literature that grapevine roots use these alternative mechanisms for obtaining soil P. Given that less energy is required to produce and maintain fungal hyphae in comparison to fine roots (500 to 1000 times larger in diameter) (Smith and Read 1997), it becomes apparent why this symbiosis has been so highly conserved in plants, in general, and in grapevines, in particular (Schreiner 2003).

Mycorrhizal fungi also benefit plants and soil ecosystems in ways that may be independent of enhanced nutrient uptake. AMF may play a role in protecting plants from soilborne pathogens either through direct competition for root occupancy or by modifying the microbial community in the rhizosphere (see Paulitz and Linderman 1991). AMF can improve the drought resistance of many plant species, although it is not always clear that the fungi affect plant water relations independent from their role in nutrition (Augé 2001). AMF are also a primary determinant of soil aggregate stability in many soils (Schreiner and Bethlenfalvay 1995, Miller and Jastrow 1992). Improved aggregate stability can arise from the physical entanglement of soil particles by the external hyphae of AMF (Tisdall and Oades 1982) and from the excretion of a recalcitrant, glycoprotein (glomalin) that binds soil particles together (Wright and Upadhyaya 1998). Indeed, the level of soil aggregation has been linked to the quantity of external AMF hyphae in soil under greenhouse conditions (Schreiner et al. 1997) and in the field (Miller and Jastrow 1990). Therefore, AMF can enhance both short-term nutrient uptake, by increasing nutrient availability to roots, and long-term nutrient dynamics of soils, by enhancing aggregation and protecting soil organic matter from degradation. In turn, greater aggregate stability of soils improves infiltration rates, gas exchange with the atmosphere, and resistance to erosion (Harris et al. 1966), which is of particular importance for hillside vineyards.

The focus of this review is to summarize what is known about AMF and the growth and mineral nutrient uptake in grapevines. Since there is relatively little published information on AMF and mineral nutrition in grapevines, examples from other higher plants will be used to illustrate some points. Whole-vine nutrient uptake and partitioning research will also be discussed. The role AMF may play in the drought resistance of grapes and aspects of managing AMF in vineyards will also be presented.

Mycorrhizal Dependency of Grapevines

Based on root-system characteristics (Richards 1983, Van Zyl 1988) and the field studies conducted by Menge et al. (1983), grapevines appear to be highly dependent on AMF to obtain ample nutrients and water for normal growth. Plant species that benefit the most from mycorrhizas are typically those that have low root densities in soil (low quantity of roots per volume of soil), produce few and/or short root hairs, or have relatively large diameter fine roots (Baylis 1975, Hetrick 1991, Schweiger et al. 1995). Grapevines appear to have low root densities in soil, as compared to other crops (Smart and Coombe 1983, Mohr 1996, Schreiner and Linderman 2004), and produce relatively large diameter fine roots (Richards 1983, Mohr 1996). In addition, while root hairs can be numerous on grapevines under some conditions (Richards 1983), I have rarely observed root hairs on grapevine roots collected from many vineyards in the Pacific Northwest (Schreiner, unpublished data). A strong dependency on AMF during the establishment of grapevines was shown by Menge et al. (1983) in fumigated vineyards of California. Survival of grapevines was closely linked to the establishment of AMF in roots. Even after three years, grapevines that were severely stunted in the field (~50% of planted stock) were not colonized by AMF, while all grapevines that had achieved normal levels of growth had roots that were completely colonized by AMF. It is noteworthy that these vines were planted in relatively deep (~1.5 m), fertile soils. Grapevines are likely to be even more dependent on AMF for estab-

lishment and growth in lower fertility soils, common in many vineyards.

Numerous reports of enhanced growth of grapevines resulting after inoculation with AMF are known (Possingham and Obbink 1971, Schubert and Cammarata 1986, Linderman and Davis 2001). Research conducted in two Oregon soils under controlled conditions has shown that soil type can influence mycorrhizal dependency of grapevines. Growth of nonmycorrhizal Pinot noir cuttings essentially stopped between 8 and 16 weeks in a low-fertility Ultisol, while the shoot length of mycorrhizal plants increased more than 4-fold over the same time period (Table 1). However, vines grew equally well with or without AMF in a high-fertility Mollisol. In fact, addition of AMF to the Mollisol initially depressed shoot growth in comparison to nonmycorrhizal grapevines, which probably reflected the carbon cost of establishing AMF in roots and soil. Similar results were observed in citrus. The total cost of producing and maintaining mycorrhizal citrus roots was shown to exceed that of nonmycorrhizal roots at high soil P, resulting in depressed shoot growth (Eissenstat et al. 1993). By 16 weeks, the AMF-inoculated vines in the Mollisol reached the same growth as control vines and appeared to be on a trajectory to surpass them (Table 1). The dependency of grapevines on AMF in the Ultisol was primarily related to improved P uptake, since both P concentrations and contents were vastly increased by AMF in shoots and roots in the Ultisol, while other nutrients showed only modest differences (data not shown).

Mycorrhizas and Mineral Uptake in Grapevines

Of the roughly 30 papers published on AMF in grapevines over the past three decades, only 12 studies have reported effects on mineral nutrition that can be ascribed to AMF (Possingham and Obbink 1971, Deal et al. 1972, Schubert and Cammarata 1986, Giovannetti et al. 1988, Waschkies et al. 1994, Karagiannidis et al. 1995, Biricolti et al. 1997, Petgen et al. 1998a, Karagiannidis and Nikolaou 2000, Nikolaou et al. 2002, 2003, Motosugi et al. 2002). Results from these studies conducted under controlled conditions in pots showed that AMF enhanced the growth of grapevines in all cases. Growth increases due to the presence of AMF in soils have been found in all grapevine varieties and rootstocks examined. In all cases but one (Waschkies et al. 1994), the presence of AMF increased P concentrations in grapevine shoots or leaves. Since growth was always enhanced by AMF in these studies, we can conclude that P uptake was increased. K and Cu concentrations in grapevine leaves or shoots were increased by AMF in two of the 12 aforementioned studies (Deal et al. 1972, Biricolti et al. 1997, Petgen et al. 1998a, Nikolaou et al. 2002). N, Ca, or Zn were each found to be increased in grapevine leaves or shoots by AMF in one study out of 12 (Petgen et al. 1998a, Nikolaou et al. 2002), although Motosugi et al. (2002) found reduced concentrations of Ca and Mg after inoculating tetraploid rootstocks with AMF. It is not uncommon for the concentration of some nutrients to be reduced in mycorrhizal plants when compared to uninoculated plants because of the dilution effect caused by enhanced growth in response to increased P uptake (Smith and Read 1997). Karagiannidis et al. (1995) and Biricolti et al. (1997) reported reduced Mn levels in mycorrhizal grapevines in comparison to nonmycorrhizal vines. Reduction in Mn concentrations may not be related to a dilution effect because AMF are known to alleviate plant toxicity to high soil Mn levels in other plant species (Bethlenfalvay and Franson 1989). Reduced Mn uptake in mycorrhizal plants grown at high Mn supply appears to result from altering the populations of Mn-reducing bacteria in the rhizosphere (Kothari et al. 1991).

The limited research that has been conducted on AMF and the mineral nutrition of grapevines is a reflection of the overall body of literature on AMF, which has primarily been conducted on annuals. Improved P uptake is clearly most important, but other nutrients may or may not be affected by AMF depending on conditions. P is often the only element examined in mycorrhizal studies (including several of the 12 studies highlighted above for grapevines), and most studies have been conducted in soils with low P availabilities.

Table 1 Effect of arbuscular mycorrhizal fungi (AMF) on growth of Pinot noir (UCD2A) cuttings in two silty-clay-loam soils in the greenhouse (n = 6).

		Soil nutrients at planting (mg kg^{-1})				Shoot length (cm)	
Treatment[a]	Soil pH	P (Bray1)	K	Ca	Mg	8 wk	16 wk
Ultisol -AMF	5.7	35	91	902	158	19.2a[b]	26.3a
Ultisol +AMF	5.7	35	91	902	158	18.7a	85.3b
Mollisol -AMF	5.6	66	166	1623	304	37.8b	82.8b
Mollisol +AMF	5.6	66	166	1623	304	21.7a	89.0b

[a]Both soils were dry-heated (150°C) to eliminate AMF. +AMF treatments received a mixture of *Scutellospora calospora*, *Glomus mosseae,* and *Glomus intraradices* inoculum from pot cultures. –AMF treatments received washings of AMF inoculum to ensure that microbes associated with AMF were similar among soils. Dolomite lime (50% $CaCO_3$, 40% $MgCO_3$) was added to the Ultisol soil at the rate of 50 g kg^{-1} dry soil prior to planting.

[b]Shoot lengths followed by the same letter within a column are not significantly different at $p > 0.05$.

Therefore, our knowledge regarding the effects of AMF on plant nutrition is heavily biased toward P. Also, most studies have been conducted under well-watered conditions, where many soil nutrients are in greater supply to roots than what occurs under field conditions, where some degree of drought stress is often encountered.

Increased P uptake in grapevines by AMF does not appear to be influenced by soil pH or soil texture. The range of soil pH reported in the studies addressed above was 5.9 to 8.4, although more research has been conducted in slightly alkaline soils. AMF have enhanced growth and P uptake in both acidic and basic soils (Biricolti et al. 1997, Petgen et al. 1998a). Similarly, AMF have increased growth and P uptake in a variety of soil textures including sandy loam soils, clay loam soils, and silty clay loam soils (Table 1, Biricolti et al. 1997, Nikolaou et al. 2003).

A relationship between soil pH and colonization of roots by AMF has, however, been found in field surveys of vineyards in different grapegrowing regions. Schubert and Cravero (1985) found a positive correlation between AMF colonization in grafted winegrapes and soil pH across the range of 4.6 to 7.9 in nine vineyards in Italy. Schreiner and Linderman (2004) found a similar correlation between arbuscular colonization and soil pH across the range of 5.3 to 6.4 in 31 winegrape vineyards in Oregon. However, no relationship was found by Nappi et al. (1985) in nine vineyards in Italy ranging in pH from 5.2 to 8.5. The lack of such relationship in the latter case may be due to the fact that roots were sampled during the winter. These findings suggest that soil pH values in the range of 5 to 5.5 can reduce AMF colonization in grapevines.

It appears that high levels of soil fertility or high plant nutrient status reduces colonization of grapevine roots by AMF. Schubert and Cravero (1985) found that root colonization by AMF was negatively correlated to soil N and P availabilities. Schreiner and Linderman (2004) found a negative correlation between root colonization and leaf N and P concentrations, but no correlation to soil nutrient levels. A negative correlation between colonization and soil P availability was also found in a survey of 45 vineyards in Greece (Karagiannidis and Nikolaou 1999). Cluster analysis of this data also indicated that vineyards with low levels of AMF colonization were associated with high leaf and soil K concentrations. High levels of plant or soil P are known to reduce AMF colonization of roots in other plants (Smith and Read 1997). Indeed, arbuscular mycorrhizal associations with plants have been deemed a self-regulatory symbiosis (Hayman 1983), since root colonization by the fungi is reduced when plants have ample nutrients. It should be noted that the work on AMF in grapevines must be viewed with some caution, because in many cases only concentrations of nutrients were examined. Nutrient concentration changes alone cannot be taken as an indication of changes in nutrient uptake.

Nutrient Uptake in Whole Vines

There is a wealth of data collected on the concentrations of minerals in leaves and especially petioles of grapevines, on which plant nutrient status is inferred and fertilizer recommendations are based (Cook 1966, Christensen 1984, Robinson 1992, Gärtel 1996). These mineral concentration guidelines are useful for identifying deficient or overly high concentrations of nutrients within grapevines, but they are based on limited field trials with a small number of cultivars. Because there is wide variation in the concentrations of various elements in leaves or petioles of different cultivars (Christensen 1984) and different rootstocks (Ruhl 1989), growers are encouraged to use other information regarding plant growth and fruit quality, specific to their site, to aide in the interpretation of leaf or petiole nutrient data. Concentrations of minerals within leaves and petioles, while somewhat diagnostic, do not provide accurate information on nutrient uptake or reflect how viticulture practices influence nutrient uptake or allocation of nutrients in various organs. The situation is reminiscent of Coombe's (1992) observation regarding the developmental changes in fruit during ripening: "The concentration of compounds is the aspect that concerns users of grapes or juice and, hence is the variable most measured and quoted. However, for those who wish to interpret developmental changes in a compound, the amount per berry gives valuable additional information: this can be simply derived from concentration and recorded measurements of berry weight at the time of sampling." This also applies to mineral uptake and partitioning within various plant organs of grapevines. Changes in whole-vine nutrient contents (concentration x biomass) are exceptionally important to understand mineral nutrient uptake in grapes, since grapevines have the capacity to store and re-allocate potentially large quantities of carbon and mineral nutrient reserves (Yang and Hori 1979, Koblett and Perret 1990, Roubelakis-Angelakis and Kliewer 1992).

Hiroyasu (1961) appears to have performed the first work on whole-vine mineral uptake, but only the summary is available in English. Conradie (1980, 1981a) studied whole-vine nutrient uptake and allocation in Chenin blanc vines grown in sand provided with nutrient solution. This research showed that the bulk of macronutrient uptake (N, P, K, Ca, Mg) occurred between bloom and veraison. Very little nutrient uptake occurred between veraison and harvest. The postharvest period was important for resupplying reserves of nutrients depleted from the roots and trunk. However, there may be problems applying these results to field-grown grapevines because the plants used in this work were only two years old and were grown under a constant, high supply of nutrients (particularly N; see Kliewer 1971). Data from this research and other whole-vine nutrient studies, including a recent study in Oregon, are compared in Table 2. The percent of total vine uptake of individual nutrients between the major phenological stages in a growing

Table 2 Seasonal uptake of macronutrients reported for grapevines in whole-plant studies.

Vine/growth conditions	Element	% of total vine uptake[a]				Reference
		Budbreak-bloom	Bloom-veraison	Veraison-harvest	Harvest-leaffall	
2 yr Chenin blanc, irrig., pot	N	24	39	0	37	Conradie 1980
2 yr Chenin blanc, irrig., pot	N	21	32	20	27	Conradie 1986
2 yr Thompson, irrig., field	N	65	25	10	nd	Araujo and Williams 1988
18 yr Cabernet S., dry, field	N	nd	86	14	nd	Williams and Biscay 1991
10 yr Chenin blanc, irrig., field	N	62	25	13	nd	Mullins et al. 1992
10 yr Concord, irrig., field	N	21	70	33	-24	Hanson and Howell 1995
3 yr Concord, dry, field	N	13	132	-28	-17	Bates et al. 2002
23 yr Pinot noir, dry, field	N	52	35	13	1	Schreiner and Baham[b]
2 yr Chenin blanc, irrig., pot	K	27	49	9	15	Conradie 1981a
18 yr Cabernet S., dry, field	K	nd	100	0	nd	Williams and Biscay 1991
10 yr Chenin blanc, irrig., field	K	48	17	35	nd	Mullins et al. 1992
23 yr Pinot noir, dry, field	K	24	55	18	3	Schreiner and Baham[b]
2 yr Chenin blanc, irrig., pot	P	33	41	-3	29	Conradie 1981a
23 yr Pinot noir, dry, field	P	55	51	0	-6	Schreiner and Baham[b]
2 yr Chenin blanc, irrig., pot	Ca	26	47	8	19	Conradie 1981a
23 yr Pinot noir, dry, field	Ca	28	49	17	6	Schreiner and Baham[b]
2 yr Chenin blanc, irrig., pot	Mg	20	42	13	25	Conradie 1981a
23 yr Pinot noir, dry, field	Mg	18	51	28	3	Schreiner and Baham[b]

[a]Data calculated from original tables or figures appearing in cited puiblications, rounding to the nearest integer; **nd: not determined.**
[b]Unpublished data from Schriener and Baham calculated from the average percentage of total uptake over a two-year period, 2001–2002.

season were calculated from original reports. Note that some studies reported in Table 2 did not follow nutrient contents over the entire growing season (budbreak to leaf-fall), and the relative uptake of nutrients is therefore skewed as compared to studies that did.

Nitrogen has been the primary nutrient examined in whole-vines studies. All the studies indicate that N uptake before veraison is greater than N uptake after veraison (Table 2). That makes sense, since the majority of N needed by grapevines occurs in the leaves and shoots of the canopy where it is used primarily for generating photosynthetic capacity (Mullins et al. 1992). Differences in the timing of N uptake between studies are also evident, particularly in the periods between budbreak and bloom and between bloom and veraison.

Of the five studies shown in Table 2 that examined N uptake from budbreak to leaf-fall, four showed peak N uptake occurring between bloom and veraison, while only our study in Oregon showed peak uptake of N before bloom. I believe that this difference is primarily explained by the fact that three of the four studies showing peak N uptake after bloom were irrigated and the fourth was conducted in New York state, where significant summer rainfall occurs. N uptake was probably limited by low soil moisture in the Oregon study, which was conducted under dryland conditions with very low summer rainfall. Interestingly, if we assume that little N uptake took place after harvest in the studies by Araujo and Williams (1988) and Mullins et al. (1992), which is consistent with the other studies that followed N uptake all season, then these studies would also indicate that peak N uptake occurred between budbreak and bloom. The dogma that grapevines take up the most N between bloom and veraison is not supported by all of the whole-vine studies.

Another difference among the five studies that were carried out over the entire growing season is that substantial N uptake after harvest only occurred in the two-year-old Chenin blanc vines grown in sand culture (Conradie 1980, 1986). Both studies on Concords showed fairly large N losses between harvest and leaf-fall (Hanson and Howell 1995, Bates et al. 2002), which may be due to the shorter growth period that occurs after harvest in the North American studies, as suggested by Hanson and Howell (1995). However, the high fertility of the nutrient solutions used in the South African studies (Conradie 1980, 1986) may also be a factor. These findings suggest that postharvest application

of fertilizer N should be avoided in cooler regions, since uptake does not appear to occur after harvest and leaching of nitrate would likely occur.

Of the four studies that examined K uptake in whole vines (Table 2), only two had sampled vines throughout the entire growing season. These studies show that the bulk of K uptake occurred between bloom and veraison. The study conducted by Williams on field-grown, Chenin blanc (reported in Mullins et al. 1992) showed peak uptake occurring prior to bloom, which was similar to N uptake in that study. It is unclear whether these differences may have been due to the timing or amount of fertilizers applied.

Only Conradie (1981a) and Schreiner and Baham (unpublished data) (Table 2) examined P, Ca, and Mg uptake in their whole-vine studies. There is agreement in the time of uptake for Ca and Mg in both studies showing maximal uptake between bloom and veraison. However, the Oregon study showed that most P uptake occurred before bloom, while the South African study showed peak uptake between bloom and veraison. In contrast to the South African study, the Oregon study showed relatively little or no uptake of P, Ca, or Mg after harvest. These differences are most likely due to the continuous supply of nutrients given to the potted Chenin blanc vines throughout the year.

The grapevines studied by Conradie (1980, 1981a, 1986) were probably accumulating luxury amounts of nutrients. For example, the two-year-old Chenin blanc vines took up 9.7 g of N from budbreak to leaf-fall (Conradie, 1980), while the 23-year-old Pinot noir vines, which were ~7 times larger, only took up 7.7 to 8.1 g of N over the same period (Schreiner and Baham, unpublished data). In addition, the leaf blade and petiole N concentrations of the two-year-old Chenin blanc vines were high (Conradie 1981b) compared to the values we obtained in Oregon and to those values typically found in field surveys (Christensen 1984, Colugnati et al. 1997).

The large differences in vine age (2 to 23 years), variety (winegrapes and Concords) and growth conditions (soil type, nutrient supply, water availability) among the studies summarized in Table 2 also account for some of the observed differences in nutrient uptake. While we should be cautious in applying the results on whole-vine nutrient uptake gathered from pot experiments to the field setting, the variability of vine size and soil properties within the field makes it difficult to obtain accurate field data on vine nutrient uptake. This is largely because of the difficulty in obtaining accurate biomass data on roots. Treating the belowground component as a black box, however, can lead to an overestimation of actual nutrient requirements (Williams 1987). It is clear from these studies that a single model of nutrient uptake will not apply to all growing regions, growing conditions, and grapevine varieties.

We had hoped that our whole-vine mineral research conducted in Oregon would shed some light on the specific nutrients that AMF help grapevines obtain from soil, since we carefully monitored root colonization in that study. However, the extent that fine roots were colonized by arbuscules rapidly increased after budbreak and remained high until after leaf-fall (Schreiner and Baham, unpublished data). High rates of arbuscular colonization occurred in roots when N and P uptake was maximal and when K, Ca, and Mg uptake was maximal. So, it is unclear what nutrients may have been enhanced by AMF under our conditions. It is possible that the uptake of many nutrients was enhanced by AMF as soil moisture declined over the summer in this dryland vineyard.

Nutrient Partitioning and Fruit Quality

The whole-vine studies shown in Table 2 generally agree that most N movement to the fruit clusters occurs between bloom and veraison. Conradie (1980), Araujo and Williams (1988), Williams and Biscay (1991), Bates et al. (2002), and Schreiner and Baham (unpublished) found that the bulk of N movement (70 to 100%) to the developing fruit clusters had occurred by veraison, and very little N was imported into the clusters after veraison. However, Williams (reported in Mullins et al. 1992) and Hanson and Howell (1995) found that more N moved to the clusters after veraison than before veraison. These differences are probably due to the higher crop loads in these two studies (2.9 to 5.2 kg cluster dry mass per vine). The studies showing peak movement of N to the fruit prior to veraison were conducted with young grapevines or on vines carrying relatively low crop loads (0.4 to 2.1 kg cluster dry mass per vine). The concentration of N in the clusters declined over the season, in all studies, as berry weights increased.

In contrast to N, the movement of K into the fruit appears to be more consistent among studies, showing a nearly linear increase in K content from bloom to harvest (Conradie 1981a, Williams and Biscay 1991, Mullins et al. 1992, Schreiner and Baham, unpublished data). Clusters are a strong sink for K throughout their development, under a variety of conditions. Conradie (1981a) and Schreiner and Baham (unpublished data) found P, Ca, and Mg import to the clusters to be maximal from bloom to veraison, as was found for N. Of the macroelements, only K appears to accumulate at a significant rate in the clusters after veraison, while other nutrients appear to slow down or even stop moving into clusters after veraison. Understanding when specific nutrients accumulate in the fruit is critical in our efforts to manipulate juice quality as it relates to mineral composition.

Low N in musts is a common factor limiting the fermentation rate and wine quality in many grapegrowing regions, including Oregon (Bell et al. 1979, Bisson 1999, Barney Watson personal communication). Low N status of grapevines can reduce yield and fruit quality and delay ripening by inhibiting leaf expansion and photosynthetic capacity (Winkler et al. 1974). High N status can also reduce yield and fruit quality by fostering excessive canopy growth,

which also delays ripening, and reduces sun exposure of clusters, thereby reducing color development in red wines (Kliewer, 1971, Spayd et al. 1994, Keller and Hrazdina 1998, Keller et al. 1998). Finding the optimal level of N that allows for sufficient, but not excessive, canopy growth, while providing ample N concentrations in musts may be difficult in some grapegrowing regions, such as Oregon. Oregon vineyards generally have sufficient soil N and soil moisture in early summer, which encourages development of large canopies, but there is a history of low N concentrations in musts (B. Watson, personal communication). Since most N movement to the clusters occurs before veraison, when shoots are growing rapidly, attempts to boost cluster N concentrations by increasing N supply in soil may instead encourage excessive canopy growth. Small applications of late summer irrigation water may produce the desired increase in fruit N concentrations, without further stimulating canopy growth. However, this approach to boost N in clusters could also lead to problems with an oversupply of K (Klein et al. 2000, Poni et al. 2003), particularly for Oregon vineyards where low crop loads (~5 t ha^{-1}) are common.

K affects fruit and wine quality primarily through its influence on pH. Must and wine pH are dictated largely by the balance of K concentrations and acid concentrations (tartaric and malic) in developing berries (Boulton 1980). An oversupply of K resulting from high soil supply, excessive fertilizer use or irrigation, or a small crop load in relation to canopy size leads to high berry K concentrations and, quite often, high juice pH (Freeman and Kliewer 1983, Hepner and Bravdo 1985, Conradie and Sayman 1989). Low supply of K results in poor growth, low yield, premature leaf-fall, delayed ripening, and low K concentrations and pH in the fruit (Winkler et al. 1974, Conradie and Sayman 1989). The large sink-strength of the developing berries for K can result in significant redistribution of K from leaves, petioles, or canes even when K status is low (Klein et al. 2000, Poni et al. 2003). These observations suggest that an oversupply of K would be more difficult to manage in winegrape vineyards carrying low to moderate crop loads than a low supply of K. A low supply of K will show either foliar symptoms of K deficiency (Poni et al. 2003) or deficient concentrations of K in leaves or petioles sampled at veraison or harvest (Conradie and Sayman 1989, Klein et al. 2000), whereas a high supply of K will likely go unnoticed until harvest.

Phosphorus affects fruit and wine quality primarily through its requirement by yeast for growth during fermentation (Bisson 1999). Low P can limit the fermentation rate of musts and as a result reduce wine quality. P, as well as Ca and Mg, are similar to N in that these nutrients primarily move to the fruit early in the season. In order to increase the concentrations of these mineral nutrients in the fruit, it would be necessary to boost their supply or uptake prior to veraison. Therefore, managing N, P, Ca, and Mg nutrition for fruit quality will require a different approach than managing K for fruit quality.

Since AMF appear to increase the uptake of K in addition to their ability to take up P by grapevines, the role played by these fungi on the balance of P versus K uptake may be the most important aspect of fruit quality affected by mycorrhizal colonization. High levels of AMF colonization in grapevine roots during the late summer (Schreiner and Linderman 2004) probably enhances K uptake from soil (Deal et al. 1972, Nikolaou et al. 2002) similar to the effect of increased irrigation (Hepner and Bravdo 1985, Klein et al. 2000). A better understanding is needed of the role of AMF on K uptake in grapevines, particularly as it relates to soil moisture and the degree of drought stress experienced by vines.

Mycorrhizas and Drought Tolerance

AMF have long been recognized for improving drought resistance of plants (Safir et al. 1971). There has been an ongoing debate as to whether AMF enhance drought resistance of plants solely because of improved plant P uptake (Safir et al. 1972, Koide 1985, Bryla and Duniway 1998, Ruiz-Lozano 2003). When considering the totality of research published on AMF and drought resistance in plants, Augé (2001) concluded that in some cases AMF can modify plant water relations in a way entirely unrelated to improved P nutrition. However, nearly all of the research studies on AMF and drought have been conducted in pots under controlled conditions (Augé 2001). It is likely that AMF play a bigger role in drought resistance under field conditions, where drought acclimation occurs over a longer time and where the external hyphal network of AMF is well established in soil. Indeed, greater development of this hyphal network and increased soil aggregation has been found after exposing pepper plants to repeated drought cycles under controlled conditions (Davies et al. 1992).

Grapevines are drought avoiders and, as such, attempt to maintain high water status in tissues by a variety of mechanisms, including the development of deep root systems, leaf movements, and sensitive stomatal regulation (Smart and Coombe 1983). Relying on AMF to better explore the soil and presumably provide greater access to soil water by grapevines is yet another means to avoid drought. AMF and drought tolerance in grapevines was recently investigated in potted, Cabernet Sauvignon vines grafted onto eight rootstocks with differing degrees of drought tolerance (Nikolaou et al. 2003). The authors showed that mycorrhizal vines that were drought stressed had significantly less negative predawn leaf water potentials, higher rates of stomatal conductance, and higher rates of CO_2 assimilation than nonmycorrhizal vines. Mycorrhizal vines also had improved P uptake and growth as compared to the nonmycorrhizal controls. It appears that the increased resistance of the mycorrhizal grapevines to drought in this study was primarily due to enhanced P nutrition.

Drought treatment did not alter root colonization by AMF in the above study (Nikolaou et al.2003), but

increased root colonization in response to low soil moisture has been observed in grapevines in two field studies in Oregon (Schreiner 2003, Schreiner and Linderman 2004). Similar results were found in a deficit-irrigated, Cabernet Sauvignon vineyard located in the arid region of south-central Washington (Schreiner and Smithyman, unpublished data). We found significantly more arbuscules per unit fine root length in grapevines receiving reduced irrigation water (30% Et) either between fruit set and veraison or between veraison and harvest, as compared to the standard deficit treatment (60% Et from fruit set to harvest). Grapevines in both reduced water-input treatments in this trial also had lower densities of fine roots, as compared to the standard deficit treatment. Based on these field studies, it appears that mycorrhizal colonization is stimulated by greater drought stress in vineyards, suggesting that grapevines are more reliant on AMF to maintain water (and nutrient) supply as soil moisture is depleted. It is likely that Nikolaou et al. (2003) did not see increased root colonization in their study because of the short duration of the drought period in their potted vines.

A recent study conducted in watermelon is relevant to this discussion because the effects of AMF on drought-stressed and nonstressed plants were investigated under field conditions (Kaya et al. 2003). AMF improved vegetative shoot growth and root growth only under drought stress, but enhanced fruit yield under both stressed and nonstressed conditions. Water use efficiency, defined as the marketable fruit yield per amount of irrigation water applied, was higher in mycorrhizal plants under both conditions. AMF significantly increased leaf N, P, K, Ca, Mg, Fe, Mn, and Zn concentrations in both stressed and nonstressed plants. Since growth was increased in the drought-stressed plants, AMF improved the uptake of all the elements examined when plants were under drought stress. Similar effects of AMF were found in maize grown at three rates of irrigation under field conditions (Sylvia et al. 1993). AMF improved growth and grain yield at all irrigation rates, but the relative increase in growth due to AMF increased with greater drought stress. Both P and Cu concentrations were higher in inoculated maize plants. AMF may therefore play bigger role in the uptake of many soil nutrients (not only P) when plants are experiencing water stress in the field.

Further research to understand the role that AMF play in the drought avoidance of grapevines is needed to identify specific nutrients other than P that may be preferentially enhanced by AMF under water stress and to understand what specific drought-avoidance mechanisms are influenced by AMF in grapes. It seems likely that AMF play an essential role in drought avoidance by grapevines, given what we know from other plant species. As viticulture moves to using less irrigation water and lower fertilizer inputs, in an effort to increase fruit quality and mitigate nutrient runoff and leaching, grapevines will become increasingly dependent on AMF to supply the nutrients and water needed to sustain production. See Keller (2004, this volume) for further discussion of water-deficit effects on grapevine nutrition and physiology.

Managing AMF in Vineyards

Since AMF play a significant role in grapevine nutrient uptake, the impact of management practices on AMF should be considered by vineyard managers. The first thing to consider is preplant soil management. Fumigation of soils (Menge et al. 1983) or long fallow periods prior to planting (Thompson 1994, Schreiner et al. 2003) should be avoided, so that propagules of AMF are not greatly reduced in soil (AMF depend entirely on host plants for their fixed carbon needs). If soils are fumigated before planting, then reintroducing AMF will likely benefit plant establishment and growth. In many cases, field-grown nursery stock (dormant plants) have AMF in their roots, but grapevines propagated in soilless media usually do not (Schreiner et al. 2003, Cheng and Baumgartner 2004). Inoculation of greenhouse-produced vines before they are planted into fumigated soils is highly recommended. However, we have found little benefit in inoculating greenhouse-produced vines when they are planted into nonfumigated sites in Oregon (Schreiner and Price, unpublished data). The indigenous AMF populations were adequate to ensure root colonization in our soils.

Managing the indigenous population of AMF is probably a more effective means to maintain or boost AMF propagules in soils compared to inoculating with products containing AMF. Cover crops used as a preplant treatment can be used to boost the number of infective propagules of AMF and ensure high rates of AMF colonization in subsequently planted crops (Galvez et al. 1995, Boswell et al. 1998). Cover crops grown between the vine rows may also be beneficial for maintaining AMF populations in vineyards (Petgen et al. 1998b). Some cover-crop species, notably plants in the mustard family (Brassicaceae) and lupines (but not other legumes) are not hosts to AMF and will not support AMF populations in soil. Petgen at al. (1998b) found reduced propagules of AMF in soil and reduced root colonization of Sylvaner/5BB grapevines in plots with mustard cover crops as compared to plots with grass or legume cover crops.

The impact of high fertilizer inputs (especially P) are known to reduce AMF colonization of roots and propagules of AMF in many agrosystems, including vineyards (Karagiannidis and Nikolaou 1999). High rates of fertilizer inputs should be avoided, to ensure maximal colonization of roots by AMF, but this is of less significance in winegrape vineyards, where high fertilizer inputs are not generally used (Conradie and Sayman 1989, Spayd et al. 1994). Foliar application of P was linked to low AMF colonization in Oregon vineyards (Schreiner and Linderman 2004). Whether or not foliar P applications consistently reduce AMF colonization, and whether this, in turn, might influence drought stress of grapevines, is currently being investigated.

The level of water applied to vineyards and/or the inherent soil moisture appears to influence AMF colonization of grapevine roots. Reducing water inputs will likely increase AMF colonization of vines. However, if water becomes too limiting and significantly reduces photosynthetic rate, carbon flow to roots will be depressed and, in turn, AMF colonization will be reduced (Smith and Read 1997). Using low water supply in young vines is not recommended, as we have found a high increase in AMF colonization and root growth of grafted, nursery stock after the rate of irrigation applied to production beds was increased (Schreiner and Lodge, unpublished data).

The negative impact of tillage on AMF is well known (McGonigle and Miller 1993, Douds et al. 1995, Kabir et al. 1997). Increased tillage of soil disrupts the hyphal network of AMF and reduces root colonization of crops. Often, tillage results in reduced P uptake of the newly planted crops (McGonigle and Miller 1993). Tillage may also decrease AMF colonization indirectly by increasing the concentration of soil P and root P, thus depressing root colonization through host-plant regulation of infection (Duke et al. 1994). Reduced AMF colonization of grapevine roots retrieved from tilled alleyways (between vine rows) can persist for more than one year after the time of tillage (Schreiner unpublished data). However, shallow cultivation within the vine row, used in many vineyards for weed control, did not adversely affect mycorrhizal colonization of grapevines in a California vineyard (Baumgartner et al. 2004).

Managing soil pH appears to be another practice that will influence AMF in vineyards. Based on surveys of vineyards in Oregon (Schreiner and Linderman 2004) and Italy (Schubert and Cravero 1985), soil pH values below 5.5 may depress AMF colonization in grapevine roots. These results are not consistent with other annual plant species where colonization can be quite high at soil pH values as low as 4.0 (Wang et al. 1993, Clark 1997). It is not known whether this difference is due to a low tolerance of acid pH by grapevine roots **or in the species** of AMF that colonize grapevine roots. Mycorrhizal colonization of grapevines is also expected to be reduced in highly alkaline soils, but the upper limit of soil pH that can reduce AMF colonization in vineyards is not known. AMF colonization of grapevines was not reduced in potted vines grown at pH 8.9 (Bavaresco and Fogher 1996) or in vineyards located in the Yakima Valley, Washington at soil pH values up to 9.4 (Schreiner and Pinkerton, unpublished). It appears that liming acid soils that are below a pH of 5.5 will improve AMF colonization in vineyards, but managing soil pH to improve AMF colonization is probably not an issue for grapevines grown in alkaline soils.

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