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Weed control and cover crop management affect mycorrhizal colonization of grapevine roots and arbuscular mycorrhizal fungal spore populations in a California vineyard

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Abstract Arbuscular mycorrhizal (AM) fungi naturally colonize grapevines in California vineyards. Weed control and cover cropping may affect AM fungi directly, through destruction of extraradical hyphae by soil disruption, or indirectly, through effects on populations of mycorrhizal weeds and cover crops. We examined the effects of weed control (cultivation, post-emergence herbicides, pre-emergence herbicides) and cover crops (*Secale cereale* cv. Merced rye, × *Triticosecale* cv.Trios 102) on AM fungi in a Central Coast vineyard. Seasonal changes in grapevine mycorrhizal colonization differed among weed control treatments, but did not correspond with seasonal changes in total weed frequency. Differences in grapevine colonization among weed control treatments may be due to differences in mycorrhizal status and/or AM fungal species composition among dominant weed species. Cover crops had no effect on grapevine mycorrhizal colonization, despite higher spring spore populations in cover cropped middles compared to bare middles. Cover crops were mycorrhizal and shared four AM fungal species (*Glomus aggregatum*, *G. etunicatum*, *G. mosseae*, *G. scintillans*) in common with grapevines. Lack of contact between grapevine roots and cover crop roots may have prevented grapevines from accessing higher spore populations in the middles.

Keywords Arbuscular mycorrhizal fungi · Cover crops · Herbicides · *Vitis vinifera* · Weeds

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Introduction

All mycorrhizal fungi identified from grapevines are arbuscular mycorrhizal (AM) fungi (Deal et al. 1971; Menge et al. 1983; Nappi et al. 1985; Possingham and Groot-Obbink 1971). Greenhouse studies showed that inoculated grapevines have higher shoot and root weights in P-sufficient (Biricolti et al. 1997; Schubert et al. 1988) and P-limiting (Linderman and Davis 2001) soil, higher tissue concentrations of P in P-sufficient soil (Biricolti et al. 1997), and more compact, highly branched, roots than non-inoculated grapevines (Schellenbaum et al. 1991). Grapevines not only respond positively to colonization, but may also suffer in the absence of mycorrhizae. Grapevines planted in soil fumigated with methyl bromide, which kills AM fungal propagules, may become severely stunted if mycorrhizae do not form within a year of planting (Menge et al. 1983).

Vineyard floor management practices, specifically weed control and cover cropping, may impact mycorrhizal colonization of grapevine roots. Weeds are controlled on the vineyard floor directly beneath grapevines, mainly to keep climbing weeds from growing up into the grapevine canopy, where they interfere with harvest. Potential effects of weed control practices on mycorrhizal colonization may be direct, through disturbance of hyphal networks by mechanical cultivation (McGonigle et al. 1990), or indirect, by killing weeds that host AM fungi (Schreiner et al. 2001). Cover crops are planted and managed in vineyard middles, the area in between vinerows, mainly to reduce soil erosion from winter rains. Dormant season cover crops have been shown to increase mycorrhizal colonization in *Zea mays* L. (Boswell et al. 1998; Kabir and Koide 2000, 2002). Mycorrhizal cover crops may increase mycorrhizal colonization of grapevines, assuming the cover crops and grapevines share AM fungal species in common.

We examined the effects of chemical and non-chemical weed control practices and two cover crops on AM fungi in a California vineyard. Specific objectives were: (1) to determine if weed control practices differ in their effects

on mycorrhizal colonization of grapevines, (2) to determine if mycorrhizal cover crops enhance colonization of grapevines, (3) to examine the diversity of AM fungal species of grapevines and cover crops, and (4) to evaluate the importance of vineyard weeds in maintaining populations of AM fungi in California vineyards.

Materials and methods

Experimental design

Our study was established in a drip-irrigated vineyard in the Central Coast grape-growing region of California, USA, in the town of Greenfield (approximately 200 km southeast of San Francisco). Greenfield has a Mediterranean climate; annual rainfall for the winter of 2001–2002 was 12 cm, and 19 cm for the winter of 2002–2003. The vineyard was established in 1996 with *Vitis vinifera* L. cv. Chardonnay on Teleki 5C (*V. berlandieri* Planch. × *V. riparia* Michx.) rootstock. Vine spacing was 2.4 m between rows and 1.8 m within rows. The soil was Elder Loam with gravelly substratum.

Weed control treatments included: in-row soil cultivation (cultivation), a post-emergence herbicide program (post-emergence), and a pre-emergence herbicide program followed by post-emergence herbicide applications (pre-emergence), which is standard practice for this grape-growing region. Herbicide applications and cultivations were timed in accordance with grower practices and labeling instructions for the herbicides (Table 1). Cultivation was carried out monthly during the growing season with the Radius Weeder (Clemens, Wittlich, Germany), which consists of a metal bar held perpendicular to the direction of tractor movement. When inserted slightly below the soil surface, it severs weed shoots from their roots.

Cover crop treatments included: no cover crop (bare ground), *Secale cereale* L. cv. Merced rye (rye), and × *Triticosecale* Wittm. ex A. Camus cv.Trios 102 (triticale). Cover crops were planted with a vineyard seed drill in the central 0.8 m of the 2.4 m-wide middles in November 2000, 2001, and 2002, just before the start of the rainy season. They were mowed in spring for frost protection and they died in summer. Before planting new cover crop seed each November, middles were disced to smooth out dried stubble remaining from the previous winter's dead cover crop and any weeds that became established during the growing season. Bare ground middles were kept free of weeds with monthly discing.

Table 1 Weed control practices associated with three weed control treatments. Chemical names of herbicides: *Glyphosate N*-(Phosphonomethyl)glycine, *oxyfluorfen*[2-chloro-1-(3-ethoxy-4-nitrophenoxy)-4-(trifluoromethyl)benzene], *simazine* 2-chloro-4,6-bis-ethylamino-*s*-triazine

Year	Weed control treatment	Date applied	Common name[a]	Amount applied (kg active ingredient ha^{-1})
2002	Cultivation	6 March	In-row cultivation	In-row cultivation
	Cultivation	8 April	In-row cultivation	In-row cultivation
	Cultivation	8 May	Hand weeding	Hand weeding
	Cultivation	4 June	In-row cultivation	In-row cultivation
	Cultivation	9 July	In-row cultivation	In-row cultivation
	Cultivation	15 August	In-row cultivation	In-row cultivation
	Post-emergence	19 March	Glyphosate	0.62
	Post-emergence	19 March	Oxyfluorfen	0.46
	Post-emergence	21 May	Glyphosate	0.62
	Post-emergence	10 July	Glyphosate	0.62
	Post-emergence	20 August	Glyphosate	0.62
	Pre-emergence	29 January	Glyphosate	0.62
	Pre-emergence	29 January	Oxyfluorfen	1.38
	Pre-emergence	29 January	Simazine	0.92
	Pre-emergence	21 May	Glyphosate	0.62
	Pre-emergence	20 August	Glyphosate	0.62
	Pre-emergence	20 August	Oxyfluorfen	0.46
2003	Cultivation	11 February	In-row cultivation	In-row cultivation
	Cultivation	8 May	In-row cultivation	In-row cultivation
	Post-emergence	10 February	Glyphosate	0.62
	Post-emergence	22 May	Glyphosate	0.62
	Pre-emergence	6 January	Glyphosate	0.62
	Pre-emergence	6 January	Oxyfluorfen	1.38
	Pre-emergence	6 January	Simazine	0.92

[a]In-row soil cultivation was carried out with a Radius Weeder (Clemens, Wittlich, Germany)

Weed control treatments (established in the vinerows) and cover crop treatments (established in the middles) were arranged in a 3×3 split-block design with three replicate blocks, covering a total of 23 vineyard rows (2.8 ha). Each block contained six vinerows and six adjacent middles. Weed control treatments, the mainplot treatments, were applied along the entire length of each vinerow, which included approximately 300 grapevines. Cover crop treatments, the subplot treatments, were applied along one-third of each middle and were continuous across mainplot treatments in each block. Each replicate mainplot × subplot treatment combination included approximately 100 grapevines and covered an area of 0.045 ha. Data was collected from every other vinerow and adjacent middle.

Sample collection

Grapevine roots and soil were collected on three dates: 25 July 2002 (summer), 19 February 2003 (winter), and 16 April 2003 (spring). Sampling dates corresponded to the following grapevine phenological stages: summer, 25% veraison (onset of ripening); winter, 10% bud break; spring, 25% bloom. Cover crop roots were collected while cover crops were actively growing (winter and spring). A shovel was used to collect approximately 8 cm grapevine root length and approximately 10 g surrounding soil from every fourth grapevine, giving a composite sample that consisted of roots/soil from a total of 20 grapevines per replicate vinerow. Grapevine roots and vinerow soil were collected from within 40 cm of the vine trunk, in the upper 30 cm soil. Cover crop roots and middle soil were collected in middles adjacent to sampled grapevines (approximately 1 m from sampled grapevines).

Mycorrhizal colonization and AM fungal spore populations

A subsample of roots was taken from each composite sample and stained using the method of Koske and Gemma (1989). Percent root length colonization of each weighed subsample (0.75 g fresh grapevine roots, 0.25 g fresh cover crop roots) was estimated using the grid-line intersect method (Giovannetti and Mosse 1980). Mycorrhizal colonization was expressed as the percentage of intersects where AM fungal structures were present out of the total number of intersects examined (100 intersects) for an average of three grid rearrangements per subsample. Mycorrhizal colonization per 100 intersects was adjusted for percent root length, where root length was estimated from 100 intersect counts using the method of Newman (1966). Spores were extracted from three, 5-g subsamples of soil per composite sample by sucrose gradient centrifugation (Daniels and Skipper 1982) and counted at 48× magnification using a dissecting microscope.

We established trap cultures with roots from grapevines, rye, and triticale on potted *Sorghum vulgare* Pers. (Sudan grass) using the procedure of Morton et al. (1993). While collecting roots for quantification of mycorrhizal colonization on 19 February 2003, we collected an additional 8 cm root length per grapevine and adjacent cover crop. Extra roots from each treatment were pooled and used as inoculum for trap cultures. Roots were chopped into 1–2 cm segments and mixed with sterile sand. The root and sand mixture was divided among four 10-cm diameter pots for each plant species and sown with approximately 30 Sudan grass seeds per pot. Sudan grass was fertilized weekly with Hoagland's nutrient solution with 0.25-strength P. After 4 months growth in the greenhouse, replicate trap cultures were pooled and mixed. Spores were extracted from a 100-cm^3 subsample of soil by wet-sieving and sucrose centrifugation. Spores were viewed with dissecting and compound microscopes, and identified based on spore color, size, surface ornamentation, and wall structure using the species descriptions of Schenck and Pérez (1990).

Weed frequency

Weed species frequency was quantified in replicate vinerows on three dates: 24 June 2002 (summer), 13 March 2003 (winter), and 15 May 2003 (spring). Frequency was measured by placing a 30.5 m-long transect line parallel to the vinerow and noting the presence or absence of a weed and the weed's identity every 0.3 m. Weed frequency (%) was expressed as the percentage of 100 points along the transect line examined where an individual weed was present. Cover crops were considered weeds when present in vinerows.

Statistical analysis

A three-way analysis of variance (ANOVA) was used to determine the effects of cover crop (bare ground, rye, triticale), season (summer, winter, spring), weed control (cultivation, post-emergence, pre-emergence), and their interactions on grapevine mycorrhizal colonization, spore populations, and weed frequency. A $\log_{10}$ transformation was performed on grapevine colonization data and spore population data before analysis to reduce heterogeneity of variance. A square root transformation was performed on weed frequency data. A three-way ANOVA was used to determine the effects of cover crop (rye, triticale), season (summer, winter, spring), weed control (cultivation, post-emergence, pre-emergence), and their interactions on cover crop mycorrhizal colonization. A square root transformation was performed on cover crop colonization data before analysis.

The Mixed procedure in SAS (SAS System, version 8.2, SAS Institute, Cary, N.C.) was used for analyses of variance. Cover crop, season, weed control, and their interactions were treated as fixed effects. Block effects and the interactions of block with cover crop, season, and weed control were treated as random effects. Season was

treated as a repeated measure and incorporated into the SAS model using a repeated statement. Treatment means were separated according to Tukey's test. Treatment means and 95% confidence intervals were reversed transformed for presentation in Table 4 and Figs. 1, 2 and 3.

Results

Grapevines

Seasonal changes in grapevine mycorrhizal colonization differed among weed control treatments (season × weed control interaction significant at P=0.0206) (Table 2). In summer, mycorrhizal colonization in the cultivation treatment was significantly higher than that of the pre-emergence treatment (Fig. 1A). Summer mycorrhizal colonization in the post-emergence treatment was intermediate; it was significantly different from neither that of the cultivation treatment, nor that of the pre-emergence treatment. For both the cultivation and post-emergence treatments, grapevine mycorrhizal colonization dropped significantly in spring, while that of the pre-emergence treatment did not drop significantly. Although mycorrhizal colonization in the pre-emergence treatment was low for all three seasons, winter and spring colonization levels were not significantly different from that of the post-emergence treatment, based on very slight overlap among confidence intervals.

Seasonal changes in vinerow spore populations differed among weed control treatments (season × weed control interaction significant at P=0.0258) (Table 2). From summer to winter, vinerow spore populations declined significantly in all weed control treatments (Fig. 1B). Winter spore populations were lowest in the post-emergence treatment (4 spores/g soil). From winter to spring, spore populations returned to high levels in all weed control treatments, but increases were significant only for the post-emergence treatment.

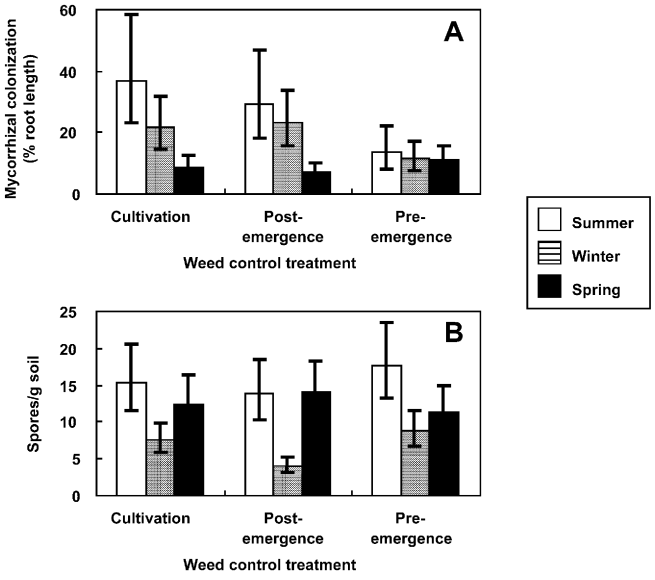

Fig. 1 Effects of three weed control treatments, over the course of three consecutive seasons, on **A** mycorrhizal colonization of grapevines and **B** arbuscular mycorrhizal (AM) fungal spore populations in vinerow soil in a California vineyard. Weed control treatments included: in-row soil cultivation (cultivation), a post-emergence herbicide program (post-emergence), and a pre-emergence herbicide program followed by post-emergence herbicide applications (pre-emergence). Seasons correspond to the following dates: 25 July 2002 (Summer), 19 February 2003 (Winter), and 16 April 2003 (Spring). Each column is the mean of nine observations. *Error bars* 95% Confidence intervals. Columns without overlapping confidence intervals are significant at $P \leq 0.05$, Tukey's test

Despite significant effects of the season × weed control interaction on grapevine mycorrhizal colonization and vinerow spore populations (Table 2), trends in seasonal changes in colonization (highest in summer, lowest in spring) (Fig. 1A) differed from that of spore populations (high in summer and spring, low in winter) (Fig. 1B). Cover crop treatment had no effect on grapevine

Table 2 Denominator degrees of freedom (*Den DF*) and *F* values from analyses of variance for seasonal grapevine $\log_{10}$ mycorrhizal colonization and $\log_{10}$ spore concentrations in vinerows and middles with three cover crop treatments and three weed control treatments. *Num DF* Numerator degrees of freedom

Source[a]		Den DF			*F* Values		
	Num DF	Mycorrhizal colonization	Vinerow spores	Middle spores	Mycorrhizal colonization	Vinerow spores	Middle spores
Cover crop	2	12.50	4.81	5.21	1.35	0.57	6.39*
Season	2	12.40	3.12	5.47	20.87***	32.04**	22.06**
Cover crop × season	4	12.90	5.22	22.60	0.55	0.94	4.69**
Weed control	2	8.31	4.52	12.50	4.10	4.53	4.42*
Cover crop × weed control	4	12.50	7.16	9.62	1.14	0.06	0.90
Season × weed control	4	12.80	6.20	10.50	4.27*	5.97*	0.10
Cover crop × season × weed control	8	13.40	8.47	22.40	1.76	1.24	0.93

*P<0.05; **P<0.01; ***P<0.0001

[a]Source of variation: bare ground, rye, or triticale (cover crop); summer, winter, or spring (season); cultivation, post-emergence, or pre-emergence (weed control)

mycorrhizal colonization or vinerow spore populations (Table 2).

Cover crops

There were no significant effects of cover crop, season, weed control, or their interactions on cover crop mycorrhizal colonization (data not shown). Cover crop mycorrhizal colonization was extremely low (0.13% and 0.09% for all rye and triticale samples, respectively). In fact, of the 36 cover crop root samples, only 21 were colonized. Despite low cover crop colonization, there were high spore populations in middle soil (Fig. 2). Seasonal changes in middle spore populations differed among cover crop treatments (cover crop × season interaction significant at P=0.0066) (Table 2). Middle spore populations were highest in spring in cover-cropped treatments (Fig. 2). There was a significant main effect of weed control treatment on middle spore populations (P=0.0354) (Table 2). Middles adjacent to the post-emergence treatment had more spores (85.40 spores/g soil) than those of the pre-emergence treatment (60.14 spores/g soil). Spore populations in middles adjacent to the cultivation treatment (63.64 spores/g soil) were intermediate; they were significantly different from neither that of the post-emergence treatment, nor that of the pre-emergence treatment.

AM fungal species

We identified a total of eight AM fungal species from trap cultures established with roots of grapevines, rye, and triticale (Table 3). There were only two species, *Glomus aggregatum* Schenck & Smith emend. Koske and *G. etunicatum* Becker & Gerd., in common among grapevines and both cover crops. *Glomus intraradices* Schenck & Smith was found on grapevine and triticale, but not rye, while *G. mosseae* (Nicol. & Gerd.) Gerd. & Trappe was found on both grapevine and rye, but not triticale. Rye and triticale shared two species in common, *G. scintillans* Rose & Trappe and *Paraglomus occultum* Morton & Redecker, that were not found on grapevine. Only triticale had unique AM fungal species: *G. geosporum* (Nicol. & Gerd.) Walker and *Scutellospora calospora* (Nicol. & Gerd.) Walker & Sanders.

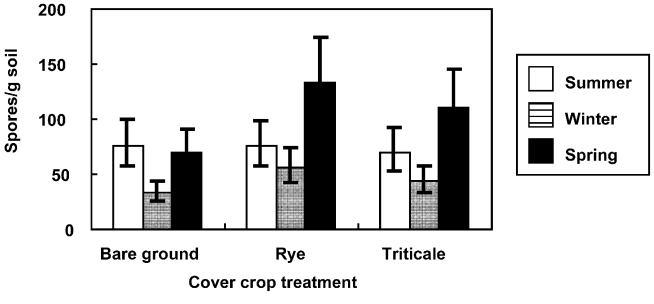

Fig. 2 Effects of three cover crop treatments, over the course of three consecutive seasons, on AM fungal spore populations in vineyard middles in a California vineyard. Season dates as in Fig. 1. Cover crops were planted in November 2002 (no cover crop was planted in bare middles) and were actively growing in winter and spring. Each column is the mean of nine observations. *Error bars* 95% Confidence intervals. Columns without overlapping confidence intervals are significant at $P \leq 0.05$, Tukey's test

Weeds

Seasonal changes in weed frequency varied significantly among weed control and cover crop treatment combinations (cover crop × season × weed control interaction significant at P=0.0046). In the cultivation and post-emergence treatments, vinerows adjacent to cover cropped middles had higher winter weed frequencies than vinerows adjacent to bare middles (Fig. 3A–C). Increased winter weed frequency in vinerows adjacent to cover cropped middles was significant only for the cultivation treatment. While there were higher spring weed frequencies in all three weed control treatments in vinerows adjacent to cover cropped middles, compared to bare middles, differences were not significant.

Dominant weed species varied among cover crop × season × weed control treatment combinations (Table 4). *Cyperus esculentus* L. (nutgrass) was the most common summer weed in all cover crop × weed control treatment combinations, but there were no weeds consistently common in all cover crop × weed control treatment combinations in winter or spring. Cover crops in vinerows (where they were considered weeds) were most common in summer, but were extremely rare in winter and spring, when the cover crop was actively growing in the middles. As summer weeds in the vinerows, cover crops were more common in cultivated and post-emergence treatments than in the pre-emergence treatment. The most common winter weed in the cultivation treatment for all cover crop treatments was *Capsella bursa-pastoris* (L.) Medic (shepherd's purse).

Discussion

Weed control effects

Seasonal changes in grapevine mycorrhizal colonization varied among weed control treatments. Colonization declined from summer to spring in all weed control treatments; declines were significant in the cultivation and post-emergence treatments. However, seasonal changes in colonization did not correspond with seasonal changes in total weed frequency. This is in contrast to past findings of a direct relationship between weed populations and AM fungi (Johnson et al. 1991; Kurle and Pfleger 1994; Schreiner et al. 2001; Sieverding and Leihner 1984). Weed control treatments clearly had differential effects on weed species frequency, suggesting that weed species may have differed in mycorrhizal status. For example, the most common winter weed in the cultivation treatment was

Table 3 Arbuscular mycorrhizal (AM) fungi associated with grapevines and two vineyard cover crops, rye and triticale, in a California vineyard

[a]Fungi were identified based on morphology of spores extracted from *Sorghum vulgare* Pers. (Sudan grass) trap cultures established with field-collected roots of grapevine, rye, and triticale

AM fungal species[a]	Grapevine	Rye	Triticale
Glomus aggregatum Schenck & Smith emend. Koske	+	+	+
Glomus etunicatum Becker & Gerd.	+	+	+
Glomus geosporum (Nicol. & Gerd.) Walker			
Glomus intraradices Schenck & Smith	+		+
Glomus mosseae (Nicol. & Gerd.) Gerd. & Trappe	+	+	
Glomus scintillans Rose & Trappe		+	+
Paraglomus occultum Morton & Redecker			+
Scutellospora calospora (Nicol. & Gerd.) Walker & Sanders			+

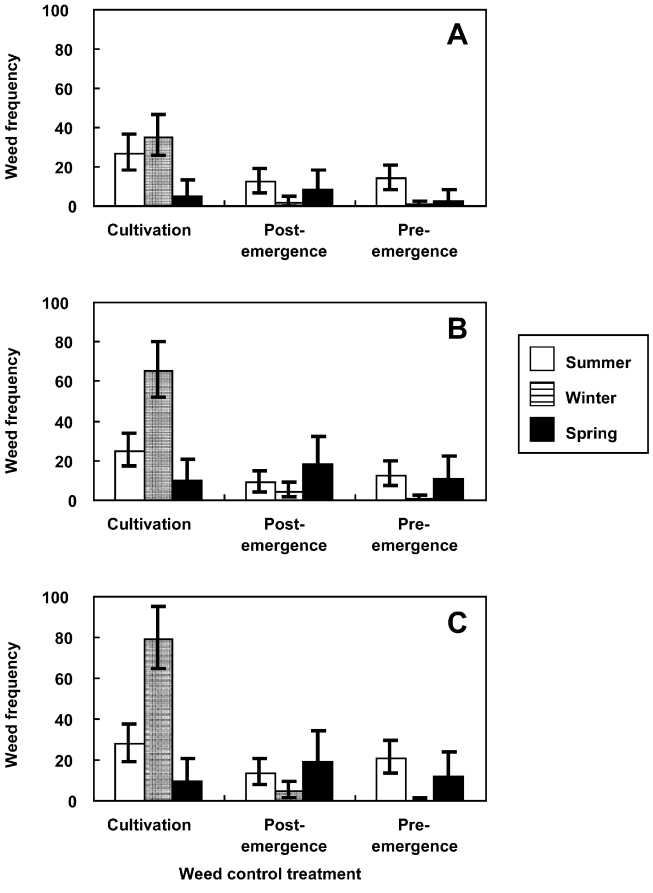

Fig. 3 Effects of three weed control treatments, over the course of three consecutive seasons, on weed frequency in vineyard rows adjacent to vineyard middles with three cover crop treatments: **A** bare ground, **B** rye, and **C** triticale. Weed control treatments as in Fig. 1. Seasons correspond to the following dates: 24 June 2002 (summer), 13 March 2003 (winter), and 15 May 2003 (spring). Cover crops were planted in November 2002 (no cover crop was planted in bare middles) and were actively growing in winter and spring. Each column is the mean of three observations. Error bars represent 95% confidence intervals. Columns without overlapping confidence intervals are significant at $P \leq 0.05$, Tukey's test

shepherd's purse, a member of the Brassicaceae, a plant family known to have a high proportion of non-mycorrhizal species. Shepherd's purse and members of the Chenopodiaceae, *Salsola iberica* Sennen (Russian thistle) and *Chenopodium album* L. (common lambsquarters), likely contributed little AM fungal inoculum.

It is difficult to associate individual weed species frequencies with grapevine mycorrhizal colonization because dominant weed species varied among cover crop × season × weed control treatment combinations. Higher frequency of cover crops as summer weeds in the cultivated and post-emergence treatments may partially explain higher summer mycorrhizal colonization of grapevines in these weed control treatments. However, given that cover crop mycorrhizal colonization was extremely low and that cover crop treatment had no effect on grapevine mycorrhizal colonization, it seems unlikely that cover crops as summer weeds contributed much AM fungal inoculum. Weed species may have differed not only in mycorrhizal status, but also in AM fungal species composition. Just as we identified AM fungal species that were unique to grapevine, rye, and triticale, it is possible that some weeds host AM fungal communities that overlap more with that of grapevines than others.

Grapevines in the cultivation treatment had higher summer mycorrhizal colonization than those in the pre-emergence treatment. We anticipated finding low colonization in the cultivation treatment, based on past reports of the negative effects of soil cultivation on mycorrhizal colonization and, in turn, shoot P concentrations of *Z. mays* (Evans and Miller 1990; McGonigle et al. 1990). Given that grapevine petiole concentrations of P were not significantly different among weed control treatments (data not shown), it is possible that the degree of soil disturbance from cultivation was not severe enough to disturb enough fine roots and their external hyphal network to reduce P uptake.

Low summer and winter mycorrhizal colonization of grapevine roots in the pre-emergence treatment (seasons when grapevines in the other weed control treatments had higher colonization) may be attributable to direct negative effects of the herbicides on grapevine roots. Glyphosate, oxyfluorfen, and simazine impair a variety of plant biochemical processes (Ahrens 1994), thereby potentially disrupting the supply of assimilates to AM fungi. Past research has demonstrated indirect negative effects of glyphosate (Mujica et al. 1999), oxyfluorfen (Sieverding and Leihner 1984), and simazine (Nemec and Tucker 1983) on mycorrhizal colonization of hosts other than grapevine. Since glyphosate was used in both post-emergence and pre-emergence treatments in similar frequency, additional oxyfluorfen and simazine applications in the pre-emergence treatment may have been

Table 4 Seasonal weed species frequency with three weed control treatments and three cover crop treatments in a California vineyard

Weed control	Season	Cover crop	Weed frequency[a]												
			Capsella	*Chenopodium*	*Convolvulus*	*Conyza*	*Cyperus*	*Lamium*	*Malva*	*Polygonum*	*Portulaca*	*Salsola*	*Solanum*	*Sonchus*	*X Triticosecale/Secale*
Cultivation	Summer	Bare	0	0.33	0	0	12.67	0	0	0	2.33	0.33	5.00	5.67	0.67
		Rye	0	0.67	0	0	8.67	0	0	0	5.33	0	2.00	2.00	6.33
		Triticale	0	0.67	0	0	11.00	0	0.33	0	4.00	0	3.00	0.33	8.67
	Winter	Bare	21.33	0	0	0.67	0	1.33	2.33	0.67	0	0	2.67	7.00	0
		Rye	27.67	0	0.33	0	0.33	0.67	4.67	14.33	0.33	0	1.67	14.33	1.00
		Triticale	42.67	1.33	0	0	0.33	0.33	7.67	11.67	0.33	0	0.33	13.00	1.67
	Spring	Bare	0	0	0	0	1.33	0.33	0	0	0	0	1.00	2.33	0
		Rye	0.33	0.33	0.33	0	0	0	3.33	2.00	1.00	0	0	2.67	0
		Triticale	0	0	0	0	0.33	0.33	3.33	2.00	1.00	0	0.33	2.67	0
Post-emergence	Summer	Bare	0	0.33	0	0	7.00	0	0	0	0	0	0.33	0.67	4.00
		Rye	0	0	0	1.33	6.00	0	0	0	0.33	0	0	0	1.33
		Triticale	0.33	0	0.67	1.33	9.67	0	0	0	0	0	0	0	3.00
	Winter	Bare	0	0	0	1.67	0	0	0	0	0	0	0	0	0
		Rye	0.33	0	0	4.67	0	0	0	0	0	0	0	0	0
		Triticale	0	0	0	5.67	0	0	0	0	0	0	0	0	0
	Spring	Bare	0.33	0.67	0	5.00	1.33	0	0.33	0	0	0	0	1.00	0
		Rye	0	0	0	14.67	2.67	0.33	1.00	0.33	0	0	0.33	0.67	0
		Triticale	0	0.33	1.00	15.00	0	0.67	0.33	3.00	0	0	0.33	0.67	0
Pre-emergence	Summer	Bare	0	0	0	2.67	10.33	0	0	0	0	0	0	0	1.33
		Rye	0	0	1.00	0	11.00	0	0	0	0	0	0	0	1.00
		Triticale	0	0	0	3.33	17.00	0	0	0	0	0	0	0	0.33
	Winter	Bare	0	0	0	0.33	0.33	0	0	0	0	0	0	0	0
		Rye	0	0	0.33	0	0.67	0	0	0	0	0	0	0	0
		Triticale	0	0	0	0	0.33	0	0	0	0	0	0	0	0
	Spring	Bare	0.33	0	0	0.33	1.33	0	0.33	0	0	0	0	0	0
		Rye	0.33	0	1.67	0	3.00	0.33	0	5.00	0	0	0.67	0	0
		Triticale	0	0	0.33	0	4.33	0	0	10.00	0	0	0	0	0.33

[a]Weed species identified in the vinerows:*Capsella bursa-pastoris* (L.) Medic (shepherd's purse), *Chenopodium album* L. (common lambsquarters), *Convolvulus arvensis* L. (morning glory),*Conyza canadensis* L. Cronq. (mare's tail), *Cyperus esculentus* L. (nut grass), *Lamium amplexicaule*L. (henbit),*Malva parviflora* L. (malva),*Polygonum arenastrum*Boreau (knotweed), *Portulaca oleracea* L. (purslane), *Salsola iberica* Sennen (Russian thistle),*Solanum sarrachoides*Sendtner (nightshade), *Sonchus oleraceus* L. (sow thistle), *Secale cereale* L. cv. Merced rye (rye cover crop), and X *Triticosecale* Wittm. ex A. Camus cv.Trios 102 (triticale cover crop). Weed frequency represents the percentage of 100 points (spaced 0.3 m apart) along a 30.5 m-long transect line where an individual weed was present. Each weed frequency measurement is the mean of three observations

responsible for reduced grapevine mycorrhizal colonization. If grapevines in the pre-emergence treatment suffered direct root damage from oxyfluorfen and simazine, this was not reflected in yield measurements taken at harvest in September 2002 or in pruning weights collected in January 2003, neither of which differed among weed control treatments (data not shown). However, herbicides may cause sublethal inhibition of photosynthesis, which may result in reduced mycorrhizal colonization in the absence of obvious damage to the plant (Moorman 1994).

Seasonal changes in grapevine mycorrhizal colonization did not correspond to seasonal changes in vinerow spore populations. Lack of correlation between colonization and spore populations has been reported in other studies (e.g., Kurle and Pfleger 1994). Colonization of grapevine roots may be initiated primarily by propagules other than spores, such as mycorrhizal grapevine or weed roots, or the roots may have been "saturated" with fungi such that additional spores had no impact on colonization (Jacobsen and Heidman 1989). The proportion of viable spores may change on a seasonal basis, but without spore viability data, it is difficult to draw conclusions about the relationship between spore populations and colonization.

Even though weed control treatments were carried out in vinerows, they had a significant effect on spore populations in middles. The highest spore populations were found in middles adjacent to the post-emergence treatment; the lowest, in middles adjacent to the pre-emergence treatment (cultivation treatment was intermediate). Assuming that differences in middle spore populations are due to effects of vinerow weed control treatments on weed establishment in the middles, we might expect that some common vinerow weeds were also common in adjacent middles. Some common weeds in certain weed control treatments, such as *Conyza canadensis* L. Cronq. (mare's tail) in the post-emergence treatment and *Malva parviflora* L. (malva) in the cultivation treatment, grew in large clusters that appeared to spread from vinerows to adjacent middles. Without weed frequency data from the middles, we do not know how vinerow weed control treatments affected weed establishment in the middles.

Cover crop effects

Neither cover crop had significant effects on grapevine mycorrhizal colonization or vinerow spore populations. This is in contrast to past research that found increased colonization of *Z. mays* planted following a dormant season cover crop (Boswell et al. 1998; Kabir and Koide 2000, 2002). The cover crops were mycorrhizal, albeit at extremely low levels, and shared four AM fungal species in common with adjacent grapevines. Higher spore populations in cover cropped middles in spring coincided with peak cover crop growth. However, given that the cover crops were planted 0.8 m away from the grapevines, it seems likely that there were few grapevine roots that extended into the middles and, in turn, few cover crop roots that extended into the vinerows. We gathered preliminary data on root distribution from soil cores taken to a depth of 50 cm in February 2003 (data not shown). For five grapevines, at 0.9 m and 1.2 m away from their trunks (where cover crops were planted in the middles), cover crop roots were present in the upper 30 cm soil, but no grapevine roots were found in the upper 50 cm soil. It is possible that little or no overlap between their root systems prevented grapevine roots from accessing AM fungal propagules in the middles.

Cover crops had a significant effect on weed frequency when cover crops were actively growing for all weed control treatments. Winter and spring weed frequencies were higher in the cultivation and post-emergence treatments in vinerows adjacent to cover cropped middles. The same trend was found in spring weed frequencies in the pre-emergence treatment. It is likely that monthly discing in the bare middles, which was done to keep them bare, kept weed seedlings from becoming established. It is also possible that the cover crop plants provided a better microclimate for weed seed germination.

There were much higher spore populations in the middles than in the vinerows. The fact that we observed this trend in bare middles as well as cover cropped middles suggests that vineyard weeds, the only mycorrhizal hosts in bare middles, may be an important source of AM fungal inoculum. A positive correlation between weed populations and spore populations has been noted in annual cropping systems (Johnson et al. 1991; Kurle and Pfleger 1994; Sieverding and Leihner 1984). Many California grape-growers do not plant cover crops. Instead, they allow whatever colonizes the vineyard floor (also known as resident vegetation) to grow during winter. In some grape-growing regions of California, resident vegetation includes species used as planted vineyard cover crops such as *Vicia sativa* ssp. *sativa* L. (common vetch), *Trifolium hirtum* All. (rose clover), and *Medicago polymorpha* L. (California burclover). Resident vegetation may help maintain AM fungal populations in vineyards during the dormant season, especially in the absence of planted cover crops.

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