

Endotrophic mycorrhiza and the nutrition of grape vines

by

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Introduction

In 1900 STAHL reported an association between fungal hyphae and the roots of grape vines escaped from German vineyards. Subsequently PETRI (1907) suggested that the incidence of mycorrhiza and the insect disease phylloxera in grape vines might be related. Later PEYRONNELL (1923) and RIVES (1926, 1927) provided detailed descriptions of the fungal-root association found in grape vines and established that the roots of *Vitis vinifera* cultivars can be infected with vesicular-arbuscular mycorrhiza. More recently STANCAK-BORATYNSKA (1954) and KOSTYUK and SHTERENBERG (1959) reported that grape vines infected with mycorrhiza are darker green and better developed than uninfected plants.

Endotrophic mycorrhizas have been shown to be present in a wide range of horticultural species including apple, walnut, almonds, citrus, avocado, strawberry (MOSSE 1963, HARLEY 1969); and in a wide range of forest trees (BAYLIS 1967, NICOLSON 1967, GERDEMANN 1968, and HARLEY 1969, 1970). In many cases the mycorrhizas have been shown to markedly improve the growth of plants, especially in the case of forest species growing in soils of low fertility.

The purpose of the experiments described in this paper was to establish whether endotrophic mycorrhizas are present in the roots of Australian grape vines. A number of different grape vine species and varieties was examined and roots were collected from the main viticultural regions of the continent to determine the general incidence of infection. In addition, a series of experiments was conducted to establish whether the presence of mycorrhizas in grape vine roots confers a nutritional advantage on the plant.

Methods

Preparation and staining of vine roots for mycorrhiza

For routine observation small 1—2 mm lengths of vine root were fixed in F.A.A. and then softened in 1 n HCl at 60° C for 10 minutes. They were cleared by placing them in a boiling saturated solution of chloral hydrate for 10 minutes, after which they were stained for 10 minutes in a hot solution of 0.1% acid fuchsin. They were washed in two changes of lacto-phenol and mounted in and tapped out in this same medium. In a few cases roots were paraffin embedded and sectioned. These were stained as described above and examined for mycorrhiza.

Culture of experimental vines

Seedlings of the variety Raisin de Dame were used in these experiments. The seeds were collected from field grown vines and after sterilization for 10 minutes

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in 5% hypochlorite solution were germinated in vermiculite. The seedlings were grown for 3—4 weeks in vermiculite after which they were transferred to soil.

The seedling vines were grown in a glasshouse in which temperature was controlled to between 22 and 26° C dependent on season. One litre metal containers were used as pots and were sterilized by autoclaving. The soils were sterilized by exposing them to 2.5—3.5 megarads of gamma ionizing irradiation. Each container held between 1000—1200 g of soil, the surface of which was covered with 200 g of sterile river sand to reduce micro-organism infection. All watering was with sterile water, and sterile (autoclaved) plastic tubes placed at the side of each pot carried water to the base of the pots. The tubes were plugged with cotton wool and capped with a plastic seal to prevent washing airborne microorganisms into the soil.

Chemical analyses

In our laboratory the levels of phosphorus present in dried ground plant material were measured using the molybdovanadate method of CAVELL (1955) following acid digestion. The levels of other inorganic nutrients present in vine shoots were measured by the Australian Mineral Development Laboratories using standard methods of analysis as described by HUMPHRIES (1956).



Fig. 1: Survey of endotrophic mycorrhiza in Australian vineyards. Dots indicate areas where root samples were taken, and in all cases mycorrhiza was present.

Experimental and Results

1. Anatomy of vine mycorrhizas

The anatomy of vine mycorrhizas was found to be essentially similar to that of endotrophic mycorrhizas infecting other plants (HARLEY 1969). The hyphae were generally aseptate with angular projections invading mainly the cortical tissue of roots and often forming numerous vesicles (Figs. 2, 3). Within host cells the fungus forms haustoria which develop into arbuscules and sporangioles (Figs. 4, 5).

2. Distribution of vine mycorrhiza within Australia and between vine varieties

Fig. 1 shows the vineyards within Australia and the Territory of Papua and

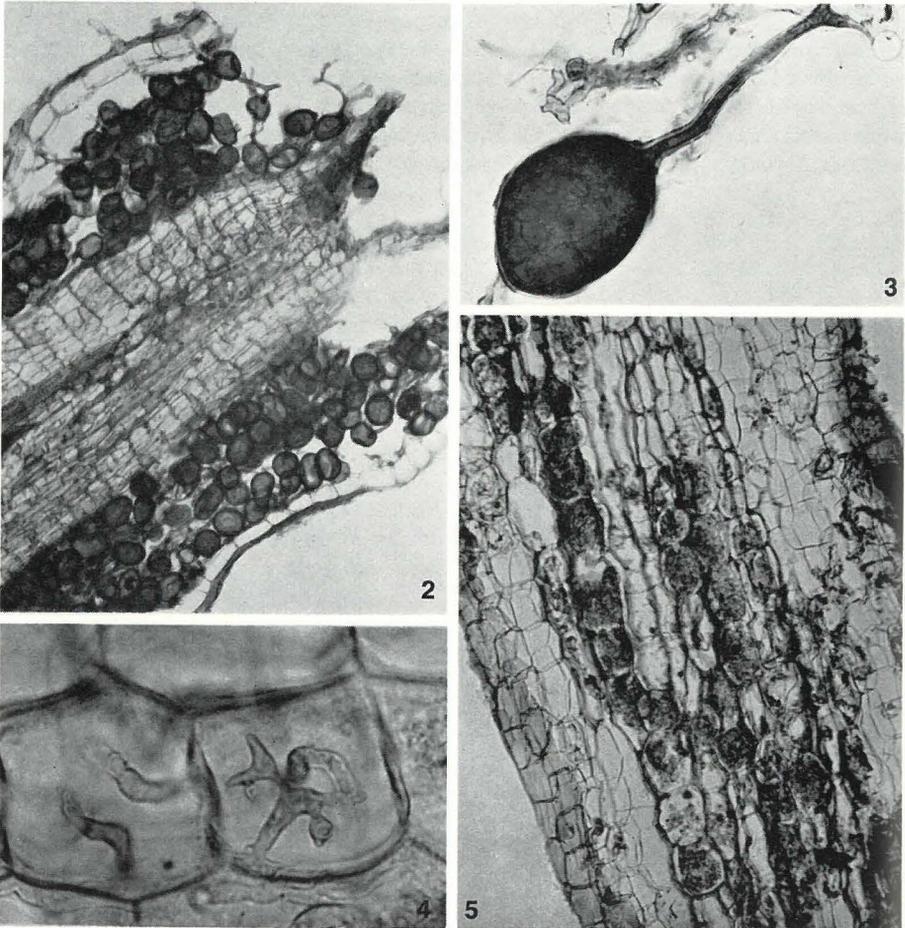


Fig. 2: Grape vine root (variety Sultana) heavily infected with mycorrhiza. Note hyphae and numerous vesicles in cortical region of root (\times ca. 110).

Fig. 3: Single vesicle of *Endogone* sp. with aseptate mycorrhizal hyphae attached (\times ca. 355).

Fig. 4: Mycorrhizal haustoria growing internally in cortical cells of infected vine roots (\times ca. 620).

Fig. 5: Grape vine root heavily infected with endotrophic mycorrhiza. Tangential root section shows numerous cortical cells containing arbuscules (\times ca. 130).

New Guinea where endotrophic mycorrhizas have been identified on vine roots. Three common grape varieties, Sultana (drying), Cabernet Sauvignon (wine making), and Muscat Hamburg (table), which are grown extensively throughout southern Australia were principally examined. Where these varieties were not available roots of other vine varieties were sampled.

All the roots examined were infected, indicating that *Endogene* spp. are widespread, if not universally present, in Australian vineyards. However, fungal hyphae, vesicles and arbuscules were more prominent in roots collected during spring and summer than in those taken from the field in winter.

Table 1 shows a list of different *Vitis* sp., *Vitis* hybrids and varieties of *V. vinifera* grown at the CSIRO vineyards at Merbein, Victoria, from which root samples were taken. All species and cultivars were infected.

3. Growth and nutrient uptake of vine seedlings infected with mycorrhiza

Preliminary experiment

A small initial trial was conducted in which the growth of vine seedlings (variety Grande Glabre, *V. vulpina*) in an autoclaved soil (15 lbs pressure for 15 minutes) was compared with their growth in a comparable natural soil. The seedlings in autoclaved soil grew poorly and many of the replicates died. Fig. 6 indicates the large growth differences obtained in this experiment.

Table 1

Vitis vinifera varieties, hybrids and *Vitis* species in which endotrophic mycorrhiza have been identified in vines grown at Merbein, Victoria. Roots were collected during 1969-70

<i>Vitis vinifera</i> varieties	Hybrids and <i>Vitis</i> species
Blanquette	Dog Ridge <i>V. champini</i> PL.
Cardinal	Salt Creek <i>V. champini</i> PL.
Cabernet Sauvignon	R 99 <i>V. berlandieri</i> PL. × <i>V. rupestris</i> SCH.
Cinsaut	1613: <i>V. longii</i> PRINCE × ([<i>V. labrusca</i> L. × <i>V. vulpina</i> L.] × <i>V. vinifera</i> L.)
Clare Riesling	101-14 <i>V. vulpina</i> L. × <i>V. rupestris</i> SCH.
Grenache	R 110 <i>V. berlandieri</i> PL. × <i>V. rupestris</i> SCH.
Gordo Blanco	Rupestris du Lot <i>V. rupestris</i> SCH.
Gros Colman	Teleki 5 BB <i>V. berlandieri</i> PL. × <i>V. vulpina</i> L.
Italia	
Listan	
Mataro	<i>Vitis</i> species
Muscat Hamburg	<i>Vitis cordifolia</i> LAM.
Ohanez	<i>Vitis longii</i> PRINCE
Purple Cornichon	<i>Vitis candicans</i> ENGELM.
Red Malaga	<i>Vitis cinerea</i> ENGELM.
Ribier	<i>Vitis rupestris</i> SCH.
Semillon	<i>Vitis berlandieri</i> PL.
Shiraz	<i>Vitis tiliaefolia</i> HUMB. and BONP.
Sultana	<i>Vitis rotundifolia</i> MICHX.
Waltham Cross	<i>Vitis labruscana</i> BAILEY
White Riesling	<i>Vitis vulpina</i> L.
Zante Currant	

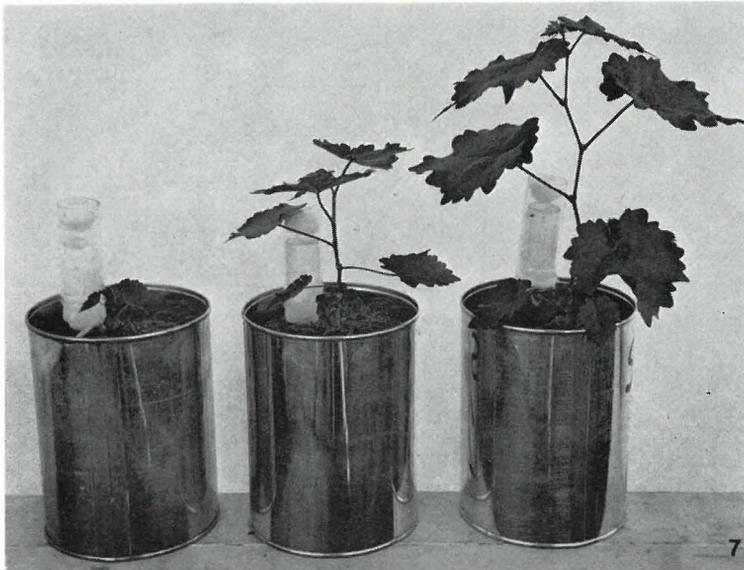
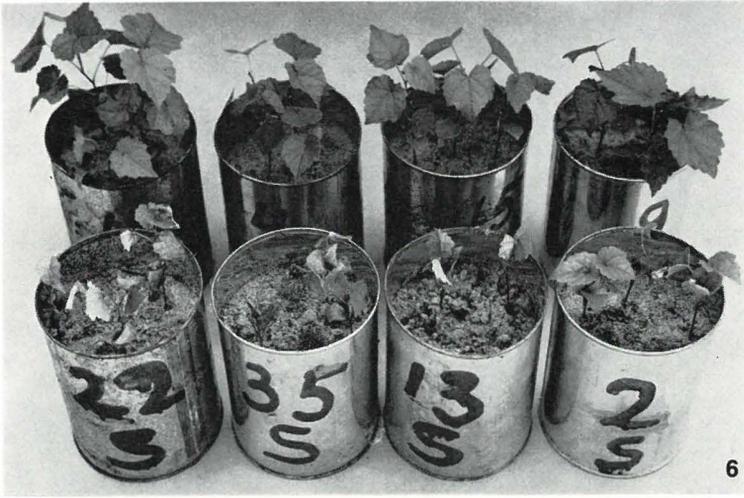


Fig. 6: Vine seedlings (variety Grande Glabre *V. vulpina*) grown in unsterilized soil (back row) and in heat sterilized soil (front row).

Fig. 7: Vine seedlings (variety Raisin de Dame) grown in Murray Sand. Note the watering tube on the side of the pots. Soil in L.H. and centre pots was sterilized. Plant in centre pot was inoculated with infected root material (live mycorrhiza inoculum) while the plant in the L.H. pot was inoculated with an autoclaved root suspension (dead mycorrhiza inoculum). The R.H. pot contained non sterile soil.

Experiment 1:

Growth of vine seedlings in two sterile soils

Vine seedlings of the variety Raisin de Dame were grown in two soils — one a light sand (Murray Sand) and the other a medium loam (Sandilong Loam) (PEN-

Table 2
Experiment 1: Growth of vine seedlings in two soils

Treatment	Murray Sand ¹⁾			Sandilong Loam ¹⁾		
	Dry weight/plant			Dry weight/plant		
	Shoot	Root	Total	Shoot	Root	Total
	g	g	g	g	g	g
Sterile soil						
Live mycorrhiza (LM)	0.91	1.37	2.28	3.83	5.68	9.51
Dead mycorrhiza (DM)	0.05	0.05	0.10	0.07	0.12	0.19
Unsterile soil (US)	0.63	2.36	2.99	3.68	5.38	9.06

1) Shoots LM ^{**} > US ^{***} > DM

1) Roots and totals US ^{***} > LM ^{***} > DM

2) Shoots, roots, and totals LM, US ^{***} > DM

*** Significant at $P < 0.01$

** Significant at $P < 0.05$

MAN 1939). The growth of the seedlings in soil which had been sterilized with gamma irradiation was compared with that in unsterilized soil. The seedlings grown in sterilized soil were inoculated at the time they were transferred from vermiculite to soil with either live or dead mycorrhizal fungus. The mycorrhizal inoculum consisted of finely chopped infected vine roots which had been washed in water, and surface sterilized by treatment with 5% hypochlorite solution for 10 minutes. The dead mycorrhiza inoculum consisted of similar roots which had been autoclaved. Approximately 0.2 g fresh weight of root inoculum was added to each pot and there were 10 replicates of each treatment.

Table 2 shows the results obtained in this experiment in which the plants were grown for 16 weeks. In both soils the growth of the plants in unsterilized soil, and in sterilized soil inoculated with live mycorrhiza was greater than the growth of plants in sterile soil which had been inoculated with dead mycorrhiza (Fig. 7). At harvest the growth differences were large as the plants grown in sterile soil and inoculated with dead mycorrhiza had virtually ceased growing.

Microscopic examinations were made of the roots of the plants of this experiment and no mycorrhiza could be found in the roots of plants grown in sterile soil which were inoculated with autoclaved roots. By contrast, clear evidence of mycorrhizal infection could be found in the roots of plants grown in non-sterile soil and in sterile soil inoculated with live mycorrhiza. In the plants inoculated with live mycorrhiza, many of the roots were infected with nematodes. In subsequent experiments mycorrhizal inoculum was prepared from the nematode resistant vine varieties of Salt Creek and 1613.

Experiment 2:

Growth of vine seedlings in sterile Murray Sand

The vine seedlings, soil, method of sterilization and growing conditions used in this experiment were as for experiment 1. However, Salt Creek rootstock vines

Table 3
Experiment 2: Growth of vine seedlings in Murray Sand

	Total dry weight ¹⁾ g	Total leaf area ²⁾ cm ²
Sterile soil		
Live mycorrhiza (LM)	3.66	265.85
Filtered soil inoculum (FSI)	0.095	7.39
Dead mycorrhiza (DM)	0.090	9.48
Unsterile soil (US)	2.01	246.86

¹⁾ LM ^{***} > US ^{***} > FSI, DM.

²⁾ LM, US ^{***} > FSI, DM.

*** Significant at P < 0.01.

infected with mycorrhiza, but not with nematodes, were used as mycorrhizal inoculum. A filtered soil inoculum was prepared by filtering (twice), through a 50 micron sieve, a suspension of 100 gms of vineyard soil in one litre of sterile water. This filtration removed all pieces of root and fungal hyphae but left bacteria and a wide range of soil organisms to act as a mixed inoculum. The growth of seedlings inoculated with either live or dead mycorrhiza or with a filtered soil inoculum was compared with the growth of seedlings in unsterile soil. There were nine replicates of each treatment, and the plants were grown for a period of 10 weeks.

Table 3 shows the mean leaf areas and dry weights of these plants. In this experiment the plants grown in sterile soil and inoculated with either dead mycorrhiza or with a filtered soil inoculum were smaller than those grown in nonsterile soil or in sterilized soil and inoculated with live mycorrhiza.

Again at the conclusion of the experiment the roots of each treatment were examined microscopically for the presence of mycorrhiza. Clear evidence of mycorrhiza was found in the plants grown in non-sterile soil and in vines grown in sterile soil where they were inoculated with a live mycorrhiza suspension. Roots of the dead mycorrhiza group were free of root fungi while the roots of plants inoculated with the filtered soil inoculum had fungal hyphae on their surfaces but displayed no evidence of characteristic mycorrhizal hyphae, vesicles or arbuscules within the cortical cells of these roots.

Experiment 3:

Growth and nutrient uptake of vine seedlings in sterile Murray Sand

In this experiment the growth of Raisin de Dame vine seedlings in non-sterile and in sterile Murray Sand was again compared in the presence of both live and dead mycorrhiza but under three differing nutritional conditions. One group of plants received a weekly supplement of Hoagland solution containing all the essential elements for plant growth. Two similar groups of plants received supplements of Hoagland solution lacking phosphorus and sulphur respectively. There were nine replicates of each treatment, and the plants were allowed to grow initially for 12 weeks when the plant tops were harvested. The plants were allowed

Table 4

Experiment 3: Growth and nutrient uptake of vine seedlings in Murray Sand. Dry weight of shoots (harvests 1, 2, and 3) and phosphorus content of shoots

Fertilizer	Dry weight of shoots		
	US g	LM g	DM g
Full nutrient	9.62	6.68	7.82
— P	9.15	5.37	4.60
— S	5.36	1.79	3.01
L.S.D. (P < 0.05)		1.27	
	Phosphorus content of shoots		
	US mg	LM mg	DM mg
Means across nutritional treatments	3.18	3.25	1.92
L.S.D. (P < 0.05)		0.51	

Abbreviations see Table 2.

to regrow for two further periods of eight weeks when two further harvests of the shoots were made.

Dry weights of shoots were taken at all harvests and the shoot material taken at harvest 2 was analysed for phosphorus while that taken at harvest 1 was analysed for a number of essential nutrient elements. The growth data are given in Table 4 and as well the pooled data from all nutritional treatments for phosphorus content per shoot at harvest 2.

Comparisons of the growth of plants receiving full Hoagland solution with those receiving Hoagland solution lacking either phosphorus or sulphur indicates that in the unsterilized condition Murray Sand is highly deficient in sulphur. However, similar growth comparisons made after sterilizing the soil with ionizing radiation indicated that the soil was both phosphorus and sulphur deficient. This change in nutrient availability as a result of sterilization is well known and is now a documented feature of a number of soils (BOWEN and CAWSE 1964, ROVIRA and BOWEN 1966).

In this experiment significant differences in shoot dry weight occurred between the plants grown in sterile soil and those grown in non-sterile soil. However, no difference in dry weight was observed between plants inoculated with either live or dead mycorrhiza. The data of Table 4 of mean phosphorus content per shoot indicates that the phosphorus content of plants grown in sterile soil and inoculated with live mycorrhiza was greater than when a dead mycorrhiza inoculum was used.

Table 5 provides data on the effect of live and dead mycorrhiza on the uptake of a range of other essential nutrient elements. These data show that inoculation with live mycorrhiza did not affect the uptake of any other nutrients except that of phosphorus. However chloride uptake was higher in unsterilized soil than in sterile but was not influenced by inoculation with mycorrhiza.

Discussion

The results of this series of experiments together with unpublished observations by BARNARD in 1927 establish that Australian grape vines join the list of plants

Table 5
Experiment 3: Nutrient uptake of vine seedlings in Murray Sand

Nutrition	Treatment	Percent of dry weight ¹⁾							
	Mycorrhiza	N	P	K	Na	Ca	Mg	Cl	S
Full nutrient	US	1.25	0.14	1.70	0.03	0.83	0.28	0.09	0.11
	LM	1.53	0.20	1.88	0.02	1.16	0.31	0.04	0.12
	DM	1.48	0.13	1.54	0.03	1.04	0.38	0.04	0.13
— P	US	1.18	0.11	1.42	0.03	1.07	0.27	0.08	0.10
	LM	1.73	0.18	1.67	0.01	1.07	0.30	0.05	0.10
	DM	2.03	0.11	1.65	0.02	1.41	0.37	0.05	0.13
— S	US	1.90	0.17	1.56	0.06	1.04	0.35	0.06	0.09
	LM	2.59	0.33	1.57	0.02	1.42	0.40	—	0.08
	DM	1.74	0.15	1.22	0.01	1.35	0.40	0.03	0.07

¹⁾ Shoot contents at harvest 1.

which are commonly infected with vesicular-arbuscular mycorrhiza. The anatomy of the fungal-root associations recorded for this plant are essentially the same as those found in other woody perennials. It is noteworthy that all of the species of *Vitis* and all of the various cultivars of *V. vinifera* examined in the present study were infected. Furthermore, all of the vineyards which were sampled had vines with infected roots, indicating that this symbiont is widespread and possibly universal in vines. This conclusion is supported by the work of Mosse and Bowen (1968 a, b) who found that spores of *Endogone*, capable of forming vesicular arbuscular mycorrhiza with inoculated host plants, were widespread in Australian soils.

Only a limited number of reports are available on the incidence of endotrophic mycorrhiza in grape vines from other parts of the world. As mentioned earlier, infected vine roots have been observed by workers in France (RIVES 1926), U.S.S.R. (KOSTYUK and SHTERENBERG 1959) and Poland (STANCAK-BORATYNSKA 1954) and in the latter cases their stimulating effect on vine growth has been noted. It is of interest here that STANCAK-BORATYNSKA (1954) and even STAHL (1900) noted that infected plants absorb more water than those lacking mycorrhiza. In our experiments we observed that the water consumption was higher of plants inoculated with live mycorrhiza, e. g. in experiment 2 over an 8-week period the average amounts of water (ml) used per cm² of leaf per week were; plants in non-sterile soil 1.06, plants in sterile soil inoculated with live mycorrhiza 1.25, inoculated with dead mycorrhiza 0.94, inoculated with a filtered soil suspension 0.98.

The growth data of experiment 1 and 2 indicate that inoculating grape vines grown in sterile soil with endotrophic mycorrhizal suspension can dramatically increase their growth. In these experiments very large growth responses attributable to mycorrhiza were obtained. By contrast, no growth response due to mycorrhizal inoculation were recorded in experiment 3. It is suggested that the altered growing conditions which included the repeated application of nutrient solutions to all treatments, a longer (winter) growing period and the complex effect of repeated shoot removal were amongst those factors affecting the growth response. In this connection, HARLEY (1969), MOSSE (1963) and PEUSS (1958) have all reported that

environmental variables such as light intensity and nitrogen fertilization can alter the incidence and effectiveness of mycorrhizal infections of the vesicular-arbuscular type.

In experiment 3 it was found that the plants inoculated with live mycorrhiza, regardless of their nutritional regime, had a higher phosphorus content per shoot than plants inoculated with dead mycorrhiza. This result is in agreement with the results of a number of workers who have shown that infection of plants with endotrophic mycorrhiza increases their capacity to absorb soil phosphorus (BAYLIS 1959, 1962, 1967, MOSSE 1957). In our experiments the uptake of other essential nutrients was not increased in the same way as phosphorus, whereas BAYLIS (1959) found that the shoots of mycorrhizal infected *Griselinia* had higher contents of a number of nutrient elements.

There are few documented cases in Australia of grape vines responding to the application of fertilizers although some 150,000 acres of them are grown and a number of long term manurial trials have been conducted. In Europe where grape vines are very widely grown they are traditionally relegated to infertile soils such as the upper slopes of the Rhine and Rhone Valleys, the Midi area of Southern France and the Douro Valley of Portugal. The centre of origin of *V. vinifera* grapes is the Middle East where they also grow on soils of low fertility and form part of the plant association of forests. Like forest trees such as *Podocarpus*, *Agathis*, *Grise-linia*, which are the colonizers of infertile soils, the survival of grape vines in many of their present habitats is possibly dependant on their ability to form vesicular-arbuscular mycorrhizal associations.

Summary

The roots of grape vines collected from a number of different localities throughout the Australian continent were all infected with mycorrhiza of the vesicular-arbuscular type. Similarly a range of *Vitis* species and hybrids and a number of *V. vinifera* cultivars all displayed microscopic evidence of mycorrhizal infection.

The growth of vine seedlings in soils sterilized either by autoclaving or by gamma irradiation was less than in similar non-sterile soil. The vine seedlings in sterile soils were not infected with mycorrhiza while those in non sterile were. Normal growth of vine seedlings in sterile soils was obtained by inoculating them with vine roots infected with live mycorrhiza. Inoculation of vine seedlings grown in sterile soils with roots containing dead mycorrhiza (autoclaved) or with filtered soil suspensions does not stimulate their growth. The shoots of vine seedlings grown in non-sterile soil or in sterile soils and inoculated with live mycorrhiza had a significantly higher phosphorus content than seedlings not infected with mycorrhiza.

It is suggested that in many of the habitats in which vines are grown in Australia and in Europe vesicular-arbuscular mycorrhiza aids their nutrition.

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