Impact of nematodes on grapevine growth and productivity: current knowledge and future directions, with special reference to Australian viticulture

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Abstract

Grapevines, like most other crops and especially horticultural crops, suffer from attacks by plant-pathogenic nematodes. The types of nematodes found in vineyards and their distribution in Australia and other regions of the world are described, together with an assessment of their impact on vineyard productivity. Relationships between nematode population density and potential damage to grapevines is tabulated, based on published data. Information on reducing nematode impact by means of rootstocks is summarised and also tabulated. Control by other means is discussed, including soil fumigants and nematicides, biological control agents and plants with nematicidal properties. Special attention is paid to improving nematode resistance in rootstocks or even own-rooted *Vitis vinifera* cultivars by conventional breeding and by genetic engineering. Areas for future research are identified, and we provide conceptual tools plus information for long term control of nematodes in vineyards.

Keywords: *nematodes, grapevine, Australian viticulture, rootstocks, resistance, plant breeding*

1 Introduction

Grape production in Australia, in contrast to most other viticultural regions, is predominantly based on own-rooted *Vitis vinifera*, a species of grapevine highly susceptible to two soil-borne pests, the aphid-like insect phylloxera (*Daktulosphaira vitifoliae*) and microscopic roundworms, nematodes. Only about 2% of the total vineyard area of Australia is infested with phylloxera and strict quarantine regulations control the export of all living grapevine material from infested areas. By contrast, plant-pathogenic nematodes are found in all viticultural regions. However, much less attention is given to nematodes, and fewer legal requirements exist to control the movement of nematode-infested material from one vineyard to another. Due to their widespread distribution, nematodes present a serious challenge to productivity in Australian viticulture.

At least 2000 species of plant-parasitic nematodes have been described and they are characterised by a stylet which is used for penetration of root tissue and subsequent feeding. Some species are endoparasitic, entering host root tissue and feeding within it, others are ectoparasitic, living outside the plant and feeding on cells near the root surface. Nematode biology is thus diverse, not only with respect to feeding but also with respect to reproduction, which can be both heterosexual and parthenogenetic.

In this review we describe which nematodes are most likely to cause damage to grapevines in Australia. We also present current information on control measures that might be used to reduce the damage they cause, and make suggestions for future research.

2 Nematodes found in vineyards

World-wide, 162 species of plant-parasitic nematodes, belonging to 35 genera, have been found on grapevines (Lamberti 1988). However, not all of these species have been recognised as causing economically significant damage. Those nematodes which are thought to be most important in vineyards are described below.

2.1 Root-knot nematodes (*Meloidogyne* spp.)

Meloidogyne spp. are sedentary endoparasites whose biology and life cycle have been described in detail in many standard texts such as Eisenback and Triantaphyllou (1991) and Brown et al. (1993). These nematodes hatch from their eggs as second-stage juveniles and migrate through soil to find a host plant root. After entering a root they establish a feeding site by inducing the forma-

tion of 'giant' cells. The infested root cortex swells to form a characteristic gall. A further three moults occur within the root as the second stage juvenile develops into an adult. These moults are superimposed so that no feeding or growth takes place until their completion (Bird 1978). Many of the adults are female, but some develop into males which then discontinue their feeding, leave the roots and move freely within the soil. In grapevine roots, one gall may contain one or several females, each of which may lay up to 1500 eggs in a gelatinous matrix on the root surface. Each life cycle takes just over a month under optimal conditions (Bird 1978) and several generations may be produced per season (McKenry 1992, Brown et al. 1993). Thus, with adequate food and no competition or predators, a single juvenile (assuming an egg mass of 500) can give rise to more than 125 million progeny in a season lasting 3–4 months.

Root-knot nematodes have a broad host range, and are known to parasitise almost every cultivated crop as well as those of many other plant species, among them those classified as weeds. More than 50 *Meloidogyne* species have been described and are known to differ in their pathogenicity on different host plants. At least four species, *M. incognita, M. javanica, M. hapla* and *M. arenaria* are considered to be important pests of grapevines. Two other species have also been found on grapevines in Australia, namely *M. thamesi* (McLeod and Khair 1973) and *M. hispanica* (Hugall et al. 1994), but their importance is unknown. *M. incognita* is considered the most virulent on grapevines under South Australian (Stirling and Cirami 1984, Walker 1997a) and South African conditions (Loubser 1988). However due to the limited number of studies and the difficulties in identifying *Meloidogyne* species (see below), this needs to be confirmed. Within the *Meloidogyne* species, differences in virulence between populations have been identified. For example, nine populations of *M.hapla* in France were found to vary considerably in their virulence when tested against six rootstocks (Dalmasso and Cuani 1976). Variation in the virulence of populations of *M. incognita* and *M. arenaria* has also been reported (Lider 1954, McKenry 1992, Cain et al. 1984, McKenry and Kretsch 1995, Walker 1997b).

Root-knot nematodes have been traditionally identified using perineal patterns, but because a certain amount of variability occurs within all *Meloidogyne* populations, such identification may not be reliable. Other methods, such as the differential host range test (Hartman and Sasser 1985) can be used to confirm a tentative diagnosis but recent results indicate that they too are imperfect and can lead to mis-identification (Stanton and O'Donnell 1998). The most accurate method of identification is based on true genetic groupings as determined by DNA-based tests such as mitochondrial DNA patterns (Stanton et al. 1997) or ribosomal DNA sequences (Zijlstra et al. 1997). Use of these methods will enable a more definitive identification of and differentiation between *Meloidogyne* species. Possible mis-identification of *Meloidogyne* species therefore needs to be kept in mind when considering the results of the studies presented throughout this review.

2.2 Dagger nematodes (*Xiphinema* spp.)

Detailed information on the life cycle and biology of dagger nematodes can be found in Siddiqi (1974a). Dagger nematodes are widely dispersed in vineyard soils but congregate at vine root tips where they feed ectoparasitically. Their feeding retards root extension, causing swelling and gall formation. Cells within gall tissue are enlarged and sometimes multinucleate (Cohn 1975, Boubals and Pistre 1978, Raski and Krusberg 1984, Brown et al. 1993). Radewald (1962) found that in California the life cycle of *X. index* takes 22–27 d at 24°C. However, studies in Israel have indicated that a much longer period (up to nine months at 20–23°C) may be required (Cohn and Mordechai 1969).

At least 28 species of this genus have been reported to occur on grapevines. The species of greatest importance is *X. index* which is the vector of the destructive Grapevine Fanleaf Virus (GFLV). *Xiphinema index* can also cause direct injury to the roots and in this respect populations derived from Italy, California, Israel and France have been shown to differ in their virulence on grapevines (Coiro et al. 1990). *Xiphinema* species other than *X. index* can be vectors for transmission of nepoviruses such as tobacco and tomato ringspot, and arabis mosaic virus (Krake et al. 1999 p. 43). *Xiphinema americanum*, one of the more common species, affects grapevine growth and yields in California (Ferris and McKenry 1975).

2.3 Citrus nematode (*Tylenchulus semipenetrans*)

Tylenchulus semipenetrans has a sedentary, semi-endoparasitic life cycle (Dalmasso et al. 1972). This nematode hatches from eggs as second-stage juveniles, and then feeds ectoparasitically on root epidermal cells. After a further moult, the nematodes bury their head within the root tissue, leaving their body outside, and develop into females. Eggs are laid in a gelatinous matrix on the root surface, and subsequently become dispersed within the soil. Their life cycle is completed within 2–3 months. Optimum temperature for development and reproduction is 25°C (reviewed by Siddiqi 1974b). Males develop from eggs to maturity within 7 d without feeding, apparently causing no damage to the plant host (Brown et al. 1993).

The host range of *T. semipenetrans* is restricted to only a few plant genera: various grapevine and citrus species, lilac, persimmon, loquat, olive and pear, according to reports summarised by Siddiqi (1974b).

Races and pathotypes of *T. semipenetrans* have been detected which differ in their host specificity. Some populations collected from citrus or olive fail to infect grapevines (Gottlieb et al. 1986, Scotto La Massese, quoted by Brown et al. 1993). In California, at least five different races have been identified on grapevines (McKenry 1992).

2.4 Root-lesion nematodes (*Pratylenchus* spp.)

A detailed description of the life cycle and biology of root-lesion nematodes is given in Loof (1991). All species are migratory endoparasites. They hatch as second-stage juveniles from eggs laid in the soil or within host root

tissue. Until they reach maturity, the nematodes may live freely in the soil, or enter a host plant root to feed on cortical tissue. Infested root tissue, or 'lesions', assume a dark red or brown colour caused by necrosis of invaded plant cells. Their life cycle is completed within 6–8 weeks, allowing several generations to occur in one season.

Several species of *Pratylenchus* have been associated with poor growth in grapevines (Raski and Krusberg 1984). These include *P. vulnus*, *P. neglectus*, *P. scribneri*, *P. brachyurus*, *P. coffeae*, *P. pratensis*, *P. macrodorus* and *P. jordanensis* (Sauer 1962, 1972, 1984, and reviews by Raski (1986) and Brown et al. (1993)).

2.5 Other nematodes

A number of different genera and species of ring nematodes have been reported on grapevines. *Criconemella xenoplax*, a widely distributed species, feeds on root cortical cells and root tips. Since this nematode feeds over long periods on single cells it is classified as a sedentary ectoparasite (Hussey et al. 1991). Reproduction is presumed to be parthenogenetic since males are rarely found. *C. xenoplax* females lay 8–15 eggs over a 2–3 d period with the complete life cycle taking 25–34 d at 22–26°C (Seshadri 1964).

Needle nematodes (*Longidorus* and *Paralongidorus* spp.) are migratory ectoparasites with a life cycle that can take up to two years to complete (Hooper and Evans 1993). These nematodes are not considered to be common pests in vineyards, although they have been identified as vectors of some uncommon grapevine viruses in Europe and North America (Krake et al. 1999).

A number of other nematodes from genera such as *Paratylenchus* (pin nematode), *Paratrichodorus* (stubby root nematode), *Tylenchorhynchus* (stunt nematode), *Helicotylenchus* (spiral nematode), *Rotylenchulus* (reniform nematode), and *Hoplolaimus*, *Telotylenchus* and *Zygotylenchus* (lance nematodes) have been found on grapevine roots and in vineyard soils (Raski 1986, McKenry 1992, McLeod et al. 1994). Their pathogenicity to vines, and therefore their importance to commercial viticulture, is unknown.

3 Geographic distribution of nematodes

Only limited surveys of nematode distribution in vineyards, both in Australia and worldwide, have been published. They indicate that nematodes pathogenic to grapevines are widespread, with the specific distribution pattern of each nematode species being determined by a range of factors such as climate, soil type and history of land use. Survey results are summarised below, and in Nicol and van Heeswijck (1997). This information is limited not only in scope, but also in reliability. This is due (a) to past difficulties in differentiating between species, especially of *Meloidogyne*, and (b) to differences in quantification due to the use of different methods of sampling and nematode extraction. Furthermore, most studies dealt only with root-knot and dagger nematodes, and contained little information on whether other nematodes were present, possibly even at damaging concentrations. Most were carried out more than 20 years ago.

Many of the vineyards previously surveyed in Australia have been, or will soon be, replanted, and new viticultural regions are being established. Land previously planted with grapevines or other horticultural crops is likely to harbour nematodes, particularly root-knot and root-lesion nematodes. It is important to obtain current information on areas to be planted or replanted with regard to the types of nematodes present, their population densities, and their potential to cause economically significant damage. This applies particularly to some of the new regions into which viticulture has expanded in the last twenty years, for example the Mornington Peninsula in Victoria, the Western Slopes of the Dividing Range in New South Wales, the Manjimup-Pemberton region of Western Australia, the sub-tropical regions of Queensland and the Northern Territory and parts of the Fleurieu Peninsula in South Australia.

3.1 Root-knot nematodes (*Meloidogyne* spp.)

In Australia, root-knot nematodes are widely distributed in vineyards. Almost all vineyards on sandy soils are infested, and overall infestation levels are probably similar to those in overseas areas with similar climates (Seinhorst and Sauer 1956, Meagher 1960, Sauer 1962, 1972, Meagher et al. 1976, Stirling 1976a, Sauer 1977, Harris 1984, McLeod and Gendy 1996). In California up to 65% of all vineyards are probably infested with root-knot nematodes (M.V. McKenry, University of California, Riverside, personal communication), while in South Africa's Western Cape Province 77% of surveyed vineyards contained root-knot nematodes (Smith 1977).

M. hapla is predominant in the cooler areas of southern Australia (Sauer 1974a, Stirling and Cirami 1984). It is also the predominant species in cooler northern vineyards of California (McKenry 1992) and in France (Dalmasso and Cuani 1976, Boubals 1979). *M. javanica* tends to predominate in regions with a hot summer climate, namely in the Murray Valley of Australia, the Central Valley of California (McKenry 1992) and in South Africa's Western Cape Province (Loubser 1988). *M. incognita* and *M. arenaria* as well as *M.hapla* were also listed by McKenry (1992) and Loubser (1988), while *M. arenaria* is present in France (Bouquet and Dalmasso 1976, Boubals 1979). It is not uncommon to find more than one species in any one region, such as the South Australian Barossa Valley where Stirling (1976a) found all four species.

3.2 Dagger nematodes (*Xiphinema* spp.)

Xiphinema index has been found in Australia in only a small region of north-eastern Victoria (Meagher et al. 1976, Harris 1977, Harris 1983a). This area is the same as that proclaimed as a grapevine quarantine district because of phylloxera infestation (Corrie et al. 1997). In other parts of the world *Xiphinema index* is widespread. In North America it is found in vineyards of the North Coast and Central Coast and the Lodi–Livermore area of California (McKenry 1992), in Mexico (Arrenondo 1992), and more recently in Napa and Sonoma County, California (M.V. McKenry, University of California, Riverside, personal

communication). *Xiphinema index* has been found in France in soils of grapegrowing regions extending from the Mediterranean coast to the Champagne region and to Alsace (Dalmasso and Caubel 1966), and other parts of Europe (Pinochet and Cisneros 1986, Coiro et al. 1989, Vallotton and Perrier 1990, Coiro et al. 1992, Arias et al. 1994).

Another species, *X. americanum*, has been reported from Australian vineyards (Harris 1980), but there have been no detailed studies on this or any other *Xiphinema* species. Nevertheless, dagger nematodes are commonly found in soil samples from Australian vineyards and are probably an important component of the nematode pest complex that occurs on grapevines.

3.3 Citrus nematode (*Tylenchulus semipenetrans*)

This nematode was first reported on grapevines in Australia by Seinhorst and Sauer (1956). It is widely distributed in vineyard regions where citrus plantings are common, i.e. in the Murray Valley districts of Sunraysia, Swan Hill, Robinvale and the Riverland (Seinhorst and Sauer 1956, Sauer 1962, 1967, Stirling 1976a, Harris 1977, 1984). Citrus nematode is also found occasionally in diagnostic samples from regions in which citrus is not widely grown (e.g. the Hunter Valley), implying that this nematode is being distributed on planting material.

Citrus nematodes spread slowly in soil, but are commonly spread over large distances by irrigation water (Sauer 1962, Meagher et al. 1976, Smith et al. 1973) which may explain their distribution along the Murray River. In this region, root-knot and citrus nematodes occur together, but root-knot nematodes predominate in sandy soils and citrus nematodes in heavier soils (Stirling, unpublished). Similar observations have been made in California where citrus nematodes were found to favour loam, sandy loam or clay loam soils rather than sands (McKenry 1992).

3.4 Root-lesion nematodes (*Pratylenchus* spp.)

In Australia, surveys by Seinhorst and Sauer (1956), Sauer (1962, 1972), Meagher et al. (1976), Stirling (1976a) and Harris (1984) found *Pratylenchus* spp. in soil and root samples from major viticultural regions. Species found included *P. vulnus*, *P. coffeae* and *P. jordanensis* (reassigned as such by Sauer (1984) and initially identified as *P. scribneri*).

Pratylenchus vulnus is considered an important grapevine pest in California and has also been found in Europe (Pinochet and Cisneros 1986, Raski 1986). *Pratylenchus* spp. have also been reported on grapevines in South Africa (Raski 1986) and in soils of the Hermosilla Coast, Mexico (Arrenondo 1992), and are estimated to occur in 60–70% of vineyards in California (M.V. McKenry, University of California, Riverside, personal communication), but little is known about their pathogenicity. Since *Pratylenchus* species are involved in decline and replant diseases in many crops other than grapevines they are a group of nematodes on which more research is justified.

3.5 Other nematodes

In Australia, a number of other nematode species have been reported to be present in vineyards (Sauer 1962, Meagher et al. 1976, Harris 1983a, Harris 1984). Among these are species of *Tylenchorhynchus*, *Paratylenchus*, *Scutellonema*, *Paratrichodorus*, *Helicotylenchus* and *Rotylenchus*. *Criconemella xenoplax* is commonly found in horticultural plantings (Walker 1995). In South Australia, Stirling (1976a) found *Paratrichodorus* spp., and especially *P. minor*, widely distributed in sandy soils of South Australia. These and other species have been found in vineyards in other parts of the world.

4 Impact of nematode infestation on vineyard productivity

Effects of plant-parasitic nematodes on grapevine growth and productivity are influenced by a number of factors. Some varieties of *V. vinifera* appear to be less susceptible to particular nematode species than others. Sultana, for example, is moderately resistant to *Meloidogyne arenaria* compared with many other varieties (Ferris et al. 1982).

Nematode population density is another important factor, but its relationship with grapevine performance remains ill-defined. There are only a few reports where population densities are ranked according to their damage potential. These rankings are summarised in Table 1 and provide some useful guidelines but are not definitive, as different methods for sampling roots and soil and for extracting nematodes confound comparisons of studies. Moreover, differences in climate, soil characteristics and grape variety may modify responses of grapevines to varying levels of nematode population density. Such interrelations are poorly understood and further studies are needed.

Poor characterisation of the relationship between population density and vine damage leads to uncertainty about what population density, as estimated from soil or root samples, justifies the implementation of control measures. Decision making about whether there are advantages in using rootstocks would be improved if data on nematode populations and yield were available from a series of regional trials containing four basic treatments (vines on own roots and a rootstock, growing in nematicide-treated or untreated soil). There is also an urgent need to improve quality control in laboratories providing nematode diagnostic services. Guidelines on how this can be achieved have been published (Stirling et al. 1999).

4.1 Effect on grapevine growth and physiology

Plant-parasitic nematodes feed on grapevine roots and cause malformations or necrosis. This leads to destruction of physiologically active roots and an overall reduction in water and nutrient uptake. Above-ground parts of grapevines show no specific visual symptoms on leaves, shoots or fruit, but there is a general reduction in vigour. Similar symptoms could be due to, and confused with, other conditions such as poor physical characteristics of the soil, mineral excess or deficiency, water stress, or other soil-borne pests and diseases. Confirmation that

Table 1. Relationship between numbers of nematodes in roots and soil and estimated damage potential in *Vitis vinifera* grapevines.

Nematode species	Damage potential	In root Nematodes/g (Sauer 1977)	In soil Nematodes/500g McKenry (1992)	
			winter	summer
Root-knot	low	40-80	<37	< 12
Meloidogyne spp.	medium	150	37–250	100
	high	300–500	>250	>100
	very high	>500	not available	
Lesion	low	10	<10	
Pratylenchus spp.	medium	20–30	10–50	
	high	60–80	>50	
Dagger	low		<10	
Xiphinema index	medium		10–100	
X. americanum	high		>100	
Citrus	low	20-40	<25	
Tylenchulus semi-	medium		25–250	
penetrans	high	60-70	>250	
Ring	low		<12	
Criconemella	medium		12–125	
xenoplax	high		>125	
Pin	low		<50	
Paratylenchus spp.	medium		50–500	
	high		>500	
Stubby root	low		<10	
Paratrichodorus spp.	medium		10–100	
	high		>100	

symptoms are attributable to nematodes on roots is therefore an important component of correct diagnosis.

Specific physiological responses of grapevines to nematode attack have been documented in only a few studies. A significant reduction in whole-plant net photosynthesis and respiration, and hence growth was recorded for container-grown *V. vinifera* cv. Colombard infested with *M. incognita* (Melakeberhan and Ferris 1989), leading to reduced assimilation (Melakeberhan et al. 1990). Total leaf area, transpiration rate, stomatal conductance, intercellular CO_2 concentration in leaves and total amount of fixed CO_2 did not appear to change. In an experiment by Anwar and Van Gundy (1989), container-grown *V. vinifera* cv. Colombard showed severely reduced root and shoot growth after infestation by *M. incognita*, *P. vulnus* and *X. index* but not *T. semipenetrans*. Similarly infested vines of cv. Rubired (Tinta Cao × (Aramon × *V. rupestris*)) showed reduced root growth, but shoot growth was only reduced by infestation with *X. index*. Container-grown vines of Colombard (*V. vinifera*) and Ramsey (*V. champini*) suffered a 35% reduction of shoot dry weight with a virulent strain of *M. incognita*, a lesser reduction upon infestation with *M. hapla*, and no reduction upon infestation with *M. javanica* (Walker 1997a).

Xiphinema index, free of grapevine fanleaf virus (GFLV) and present on roots for two seasons, reduced various components of vegetative and reproductive growth of container-grown *V. vinifera* vines by 20–90%, confirming that this nematode is a damaging pest in its own right, quite apart from its activity as a virus vector (Kirkpatrick et al. 1962).

Studies listed above dealt predominantly with effects from a limited number of root-knot and dagger nematode species. Clearly there is need for more detailed information on the physiological response of *V. vinifera* and other *Vitis* species and their hybrids, to other species of *Meloidogyne* and *Xiphinema*, and also to representatives of other genera of plant-parasitic nematodes. A better understanding of effects of nematode attack on roots, and consequent effects on the interplay between below-ground and above-ground vine parts may allow for better control of nematode damage to the vine through cultural practices such as enhanced irrigation and application of plant nutrients. An improved understanding of host-pathogen interaction may also assist development of nematode-resistant vine material through conventional or molecular breeding approaches.

4.2 Effect on grape yield and quality

Stirling et al. (1992) estimated that Australian viticultural industries lose 7% of production to nematodes. In California the losses estimated from root-knot nematodes alone are even higher, at about 20% of production (Raski 1986). There is no doubt that nematodes cause significant yield losses in many grapegrowing regions, but the magnitude of these losses is difficult to determine. Estimates of crop losses in viticulture have been derived from experiments in which the yields of 'nematode-free' vines growing in fumigated or nematicide-treated soils, are compared with the yields of vines growing in nematode-infested soils. Comparisons have also been made between the performance of *V. vinifera* vines on their own roots and those grafted onto nematode-resistant rootstocks, both growing in nematode-infested soils. Both methods have their limitations. Most fumigants have short-term effects on nitrogen nutrition, control other potential pathogens and affect beneficial microbes. Non-volatile nematicides tend to be more specific but are likely to affect root-feeding arthropods. Thus observed yield differences may not be entirely due to nematodes. The results of rootstock trials may be confounded by the many effects exerted by the rootstock on the scion that are unrelated to nematode infestation.

There are several reports of fumigants and nematicides being used to demonstrate the impact of nematodes on grapevines. Yield losses due to *T. semipenetrans* were recorded in nematicide trials in the Murray Valley of Australia (Sauer 1966) and in California (Van Gundy 1961, McKenry 1992). Application of the non-volatile nematicide fenamiphos (Nemacur®) to irrigated vineyards reduced the population densities of *T. semipenetrans* and *Meloidogyne* spp., and subsequently increased yields from

Valdiguie vines by 20–30% in South Australia (Walker 1989), and from Sultana vines by about 20% in some seasons in Victoria (Edwards 1991). Reduction of a range of parasitic nematodes by fumigation increased yields on average by more than two-fold in five commercial vineyards in California (McKenry and Ferris 1979).

The most extensive rootstock trials in Australia were conducted by Sauer (1966, 1967, 1972, 1974a, 1974b, 1977) in sites containing root-knot nematode or citrus nematode. Some rootstocks, such as Ramsey, clearly showed enhanced levels of production relative to own-rooted vines. Later studies by Hedberg et al. (1986), Wachtel (1986), Cirami and McCarthy (1988) and Edwards (1988, 1989) on sites infested with root-knot and citrus nematode have produced similar findings. However, as already discussed, it is unlikely that the yield benefits obtained are entirely due to nematode resistance or tolerance as some rootstocks such as Ramsey have other growth-enhancing characteristics.

Xiphinema index has also been shown to be associated with yield reductions but losses become more extensive when combined with GFLV (McKenry 1992). In long-term rootstock trials in California it was demonstrated that the yield of vines of Cabernet Sauvignon grafted onto the rootstocks St George (syn. du Lot) or Harmony, which are susceptible to *X. index*, decreased to about 10% of that obtained when the *X. index* resistant rootstock VR-039-16 was used (Walker et al. 1994b).

There have been numerous rootstock trials in Australia, listed by May (1994); many of these were not designed to test responses to nematode infestation, and the nematode status of the sites was hardly ever determined. Even though these trials suffer from the problems described above, revisiting these sites may give useful indications of the response of the various rootstocks to the presence or absence of nematodes.

All the available evidence shows that root-knot and citrus nematodes and the *X. index*/GFLV complex cause significant yield losses in grapevines. However, there are insufficient data on the quantitative effects of other plant-parasitic nematodes such as root lesion nematodes, ring nematodes and other species of dagger nematodes. Until such data are collected, the economic importance, and the need to control these nematodes, remains unknown.

Although grape quality is probably not directly affected by nematode infestation, and such effects would be difficult to prove, indirect effects of severe infestations are likely through the damage caused to overall metabolic activity. As already described, such infestations have detrimental effects on water uptake, nutrient supply, photosynthesis and sugar accumulation, all of which need to be optimal for producing grapes of good quality.

4.3 Interactions with other soil organisms

Mechanical injuries to roots inflicted by plant-parasitic nematodes favour entry of microbial pathogens (Prot and Khan 1993). Field observations by Walker (1994) showed that the fungal pathogen *Rhizoctonia solani* was isolated from 86% of roots damaged by root-knot nematode compared to 22% of roots without such damage. The severity of fungal root rot increased in both Colombard (*V. vinifera*) and Ramsey (*V. champini*) by co-inoculation with the fungus and root-knot nematodes (Walker 1997a). Root rot was even more severe when the nematodes were inoculated before the fungus.

Grapevine roots damaged by nematodes are also believed to be more prone to infection by other fungal pathogens, including *Phytophthora* spp. (especially *P. cinnamomi*), *Pythium* spp. (especially *P. ultimum*) (Chiarappa 1959, McGechan 1966, van der Merwe et al. 1972, Walker 1995), *Verticillium dahliae*, *Thielaviopsis basicola*, *Dematophora necatrix* (Walker 1995), and *Armillaria* spp. (B.B. Westerdahl, University of California, Davis, personal communication). Direct experimental evidence for this is lacking, as is any quantitative measurement of the effects on grapevine health and productivity that might be expected from these interactions. The general lack of knowledge of soil ecology and of interactions between soil organisms makes it difficult to recognise the conditions under which pathogens and pests, including nematodes, act together to become a significant problem in grape production.

5Nematode control in vineyards and nurseries

5.1 Rootstocks

Rootstocks constitute an old management tool in horticulture, and became widespread last century in European vineyards after the introduction and spread of phylloxera. Rootstocks are now used almost universally throughout the world, although not in all regions of Australia. Recognition, mainly in California and Australia, of serious damage caused by nematodes made testing of rootstocks to ameliorate the deleterious effects of this pest an obvious research priority. Tables 2a and 2b give a summary of those tests in which a distinction was made between resistance, susceptibility and tolerance. Similar tables have been published in the past (Whiting et al. 1987, Howell 1987, Hardie and Cirami 1988, McKenry 1992) but they do not contain the detailed information collected here.

Resistance is defined here as a plant's ability to inhibit nematode reproduction, while tolerance describes the ability of a plant to grow and produce satisfactory yields despite nematode infestation (Wallace 1963). Resistance is a more desirable characteristic than tolerance since the latter may not reduce nematode reproduction, and yields may still be lowered. Moreover, tolerance is difficult to estimate quantitatively because rootstocks exert other effects on scion performance apart from protection from nematode (and phylloxera) damage. Such effects include modification of salt or drought tolerance, and variation in root volume, including numbers of root tips. In agreement with Robinson (1969), the term 'intolerance' is not used. Immunity, an extreme from of resistance in which a nematode's stylet does not penetrate the plant root at all, is found only in the sub-genus *Muscadinia* and possibly in a few *Vitis* species (e.g. *Vitis cinerea*) and is therefore not mentioned in Tables 2a and 2b.

The reports on which the data in Tables 2a and 2b are

Table 2a. Resistance (R), susceptibility (S) and tolerance (T) of rootstock cultivars to root-knot nematode *Meloidogyne* spp., summarised and categorised by extrapolation from information contained in the literature. The letters in the body of the table refer to the references listed below. Underlined letters indicate an estimate of highly resistant. Where cells are empty no reliable information was found.

Rootstock	*M.* spp. (indeterminate)			*M. javanica*			*M. incognita*			*M. hapla*			*M. arenaria*		
	R	S	T	R	S	T	R	S	T	R	S	T	R	S	T
Ramsey	bmn^{a}n^{c}opstu	n^{b}	g	ikmnr	.	k	dklmnv	m^{a}	k	k	.	.	cdj	knn^{d}	k
Dog Ridge	bmn^{a}opstu	.	.	kmnr	.	k	dklmnv	m^{a}	k	.	.	.	cdj	knn^{d}	k
Freedom	mn^{a}n^{b}otu	n^{c}	g	mn	.	.	lmnv	m^{a}	.	.	.	.	.	nn^{d}	.
Harmony	mn^{a}opu	n^{b}n^{c}op	.	f^{a}imn	f^{b}	f	f^{a}dlmv	f^{b}m^{a}n	.	.	.	.	df^{a}j	f^{b}nn^{d}	.
1613C	bmopsu	n^{a}n^{b}n^{c}op	.	af^{a}mnr	f^{b}k	k	adf^{a}mnv	f^{b}km^{a}	k	.	.	.	df^{a}	cf^{b}knn^{d}	k
1616C	bestu	.	.	.	.	.	d	v	.	.	.	.	cd	.	.
K51-32	t	n^{a}u	.	.	n	.	n	.	.	.	.	.	.	n^{d}	.
K51-40	tu	.	.	.	.	.	.	.	.	.	.	.	.	.	.
J17-69	.	u	g	.	.	.	.	.	.	.	.	.	.	.	.
Rupestris du Lot	u	beps	.	i	qr	q	.	dv	.	.	h	.	.	cdj	.
Riparia Gloire	e	bsu	.	.	.	.	.	d	.	.	h	.	.	cd	.
Schwarzmann	tu	mn^{a}	.	i	mn	.	.	mm^{a}n	.	.	.	.	.	nn^{d}	.
3306C	u	bs	.	.	r	.	.	dl	.	.	.	.	c	d	.
3309C	e	bn^{a}su	.	.	nr	.	.	dln	.	.	.	.	.	cdnn^{d}	.
101-14	e	bsu	.	qr	.	q	dl	.	.	.	.	.	cd	.	.
5BB-5A[1]	.	u	.	i	.	k	.	.	k	.	.	.	.	.	k
5BB	beu	.	.	i	.	.	dl^{a}	l^{b}	.	.	h	.	c	d	.
5C	.	n^{a}u	.	.	nr	.	.	ln	.	.	.	.	.	nn^{d}	.
SO4	beu	n^{a}	.	i	n	.	dl	n	.	.	h	.	c	dn^{d}	.
34 EM	u	bs	.	.	.	.	d	.	.	.	.	.	d	c	.
420A	u	beks	.	.	qr	.	d	.	.	.	.	.	d	c	.
1103P	eu	.	.	.	.	.	.	dl	.	.	.	.	c	d	.
161-49	u	bes	.	.	.	.	.	dl	.	.	.	.	.	cd	.
99R	be	n^{a}u	.	.	nr	.	l^{a}	dl^{b}n	.	.	h	.	cd	n^{d}	.
110R	u	bes	.	i	r	.	.	dl	.	.	.	.	.	cd	.
140Ru	u	.	.	.	.	.	.	dl	.	.	.	.	d	.	.
ARG 1	.	psu	.	.	f iq	.	.	f	.	.	.	.	.	f j	.
VR039-16	.	mn^{a}	.	.	mn	.	.	mm^{a}n	.	.	.	.	.	nn^{d}	.
6-19B[2]	n^{a}n^{b}	n^{c}	.	n	.	.	n	.	.	.	.	.	.	n^{d}	.
10-17A[3]	n^{a}n^{b}n^{c}	.	.	n	.	.	n	.	.	.	.	.	n^{d}	.	.
10-23B[4]	n^{a}n^{b}n^{c}	.	.	n	.	.	n	.	.	.	.	.	n^{d}	.	.
RS-9[5]	n^{a}n^{b}n^{c}	.	.	n	.	.	n	.	.	.	.	.	nn^{d}	.	.
RS-3[5]	n^{a}	.	.	n	.	.	n	.	.	.	.	.	.	n^{d}	.
V. rotundifolia	.	.	.	a	.	.	av	.	.	.	.	.	a	.	.

[1] This selection was initially identified as 5A Teleki and later reassigned as 5BB Kober.
[2,3,4] USDA selections (Cavanaugh 1995, listed in McKenry and Kretsch 1995): [2] GA-3-4-5 × Dog Ridge 5; [3] Edna × *V. simpsoni;* [4] *V. doaniana.*
[5] Ramsey × Schwarzmann selections (listed in McKenry and Kretsch 1995).
f^{a}: at soil temperatures ≤ 26°C; f^{b}: at soil temperature 36°C.
l^{a}, l^{b}: two different sites.
m^{a}: virulent population.
n^{a}, n^{b}, n^{c}: three mixed *Meloidogyne* populations of varying virulence; n^{d}: *Meloidogyne arenaria* pathotype H (McKenry & Kretsch 1995).

Authors have used various methods and standards of susceptibility to determine host status and to categorise rootstock resistance and/or susceptibility. Here, based on the comments and data reported, a rootstock was taken as highly resistant (reference index underlined), resistant or susceptible, but where there was no clear indication of resistance or susceptibility, the data has been excluded.

Reference identification (References to nematodes in Australia are underlined):
a-Bloodworth et al. 1980; b-Boubals 1954; c-Boubals 1979; d-Boubals 1992; e-Bouquet & Dalmasso 1976; f-Chitambar & Raski 1984; g-Cirami 1994; h-Dalmasso & Cuani 1976; i-Edwards 1989; j-Ferris et al. 1982; k-Lider 1960; l-Loubser & Meyer 1987; m-McKenry 1992; n-McKenry & Kretsch 1995; o-Raski 1986; p-Raski et al. 1973; q-Sauer 1967; r-Sauer 1977; s-Snyder 1936; t-Stirling & Cirami 1984; u-G.E. Walker 1995; v-M.A. Walker et al. 1994a

Table 2b. Resistance (R), susceptibility (S) and tolerance (T) of rootstock cultivars to *Xiphinema* spp., *Tylenchulus semipenetrans*, *Pratylenchus* spp. and *Criconemella xenoplax*, summarised and categorised by extrapolation from information contained in the literature. The letters in the body of the table refer to the references listed at the bottom of the table. Underlined letters indicate an estimate of highly resistant. Where cells are empty no reliable information was found.

Rootstock	Dagger (*Xiphinema*)						Citrus (*Tylenchulus*)			Root lesion (*Pratylenchus*)						Ring (*Criconemella*)		
	X. index			*X. americanum*			*T. semipenetrans*			*P. vulnus*			*P.* spp.			*C. xenoplax*		
	R	S	T	R	S	T	R	S	T	R	S	T	R	S	T	R	S	T
Ramsey	c^{a}hi	ac^{bcd}gk	.	.	i	.	den	il	.	bik	.	.	.	l	.	.	io	.
Dog Ridge	ac^{abcd}	gik	.	.	hi	.	.	iln	n	bk	hi	.	.	l	.	.	io	.
Freedom	fhi	.	.	i	h	.	.	hi	.	.	i	.	.	.	.	.	io	.
Harmony	c^{bcd}fk	c^{a}i	.	.	hi	.	.	dehin	de	.	bhi	b	.	.	.	.	io	.
1613C	c^{bcd}ghik	ac^{a}f	.	.	hi	.	.	hil	.	.	bhik	b	.	l	.	.	io	.
1616C	.	af	.	.	.	.	.	no	n	.	.	.	.	o	.	.	.	.
K51-32	i	f	.	.	i	.	.	din	dn	i	.	.	.	.	.	.	io	.
K51-40	.	.	.	.	.	.	.	n	n	.	.	.	.	.	.	.	o	.
J17-69	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o	.
Rupestris du Lot	a	c^{abcd}gkm	.	.	.	.	.	l	.	j	kl	.	.	l	.	.	o	.
Riparia Gloire	a	g	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o	.
Schwarzmann	fhi	.	.	.	hi	.	.	dhin	dn	.	hi	.	.	.	.	.	io	.
3306C	a	g	.	.	.	.	.	l	.	.	.	.	l	.	.	.	o	.
3309C	af	im	.	.	i	.	.	il	.	.	i	.	l	.	.	.	io	.
101-14	.	af	.	.	.	.	.	l	.	.	.	.	.	lo	.	.	.	.
5BB-5A[1]	c^{bcd}	c^{a}	.	.	.	.	.	o	.	.	.	.	.	o	.	.	.	.
5BB	.	ac^{abcd}m	.	.	.	.	.	d	d	.	.	.	.	.	.	.	o	.
8B	.	ac^{abcd}	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o	.
5C	i	ac^{abcd}m	.	.	i	.	.	il	.	.	i	.	.	l	.	.	io	.
SO4	ai	c^{abcd}mf	.	.	i	.	.	i	.	j	i	.	.	o	.	.	io	.
34 EM	.	af	.	.	.	.	.	.	.	.	.	.	.	.	.	.	o	.
420A	.	a	.	.	.	.	.	l	.	.	.	.	.	l	.	.	o	.
1103P	.	a	.	.	.	.	.	.	.	j	.	.	.	.	.	.	o	.
161-49	a	.	.	.	.	.	.	.	.	.	j	.	.	.	.	.	o	.
99R	.	agi	.	.	i	.	.	il	.	.	i	.	.	l	.	.	io	.
110R	a	fm	.	.	.	.	.	dl	d	.	j	.	.	l	.	.	o	.
140Ru	.	a	.	.	.	.	.	.	.	.	.	.	.	o	.	.	.	.
ARG 1	.	afgk	.	.	.	.	.	l	.	.	bk	.	.	.	.	.	o	.
VR039-16	hi	.	.	hi	.	.	.	i	.	.	hi	.	.	.	.	.	.	.
6-19B[2]	.	i	.	i	.	.	i	.	.	i	.	.	.	.	.	.	i	.
10-17A[3]	i	.	.	.	.	.	i	.	.	i	.	.	.	.	.	.	i	.
10-23B[4]	i	.	.	.	.	.	i	.	.	i	.	.	.	.	.	.	i	.
Vitis rotundifolia	a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

[1] This selection was initially identified as 5A Teleki and later reassigned as 5BB Kober.
[2,3,4] USDA selections (Cavanaugh 1995, listed in McKenry and Kretsch 1995): [2] GA3-4-5 × Dog Ridge 5; [3] Edna × *V. simpsoni* [4] *V. doaniana;*
c^{a}: population from California, c^{bcd}: populations from Italy, France and Israel.

Authors have used various methods and standards of susceptibility to determine host status and to categorise rootstock resistance and/or susceptibility. Here, based on the comments and data reported, a rootstock was taken as highly resistant (reference index underlined), resistant or susceptible, but where there was no clear indication of resistance or susceptibility, the data has been excluded.

Reference identification (References to Australian nematodes are underlined):
a-Boubals & Pistre 1978; b-Chitambar & Raski 1984; c-Coiro et al. 1990; d-Edwards 1988; e-Edwards 1989; f-Harris 1983b; g-Kunde et al. 1968; h-McKenry 1992; i-McKenry & Kretsch 1995; j-Pinochet et al.1992; k-Raski et al. 1973; l-Sauer 1977; m-Vallotton & Perrier 1990; n-Wachtel 1986; o-Walker 1995.

based do not always agree with respect to the levels of resistance and tolerance of grapevine rootstocks to nematodes. This is probably related to differences in methods of experimentation and evaluation of results but may also reflect variation in virulence of the resident nematode population. For example, laboratory or glasshouse tests generally involve a selected isolate of a single nematode species, while field tests are done in the presence of a whole array of root pathogens, usually including mixed populations of various nematode species. Also, the concept of a nematode species has altered over the last 50 years or so, and this, together with the difficulty of species identification, creates doubt about the actual identity of some of the species reported on.

It is clear from Tables 2a and 2b that most studies on the response of rootstocks to nematodes have been directed towards species of *Meloidogyne* and *Xiphinema*. Little is known about the resistance of many currently used rootstocks to the full range of plant-parasitic nematodes found in vineyard soils (Wicks and Walker 1995). Indeed, from what is known, it appears that many of the rootstocks possess resistance to only a limited range of nematodes. This brings with it the danger that the use of rootstocks that are resistant and/or tolerant to certain nematodes, while being susceptible to other nematodes, may slowly change the range of species or pathotypes of nematodes present at any given site.

5.1.1 Rootstocks resistant to Meloidogyne *spp.*

Snyder (1936) examined the response of over 150 selections of *Vitis* spp. and species hybrids, including *V. vinifera* and those used as phylloxera-resistant rootstocks, while growing in soil infested with root-knot nematodes. Only selections of *V. champini*, *V. longii* (syn. *V. solonis*) and *V. cinerea* showed some resistance to root-knot nematodes. Subsequently Lider (1954) ascribed resistance against *M. incognita* var. *acrita* Chitwood to *V. champini*, *V. longii* and also to *V. berlandieri*, but noted that the grapevine response depended on the aggressiveness of the nematode population. More recently, Walker et al. (1994a) added some selections of *V. aestivalis*, *V. cinerea*, *V. rufotomentosa* and *V. rupestris* to this list.

The most significant result of these studies was an early recognition of superior resistance to root-knot nematodes in *V. champini*. This observation led to selection of Ramsey and Dog Ridge. They were introduced into Australia in the mid 1950s. Subsequent tests (Sauer 1972, 1974b) proved Ramsey to be the most satisfactory rootstock for Sultana vines in light soils of the Murray Valley, ensuring strong growth and good yields even in the presence of large *Meloidogyne* populations (predominantly *M. javanica*). Stirling and Cirami (1984) later demonstrated good resistance of Ramsey and Dog Ridge in both field- and container-grown vines to other populations of root-knot nematodes.

Ramsey has performed well for two decades or more in soils infested with root-knot nematodes in a number of grapegrowing regions of the world. However, there are virulent populations of root-knot nematodes that are able to infest these usually resistant grapevine types. For instance Lider (1954) found *V. champini* and *V. longii* to be as susceptible as *V. vinifera* to populations of *M. incognita* present at two test sites in California. Similarly, a virulent population of *M. incognita* was later found causing severe galling on the 'resistant' rootstocks Harmony and Freedom (Cain et al. 1984). McKenry (1992) and McKenry and Kretsch (1995) reported a number of rootstocks including Ramsey, Harmony, Freedom, and 1613C to be susceptible to some populations of *M. incognita* or *M. arenaria* in field plots in California, but not to other populations of the same species. In Australia also, a population of *M. incognita* sufficiently aggressive to overcome both the resistance and tolerance of Ramsey was found by Walker (1997a,b). While these results are alarming, they must be kept in perspective: in Lider's experiments, the resistance of *V. champini* and *V. longii* to *M. incognita* was maintained at 17 of the 19 test sites in California. In Australia, the virulent population of *M. incognita* was identified in only one Australian site, and even then Ramsey was still significantly less damaged than *V. vinifera* (Walker 1997a,b).

Harmony and Freedom have shown satisfactory resistance to root-knot nematodes under Australian conditions, as has 1613C (Stirling and Cirami 1984), presumably due to having *V. longii* in its parentage. The use of Harmony and Freedom is now being questioned however, since they are hybrids of *V. vinifera*. This makes them potentially susceptible to phylloxera damage, with Harmony having already declined due to phylloxera in California (Granett et al. 1996). A number of other rootstocks with *V. champini* or *V. longii* parentage (1616C, K51-32, K51-40) and others with only *V. riparia*, *V. rupestris* or *V. berlandieri* parentage (99R, 34EM, Schwarzmann, 5BB Kober-5A Teleki[1]), have also been tested in Australia and world-wide and generally demonstrate moderate to good resistance to root-knot nematodes (Table 2a). In general, however, selections of *V. champini* have shown better performance.

The mechanisms of resistance in *V. champini* to *Meloidogyne* spp. have not been investigated in detail but Ferris et al. (1982) established a mathematical relationship between the number of *Meloidogyne arenaria* penetrating or establishing infection sites in grapevine roots and degree days above 10°C. They demonstrated that Harmony, Salt Creek and Dog Ridge were all highly resistant to *M. arenaria*, and that this resistance was expressed primarily through reduced penetration of the root system, in combination with failure of the nematodes to establish infection sites and/or induction of host biochemical defences.

Vitis rotundifolia, a species of the *Vitis* sub-genus *Muscadinia*, has been reported as being resistant or even immune to *Meloidogyne* spp. (Lider 1954, Bloodworth et al. 1980, Firoozabady and Olmo 1982, Walker et al. 1994a), and for this, and other reasons, has been included in rootstock breeding programs. Hybridisation with

1. A clone was imported from California under the name 5A Teleki. This was subsequently indentified as 5BB Kober (Walker and Liu 1995).

other *Vitis* species has proved difficult due to cytogenetic differences between the two sub-genera (2n = 40 for *Muscadinia* and 2n = 38 for *Euvitis*) (Patel and Olmo 1955). Nevertheless, the so-called VR hybrids (crosses of *V. rotundifolia* and *V. vinifera*) have been produced, some of which show root-knot nematode resistance combined with reasonable ease of rooting and grafting (Davidis and Olmo 1964, Bloodworth et al. 1980, Bouquet 1980, Firoozabady and Olmo 1982, Walker et al. 1994a). These VR hybrids have not been widely adopted, presumably at least in part because of the risk that their *V. vinifera* parentage reduces their long-term phylloxera resistance (Granett et al. 1987, 1996).

5.1.2 Rootstocks resistant to X. index

Rootstocks used to prevent damage from *X. index* should be immune in order to prevent infection with GFLV. Such a rootstock has not yet been produced. *Vitis* species showing some resistance or tolerance are *V. candicans*, *V. longii*, *V. arizona*, *V. smalliana* and, especially, *V. rufotomentosa* (Kunde et al. 1968). Some of these species were used in grapevine breeding by L.A. Lider (University of California, Davis) and tested in Australia by Harris (1983b). Although at least two hybrids of *V. rufotomentosa* were thought to be immune, long-term field trials in California clearly demonstrate that they are neither resistant to GFLV transmission (Walker et al. 1994c) nor do they confer tolerance to the detrimental effects of *X. index* and GFLV on cropping (Walker et al. 1994b). The same applies to rootstocks with *V. champini* heritage such as 1613C, Dog Ridge, Ramsey, Freedom and Harmony, which, despite their resistance or tolerance to *X. index* (Harris 1983b, Coiro et al. 1990, Meredith et al. 1982 , Malan and Meyer 1993), can be infected by GFLV (Malan and Meyer 1993, Walker et al. 1994c).

Vitis rotundifolia has shown strong resistance to both *X. index* and grapevine fanleaf virus (GFLV) (Boubals and Pistre 1978, Bouquet 1981, Torregrosa and Bouquet 1995). Studies of the above-mentioned VR hybrids have demonstrated that while some have good levels of resistance to *X. index*, transmission of GFLV still occurs, although scion infection can be delayed for years in some cases (Walker et al. 1994b, 1994c). Failure to completely prevent transmission of GFLV is perhaps not unexpected since transmission can be accomplished by a single nematode feeding for only a few minutes. Interestingly, Cabernet Sauvignon grafted to VR-039-16 or VR-043-43 still maintained consistent crop yields during the 12 years of a field trial despite the presence, especially in the latter years, of high titres of GFLV in scions on both rootstocks (Walker et al. 1994b, 1994c). This indicates that these rootstocks are able to confer both some resistance and tolerance to GFLV. As mentioned above, the current VR hybrids have not been widely used. Nevertheless VR-039-16, which has the strongest phylloxera and nematode resistance, has been recommended for use in land infested with *X. index* that is likely to carry GFLV (Walker et al. 1994b, Wolpert et al. 1994).

Assessment of *Vitis* germplasm to find *X. index* resistance is continuing (Walker et al. 1994b). *V. cinerea* Arnold, and rootstocks derived from it, such as Börner, have been reported to be immune to both phylloxera and *X. index* and to prevent transmission of GFLV (Becker 1989). While Börner is a potentially important addition to the range of rootstocks available for either nematode or phylloxera control, further documentation of the hitherto limited range of experimental results with this rootstock in Germany and extension of the trial work to other viticultural regions, including Australia, is needed.

5.1.3 Rootstocks resistant to other nematodes

It would appear, from Table 2b, that many rootstocks used for root-knot nematode control are not suitable for the control of nematodes of the genus *Pratylenchus*. Australian studies by Sauer (1977) indicate that only moderate resistance to *Pratylenchus* spp. can be found in 5C Teleki, 420A, 99R and 110R, and that resistance can be found in 3306C and 3309C. Studies from elsewhere (McKenry 1992, McKenry and Kretsch 1995) indicate that most of the commonly used rootstocks are susceptible to *Pratylenchus vulnus*.

Conflicting results about rootstock resistance to *Tylenchulus semipenetrans* make generalisation difficult. In the studies done in Australia, all tested rootstocks were found to be tolerant to these nematodes (Wachtel 1986, Edwards 1988, 1989) except for K51-32 (*V. champini* × *V. riparia*) which, although resistant, gave reduced yields in the study of Wachtel (1986). Ramsey and Dog Ridge were found to be the most resistant rootstocks.

5.1.4 Rootstocks used in Australian viticulture

Australia's viticulture is still predominantly based on own-rooted vines (Hardie and Cirami 1988, May 1994), although the use of grafted vines has increased in recent years (deLaine 1998). One of the main reasons for this increase has been the need to limit damage from nematodes (May 1994). Ramsey and Schwarzmann continue to be the preferred varieties, followed by 140 Ruggeri, K51-40, 5BB Kober-5A Teleki, 1103 Paulsen, 5BB Kober and 99 Richter (deLaine 1998). Characteristics of the commonly used rootstocks, including their phylloxera resistance, scion vigour and tolerance to various soil conditions can be found in Whiting et al. (1987), Whiting and Buchanan (1992), May (1994) and Nicholas (1997). There is little doubt that rootstocks will remain the preferred form of nematode control into the foreseeable future. Further development is required, however, to extend the range of nematode resistance available to ensure that the rootstocks can withstand the possible evolution of more virulent biotypes, and to increase the range of nematode species controlled. To this end, research is required to identify the genetic resources available, and to use these resources in new breeding strategies.

5.1.5 Conventional breeding of nematode-resistant rootstocks

As described above, part of the search for nematode-resistant rootstocks involved the conventional method of cross-breeding, used for over four decades. While many *Vitis* species evidently have genes which confer resistance

to at least one or more species of nematodes, little is known about the mechanisms by which this resistance is expressed. This limits the ability of breeders to predict how resistance is inherited, whether different resistance genes might complement each other, or whether they may even act synergistically. Selection for resistance to *Meloidogyne* spp. has resulted in only a few releases, including single-species cultivars such as Ramsey and Dog Ridge, or species hybrids such as Harmony and Freedom. Breeding for resistance to *X. index* has proved to be even less rewarding, with the possible exception of the new rootstock Börner (Becker 1989). No information is yet available on any attempts to breed for resistance to other nematodes.

Production of VR hybrids in an attempt to incorporate the relatively broad resistance or immunity of *V. rotundifolia* to nematodes and other root pests has already been mentioned. Although promising, these F_1 hybrids need further improvement, but this cannot be done using conventional techniques since they are sterile. Fertile hybrids have recently been produced from crosses between *V. rotundifolia* and *V. rupestris.* Preliminary assessment indicates that they have good resistance to *Meloidogyne* spp. and *X. index* (M.A Walker, University of California, Davis, personal communication).

5.2 Nematode-resistant transgenic plants

Genetic engineering offers new techniques for the introduction of nematode resistance into rootstock cultivars which have other desirable traits such as low scion vigour or salinity tolerance. Genetic engineering might even eliminate a need for rootstocks by creating *V. vinifera* cultivars that are nematode-resistant. Development of nematode-resistant transgenic plants of many genera is under way in many laboratories around the world (Williamson and Hussey 1996, Gheysen et al. 1996, Fenoll et al. 1997, Williamson 1998). Recent success with genetic engineering of grapevines, including *V. vinifera* (Mauro et al. 1995, Perl et al. 1996, Scorza et al. 1996, Franks et al. 1998) introduces the possibility of applying this technology for the control of nematodes in viticultural production. A range of approaches is being pursued, from *in vitro* transfer of natural nematode genes to identification of novel anti-nematode metabolites. A few of these approaches are described in more detail below.

5.2.1 Transfer of natural nematode resistance genes to new plant hosts

Many plant species have natural resistance genes which confer resistance to nematodes, and some of these have now been genetically mapped in crops such as tomato, potato and wheat (Williamson and Hussey 1996). Some of these genes encode a relatively narrow resistance which controls only specific pathotypes of a single nematode species. Others encode broad resistance, effective against several nematode species. If the DNA encoding these genes can be isolated, it can be moved into other plants species by methods of genetic engineering. Recent isolation of the *Hs1* and *Mi* resistance genes, and their use in genetic engineering to produce nematode-resistant cultivars of sugar beet and tomato are promising examples of this new technology (Cai et al. 1997, Milligan et al. 1998).

5.2.2 Disruption of changes in root cells required for nematode feeding and reproduction

A great deal of information is now available on the cellular events that take place when nematodes infest a plant, and a number of genes switched 'on' during this process have now been identified (reviewed in Fenoll et al. 1997).

Sedentary endoparasitic nematodes such as *Meloidogyne* spp. are known to be totally dependent upon establishment of specialised feeding sites within the host root for survival and reproduction. One strategy for production of nematode-resistant plants is therefore to interfere with the formation of these feeding sites by using genetic engineering to switch 'off' some of the genes normally required (Gheysen et al. 1996, Williamson and Hussey 1996, Fenoll et al. 1997). This approach is still experimental and has not yet been proved to work, although there is a reported success of this approach in producing transgenic tobacco plants with enhanced resistance to root-knot nematode (Opperman and Conkling 1996).

5.2.3 Production of anti-nematode metabolites in grapevine roots

Genetic engineering opens up a potential option for introducing novel genes which encode anti-nematode chemicals into grapevines. These genes might encode peptides or proteins such as the *Bacillus thuringiensis* crystal proteins, proteinase inhibitors, enzymes such as collagenase and cutinase or, alternatively, enzymes that convert normal plant metabolites into chemicals inhibitory to nematode growth and development (Burrows and De Waele 1997, McPherson et al. 1997). Results from current research indicate that many of these are likely to be effective for controlling nematodes when expressed in transgenic plants. Introduction of a proteinase inhibitor gene into *Arabidopsis thaliana*, for example, has been shown to confer resistance to both cyst and root-knot nematodes (Urwin et al. 1997).

5.2.4 Engineered resistance to GFLV

As discussed previously, enhanced resistance to the nematode *X. index* is, in itself, unlikely to control transmission of GFLV. Full resistance to *X. index*/GFLV is likely to require a combination of virus resistance as well as resistance to the nematode. Synthetic virus resistance has now been successfully engineered in a number of crop plants through insertion of genes encoding, for example, a virus coat protein or a virus replicase (Scholthof et al. 1993). Work is under way to apply these strategies to GFLV resistance in *Vitis* spp. (Krastanova et al. 1995, Mauro et al. 1995). It remains to be seen whether genetic engineering will be useful in enhancing resistance to the vector of GFLV. *X. index* is a migratory ectoparasite and most interest in engineering resistance has centred on sedentary endoparasites such as root-knot and cyst nematodes. Perhaps knowledge of nematode biology that

has been gained from studies of the genome of *Caenorhabditis elegans* (Bird et al. 1999) will open up new opportunities for control of other types of nematodes.

5.3 Systemic acquired resistance

Systemic acquired resistance is a phenomenon whereby infection of a plant by a pathogen or treatment with certain chemicals induces an active response in the plant which results in increased disease resistance. This resistance response is characterised by an induction of a long-lasting, systemic resistance that often has a broad spectrum of activity against viral, bacterial and fungal pathogens (Gorlach et al. 1996).

There have been few attempts to use this phenomenon against nematodes, but one recent study (Owen et al. 1998) showed that benzothiadiazole (a well-known inducer of systemic resistance) reduced egg production by root-knot nematodes on grapevines. If this promising result is confirmed and mechanisms of action determined, longer-term field studies of resistance-inducing chemicals may well be justified.

5.4 Fumigants and nematicides

Chemicals for nematode control are classified as either fumigants or nematicides, based on their spectrum of activity. The broad toxicity of fumigants means that many soil-borne pests, including nematodes, fungi, bacteria and insects, are killed on contact. Most fumigants are also phytotoxic and can only be used before planting (Van Gundy and McKenry 1977). Nematicides are generally more specific in their nature, giving control of nematodes but little or no control of fungi and bacteria (Van Gundy and McKenry 1977). They affect nematode reproduction and development by impairing neuromuscular activity, thus interfering with movement and root invasion, and probably with hatching and feeding.

Soil fumigation has been widely used since the 1880s when carbon disulfide was used in attempts to combat phylloxera (Hague and Gowen 1987). Since then, various halogenated hydrocarbons—methyl bromide (MBr), ethylene dibromide (EDB), 1,2-dibromo-3-chloropropane (DBCP), 1,3-dichloropropene (1,3-D) and its mixture with 1,2-dichloropropene (DD), and trichloronitromethane (chloropicrin)—have been used for nematode control. During the 1960s various non-volatile organophosphate and carbamate compounds became available for use against both nematodes and insects (Hague and Gowen 1987).

Chemical control of nematodes (particularly *Meloidogyne* spp. and *X. index*) has been effectively practised within established vineyards and prior to planting, in California (Raski and Schmitt 1972, McKenry and Ferris 1979, Lear et al. 1981, Raski 1986, Radewald et al. 1987, McKenry 1992) and in South Africa (Malan 1995). In Australia, pre-plant soil fumigation was common prior to the mid-1970s (Stirling 1976b) but since then nematicide use has mainly been confined to commercial field nurseries. One of the main limitations of chemical control is the difficulty of delivering the chemical to the site of the pest. This is especially difficult for some nematode species that have been found at depths of up to 3 m (McKenry 1992).

Many fumigants that were once available for nematode control in vineyards are now being withdrawn from use (Hague and Gowen 1987). In Australia, EDB, DBCP and DD have been deregistered, while methyl bromide (which was sometimes used in nurseries) is to be phased out by the year 2005 (Price 1996). Remaining fumigants (chloropicrin and 1,3-D) are unlikely to find a place in viticulture because they are expensive, and their high volatility can result in atmospheric pollution. This means that metham sodium (a carbamate compound with limited fumigant activity; National Registration Authority 1997) is likely to be the only chemical in this group that will be available in future.

Organophosphate and carbamate nematicides have high mammalian toxicity and are susceptible to enhanced biodegradation (Van Gundy and McKenry 1977, McKenry 1991), characteristics that will limit their future use. They also have a short half-life in soil and viticulturists need to question whether it makes sense to try and control nematodes that are active for 8–9 months of the year with chemicals that are effective for only 4–6 weeks. If such chemicals are to be successfully used, controlled-release formulations and more targeted application methods must be developed. In Australia, fenamiphos is the only non-fumigant available for nematode control on grapevines, but it is not registered for use in Victoria and the Northern Territory.

5.5 Nursery hygiene

Distribution of nematode-infested grapevine rootlings is one of the main routes for spread of nematodes into new vineyard areas. In fact, the occurrence of endoparasitic nematodes such as root-knot, citrus and lesion nematodes in newly planted vineyards is usually the direct result of planting infested rootlings. Standard nursery practice in Australia is to produce rootlings in in-ground nurseries using soil that has been fumigated or treated with nematicides. Since such practices do not eradicate nematodes, rootlings are likely to be infested by the time they are ready for sale. Meagher (1960) estimated that without hot-water treatment almost 50% of the 800,000 cuttings raised that season in Victoria were infested with root-knot nematodes. Visual inspection of bare rooted vines for symptoms is not an adequate quality control procedure, as it will only reveal heavy infestations of root-knot nematode. Lesion nematode, citrus nematode and low levels of root-knot nematode will not be detected.

If rootlings are infested with root-knot nematodes, hot water treatment at temperatures near 50°C for 5–15 min is sufficient to eradicate them (Lear and Lider 1959, Meagher 1960, Suatmadji et al. 1982, Barbercheck 1986, Gokte and Mathur 1995). The requirements for eradicating other plant-parasitic nematodes are likely to be similar. Although there are some inconsistencies in the literature concerning the conditions and efficacy of hot water treatment, the Australian Vine Improvement Association currently recommends 50°C for 30 min (Caudwell et al. 1997) in response to recent concerns

about the spread of Australian Grapevine Yellows (Hamilton 1997). This treatment is assumed to be sufficient to eradicate nematodes and all internal pathogens (except viruses).

Because there are always doubts about the efficacy of hot water treatment when large numbers of rootlings are treated in a commercial operation, a more satisfactory procedure is to produce rootlings in containers of sterilised potting media. This is standard practice for most other perennial horticultural crops, and is done for vines in other areas of the world (Foulonneau 1971, Weinberger and Loomas 1972). Provided basic nursery hygiene practices are employed, container-grown vines will be free of all potentially important nematodes.

5.6 Biological control

If a vineyard is to be established or replanted in a site infested with root-knot nematodes, the use of resistant rootstocks is likely to be the best available control option in the foreseeable future. However, there are large areas of existing vineyards that are infested with nematodes and, in these situations, other integrated pest management options, such as biological control, should be considered (Stirling et al. 1991a). Such control measures may be able to keep nematode populations at levels below that where nematodes cause significant damage, i.e. below the damage threshold level, and may thus present an economical solution.

Biological control is defined as the action of one or several organisms to reduce the population of a commercially damaging organism to a level lower than would occur without this control (De Bach 1964). Nematodes are difficult to control by such means because they have a high reproductive potential and have evolved a number of structures and mechanisms which protect them from attack by most other predators or pathogens (reviewed by Stirling 1991b). They have a multi-layered, proteinaceous cuticle and their eggs are covered by a triple-layered shell comprised mainly of chitin (Bird and Bird 1991). They are also able to survive stress conditions such as drought by reducing their metabolic rate (Womersly 1987), and behavioural responses such as coiling reduce their susceptibility to attack by biological control agents.

Pasteuria penetrans is a mycelial- and endospore-forming bacterium known to be parasitic on certain root-knot nematodes (Mankau 1975, Stirling and White 1982, Stirling 1984). Stirling and White (1982) found it to be widely distributed in South Australian vineyards and suggested that this may be associated with the reduced numbers of root-knot nematodes found in vineyards older than 25 years. This view was supported by the results of an experiment where root-knot nematodes showed reduced rates of reproduction when added to vineyard soils containing *Pasteuria penetrans* (Bird and Brisbane 1988). *Pasteuria thornei*, a related parasite that attacks lesion nematodes, has been found in Australia in association with the nematode *Pratylenchus brachyurus* (Stirling, unpublished). Thus further studies on the population dynamics of *Pasteuria* species and plant-parasitic nematodes seem warranted as these parasites may play a role in the natural suppression of root-knot and other nematodes. Such studies should concentrate on manipulating naturally-occurring populations of *Pasteuria*, as practical methods of mass producing the parasite and introducing it into the soil have not yet been developed.

A range of fungal biological control agents are also active in vineyards. *Paecilomyces lilacinus* and *Verticillium chlamydosporium* parasitised 23–87% of *Meloidogyne* egg masses in Queensland vineyards (Mertens and Stirling 1993) but, despite this level of egg mortality, nematode populations remained high and nematode damage on roots was still apparent. *Xiphinema index* and *X. diversicaulatum* are attacked by the fungi *Hirsutella rhossiliensis* and *Catenaria anguillulae* (Ciancio et al. 1986, Ciancio and Chinappen 1987), but information on their efficacy in vineyards is lacking.

Currently, there is interest in developing biological control agents that can be applied to crops as inundative inoculants. However, in a perennial crop such as grapevine, such approaches may be limited by cost, as repeated applications are likely to be necessary. A better approach may be to develop a soil ecology which has sustainable suppressiveness to nematodes (Stirling 1999). Investigation of these opportunities would require the measurement and comparison of the level of suppressiveness of different soils, characterisation of their soil biota, and determination of the soil conditions which encourage the presence and activity of parasites and predators effective against the nematodes. The presence and activity of many different soil microbes can be stimulated by addition of organic amendments (reviewed by Stirling 1991b).

5.7 Agronomic measures

Such measures include crop rotation, fallowing, cover crops, inter-row plantings and use of mulches. One classical method of nematode control in agriculture is rotation of crops and/or the use of fallow. This involves the interspersing of non-susceptible crops, or a complete break from cropping, into a sequence of susceptible crops. The rotation needs to be of sufficient duration to reduce the nematode population below damage threshold levels. Such practices should be considered before replanting vineyards, or where land to be planted with vines has been used for horticulture. Soil in either situation may have high nematode population densities.

Fallowing soil is not effective unless the break from cropping is maintained for long periods because eggs and other survival stages of many nematode species, including *Meloidogyne*, persist for up to 18 months, even in the absence of live roots. Since the risk of erosion is increased with bare soil, a better alternative is to use a green manure crop such as forage sorghum cv. Jumbo as it is a poor host of root-knot nematodes(Stirling et al. 1996).

In perennial crops such as grapevines, an opportunity to use crop rotation only occurs prior to planting. Removal of old roots after vine removal, and continued elimination of nematode-supporting plant species during the rotation will assist in reducing the rotation time. Management techniques such as irrigation and deep-

ripping of soil can accelerate decomposition of the roots, and quicken the hatching of nematode eggs, which will also reduce the rotation period.

Once a vineyard is planted, nematode-suppressive crops can be sown between the rows, or organic materials added as mulch. A recent compilation of plants likely to be found in Australian vineyards, whether sown, or as volunteer growth (Nicol and van Heeswijck 1997), shows that most weeds likely to be present can be hosts to nematodes. This is also the case with most of the cover crops commonly planted, with the exception of some oat and barley cultivars. Viticultural advantages of using cover crops or maintaining volunteer growth may therefore need to be balanced against the disadvantage of increasing nematode populations. Since minimum tillage usually enhances biological control (Stirling 1999) it is possible that permanent cover crops will reduce nematode problems. Further testing should therefore be done to determine the long-term effects of cover crops on nematode control, soil fertility and grapevine productivity.

Potential use of plants with nematicidal properties as cover crops or mulch has been investigated in Australia (McLeod and Warren 1993, McLeod and Da Silva 1994, McLeod and Gendy 1996, McLeod et al. 1998, Stirling and Potter 1998, McLeod and Steel 1999) and USA (Mojtahedi et al. 1991, 1993, McKenry 1992, 1994). Members of the Cruciferae, especially species of the genus *Brassica*, are known to produce glucosinolates that degrade to isothiocyanates (Fenwick et al. 1994). These isothiocyanates are fatal to a range of insects, fungi and nematodes (Kirkegaard et al. 1993). Conversion to isothiocyanate occurs within plant tissue that is damaged by biological or mechanical means, and through natural decomposition. McLeod and colleagues (see above) have examined the usefulness of *Brassica* spp. and other crops in Australian vineyards. Most studies have shown that populations of *M. javanica* and *M. incognita* actually increase on the *Brassica* spp. tested. Clearly, any potential use of *Brassica* spp. and other plants to control nematodes in commercial vineyards requires a better understanding of the release, concentration and distribution of natural nematicidal compounds in soil and of the effects of these compounds on nematodes and their natural enemies. More effort also needs to be directed towards selecting plant species that do not host the key nematode pests of grapevines.

6 Conclusions and future directions

Plant-parasitic nematodes are always found within vineyards. Whether they have an impact on grapevine growth and physiology, and ultimately on crop yield, will depend on the nematode species present, their population levels and damage potential, and the genotype of the grapevine root system (*V. vinifera* or other *Vitis* species). These factors also interact in a complex way with climate, soil type and management practices, while other soil organisms may serve to modulate nematode population size and thus the potential for damage.

It is clear from the information here reviewed that there are significant knowledge gaps. Much of the information already available relates to root-knot nematodes, perceived as the most significant nematode pest of grapevines in Australia. The dagger nematode *X. index* has also received some attention, less due to its direct pathogenic effect than to its role in transmitting GFLV. Little is known about most of the other nematode species in regard to both their incidence and potential effects on the grapevine. Lesion nematodes (*Pratylenchus* spp.) are perhaps the group that most deserves future attention, as they are common on grapevines in Australia and are frequently associated with decline and replant problems.

Chemical control of nematodes is not a sustainable option in any viticultural situation. Even in grapevine nurseries a move to use of containers for growth of rootlings is preferable to using relatively ineffective nematicides. Utilisation of host-plant resistance imparted by rootstocks continues to be the best form of control, although there are also significant gaps in our knowledge of grapevine and nematode genetics, mechanisms of resistance and species differences in the grapevine-nematode interaction. This lack of knowledge may threaten the durability of rootstock resistance.

The following priorities for research concerned with grapevine nematology are proposed.

1. Consolidate and standardise methods for sampling vineyards, and for extracting and identifying nematodes in those samples. Such methods should then be adopted universally.
2. Establish better defined relationships between population size and damage potential for various nematodes. This will involve collection of information on the influence of factors such as climate, characteristics of host plants and soil features (including soil microbial status).
3. Assess nematode distribution, especially in new grapegrowing regions.
4. Collect information on variation in pathogenicity between and within *Meloidogyne* species, with an emphasis on investigation of the incidence, distribution and likely spread of virulent, or ‘resistance-breaking’, populations.
5. Further assess rootstocks presently used in Australia for their resistance or tolerance to the range of nematodes encountered, especially *Meloidogyne* spp. and the more common *Pratylenchus* spp., using local nematode isolates.
6. Extend the presently available range of nematode-resistant rootstocks by local breeding and by importation, taking into consideration essential rootstock characteristics other than nematode-resistance.
7. Explore and utilise the potential of genetic engineering for introducing and strengthening resistance in rootstocks or even in *V. vinifera.*
8. Enhance natural suppressiveness of soils to plant-parasitic nematodes and develop methods to sustain such suppressiveness.
9. Identify parasites and predators that limit nematode reproduction, and develop commercially viable

methods of using promising organisms as inundative biological control agents.

10. Expand knowledge of nematode-suppressive and nematode-promoting plants to establish guidelines for manipulating inter-row ecology.

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