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Luma Al-Banna

University of Jordan, lalbanna@ju.edu.jo

Scott Lyell Gardner

University of Nebraska - Lincoln, slg@unl.edu

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Nematode diversity of native species of *Vitis* in California

Luma Al Banna and Scott Lyell Gardner

Abstract: From 1990 through 1992, nematodes were extracted from soil samples taken from the rhizosphere of native species of grapes from four areas of northern California and two areas of southern California. For comparison, samples from domestic grapes as well as a putative hybrid of *Vitis californica* and *V. vinifera* were also taken. Rhizosoil from California native grapevine contained many more species of nematodes than did soil obtained from cultivated forms of *V. vinifera*. Taxonomic and trophic diversity was much higher in nematodes from sampling sites from native grapes than in those from grapes maintained in vineyard situations. Ordination methods using correspondence analysis showed both similarities and differences in the faunal assemblages of nematodes from the different sampling sites, based on indexes of species and trophic groups. Collected data indicate that nematode communities with high trophic and taxonomic diversity have a lower numerical density of plant parasites.

Résumé : De 1990 à la fin de 1992, des nématodes ont été extraits d'échantillons de sol recueillis dans la rhizosphère d'espèces indigènes de raisins, en quatre régions du nord et en deux régions du sud de la Californie. Pour fins de comparaison, des échantillons de raisins domestiques et d'un hybride soupçonné de *Vitis californica* × *V. vinifera* ont également été récoltés. Le sol autour des racines des espèces indigènes de Californie contenait une faune beaucoup plus diversifiée de nématodes que le sol échantillonné autour des racines des formes cultivées de *V. vinifera*. La diversité taxonomique et trophique des nématodes était beaucoup plus élevée autour des racines de raisins indigènes que dans les entreprises viticoles. Une méthode d'ordination basée sur l'analyse des correspondances a mis en lumière des similarités et des différences dans les associations de nématodes des différents points d'échantillonnage, d'après les indices relatifs aux espèces et aux groupes trophiques. Les données recueillies indiquent que les communautés de nématodes à diversité trophique et taxonomique élevée ont une densité numérique de parasites moins importante.

[Traduit par la Rédaction]

Introduction

Invasion and destruction of crop plants by undescribed, unknown, or presumed nonpathogenic species of organisms represent a continuous threat to international agricultural production (Giovani 1986; Morrison et al. 1988). Examples of contemporary invasions of agro-ecosystems include the Russian wheat aphid, *Diuraphis noxia* Mordvilko, in North America (Morrison et al. 1988), the brown rice planthopper, *Nilaparvata lugens* Stål, in Asia (Dyck and Thomas 1979), and a new "strain" of pathogenic phylloxera, *Daktulosphaira vitifoliae* Fitch, on grapes in California (Granett et al. 1985).

Production of grapes (species of *Vitis* L.) in various regions of the world has been threatened by the invasion or infestation of many species of parasitic nematodes (Pinochet et al. 1976; Rüdel 1985; Allen et al. 1988; Loubser 1988; Jenser et al. 1991) and continuous research is being conducted to increase the resistance of grape rootstock to various soilborne pathogens (Wachtel 1986; Frascini 1990; Melakeberhan et al. 1990).

A large amount of research (we have found >300 citations) has been conducted on various aspects of interactions of nematodes in vineyards, including studies of the geographic distributions, population dynamics, management, and control of important parasitic nematodes of grapevine. However, very little work has been done on the diversity of nematodes in vineyards. In contrast to the data base on nematodes in vineyards, virtually no information is available in the literature regarding the ecological relationships of nematodes associated with native species of Vitaceae of the world. For example, there have been no studies on the potential of native species of grapes to serve as reservoirs or sources of plant-parasitic nematodes.

Plant-parasitic nematodes in vineyards can increase in density to levels that severely affect the health and productivity of the grapevine (Hafez et al. 1981; Lal et al. 1982). Pathogenesis may be caused by direct feeding on the roots, as with species of the genus *Pratylenchus*, or the nematodes may vector viruses, such as those of *Xiphinema* spp. Feeding by nematodes physically damages roots by creating wounds (allowing entrance of fungi or bacteria) and altering the physiology of the root and thus of the whole plant.

Studies of the diversity of native or wild species of grapes have not been conducted; thus, meaningful comparisons between the diversity of species of nematodes and density or pathogenicity of plant-parasitic species cannot be made. The present study provides information on the diversity of nematodes in both vineyard and naturally occurring grapevine.

In our comparative studies of nematode associates of grapes we examined the diversity of nematodes from two

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L. Al Banna. Department of Nematology, University of California, Davis, CA 95616, U.S.A.

S.L. Gardner.¹ Harold W. Manter Laboratory of Parasitology, W-529 Nebraska Hall, University of Nebraska State Museum, University of Nebraska, Lincoln, NE 68588-0514, U.S.A. (e-mail: slg@unl.edu).

¹ Author to whom all correspondence should be addressed.

general habitat types: (i) anthropogenically modified habitats (vineyards) with low microvariation in soil structure, and (ii) relatively undisturbed natural habitats with much greater microvariation in soil structure. A central question of applied biodiversity relative to the Nemata is whether or not the pathogenicity of nematodes in vineyards or other crop situations is related to the taxonomic or trophic diversity of the nematodes in the soil. A testable hypothesis can be formulated as follows: the pathogenicity of nematodes (in crop situations) is high when the overall taxonomic diversity of nematodes in the soil is low.

In the present study we survey, describe, summarize, and compare the "community structure" of nematodes associated with native species of *Vitis*. We also compare the results of our studies on sylvatic grapevine with data derived from studies of nematode diversity in vineyard situations. Two general areas were selected for this work, including several sites in northern California with *Vitis californica* Benth and two different sites in Southern California with *Vitis girdiana* Munson. For each sampling site the nematode species associated with grapevine were determined. Although we maintain a holistic view of "community" and do not restrict the definition of a community to a single taxonomic group (i.e., the Nemata), in the present paper we summarize our data and compare the community structure of nematodes among the different localities using several different comparative methods. These techniques were used to assess relative diversity and abundance of species of nematodes. Ordination methods were used to summarize information among sampling units and their nematode faunas.

Materials and methods

From 1990 through 1992, rhizosoil was collected from native species of grapes occurring in six different sites in California: *Vitis californica* (California native grape) was sampled from four localities in northern California and *V. girdiana* (California desert grape) was sampled from two localities in southern California. Subsamples of rhizosoil were taken from accessible roots of grapes in each collection locality. In all cases, soil was taken from the upper 15 cm of the soil horizon. During this study all subsamples were treated as one sampling unit except when constructing the species volume curves; in this case each subsample was treated as one sampling unit.

Description of sampling localities

Samples of soil and root segments from the rhizosoil of *V. californica* were collected from a relatively isolated area in the foothills of the Sierra Nevada along the Cosumnes River (12 km south by road from Placerville, El Dorado County, Calif., 38°40'N, 121°26'W). *Vitis californica* was also sampled in three less isolated locations. Two of these sites, located about 45 km west by road from Davis, were Gates Canyon, Solano County (38°22'N, 122°24'W), and Mix Canyon, Solano County (38°24'N, 122°02'W). The third site, situated well into the central valley of California, was Bobelaine Audobon Wildlife Preserve, 32 km by road south of Yuba City, Placer County (38°55'N, 121°34'W) (Fig. 1).

Two samples of rhizosoil of the desert grape (*V. girdiana*) were collected, one from a botanical garden at the University of California, Riverside, Riverside County (33°58'N, 117°20'W), and the second from Grapevine Mountain, in Anza Borego Desert Reserve, Riverside County (33°07'N, 116°28'W).

For comparison, eight vineyards and a putative hybrid of *V. vinifera* × *V. californica* were included in this study. Cultivated

forms of *V. vinifera* were sampled from the following localities: Napa valley, Napa County (38°15'N, 122°17'W); Sonoma, Sonoma County (38°12'N, 122°25'W); San Jose, Santa Clara County (37°20'N, 121°53'W); Davis, Yolo County (three sublocalities) (38°32'N, 121°44'W); and Pope Valley, Napa County (38°36'N, 122°23'W) (Fig. 1). A putative hybrid of *V. californica* and *V. vinifera* was sampled at a location 6.92 km by road southwest of Lone, Amador County (38°21'N, 120°56'W) (Fig. 1).

From each specimen of grapevine root that was sampled, vouchers of the grape leaves were collected and deposited in the J.M. Tucker Herbarium, University of California, Davis (Nos. 120480, 120481).

Soil samples were processed immediately after collection. For each sample, nematodes were extracted from 200 cc of soil, using both Baermann funnel (Christie and Perry 1951) and centrifugation – sugar flotation methods (Niblack and Hussey 1985). All nematodes recovered were killed and fixed using equal volumes of hot 10% buffered formalin solution (1000 cc 10% formalin, 4 g sodium acid phosphate, and 6.5 g anhydrous disodium phosphate) (Humason 1972). All nematodes were counted and the number of individuals of each species was tabulated for every locality.

Permanent mounts were made using the "rapid method" of Seinhorst (1959). Specimens were prepared permanently in pure anhydrous glycerin, placed on Cobb mounts, and examined using a Leitz Ortholux II compound microscope. Measurements were taken using both an ocular micrometer and computer video imaging system (Java™). Both quantitative and qualitative data were used to identify nematodes to the level of the species.

Two measures of diversity were applied to data that were collected from field sites, the reciprocal of Simpson's index (λ), and the evenness index (E). The reciprocal of Simpson's index ($1/\lambda$; $\lambda = \sum p_i^2$, where p_i is the proportion of individuals in the i th species) reflects the number of extremely abundant nematode species in each locality (Hill 1973). This diversity index, also known as Hill's second diversity number (N_2), was employed because it is less sensitive to variation in sample size and gives less weight to rare species (Hill 1973; Peet 1974; Routledge 1979).

The evenness index, E (the modified Hill's ratio of Alatalo 1981), was calculated to characterize cases where the abundances of species were very unequal. The modified Hill's ratio was used as a measure of evenness, E , because it is easy to interpret and is independent of the number of species in the sample (Hill 1973; Alatalo 1981). Alatalo (1981) recommended the use of the modified Hill's ratio as an evenness index, since this value approaches zero as a single species becomes increasingly dominant in a community. Furthermore, Alatalo stated that this ratio is very useful, especially when species diversity is low, as in the case of cultivated grapes. The evenness index was calculated using the equation

$$\Sigma E = \frac{(1/\lambda) - 1}{\exp H' - 1}$$

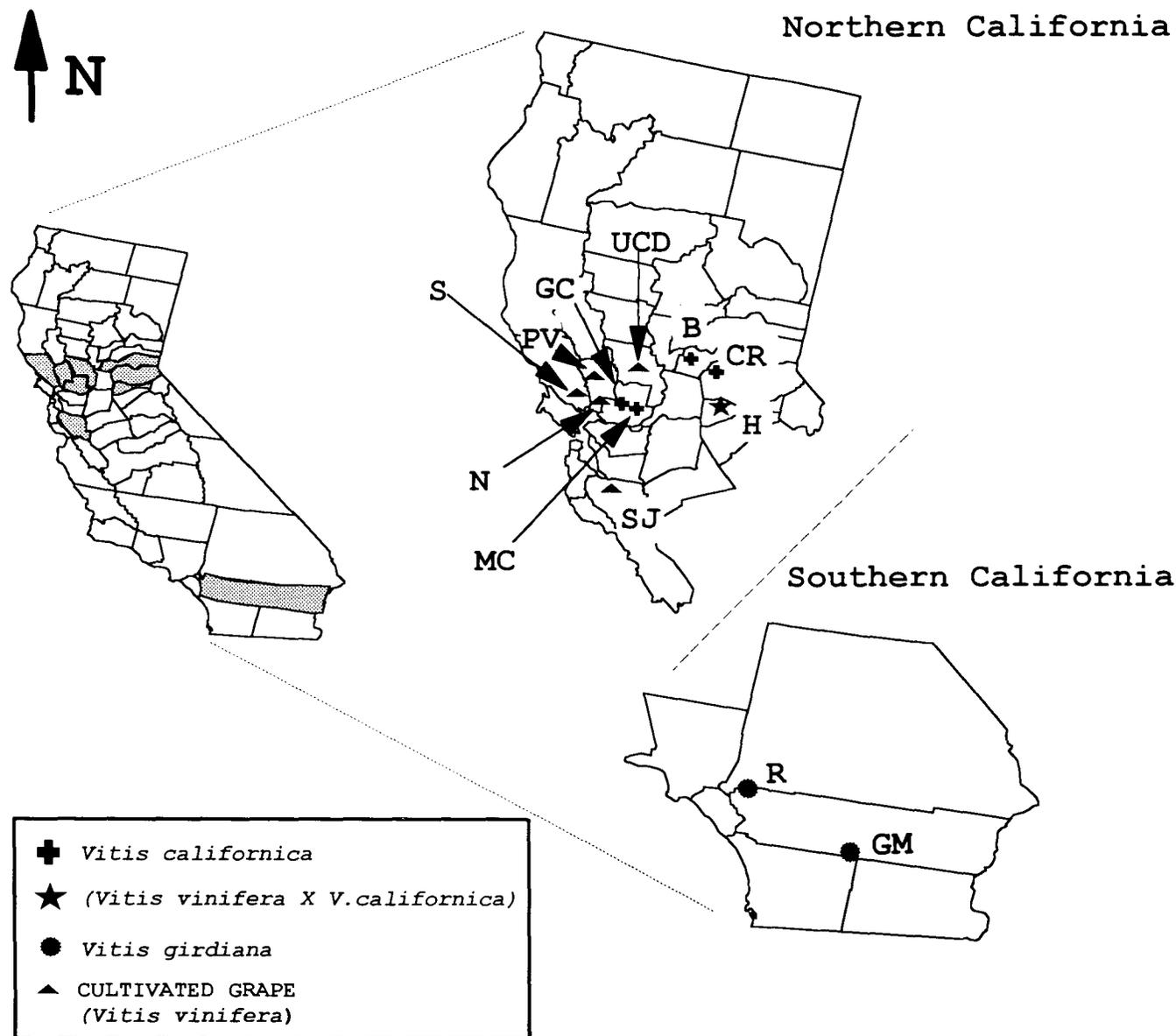
where λ is Simpson's diversity index and H' is Shannon's entropy (Hill 1973).

A t test (based on the Shannon formula) was used to test whether the nematode community composition in two geographically proximate canyons (Gates Canyon and Mix Canyon) was statistically different. The formula of the t test is $t = (H'_1 - H'_2) / (\text{var } H'_1 + \text{var } H'_2)^{1/2}$, where H'_1 is Shannon's entropy at site 1 and $\text{var } H'_1$ is its variance.

Ordination of the different sites in which species of *Vitis* were sampled was performed using multivariate statistical procedures in NTSYS-PC (Rohlf 1990). Correspondence analysis was used to examine the relationships of communities from different collection localities in a graphical context.

For classification at the higher levels we follow the classification of the Nemata by Maggenti (1991).

Fig. 1. Map of California, showing all collection localities of native and cultivated grapes utilized in this study: GC, Gates Canyon; MC, Mix Canyon; B, Bobelaine; CR, Cosumnes River; R, Riverside; GM, Grapevine Mountain; PV, Pope Valley; UCD, University of California, Davis; N, Napa Valley; S, Sonoma; SJ, San Jose; H, hybrid from Amador County.



Results

Ninety species of Nemata were recovered from the rhizosoil of *V. californica* from four different collection localities in northern California (Table 1). These species can be assigned to 19 families and include forms that are predators, bacteria feeders, fungus feeders, and specialists on unicellular protists (Yeates et al. 1993). Individuals of *Xiphinema index* Thorne and Allen, 1952 (the vector of the grape fan-leaf virus) were recovered from both the rhizosoil and roots of *V. californica* about 4 m from the Cosumnes River in the foothills of the Sierra Nevada (see Materials and methods).

A few species were found in all collection localities of *V. californica*; they included *Acrobeles singulus* Heyns, 1969, *Alaimus parvus* Thorne, 1939, *Aporcelaimellus obtusicaudatus*

(Bastian, 1865), *Filenchus* sp., *Mesorhabditis spiculigera* (Steiner, 1936), and *Prionchulus muscorum* (Dujardin, 1845).

Of the 90 species of nematodes associated with *V. californica*, 63 (70%) were recorded from Gates Canyon (Table 1) and can be placed in the following orders: Araeolaimida, Chromadorida, Dorylaimida, Enoplida, Mononchida, Rhabditida, Tylenchida, and Tripylida (Fig. 2). The percentage of each nematode order, based on number of individuals in each, is shown in Fig. 3.

Thirty-nine species were found in the Mix Canyon samples (Table 1), of which 50% also occurred in the samples from Gates Canyon. These two canyons parallel each other and are separated by only a few kilometres. Based on the *t* test (see Materials and methods), a significant difference in community structure ($P < 0.001$) between these two localities is

Table 1. Nematodes from soil from California native grape (*Vitis californica*) sampling sites.

	Feeding type ^a	Collection locality ^b			
		GC	MC	B	CR
<i>Achromadora walkeri</i> Al Banna and Gardner, 1994	(5)		x		
<i>Achromadora pseudomicoletzkyi</i> van der Linde, 1938	(5)	x			
<i>Achromadora ruricola</i> (de Man, 1880)	(5)		x		
<i>Acrobeles cylindricus</i> Ivanova, 1968	3	x	x	x	
<i>Acrobeles singulus</i> Heyns, 1969	3	x	x	x	x
<i>Acrobeloides apiculatus</i> (Thorne, 1925)	3			x	
<i>Acrobeloides buetschlii</i> (de Man, 1884)	3	x			
<i>Acrobeloides clavicaudatus</i> (Thorne, 1925)	3			x	
<i>Acrobeloides minor</i> (Thorne, 1925)	3	x			
<i>Acrobeloides nanus</i> (de Man, 1880)	3	x	x		
<i>Acrobeloides syrtisus</i> Yeates, 1967	3		x		
<i>Alaimus parvus</i> Thorne, 1939	3	x	x	x	x
<i>Aphelenchoides</i> sp.	1 or 2	x			
<i>Aphelenchoides fragariae</i> (Ritzema Bos, 1891)	1 or 2		x		
<i>Aphelenchoides saprophilus</i> Franklin, 1957	1 or 2	x	x	x	
<i>Aphelenchus</i> sp.	1 or 2	x			
<i>Aphelenchus avenae</i> Bastian, 1865	1 or 2	x	x		
<i>Aporcelaimellus amylovorus</i> (Thorne and Swanger, 1936)	4, 6	x		x	
<i>Aporcelaimellus hylophilus</i> Tjepkema, Ferris, and Ferris, 1971	4, 6	x		x	
<i>Aporcelaimellus laevis</i> Tjepkema, Ferris, and Ferris, 1971	4, 6		x		
<i>Aporcelaimellus obtusicaudatus</i> (Bastian, 1865)	4, 6	x	x	x	x
<i>Aporcelaimellus vanderlaani</i> (Meyl, 1957)	4, 6				x
<i>Aporcelaimus latificanus</i> (Andrassy, 1956)	4, 6	x			
<i>Boleodorus thylactus</i> Thorne 1941	1 or 2	x	x	x	
<i>Cephalenchus hexalineatus</i> (Geraert, 1962)	1	x			
<i>Chiloplacus symmetricus</i> (Thorne, 1925)	3	x			
<i>Clarkus papillatus</i> (Bastian, 1865)	4			x	
<i>Clarkus sheri</i> (Mulvey, 1967)	4	x	x		
<i>Coslenchus</i> sp.	1	x	x		
<i>Coslenchus turkeyensis</i> Siddiqi, 1980	1	x			
<i>Criconemoides</i> sp.	1			x	
<i>Criconemoides annulifer</i> (de Man, 1921)	1	x			
<i>Criconemoides featherensis</i> Al Banna and Gardner 1993	1			x	
<i>Criconemoides macrodorus</i> (Taylor, 1936)	1		x		
<i>Criconemoides morgense</i> (Hoffmann and Menzel, 1914)	1	x		x	
<i>Criconemoides variabile</i> (Raski and Golden, 1966)	1	x	x		
<i>Criconemoides xenoplax</i> Raski, 1952	1			x	
<i>Ditylenchus convallariae</i> Sturhan and Friedman, 1965	1 or 2		x		
<i>Ditylenchus indicus</i> (Sethi and Swarup, 1967)	1 or 2	x			
<i>Dorylaimus</i> sp.	6			x	
<i>Eucephalobus oxyuroides</i> (de Man, 1876)	3		x	x	
<i>Eucephalobus striatus</i> (Bastian, 1865)	3	x	x	x	
<i>Eudorylaimus altherri</i> Tjepkema, Ferris, and Ferris, 1971	4, 6	x			
<i>Eudorylaimus brevidens</i> (Thorne and Swanger, 1936)	4, 6		x		
<i>Eudorylaimus carteri</i> (Bastian, 1865)	4, 6	x			
<i>Eudorylaimus curvatus</i> (Thorne and Swanger, 1936)	4, 6		x		
<i>Eudorylaimus granuliferus</i> (Cobb, 1893)	4, 6	x			
<i>Eudorylaimus kirjanovae</i> (Tulaganov, 1949)	4, 6			x	
<i>Eudorylaimus leptus</i> Tjepkema, Ferris, and Ferris, 1971	4, 6	x			
<i>Eudorylaimus modestus</i> (Altherr, 1952)	4, 6	x		x	
<i>Eudorylaimus modicus</i> (Kirjanova, 1951)	4, 6	x		x	
<i>Eudorylaimus noterophilus</i> Tjepkema, Ferris, and Ferris, 1971	4, 6	x	x		
<i>Eudorylaimus nothus</i> (Thorne and Swanger, 1936)	4, 6			x	x
<i>Eudorylaimus parvus</i> (de Man, 1880)	4, 6	x			
<i>Eudorylaimus rapsus</i> Heyns, 1963	4, 6	x	x		

Table 1 (concluded).

	Feeding type ^a	Collection locality ^b			
		GC	MC	B	CR
<i>Eudorylaimus thornei</i> Tjepkema, Ferris, and Ferris, 1971	4, 6	x			
<i>Eudorylaimus vitrinus</i> (Thorne and Swanger, 1936)	4, 6	x			
<i>Filenchus</i> sp.	1	x	x	x	x
<i>Filenchus conicephalus</i> Siddiqui and Khan, 1983	1	x			
<i>Hemicriconemoides</i> sp.	1	x		x	
<i>Hemicriconemoides mangiferae</i> Siddiqui, 1961	1	x			
<i>Hemicriconemoides parvus</i> Dasgupta, Raski, and Van Gundy, 1969	1	x			
<i>Longidorus elongatus</i> (de Man, 1876)	1	x			
<i>Merlinius brevidens</i> (Allen, 1955)	1	x	x		
<i>Mesodorylaimus ghanae</i> Andrassy, 1965	6	x	x		
<i>Mesodorylaimus usitatus</i> Basson and Heyns, 1974	6	x			
<i>Mesorhabditis spiculigera</i> (Steiner, 1936)	3	x	x	x	x
<i>Paraphelenchus</i> sp.	2	x			
<i>Paraphelenchus tritici</i> Baranovskaya, 1958	1 or 2	x	x		
<i>Plectus</i> sp. 1	3	x			
<i>Plectus</i> sp. 2	3	x			
<i>Plectus acuminatus</i> Bastian, 1865	3				x
<i>Plectus armatus</i> Buetschli, 1873	3	x			
<i>Plectus elongatus</i> Maggenti, 1961	3	x	x		
<i>Plectus parietinus</i> Bastian, 1865	3	x	x	x	
<i>Plectus parvus</i> Bastian, 1865	3		x		
<i>Pratylenchus thornei</i> Sher and Allen, 1953	1	x		x	
<i>Prionchulus muscorum</i> (Dujardin, 1845)	4	x	x	x	x
<i>Prionchulus verscus</i> Eroshenko, 1975	4		x		
<i>Prismatolaimus</i> sp.	3?	x	x		
<i>Psilenchus hilarus</i> Siddiqui, 1963	1			x	
<i>Trichodorus californicus</i> Allen, 1957	1	x	x		
<i>Tripyla</i> sp.	4				x
<i>Turbatrix</i> sp.	3	x	x		
<i>Tylencholaimellus montanus</i> Thorne, 1939	2	x	x		
<i>Tylenchorhynchus dubius</i> (Buetschli, 1873)	1		x		
<i>Tylenchus maius</i> Andrassy, 1979	1, 2?	x			
<i>Wilsonema otophorum</i> (de Man, 1880)	3	x			
<i>Xiphinema americanum</i> Cobb, 1913	1	x		x	x
<i>Xiphinema index</i> Thorne and Allen, 1950	1				x

^a1, plant feeding; 2, hypha feeding; 3, bacteria feeding; 4, animal predation; 5, unicellular eucaryote feeding; 6, omnivorous. Parentheses indicate a tentative assignment.

^bGC, Gates Canyon; MC, Mix Canyon; B, Bobelaine; CR, Cosumnes River.

evident. However, the nematode community structure in the Mix Canyon samples, based on both species and number of individuals, followed the same trend as in Gates Canyon (Figs. 2 and 3).

In samples from the Bobelaine locality, 29 species of nematodes were associated with rhizosoil of *V. californica* (Table 1). In this locality the percentage (based on both number of species and number of individuals) of bacteria-feeding nematodes of the order Rhabditida was higher than those recovered from both Gates and Mix canyons (Fig. 3).

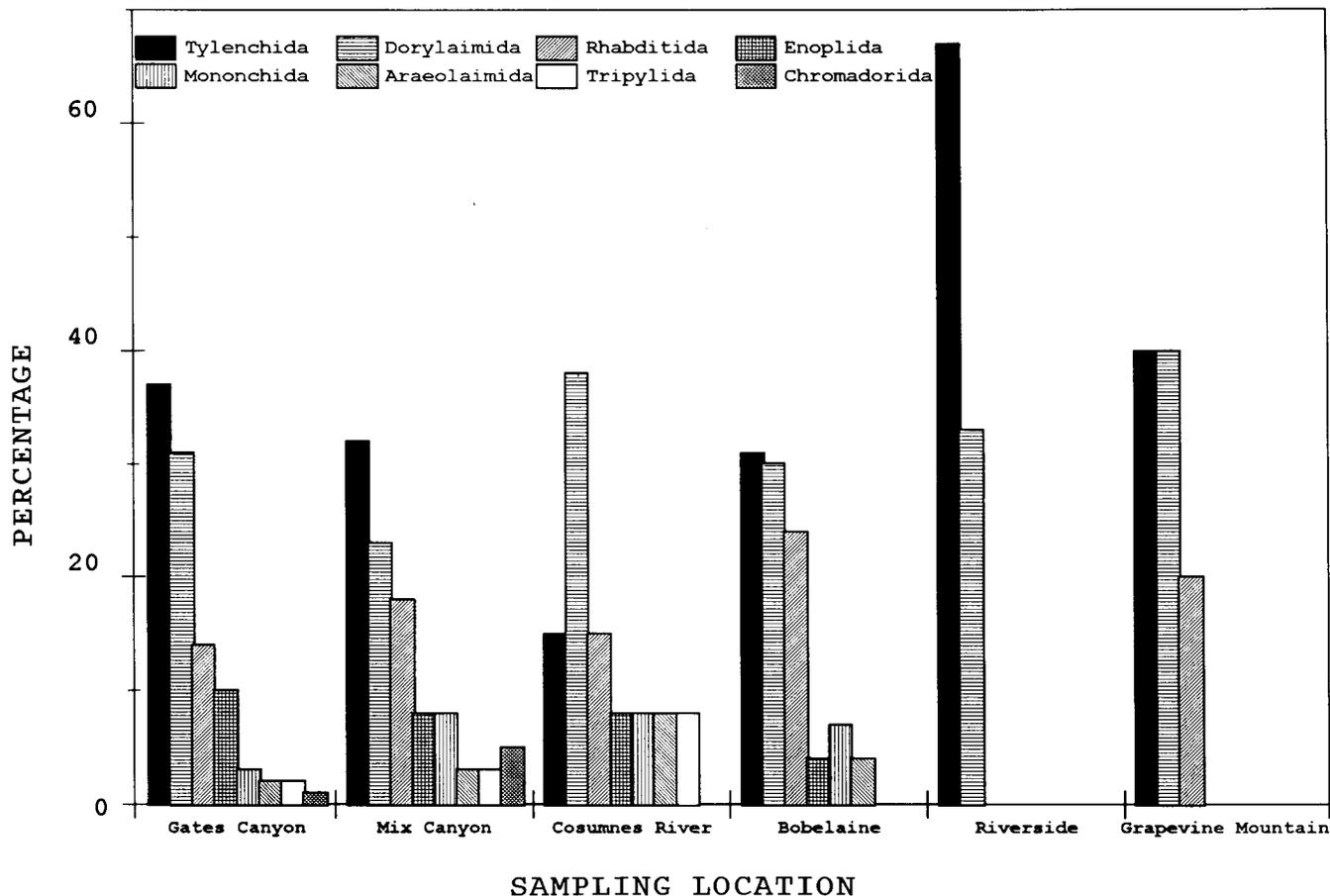
In the foothills of the Sierra Nevada and along the Cosumnes River, 13 species of nematodes representing 7 orders were recovered (Fig. 2, Table 1). Here the dominant species of Nematoda (i.e., with the greatest numerical density) belong to the order Dorylaimida (*Xiphinema americanum* Cobb, 1913) (Fig. 3). This was the only locality of native

grapes from which *X. index* was identified. Of the nematodes recovered from the Cosumnes River locality, 46% were also recorded from the other localities.

Species area or, in this case, species volume curves (because of the volumetric nature of the soil habitat of the nematodes) showed that more species of nematodes were encountered as the number of sampling sites was increased with each locality of *V. californica* (Fig. 4). Approximately 50% of the total number of species encountered during the study in both costal canyon sites were present after analysis of only five samples from Gates Canyon and only three samples from Mix Canyon. The species volume curve for the Bobelaine locality in the middle of the central valley in California shows that 100% of the species encountered were present in the first six soil samples.

The two sampling localities of *V. girdiana* from southern

Fig. 2. Percentages of nematode orders at sampling sites of *V. californica* and *V. girdiana*, based on the number of species of nematodes per taxonomic order.



California (Riverside and Grapevine Mountain) were found to harbor 11 species of nematodes. Six species belonging to 2 orders were collected from the Riverside locality (Table 2, Figs. 2 and 3). At this site, second-stage juveniles of *Tylenchulus semipenetrans* Cobb, 1913 were recorded at a numerical density of >1000 individuals/200 cc soil. *Criconemoides xenoplax* Raski, 1952 also occurred in large numbers (350 individuals/200 cc soil). From the Grapevine Mountain locality, nematodes representing 5 species and 3 orders were recovered (Table 2, Figs. 2 and 3). From this location a new species of plant-parasitic nematode of the genus *Hemicylichophora* was identified (Al Banna and Gardner 1993).

The density of nematode species in cultivated vineyards was much lower than in localities in natural habitats from which samples were taken. *Xiphinema americanum* was the dominant species in vineyards on the campus of the University of California, Davis (UC Davis), as well as in a commercial vineyard in Pope Valley (Table 3). In one vineyard at UC Davis, large numbers (350 individuals/200 cc soil) of *Criconemoides xenoplax* were found. In the three commercial vineyards sampled in Napa, Sonoma, and San Jose, *Xiphinema index* was the dominant species (Table 3). The rhizosoil of an old (>50 years) putative hybrid vine of *V. vinifera* × *V. californica* in Amador County harbored 6 species (Table 4), with *Prionchulus muscorum* (Dujardin, 1845) predominating.

The ecological diversity of nematode species among the sampling sites was analyzed using the reciprocal of Simpson's

index ($1/\lambda$) and the evenness index. The values of the reciprocal of Simpson's index varied among sampling sites (Fig. 5). The values were the same for Gates and Mix canyons, even though more species were found in the Gates locality. The equality of these values appears to be due to the presence of around 20 rare species in Gates Canyon that were not included in the estimation of the species abundance index (Fig. 5). The evenness indexes generally varied little among sampling sites, except at Riverside and one location on the UC Davis campus (where one species of nematode predominates). In Gates Canyon the evenness index was lower than in other localities from which *V. californica* was sampled, evidently because of the presence of uncommon species of nematodes (Fig. 5).

Ordination of sampling sites using the presence or absence of species of nematodes from each collection locality (Fig. 6) showed that the Gates Canyon locality segregated from all other samples. This locality had the most unique fauna of nematodes; 40% of the taxa found in Gates Canyon did not occur anywhere else. Mix and Gates canyons shared 50% of the nematode species. The nematode fauna from grape rhizosoil at Bobelaine was more similar to that in Mix and Gates canyons on one axis, but it was also grouped by itself. The Cosumnes River locality, with fewer species of nematodes, was placed close to the domestic grapes because they shared several species, including *X. index*. The nematode faunas of both localities from which *V. girdiana* was sampled do not

Fig. 3. Percentages of nematode orders at sampling sites of *V. californica* and *V. girdiana*, based on the number of individual nematodes per taxonomic order.

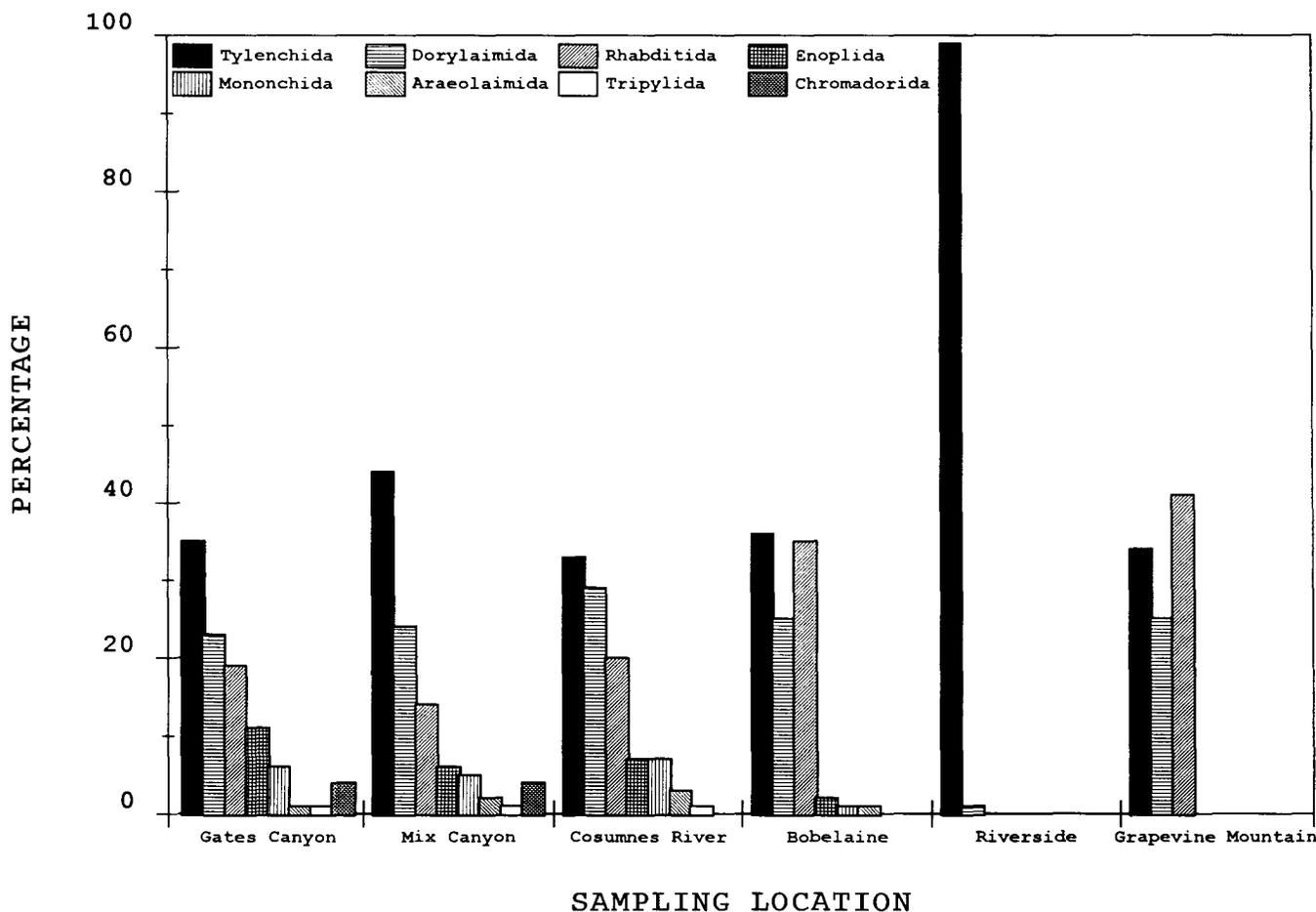
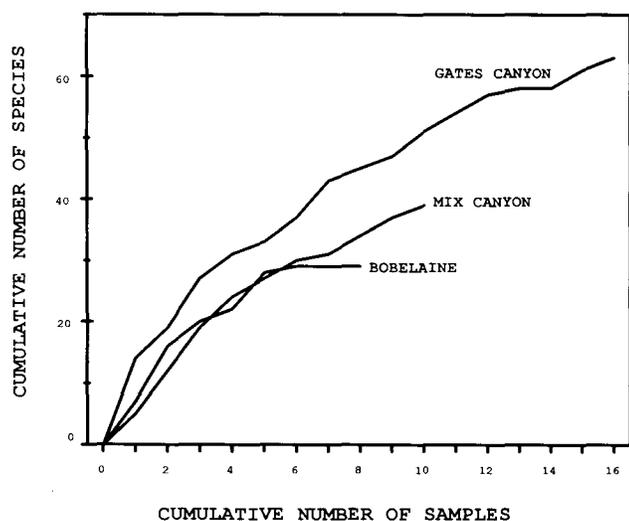


Fig. 4. Species volume curve for sampling sites of *V. californica*.



group together because the nematode species found in each locality were different. The nematode faunas of the cultivated forms of *V. vinifera* clustered into two groups. The first group clustered together because they all shared the species *X. index*. The second group was distinguished by

the presence of *X. americanum* (Fig. 6). The hybrid locality was placed in the vicinity of the second group of cultivated grapes (Fig. 6).

Ordination based on the number of individual nematodes per species (Fig. 7) corresponds to the results of the presence or absence of species ordination. The exception was the locality U2, which was separated because of the large number of *Criconemoides xenoplax* in the sample (Fig. 7).

Ordination (Fig. 8) using the presence or absence of taxonomic groupings at the level of the family indicates that the nematode faunas of Gates and Mix canyons were similar. The Riverside locality (*V. girdiana*) segregated from the rest of the sampling localities because of the unique occurrence of species of the families Tylenchulidae and Hoplolaimidae. The Cosumnes River locality harbored a unique family (Tripylidae), thus increasing the spread along the Z axis in the ordination plot (Fig. 8). The sublocality U3 was placed apart from the rest of the localities from which samples of nematodes were taken from cultivated grapes because of the unique presence of the family Mylonchulidae.

Discussion

Our comparison of nematode diversity in natural and agricultural habitats indicates that rhizosols from native California grapevines contained many more species of nematodes than

Table 2. Nematodes from soil of the desert grape (*Vitis girdiana*).

	Feeding type ^a	Collection locality ^b	
		R	GM
<i>Acrobeles crossotus</i> Steiner, 1929	3		x
<i>Aporcelaimellus obtusicaudatus</i> (Bastian, 1865)	4, 6		x
<i>Aporcelaimellus</i> sp.	4, 6	x	
<i>Criconemoides xenoplax</i> Raski, 1952	1	x	
<i>Dorylaimus</i> sp.	6	x	
<i>Eudorylaimus nothus</i> (Thorne and Swanger, 1936)	4, 6		x
<i>Filenchus conicephalus</i> Siddiqui and Khaun, 1983	1	x	
<i>Hemicriconemoides chitwoodi</i> Esser, 1960	1		x
<i>Hemicyclophora armandae</i> Al Banna and Gardner, 1993	1		x
<i>Helicotylenchus californicus</i> Sher, 1966	1	x	
<i>Tylenchulus semipenetrans</i> Cobb, 1913	1	x	

^a1, plant feeding; 2, hypha feeding; 3, bacteria feeding; 4, animal predation; 5, unicellular eucaryote feeding; 6, omnivorous.

^bR, Riverside; GM, Grapevine Mountain.

Table 3. Nematodes recovered from the rhizosoil of the roots of domestic grape.

	Feeding type ^a	Collection locality ^b						
		P	U1	U2	U3	N	S	SJ
<i>Acrobeloides bodenheimeri</i> (Steiner, 1936)	3		x	x				
<i>Aphelenchoides</i> sp.	1					x		
<i>Aphelenchoides saprophilus</i> Franklin, 1957	1			x	x			
<i>Aphelenchus cylindricaudatus</i> (Steiner, 1926)	1						x	
<i>Aporcelaimellus adoxus</i> Tjepkema, Ferris, and Ferris, 1971	4, 6	x		x				
<i>Aporcelaimellus hylophilus</i> Tjepkema, Ferris, and Ferris, 1971	4, 6		x					
<i>Boleodorus thylactus</i> Thorne, 1941	1				x			
<i>Chiloplacus symmetricus</i> (Thorne, 1925)	3							x
<i>Cephalobus pinguimicronatus</i> Andrassy, 1968	3							x
<i>Clarkus sheri</i> (Mulvey, 1967)	4						x	
<i>Coslenchus</i> sp.	1	x						
<i>Criconemoides xenoplax</i> Raski, 1952	1		x	x				
<i>Ditylenchus</i> sp.	1					x		
<i>Discolaimus similis</i> Thorne, 1939	6		x					
<i>Eudorylaimus noterophilus</i> Tjepkema, Ferris, and Ferris, 1971	4, 6					x		
<i>Hemicriconemoides mangiferae</i> Siddiqui, 1961	1				x			
<i>Merlinius brevidens</i> (Allen, 1955)	1		x					
<i>Mylonchulus sigmaturus</i> (Cobb, 1917)	4				x			
<i>Plectus elongatus</i> Maggenti, 1961	3	x						
<i>Plectus parvus</i> Bastian, 1865	3						x	
<i>Xiphinema americanum</i> Cobb, 1913	1	x	x	x	x			
<i>Xiphinema index</i> Thorne and Allen, 1950	1					x	x	x

^a1, plant feeding; 2, hypha feeding; 3, bacteria feeding; 4, animal predation; 5, unicellular eucaryote feeding; 6, omnivorous.

^bP, Pope Valley; U1–U3, University of California, Davis, sites 1–3; N, Napa Valley; S, Sonoma; SJ, San Jose.

rhizosoils from cultivated forms of *V. vinifera*. The relatively high diversity of species of nematodes associated with native grapes (especially in the localities in the coastal range) is probably due to the less disturbed nature of the habitat. Atlas et al. (1991) and Jarosic (1983) reported that the taxonomic diversity of microbial communities was lower in disturbed or polluted locations than in undisturbed or nonpolluted locations.

Using comparative methods we tested the hypothesis that high nematode diversity in the rhizosoil of grapes may have a negative effect on abundance or numerical density of plant-

parasitic species. Our results indicate that increased diversity of species of nematodes does appear to have a negative effect on the numerical density of individuals of plant-parasitic nematodes. This may be the case in the sampling sites of *V. californica* at Gates and Mix canyons and perhaps to a lesser extent at Bobelaine; at these sites there was a wide diversity of nematode species (various taxonomic as well as trophic groups), with relatively few individuals of each species occurring in the soil (the evenness value was 0.6, 0.7 and 0.9, respectively; Fig. 5). In contrast, the low diversity of

Fig. 5. Diversity and evenness of nematodes from each collection locality (GC, Gates Canyon; MC, Mix Canyon; B, Bobelaine; CR, Cosumnes River; R, Riverside; GM, Grapevine Mountain; PV, Pope Valley; U1–U3, University of California, Davis, sites 1–3; N, Napa Valley; S, Sonoma; SJ, San Jose; H, hybrid from Amador County). Diversity is represented by the reciprocal of Simpson's index ($1/\lambda$ = number of very abundant species). Species evenness (modified Hill's ratio) is measured as $[(1/\lambda) - 1] / (eH' - 1)$, where λ is Simpson's diversity index and H' is Shannon's entropy.

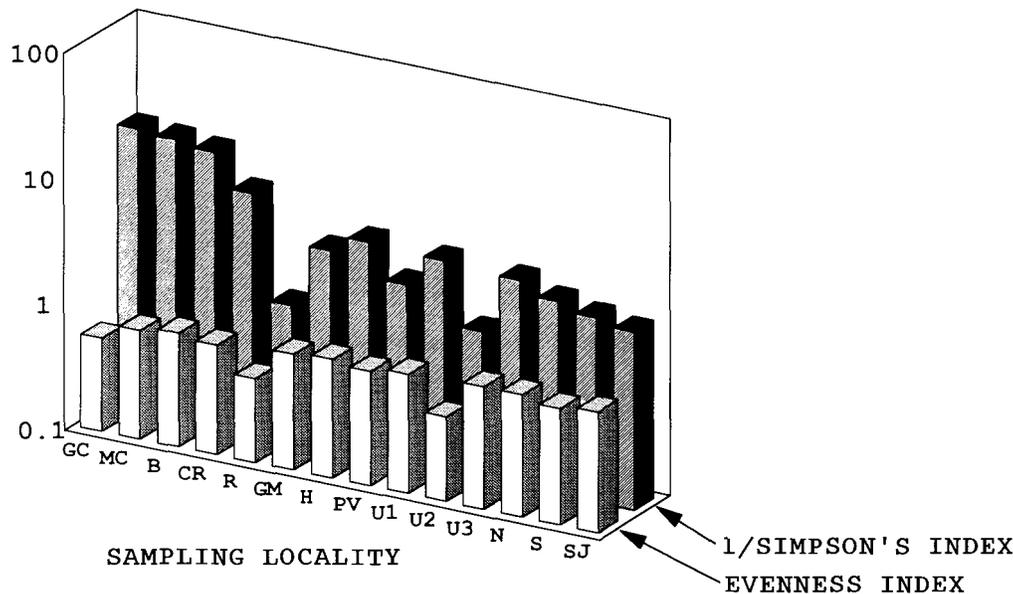


Table 4. Nematode associates of a putative hybrid vine (*V. vinifera* × *V. californica*) in Amador County.

	Feeding type ^a
<i>Alaimus parvus</i> Thorne, 1939	3
<i>Aphelenchus avenae</i> Bastian, 1865	1, 2
<i>Aporcelaimellus obtusicaudatus</i> (Bastian, 1865)	4, 6
<i>Boleodorus thylactus</i> Thorne, 1941	1
<i>Filenchus conicephalus</i> Siddiqui and Khan, 1983	1
<i>Plectus parietinus</i> Bastian, 1865	3
<i>Prionchulus muscorum</i> (Dujardin, 1845)	3

^a1, plant feeding; 2, hypha feeding; 3, bacteria feeding; 4, animal predation; 5, unicellular eucaryote feeding; 6, omnivorous.

nematode species in soil may allow one or two species of nematodes parasitic on plant roots to increase to great numerical density, as is the case in the Riverside and U2 localities. Similarly, Oostenbrink (1966) stated that plant-parasitic nematodes are widespread, and are found in natural communities at low densities but become established at greater numerical densities as natural habitats are disturbed by clearing or cultivation. The increase of plant-parasitic nematodes in number of species and in numerical density in anthropogenically modified soils is probably due to many factors, including (i) the polyphagous nature of many of these species (they can persist on weeds and crop plants alike), (ii) their ability to persist in the soil for a long time, (iii) low interspecific competition, and (iv) the dispersal of plant-parasitic nematodes anthropogenically.

Quantitative analysis of the number of individual nematodes per collection locality provided information on the dominance

of certain species. For example, the Riverside locality of *V. girdiana* is grouped by itself because of the presence of large numbers of individuals of two plant-parasitic nematodes, *Tylenchulus semipenetrans* and *Criconemoides xenoplax*.

The two localities of the desert native grape (*V. girdiana*) have an interesting nematode fauna. In these two localities, plant-parasitic nematodes were dominant and it is probable that they were introduced into the Riverside site by human activities. Second-stage juveniles of *T. semipenetrans* and *C. xenoplax* could have invaded this site from the nearby cultivated cropland. The presence of the sheath nematode, *Hemicycliophora armandae* Al Banna and Gardner, 1993, in an isolated area (Grapevine Mountain) indicates that this species is native to *V. girdiana* in that region and that it probably became isolated because of the desertification of the area since the Pleistocene.

The shapes and the slopes of the species volume curves of the three localities, Gates Canyon, Mix Canyon, and Bobelaine, were different (Fig. 4). These differences indicate that the species richness index, the total number of species in a defined sampling unit, cannot be applied as a diversity measure to discriminate between sampling localities. The species volume curves for the two sites in the coastal foothills indicate that additional sampling would have yielded more species at about the same rate. In the Bobelaine locality the curve flattens out after six samples were processed (no new species were found after six samples), therefore we are confident that we collected most of the species present in that locality (Fig. 4).

Three-dimensional ordination provided a good view of the community structure of the nematode fauna associated with the rhizosol of species of *Vitis*. Analysis of data at the level

Fig. 6. Three-dimensional ordination, showing different collection localities of species of *Vitis* in California, based on the communities of nematodes from each locality. For an explanation of abbreviations for localities see Figs. 1 and 5.

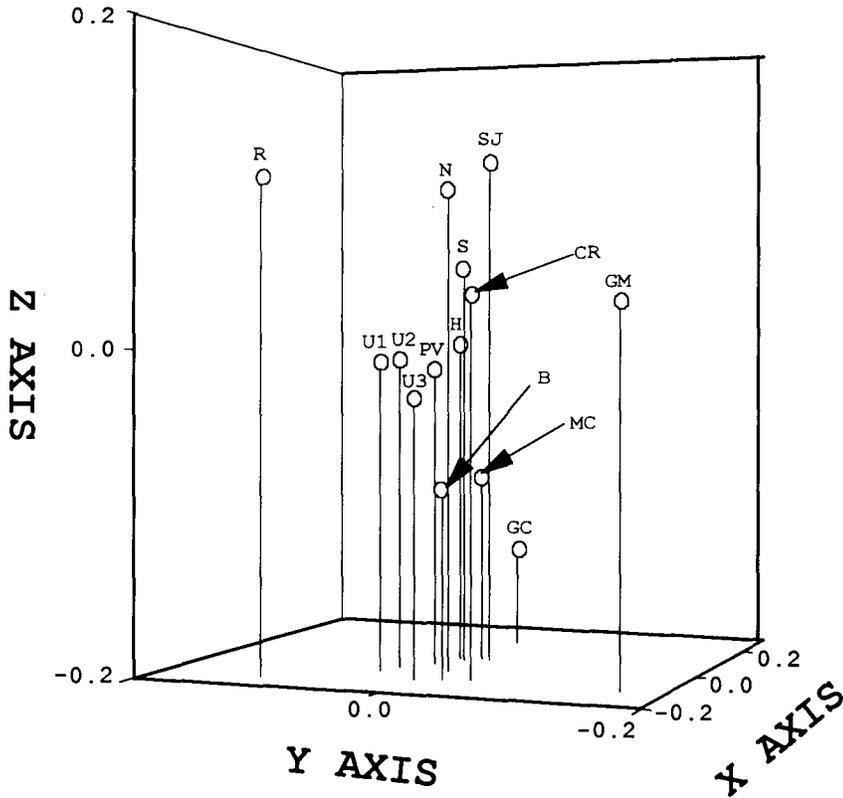


Fig. 7. Three-dimensional ordination, showing different collection localities of species of *Vitis* in California, based on the number of individuals or species from each locality. For an explanation of abbreviations for localities see Figs. 1 and 5.

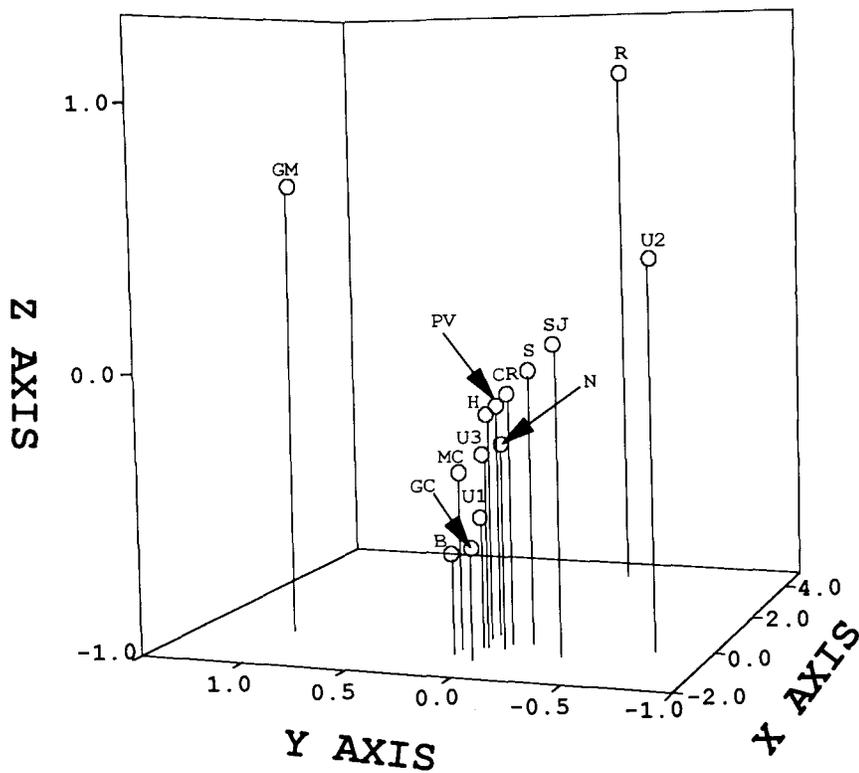
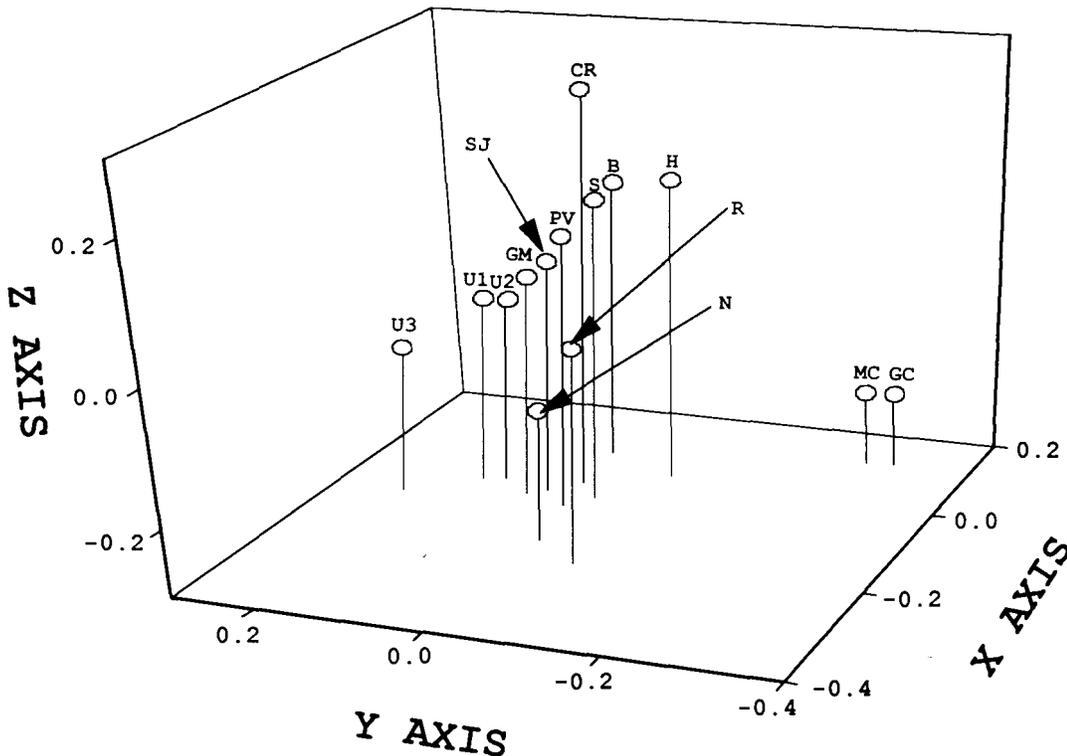


Fig. 8. Three-dimensional ordination, showing different collection localities of species of *Vitis* in California, based on the number of families of nematodes from each locality. For an explanation of abbreviations of localities see Figs. 1 and 5.



of families or species or numerical density of individuals provided different levels of resolution into the aggregations of nematodes among the different collection localities. The analyses based on either the presence or absence or the number of individuals of each nematode species provided the most realistic interpretation of the pattern of diversity and composition of the nematode communities among localities.

The results of this survey indicate that both species of California native grape could act as reservoirs of plant-parasitic nematodes that have the potential to infest domestic grapes and other crops of economic importance. The biology and feeding habits of many of the nematode species found in this study are poorly known, making interpretation of the associations difficult. However, from data we compiled on nematodes from both cropland and natural situations, we conclude that little meaningful ecological or numerical—population information can be derived from studies of nematodes from cultivated crop plants only. Our data indicate that the soil faunas in vineyard agro-ecosystems are completely different from those found in natural systems. It appears that the nematode faunas of vineyard soils are completely depauperate (collapsed ecosystems) and are maintained in this state only through direct anthropogenic inputs. These types of system do not allow generalizations to be made, concerning either other agricultural systems or, more importantly, natural systems. Our data imply that soil nematode faunas with great trophic diversity act as “trophic buffers,” preventing nematodes of only one trophic type or another from increasing to extremely high numerical densities. The present study does show that nematode communities with great trophic and taxonomic diversity have lower numerical densities of plant-parasitic forms.

To understand the faunal and structural complexity of nematode associates of crop plants, more comparative studies of the diversity of nematodes associated with native relatives of cultivated crops must be conducted. Only by comparing the nematode faunas of native species of plants with those faunas associated with anthropogenically maintained crop plants can we obtain robust data on relationships among nematode species or populations in agricultural situations. These types of comparison will also help to guide researchers in the search for self-maintaining low-input agricultural systems. Additional studies of the biodiversity of nematodes in soils from both unexplored and well-known parts of the earth must continue to be conducted. These kinds of basic investigations will allow researchers to analyze incoming data on the biodiversity of the earth in multifarious ways.

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