Chapter 6
Plant Parasitic Nematodes in California Agriculture

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6.1 Introduction

California continues to lead the United States in agricultural production and is a main provider of food for the nation and much of the world. As the nation's third largest state by land area comprising of distinct topographical contrasts, California produces numerous agricultural crops primarily within its valley regions. Plant parasitic nematodes are associated with these crops and can be a significant threat to the state's agricultural production. An overview of California's agricultural crop production and associated plant parasitic nematode problems and management strategies are provided in this chapter.

6.2 California's Major Agricultural Crops

California's climate and geography allows the production of the largest diversity of agricultural crops in the U.S. (Table 6.1; Fig. 6.1). In 2016, fruits, nuts and vegetables continued as the state's leading crops and accounted for 56% of the nation's non-citrus fruit and nut production and over 46% of the nation's citrus production. The total value of all fruits and nuts produced in California was $19.7 billion. California is the number one producer of grapes in the nation, producing 88% of the

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Table 6.1 Selected economically important crops of California for 2016 (California Agricultural Statistics Review 2016–2017)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Fruit and nut crops					
Almonds	376.0	1	100.0	5,158,160	Kern, Fresno, Stanislaus, Merced, Madera
Apples	5	6	1.6	54,013	El Dorado, San Joaquin, Santa Cruz, Fresno, Sonoma
Apricots	3.4	1	85.2	48,929	Stanislaus, Fresno, Kings, Tulare, San Joaquin
Avocados	20.8	1	93.6	412,050	San Diego, Ventura, Santa Barbara, San Luis Obispo, Riverside
Blueberries	2.5	2	14.5	108,765	Tulare, Kern, San Joaquin, Ventura, Fresno
Cherries, Sweet	13.2	2	21.4	184,490	Kern, San Joaquin, Fresno, Tulare, Kings
Dates	4.0	1	68.9	46,650	Riverside, Imperial
Figs	2.4	1	100.0	29,230	n/a[b]
Grapefruit, all	3.8	2	26.6	67,664	Riverside, San Diego, Tulare, Kern, Imperial
Grapes, all	336.4	1	89.2	5,581,410	Kern, Napa, Fresno, Tulare, Sonoma
Kiwifruit	1.4	1	100.0	44,431	Tulare, Yuba, Butte, Fresno, Sutter
Lemons	18.8	1	78.6	(Withheld)	Ventura, Riverside, Tulare, Kern, San Diego
Nectarines	7.6	1	92.6	137,418	Fresno, Tulare, Kings, Kern, Contra Costa
Olives	14.0	1	100.00	138,090	Tehama, Tulare, Glenn, San Joaquin, Yolo
Oranges, all	62.8	2	42.9	826,294	Tulare, Kern, Fresno, San Diego, Madera
Peaches, all	16.0	1	55.7	350,285	Fresno, Tulare, Stanislaus, Sutter, Kings
Pears, all	1.7	3	19.7	93,585	Sacramento, Fresno, Lake, Mendocino, Tulare
Pecans	n/a	6	2.1	14,656	n/a

(continued)

Table 6.1 (continued)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Pistachios	95.6	1	100.0	1,506,120	Kern, Tulare, Fresno, Madera, Kings
Plums and Prunes	25.4	1	100.0	195,754	Fresno, Tulare, Kings, Kern, Madera[c]
Raspberries	4.1	1	83.1	380,447	Ventura, Santa Cruz, Monterey, Santa Barbara
Strawberries, all	15.1	1	78.5	1,834,783	Monterey, Ventura, Santa Barbara, San Luis, Obispo, Santa Cruz
Tangerines, Mandarins, Tangelos and Tangors	22.8	1	93.3	(Withheld)	Kern, Tulare, Fresno, Madera, Riverside
Walnuts	126.0	1	100.0	1,241,660	San Joaquin, Butte, Glenn, Tulare, Stanislaus
Vegetable and melon crops					
Artichokes	2.7	1	100.0	69,119	n/a
Asparagus	3.2	1	35.5	26,624	Fresno, Monterey, San Joaquin, Kern, Imperial
Beans, fresh	2.8	2	20.3	55,020	n/a
Broccoli	49.2	1	91.5	779,186	Monterey, Santa Barbara, Imperial, San Luis Obispo, Fresno
Cabbage, fresh market	5.7	1	39.5	158,976	Monterey, Ventura, Imperial, Santa Barbara, Kern
Carrots, fresh	26.9	1	89.8	702,030	Kern, Imperial, Monterey, Riverside, Fresno
Cauliflower	12.9	1	82.7	322,154	Monterey, Santa Barbara, Imperial, San Luis Obispo, Riverside
Celery	10.8	1	94.8	340,035	Ventura, Monterey, Santa Barbara, Imperial, San Benito
Corn, fresh sweet	13.9	1	18.3	163,751	Imperial, Contra Costa, Fresno, Riverside, Santa Clara
Cucumber, fresh market	3.7	2	20.9	36,285	n/a

(continued)

Table 6.1 (continued)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Garlic	11.0	1	100.0	268,665	Fresno, Kern, Riverside, Santa Clara, Madera
Lettuce, all	83.6	1	68.0	1,960,266	Monterey, Imperial, Santa Barbara, San Benito, Fresno
Melons, cantaloupe	10.2	1	43.9	91,035	Fresno, Imperial, Merced, Riverside, Kern
Melons, honeydew	4.4	1	100.0	67,584	Fresno, Riverside, Imperial, Sutter
Melons, watermelon	5.0	2	21.2	122,850	San Joaquin, Kern, Riverside, Fresno, Imperial
Onions, all	17.7	1	24.6	183,386	Imperial, Fresno, Kern, Monterey, San Benito
Peppers, all	10.6	1	55.3	496,770	Riverside, Ventura, Kern, San Benito, Santa Clara[d]
Pumpkin	2.0	5	7.3	15,255	n/a
Spinach, fresh market	11.4	1	57.7	174,406	Monterey, Imperial, San Benito, Santa Clara, Santa Barbara
Squash	2.5	1	21.9	35,925	n/a
Tomatoes, all	116.6	1	64.7	1,329,523	Fresno, Merced, San Diego, Kern, Santa Clara[e]
Field and seed crops					
Beans, dry	19.6	5	9.5	70,286	Stanislaus, Tulare, San Joaquin, Fresno, Sutter
Cotton lint, all	86.4	3	7.5	(Withheld)	Kings, Fresno, Merced, Kern, Tulare
Cottonseed	n/a	3	6.7	75,175	Kings, Fresno, Kern, Tulare, Merced
Hay, alfalfa and others	480.0	1	12.5	966,192	Imperial, Kern, Merced, Tulare, Riverside[f]
Potatoes (excl. sweet)	13.2	5	6.8	265,305	Kern, San Joaquin, Imperial, Siskiyou, Riverside
Potatoes, sweet	8.0	2	21.4	151,280	Merced, Stanislaus, Kern

(continued)

Table 6.1 (continued)

Crops[a]	Area harvested 1000 ha	U.S. rank	CA share of U. S. receipts percent	Total value $1000	Five leading counties by gross value of production
Rice	214.4	1	29.1	649,289	Colusa, Butte, Sutter, Glenn, Yolo
Sugar beets	10.0	7	3.0	n/a	Imperial

[a]Crops in bold are included in California's top 20 commodities for 2016, by value and rank
[b]*n/a* Not available
[c]Five leading counties for plums; five leading counties for dried plums (prunes) in 2016 were Tulare, Butte, Yuba, Sutter and Tehama
[d]Leading counties for bell peppers
[e]Leading counties for fresh market tomatoes only
[f]Leading counties for alfalfa hay only

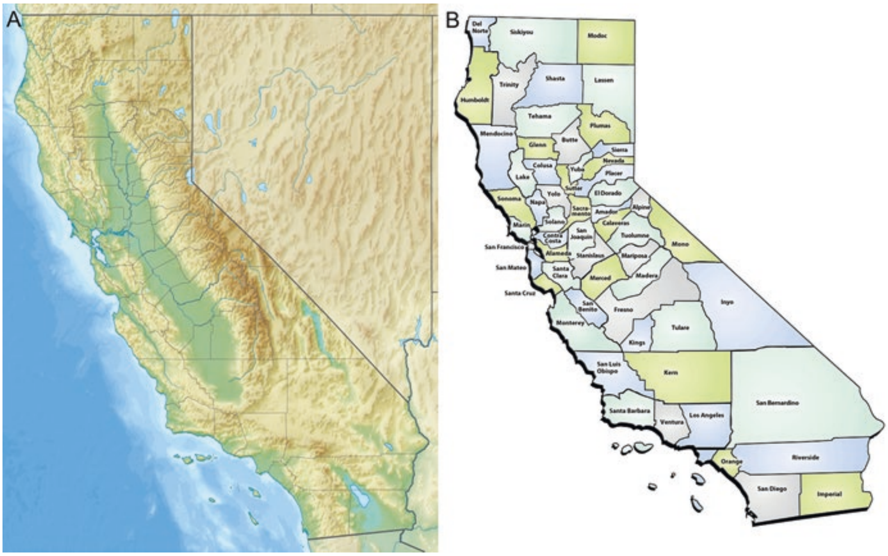

Fig. 6.1 (**a**) California physical map; (**b**) California county map. (Source **a** quazoo.com; **b** picquery)

nation's total tonnage. The state also produces 80% of worldwide almond production. The total value of fresh and processing vegetables and melon production was $7.4 billion with lettuce as the leading vegetable crop, in value of production ($2.0 billion), followed by tomatoes ($1.3 billion). Furthermore, California is the nation's sole producer of 99% or more of almonds, artichokes, dates, figs, garlic, grapes (raisins), kiwifruit, Honeydew melons, olives, peaches (clingstone), pistachios, rice (sweet), seed (Ladino clover) and walnuts (CDFAa 2016–2017). California is the largest producer of almonds in the world, with approximately 80% in global production, and the second largest producer of walnuts in the world. Almonds continue to be the state's top valued agricultural export commodity, with $4.50 billion in foreign sales in 2016. California is, also, the nation's largest agricultural exporter of 14.9% of total U.S. agricultural exports in 2016, and the sole exporter of 99% or more of almonds, artichokes, dates, dried plums, figs, garlic, kiwifruit, olives and olive oil, pistachios, raisins, table grapes and walnuts (CDFAb 2016–2017). California's nursery, greenhouse and floriculture crop production, which includes cut flowers, potted plants, foliage plants, bedding plants and indoor decorative, was valued at $947 million in 2015. California's numerous public and private golf courses are major users of turfgrasses and represent 3.5% of total turf grass cultivated in the state. The golf industry ($6.3 billion in 2011), is comparable in size to other important state industries including greenhouse/nursery crops, and therefore, the use and importance of turf grass management cannot be under rated (SRI International 2013).

6.3 California's Major Agricultural Regions

The Central Valley, which includes all or part of 18 Northern California counties and extends through the center of the state from Shasta County in the north to Kern County in the south, is the state's agricultural heartland that produces more than 250 different crops with an estimated value of $17 billion per year. The Valley alone accounts for one-fourth of the nation's food including 40% of the nation's fruit, nut and other agricultural crops, on less than 1% of the nation's total farmland and is marked by a hot Mediterranean climate in the north, and a dry, desert-like climate in the southernmost regions (USGS 2017). The top four agricultural counties namely Kern, Tulare, Fresno and Monterey Counties, that lead in total value of production and leading commodities are in the Central Valley and experience a growing season of 9–10 months (CDFAa 2016–2017; Morgan and McNamee 2017). The Central Valley is subdivided into (1) the Sacramento Valley which encompasses the region north of the Sacramento-San Joaquin River Delta and comprises all or part of ten Northern California counties, and (2) the San Joaquin Valley which extends from the Delta to the Tehachapi Mountains in the south and includes seven northern counties as well as most of Kern County in Southern California.

The Salinas Valley lies within Monterey County, west of the San Joaquin Valley and south of San Francisco Bay, with cool summers and relatively mild winters in the northern region and warmer summers and colder winters in the southern region. The Salinas Valley is the State's major producer of salad and vegetable crops as well as strawberries and wine grapes.

The Coachella Valley is part of the Colorado Desert extending from the Salton Sea through Riverside County to the San Gorgonio Pass in Southern California, with warm climates through the year and generally, extremely arid climate with most precipitation occurring during the winter months. Irrigation and warm climates have resulted in production of varied vegetables, fruits including date palms, citrus and mangoes, cotton and alfalfa (Britannica 2018).

The Imperial Valley, lying within Southern California's Imperial County and extending south of the Coachella Valley to the Gulf of California, has desert climate and extreme daily temperatures. Summer temperatures are usually greater than

38 °C, whereas, temperatures from late October to mid-April are relatively mild. The Imperial Valley comprises thousands of hectares of irrigated farmland and is a major producer of winter fruits that cannot endure cool temperatures, and vegetables, cotton and grain crops.

The Napa and Sonoma Valleys lie adjacently north of San Francisco along the coastal mountain ranges. These regions have a Mediterranean climate of warm and dry days and cool nights during summers and wet and cool winters, well-suited for the cultivation of premium wine grapes.

Several small valleys lie within California's Central Coast which includes parts of San Luis Obispo, Santa Barbara and Ventura Counties and provide unique climate niches and soil types ideal for year-round production of fruits, wine grapes, cool and warm season vegetables and seed crops (UCCE 2005).

6.4 Nematology in California: Early Discoveries

Nematode problems in agriculture were not fully recognized in the USA until the early 1900s. The early development of Nematology was mainly limited to reports on root knot nematodes and initial work was concentrated on the US east coastal region. This recognition soon led to initial nematode surveys in California during 1907 and a first report by E. A. Bessey in 1911 of the presence of root knot nematodes (*Meloidogyne* spp.) and sugar beet cyst nematodes (*Heterodera schachtii*) in several regions of the State. With growing awareness of nematode problems in California, in 1912, the citrus nematode was discovered by a Los Angeles County Agricultural Inspector, J. R. Hodges., and in 1928, was shown to cause serious damage to citrus seedlings, by E. E. Thomas at the Citrus Experiment Station in Riverside. Initial surveys in the early 1920s also detected the stem and bulb nematode, *Ditylenchus dipsaci*, and in 1927 the root lesion nematodes, *Pratylenchus* spp., were first reported on fig. In the decade that followed, root lesion nematode damage to fig, walnut and cherry trees was found to be widespread in California. Critical to the initial detections, research and management of plant parasitic nematodes in California agriculture, was the development of the Department of Nematology at the University of California and the Nematology Regulatory Program at the California Department of Agriculture. At that time, the State Department of Agriculture estimated the value of nursery stock rejected due to root knot nematode infestation, during the December 1922 to April 1923 planting season, to be $100,000 (Siddiqui et al. 1973; Raski et al. 2002). Losses caused by nematodes were difficult to assess then as several species of ectoparasitic nematodes were being discovered to feed on plant roots without causing distinct symptoms other than restricted root growth. Much about their damage potential and distribution was unknown and their impact on crop growth was recognized only when nematicides were applied to areas where poor plant growth occurred by unknown cause. With the advent of fumigant nematicides, several ectoparasitic nematodes were soon recognized to cause more damage to crops than that caused by endoparasites. In 1959, the Department of

Nematology estimated annual crop losses due to nematodes at $89,442,000–$141,721,000 (Allen and Maggenti 1959). In 1951, after review of the nematode situation at that time, the Department of Agriculture and the University of California produced the first distribution record of plant parasitic nematodes in California (Raski et al. 2002). Since then, several in-state surveys have been conducted collaboratively or individually by federal, state, county and University of California agencies, for targeted plant parasitic nematodes such as the burrowing nematode, sugar beet cyst nematode, golden nematode, potato pale cyst nematode, Columbia root knot nematode, sting nematode, strawberry foliar nematode, reniform nematode and other exotic and non-exotic species associated with host plants in cultivated and non-cultivated crop fields, orchards, nurseries and golf greens.

6.5 Economically Important Plant Parasitic Nematodes of Major Crops in California

Plant parasitic nematodes can significantly impact crop production in California. While several species have been found to be associated with different plants grown in the state (Table 6.2), in this chapter, only certain main, economically important plant parasitic nematode species associated with major crops of the state are discussed. These species include the root knot, lesion, stem and bulb, citrus, dagger, ring, pin and sting nematodes and a few others.

6.5.1 Root Knot Nematodes, Meloidogyne *spp.*

Since first being reported in California by E. A. Bessey in 1911, root knot nematodes (*Meloidogyne* spp.) have become the most extensively studied genus in the state. Six species are of significant economic concern: *M. incognita, M. javanica, M. arenaria, M. hapla, M. chitwoodi* and *M. naasi*. Another three species have been reported: *M. graminis, M. marylandi* and *M. fallax* (Table 6.2; Fig. 6.2).

The host ranges of the various species are highly varied (Table 6.2), but as a whole encompass most of the economically important annual perennial, and ornamental crops grown in California (Table 6.1). Species are distributed throughout California's agricultural areas but show some regional and crop distribution preferences. For example, *M. chitwoodi* is found on potatoes and small grains in the northern part of the state in Modoc and Siskiyou Counties. In this same area, *M. naasi* parasitizes barley, wheat and grasses. An isolated occurrence of *M. naasi* has also been found on a bowling green in the Los Angeles area. The northern root knot nematode *M. hapla* is found statewide, particularly in fields cropped to alfalfa where it can reduce alfalfa stand densities by 62% (Noling and Ferris 1985). As the only species that parasitizes cotton, *M. incognita* may be more common on land regularly cropped with cotton (McKenry and Roberts 1985).

Table 6.2 Plant parasitic nematodes associated with various crops in California

Species	Crop	References
Anguna agrostis	Creeping bentgrass	Siddiqui et al. (1973)
A. pacificae	Bluegrass	Cid Del Prado Vera and Maggenti (1984) and McClure et al. (2008)
Aphelenchoides fragariae	Strawberry, ornamentals	Siddiqui et al. (1973) and McKenry and Roberts (1985)
A. ritzemabosi	Strawberry, alfalfa, ornamentals	Siddiqui et al. (1973) and McKenry and Roberts (1985)
Ataloderа gracililanceae	*Festuca* sp.	Robbins (1978a)
Belonolaimus longicaudatus	Grasses	Mundo-Ocampo et al. (1994)
Cacopaurus pestis	Walnut	Thorne (1943)
Criconemoides annulatus	Plum, beet, barley, citrus, apple, cotton, strawberry, alfalfa, tomato, tobacco, sorghum, clover, corn, walnut	Raski (1952a) and Siddiqui et al. (1973)
Criconema permistum	Grape	Siddiqui et al. (1973)
Ditylenchus dipsaci	Alfalfa, garlic, onion, sugar beet, alfalfa, phlox, pea, clover, barley	Siddiqui et al. (1973) and McKenry and Roberts (1985)
D. destructor	Potato	Ayoub (1970)
Gracilacus anceps	Tomato	Siddiqui et al. (1973)
G. idalimus	Grape	Dong et al. (2007)
G. mirus	Grape	Raski (1962)
Helicotylenchus digonicus	Oat, beet, citrus, fig, barley, tomato, bean, wheat, grape, corn, nectarine	Siddiqui et al. (1973) and Dong et al. (2007)
H. dihystera	Grape, bermudagrass, onion, beet, citrus, cotton, barley, tomato, rice, almond potato, sorghum, grape, corn, apricot, cherry, peach, plum	Siddiqui et al. (1973), McKenry and Roberts (1985), Subbotin et al. (2015b), and Dong et al. (2007)
H. erythrinae	Beet, cotton, apple, grape	Siddiqui et al. (1973)
H. microlobus	Corn	Subbotin et al. (2015b)
H. paragiris	Apricot, cherry, nectarine, plum	Dong et al. (2007)
H. paxilli	Grasses	Subbotin et al. (2015b)
H. pseudorobustus	Grasses, rice, grape, beet, apricot, cherry, nectarine, plum	Siddiqui et al. (1973), Subbotin et al. (2015b), and Dong et al. (2007)
Hemicriconemoides californianus	Grape	Pinochet and Raski (1975)
Hemicycliophora arenaria	Citrus, tomato	Siddiqui et al. (1973) and Dong et al. (2007)
H. biosphaera	Citrus	Dong et al. (2007)
H. sheri	Prune	Dong et al. (2007)
H. striatula	Nectarine	Dong et al. (2007)

(continued)

Table 6.2 (continued)

Species	Crop	References
Heterodera cruciferae	Table beets, cabbage, Brussels sprouts, broccoli, cauliflower	Siddiqui et al. (1973) and McKenry and Roberts (1985)
H. fici	Fig	Sher and Raski (1956)
H. schachtii	Sugar beet, table beet, cabbage, Brussels sprouts, broccoli, cauliflower, radish, spinach, turnips	Siddiqui et al. (1973) and McKenry and Roberts (1985)
H. trifolii	Clover	McKenry and Roberts (1985)
Hirschmanniella belli	Rice	Siddiqui et al. (1973) and McKenry and Roberts (1985)
Longidorus africanus	Bermudagrass, lettuce, cotton, orange	McKenry and Roberts (1985), Ploeg (1998), and Dong et al. (2007)
L. elongatus	Grape	Siddiqui et al. (1973) and Robbins and Brown (1991)
L. ferrisi	Citrus	Robbins et al. (2009)
L. orientalis	Date palm	Subbotin et al. (2015a)
Meloidogyne arenaria	Alfalfa, apple, grape, nectarine, peach, plum, prune, beans (dry), broccoli, cabbage, cauliflower, carrots, lettuce, cucurbits, sugar beet, wheat, barley, potato	Siddiqui et al. (1973)
M. chitwoodi	Barley, oat, potato	McKenry and Roberts (1985)
M. hapla	Strawberry, sugar beet, carrot, table beets, cabbage, Brussels sprouts, broccoli, cauliflower, celery, lettuce, garlic, onion, tomato, alfalfa, clover, tomato, potato, grape	Raski (1957), Siddiqui et al. (1973), McKenry and Roberts (1985), and Dong et al. (2007)
M. incognita	Beet, cucumber, onion, soybean, olive, alfalfa, bean, tomato, hop, potato, nectarine, grape	Siddiqui et al. (1973) and Dong et al. (2007)
M. graminis	Grasses	McClure et al. (2012)
M. fallax	Grasses	Nischwitz et al. (2013)
Meloidogyne floridensis	Almond	Westphal et al. (unpublished) and Chitambar (2018)
M. marylandi	Grasses	McClure et al. (2012)
M. naasi	Grasses, barley, oat, rye, wheat, turfgrass	Radewald et al. (1970), Siddiqui et al. (1973), McKenry and Roberts (1985), and McClure et al. (2012)
M. javanica	Beet, citrus, tomato, olive, potato, grape, peach	Siddiqui et al. (1973) and Dong et al. (2007)
Merlinius brevidens	Grasses, artichoke, corn, lettuce, alfalfa, cereals, cabbage, carrot, cotton, rice, pea, almond, grape, prune, corn, wheat, potato	Allen (1955), McKenry and Roberts (1985), and Dong et al. (2007)
Mesocriconema rusticum	Grape	Siddiqui et al. (1973)

(continued)

Table 6.2 (continued)

Species	Crop	References
M. xenoplax	Grape, citrus, tomato, apple, plum, walnut, rice, apricot, cherry, peach	Raski (1952a), Siddiqui et al. (1973), and Dong et al. (2007)
Nacobbus dorsalis	Barley, corn	Siddiqui et al. (1973)
Nanidorus minor	Alfalfa, almond, cabbage, barley, bean, carrot, cotton, corn, peppers, sugar beet, onion, tomato, olive, plum	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Kumari and Subbotin (2012)
Paralongidorus microlaimus	Walnut	Robbins (1978b)
Paratrichodorus allius	Onion	Norton et al. (1984)
P. porosus	Fig, tomato, apple, alfalfa, olive, plum, peach	Siddiqui et al. (1973)
Paratylenchus baldacci	Prune, citrus	Dong et al. (2007)
P. bukowinensis	Apricot, cherry, citrus, nectarine, plum, prune	Dong et al. (2007)
P. dianthus	Citrus	Dong et al. (2007)
P. hamatus	Fig, peach, plum, apricot, beet, carrot, cabbage, barley, alfalfa, apple, potato, grape, peach, almond, cherry, nectarine, plum, prune, citrus	Thorne and Allen (1950), Siddiqui et al. (1973), Raski (1975), Dong et al. (2007), and Van den Berg et al. (2014)
P. holdemani	Citrus	Dong et al. (2007)
P. lepidus	Apricot, cherry	Dong et al. (2007)
P. nanus	Grasses, walnut, alfalfa, cabbage	Siddiqui et al. (1973), Raski (1975), and Van den Berg et al. (2014)
P. neoamblycephalus	Plum, apricot	McKenry and Roberts (1985) and Dong et al. (2007)
P. projectus	Bean, plum	Siddiqui et al. (1973)
P. similis	Citrus	Dong et al. (2007)
P. straeleni	Prune	Van den Berg et al. (2014)
Pratylenchus brachyurus	Cotton, barley, alfalfa, grape, corn, prune	Siddiqui et al. (1973), McKenry and Roberts (1985), and Dong et al. (2007)
P. crenatus	Beet, carrot, barley, olive, tomato, peach, potato, corn	Siddiqui et al. (1973)
P. hexincisus	Grape	Dong et al. (2007)
P. penetrans	Cowpea, cherry, strawberry, oat, cabbage, barley, tomato, alfalfa, pea, potato, wheat, almond, corn, apricot, cherry, plum, grape	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)
P. scribneri	Sudan grass, beans, alfalfa, corn, grape, apple, beet	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)

(continued)

Table 6.2 (continued)

Species	Crop	References
P. thornei	Grasses, sorghum, wheat, onion, sugar beet, cabbage, alfalfa, beans, sorghum, corn, apricot, cherry, grape	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)
P. neglectus	Onion, sugar beet, oat, cabbage, citrus, carrot, alfalfa, barley, soybean, peach, bean, tomato, apple, potato, bean, wheat, corn, clover, grape, apricot, cherry, nectarine, plum, prune, barley	Siddiqui et al. (1973), Dong et al. (2007), and Subbotin et al. (2008)
P. vulnus	Walnut, grape, fig, citrus, apricot, avocado, cherry, olive, peach, almond, plum, raspberry, boysenberry, apple, strawberry, pear, pistachio, nectarine	Allen and Jensen (1951), Hart (1951), Lownsbery (1956), Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Subbotin et al. (2008)
Quinisulcius acutus	Apple, sorghum, peach, grape	Siddiqui et al. (1973)
Rotylenchulus parvus	Alfalfa, cotton, olive, sugar beet, sorghum	Siddiqui et al. (1973) and Dong et al. (2007)
Rotylenchus robustus	Apple, potato, olive, grape, grasses	Siddiqui et al. (1973), Dong et al. (2007), and Cantalapiedra-Navarrete et al. (2013)
Scutellonema brachyurus	Peach, plum	Dong et al. (2007)
S. clathricaudatum	Apricot	Dong et al. (2007)
S. conicephalum	Apricot, cherry, plum	Dong et al. (2007)
Trichodorus californicus	Rose	Siddiqui et al. (1973)
Tylenchulus semipenetrans	Persimmon, citrus, grape, olive	Baines and Thorne (1952), McKenry and Roberts (1985), Dong et al. (2007), and Tanha Maafi et al. (2012)
Tylenchorhynchus agri	Cherry	Dong et al. (2007)
T. aspericutis	Nectarine	Dong et al. (2007)
T. annulatus	Plum	Dong et al. (2007) and Handoo et al. (2014)
T. capitatus	Pear, cabbage, carrot, barley, apple, rye, corn, plum	Allen (1955) and Siddiqui et al. (1973)
T. claytoni	Citrus, tomato, apple, peach, grape, corn	Siddiqui et al. (1973)
T. clarus	Citrus, alfalfa, barley, beans, bermudagrass, cotton, carrot, barley, olive, rice, plum, peach, potato, corn, grape, clover, wheat	Allen (1955), Siddiqui et al. (1973), McKenry and Roberts (1985), and Handoo et al. (2014)

(continued)

Table 6.2 (continued)

Species	Crop	References
T. cylindricus	Cotton, apple, olive, almond, potato, grape, corn, bean	Allen (1955) and Siddiqui et al. (1973)
T. ebriensis	Peach	Dong et al. (2007)
T. elegans	Cherry, plum, grape	Dong et al. (2007)
T. mashhoodi	Apricot, cherry peach, plum, grape	Dong et al. (2007)
T. microconus	Cherry	Dong et al. (2007)
T. nudus	Apricot	Dong et al. (2007)
Xiphinema americanum sensu lato	Plum, apricot, grape, grasses, orange, pecan, walnut, cherry, peach, cherry, alfalfa, apricot, apple, citrus pear, pistachio, raspberry, strawberry, tomato, rice, sorghum, bean	Siddiqui et al. (1973), McKenry and Roberts (1985), Dong et al. (2007), and Orlando et al. (2016)
X. californicum	Orange, grape, grapefruit, lemon, peach, cherry, plum, lemon, walnut, olive, alfalfa,	Lamberti and Bleve-Zacheo (1979), Lamberti and Golden (1984), Robbins (1993), and Orlando et al. (2016)
X. pachtaicum	Plum, lemon	Robbins (1993) and Orlando et al. (2016)
X. rivesi	Grasses	Orlando et al. (2016)
X. index	Fig, grape	Thorne and Allen (1950) and Siddiqui et al. (1973)
X. insigne	Plum, grasses	Luc and Southey (1980) and Cai et al. (2018)
X. vuittenezi	Grape, fig, citrus, carrot	Luc et al. (1964) and Siddiqui et al. (1973)

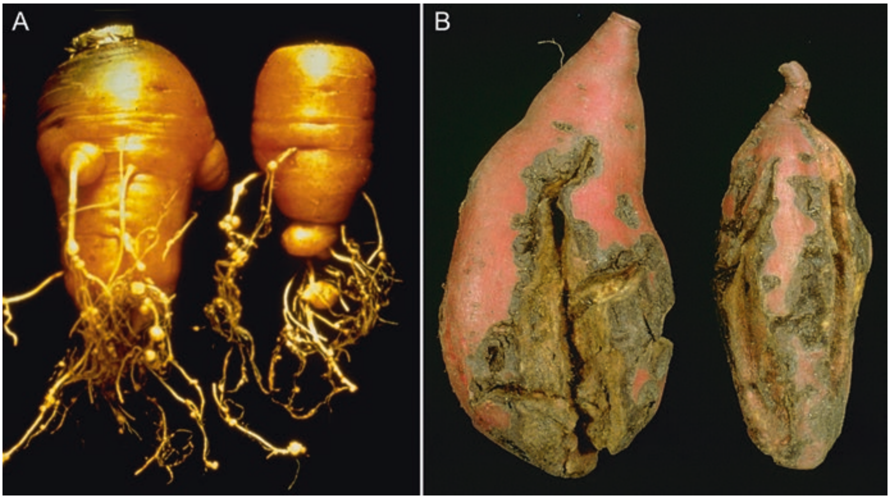

Fig. 6.2 *Meloidogyne* spp. damage (**a**) Carrot; (**b**) Sweet potato. (Credit: J. Radewald and University of California, Riverside)

Characteristic aboveground symptoms of *Meloidogyne* infestation include stunting, loss of quantity and quality of yield, wilting during hot periods of the day, and increased susceptibility to foliage diseases and vascular wilts. In contrast, mild infections can actually stimulate an increase in growth and yield. Belowground, *Meloidogyne* infection causes both a decrease in the size of the root system and the development of root galls. Depending upon the nematode-host combination and the number of nematodes present, galls vary in size from minute to extremely large. Galls on trees and vines, are typically smaller than those on annual crops. In some cases, infections may cause an aesthetic problem rather than growth reduction. In carrots, for example, an early attack on the developing tap root can cause disfiguration through galling and splitting of the tap root, rendering the plant unmarketable (McKenry and Roberts 1985).

Heavily infected roots are often badly discolored and rotted due to the invasion of roots by fungi such as *Rhizoctonia*, *Fusarium* and *Pythium* which cause rotting and breakdown of galled tissue, and by bacteria. A severe root rot of tomato caused by *M. incognita* and *R. solani* was associated with nutrient mobilization into gall tissue and root exudations, but root decay did not develop when root exudates were continuously removed by leaching (Van Gundy et al. 1977).

Second-stage juveniles (J2) of this sedentary endoparasitic nematode that hatch from eggs and move within the film of water that lines soil pores, are the infective stage. Photoperiod influences the migration of *M. incognita* juveniles toward tomato root (Prot and Van Gundy 1981b). The stylet is used to penetrate root tips at the zone of elongation. After penetrating the plant root, J2 migrate towards the vascular cylinder where they establish a feeding site and initiate feeding using their stylets. Gall formation may be influenced by secretion of plant-growth regulators by the nematode (Viglierchio and Yu 1965). Once feeding is initiated, J2s become sedentary and undergo three additional moults to become pear or nearly spherical-shaped adults. The adult female lays 150–250 eggs in a gelatinous matrix on or below the surface of the root. From the eggs new infective J2s hatch and start a new cycle (Atamian et al. 2012). The number of males in a population are typically low, but larger numbers may be found toward the end of the growing season, when populations are dense and host plants are under stress (McClure and Viglierchio 1966).

Distinguishing between the species of *Meloidogyne* can be a difficult problem. The female cuticle is finely striated and assumes patterns in the perineal region which are characteristic of the species. Variations of the perineal patterns within a given species are wide, so identification is often difficult and must be based upon examination of many specimens. Cultural management techniques such as crop rotation and trap cropping, rely on knowing the species present in a field. The ability to analyze DNA has progressively led to more advanced and accurate methods of species identification (Hyman et al. 1990) including the ability to distinguish mixed populations of single juveniles (Williamson et al. 1997), and juveniles extracted directly from soil (Qiu et al. 2006). Host races occur within root knot nematode species. Four host races within *M. incognita* can be differentiated by a host differential test. M. *incognita* races 3 and 4 will reproduce on cotton, whereas races 1 and 2 will not (McKenry and Roberts 1966).

Meloidogyne species occur in a wide range of soil textures, but they appear to predominate in coarse textured sandy and sandy loam soils where plant damage is often accentuated in sandy patches or streaks within a field. However, clay particles may aid in the migration of root knot juveniles to plant roots by absorbing and holding root exudates or bacterial by-products which form a concentration gradient enabling nematodes to locate roots (Prot and Van Gundy 1981a). Soil oxygen concentrations below 3.5% reduced root growth, size of developing females, production of nematode eggs and root galls of *M. javanica* (Van Gundy and Stolzy 1961).

6.5.1.1 Management

Resistant cultivars of some *Meloidogyne* susceptible crops are available including tomato, cotton, cowpea, lima bean and sweet potato (Roberts 1993). Nemaguard rootstock is resistant to root knot nematodes and is widely used in California for perennial crops including almonds and peaches. Processing tomatoes are a major California crop (Table 6.1). Tomato cultivars are available with the *Mi* gene located on chromosome 6 that are resistant to *M. incognita, M. javanica* and *M. arenaria* but not to *M. hapla* (Ho et al. 1992). *Mi*-mediated resistance is characterized by a localized necrosis of host cells near the invading nematode that begins about 12 h after infestation occurs. Resistance mediated by *Mi* is lost above 30 °C (Williamson and Hussey 1996). The use of resistant varieties became increasingly popular following field trials demonstrating the effectiveness of the resistance (Roberts and May 1986). The selection of resistance breaking populations in fields cropped to resistant varieties for multiple years began to be seen in 1995 (Kaloshian et al. 1996).

Another resistance gene, *Mi-3*, identified in *Lycopersicon peruvianum* on the short arm of chromosome 12 confers resistance to nematodes that are virulent on tomato lines that carry *Mi-1*, and is effective at temperatures at which *Mi-1* is not effective (Ammati et al. 1986; Williamson 1998; Yaghoobi et al. 1995, 2005). A heat-stable resistance gene, *Mi-9* from *Lycopersicon peruvianum* has been found that is localized on the short arm of chromosome 6 (Ammiraju et al. 2003).

Following a field observation that nematode resistant tomatoes were also resistant to the potato aphid, *Macrosiphum euphorbiae*, it was determined these traits are tightly linked (Kaloshian et al. 1995; Martinez De Ilarduya and Kaloshian 2001). Subsequently, it was determined that on the short arm of tomato chromosome 6, a cluster of disease resistance genes have evolved harboring the *Mi-1* and *Cf* genes. The *Mi-1* gene confers resistance to root knot nematodes, aphids, and the sweet potato whitefly (*Bemisia tabaci*) (Nombela et al. 2003). Ol-4 and Ol-6 that confer resistance to tomato powdery mildew are also in this cluster (Seifi et al. 2011). Changes in expression of jasmonic acid (JA)- and salicylic acid (SA)- dependent defense genes in response to potato and green peach aphids suggest that aphid feeding involves both SA and JA/ethylene plant defense signaling pathways and that *Mi-1*-mediated resistance might involve a SA-dependent signaling pathway (Martinez De Ilarduya et al. 2003).

Genetic material is being developed to transfer root knot (*M. incognita, M. javanica, M. arenaria)* resistance from ‘Brasilia’ carrot germplasm into California fresh market carrots via two resistance genes found on chromosome 8 (Roberts 1993; Ali et al. 2014). In fields with medium or high levels of nematode infestation, root galling in NemX, an Acala-type upland cotton, resistant to *M. incognita* was reduced and lint yields were increased compared to those on a susceptible variety (Ogallo et al. 1997). The variety was also highly effective in protecting plants from race 1 of *Fusarium* wilt as a disease complex (Wang and Roberts 2006). In resistant cowpea, the induction of resistance is relatively late compared to that in tomato. Nematodes were able to develop normal feeding sites similar to those in susceptible roots up to 9–14 days post inoculation. Following this, giant cell deterioration was observed and the female nematodes showed arrested development, failed to reach maturity and did not initiate egg laying in resistant roots (Das et al. 2008).

Optimum temperatures for *Meloidogyne* vary among different species and even among the different life stages (Ploeg and Maris 1999). The *M. incognita* life cycle is completed in 4–6 weeks at 26–28 °C (Atamian et al. 2012). Nematode reproduction was directly proportional to temperature between 14 and 30 °C for *M. incognita* and between 18 and 26 °C for *M. javanica* (Roberts and Van Gundy 1981). The migration of *M. incognita* juveniles begins at about 18 °C and reaches its maximum at 22 °C. Juveniles of *M. hapla* are able to migrate at a lower temperature than those of *M. incognita* (Prot and Van Gundy 1981b). For *M. incognita*, delay of planting date for a host crop until soil temperature is below 18 °C can be used to minimize damage because the plants will not be infected, and therefore, nematode development and reproduction will not occur (Roberts et al. 1981a). If plantings are made at temperatures above this threshold, nematode development and reproduction may occur during winter. Planting at cool soil temperatures will mean that nematode activity is low and young root systems can establish before nematode activity increases as soil temperature rises during the spring. Certain crops may be planted during the winter months and harvested before injury occurs in the spring. The potato industry of the San Joaquin Valley has utilized this method. Plantings can be made during cool months and harvested before June without visible infestation. If allowed to remain a month or two longer, the entire crop would be unsalable. For crops due for harvest that are infested with nematodes, growers should schedule the infested crop for an early harvest to prevent additional nematode reproduction and buildup (McKenry and Roberts 1985).

Determination and use of economic thresholds is an important consideration in nematode pest management programs, but their development has been limited by reliability of nematode population assessment techniques (Ferris 1978). A computer-simulation model of a *Meloidogyne*-grapevine system (Ferris 1976) developed in conjunction with extensive field sampling, greenhouse and laboratory research has contributed to our knowledge of the biology and management of nematodes in vineyards (Ferris and McKenry 1974, 1975, 1976; Melakeberhan et al. 1989). The economic importance of grapes statewide (Table 6.1), and their status as hosts to multiple genera of plant parasitic nematodes has led to extensive host range testing and breeding to develop rootstocks resistant not only to multiple genera of nematodes, but to virus and insect pests as well (Chitambar and Raski 1984; Anwar and McKenry 2002; McKenry et al. 2004). After a 15-year screening process, 13 selections emerged with either almost complete or complete combined resistance to *M. incognita* Race 3, *M. incognita* pathotype Harmony C, *M. arenaria* pathotype Harmony A, and *X. index*. After a total of 204 separate trials, the rootstocks were released to the grape industry as UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD GRN5 (Ferris et al. 2012, 2013).

A number of studies in California have increased our knowledge of the potential for using biological control to manage *Meloidogyne* spp. Second stage juveniles of *Meloidogyne* spp. were readily infected with the endoparasite *Pasteuria penetrans* (Mankau and Prasad 1977). Hyphae of *Dactylella oviparasitica* proliferated rapidly through *MeIoidogyne* egg masses, and appressoria formed when they contacted eggs (Stirling and Mankau 1979). The nematophagous fungi, *Paecilomyces lilacinus* and *Verticillium chlamydosporium*, were found in a high proportion of Northern California tomato fields but were determined to not be effectively suppressing populations of *M. incognita* (Gaspard et al. 1990). The nematophagous fungus *Hirsutella rhossiliensis* infested *M. javanica* but did not provide effective control (Tedford et al. 1993). Three species of the nematode-trapping fungi *Arthrobotrys* and two of *Nematoctonus* were detected in both organic and conventional field plots but did not suppress *M. javanica* in a laboratory bioassay (Jaffee et al. 1998). Three *Pochonia chlamydosporia* var. c*hlamydosporia* strains isolated from a *M. incognita*-suppressive soil showed potential as biological control agents against root knot nematodes in greenhouse trials (Bent et al. 2008; Yang et al. 2012). Chitinolytic microflora may contribute to biological control of *Meloidogyne* by causing decreased egg viability through degradation of egg shells as shown by laboratory trials with *Lysobacter enzymogenes* strain C3 (Chen et al. 2006) and field trials with a chitin-urea soil amendment (Westerdahl et al. 1992). Various formulations of four entomopathogenic nematode (EPN) species and the supernatants of their mutualistic bacteria were found to suppress *M. incognita* and *M. arenaria* in tomato roots (Kepenekci et al. 2016).

Crop rotation and related techniques are seeing increasing use. Greenhouse and field trials found cultivars of alfalfa, amaranth, oilseed radish, oilseed rape, and safflower that were suitable rotation crops for *M. chitwoodi* (Ferris et al. 1993). *Crotalaria juncea* and *Sesamum indicum* have potential as cover crops to reduce *M. javanica* numbers (Araya and Caswell-Chen 1994). All cultivars of oilseed radish, white mustard, buckwheat, and phacelia tested were hosts to *M. incognita* and *M. javanica* (Gardner and Caswell-Chen 1994). Grafting susceptible melons on *Cucumus metuliferus* rootstocks reduced levels of root galling, prevented shoot weight losses, and resulted in significantly lower levels of *M. incognita* at harvest (Sigüenza et al. 2005). Aguiar et al. (2014) found resistant bell pepper cultivars to be effective in reducing damage by *M. incognita.* Weed hosts of *Meloidogyne* such as the solanaceous nightshade plants, need to be controlled if rotation crops are to be used successfully (McKenry and Roberts 1985).

Field corn and wheat are hosts for root knot nematodes but are tolerant to damage and can yield well under moderate-to-heavy infection. They will maintain or even build up root knot nematode populations in the soil, but they have been grown on infested land without significant yield reduction (McKenry and Roberts 1985). The wheat cultivar Lassik with the *Rkn3* gene is resistant to several isolates of *M. incognita* and *M. javanica* including those that can reproduce on tomato with the resistance gene *Mi-1* (Williamson et al. 2013). Wheat varieties resistant to *M. chitwoodi* have also been found (Kaloshian et al. 1989). Mixed populations of two or more species of *Meloidogyne* are possible in a field, as are the presence of other nematode genera complicating the use of crop rotation and resistant varieties. For example, five plant-parasitic species were found in an alfalfa field: *M. arenaria, Pratylenchus minyus, Merlinius brevidens, Helicotylenchus digonicus,* and *Nanidorus minor* (Goodell and Ferris 1980). Root systems of perennial crops are commonly fed upon simultaneously by multiple nematode species (McKenry and Anwar 2007).

Biofumigation is a technique investigated for management of weeds and fungi as well as nematodes. Brassica species such as broccoli produce glucosinolates, and when these degrade in the soil they release isothiocyanates that are similar to the active ingredient in metam sodium which is one of the more widely used nematicides (Westerdahl 2011; Zasada and Ferris 2003; Edwards and Ploeg 2014; López-Pérez et al. 2010). Marigolds have also been found to reduce damage by *Meloidogyne* on subsequent crops (Ploeg 1999; Huang and Ploeg 1999). Trap cropping can be utilized for sedentary endoparasitic nematodes such as root knot (Westerdahl 2011). A susceptible host is planted and larvae of a sedentary parasitic nematode are induced to enter and establish a feeding site within the roots. Once this has occurred, and the female nematode begins to mature, it is unable to leave the plant root. The plants are then destroyed before the life cycle of the nematode can be completed, trapping nematodes within the root. Soil solarization has shown mixed results, but in some field experiments *M. incognita* J2 were significantly reduced and yield of carrot and survival of cotton seedlings was increased (Stapleton et al. 1987). Goodell et al. (1983) showed that *M. incognita* populations were reduced by approximately 40% (within the tilled zone) for each plowing, following destruction of a cotton crop.

A number of chemicals have been shown to be effective against *Meloidogyne* spp. including aldicarb (Hough and Thomason 1975), phenamiphos (Greco and Thomason 1980), avermectins (Garabedian and Van Gundy 1983), ozone gas (Qiu et al. 2009), DMDS (Cabrera et al. 2014), and fluensulfone (Westerdahl et al. 2014). Sublethal effects of aldicarb stimulated hatch of *M. javanica* (Hough and Thomason 1975).

6.5.2 Citrus Nematode, Tylenchulus semipenetrans

Tylenchulus semipenetrans is commonly referred to as the "citrus nematode" because of its historical association with citrus. Yield losses to citrus due to *T. semipenetrans* are in the range of 10–30% depending on the level of infestation

(Verdejo-Lucas and McKenry 2004). *Tylenchulus semipenetrans* was discovered on citrus roots in Los Angeles County in 1912, and subsequently described by Cobb (1913, 1914). Within a few months of its discovery, it was found to also be present in other citrus growing areas around the world, probably due to distribution on infested nursery stock (Cobb 1914). E. E. Thomas of the Riverside Citrus Experiment Station (predecessor to the Riverside campus of the University of California) conducted the early research on pathogenicity and management of this nematode (Cobb 1914). In 1939, J. C Johnston and G. Thorne examined more than 100 samples from citrus orchards in various parts of the state and found all but one to be infested with *T. semipenetrans* (Thorne 1961).

Van Gundy (1958) conducted a detailed study on the life history and morphology of citrus nematode. Juveniles penetrate the root 2–3 weeks after hatching. A juvenile burrows its anterior end deep inside the root cortex while the posterior end remains outside in the soil. Young females become embedded in the cortex with their anterior regions retaining the ability to move about in a cavity formed from a single plant cell. Feeding occurs on six to ten so-called "nurse cells," which are cortical parenchyma cells about the nematode anterior regions. Eggs are laid in a gelatinous matrix deposited by the female nematode on the root surface. The life cycle from egg to egg takes 6–8 weeks. Reproduction occurs over a wide range of temperatures, soil types, and pH values (Kirkpatrick et al. 1965b). Maximum population growth occurs between 28 and 31 °C, although some reproduction occurs as low as 21 °C, but not above 31 °C. Van Gundy and Martin (1961) found a correlation between nematode injury and plant nutrition. The greatest retardation in growth of citrus was caused by *T. semipenetrans* in soils that were deficient or nearly deficient in calcium, sodium, and potassium. The leaf content of calcium and zinc was less in plants grown in these soils. Higher population densities of *T. semipenetrans* were found in alkaline than in acid soils. Soil moisture affects reproduction with a dry soil being more favorable than a wet one, probably due to an oxygen deficiency when soil moisture is high (Van Gundy and Tsao 1963; Van Gundy et al. 1964).

R. C. Baines conducted extensive host range studies (Baines 1950; Baines et al. 1948). In addition to citrus, *T. semipenetrans* parasitizes grape, lilac, olive, and persimmon. It is common in table grape vineyards in the Coachella Valley (Riverside County). It has also been found in peach and almond orchards on "Lovell" rootstock in the San Joaquin Valley (Duncan et al. 1992), and on ponderosa pine (Viglierchio 1979). Baines et al. (1974) found four citrus nematode biotypes in California that could be differentiated by means of a host range test utilizing four citrus rootstocks.

Baines identified *Poncirus trifoliata* rootstock as having resistance to *T. semipenetrans*. In resistant plants, juveniles penetrate epidermal and hypodermal cells. These cells and the first row of cortical parenchyma cells then collapse and often become necrotic. A wound periderm forms in the parenchyma, effectively isolating the area of penetration. Penetration does not progress, and nematodes neither mature nor reproduce. In addition to this mechanical resistance, there appears to be a toxic chemical associated with nonhost plants (Verdejo-Lucas and McKenry 2004).

6.5.2.1 Management

Of 15 grape rootstocks tested, McKenry and Anwar (2006) found Ramsey and SO4 to be resistant to *T. semipenetrans*, Thompson seedless to be highly susceptible, and the others to be susceptible. Ferris et al. (2012) reported that of 13 grape rootstocks tested, 8 were susceptible, three were resistant, 1 was moderately resistant, and 1 was moderately susceptible. Two newly released grape rootstocks GRN-1 and GRN-3 were resistant, and a third GRN-2 was susceptible.

Mature citrus trees can tolerate a considerable number of citrus nematode before showing lack of vigor and decline symptoms. Susceptible trees planted in lightly infested soil may grow for many years without apparent damage and then suffer a "slow decline". Typical above ground signs consist of reduced vigor, the death of terminal buds, chlorosis and dying of leaves, early wilting under moisture stress, and twig dieback. Fruit is reduced in size, quantity and quality. Damage is greater when trees are predisposed by other factors such as *Phytophthora* root rot and water stress. Infested root systems are smaller than noninfested ones and have a dirty appearance because of the adhesion of soil particles to the gelatinous matrix deposited by the female nematode on the root surface during laying of eggs.

Baines researched and recommended use of soil fumigants for pre-plant management (Baines et al. 1957). Post-plant nematicide treatments are warranted if more than 400 nematode females/g root are found in samples collected in February to April or 700 females/g root in May and June. The same is true for populations of juveniles greater than 5000 per 500 g of soil in February to April, or greater than 8000 in May to July (Becker and Westerdahl 2009). Little effect of treatment on yield and fruit quality may be obtained the 1st year after a post-plant application, but with continued treatment, efficacy can often be demonstrated in the 2nd year (Verdejo-Lucas and McKenry 2004). Duncan et al. (1992) found that placement of a 3-m-wide, black, polyethylene film mulch down rows of peach (*Prunus persica* 'Red Haven' on 'Lovell' rootstock) and almond (*Prunus dulcis* 'Nonpareil' on 'Lovell') trees in the San Joaquin Valley for water conservation, also resulted in reductions of levels of citrus nematode. It is common to be able to recover several thousand citrus nematode juveniles from just 50 g of soil. This has led to use of citrus nematode infested soil as a model system for bioassaying the efficacy of potential new nematicides as alternatives to methyl bromide (Wang et al. 2004; Westerdahl et al. 1992). Such studies have shown toxicity of nematicides to citrus nematode to be similar to that for root knot nematode (Roberts and Thomason 1988; Zasada and Ferris 2003).

6.5.3 *Stem and Bulb Nematode,* **Ditylenchus dipsaci**

One of the earliest nematode problems recognized in California was the impact of the stem and bulb nematode on garlic and narcissus production. In 1925, D. G. Milbrath of the California Department of Agriculture, reported 5% losses of garlic due to *Ditylenchus dipsaci* (Siddiqui et al. 1973). Soon afterward, the use of hot water treatments, first developed by the Europeans, proved most successful in controlling *D. dipsaci*-infested narcissus bulbs in the northern coastal counties (Allen and Maggenti 1959; Siddiqui et al. 1973). Presently, *D. dipsaci* is a major nematode pest mainly of garlic, onion and alfalfa in California and, if not managed, can impact all regions of production. California is the largest producing state in the U.S. for garlic and onion with major production regions for garlic located within the Western San Joaquin Valley and minor production regions within few southeast desert counties, northern and central coastal counties (CGORAB 2007). Onions are grown throughout the state and alfalfa is mostly produced in Southern California and the San Joaquin Valley (Table 6.1; CDFAa 2016–2017; Geisseler and Horwath 2016). By 1959, host-specific biological races of *D. dipsaci* on alfalfa, narcissus, onion and garlic were found to be generally distributed whereas, other races were not (Allen and Maggenti 1959). Subsequently, in 1960, at the request of seed garlic growers, the California Seed Certification Program was established by the California Department of Agriculture and continues to date. In this Program, garlic plants are approved as propagative stock when tested by laboratory examination and found free from the stem and bulb nematode and the white rot fungal pathogen, *Sclerotium cepivorum*, and when found to meet certain minimum requirements. The program has proven successful, and from 1983 to 2017 a total of 16,637 garlic seed samples examined by the CDFA, have resulted in issuance of certified commercial planting stock free of the stem and bulb nematode. Brendler et al. (1971), reported a serious problem of tulip root disease incited by *D. dipsaci* in oat varieties cultivated in the coastal areas of Southern California.

Ditylenchus dipsaci, the stem and bulb nematode, is an obligate migratory endoparasite of more than 500 host plants (Fig. 6.3). *Ditylenchus dipsaci* has been documented in early reports as a complex containing several species (Sturhan and Brzeski 1991). However, *D. dipsaci sensu stricto* can now be distinguished from other related species by host plant range, chromosome number, morphometric values and gene sequences (Subbotin et al. 2005). The nematode feeds mainly on aerial parts of plants, within parenchymatous tissue of stems, bulbs, leaves, inflorescences and buds, but is also found within bulbs, tubers, rhizomes, stolons and rarely in roots (Sturhan and Brzeski 1991). A single female can lay 200–500 eggs within garlic and onion tissue and with a life cycle of about 21 days at 15 °C, several generations can occur in one crop season causing substantial damage. All postembryonic stages of *D. dipsaci* can infect plants, but fourth stage larvae are the most important infective stage as they have the unique capability of withstanding desiccation by undergoing anabiosis and surviving for long periods within stems, leaves, bulbs and seeds. Plants are invaded through stomates or tissue are directly penetrated at the base of stems and leaf axils (Becker and Westerdahl 2018). The nematodes may invade seedlings below the soil surface causing their retarded emergence and malformation or migrate upwards to apices of shoots.

As a result of nematode feeding, general symptoms develop that include swelling, distortion, discoloration and stunting of aerial plant parts and necrosis and rotting of bulbs and tubers (Anon 2008). Germinating onion and garlic cloves are

Fig. 6.3 Stem and bulb nematode, *Ditylenchus dipsaci.* (**a**) Alfalfa normal stem on left and ones with shortened internodes infected with *D. dipsaci* on right; (**b**) Daffodil bulb infected with nematodes; (**c**, **d**) Raised spikkels on leaves of daffodil. (Credit: W. Hart and J. Radewald; University of California, Davis and Riverside)

penetrated by *D. dipsaci* and surviving plants are stunted with distorted and bloated tissue appearing spongy; leaves are thickened and shortened, often with yellowish or brown lesions; softening of bulb tissue initiates at the stem and neck and proceeds downward into the scales which become soft, loose and pale gray or brown in concentric circles when observed in transverse section, and bulbs split at the base under dry conditions, or become malformed. Under moist conditions, bulbs rot due to the presence of secondary invading fungi, bacteria and onion maggots (Becker and Westerdahl 2018; Sturhan and Brzeski 1991). Infected alfalfa plants are stunted with few shoots and deformed buds. Infected stems are enlarged and discolored and, when nematode population numbers are high, lower stems may turn black, especially under moderate temperatures and high humidity. 'White flags' are formed when the nematodes move into leaf tissue and destroy chloroplast (Westerdahl et al. 2017a, b). Damage to alfalfa is most severe in moist, cool weather in cooler, sprinkler-irrigated inland valley and foggy coastal areas of California. Damage is usually seen in the first and second cuttings of alfalfa under cool and optimum conditions (15–20 °C) for nematode development, and less often later in the season under hot and dry conditions when nematode activity diminishes. The species may be found as far south in the Central Valley as Madera County (Westerdahl 2007).

6.5.3.1 Management

The development of control strategies for *D. dipsaci* in bulbous plants and alfalfa gained much attention particularly during the 1960s through 1990s with increased problems in garlic, narcissus and alfalfa crop production and loss of registration of pesticides. With the establishment of the California Seed Certification Program in 1960, authorized by the California Food and Agriculture Code, California growers continue to be provided with a strong preventive measure to guard against the stem and bulb nematode. This measure has resulted in far less problems in production fields (CGORAB-CSCC 2007). The use of clean nematode-free seeds is the primary preventative step against nematode infestation. The Program allows for seed garlic to be approved as propagative stock when tested by laboratory examination and found free from the stem and bulb nematode, *Ditylenchus dipsaci*, and certified when inspected and found free of the white rot fungus, *Sclerotium cepivorum*, in fulfilment of minimum requirements as specified by regulation. Grower participation is voluntary, but strongly encouraged. Essential elements of the Program include (1) use of clean "foundation" or "registered" or stock with an equivalent history for planting, (2) geographic areas for planting are protected by county ordinances and where contamination by the stem and bulb nematode and white rot fungus is not likely to occur, on which no *Allium* sp. has grown for 5 years prior to planting, no white rot has been detected and located at least 152 m from *Allium* sp. not entered in the program, (3) sanitation measures to protect seed garlic from contamination by the nematode and fungus, (4) sampling and laboratory testing for the stem and bulb nematode and (5) inspection by the CDFA and county personnel. In support of the above requirements it would be necessary to obtain information on the potential presence and identity of the nematode species and its population density in the target field as well as the cropping history of the field.

Hot water-formalin treatment of bulbs has been used historically in California against the stem and bulb nematode in narcissus bulbs. Lear and Johnson (1962) and Johnson and Lear (1965) refined the treatments to handle small volumes of garlic cloves. However, during the late 1980s, this technique decreased mainly due to uncertainty in registration of formalin, grower perception that hot water treatment resulted in deformed flowers, length of time required for dipping, safety concerns over handling of formalin-treated bulbs and disposing of large volume of formalin. This lead to evaluative studies of hot water treatment against *D. dipsaci* in daffodil bulbs and Qiu et al. (1993) determined that hot water treatment with 0.37% formaldehyde at 44 °C for 150 min controlled the nematode without detrimental effects on plant growth and flower production. Alternatively, nematode control was also obtained with hot water treatment at 44 °C for 240 min without chemicals. Roberts and Mathews (1995) reported the use of abamectin and sodium hypochlorite as effective alternatives to replace formalin. Abamectin at 10–20 ppm as a 20-min cool dip (18 °C) following a 20-min hot water dip and sodium hypochlorite at 1.052–1.313% aqueous solution as the 20-min hot dip were highly effective in controlling *D. dipsaci*, although neither treatment was effective as a hot water-formalin treatment and did not eradicate the nematode. Hot water treatment can reduce stem and bulb nematode in garlic cloves but is not completely eradicative (Becker and Westerdahl 2018).

The standard management of *D. dipsaci* in daffodils in California was hot water-formalin treatment of bulbs and preplant chemical treatment of soil. In addition, growers used preplant fumigation with 1,3-dichloropropene (1,3-D) and 1,2-dichloropropane (1,2-D) and/or at-planting application of aldicarb. However, after 1,2-D and aldicarb were found in groundwater and subsequently removed from the market, the latter was replaced with fenamiphos (Nemacur) which met the same fate in 1986. Since then, 1,3-D and phorate (Rampart) were used as preplant control treatments. Several non-fumigant nematicides applied directly onto garlic seed cloves in seed furrows in different types of soil gave differing results in suppressing *D. dipsaci* infection (Roberts and Greathead 1986). Westerdahl et al. (1991) found that foliar applications of oxamyl reduced nematode infestation in daffodil bulbs without phytotoxicity but not as well as hot water-formalin dipping. Currently, nematicides registered in California for use in garlic and onion are preplant fumigants, 1.3-Dichloropropene/chloropicrin (inline), 1,3-Dichloropropene (Telone EC), metam sodium (Vapam HL) and metam potassium (K-Pam HL). Oxamyl (Vydate L) is applied at or after planting (Becker and Westerdahl 2018).

There are no nematicides presently registered for use against the alfalfa stem nematode in California (Westerdahl et al. 2017a).

Planting resistant varieties is regarded the most effective control measure against *D. dipsaci* in alfalfa. Currently, greater than 50% resistance to *D. dipsaci* is available in several resistant varieties (Alfalfa Variety Ratings 2018).

Rotation with non-host crops provides some reduction of alfalfa stem nematode populations, which has a very limited host range. Rotating with non-host crops such as tomato, small grains, beans and corn for 2–4 years has resulted in reduced nematode numbers, whereas, growing no-hosts or poor hosts such as corn for 3–4 years can reduce stem and bulb nematode in garlic and onion (Westerdahl et al. 2017a; Becker and Westerdahl 2018).

6.5.4 Cyst Nematodes, Heterodera *spp.*

6.5.4.1 Sugar Beet Cyst Nematode, *Heterodera schachtii*

In California, *Heterodera schachtii* was first detected in 1907 in Alameda, Los Angeles and Salinas Counties (Caswell and Thomason 1985) (Fig. 6.4). In 1920, an intra-state survey revealed more than 1000 ha to be infected by this nematode (Thorne and Gidding 1922). Since then, *H. schachtii* has been detected in 23 countries (Siddiqui et al. 1973) and is widespread in all former and present California sugar beet growing areas, especially the Imperial Valley, central regions of the

Fig. 6.4 (**a**) Sugar beets – healthy and infected with *Heterodera schachtii*; (**b**) Sugar beet field infected by *H. schachtii.* (Credit: I. Thomason and J. K. Clark, University of California)

Central Valley, the Salinas Valley, and Monterey, Santa Barbara and Ventura Counties where sugar beet production is most concentrated (Caveness 1958; Cooke and Thomason 1978; Caswell and Thomason 1985). Sugar beet nematode has been recovered from all soil types. In the Imperial Valley 11% of the total cultivated acreage were infected. It is assumed that this cyst nematode was introduced to the Central Coast Valley during the time when sugar beet production was a primary crop in this area. Estimates of yield loss can reach 25 t/ha in untreated fields. Damage threshold levels vary with soil temperature, type and moisture and are characteristic for different sugar beet growing areas. The damage threshold in the Imperial Valley, California, is attained with 1–2 eggs/g soil (Cooke and Thomason 1979). In California, beside sugar beet, *Heterodera schachtii* was also found in Brussels sprouts, broccoli or cauliflower and cabbage (*Brassica oleracea*).

The life history and morphology of the sugar beet nematode was studied in detail by Raski (1949). In the laboratory, plant host tests conducted by Raski (1952c) with infested field soil collected near Salinas, California, resulted in detection of some cysts from roots of Golden Queen and Jubilee tomatoes, annual lupin, Golden Wax bush bean, Iron cowpea, garden pea, sweet pea (*Lathyrus odoratus*) and purple vetch. Steele (1965) also provided a list of plant hosts among weeds and agricultural plants belonging to seven families for California populations of *H. schachtii. Heterodera schachtii* females were also collected from the roots of *Amaranthus retroflexus*, *A. graecizans*, *Chenopodium murale* and *Solanum nigrum,* but only rarely (Raski 1952c). The penetration, development, and reproduction of a California population of the sugar beet cyst nematode were observed on phacelia (*Phacelia tanacetifolia*), buckwheat (*Fagopyrum esculentum*), oilseed radish (*Raphanus sativus*), and white mustard (*Sinapis alba*) (Gardner and Caswell-Chen 1993).

6.5.4.1.1 Management

Crop rotation and nematicidal application minimized yield losses (Cooke and Thomason 1978). However, high cost of treatment in relation to sugar prices often restricts nematicide use. To reduce crop damage caused by *H. schachtii*, representatives of the local sugar beet factory, growers, the County Agricultural Commissioner and nematologists from the University of California designed a cropping scheme based on a cyst nematode dump-sample survey (Roberts and Thomason 1981). A dump sample is a 500-cm^3 representative soil sample collected from sugar beets harvested from an approximately 2-ha area. Fields are considered infested if three or more cysts are found in a sample. Sugar beets cannot be planted in non-infested fields more than two consecutive years and not more than 4 out of 10 years. Sugar beets can be grown only once every 4 years in infested fields. The success of this program is due to the natural decline of *H. schachtii* in the absence of host plants. For example, in the Imperial Valley, annual population decline rates of more than 50% have been reported. In addition, egg densities in four different fields dropped below the detection level during the 4th year under continuous non-host alfalfa (Roberts et al. 1981b).

It has been shown that egg parasitism by *Fusarium oxysporum*, *Acremonium strictum, Hirsutella rhossiliensis, Dactylella oviparasitica* and other fungi (Nigh et al. 1980; Jaffee et al. 1991; Westphal and Becker 1999; Becker et al. 2013) play a major role in *H. schachtii* egg destruction and consequently contribute to the decline of the nematode population. Soil moisture in relation to type of cropping sequence apparently influenced egg hatch and activity of fungal parasites (Roberts et al. 1981a).

Westphal et al. (2011) studied soil suppressiveness against the sugar beet cyst nematode, *Heterodera schachtii*, using 11 soils from Southern California locations. The study illustrated that the comparison of population development of *H. schachtii* in non-treated and fumigated portions of field soils had the potential to detect suppressiveness in multiple soil texture classes. It has been shown that soil suppressiveness existed in various soil texture classes, suggesting the broad potential for directly exploiting the natural mechanisms that reduce population densities of nematodes for sustainable agricultural production.

6.5.4.2 Cabbage Cyst Nematode, *Heterodera cruciferae*

In the USA, *Heterodera cruciferae* is only known to occur in California (Raski 1952b; Raski and Sciaroni 1954). This nematode species is known from Yolo, San Mateo, Santa Cruz, Monterey and Santa Barbara Countries (Siddiqui et al. 1973) and recognized as economically important (Lear et al. 1965).

6.5.4.3 Clover Cyst Nematode, *Heterodera trifolii*

In California, *H. trifolii* was reported by Raski and Hart (1953) from white clover in the lawn of a private residence in Camarillo, California. The nematode also developed on carnation (*Dianthus caryophyllus),* Golden Wax bush bean (*Phaseolus vulgaris*) *and Sesbania macrocarpa*. Later, this nematode was collected from other places in California, but its pathogenicity was not reported.

6.5.4.4 Fig Cyst Nematode, *Heterodera fici*

In California, *Heterodera fici* was first detected in *Ficus elastica* showing poor growth in a nursery at San Bernardino and in field-grown commercial fig*, Ficus carica*, in Yolo County. Later, this nematode was also found in other counties. Infection of plants under greenhouse conditions has been successful only in the genus *Ficus*. Fig cyst nematode pathogenicity in commercial cultivars of fig has not been determined (Sher and Raski 1956).

6.5.5 Ring Nematode, Mesocriconema xenoplax

The ring nematode, *Mesocriconema xenoplax*, was first discovered and described by Raski (1952a) as *Criconemoides xenoplax* (= *Macroposthonia xenoplax*, *Criconemella xenoplax*) from specimens collected from a California vineyard. At that time, the species was also commonly encountered in walnut and prune orchards and vineyards (Raski 1952a; Siddiqui et al. 1973; Lownsbery et al. 1974). In 1968, the species was detected in 26 of 29 walnut orchards in San Joaquin County and by 1974, *M. xenoplax* was found in all four, main prune-cultivation regions of the state, namely Santa Clara, Napa-Sonoma, Sacramento and San Joaquin Valleys (Lownsbery et al. 1974). During a survey of 14 out of 17 almond-producing counties of California, McKenry and Kretsch (1987) found *Mesocriconema xenoplax* to be the most damaging nematode of almond production in the Northern San Joaquin region (San Joaquin, Stanislaus and Merced Counties), in sandy soils in the Southern San Joaquin region (Fresno, Kings, Tulare and Kern Counties), and occasionally in the Sacramento Valley and a coastal region of non-irrigated hillside near Paso Robles. The species is widely distributed in vineyards and several other perennial crops planted throughout the state (Ferris et al. 2012). Currently, *M. xenoplax* is becoming more prevalent and increasing in population levels in California. This increase is probably associated with the advent of drip irrigation plus soil additives that increase size of pore spaces (McKenry, UCR pers. comm.). During statewide detection surveys for the presence or absence of 22 economically important nematode species in major agricultural crops and nursery production areas within California, the CDFA reported higher frequencies of detection of *M. xenoplax* in rhizosphere soils of apricot, cherry, plum, prune, grape, peach, walnut and alfalfa, and relatively few detections in soils of cotton, long bean, oats, orange and tomato, from 16 counties (Dong et al. 2007).

Mesocriconema xenoplax is a sedentary ectoparasitic nematode that inhabits the rhizosphere soil of host plants and feeds on root tissue through an elongate stylet inserted into a root while the body remains outside. Feeding is completed in 1–2 weeks resulting in the death of fine roots. During the 1st year after transplanting, up to 85% of fine roots can be absent (Westerdahl and Duncan 2015). Seshadari (1964) determined that *M. xenoplax* reproduced best in very sandy soils than in loam or silty loam, and at the highest soil moisture level (sticky point = 15.5%). The nematode had a life cycle of 25–34 days at 22–26 °C (Seshadari 1964). High populations are attained on stone fruit and grape and the nematode is associated with orchards with a replant history (McKenry and Kretsch 1987; Ferris et al. 2004). In studies conducted during the mid-1970s, *M. xenoplax* was experimentally shown to adversely affect growth of stone fruit including peach, Myrobalan and Marianna 2624 plum (Braun et al. 1975; Lownsbery et al. 1977; Mojtahedi et al. 1975), almond (McKenry and Kretsch 1987), and walnut (Lownsbery et al. 1978). Damage caused by *M. xenoplax* alone in a walnut orchard was difficult to assess due to the combined presence of *Pratylenchus vulnus*, as both species were found to retard plant growth by causing lesions and longitudinal cracks in plant roots, however, Lownsbery et al. (1978) gave experimental evidence that initial non-coalesced lesions caused by *M. xenoplax* were smaller than those caused by *P. vulnus*. Ring nematode reduced number and volume of feeder roots, destroyed cortical root tissue, darkened roots, altered water stress, lowered nutrient levels in leaves, reduced fresh and dry weight, and caused stunted growth in Myrobalan and Marianna 2624 plum, Nemaguard and Lovell peach and French prune (Braun et al. 1975; English et al. 1982; Lownsbery et al. 1977; Mojtahedi and Lownsbery 1975; Mojtahedi et al. 1975). Ring nematode also damages young grape vines and while it may be difficult to assess damage and crop loss in older grape vines, both symptoms are highly probable given the high ring nematode population levels often encountered in California vineyards (Ferris et al. 2012). McKenry (1992) reported reduction of 10–25% in grapevine yield with more than 500 *M. xenoplax* kg^{-1} soil (0.5 nematodes/g^{-1} soil). However, the greater economic damage caused by *M. xenoplax* is its ability to predispose *Prunus* spp. and *Malus* spp. to bacterial canker caused by *Pseudomonas syringae* pv. *syringae*, contributing to peach decline and mortality in the San Joaquin Valley of California (Lownsbery et al, 1973; English et al. 1980) and *Cytospora* canker of prune caused by *Cytospora leucostoma* (English et al. 1982). Bacterial canker was severe when associated with *M. xenoplax* (Lownsbery et al. 1977) and higher densities of the nematode resulted in higher incidence of bacterial canker (Underwood et al. 1994). *Mesocriconema xenoplax* was the most damaging nematode of almonds because of the associated bacterial canker complex in the San Joaquin Valley where about half the orchards had both pathogens (McKenry and Kretsch 1987). In the Southeastern United States *M. xenoplax* is a major contributor to a similar association with *P. syringae* pv. *syringae* and cold injury resulting in Peach tree short life disease complex (Nyczepir et al. 1983).

While earlier reported studies on *M. xenoplax* in California largely involved container experiments, through the years experimental evidence obtained under field conditions have furthered our knowledge on ring nematode, host and environment interactions over time with relevance to appropriate management choices. Seasonal effects on ring nematode population under field conditions have been reported. In a 3-year study on population fluctuations of ring nematode in five prune orchards in California, Westerdahl et al. (2013) found highest number of ring nematodes at depths of 0–30 cm in the summer months and 30–60 cm in the fall and winter, with nematode numbers being lowest before irrigation and sharply increased after irrigation. The type of sampling tool had no effect on nematode recovery. An optimum sampling strategy to detect the presence of ring nematodes in a prune orchard would therefore, incorporate those determined results. On the other hand, Ferris et al. (2012) found all life stages of *M. xenoplax* to be present through the year but with lower ratios of juveniles to adults and lower proportions of nematode populations in the upper 30 cm than at 30–90 cm depths in the summer months in California *Prunus* orchards where trees were irrigated by flooding of large basins when the soil became dry thereby, resulting in root zone soil being subject to extreme wet and dry cycles, particularly in the upper 30 cm. They determined that two samplings, one in spring and the other in fall, are needed to determine the annual trajectory of ring nematode dosage in *Prunus* orchards.

The initial management measure to prevent spread of *Mesocriconema xenoplax* to non-infested fields includes the use of certified planting stock, removal of soil from equipment prior to moving between orchards and avoidance of recycling irrigation water (McKenry and Westerdahl 2009).

6.5.5.1 Management

In 1960, the development of the 'Approved Treatment and Handling Procedures for the Control of Nematodes in Deciduous Fruit and Nut Tree, Grapevine, Berry and Vegetable Plant Growing Ground Inspection Program' based on acre-by-acre composite sampling and laboratory examination for nematodes, soon resulted in significant improvement in nematode cleanliness of California-grown nursery stock. Sampling was waived if the land had been pre-fumigated at high rates. This program is continued to date under the CDFA's Nursery Stock Nematode Control Program (NIPM #7) that specifies soil treatment and handling procedures to ensure field and container grown nematode-free nursery stock for farm planting (Raski et al. 2002).

Most *Prunus* rootstocks support populations of *M. xenoplax* but differ in response to other plant parasitic nematodes. Nemaguard rootstock is planted to 90% of the peach industry in California. In earlier studies, Lownsbery et al. (1977) found scions on Nemaguard and Lovell rootstocks to be highly susceptible to bacterial canker and *M. xenoplax* in container experiments and indicated the need for comparison of the rootstocks under field conditions. Although Nemaguard rootstock is resistant to root knot nematodes, it is damaged by *M. xenoplax* and is a better host to the ring nematode than Lovell rootstock, which is more tolerant to bacterial canker and resistant to root knot nematode. Furthermore, Nemaguard is among the most difficult to successfully replant because of the 'rejection component' of the replant problem. Marianna 2624 and Myrobalan 29C rootstocks also commonly used in California, although resistant to root knot nematodes, are highly susceptible to *M. xenoplax*. Viking rootstock is reported to offer some tolerance to ring nematode similar to Lovell rootstock with comparable protection against bacterial canker (McKenry and Westerdahl 2009).

Over a 15-year period, Ferris et al. (2012) tested five new grape rootstocks with broad and durable nematode resistance at four general grape-growing regions of the state: north coast, Northern San Joaquin Valley, central coast region and the Central and Southern San Joaquin Valley. They reported UCD GRNI, UCD GRN5 and VR 039-16 to be resistant to ring nematode. UCD GRN1 has broad nematode resistance and these studies resulted in the patenting and release of the five rootstocks to the grape industry. Furthermore, populations of *M. xenoplax* from the five locations differed in virulence – as indicated by their reproduction on susceptible rootstock. Resistance to *M. xenoplax* was not compromised at high soil temperature, even at 30 °C where the nematode was still biologically active (Ferris et al. 2013).

Preplant and postplant nematicides have been important in the chemical control of ring nematodes and bacterial canker. The earliest choice of postplant nematicide was dibromochloropropane (DBCP). However, with its removal from the market as well as the removal of other nematicides, the choice got narrower. Ferris et al. (2012) reported that applications of phenamiphos in spring and summer were most effective for controlling ring nematode and reducing annual tree mortality due to bacterial canker in California *Prunus* orchards. Currently, preplant nematicides registered for use in California are methyl bromide (under Critical Use Exemption), metam sodium (Vapam^{R}) and 1, 3-Dichloropropene (Telone II^{R}).

Among postplant products, Ditera^{R} (a toxin produced by *Myrothecium verrucaria*), Nema-Q^{R} (an extract of Quillaja, the soapbark tree) (Westerdahl et al. 2013), Enzone^{R} (sodium tetrathiocarbonate) and Movento^{R} (Spirotetramat) are available for use against nematodes infesting fruit and nut crops (Bettiga et al. 2016; McKenry and Westerdahl 2009).

Preplant applications of different rates of lime ($CaCO_3$) in peach and almond orchards (0, 13.2, 18.2, 27.3 or 54.2 kg lime/peach tree and 0, 6.4, 12.8, or 25.0 kg lime/almond tree) altered soil pH but did not affect numbers of *C. xenoplax* in peach and almond, nor did it reduce incidence of bacterial canker in peach (Underwood et al. 1994).

The nematophagous fungus *Hirsutella rhossiliensis* naturally parasitizes *Mesocriconema xenoplax* in a density-dependent manner in many stone fruit orchards in California (Jaffee et al. 1989) and there have been several studies aimed at its exploitative use as a biocontrol agent against the ring nematode under field conditions in California. However, *H. rhossiliensis* was found to be a weak regulator of *M. xenoplax* population density (Jaffee et al. 1989) and did not regulate ring nematode populations in a newly planted *Prunus* orchard in California (Ferris et al. 2004). Efforts to enhance parasitism of nematodes by *H. rhossiliensis* through the addition of organic matter have been unsuccessful. In a related study, Jaffee et al. (1994) determined that parasitism of *M. xenoplax* by *H. rhossiliensis* was only slightly suppressed and numbers of nematodes were not affected by the addition of 73 mt of composted chicken manure/ha to a peach orchard in California.

6.5.6 *Root Lesion Nematodes,* Pratylenchus *spp.*

Pratylenchus spp. were first discovered in California in 1927, however their importance as plant pathogens was not realized until investigations held from 1930 to 1943 revealed damages caused by root lesion nematodes to walnut, fig and cherry trees. At that time, confusion over species identities, distribution and host range made it difficult for state and county regulatory agencies to restrict the spread of root lesion nematodes until the group was revised by Sher and Allen (1953). By 1959, *P. brachyurus, P. penetrans, P. vulnus, P. scribneri* and *P. hexincisus* were recognized as root lesion nematodes of economic importance in California, while *P. pratensis, P. thornei, P. minyus* and *P. coffeae* were also present in the state, but their importance was not known (Allen and Maggenti 1959). In the early 1960s, a nematode survey of pear orchards was conducted in response to the occurrence of pear decline in California. Of the several different *Pratylenchus* species found in pear orchards, only *P. vulnus* and *P. penetrans* were recovered from pear roots. *Pratylenchus zeae*, a species not generally distributed in California, was discovered in 10 or 20 pear orchards in Placer County (French et al. 1964). *Pratylenchus penetrans*, *P. vulnus, P. neglectus* and *P. thornei* are discussed in this section in further detail.

In general, *Pratylenchus* spp. are migratory endoparasitic nematodes that feed within root cortical tissue and are also found in the surrounding soil. Infected plants have roots with black lesions and fewer feeder roots than non-infected plants thereby resulting in stunted root growth. Top growth may exhibit general symptoms of an impaired root system including lack of vigor, dieback, chlorotic and small leaves and reduction of yield.

6.5.6.1 *Pratylenchus vulnus*

Pratylenchus vulnus was first reported in 1951 in California as a new species and important plant parasite of various trees and vines, namely walnut, grape, fig, citrus, apricot, avocado, weeping willow, cherry, olive, peach, almond, plum, raspberry and boysenberry (Allen and Jensen 1951). *Pratylenchus vulnus* is the most common root lesion nematode found associated with almonds in the Sacramento Valley (McKenry and Kretsch 1987) and is commonly distributed in California vineyards seriously affecting grape yield (Lider 1960; Raski et al. 1973). Root systems of young grapevines may be restricted in growth with absence of major roots and dead feeder roots while root lesions at feeding sites may not be present. *Pratylenchus vulnus* is also the root lesion species most commonly found in walnut orchards in California (Westerdahl et al. 2017b). Walnut tree vigor and yields are reduced by the feeding activity of *P. vulnus* which places infected trees under stress (Lownsbery 1956). In California, as in many regions worldwide, this nematode is the primary cause of tree decline and replant problems in orchards (Nyczepir and Halbrendt 1993; McKenry 1999). Growth of young walnut trees can be arrested by *P. vulnus* and the replant problem, even at 1 nematode/250 cm^3, and established walnut orchards in California are able to support 500 *P. vulnus*/250 cm^3 soil (Buzo et al. 2009). *Pratylenchus vulnus* reduced plum yields by 16%, 16%, 10% and 6.4% in Lovell, Nemaguard, Myrobalan 29C and Marianna 2624 plum rootstocks, respectively, with reduced levels of calcium and magnesium in scion petioles. Monthly and annual fluctuations of *P. vulnus* populations were observed in a plum orchard, with the most stable levels occurring during fall months and at higher population levels in the top 30 cm than lower 30–60 cm depths (McKenry 1989). During the 1970s, *Pratylenchus vulnus* was also found to affect rose production in California (Lear et al. 1970) and was involved in a disease of Manetti rose rootstocks with optimum nematode reproduction in silt loam soil at 20 °C (Santo and Lear 1976).

6.5.6.1.1 Management

Non-chemical control of *Pratylenchus vulnus* begins with preventive measures taken by planting nematode-free planting stock. In California, the CDFA's Nursery Stock Nematode Control Program (NIPM #7) specifies soil treatment and handling procedures to ensure field and container grown nematode-free nursery stock for farm planting.

The loss and restriction of nematicides has resulted in reliance on alternate options, in particular use of resistant plants, for control of soil-borne nematodes. Over the years, the host status of fruit and nut and grape rootstock varieties to *Pratylenchus vulnus* and other important plant parasitic nematodes have been assessed for resistance, susceptibility, tolerance and intolerance in California. Screening and monitoring plant response to plant parasitic nematode and plant vigor over several years was found necessary as nematode reproductive values can differ after the 1st year of growth (Westphal et al. 2016a). Currently, no resistance to *P. vulnus* has been found in *Juglans* spp. English and black walnut are very susceptible to root lesion nematode, but their hybrid Paradox is more tolerant than either parent, when nematode population numbers are not too high. Of the presently available clonal Paradox walnut rootstocks in California, clonal Paradox VX211 is nematode-tolerant and was released to California growers in 2007 (Buzo et al. 2005, 2009; Hasey et al. 2018; Westerdahl et al. 2017b). Buzo et al. (2005) determined *P. vulnus* population increases about three times the initial inoculum density in fleshy root tips than within primary roots of four walnut cultivars including the more aggressively-growing Paradox hybrid. Hybrid vigor is a primary quality of VX211 (Buzo et al. 2009).

Studies on host status of grape rootstocks included interactions of 18 and 16 grape cultivars and *Pratylenchus vulnus* in microplots trials that revealed root lesion nematode resistance in cultivars Ramsey and K51–32 after 10 and 24-month periods (McKenry et al. 2001; McKenry and Anwar 2006). McKenry and Anwar found that certain cultivars selected for nematode resistance such as Dogridge, Freedom, Ramsey and 3309C, often stimulated vine growth when fed upon by the nematode, and regarded this growth-stimulating response as a form of tolerance associated with resistance. Ferris et al. (2012) found moderate resistance to *P vulnus* in five new grape rootstocks, UCD GRN1, UCD GRN2, UCD GRN3 UCD GRN 4 and UCD GRN 5, after a 15-year screening process in the Northern, Central and Southern San Joaquin Valley, and central and north coast regions, which resulted in their eventual release to the grape industry. Furthermore, they provided a compilation of current knowledge of host status of 27 other rootstock cultivars to plant parasitic nematodes including USDA-ARS rootstocks, USDA 10-17A, USDA 10-23B and USDA 6-19B which were evaluated as resistant to *P. vulnus* (Ferris et al. 2012; Gu and Ramming 2005a, b).

Pistachio is an expanding nut crop in California and the selection of rootstocks is critical to mitigate potential risk for increase of *Pratylenchus vulnus* populations in orchards. Westphal et al. (2016b) determined that an aggressive population of *P. vulnus* was more aggressive on the popular 'UCB1' pistachio rootstock which in turn, was less susceptible to the nematode than various *Prunus* rootstocks.

Experimental efforts to control root lesion through genetic engineering involving gene silencing and crown gall and nematode resistance gene stacking technologies resulted in simultaneous control of crown gall and *Pratylenchus vulnus* (Walawage et al. 2013).

6.5.6.2 *Pratylenchus penetrans*

Pratylenchus penetrans is another economically important root lesion nematode species found throughout the state on various host plants including apple, cherry, peach, apricot, plum, pear, strawberry, alfalfa, garlic, ornamentals and several other crops (French et al. 1964; Siddiqui et al. 1973; McKenry and Roberts 1985; Dong et al. 2007; Westerdahl et al. 2017b). Of particular economic importance is the species' detrimental impact to commercial productions of Easter lily and Oriental lily in Humboldt and Del Norte counties in California which, along with Curry County, Oregon, is the only area in the United States where Easter lily bulbs are grown commercially (Westerdahl et al. 1993, 1998). *Pratylenchus penetrans* has been found in Easter lilies since 1946 (Butterfield 1947) causing restricted root growth and retarded top growth as well as of non-emergence of shoots from bulbs. *Pratylenchus penetrans* is frequently found in apple orchards in Northern California and is occasionally associated with apple replant disease (Westerdahl 2015), whereas, in alfalfa, it is present only in localized areas of the state (Westerdahl et al. 2017a).

6.5.6.2.1 Management

In California, early studies on the control of *Pratylenchus penetrans* have mainly been on Easter lily (Maggenti et al. 1967, 1970; Hart et al. 1967). Chemical control of *P. penetrans* in Easter lily fields has traditionally consisted of a preplant fumigation with a mixture of 1,3-dichloropropene (1,3-D) and 1,2-dichloropropane (1,2-D) followed by at-planting applications of an organo-phosphate or carbamate, since the nematode infests both planting stock and soil. However, the withdrawal of 1,2-dichloropropane, aldicarb and fenamiphos (Nemacur) in the early and mid-1980s, following their discovery in groundwater, left the use of 1,3-dichloropropene (1,3-D, Telone II) which was suspended in California from April 1990 until early 1996. Consequently, growers used metam sodium or methyl bromide plus an at-planting application of an organophosphate, phorate (Rampart^{R}) (Westerdahl et al. 1998). Following the phase-out of methyl bromide, currently, effective preplant soil fumigation with chloropicrin or Telone II and metam sodium (Vapam^{R}) are available for use in strawberry and apple. Effective application methods of nematicides have been studied (Westerdahl et al. 1993), but subsequently, concerns over groundwater pollution through use of nematicides in sandy soils of Del Norte County led to investigations of alternative management strategies.

Due its very wide host range, non-chemical control of *P. penetrans* through crop rotation and resistant varieties have not been feasible. In California, lily bulbs are usually rotated with pasture grasses. Westerdahl et al. (1998) determined that *P. penetrans* populations fluctuated under pasture grass and continuous fallow following Easter lilies but generally increased on pasture grasses and decreased under fallow, although not completely. In alfalfa, a field left fallow and weed-free can reduce lesion nematode numbers but not sufficiently to prevent damage to newly-planted alfalfa. Currently, there are no commercially certified alfalfa varieties with resistance to root lesion nematodes (Westerdahl et al. 2017a). For apple, some nematode tolerance to *P. penetrans* has been observed in standard and certain dwarfing rootstocks, however, the latter are known to be susceptible to *P. vulnus* (Westerdahl 2015).

Hot water and ozone treatments of Easter lily for control of *P. penetrans* gave varying results in a 3-year field trial study. Giraud et al. (2001) found that several treatments performed better than the untreated control but not as well as commercial chemical standard treatment. Hot water treatment at 39 °C for 35 min or 46 °C for 90 min reduced nematode numbers but did not improve bulb growth, however, this was the reverse case for ozone.

New natural products are being tested against *P. penetrans* with some promising results. Nema-Q®, a bionematicide, has been tested in vitro, greenhouse and field environments against several important plant parasitic nematodes including lesion nematode *P. penetrans,* and was found effective in controlling them at a concentration of 10,00 ppm. Lesion nematodes were reduced from 1200 to 350 per 205-g soil in Cabernet wine grapes (Marais et al. 2010). During a 2-year field trial study, Giraud et al. (2011) tested meadowfoam seed meal, mustard bran, *Quillaja*, DiTera®, the fungi *Paecilomyces lilacinus* and *Muscodor albus* for management of lesion nematode and improvement of plant health. *Muscodor albus* applied with

Thimet at planting, and meadowfoam seed meal had lower numbers of lesion nematodes than the controls. Similar studies were conducted with essential oil products Dougard, EF400, EF300 and Cinnamite tested as preplant dips of bulblet planting stock and *Paecilomyces lilacinus* as a soil treatment showed varying levels of lesion nematode reduction within roots over the controls (Westerdahl and Giraud 2017).

6.5.6.3 *Pratylenchus neglectus*

Pratylenchus neglectus, reported earlier as *P. minyus*, is the most widely distributed root lesion nematode species in California (Allen and Maggenti 1959; McKenry and Roberts 1985).

Although particularly associated with grasses and cereal crops, *P. neglectus* has a very wide host range and in California is frequently found in annual crops such as barley, oats and potatoes as well as perennial crops such as alfalfa and other forage crops (Siddiqui et al. 1973; McKenry and Roberts 1985; Dong et al. 2007). In recent surveys conducted by the CDFA, *P. neglectus* was found more frequently in grape than in other commercial field-grown fruit and nut trees in California (Dong et al. 2007).

During the early 1980s, the discovery of *Pratylenchus neglectus* and the Columbia root knot nematode, *Meloidogyne chitwoodi,* in potato and barley fields in the Klamath basin in Northeastern California, led to further studies on the effects of temperature and host plant interaction of the lesion nematode and barley, a crop that was then being used in rotation with potato and alfalfa (Ferris et al. 1993). Umesh and Ferris (1992) determined a low threshold temperature of 7.75 °C required for the development of a Klamath basin population of *P. neglectus* in petri-dish trials, whereas the optimum temperature for development of this population was about 25 °C, which differed from higher optimal temperatures for reproduction and development of *P. neglectus* reported from other regions and hosts in the country. Temperatures above 25 °C did not favour the Klamath basin population on barley and total nematode numbers were greatest at 25 °C but lower above and below that temperature. Maximum nematode activity occurred at 20 °C through 2-cm sand in lab studies and corresponded to the cool spring soil temperatures of the Klamath basin. In further experimental trails, Umesh and Ferris (1994) showed that *P. neglectus* and *M. chitwoodi* interacted competitively and this interaction was affected by soil temperature and the host plants, barley and potato. The restrictive effect of *M. chitwoodi* on *P. neglectus* was greatest at 25 °C on barley and potato, while the restrictive effect of *P. neglectus* on *M. chitwoodi* was greatest at 15 °C in barley and at 25 °C in potato. They inferred that *P. neglectus* has the potential to suppress *M. chitwoodi* populations and reduce the damage it causes to potato and barley, but further studies in this area are needed.

Pratylenchus neglectus was found to be a weak pathogen of barley in pot experiments (Umesh and Ferris 1992) and a weak or non-pathogen of wheat and barley in field trials, as its rates of increase were highest in the highest yielding cereal varieties but could become important if it were to increase in prevelance (Ferris et al. 1993). Similar observations were made of *P. neglectus* inoculated into six alfalfa cultivars resulting in either absent or at low population levels after 4 years (McKenry and Buzo 1985). Although *P. neglectus* increases susceptibility of potato plants to *Verticillium*, the nematode has not been shown to damage potatoes in California (Westerdahl and Kodira 2012).

In studies conducted over a 7-year period in fields used for potato cultivation and infested with *M. chitwoodi* and *P. neglectus* in the Klamath basin of Northeast California, Ferris et al. (1994) determined nematode population changes under different crop rotation sequences and the impact of those changes on potato yield and quality. Season multiplication rates and overwinter survival rates of both species were related to populations measured in the previous fall, and spring, and in fall respectively. A positive relationship occurred between potato tuber blemish and population levels of *P. neglectus* measured in the previous fall and yields were associated with higher population levels of *P. neglectus*. By their analyses, potato yield and quality can be expected based on population levels of *P. neglectus* (or *M. chitwoodi*) measured either in the previous fall or in the spring before planting, whereas winter survival rates of both nematodes are a function of nematode population measured in the fall and increase or decrease in nematode population can occur on various crops or fallow conditions. These predictions of crop damage and nematode population changes had direct implications on nematode management decisions.

6.5.6.4 *Pratylenchus thornei*

Pratylenchus thornei is found in all climatic conditions throughout California, particularly in clay and loam soils such as those in the Imperial Valley, Sacramento Valley and eastern slopes of the San Joaquin Valley (McKenry and Roberts 1985). This lesion nematode has a wide host range comprising annual field, vegetable crops, fruit and nut trees and ornamentals (Siddiqui et al. 1973). It is also associated with small grains causing probable damage particularly in warm areas such as the Imperial Valley (Westerdahl and Kodira 2007). However, their effect on associated crops has not been studied in California. While *P. thornei* has been found mainly associated with small grains: sorghum, wheat, barley, oats in the state (McKenry and Roberts 1985; Westerdahl and Kodira 2007; Dong et al. 2007) during recent surveys, the CDFA also found it associated with alfalfa, grape, apricot, cherry, cotton, prune and walnut (Dong et al. 2007). Grain crops infested with *P. thornei* are stunted and yellow in patches in a field, with brown leaf tips, fewer tillers and smaller heads (Westerdahl and Kodira 2007).

6.5.7 Dagger Nematodes, Xiphinema *spp.*

6.5.7.1 California Dagger Nematode, *Xiphinema index*

Xiphinema index was first described by Thorne and Allen (1950) from specimens extracted from soil around fig trees showing leaf drop and poor growth in Madera Country. In California, *X. index* is found in approximately 10% of California vineyards (Feil et al. 1997; McKenry et al. 2004). Hewitt et al. (1958) showed that *X. index* is the natural vector of the *Grapevine fanleaf virus* (GFLV) which is soil-borne. This study was also the first to prove that nematodes are able to vector soil-borne viruses and that spread is typically slow and in a concentric pattern (Hewitt et al. 1958). Just as with GFLV, *X. index* almost certainly was introduced into California, because no evidence exists that suggests it is native to the state. Several plants in California were also identified by Weiner and Raski (1966) as hosts: *Pistacia vera, P. mutica, Ampelopsis aconitifolia* and *Parthenocissus tricuspidata.*

In California, *Xiphinema index* significantly reduced root and shoot growth of the grape cultivar French Colombard. Bud break was delayed and buds were less vigorous than in the control (Anwar and Van Gundy 1989). Grapevine plants grown at 16.6 °C and inoculated with 500 *X. index* had, in the 1st year, 23% increased abscission of oldest leaves, and in the 2nd year, 65% and 38% reduction in top and root weights, respectively. Inoculated plants also had 60% fewer inflorescences and 89% reduced fruit size (Kirkpatrick et al. 1965a).

The length of the life cycle of *X. index* is reported as 27 days in California (Radewald and Raski 1962). *Xiphinema index* counts were always highest in the winter months. Temperature likely limits *X. index* reproduction in California because the summers are hotter and the growing season is longer than in most other grape-growing regions of the world. The findings of the study by Radewald and Raski (1962) showed that *X. index* populations fluctuate throughout the year and can be correlated with soil temperature. The possibility of detecting *X. index* in a vineyard can be maximized by sampling within rows during the winter months (Feil et al. 1997). Raski and Hewitt (1960) noted that under starving conditions, *X. index* retained the ability to transmit *Grapevine fanleaf nepovirus* for up to 9 months. The virus did not affect the rate of reproduction of *X. index* but did improve its survival rate during starvation (Das and Raski 1969).

6.5.7.1.1 Management

Soil fumigation with methyl bromide or 1,3-dichloropropene was successful over a 3-year period in controlling *X. index.* Such treatments can also give 99.9% reduction of all nematode species in the top 1.5–2 m of soil when properly applied (Raski et al. 1971). However, in 1990, the use of 1,3-dichloropropene was halted in California.

Nematode-resistant rootstocks are a promising alternative to the ban of nematicides. Since the 1970s, the University of California, Davis has been developing rootstocks to resist fanleaf degeneration. During the development of this breeding program two *V. vinifera* x *M. rotundifolia* (VR) hybrids, O39-16 and O43-43 were found to be highly resistant to *X. index* and prevent fanleaf degeneration. These root-stocks were derived from crosses of *V. vinifera x Muscadinia rotundifolia* Small (VR hybrids) and eventually patented and released (Walker et al. 1985, 1989, 1991; McKenry et al. 2004). After a 15-year sequence of intensive studies involving 204 separate trials, the five rootstocks (UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD GRN5) with broad and durable resistance to root knot and dagger nematodes were released to nurseries in California in 2009 and were available commercially in 2011 (Ferris et al. 2012). Based on nematode densities, Harmony and Freedom, commercially acceptable for their resistance to root knot nematode, were rated resistant to *X. index* (McKenry et al. 2004).

Crop rotation is also a possible management strategy in California dagger nematode control. Before vineyards are replanted with grapevines, the land can be cropped with cereals or grains to suppress nematodes. An early study by Raski (1955) suggested that 3 years is an adequate period for crop rotation. However, more recent studies suggested that *X. index* infested sites should be left fallow or rotated to crops other than grapes or figs for at least 10 years (McKenry 2000). In moist sterile soil without food, *X index* died after 9–10 months, but survived for 4–5 years in soil where grapevines were removed, but roots remained (Raski et al. 1965).

6.5.7.2 American Dagger Nematode, *Xiphinema americanum*

The *Xiphinema americanum*-group is a large species complex comprising 55 nominal taxa of dagger nematode. At present, five valid species of the *X. americanum*-group: *X. americanum s. str.*, *X. brevicolle*, *X. bricolense*, *X. californicum, X. pachtaicum* and *X. rivesi* have been reported in California (Robbins 1993; Orlando et al. 2016). At least two unidentified *Xiphinema* species were also reported using molecular methods (Orlando et al. 2016). Representatives of this group are very widely distributed in agricultural fields and orchards in California. For example, sampling from 126 orchards showed that *X. americanum* and *Paratylenchus hamatus* occurred in more than 90% of the orchards and in all pear-growing areas of the state (French et al. 1964). Although, there are no studies showing direct evidence of pathogenicity of *X. americanum* group species in California, it has been shown that they transmit viruses: *X. americanum sensu stricto – Cherry rasp leaf virus* (CRLV), *Tobacco ringspot virus* (TRSV), *Tomato ringspot virus* (ToRSV) (Teliz et al. 1966; Brown and Halbrendt 1992) and *X. californicum – Cherry Rasp leaf virus* (CRLV), *Tobacco ringspot virus* (TRSV), *Tomato ringspot virus* (ToRSV) (Hoy et al. 1984; Brown and Halbrendt 1992).

6.5.8 Pin Nematodes, **Paratylenchus** *spp.*

Paratylenchus hamatus and *P. neoamblycephalus* are the two most common species of pin nematode encountered in California. Because of their small size, all species of *Paratylenchus* have the common name of "pin nematode". Among other characteristics, these two species can be differentiated by lack of a stylet in the males of *P. neoamblycephalus*. *Paratylenchus hamatus* was first collected in 1944 from a fig orchard in Merced County, and identified by Thorne (Thorne and Allen 1950). In California, it has also been identified from Butte, El Dorado, Fresno, Kern, Marin, San Joaquin, San Mateo, Santa Barbara, Stanislaus, Sutter, Tehama and Tulare Counties by Raski (1975) from grape, peach, prune, oak, rose, plum, pear and walnut.

Paratylenchus neoamblycephalus was described by Geraert (1965). In California, Raski (1975) identified it from Alameda, Contra Costa, Kings, Monterey, San Francisco, San Joaquin, Solano and Yolo Counties associated with prune, apricot, plum on peach root, rose, walnut, fig, apple, pear, grape and peach.

Paratylenchus was found in 65 of 97 prune orchards sampled (Lownsbery et al. 1974). In this survey, *P. neoamblycephalus* was the most common species, and was found in all four of the important prune growing districts in the state. Braun et al. (1975) and Braun and Lownsbery (1975) demonstrated pathogenicity of *P. neoamblycephalus* to Myrobalan plum by several methods including comparison of plant growth in fumigated and nonfumigated soil and inoculating plants with suspensions of extracted nematodes. Roots of Myrobalan seedlings inoculated with surface-sterilized nematodes were smaller, darker and had fewer feeder roots than those of non-inoculated controls. Nematodes were observed feeding ectoparasitically, but with heads embedded in roots as deep as the cortex. They were associated with small lesions and dead lateral roots. Clusters of nematodes were common at ruptures in the epidermis and where lateral roots emerged.

Paratylenchus hamatus, on the other hand, is somewhat of a conundrum because it is not uncommon to find high numbers of nematodes occurring in perennial cropping systems without causing apparent harm. For example, Ferris and McKenry (1975) found that in a vineyard in which vine yield growth and vigor were negatively correlated with populations of *Xiphinema americanum*, there was a positive correlation of *P. hamatus* with the same factors. In contrast, trees in a fig orchard infested with *P. hamatus* had dieback of twigs, and chlorotic leaves that died and fell from the tree along with undersized fruit. Infested roots exhibited enlarged and spongy cells which caused a slight swelling of the entire root, and growth of the growing point was apparently blinded (Thorne 1961). Feeding of large numbers on grape roots produced shallow, localized lesions (Raski and Radewald 1958). Ferris and McKenry (1975) found densities of *P. hamatus* were greater in fine-textured soils.

Ferris et al. (2012) studied the susceptibility of five newly released UCD series grape rootstocks to *P. hamatus*. Four of the new rootstocks (GRN1, GRN2, GRN3, and GRN5) were moderately resistant and one (GRN4) was found to be moderately susceptible. In contrast, of 22 rootstocks tested in previous studies, 15 were susceptible, 4 were moderately susceptible, and 3 were moderately resistant to this nematode.

6.5.9 Needle Nematode, **Longidorus africanus**

During the fall of 1967, the nematode *Longidorus africanus* was found in soil around the roots of stunted lettuce seedlings in the Imperial Valley of Southern California (Fig. 6.5). Root tips of lettuce seedlings attacked by this nematode are

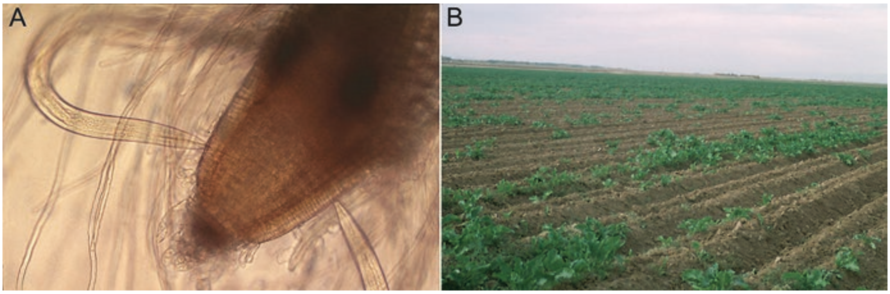

Fig. 6.5 (**a**) Needle nematode, *Longidorus africanus* feeding on root tip; (**b**) *Longidorus africanus* sugar beet field damage, Imperial Valley, California (A. Ploeg and University of California, Riverside)

swollen and usually have necrotic spots. Seedlings are severely stunted and because it feeds on root tips, plants are often severely stunted before the first true leaf develops (Radewald et al. 1969a). As infected plants mature, stunting continues, and they may never reach harvest-maturity. Root systems of older infected plants are greatly reduced in size. *Longidorus africanus* can cause a serious seedling disease at relatively low population levels in soil (Kolodge et al. 1986). This study showed that *L. africanus* can cause severe growth reductions in both carrot and lettuce, especially when nematode attack occurs within 10 days of seedling. Tolerance levels for carrot and lettuce exposed to *L. africanus* at seeding were less than 5 nematodes per 250 g soil (Huang and Ploeg 2001a).

The experimental work showed that this nematode has a wide host range including sorghum, barley, Bermuda grass, corn, wheat, cotton, okra, snap bean, lima bean, cucumber, cantaloupe, eggplant, and sugar beet. Most valley crops, with the exception of the crucifers, should be considered capable of supporting populations high enough to cause economic damage to fall-planted crops. In a state-wide survey for certain exotic and economically important plant parasitic nematodes in California, the CDFA detected *L. africanus* populations associated with commercial cotton and orange plants in the Imperial Valley (Dong et al. 2007).

The life cycle of *L. africanus* was completed in 7 weeks (Kolodge et al. 1986, 1987). *L. africanus* population densities increased with increasing depth. Chances for detecting this nematode were greatest in summer at depths of 60–90 cm (Ploeg 1998). Field studies in the Imperial Valley showed a strong correlation between the vertical distribution of *L. africanus* and soil temperature, with high populations occurring in the upper soil layers during the hot summer months (Ploeg 1998). Nematode multiplication is greatest at relatively high soil temperatures, ca. 28 °C. The results suggested that seeding of carrot or lettuce at soil temperatures less than 17 °C would significantly reduce damage by *L. africanus* (Huang and Ploeg 2001b). In the Imperial Valley, where *L. africanus* occurs, this would correspond to the period from November through March.

Longidorus africanus can be effectively controlled with nematicides (Radewald et al. 1969b), but because of increasing costs and restrictions on their use, alternative methods need to be developed.

6.5.10 *Rice White Tip Nematode,* Aphelenchoides besseyi

The first documentation of the possible presence of *Aphelenchoides besseyi* in California was in 1963 when the species was found in a culture of the fungus, *Sclerotium oryzae,* which had been isolated from a sample collected from a rice field in Butte County. The rice field was used by a research facility that exchanged seed with regions in Southeastern USA where *A. besseyi* was known to parasitize rice (Chitambar 1999). During 1997, in response to developing international trade agreements between Turkey and the USDA APHIS, the CDFA conducted intensive surveys of paddy rice seed in county driers of 13 rice-producing counties in California. *Aphelenchoides besseyi* was detected in few samples obtained from Butte and Sutter Counties. Subsequent detections were from paddy rice seed shipments intended for export in 1999, 2001, 2002, 2005 and 2008 in Sutter and Yolo Counties. This nematode species remains very limited in its distribution and infrequent occurrence within rice fields of Butte, Sutter and Yolo Counties and therefore, a 0% loss of rice yield due to *A. besseyi* was estimated for California in 1994 (Koenning et al. 1999). Based on international trade agreements, export shipments of paddy rice are handled on a per shipment basis and disqualify for phytosanitary certification if found contaminated with the white-tip of rice nematode (Chitambar 2008). The origin of the nematode species in California is not known. If it was introduced, then its low rate of detection and sporadic occurrence in cultivated field is an indication of its inability to fully establish to damaging levels within the state. Chitambar (2008) reasoned that certain biological, cultural and ecological factors, such as insufficient moisture, planting by airplane directly into flooded fields, presence of resistant varieties and high ambient temperatures, may be working against the nematode's ability to successfully establish and spread within California.

6.5.11 *Sting Nematode,* Belonolaimus longicaudatus

The sting nematode, *Belonolaimus longicaudatus* (Fig. 6.6) was discovered for the first time in 1992, associated with dying Bermuda turfgrass at a golf course near Rancho Mirage, Riverside County. Consequently, intensive delimiting surveys in the Coachella Valley were conducted by the CDFA and the Riverside County Department of Agriculture and by late 1993, the sting nematode was detected on Bermuda and rye turfgrass in eight golf courses (Chitambar 2008). The nematodes suppressed turfgrass root growth and caused stunting and chlorosis (Mundo-Ocampo et al. 1994). Based on its morphology, the nematode species was identified as *B. longicaudatus* and later confirmed by rDNA characterization (Cherry et al. 1997). Cherry et al. (1997) hypothesized that the California sting nematode was introduced from the Eastern United States. There had been earlier detections of the sting nematode in few interstate shipments of plant samples to California that were intercepted on entry and consequently, destroyed by state regulatory action. The current known distribution of the sting nematode is restricted to the original eight

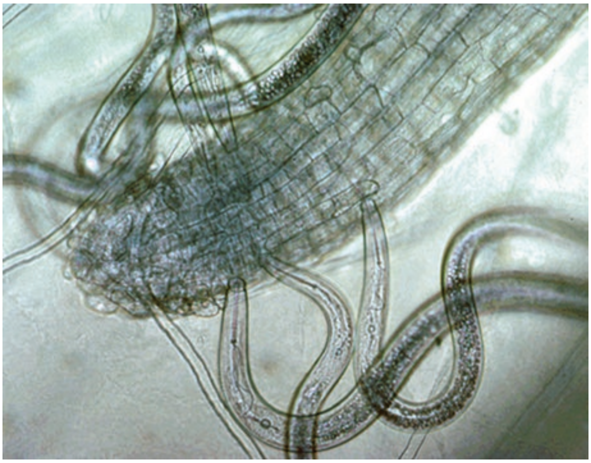

Fig. 6.6 Sting nematode, *Belonolaimus longicaudatus* feeding on root tip (O. Becker and University of California, Riverside)

golf courses in the Coachella Valley. This was confirmed by surveys of several major golf courses in California, conducted in 2012–2013 by the CDFA and sponsored by the USDA APHIS Cooperative Agricultural Pest Survey (CAPS) Program survey.

The Bermuda turfgrass in the Coachella Valley golf courses typically exhibited chlorosis at the beginning of April when the sting nematode populations began to increase. In a study on population dynamics of the sting nematode monitored at monthly intervals at three golf courses in Rancho Mirage, Coachella Valley, soil temperature and fluctuation of nematode densities were significantly correlated. At one golf course, population density peaked in October, with 1000 nematodes per 100 cm^3 of soil, but declined rapidly, with the lowest population density occurring in December with approximately 50 nematodes per 100 cm^3 of soil. Significant increases in nematode populations did not occur until temperature reached 20 °C or late spring. Nematode distribution was greatest in the top 15 cm of soil except during the hottest summer months, when the population was higher at depths of 15–30 cm (Bekal and Becker 2000b).

Belonolaimus longicaudatus is a major parasite of grasses and is also capable of parasitizing a wide range of crops including grapes, citrus, cantaloupes, lettuce tomatoes, cotton, ornamentals and weeds, however, its host range is not restricted to horticultural grasses or agricultural crops (Bekal and Becker 2000a). Many weeds, such as *Euphorbia glyptosperma*, *Sisymbrium irio*, *Paspalum dilatatum*, *Portulaca oleracea*, *Sorghum sudanense* and *Cyperus esculentus*, can serve as hosts for *B. longicaudatus* and only *Abelmoschus esculentus*, *Citrullus lanatus* and *Nicotiana tabacum* were non-hosts among the tested species. In the Coachella Valley, the sting nematode has not been found in grapes, citrus and other agricultural crops. *Belonolaimus longicaudatus* had a high reproductive fitness on a majority of species tested and is considered a major threat for most agricultural and horticultural crops grown in sandy soils (>80% sand) (Bekal and Becker 2000a).

Following its 1992–1993 detection, quarantine restrictions were imposed by State and County in order to contain or suppress the sting nematode within the Coachella Valley. Eradication was not deemed a practical alternative, due to high cost of operations, extensive sampling required and nature of dissemination of the nematode. Restrictions were placed on movement and disposal of mowed grass clippings from sting nematode-infested properties to non-infested properties or agricultural lands. Composting with sewer sludge was chosen as control of potentially infested grass clippings or thatch. Compliance agreements were established with golf course superintendents accordingly. Regulatory restrictions continue to keep *B. longicaudatus* under suppression in the Coachella Valley (Chitambar 2008).

6.5.12 *Stubby Root Nematodes,* **Trichodorus** *spp.,* **Paratrichodorus** *spp. and* **Nanidorus** *spp.*

Nematological surveys revealed that the stubby root nematodes are widely distributed in California. Presently, several valid species are reported: *Nanidorus minor, Paratrichodorus allius, P. grandis, P. porosus, Trichodorus aequalis, T. californicus, T. intermedius* and *T. dilatatus* (Allen 1957; Siddiqui et al. 1973; Rodriguez-M and Bell 1978). However, molecular analysis of trichodorid samples collected from non-agricultural areas revealed its high genetic diversity and indicated the presence of at least eight unidentified or putatively new species from the genus *Trichodorus* (Subbotin and Decraemer unpublished). *Nanidorus minor* and *P. porosus* are the mostly distributed species in agricultural fields and orchards. French et al. (1964) reported *N. minor* occurred in 12 pear orchards and *P. porosus* in 6 pear orchards in Placer County. Influence of the stubby-root nematode on growth of alfalfa was studied by Thomason and Sher (1957). Ayala and Allen (1968) tested four stubby root nematode species for their ability to transmit *Tobacco rattle virus* (TRV). *Paratrichodorus allius* was a good vector and was used in all experiments on nematode-virus interrelationships, whereas *N. minor* and *P. porosus* were moderately good vectors. The results showed that the populations of *P. allius* became infective after feeding on virus-infected tobacco for 1 h. Efficacy increased as the feeding time was increased up to 24 h. Populations remained infective for 20 weeks when kept at 20 °C without a host and 27 weeks when feeding on a virus immune host (Ayala and Allen 1968).

6.5.13 *Citrus Sheath Nematode,* **Hemicycliophora arenaria**

A brief account of the citrus sheath nematode, *Hemicycliophora arenaria*, is included here as this species has for long, only been reported from California, until more than 25 years later, when it was also reported from Australia and Southern

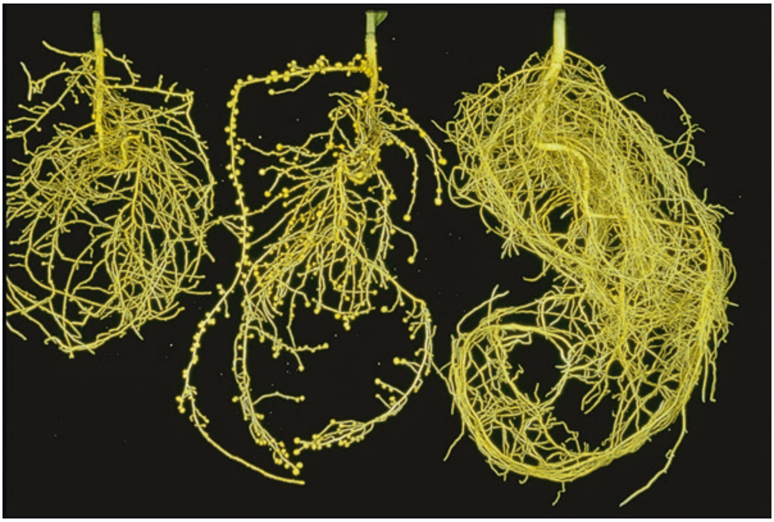

Fig. 6.7 Citrus root systems infected with *Hemicycliophora arenaria* (left and middle) and healthy root system (right). (Credit: F.D. McElroy and S.D. Van Gundy, University of California, Riverside)

Argentina (Reay 1984; Brugni and Chaves 1994; Chitambar and Subbotin 2014). The nematode was first reported by Van Gundy (1957) as an unknown species parasitizing rough lemon seedlings in a grower's nursery in the Coachella Valley, near Mecca, Southern California, causing 'peculiar galling' of infected roots quite unlike those caused by the root knot nematode (Fig. 6.7). A year later, the species was named and described by Raski (1958) as *H. arenaria.* By 1964, *H. arenaria* was found in a citrus ranch approximately 3.2 km from the original site in Riverside County and on citrus land in Imperial County. All properties were planted with citrus trees from a commercial nursery located near Niland in Imperial County, approximately 40 miles from the original site in Riverside County. This nursery had been planted on virgin desert soil and failed due to lack of moisture, and consequently, was abandoned in 1956. Surveys were conducted by the CDFA at that time to establish origin and extent of spread of the nematode species. In 1965, *H. arenaria* was found in a number of soil samples collected from cheese bush, a California native plant, growing in a virgin desert region about 1 mile north of the original abandoned nursery. At about the same time, the nematode species was also found on cheese bush in another native situation near Palm Springs, about 30 miles northwest from the infestation in Mecca. Additionally, another California native plant, coyote melon, was experimentally shown to be a host of the nematode species (McElroy and Van Gundy 1967). In 1971, *H. arenaria* was found in soil and root samples collected from roadside cheese bush plants near the entrance of a desert state park in San Diego County. These detections indicated that *H. arenaria* is indigenous to native plants in low and high elevation deserts within Imperial, Riverside and San Diego Counties of California and had been spread with citrus nursery stock from the abandoned nursery planting near Niland. Subsequent regulatory action taken by the

CDFA established the nematode as quarantine actionable and limited in distribution within California (Chitambar 2016). In 2006, CDFA once again detected this species in lemon and grapefruit soil in Imperial County (Chitambar 2008).

The preference of high temperature and sandy soils explains the very limited distribution of the citrus sheath nematode within desert regions of California, where it was discovered to be endemic on native desert plants (McElroy et al. 1966; McElroy and Van Gundy 1967). This ectoparasitic species reproduces at 30–32.5 °C, with 32.5 °C being the optimum, to complete a short life cycle of 15–18 days. Almost no reproduction occurs at 20 °C and is greatly reduced at 35 °C. Van Gundy and Rackham (1961) found reproduction to be greatest in sandy soil and gave experimental evidence of high reproduction in tomato plants. Subsequently, the citrus sheath nematode gained economic importance as a parasite of agricultural crops with the reclamation of Southern California deserts (Maggenti 1981). In California, citrus is the main host, while other agricultural crops have been experimentally shown to include tomato, blackeye bean, pepper, celery, squash and Tokay grape (Van Gundy 1959; Van Gundy and Rackham 1961; McElroy et al. 1966; McElroy and Van Gundy 1967, 1968; Van Gundy and McElroy 1969). Feeding of *H. arenaria* results in the production of galls at tips of lateral and terminal roots as well as a reduction in the number of feeder roots and top growth. Early studies established the damage potential of this species. The growth of rough lemon seedlings in *H. arenaria* infested soil at 30 °C for 5 months was reduced by 36% in comparison to seedlings in non-infested soil. Dry weight of tomato plants was reduced by 28%, and a 10–20% yield reduction in field-grown tomato and squash occurred at the original locality in Mecca, California. Growth of citrus and tomato was reduced from 12% at 25 °C to 37% at 30 °C (McElroy and Van Gundy 1967, 1968; Van Gundy and Rackham 1961).

6.5.14 Pacific Shoot-Gall Nematode, **Anguina pacificae**

Anguina pacificae was described by Cid del Prado Vera and Maggenti (1984) as a new species from the Northern Pacific Coast of California. This nematode causes stem galls at the base of tillers in annual bluegrass (*Poa annua*), resulting in yellow patches and irregular surfaces on North California golf course putting greens (Fig. 6.8). The disease has been found only along an approximately 20 to 30-mile-wide coastal corridor from Carmel to Mendocino (McClure et al. 2008). Over the years extensive research has been conducted to develop management strategies against *A. pacificae* (Westerdahl et al. 2005). Twenty-nine products were screened in a bioassay for efficacy against the nematode (McClure and Schmitt 2012). Of those, eight products showed some degree of control but only four were registered for use on golf course greens. McClure and Schmitt (2012) recommended biweekly application of products with the active ingredient azadirachtin that was derived from the Indian Neem tree (*Azadirachta indica*). Recently, Bayer CropScience developed fluopyram as a nematicide with excellent activity against several plant parasitic nematodes. Fluopyram significantly reduced the *A. pacificae* population and

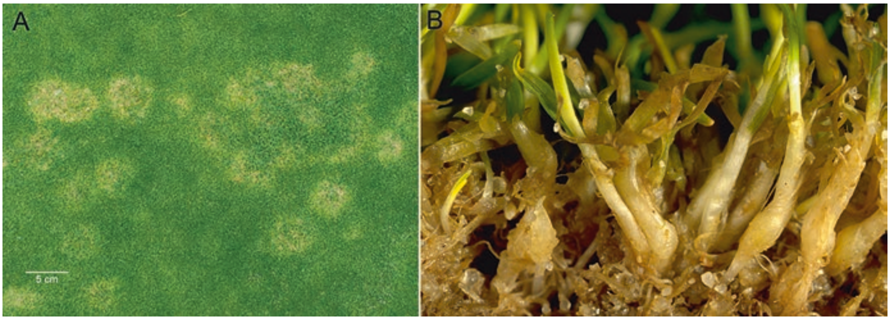

Fig. 6.8 *Anguina pacificae* on *Poa annua*. (**a**) Damaged putting green; (**b**) Galls on the crowns of infected plants. (Credit: M. McClure and L. Costello)

associated shoot galls compared to either Neemix[R] or the non-treated control by the end of the study. Two applications of fluopyram at either the low or high rate effectively restored turf health (Baird and Becker 2016).

6.5.15 Certain Plant Parasitic Nematodes of Common Occurrence in California

Plant parasitic nematodes in this category include species of genera such as *Helicotylenchus*, *Scutellonema* and *Tylenchorhynchus*, that are found frequently and distributed widely in cultivated and non-cultivated regions within California. In general, plant damage caused by high populations of these obligate migratory ecto-parasitic root feeders may be more significant in small-area production sites and containerized crops in nursery, residential and local situations, than in larger areas and environments such as parks, pastures and cultivated fields. Furthermore, crop damage under field conditions is often difficult to assess since different genera and species are often present in mixed populations (Norton 1984).

6.5.15.1 Spiral Nematodes of the Genus *Helicotylenchus* spp.

In California, *Helicotylenchus* spp. are present in soil around the root zone of a wide range of plants including agricultural crops, fruit trees, ornamentals nursery stock forest trees and shrubs, desert shrubs, grasses and weeds, however, the host status of the associated plants is not always known. Feeding of spiral nematodes results in production of small discolored lesions in the root cortex and other underground parts, on which the nematode feed. Species reproduce mainly by parthenogenesis and high nematode population levels can severely damage roots causing them to become slightly swollen, spongy, discoloured with sloughed-off cortical tissue (Maggenti 1981). While species of *Helicotylenchus* may not be identified for nematode management in cultivated fields, certain species that have been reported in

California include *H. dihystera*, *H. digonicus, H. pseudorobustus, H. erythrinae* and other species (Siddiqui et al. 1973; Dong et al. 2007). Banana spiral nematode, *H. multicinctus*, is not distributed widely in California and was reported in the mid-1960s and 1970s from Riverside, Los Angeles and San Diego Counties (Sher 1966; Siddiqui et al. 1973). Pathogenicity of *Helicotylenchus* spp. has not been studied in California.

6.5.15.2 Spiral Nematodes of the Genus *Scutellonema*

In California, *Scutellonema* spp., also called spiral nematodes, are common associates of a wide range of agricultural crops, fruit trees, ornamentals, nursery stock, forest trees and shrubs, desert shrubs, grasses, and weeds. Agricultural crops include alfalfa, cotton, potato, corn and several other crops. The host status of associated plants is not always known. *Scutellonema brachyurus* has been reported as wide spread within the state (Siddiqui et al. 1973). General plant damage associated with *Scutellonema* spp. is commonly exhibited as numerous small, brown necrotic root lesion produced as a result of their feeding. Internally, isolated root cavities are produced by the nematodes while above ground symptoms may include leaf stunting and chlorosis, and reduced growth. The shallow root lesions become avenues for secondary invaders, namely bacteria, fungi and mites. Pathogenicity of *Scutellonema* spp. detected on agricultural and ornamental crops in California, has not been studied.

6.5.15.3 Stunt Nematodes, *Tylenchorhynchus* spp.

Tylenchorhynchus spp. are associated with the roots of a wide range of plants including cotton, oats, and corn as well as other agricultural crops, fruit trees, ornamentals, nursery stock, forest trees and shrubs, desert shrubs, grasses, and weeds. The host status of associated plants is not always known. General plant damage associated with *Tylenchorhynchus* spp. includes stunting of the root system which is expressed aboveground by yellowing of foliage, stunted top growth, and sometimes wilt and defoliation (Maggenti 1981). Generally, *Tylenchorhynchus* spp. are considered mild pathogens of plants and are common associates of several plants (Norton 1984; Table 6.2). Pathogenicity of several *Tylenchorhynchus* spp. detected on agricultural and ornamental crops in California has not been studied (McKenry and Roberts 1985).

6.6 Conclusion and Future Perspectives

California's multibillion dollar investment in the nation's largest diversity of agricultural crops, nursery and turf productions, and its role as a major provider of food for the nation and global communities, more than warrants the continued and future protection of the state's crop productions against damages and losses caused by plant parasitic nematodes. To reach this goal, the state continues to recognize and resolve challenges in nematode management and biological technologies. The future is promising.

Stimulated by the restricted availability of nematicides, California is looking ahead to the use of more sustainable management scenarios for managing plant parasitic nematodes. Recent developments offer new tools to fine tune the use of cultural and biological practices for local cropping systems. The commercial availability of several biological nematicides, of products with newer and safer modes of action, of the increasing availability of nematode resistant cultivars, of the development or selection of cover crop varieties for use against particular nematode species, and the use of green manures, biofumigation, and trap cropping are promising techniques. Combining these with a strong nematode control and certification program for nursery crops, the development of molecular techniques for identification of plant parasitic nematodes, online databases to rapidly search out nematode resistant crops, computerized soil temperature monitoring equipment plus computer models for calculating nematode degree days and modeling population cycling, and a greater understanding of nematode biology and population dynamics make it possible to develop promising scenarios to reduce damaging nematode populations and increase yields.

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