

1 ***Plant Parasitic Nematodes in Sustainable Agriculture of North America***

2 ***Volume 1: Canada, Northeastern, Midwestern and Southern USA***

3 **Editors: Sergei A. Subbotin and John J. Chitambar**

4

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2 *Volume 2: Western USA and Mexico*

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Chapter 21. Plant Parasitic Nematodes in California Agriculture

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21.1 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.

22.1 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 21.1)(Fig.21.1). In 2016, fruits, nuts and vegetables continued as the state's leading crops and accounted for 56 percent of the nation's non-citrus fruit and nut production and over 46 percent of the nation's citrus production. 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 percent of the nation's total tonnage. The state also produces 80 percent of worldwide almond production. The total value of fresh and processing vegetables and melon

1 production was \$7.4 billion with lettuce as the leading vegetable crop, in value of production (\$2.0
2 billion), followed by tomatoes (\$1.3 billion). Furthermore, California is the nation's sole producer
3 of 99 percent or more of almonds, artichokes, dates, figs, garlic, grapes (raisins), kiwifruit,
4 Honeydew melons, olives, peaches (clingstone), pistachios, rice (sweet), seed (Ladino clover) and
5 walnuts (CDFAA, 2016-2017). California is the largest producer of almonds in the world, with
6 approximately 80 percent in global production, and the second largest producer of walnuts in the
7 world. Almonds continue to be the state's top valued agricultural export commodity, with \$4.50
8 billion in foreign sales in 2016. California is, also, the nation's largest agricultural exporter of 14.9
9 percent of total U.S. agricultural exports in 2016, and the sole exporter of 99 percent or more of
10 almonds, artichokes, dates, dried plums, figs, garlic, kiwifruit, olives and olive oil, pistachios,
11 raisins, table grapes and walnuts (CDFAB, 2016-2017). California's nursery, greenhouse and
12 floriculture crop production, which includes cut flowers, potted plants, foliage plants, bedding
13 plants and indoor decorative, was valued at \$947 million in 2015. California's numerous public
14 and private golf courses are a major user of turfgrasses and represent 3.5 percent of total turf grass
15 cultivated in the state. The golf industry (\$6.3 billion in 2011), is comparable in size to other
16 important state industries including greenhouse/nursery crops, and therefore, the use and
17 importance of turf grass management cannot be under rated (SRI International, 2013).

18

19 **21.3 California's Major Agricultural Regions**

20

21 The Central Valley, which includes all or part of 18 Northern California counties and extends
22 through the center of the state from Glenn and Butte Counties in the north to Kern County in the
23 south, is the state's agricultural heartland that produces more than 250 different crops with an
24 estimated value of \$17 billion per year. The Valley alone accounts for one-fourth of the nation's
25 food including 40% of the nation's fruit, nut and other agricultural crops, on less than 1% of the
26 nation's total farmland and is marked by a hot Mediterranean climate in the north, and a dry, desert-
27 like climate in the southernmost regions (USGS, 2017). The top four agricultural counties namely
28 Kern, Tulare, Fresno and Monterey Counties, that lead in total value of production and leading
29 commodities are in the Central Valley and experience a growing season of 9 to 10 months (CDFAA
30 2016-2017; Morgan and McNamee, 2017). The Central Valley is subdivided into 1) the
31 Sacramento Valley which encompasses the region north of the Sacramento-San Joaquin River

1 Delta and comprises all or part of ten Northern California counties, and 2) the San Joaquin Valley
2 which extends from the Delta to the Tehachapi Mountains in the south and includes seven northern
3 counties as well as most of Kern County in Southern California.

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

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

13 The Imperial Valley, lying within Southern California's Imperial County and extending south of
14 the Coachella Valley to the Gulf of California, has desert climate and extreme daily temperatures.
15 Summer temperatures are usually greater than 38 °C, whereas, temperatures from late October to
16 mid-April are relatively mild. The Imperial Valley comprises thousands of hectares of irrigated
17 farmland and is a major producer of winter fruits, that cannot endure cool temperatures, and
18 vegetables, cotton and grain crops.

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

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

26

27 **Table 21.1.** Selected economically important crops of California for 2016. (California
28 Agricultural Statistics Review, 2016-2017)

29

| Crops¹ | Area harvested 1000 ha | U.S. Rank | CA share of U. S. receipts Percent | Total value \$1,000 | Five leading counties by gross value of production |
|----------------------------|-----------------------------------|----------------------|---|--------------------------------|--|
| <i>Fruit and Nut Crops</i> | | | | | |
| 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 |
| 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 |
| 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 ² |
| 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 |
| <i>Vegetable and Melon Crops</i> | | | | | |

| | | | | | |
|---------------------------|------|---|-------|-----------|--|
| 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 |
| 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 ³ |
| 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 ⁴ |
| <i>Field and Seed Crops</i> | | | | | |
| 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 ⁵ |
| 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 |

| | | | | | |
|-------------|-------|---|------|---------|---------------------------------------|
| Rice | 214.4 | 1 | 29.1 | 649,289 | Colusa, Butte, Sutter, Glenn, Yolo |
| Sugar beets | 10.0 | 7 | 3.0 | n/a | Imperial |

1

2 ¹Crops in bold are included in California’s top 20 commodities for 2016, by value and rank.

3 ²Five leading counties for plums; five leading counties for dried plums (prunes) in 2016 were Tulare, Butte, Yuba,
4 Sutter and Tehama.

5 ³Leading counties for bell peppers.

6 ⁴Leading counties for fresh market tomatoes only.

7 ⁵Leading counties for alfalfa hay only

8

9

10 **21. 4 Nematology in California – Early Discoveries**

11

12 Nematode problems in agriculture were not fully recognized in the USA until the early 1900s. The
13 early development of Nematology was mainly limited to reports on root knot nematodes and initial
14 work was concentrated on the US east coastal region. This recognition soon led to initial nematode
15 surveys in California during 1907 and a first report by E. A. Bessey in 1911 of the presence of root
16 knot nematodes (*Meloidogyne* spp.) and sugar beet cyst nematodes (*Heterodera schachtii*) in
17 several regions of the State. With growing awareness of nematode problems in California, in 1912,
18 the citrus nematode was discovered by a Los Angeles County Agricultural Inspector, J. R. Hodges.,
19 and in 1928, was shown to cause serious damage to citrus seedlings, by E. E. Thomas at the Citrus
20 Experiment Station in Riverside. Initial surveys in the early 1920s also detected the stem and bulb
21 nematode, *Ditylenchus dipsaci*, and in 1927 the root lesion nematodes, *Pratylenchus* spp., were
22 first reported on fig. In the decade that followed, root lesion nematode damage to fig, walnut and
23 cherry trees was found to be widespread in California. Critical to the initial detections, research
24 and management of plant parasitic nematodes in California agriculture, was the development of
25 the Department of Nematology at the University of California and the Nematology Regulatory
26 Program at the California Department of Agriculture. At that time, the State Department of
27 Agriculture estimated the value of nursery stock rejected due to root knot nematode infestation,
28 during the December 1922 to April 1923 planting season, to be \$100,000 (Siddiqui *et al.*, 1973;
29 Raski *et al.*, 2002). Losses caused by nematodes were difficult to assess then as several species of

1 ectoparasitic nematodes were being discovered to feed on plant roots without causing distinct
 2 symptoms other than restricted root growth. Much about their damage potential and distribution
 3 was unknown and their impact on crop growth was recognized only when nematicides were
 4 applied to areas where poor plant growth occurred by unknown cause. With the advent of fumigant
 5 nematicides, several ectoparasitic nematodes were soon recognized to cause more damage to crops
 6 than that caused by endoparasites. In 1959, the Department of Nematology estimated annual crop
 7 losses due to nematodes at \$89,442,000 to \$141,721,000 (Allen and Maggenti, 1959). In 1951,
 8 after review of the nematode situation at that time, the Department of Agriculture and the
 9 University of California produced the first distribution record of plant parasitic nematodes in
 10 California (Raski *et al.*, 2002). Since then, several in-state surveys have been conducted
 11 collaboratively or individually by federal, state, county and University of California agencies, for
 12 targeted plant parasitic nematodes such as the burrowing nematode, sugar beet cyst nematode,
 13 golden nematode, potato pale cyst nematode, Columbia root knot nematode, sting nematode,
 14 strawberry foliar nematode, reniform nematode and other exotic and non-exotic species associated
 15 with host plants in cultivated and non-cultivated crop fields, orchards, nurseries and golf greens.

16

17 **21.5 Economically Important Plant Parasitic Nematodes of Major Crops in California**

18

19 Plant parasitic nematodes can significantly impact crop production in California. While several
 20 species have been found to be associated with different plants grown in the state (Table 21.2), in
 21 this chapter, only certain main, economically important plant parasitic nematode species associated
 22 with major crops of the state are discussed. These species include the root knot, lesion, stem and
 23 bulb, citrus, dagger, ring, pin and sting nematodes and a few others.

24

25 **Table 21.2.** Plant parasitic nematodes associated with various crops in California.

26

| Species | Crop | Reference |
|---------------------------------|-------------------------|---|
| <i>Anguna agrostis</i> | Creeping bentgrass | Siddiqui <i>et al.</i> , 1973 |
| <i>Anguina pacificae</i> | Bluegrass | Cid del Prado and Maggenti, 1984; McClure <i>et al.</i> , 2008 |
| <i>Aphelenchoides fragariae</i> | Strawberry, ornamentals | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; |

| | | |
|--|---|---|
| <i>Aphelenchoides ritzemabosi</i> | Strawberry, alfalfa, ornamentals | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; |
| <i>Atalodera gracililanceae</i> | <i>Festuca</i> sp. | Robbins, 1978a |
| <i>Belonolaimus longicaudatus</i> | Grasses | Mundo-Ocampo <i>et al.</i> 1994 |
| <i>Cacopaurus pestis</i> | Walnut | Thorne, 1943 |
| <i>Criconemoides annulatus</i> | Plum, beet, barley, citrus, apple, cotton, strawberry, alfalfa, tomato, tobacco, sorghum, clover, corn, walnut | Raski, 1952; Siddiqui <i>et al.</i> , 1973 |
| <i>Criconema permistum</i> | grape | Siddiqui <i>et al.</i> , 1973 |
| <i>Ditylenchus dipsaci</i> | Alfalfa, garlic, onion, sugar beet, alfalfa, phlox, pea, clover, barley | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985 |
| <i>Ditylenchus destructor</i> | Potato | Ayoub, 1970 |
| <i>Gracilacus anceps</i> | Tomato | Siddiqui <i>et al.</i> , 1973 |
| <i>Gracilacus idalimus</i> | Grape | Dong <i>et al.</i> , 2007 |
| <i>Gracilacus mirus</i> | Grape | Raski, 1962 |
| <i>Helicotylenchus digonicus</i> | Oat, beet, citrus, fig, barley, tomato, bean, wheat, grape, corn, nectarine | Siddiqui <i>et al.</i> , 1973, Dong <i>et al.</i> , 2007 |
| <i>Helicotylenchus dihystra</i> | Grape, bermudagrass, onion, beet, citrus, cotton, barley, tomato, rice, almond potato, sorghum, grape, corn, apricot, cherry, peach, plum | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Subbotin <i>et al.</i> , 2015b, Dong <i>et al.</i> , 2007 |
| <i>Helicotylenchus erythrinae</i> | Beet, cotton, apple, grape | Siddiqui <i>et al.</i> , 1973 |
| <i>Helicotylenchus microlobus</i> | Corn | Subbotin <i>et al.</i> , 2015b |
| <i>Helicotylenchus paragiris</i> | Apricot, cherry, nectarine, plum | Dong <i>et al.</i> , 2007 |
| <i>Helicotylenchus paxilli</i> | Grasses | Subbotin <i>et al.</i> , 2015b |
| <i>Helicotylenchus pseudorobustus</i> | Grasses, rice, grape, beet, apricot, cherry, nectarine, plum | Siddiqui <i>et al.</i> , 1973; Subbotin <i>et al.</i> , 2015b; Dong <i>et al.</i> , 2007 |
| <i>Hemicriconemoides californianus</i> | Grape | Pinochet and Raski, 1975 |
| <i>Hemicycliophora arenaria</i> | Citrus, tomato | Siddiqui <i>et al.</i> , 1973; Dong <i>et al.</i> , 2007 |
| <i>Hemicycliophora biosphaera</i> | Citrus | Dong <i>et al.</i> , 2007 |
| <i>Hemicycliophora sheri</i> | Prune | Dong <i>et al.</i> , 2007 |
| <i>Hemicycliophora striatula</i> | Nectarine | Dong <i>et al.</i> , 2007 |
| <i>Heterodera cruciferae</i> | Table beets, cabbage, Brussels sprouts, broccoli, cauliflower | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985 |

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

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| | cotton, rice, pea, almond, grape, prune, corn, wheat, potato | |
| <i>Mesocriconema rusticum</i> | Grape | Siddiqui <i>et al.</i> , 1973 |
| <i>Mesocriconema xenoplax</i> | Grape, citrus, tomato, apple, plum, grapevine, walnut, rice, apricot, cherry, peach | Raski, 1952a; Siddiqui <i>et al.</i> , 1973; Dong <i>et al.</i> , 2007 |
| <i>Nacobbus dorsalis</i> | Barley, corn | Siddiqui <i>et al.</i> , 1973 |
| <i>Nanidorus minor</i> | Alfalfa, almond, cabbage, barley, bean, carrot, cotton, corn, peppers, sugar beet, onion, tomato, olive, plum, | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007; Kumari and Subbotin, 2012 |
| <i>Paralongidorus microlaimus</i> | Walnut | Robbins, 1978b |
| <i>Paratrichodorus allius</i> | Onion | Norton, 1984b |
| <i>Paratrichodorus porosus</i> | Fig, tomato, apple, alfalfa, olive, plum, peach | Siddiqui <i>et al.</i> , 1973; |
| <i>Paratylenchus baldacci</i> | Prune, citrus | Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus bukowinensis</i> | Apricot, cherry, citrus, nectarine, plum, prune | Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus dianthus</i> | Citrus | Dong <i>et al.</i> , 2015 |
| <i>Paratylenchus hamatus</i> | Fig, peach, plum, apricot, beet, carrot, cabbage, barley, alfalfa, apple, potato, grape, peach, almond, cherry, nectarine, plum, prune, citrus | Thorne and Allen, 1950; Siddiqui <i>et al.</i> , 1973; Raski, 1975; Dong <i>et al.</i> , 2007; Van den Berg <i>et al.</i> , 2014 |
| <i>Paratylenchus holdemani</i> | Citrus | Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus lepidus</i> | Apricot, cherry | Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus nanus</i> | Grasses, walnut, alfalfa, cabbage | Siddiqui <i>et al.</i> , 1973; Raski, 1975; Van den Berg <i>et al.</i> , 2014 |
| <i>Paratylenchus neoamblycephalus</i> | Plum, apricot | McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus projectus</i> | Bean, plum | Siddiqui <i>et al.</i> , 1973 |
| <i>Paratylenchus similis</i> | Citrus | Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus straeleni</i> | Prune | Van den Berg <i>et al.</i> , 2014 |
| <i>Paratylenchus brachyurus</i> | Cotton, barley, alfalfa, grape, corn, prune | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007 |
| <i>Paratylenchus crenatus</i> | Beet, carrot, barley, olive, tomato, peach, potato, corn | Siddiqui <i>et al.</i> , 1973; |

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| <i>Pratylenchus hexincisus</i> | Grape | Dong <i>et al.</i> , 2007 |
| <i>Pratylenchus penetrans</i> | Cowpea, cherry, strawberry, oat, cabbage, barley, tomato, alfalfa, pea, potato, wheat, almond, corn, apricot, cherry, plum, grape | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2008 |
| <i>Pratylenchus scribneri</i> | Sudan grass, beans, alfalfa, corn, grape, apple, beet | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2008 |
| <i>Pratylenchus thornei</i> | Grasses, sorghum, wheat, onion, sugar beet, cabbage, alfalfa, beans, sorghum, corn, apricot, cherry, grape | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2008 |
| <i>Pratylenchus neglectus</i> | 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 <i>et al.</i> , 1973; Dong <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2008 |
| <i>Pratylenchus vulnus</i> | Walnut, grape, fig, citrus, apricot, avocado, cherry, olive, peach, almond, plum, raspberry, boysenberry, apple, strawberry, pear, pistachio, nectarine | Allen and Jensen, 1951; Hart, 1951; Lownsbey, 1956; Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007; Subbotin <i>et al.</i> , 2008 |
| <i>Rotylenchulus parvus</i> | Alfalfa, cotton, olive, sugar beet, sorghum | Siddiqui <i>et al.</i> , 1973; Dong <i>et al.</i> , 2007 |
| <i>Rotylenchulus robustus</i> | Apple, potato, olive, grape, grasses | Siddiqui <i>et al.</i> , 1973; Dong <i>et al.</i> , 2007; Cantalapiedra-Navarrete <i>et al.</i> , 2013 |
| <i>Scutellonema brachyurus</i> | Peach, plum | Dong <i>et al.</i> , 2007; |
| <i>Scutellonema clathricaudatum</i> | Apricot | Dong <i>et al.</i> , 2007 |
| <i>Scutellonema conicephalum</i> | Apricot, cherry, plum | Dong <i>et al.</i> , 2007 |
| <i>Trichodorus californicus</i> | Rose | Siddiqui <i>et al.</i> , 1973; |
| <i>Tylenchulus semipenetrans</i> | Persimmon, citrus, grape, olive | Baines and Thorne 1952; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007; Tanha Maafi <i>et al.</i> , 2012 |
| <i>Tylenchorhynchus acutus</i> | Apple, sorghum, peach, grape | Siddiqui <i>et al.</i> , 1973; |
| <i>Tylenchorhynchus agri</i> | Cherry | Dong <i>et al.</i> , 2007 |
| <i>Tylenchorhynchus aspericutis</i> | Nectarine | Dong <i>et al.</i> , 2007 |

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| <i>Tylenchorhynchus annulatus</i> | Plum | Dong <i>et al.</i> , 2007; Handoo <i>et al.</i> , 2014 |
| <i>Tylenchorhynchus capitatus</i> | Pear, cabbage, carrot, barley, apple, rye, corn, plum | Allen, 1955; Siddiqui <i>et al.</i> , 1973; |
| <i>Tylenchorhynchus claytoni</i> | Citrus, tomato, apple, peach, grape, corn | Siddiqui <i>et al.</i> , 1973 |
| <i>Tylenchorhynchus clarus</i> | Citrus, alfalfa, barley, beans, bermudagrass, cotton, carrot, barley, olive, rice, plum, peach, potato, corn, grape, clover, wheat | Allen, 1955; Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Handoo <i>et al.</i> , 2014 |
| <i>Tylenchorhynchus cylindricus</i> | Cotton, apple, olive, almond, potato, grape, corn, bean | Allen, 1955; Siddiqui <i>et al.</i> , 1973 |
| <i>Tylenchorhynchus ebriensis</i> | Peach | Dong <i>et al.</i> , 2007 |
| <i>Tylenchorhynchus elegans</i> | Cherry, plum, grape | Dong <i>et al.</i> , 2007 |
| <i>Tylenchorhynchus mashhoodi</i> | Apricot, cherry peach, plum, grape | Dong <i>et al.</i> , 2007 |
| <i>Tylenchorhynchus microconus</i> | Cherry | Dong <i>et al.</i> , 2007 |
| <i>Tylenchorhynchus nudus</i> | Apricot | Dong <i>et al.</i> , 2007 |
| <i>Xiphinema americanum sensu lato</i> | Plum, apricot, grape, grasses, orange, pecan, walnut, cherry, peach, cherry, alfalfa, apricot, apple, citrus pear, pistachio, raspberry, strawberry, tomato, rice, sorghum, bean | Siddiqui <i>et al.</i> , 1973; McKenry and Roberts, 1985; Dong <i>et al.</i> , 2007 Orlando <i>et al.</i> , 2016 |
| <i>Xiphinema californicum</i> | Orange, grape, grapefruit, lemon, peach, cherry, plum, lemon, walnut, olive, alfalfa, grapevine | Lamberti and Bleve-Zacheo, 1979; Lamberti and Golden, 1984; Robbins, 1993; Orlando <i>et al.</i> , 2016 |
| <i>Xiphinema pachtaicum</i> | Plum, lemon | Robbins, 1993; Orlando <i>et al.</i> , 2016 |
| <i>Xiphinema rivesi</i> | Grasses | Orlando <i>et al.</i> , 2016 |
| <i>Xiphinema insigne</i> | Plum, grasses | Luc and Southey, 1980; Cai <i>et al.</i> , 2018 |
| <i>Xiphinema vuittenezi</i> | Grape, fig, citrus, carrot | Luc <i>et al.</i> , 1964; Siddiqui <i>et al.</i> , 1973 |
| <i>Xiphinema index</i> | Fig, grape | Thorne and Allen, 1950; Siddiqui <i>et al.</i> , 1973 |

1

2 **21.5.1 Root Knot Nematodes, *Meloidogyne* spp.**

3

1 Since first being reported in California by E. A. Bessey in 1911, root knot nematodes (*Meloidogyne*
2 spp.) have become the most extensively studied genus in the state. Six species are of significant
3 economic concern: *M. incognita*, *M. javanica*, *M. arenaria*, *M. hapla*, *M. chitwoodi*, and *M. naasi*.
4 Another three species have been reported: *M. graminis*, *M. marylandi*, and *M. fallax* (Table
5 21.2)(Fig.21.2).

6 The host ranges of the various species are highly varied (Table 21.2), but as a whole encompass
7 most of the economically important annual, perennial, and ornamental crops grown in California
8 (Table 21.1). Species are distributed throughout California's agricultural areas but show some
9 regional and crop distribution preferences. For example, *M. chitwoodi* is found on potatoes and
10 small grains in the northern part of the state in Modoc and Siskiyou Counties. In this same area,
11 *M. naasi* parasitizes barley, wheat and grasses. An isolated occurrence of *M. naasi* has also been found
12 on a bowling green in the Los Angeles area. The northern root knot nematode *M. hapla* is found
13 statewide, particularly in fields cropped to alfalfa where it can reduce alfalfa stand densities by
14 62% (Noling and Ferris, 1985). As the only species that parasitizes cotton, *M. incognita* may be
15 more common on land regularly cropped with cotton (McKenry and Roberts, 1985).

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

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

31 Second-stage juveniles (J2) of this sedentary endoparasitic nematode that hatch from eggs and

1 move within the film of water that lines soil pores, are the infective stage. Photoperiod influences
2 the migration of *M. incognita* juveniles toward tomato root (Prot and Van Gundy, 1981b). The
3 stylet is used to penetrate root tips at the zone of elongation. After penetrating the plant root, J2
4 migrate towards the vascular cylinder where they establish a feeding site and initiate feeding using
5 their stylets. Gall formation may be influenced by secretion of plant-growth regulators by the
6 nematode (Viglierchio and Yu, 1965). Once feeding is initiated, J2s become sedentary and undergo
7 three additional moults to become pear or nearly spherical-shaped adults. The adult female lays
8 150-250 eggs in a gelatinous matrix on or below the surface of the root. From the eggs new
9 infective J2s hatch and start a new cycle (Atamian *et al.*, 2012). The number of males in a
10 population are typically low, but larger numbers may be found toward the end of the growing
11 season, when populations are dense and host plants are under stress (McClure and Viglierchio,
12 1966).

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

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

31

1 **21.5.1.1 Management**

2

3 Resistant cultivars of some *Meloidogyne* susceptible crops are available including tomato, cotton,
4 cowpea, lima bean, and sweet potato (Roberts, 1993). Nemaguard rootstock is resistant to root
5 knot nematodes and is widely used in California for perennial crops including almonds and
6 peaches. Processing tomatoes are a major California crop (Table 21.1). Tomato cultivars are
7 available with the *Mi* gene located on chromosome 6 that are resistant to *M. incognita*, *M. javanica*,
8 and *M. arenaria* but not to *M. hapla* (Ho *et al.*, 1992). *Mi*-mediated resistance is characterized by
9 a localized necrosis of host cells near the invading nematode that begins about 12 hours after
10 infestation occurs. Resistance mediated by *Mi* is lost above 30 C (Williamson and Hussey, 1996).
11 The use of resistant varieties became increasingly popular following field trials demonstrating the
12 effectiveness of the resistance (Roberts and May, 1986). The selection of resistance breaking
13 populations in fields cropped to resistant varieties for multiple years began to be seen in 1995
14 (Kaloshian *et al.*, 1996).

15 Another resistance gene, *Mi-3*, identified in *Lycopersicon peruvianum* on the short arm of
16 chromosome 12 confers resistance to nematodes that are virulent on tomato lines that carry *Mi-1*,
17 and is effective at temperatures at which *Mi-1* is not effective (Ammati *et al.*, 1986; Williamson,
18 1998; Yaghoobi *et al.*, 1995, 2005). A heat-stable resistance gene, *Mi-9* from *Lycopersicon*
19 *peruvianum* has been found that is localized on the short arm of chromosome 6 (Ammiraju *et al.*,
20 2003).

21 Following a field observation that nematode resistant tomatoes were also resistant to the potato
22 aphid, *Macrosiphum euphorbiae* it was determined these traits are tightly linked (Kaloshian *et al.*,
23 1995; Martinez de Ilarduya and Kaloshian, 2001). Subsequently, it was determined that on the
24 short arm of tomato chromosome 6, a cluster of disease resistance genes have evolved harboring
25 the *Mi-1* and *Cf* genes. The *Mi-1* gene confers resistance to root knot nematodes, aphids, and the
26 sweet potato whitefly (*Bemisia tabaci*). Ol-4 and Ol-6 that confer resistance to tomato powdery
27 mildew are also in this cluster (Seifi *et al.*, 2011). Changes in expression of jasmonic acid (JA)-
28 and salicylic acid (SA)- dependent defense genes in response to potato and green peach aphids
29 suggest that aphid feeding involves both SA and JA/ethylene plant defense signaling pathways and
30 that *Mi-1*-mediated resistance might involve a SA-dependent signaling pathway (Martinez de
31 Ilarduya *et al.*, 2003).

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

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

1 Determination and use of economic thresholds is an important consideration in nematode pest
2 management programs, but their development has been limited by reliability of nematode
3 population assessment techniques (Ferris, 1978). A computer-simulation model of a *Meloidogyne*-
4 grapevine system (Ferris, 1976) developed in conjunction with extensive field sampling,
5 greenhouse, and laboratory research has contributed to our knowledge of the biology and
6 management of nematodes in vineyards (Ferris and McKenry, 1974, 1975, 1976; Melakeberhan *et*
7 *al.*, 1989). The economic importance of grapes statewide (Table 21.1), and their status as hosts to
8 multiple genera of plant parasitic nematodes has led to extensive host range testing and breeding
9 to develop rootstocks resistant not only to multiple genera of nematodes, but to virus and insect
10 pests as well (Chitambar and Raski, 1984; Anwar and McKenry, 2002; McKenry *et al.*, 2004).
11 After a 15-year screening process, 13 selections emerged with either almost complete or complete
12 combined resistance to *M. incognita* Race 3, *M. incognita* pathotype Harmony C, *M. arenaria*
13 pathotype Harmony A, and *X. index*. After a total of 204 separate trials, the rootstocks were
14 released to the grape industry as UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD
15 GRN5 (Ferris *et al.*, 2012, 2013).

16 A number of studies in California have increased our knowledge of the potential for using
17 biological control to manage *Meloidogyne* spp. Second stage juveniles of *Meloidogyne* spp. were
18 readily infected with the endoparasite *Pasteuria penetrans* (Mankau and Prasad, 1977). Hyphae of
19 *Dactylella oviparasitica* proliferated rapidly through *Meloidogyne* egg masses, and appressoria
20 formed when they contacted eggs (Stirling and Mankau, 1979). The nematophagous fungi,
21 *Paecilomyces lilacinus* and *Verticillium chlamydosporium*, were found in a high proportion of
22 Northern California tomato fields but were determined to not be effectively suppressing
23 populations of *M. incognita* (Gaspard *et al.*, 1990). The nematophagous fungus *Hirsutella*
24 *rhossiliensis* infested *M. javanica* but did not provide effective control (Tedford *et al.*, 1993).
25 Three species of the nematode-trapping fungi *Arthrobotrys* and two of *Nematoctonus* were
26 detected in both organic and conventional field plots but did not suppress *M. javanica* in a
27 laboratory bioassay (Jaffee *et al.*, 1998). Three *Pochonia chlamydosporia* var. *chlamydosporia*
28 strains isolated from a *M. incognita*-suppressive soil showed potential as biological control agents
29 against root knot nematodes in greenhouse trials (Bent *et al.*, 2008; Yang *et al.*, 2012). Chitinolytic
30 microflora may contribute to biological control of *Meloidogyne* by causing decreased egg viability
31 through degradation of egg shells as shown by laboratory trials with *L. enzymogenes* strain C3

1 (Chen *et al.*, 2006) and field trials with a chitin-urea soil amendment (Westerdahl *et al.*, 1992).
2 Various formulations of four entomopathogenic nematode (EPN) species and the supernatants of
3 their mutualistic bacteria were found to suppress *M. incognita* and *M. arenaria* in tomato roots
4 (Kepenekci *et al.*, 2016).

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

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

28 Biofumigation is a technique researched for management of weeds and fungi as well as nematodes.
29 Brassica species such as broccoli produce glucosinolates, and when these degrade in the soil they
30 release isothiocyanates that are similar to the active ingredient in metam sodium which is one the
31 more widely used nematicides (Westerdahl, 2011; Zasada and Ferris, 2003; Edwards and Ploeg,

1 2014; Lopez-Perez *et al.*, 2010). Marigolds have also been found to reduce damage by *Meloidogyne*
2 on subsequent crops (Ploeg, 1999; Huang and Ploeg, 1999). Trap cropping can be utilized for
3 sedentary endoparasitic nematodes such as root knot (Westerdahl, 2011). A susceptible host is
4 planted and larvae of a sedentary parasitic nematode are induced to enter and establish a feeding
5 site within the roots. Once this has occurred, and the female nematode begins to mature, she is
6 unable to leave the plant root. The plants are then destroyed before the life cycle of the nematode
7 can be completed, trapping nematodes within the root. Soil solarization has shown mixed results,
8 but in some field experiments *M. incognita* J2 were significantly reduced and yield of carrot and
9 survival of cotton seedlings was increased (Stapleton *et al.*, 1987). Goodell *et al.* (1983) showed
10 that *M. incognita* populations were reduced by approximately 40% (within the tilled zone) for each
11 plowing, following destruction of a cotton crop.

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

17

18 **21.5.2 Citrus Nematode, *Tylenchulus semipenetrans***

19

20 *Tylenchulus semipenetrans* is commonly referred to as the "citrus nematode" because of its
21 historical association with citrus. Yield losses to citrus due to *T. semipenetrans* are in the range of
22 10% to 30% depending on the level of infestation (Verdejo-Lucas and McKenry, 2004).
23 *Tylenchulus semipenetrans* was discovered on citrus roots in Los Angeles County in 1912, and
24 subsequently described by Cobb (1913, 1914). Within a few months of its discovery, it was found
25 to also be present in other citrus growing areas around the world, probably due to distribution on
26 infested nursery stock (Cobb, 1914). E.E. Thomas of the Riverside Citrus Experiment Station
27 (predecessor to the Riverside campus of the University of California) conducted the early research
28 on pathogenicity and management of this nematode (Cobb, 1914). In 1939, J.C Johnston and G.
29 Thorne examined more than 100 samples from citrus orchards in various parts of the state and
30 found all but one to be infested with *T. semipenetrans* (Thorne, 1961).

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

18 R.C. Baines conducted extensive host range studies (Baines, 1950; Baines *et al.* 1948). In addition
19 to citrus, *T. semipenetrans* parasitizes grape, lilac, olive, and persimmon. It is common in table
20 grape vineyards in the Coachella Valley (Riverside County). It has also been found in peach and
21 almond orchards on "Lovell" rootstock in the San Joaquin Valley (Duncan *et al.*, 1992), and on
22 ponderosa pine (Viglierchio, 1979). Baines *et al.* (1974) found four citrus nematode biotypes in
23 California that could be differentiated by means of a host range test utilizing four citrus rootstocks.
24 Baines identified *Poncirus trifoliata* rootstock as having resistance to *T. semipenetrans*. In resistant
25 plants, juveniles penetrate epidermal and hypodermal cells. These cells and the first row of cortical
26 parenchyma cells then collapse and often become necrotic. A wound periderm forms in the
27 parenchyma, effectively isolating the area of penetration. Penetration does not progress, and
28 nematodes neither mature nor reproduce. In addition to this mechanical resistance, there appears
29 to be a toxic chemical associated with nonhost plants (Verdejo-Lucas and McKenry, 2004).

30

31 **21.5.2.1 Management**

1
2 Of 15 grape rootstocks tested, McKenry and Anwar (2006) found Ramsey and SO4 to be resistant
3 to *T. semipenetrans*, Thompson seedless to be highly susceptible, and the others to be susceptible.
4 Ferris *et al.* (2012) reported that of 13 grape rootstocks tested, eight were susceptible, three were
5 resistant, one was moderately resistant, and one was moderately susceptible. Two newly released
6 grape rootstocks GRN-1 and GRN-3 were resistant, and a third GRN-2 was susceptible.
7 Mature citrus trees can tolerate a considerable number of citrus nematode before showing lack of
8 vigor and decline symptoms. Susceptible trees planted in lightly infested soil may grow for many
9 years without apparent damage and then suffer a “slow decline”. Typical above ground signs
10 consist of reduced vigor, the death of terminal buds, chlorosis and dying of leaves, early wilting
11 under moisture stress, and twig dieback. Fruit is reduced in size, quantity and quality. Damage is
12 greater when trees are predisposed by other factors such as *Phytophthora* root rot and water stress.
13 Infested root systems are smaller than noninfested ones and have a dirty appearance because of the
14 adhesion of soil particles to the gelatinous matrix deposited by the female nematode on the root
15 surface during laying of eggs.
16 Baines researched and recommended use of soil fumigants for pre-plant management (Baines *et*
17 *al.*, 1957). Post-plant, nematicide treatments are warranted if more than 400 nematode females/g
18 root are found in samples collected in February to April or 700 females/g root in May and June.
19 The same is true for populations of juveniles greater than 5,000 per 500 g of soil February to April,
20 or greater than 8,000 May to July (Becker and Westerdahl, 2009). Little effect of treatment on
21 yield and fruit quality may be obtained the first year after a post-plant application, but with
22 continued treatment, efficacy can often be demonstrated in the second year (Verdejo-Lucas and
23 McKenry, 2004). Duncan *et al.* (1992) found that placement of a 3-m-wide, black, polyethylene
24 film mulch down rows of peach (*Prunus persica* 'Red Haven' on 'Lovell' rootstock) and almond
25 (*Prunus dulcis* 'Nonpareil' on 'Lovell') trees in the San Joaquin Valley for water conservation, also
26 resulted in reductions of levels of citrus nematode. It is common to be able to recover several
27 thousand citrus nematode juveniles from just 50 grams of soil. This has led to use of citrus
28 nematode infested soil as a model system for bioassaying the efficacy of potential new nematicides
29 as alternatives to methyl bromide (Wang *et al.*, 2004, Westerdahl *et al.*, 1992). Such studies have
30 shown toxicity of nematicides to citrus nematode to be similar to that for root knot nematode
31 (Roberts and Thomason, 1988; Zasada and Ferris, 2003).

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21.5.3 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, 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, 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 21.1; 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. 21.3). Presently, *D. dipsaci* comprises several races and populations that differ in host plant range, chromosome number, few morphometric values and gene sequences (Sturhan and Brzeski, 1991; 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

1 found within bulbs, tubers, rhizomes, stolons and rarely in roots (Sturhan and Brzeski, 1991). A
2 single female can lay 200-500 eggs within garlic and onion tissue and with a life cycle of about 21
3 days at 15°C, several generations can occur in one crop season causing substantial damage. All
4 postembryonic stages of *D. dipsaci* can infect plants, but fourth stage larvae are the most important
5 infective stage as they have the unique capability of withstanding desiccation by undergoing
6 anabiosis and surviving for long periods within stems, leaves, bulbs and seeds. Plants are invaded
7 through stomates or tissue are directly penetrated at the base of stems and leaf axils (Becker and
8 Westerdahl, 2018). The nematodes may invade seedlings below the soil surface causing their
9 retarded emergence and malformation or migrate upwards to apices of shoots.

10 As a result of nematode feeding, general symptoms develop that include swelling, distortion,
11 discoloration and stunting of aerial plant parts and necrosis and rotting of bulbs and tubers (Anon,
12 2008). Germinating onion and garlic cloves are penetrated by *D. dipsaci* and surviving plants are
13 stunted with distorted and bloated tissue appearing spongy; leaves are thickened and shortened,
14 often with yellowish or brown lesions; softening of bulb tissue initiates at the stem and neck and
15 proceeds downward into the scales which become soft, loose and pale gray or brown in concentric
16 circles when observed in transverse section, and bulbs split at the base under dry conditions, or
17 become malformed. Under moist conditions, bulbs rot due to the presence of secondary invading
18 fungi, bacteria and onion maggots (Becker and Westerdahl, 2018; Sturhan and Brzeski, 1991).
19 Infected alfalfa plants are stunted with few shoots and deformed buds. Infected stems are enlarged
20 and discolored and, when nematode population numbers are high, lower stems may turn black,
21 especially under moderate temperatures and high humidity. ‘White flags’ are formed when the
22 nematodes move into leaf tissue and destroy chloroplast (Westerdahl, *et al.*, 2017). Damage to
23 alfalfa is most severe in moist, cool weather in cooler, sprinkler-irrigated inland valley and foggy
24 coastal areas of California. Damage is usually seen in the first and second cuttings of alfalfa under
25 cool and optimum conditions (15-20°C) for nematode development, and less often later in the
26 season under hot and dry conditions when nematode activity diminishes. The species may be found
27 as far south in the Central Valley as Madera County (Westerdahl, 2007).

28

29 **21.5.3.1 Management**

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

23 Hot water-formalin treatment of bulbs has been used historically in California against the stem and
24 bulb nematode in narcissus bulbs. Lear and Johnson (1962) and Johnson and Lear (1965) refined
25 the treatments to handle small volumes of garlic cloves. However, during the late 1980s, this
26 technique decreased mainly due to uncertainty in registration of formalin, grower perception that
27 hot water treatment resulted in deformed flowers, length of time required for dipping, safety
28 concerns over handling of formalin-treated bulbs and disposing of large volume of formalin. This
29 lead to evaluative studies of hot water treatment against *D. dipsaci* in daffodil bulbs and Qui *et al.*
30 (1993) determined that hot water treatment with 0.37% formaldehyde at 44°C for 150 minutes
31 controlled the nematode without detrimental effects on plant growth and flower production.

1 Alternatively, nematode control was also obtained with hot water treatment at 44°C for 240
2 minutes without chemicals. Roberts and Mathews (1995) reported the use of abamectin and
3 sodium hypochlorite as effective alternatives to replace formalin. Abamectin at 10-20 ppm as a
4 20-minute cool dip (18°C) following a 20-minute hot water dip and sodium hypochlorite at 1.052-
5 1.313% aqueous solution as the 20-minute hot dip were highly effective in controlling *D. dipsaci*,
6 although neither treatment was effective as a hot water-formalin treatment and did not eradicate
7 the nematode. Hot water treatment can reduce stem and bulb nematode in garlic cloves but is not
8 completely eradicated (Becker and Westerdahl, 2018).

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

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

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

28 Rotation with non-host crops provides some reduction of alfalfa stem nematode populations, which
29 has a very limited host range. Rotating with non-host crops such as tomato, small grains, beans
30 and corn for 2 to 4 years has resulted in reduced nematode numbers, whereas, growing no-hosts

1 or poor hosts such as corn for 3-4 years can reduce stem and bulb nematode in garlic and onion
2 (Becker and Westerdahl, 2018; Westerdahl *et al.*, 2017).

3

4 **21.5.4 Cyst Nematodes, *Heterodera* spp.**

5

6 **21.5.4.1 Sugar beet cyst nematode, *Heterodera schachtii***

7

8 In California, *Heterodera schachtii* was first detected in 1907 in Alameda, Los Angeles and
9 Salinas Counties (Caswell and Thomason, 1985)(Fig.21.4). In 1920, an intra-state survey revealed
10 more than one thousand hectares to be infected by this nematode (Thorne and Gidding, 1922).
11 Since then, *H. schachtii* has been detected in 23 countries (Siddiqui *et al.*, 1973) and is widespread
12 in all former and present California sugar beet growing areas, especially the Imperial Valley,
13 central regions of the Central Valley, the Salinas Valley, and Monterey, Santa Barbara, and
14 Ventura counties where sugar beet production is most concentrated (Caveness, 1958; Cooke and
15 Thomason, 1978; Caswell and Thomason, 1985). Nematode has been recovered from all soil types.
16 In the Imperial Valley 11% of the total cultivated acreage were infected. It is assumed that this
17 cyst nematode was introduced to the Central Coast valleys during the time when sugar beet
18 production was a primary crop in these areas. Estimates of yield loss can reach 25 t/ha in untreated
19 fields. Damage threshold levels vary with soil temperature, type, and moisture and are
20 characteristic for different sugar beet growing areas. The damage threshold in the Imperial Valley,
21 California, is attained with 1-2 eggs/g soil (Cooke and Thomason, 1979). In California, beside
22 sugar beet, *Heterodera schachtii* was also found from Brussels sprouts, broccoli or cauliflower
23 and cabbage (*Brassica oleracea*).

24 The life history and morphology of the sugar beet nematode was studied in details by Raski (1949).
25 In the laboratory, plant host tests conducted by Raski (1952c) with infested field soil collected near
26 Salinas, California some cysts were found in roots of Golden Queen and Jubilee tomatoes, annual
27 lupin, Golden Wax bush bean, Iron cowpea, garden pea, sweet pea (*Lathyrus odoratus*) and purple
28 vetch. Steele (1965) also provided the list of plant-hosts among weeds and agricultural plants
29 belonging to seven families for California populations of *H. schachtii*. *Heterodera schachtii*
30 females were also collected from the roots of *Amaranthus retroflexus*, *A. graecizans*,
31 *Chenopodium murale* and *Solanum nigrum*, but only rarely (Raski, 1952c). The penetration,

1 development, and reproduction of a California population of the sugar beet cyst nematode were
2 observed on phacelia (*Phacelia tanacetifolia*), buckwheat (*Fagopyrum esculentum*), oilseed radish
3 (*Raphanus sativus*), and white mustard (*Sinapis alba*) (Gardner and Caswell-Chen, 1993).

4 5 **21.5.4.1.1 Management**

6
7 Crop rotation and nematicidal application minimized yield losses (Cooke and Thomason, 1978).
8 However, high cost of treatment in relation to sugar prices often restricts nematicide use. To reduce
9 crop damage caused by *H. schachtii*, representatives of the local sugar beet factory, growers, the
10 County Agricultural Commissioner and nematologists from the University of California designed
11 a cropping scheme based on a cyst nematode dump-sample survey (Roberts and Thomason, 1981).
12 A dump sample is a 500-cm³ representative soil sample collected from sugar beets harvested from
13 an approximately 2-hectare area. Fields are considered infested if three or more cysts are found in
14 a sample. Sugar beets cannot be planted in non-infested fields more than two consecutive years
15 and not more than four out of ten years. Sugar beets can be grown only once every four years in
16 infested fields. The success of this program is due to the natural decline of *H. schachtii* in the
17 absence of host plants. For example, in the Imperial Valley, annual population decline rates of
18 more than 50% have been reported. In addition, egg densities in four different fields dropped below
19 the detection level during the fourth year under continuous non-host alfalfa (Roberts *et al.*, 1981).
20 It has been shown that egg parasitism by *Fusarium oxysporum*, *Acremonium strictum*, *Hirsutella*
21 *rhossiliensis*, *Dactylella oviparasitica* and other fungi (Nigh *et al.*, 1980; Jaffee *et al.*, 1991;
22 Westphal and Becker, 1999; Becker *et al.*, 2013) play a major role in *H. schachtii* egg destruction
23 and consequently contribute to the decline of the nematode population. Soil moisture in relation to
24 type of cropping sequence apparently influenced egg hatch and activity of fungal parasites
25 (Roberts *et al.* 1981).

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

1 nematodes for sustainable agricultural production.

2

3 **21.5.4.2 Cabbage Cyst Nematode, *Heterodera cruciferae***

4

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

9

10 **21.5.4.3 Clover Cyst Nematode, *Heterodera trifolii***

11

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

16

17 **21.5.4.4 Fig Cyst Nematode *Heterodera fici***

18

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

24

25 **21.5.5 Ring Nematode, *Mesocriconema xenoplax***

26

27 The ring nematode, *Mesocriconema xenoplax*, was first discovered and described by Raski (1952a)
28 as *Criconemoides xenoplax* (= *Macroposthonia xenoplax*, *Criconemella xenoplax*) from
29 specimens collected from a California vineyard. At that time, the species was also commonly
30 encountered in walnut and prune orchards and vineyards (Raski, 1952a; Siddiqui *et al.*, 1973;
31 Lownsbery *et al.*, 1974). In 1968, the species was detected in 26 of 29 walnut orchards in San

1 Joaquin County and by 1974, *M. xenoplax* was found in all four, main prune-cultivation regions
2 of the state, namely Santa Clara, Napa-Sonoma, Sacramento and San Joaquin Valleys (Lownsbery
3 *et al.*, 1974). During a survey of 14 out of 17 almond-producing counties of California, McKenry
4 and Kretsch (1987) found *Mesocriconema xenoplax* to be the most damaging nematode of almond
5 production in the Northern San Joaquin region (San Joaquin, Stanislaus and Merced Counties), in
6 sandy soils in the Southern San Joaquin region (Fresno, Kings, Tulare and Kern Counties), and
7 occasionally in the Sacramento Valley and a coastal region of non-irrigated hillside near Paso
8 Robles. The species is widely distributed in vineyards and several other perennial crops planted
9 throughout the state (Ferris *et al.*, 2012). Currently, *M. xenoplax* is becoming more prevalent and
10 increasing in population levels in California. This increase is probably associated with the advent
11 of drip irrigation plus soil additives that increase size of pore spaces (M. McKenry, UCR, pers.
12 comm.). During statewide detection surveys for the presence or absence of 22 economically
13 important nematode species in major agricultural crops and nursery production areas within
14 California, the CDFA reported greater numbers of detection of *M. xenoplax* in rhizosphere soils of
15 apricot, cherry, plum, prune, grape, peach, walnut and alfalfa, and relatively few detections in soils
16 of cotton, long bean, oats, orange and tomato, from 16 counties (Dong *et al.*, 2006).

17 *Mesocriconema xenoplax* is a sedentary ectoparasitic nematode that inhabits the rhizosphere soil
18 of host plants and feeds on root tissue through an elongate stylet inserted into a root while the body
19 remains outside. Feeding is completed in one to two weeks resulting in the death of fine roots.
20 During the first year after transplanting, up to 85% of fine roots can be absent (Westerdahl and
21 Duncan, 2015). Seshadhari (1964) determined that *M. xenoplax* reproduced best in very sandy
22 soils than in loam or silty loam, and at the highest soil moisture level (sticky point = 15.5%). The
23 nematode had a life cycle of 25-34 days at 22-26 °C (Seshadhari, 1964). High populations are
24 attained on stone fruit and grape and the nematode is associated with orchards with a replant history
25 (McKenry and Kretsch, 1987; Ferris *et al.*, 2004). In studies conducted during the mid-1970s, *M.*
26 *xenoplax* was experimentally shown to adversely affect growth of stone fruit including peach,
27 Myrobalan and Marianna 2624 plum (Braun *et al.*, 1975; Lownsbery *et al.*, 1977; Mojtahedi *et al.*,
28 1975), almond (McKenry and Kretsch, 1987), and walnut (Lownsbery *et al.*, 1978b). Damage
29 caused by *M. xenoplax* alone in a walnut orchard was difficult to assess due to the combined
30 presence of *Pratylenchus vulnus*, as both species were found to retard plant growth by causing
31 lesions and longitudinal cracks in plant roots, however, Lownsbery *et al.* (1978) gave experimental

1 evidence that initial non-coalesced lesions caused by *M. xenoplax* were smaller than those caused
2 by *P. vulnus*. Ring nematode reduced number and volume of feeder roots, destroyed cortical root
3 tissue, darkened roots, altered water stress, lowered nutrient levels in leaves, reduced fresh and dry
4 weight, and caused stunted growth in Myrobalan and Marianna 2624 plum, Nemaguard and Lovell
5 peach and French prune (Braun *et al.*, 1975; English *et al.*, 1982; Lownsbery *et al.*, 1977;
6 Mojtahedi and Lownsbery, 1975; Mojtahedi *et al.*, 1975). Ring nematode also damages young
7 grape vines and while it may be difficult to assess damage and crop loss in older grape vines, both
8 symptoms are highly probable given the high ring nematode population levels often encountered
9 in California vineyards (Ferris *et al.*, 2012). McKenry (1992) reported reduction of 10% to 25%
10 in grapevine yield with more than 500 *M. xenoplax* kg⁻¹ soil (0.5 nematodes/g⁻¹ soil). However,
11 the greater economic damage caused by *M. xenoplax* is its ability to predispose *Prunus* spp. and
12 *Malus* spp. to bacterial canker caused by *Pseudomonas syringae* pv. *syringae*, contributing to
13 peach decline and mortality in the San Joaquin Valley of California (Lownsbery *et al.*, 1973;
14 English *et al.*, 1980) and *Cytospora* canker of prune caused by *Cytospora leucostoma* (English *et*
15 *al.*, 1982). Bacterial canker was severe when associated with *M. xenoplax* (Lownsbery *et al.*, 1977)
16 and higher densities of the nematode resulted in higher incidence of bacterial canker (Underwood
17 *et al.*, 1994). *Mesocriconema xenoplax* was the most damaging nematode of almonds because of
18 the associated bacterial canker complex in the San Joaquin Valley where about half the orchards
19 had both pathogens (McKenry and Kretsch, 1987). In the Southeastern United States *M. xenoplax*
20 is a major contributor to a similar association with *P. syringae* pv. *syringae* and cold injury
21 resulting in Peach tree short life disease complex (Nyczepir *et al.*, 1983).

22 While earlier reported studies on *M. xenoplax* in California largely involved container
23 experiments, through the years experimental evidence obtained under field conditions have
24 furthered our knowledge on ring nematode, host and environment interactions over time with
25 relevance to appropriate management choices. Seasonal effects on ring nematode population
26 under field conditions have been reported. In a three-year study on population fluctuations of ring
27 nematode in five prune orchards in California, Westerdahl *et al.* (2013) found highest number of
28 ring nematodes at depths of 0 to 30 cm in the summer months and 30 to 60 cm in the fall and
29 winter, with nematode numbers being lowest before irrigation and sharply increased after
30 irrigation. The type of sampling tool had no effect on nematode recovery. An optimum sampling
31 strategy to detect the presence of ring nematodes in a prune orchard would therefore, incorporate

1 those determined results. On the other hand, Ferris *et al.* (2012) found all life stages of *M. xenoplax*
2 to be present through the year but with lower ratios of juveniles to adults and lower proportions of
3 nematode populations in the upper 30 cm than at 30 to 90 cm depths in the summer months in
4 California *Prunus* orchards where trees were irrigated by flooding of large basins when the soil
5 became dry thereby, resulting in root zone soil being subject to extreme wet and dry cycles,
6 particularly in the upper 30 cm. They determined that two samplings, one in spring and the other
7 in fall, are needed to determine the annual trajectory of ring nematode dosage in *Prunus* orchards.
8 The initial management measure to prevent spread of *Mesocriconema xenoplax* to non-infested
9 fields includes the use of certified planting stock, removal of soil from equipment prior to moving
10 between orchards and avoidance of recycling irrigation water (McKenry and Westerdahl, 2009).

11

12 **21.5.5.1 Management**

13

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

22 Most *Prunus* rootstocks support populations of *M. xenoplax* but differ in response to other plant
23 parasitic nematodes. Nemaguard rootstock is planted to ninety percent of the peach industry in
24 California. In earlier studies, Lownsbery *et al.* (1977) found scions on Nemaguard and Lovell
25 rootstocks to be highly susceptible to bacterial canker and *M. xenoplax* in container experiments
26 and indicated the need for comparison of the rootstocks under field conditions. Although
27 Nemaguard rootstock is resistant to root knot nematodes, it is damaged by *M. xenoplax* and is a
28 better host to the ring nematode than Lovell rootstock, which is more tolerant to bacterial canker
29 and resistant to root knot nematode. Furthermore, Nemaguard is among the most difficult to
30 successfully replant because of the ‘rejection component’ of the replant problem. Marianna 2624
31 and Myrobalan 29C rootstocks also commonly used in California, although resistant to root knot

1 nematodes, are highly susceptible to *M. xenoplax*. Viking rootstock is reported to offer some
2 tolerance to ring nematode similar to Lovell rootstock with comparable protection against bacterial
3 canker (McKenry and Westerdahl, 2009).

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

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

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

25 Preplant applications of different rates of lime (CaCO_3) in peach and almond orchards (0, 13.2,
26 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
27 but did not affect numbers of *C. xenoplax* in peach and almond, nor did it reduce incidence of
28 bacterial canker in peach (Underwood *et al.*, 1994).

29 The nematophagous fungus *Hirsutella rhossiliensis* naturally parasitizes *Mesocriconema xenoplax*
30 in a density-dependent manner in many stone fruit orchards in California (Jaffee *et al.*, 1989) and
31 there have been several studies aimed at its exploitative use as a biocontrol agent against the ring

1 nematode under field conditions in California. However, *H. rhossiliensis* was found to be a weak
2 regulator of *M. xenoplax* population density (Jaffee, *et al.*, 1989) and did not regulate ring
3 nematode populations in a newly planted *Prunus* orchard in California (Ferris *et al.*, 2004). Efforts
4 to enhance parasitism of nematodes by *H. rhossiliensis* through the addition of organic matter have
5 been unsuccessful. In a related study, Jaffee *et al.* (1994) determined that parasitism of *M. xenoplax*
6 by *H. rhossiliensis* was only slightly suppressed and numbers of nematodes were not affected by
7 the addition of 73 metric tons of composted chicken manure /ha to a peach orchard in California.

9 **21.5.6 Root Lesion Nematodes, *Pratylenchus* spp.**

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

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

31 **21.5.6.1 *Pratylenchus vulnus***

1
2 *Pratylenchus vulnus* was first reported in 1951 in California as a new species and important plant
3 parasite of various trees and vines, namely walnut, grape, fig, citrus, apricot, avocado, weeping
4 willow, cherry, olive, peach, almond, plum, raspberry and boysenberry (Allen and Jensen, 1951).
5 *Pratylenchus vulnus* is the most common root lesion nematode found associated with almonds in
6 the Sacramento Valley (McKenry and Kretsch, 1987) and is commonly distributed in California
7 vineyards seriously affecting grape yield (Lider, 1960, Raski *et al.*, 1973). Root systems of young
8 grapevines may be restricted in growth with absence of major roots and dead feeder roots while
9 root lesions at feeding sites may not be present. *Pratylenchus vulnus* is also the root lesion species
10 most commonly found in walnut orchards in California (Westerdahl *et al.*, 2017b). Walnut tree
11 vigor and yields are reduced by the feeding activity of *P. vulnus* which places infected trees under
12 stress (Lownsbery, 1956). In California, as in many regions worldwide, this nematode is the
13 primary cause of tree decline and replant problems in orchards (Nyczepir and Halbrecht, 1993;
14 McKenzie, 1999). Growth of young walnut trees can be arrested by *P. vulnus* and the replant
15 problem, even at 1 nematode/250 cm³, and established walnut orchards in California are able to
16 support 500 *P. vulnus*/250 cm³ soil (Buzo *et al.*, 2009). *Pratylenchus vulnus* reduced plum yields
17 by 16, 16, 10 and 6.4% in Lovell, Nemaguard, Myrobalan 29C and Marianna 2624 plum rootstocks
18 respectively, with reduced levels of calcium and magnesium in scion petioles. Monthly and annual
19 fluctuations of *P. vulnus* populations were observed in a plum orchard, with the most stable levels
20 occurring during fall months and at higher population levels in the top 30 cm than lower 30-60 cm
21 depths (McKenry, 1989). During the 70s, *Pratylenchus vulnus* was also found to affect rose
22 production in California (Lear *et al.*, 1970) and was involved in a disease of Manetti rose rootstocks
23 with optimum nematode reproduction in silt loam soil at 20°C (Santo and Lear, 1976).

24

25 **21.5.6.1.1 Management**

26

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

1 The loss and restriction of nematicides has resulted in reliance on alternate options, in particular
2 use of resistant plants, for control of soil-borne nematodes. Over the years, the host status of fruit
3 and nut and grape rootstock varieties to *Pratylenchus vulnus* and other important plant parasitic
4 nematodes have been assessed for resistance, susceptibility, tolerance and intolerance in
5 California. Screening and monitoring plant response to plant parasitic nematode and plant vigor
6 over several years was found necessary as nematode reproductive values can differ after the first
7 year of growth (Westphal *et al.*, 2016a). Currently, no resistance to *P. vulnus* has been found in
8 *Juglans* spp. English and black walnut are very susceptible to root lesion nematode, but their
9 hybrid Paradox is more tolerant than either parent, when nematode population numbers are not too
10 high. Of the presently available clonal Paradox walnut rootstocks in California, clonal Paradox
11 VX211 is nematode-tolerant and was released to California growers in 2007 (Buzo *et al.*, 2005,
12 2009; Hasey *et al.*, 2018; Westerdahl *et al.*, 2017). Buzo *et al.* (2005) determined *P. vulnus*
13 population increases about three times the initial inoculum density in fleshy root tips than within
14 primary roots of four walnut cultivars including the more aggressively-growing Paradox hybrid.
15 Hybrid vigor is a primary quality of VX211 (Buzo *et al.*, 2009).

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

29 Pistachio is an expanding nut crop in California and the selection of rootstocks is critical to mitigate
30 potential risk for increase of *Pratylenchus vulnus* populations in orchards. Westphal *et al.* (2016b)
31 determined that an aggressive population of *P. vulnus* was more aggressive on the popular ‘UCB1’

1 pistachio rootstock which in turn, was less susceptible to the nematode than various *Prunus*
2 rootstocks.

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

6

7 **21.5.6.2 *Pratylenchus penetrans***

8

9 *Pratylenchus penetrans* is another economically important root lesion nematode species found
10 throughout the state on various host plants including apple, cherry, peach, apricot, plum, pear,
11 strawberry, alfalfa, garlic, ornamentals and several other crops (French *et al.*, 1964; Siddiqui *et al.*,
12 1973; McKenry and Roberts, 1985; Dong *et al.*, 2007; Westerdahl *et al.*, 2017). Of particular
13 economic importance is the species' detrimental impact to commercial productions of Easter lily
14 and Oriental lily in Humboldt and Del Norte counties in California which, along with Curry
15 County, Oregon, is the only area in the United States where Easter lily bulbs are grown
16 commercially (Westerdahl *et al.*, 1993, 1998). *Pratylenchus penetrans* has been found in Easter
17 lilies since 1946 (Butterfield, 1947) causing restricted root growth and retarded top growth as well
18 as of non-emergence of shoots from bulbs. *Pratylenchus penetrans* is frequently found in apple
19 orchards in Northern California and is occasionally associated with apple re-plant disease
20 (Westerdahl, 2015), whereas, in alfalfa, it is present only in localized areas of the state (Westerdahl
21 *et al.*, 2017).

22

23 **21.5.6.2.1 Management**

24

25 In California, early studies on the control of *Pratylenchus penetrans* have mainly been on Easter
26 lily (Maggenti *et al.*, 1967, 1970; Hart *et al.*, 1967). Chemical control of *P. penetrans* in Easter lily
27 fields has traditionally consisted of a preplant fumigation with a mixture of 1,3-dichloropropene
28 (1,3-D) and 1,2-dichloropropane (1,2-D) followed by at-planting applications of an organo-
29 phosphate or carbamate, since the nematode infests both planting stock and soil. However, the
30 withdrawal of 1,2-dichloropropane, aldicarb and fenamiphos (Nemacur) in the early and mid-
31 1980s, following their discovery in groundwater, left the use of 1,3-dichloropropene (1,3-D,

1 Telone II) which was suspended in California from April 1990 until early 1996. Consequently,
2 growers used metam sodium or methyl bromide plus an at-planting application of an
3 organophosphate, phorate (Rampart) (Westerdahl *et al.*, 1998). Following the phase-out of methyl
4 bromide, currently, effective preplant soil fumigation with chloropicrin or Telone II and metam
5 sodium (Vapam) are available for use in strawberry and apple. Effective application methods of
6 nematicides have been studied (Westerdahl *et al.*, 1993), but subsequently, concerns over
7 groundwater pollution through use of nematicides in sandy soils of Del Norte County led to
8 investigations of alternative management strategies.

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

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

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

1 meadowfoam seed meal had lower numbers of lesion nematodes than the controls. Similar studies
2 were conducted with essential oil products Dougard, EF400, EF300 and Cinnamite tested as
3 preplant dips of bulblet planting stock and *Paecilomyces lilacinus* as a soil treatment showed
4 varying levels of lesion nematode reduction within roots over the controls (Westerdahl and Giraud,
5 2017).

6

7 **21.5.6.3 *Pratylenchus neglectus***

8

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

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

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

1 barley and potato, while the restrictive effect of *P. neglectus* on *M. chitwoodi* was greatest at 15°C
2 in barley and at 25°C in potato. They inferred that *P. neglectus* has the potential to suppress *M.*
3 *chitwoodi* populations and reduce the damage it causes to potato and barley, but further studies in
4 this area are needed.

5 *Pratylenchus neglectus* was found to be a weak pathogen of barley in pot experiments (Umesh and
6 Ferris, 1992) and a weak or non-pathogen of wheat and barley in field trials, as its rates of increase
7 were highest in the highest yielding cereal varieties but could become important if it were to
8 increase in prevalence (Ferris *et al.*, 1993). Similar observations were made of *P. neglectus*
9 inoculated into 6 alfalfa cultivars resulting in either absent or at low population levels after 4 years
10 (McKenry and Buzo, 1985). Although *P. neglectus* increases susceptibility of potato plants to
11 *Verticillium*, the nematode has not been shown to damage potatoes in California (Westerdahl and
12 Kodira, 2012).

13 In studies conducted over a seven-year period in fields used for potato cultivation and infested
14 with *M. chitwoodi* and *P. neglectus* in the Klamath basin of Northeast California, Ferris *et al.*,
15 (1994) determined nematode population changes under different crop rotation sequences and the
16 impact of those changes on potato yield and quality. Season multiplication rates and overwinter
17 survival rates of both species were related to populations measured in the previous fall and spring,
18 and in fall respectively. A positive relationship occurred between potato tuber blemish and
19 population levels of *P. neglectus* measured in the previous fall and yields were associated with
20 higher population levels of *P. neglectus*. By their analyses, potato yield and quality can be expected
21 based on population levels of *P. neglectus* (or *M. chitwoodi*) measured either in the previous fall
22 or in the spring before planting, whereas winter survival rates of both nematodes are a function of
23 nematode population measured in the fall and increase or decrease in nematode population can
24 occur on various crops or fallow conditions. These predictions of crop damage and nematode
25 population changes had direct implications on nematode management decisions.

26

27 **21.5.6.4 *Pratylenchus thornei***

28

29 *Pratylenchus thornei* is found in all climatic conditions throughout California, particularly in clay
30 and loam soils such as those in the Imperial Valley, Sacramento Valley and eastern slopes of the
31 San Joaquin Valley (McKenry and Roberts, 1985). This lesion nematode has a wide host range

1 comprising annual field, vegetable crops, fruit and nut trees and ornamentals (Siddiqui *et al.*,
2 1973). It is also associated with small grains causing probable damage particularly in warm areas
3 such as the Imperial Valley (Westerdahl and Kodira, 2007). However, their effect on associated
4 crops has not been studied in California. While *P. thornei* has been found mainly associated with
5 small grains: sorghum, wheat, barley, oats in the state (McKenry and Roberts, 1985; Westerdahl
6 and Kodira, 2007; Dong *et al.*, 2007) during recent surveys, the CDFA also found it associated
7 with alfalfa, grape, apricot, cherry, cotton, prune and walnut (Dong *et al.*, 2007). Grain crops
8 infested with *P. thornei* are stunted and yellow in patches in a field, with brown leaf tips, fewer
9 tillers and smaller heads (Westerdahl and Kodira, 2007).

11 **21.5.7 Dagger Nematodes, *Xiphinema* spp.**

13 **21.5.7.1 California Dagger Nematode, *Xiphinema index***

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

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

1 The length of the life cycle of *X. index* is reported as 27 days in California (Radewald and Raski,
2 1962). *Xiphinema index* counts were always highest in the winter months. Temperature likely
3 limits *X. index* reproduction in California because the summers are hotter and the growing season
4 is longer than in most other grape-growing regions of the world. The findings of the study by
5 Radewald and Raski (1962) showed that *X. index* populations fluctuate throughout the year and
6 can be correlated with soil temperature. The possibility of detecting *X. index* in a vineyard can be
7 maximized by sampling within rows during the winter months (Feil *et al.*, 1997). Raski and Hewitt
8 (1960) noted that under starving conditions, *X. index* retained the ability to transmit grapevine
9 fanleaf nepovirus for up to 9 months. The virus did not affect the rate of reproduction of *X. index*
10 but did improve its survival rate during starvation (Das and Raski, 1969).

11

12 **21.5.7.1.1 Management**

13

14 Soil fumigation with methyl bromide or 1,3-dichloropropene was successful over a 3-year period
15 in controlling *X. index*. Such treatments can also give 99.9% reduction of all nematode species in
16 the top 1.5 to 2 m of soil when properly applied (Raski *et al.*, 1971). However, in 1990, the use of
17 1,3-dichloropropene was halted in California.

18 Nematode-resistant rootstocks are a promising alternative to the ban of nematicides. Since the
19 1970s, the University of California, Davis has been developing rootstocks to resist fanleaf
20 degeneration. During the development of this breeding program two *V. vinifera* x *M. rotundifolia*
21 (VR) hybrids, O39-16 and O43-43 were found to be highly resistant to *X. index* and prevent fanleaf
22 degeneration. These root-stocks were derived from crosses of *V. vinifera* x *Muscadinia*
23 *rotundifolia* Small (VR hybrids) and eventually patented and released (Walker *et al.*, 1985, 1989,
24 1991; McKenry *et al.*, 2004). After a 15-year sequence of intensive studies involving 204 separate
25 trials, the five rootstocks (UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD GRN5)
26 with broad and durable resistance to root knot and dagger nematodes were released to nurseries in
27 California in 2009 and were available commercially in 2011 (Ferris *et al.*, 2012). Based on
28 nematode densities, Harmony and Freedom, commercially acceptable for their resistance to root
29 knot nematode, were rated resistant to *X. index* (McKenry *et al.*, 2004).

30 Crop rotation is also possible management strategy in California dagger nematode control. Before
31 vineyards are replanted with grapevines, the land can be cropped with cereals or grains to suppress

1 nematodes. An early study done by Raski (1955) suggested that three years is an adequate period
2 for crop rotation. However, more recent studies suggested that *X. index* infested sites should be
3 left fallow or rotated to crops other than grapes or figs for at least 10 years (McKenry, 2000). In
4 moist sterile soil without food, *X index* died after 9 to 10 months, but survived for 4 to 5 years in
5 soil where grapevines were removed, but roots remained (Raski *et al.*, 1965).

6

7 **21.5.7.2 American Dagger Nematode, *Xiphinema americanum***

8

9 The *Xiphinema americanum*-group is a large species complex comprising 55 nominal taxa of
10 dagger nematode. At present, five valid species of the *X. americanum*-group: *X. americanum s.*
11 *str.*, *X. brevicolle*, *X. bricolense*, *X. californicum*, *X. pachtaicum* and *X. rivesi* have been reported
12 in California (Robbins, 1993; Orlando *et al.*, 2016). At least two unidentified *Xiphinema* species
13 were also reported using molecular methods (Orlando *et al.*, 2016). Representatives of this group
14 are very widely distributed in agricultural fields and orchards in California. For example, sampling
15 from 126 orchards showed that *Xiphinema americanum* and *Paratylenchus hamatus* occurred in
16 more than 90% of the orchards and in all pear-growing areas of the state (French *et al.*, 1964).
17 Although, there are no studies showing direct evidence of pathogenicity of *Xiphinema americanum*
18 group species in California, it has been shown that they transmit viruses: *Xiphinema americanum*
19 *sensu stricto* – *Cherry rasp leaf virus* (CRLV), *Tobacco ringspot virus* (TRSV), *Tomato ringspot*
20 *virus* (ToRSV) (Teliz *et al.*, 1966; Brown and Halbrecht, 1992) and *X. californicum* – *Cherry Rasp*
21 *leaf virus* (CRLV), *Tobacco ringspot virus* (TRSV), *Tomato ringspot virus* (ToRSV)(Hoy *et al.*,
22 1984; Brown and Halbrecht, 1992).

23

24 **21.5.8 Pin Nematodes, *Paratylenchus* spp.**

25

26 *Paratylenchus hamatus* and *P. neoamblycephalus* are the two most common species of pin
27 nematode encountered in California. Because of their small size, all species of *Paratylenchus* have
28 the common name of “pin nematode”. Among other characteristics, these two species can be
29 differentiated by lack of a stylet in the males of *P. neoamblycephalus*. *Paratylenchus hamatus* was
30 first collected in 1944 from a fig orchard in Merced County, and identified by Thorne (Thorne and
31 Allen, 1950). In California, it has also been identified from Butte, El Dorado, Fresno, Kern, Marin,

1 San Joaquin, San Mateo, Santa Barbara, Stanislaus, Sutter, Tehama, and Tulare Counties by Raski
2 (1975) from grape, peach, prune, oak, rose, plum, pear, and walnut.

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

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

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

28 Ferris *et al.* (2012) studied the susceptibility of five newly released UCD series grape rootstocks
29 to *P. hamatus*. Four of the new rootstocks (GRN1, GRN2, GRN3, and GRN5) were moderately
30 resistant and one (GRN4) was found to be moderately susceptible. In contrast, of 22 rootstocks

1 tested in previous studies, 15 were susceptible, four were moderately susceptible, and three were
2 moderately resistant to this nematode.

3

4 **21.5.8 Needle Nematode, *Longidorus africanus***

5

6 During the fall of 1967, the nematode *Longidorus africanus* was found in soil around the roots of
7 stunted lettuce seedlings in the Imperial Valley of Southern California (Fig. 21.5). Root tips of
8 lettuce seedlings attacked by this nematode are swollen and usually have necrotic spots. Seedlings
9 are severely stunted and because it feeds on root tips, plants are often severely stunted before the
10 first true leaf develops (Radewald *et al.*, 1969a). As infected plants mature, stunting continues, and
11 they may never reach harvest-maturity. Root systems of older infected plants are greatly reduced
12 in size. *Longidorus africanus* can cause a serious seedling disease at relatively low population
13 levels in soil (Kolodge *et al.*, 1986). This study showed that *L. africanus* can cause severe growth
14 reductions in both carrot and lettuce, especially when nematode attack occurs within 10 days of
15 seedling. Tolerance levels for carrot and lettuce exposed to *L. africanus* at seeding were less than
16 5 nematodes per 250 g soil (Huang and Ploeg, 2001a).

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

24 The life cycle of *L. africanus* was completed in seven weeks (Kolodge *et al.*, 1986, 1987). *L.*
25 *africanus* population densities increased with increasing depth. Chances for detecting this
26 nematode were greatest in summer at depths of 60 to 90 cm (Ploeg, 1998). Field studies in the
27 Imperial Valley showed a strong correlation between the vertical distribution of *L. africanus* and
28 soil temperature, with high populations occurring in the upper soil layers during the hot summer
29 months (Ploeg, 1998). Nematode multiplication is greatest at relatively high soil temperatures, ca.
30 28 °C. The results suggested that seeding of carrot or lettuce at soil temperatures less than 17°C
31 would significantly reduce damage by *L. africanus* (Huang and Ploeg, 2001b). In the Imperial

1 Valley, where *L. africanus* occurs, this would correspond to the period from November through
2 March.

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

5

6 **21.5.9 Rice White Tip Nematode, *Aphelenchoides besseyi***

7

8 The first documentation of the possible presence of *Aphelenchoides besseyi* in California was in
9 1963 when the species was found in a culture of the fungus, *Sclerotium oryzae*, which had been
10 isolated from a sample collected from a rice field in Butte County. The rice field was used by a
11 research facility that exchanged seed with regions in Southeastern USA where *A. besseyi* was
12 known to parasitize rice (Chitambar, 1999). During 1997, in response to developing international
13 trade agreements between Turkey and the USDA APHIS, the CDFA conducted intensive surveys
14 of paddy rice seed in county driers of 13 rice-producing counties in California. *Aphelenchoides*
15 *besseyi* was detected in few samples obtained from Butte and Sutter Counties. Subsequent
16 detections were from paddy rice seed shipments intended for export in 1999, 2001, 2002, 2005
17 and 2008 in Sutter and Yolo Counties. This nematode species remains very limited in its
18 distribution and infrequent occurrence within rice fields of Butte, Sutter and Yolo Counties and
19 therefore, a zero percent loss of rice yield due to *A. besseyi* was estimated for California in 1994
20 (Koenning *et al.*, 1999). Based on international trade agreements, export shipments of paddy rice
21 are handled on a per shipment basis and disqualify for phytosanitary certification if found
22 contaminated with the white-tip of rice nematode (Chitambar, 2008). The origin of the nematode
23 species in California is not known. If it was introduced, then its low rate of detection and sporadic
24 occurrence in cultivated field is an indication of its inability to fully establish to damaging levels
25 within the state. Chitambar (2008) reasoned that certain biological, cultural and ecological factors,
26 such as insufficient moisture, planting by airplane directly into flooded fields, presence of resistant
27 varieties and high ambient temperatures, may be working against the nematode's ability to
28 successfully establish and spread within California.

29

30 **21.5.10 Sting Nematode, *Belonolaimus longicaudatus***

31

1 The sting nematode, *Belonolaimus longicaudatus* (Fig. 21.6) was discovered for the first time in
2 1992, associated with dying Bermuda turfgrass at a golf course near Rancho Mirage, Riverside
3 County. Consequently, intensive delimiting surveys in the Coachella valley were conducted by the
4 CDFA and the Riverside County Department of Agriculture and by late 1993, the sting nematode
5 was detected on Bermuda and rye turfgrass in eight golf courses (Chitambar, 2008). The
6 nematodes suppressed turfgrass root growth and caused stunting and chlorosis (Mundo-Ocampo
7 *et al.*, 1994). Based on its morphology, the nematode species was identified as *B. longicaudatus*
8 and later confirmed by rDNA characterization (Cherry *et al.*, 1997). Cherry *et al.* (1997)
9 hypothesized that the California sting nematode was introduced from the Eastern United States.
10 There had been earlier detections of the sting nematode in few interstate shipments of plant
11 samples to California that were intercepted on entry and consequently, destroyed by state
12 regulatory action. The current known distribution of the sting nematode is restricted to the original
13 eight golf courses in the Coachella Valley. This was confirmed by surveys of several major golf
14 courses in California, conducted in 2012-13 by the CDFA and sponsored by the USDA APHIS
15 Cooperative Agricultural Pest Survey (CAPS) Program survey.

16 The Bermuda turfgrass in the Coachella Valley golf courses typically exhibited chlorosis at the
17 beginning of April when the sting nematode populations began to increase. In a study on
18 population dynamics of the sting nematode monitored at monthly intervals at three golf courses in
19 Rancho Mirage, Coachella Valley, soil temperature and fluctuation of nematode densities were
20 significantly correlated. At one golf course, population density peaked in October, with 1,000
21 nematodes per 100 cm³ of soil, but declined rapidly, with the lowest population density occurring
22 in December with approximately 50 nematodes per 100 cm³ of soil. Significant increases in
23 nematode populations did not occur until temperature reached 20°C or late spring. Nematode
24 distribution was greatest in the top 15 cm of soil except during the hottest summer months, when
25 the population was higher at depths of 15 to 30 cm. (Bekal and Becker, 2000b).

26 *Belonolaimus longicaudatus* is a major parasite of grasses and is also capable of parasitizing a
27 wide range of crops including grapes, citrus, cantaloupes, lettuce tomatoes, cotton, ornamentals
28 and weeds, however, its host range is not restricted to horticultural grasses or agricultural crops
29 (Bekal and Becker, 2000a). Many weeds, such as *Euphorbia glyptosperma*, *Sisymbrium irio*,
30 *Paspalum dilatatum*, *Portulaca oleracea*, *Sorghum sudanense* and *Cyperus esculentus*, can serve
31 as hosts for *B. longicaudatus* and only *Abelmoschus esculentus*, *Citrullus lanatus* and *Nicotiana*

1 *tabacum* were non-hosts among the tested species. In the Coachella Valley, the sting nematode has
2 not been found in grapes, citrus and other agricultural crops. *Belonolaimus longicaudatus* had a
3 high reproductive fitness on a majority of species tested and is considered a major threat for most
4 agricultural and horticultural crops grown in sandy soils (>80% sand) (Bekal and Becker, 2000a).
5 Following its 1992-93 detection, quarantine restrictions were imposed by State and County in
6 order to contain or suppress the sting nematode within the Coachella Valley. Eradication was not
7 deemed a practical alternative, due to high cost of operations, extensive sampling required and
8 nature of dissemination of the nematode. Restrictions were placed on movement and disposal of
9 mowed grass clippings from sting nematode-infested properties to non-infested properties or
10 agricultural lands. Composting with sewer sludge was chosen as control of potentially infested
11 grass clippings or thatch. Compliance agreements were established with golf course
12 superintendents accordingly. Regulatory restrictions continue to keep *B. longicaudatus* under
13 suppression in the Coachella Valley (Chitambar, 2008).

14

15 **21.5.11 Stubby Root Nematodes, *Trichodorus* spp., *Paratrichodorus* spp. and *Nanidorus* spp.**

16

17 Nematological surveys revealed that the stubby root nematodes are widely distributed in
18 California. Presently, several valid species are reported: *Nanidorus minor*, *Paratrichodorus allius*,
19 *P. grandis*, *P. porosus*, *Trichodorus aequalis*, *T. californicus*, *T. intermedius* and *T. dilatatus*
20 (Allen, 1957; Siddiqui *et al.*, 1973; Rodriguez-M and Bell, 1978). However, molecular analysis of
21 trichodorid samples collected from non-agricultural areas revealed its high genetic diversity and
22 indicated the presence of at least 8 unidentified or putatively new species from the genus *Trichodorus*
23 (S.A. Subbotin and W. Decraemer, unpublished). *Nanidorus minor* and *P. porosus* are mostly
24 distributed species in agricultural fields and orchards. French *et al.* (1964) reported *N. minor*
25 occurred in 12 pear orchards and *P. porosus* in six pear orchards these species in Placer County.
26 Influence of the stubby-root nematode on growth of alfalfa was studied by Thomason and Sher
27 (1957). Ayala and Allen (1968) tested four stubby root nematode species for their ability to
28 transmit Tobacco Rattle Virus (TRV). *Paratrichodorus allius* was a good vector and was used in
29 all experiments on nematode-virus interrelationships, whereas *N. minor* and *P. porosus* were
30 moderately good vectors. The results showed that the populations of *P. allius* became infective
31 after feeding on virus-infected tobacco for 1 hour. Efficacy increased as the feeding time was

1 increased up to 24 hours. Populations remained infective for 20 weeks when kept at 20° C without
2 a host and 27 weeks when feeding on a virus immune host (Ayala and Allen, 1968).

3 4 **21.5.11 Citrus Sheath Nematode, *Hemicycliophora arenaria***

5
6 A brief account of the citrus sheath nematode, *Hemicycliophora arenaria*, is included here as this
7 species has for long, only been reported from California, until more than 25 years later, when it
8 was also reported from Australia and Southern Argentina (Reay, 1984; Brugni and Chaves, 1994;
9 Chitambar and Subbotin, 2014). The nematode was first reported by Van Gundy (1957) as an
10 unknown species parasitizing rough lemon seedlings in a grower's nursery in the Coachella Valley,
11 near Mecca, Southern California, causing 'peculiar galling' of infected roots quite unlike those
12 caused by the root knot nematode (Fig. 21.7) A year later, the species was named and described
13 by Raski (1958) as *H. arenaria*. By 1964, *H. arenaria* was found in a citrus ranch approximately
14 3.2 km from the original site in Riverside County and on citrus land in Imperial County. All
15 properties were planted with citrus trees from a commercial nursery located near Niland in Imperial
16 County, approximately 40 miles from the original site in Riverside County. This nursery had been
17 planted on virgin desert soil and failed due to lack of moisture, and consequently, was abandoned
18 in 1956. Surveys were conducted by the CDFA at that time to establish origin and extent of spread
19 of the nematode species. In 1965, *H. arenaria* was found in a number of soil samples collected
20 from cheese bush, a California native plant, growing in a virgin desert region about one mile north
21 of the original abandoned nursery. At about the same time, the nematode species was also found
22 on cheese bush in another native situation near Palm Springs, about 30 miles northwest from the
23 infestation in Mecca. Additionally, another California native plant, coyote melon, was
24 experimentally shown to be a host of the nematode species (McElroy and Van Gundy, 1967). In
25 1971, *H. arenaria* was found in soil and root samples collected from roadside cheese bush plants
26 near the entrance of a desert state park in San Diego County. These detections indicated that *H.*
27 *arenaria* is indigenous to native plants in low and high elevation deserts within Imperial, Riverside
28 and San Diego Counties of California and had been spread with citrus nursery stock from the
29 abandoned nursery planting near Niland. Subsequent regulatory action taken by the CDFA
30 established the nematode as quarantine actionable and limited in distribution within California

1 (Chitambar, 2016). In 2006, CDFA once again detected this species in lemon and grapefruit soil
2 in Imperial County (Chitambar, 2008).

3 The preference of high temperature and sandy soils explains the very limited distribution of the
4 citrus sheath nematode within desert regions of California, where it was discovered to be endemic
5 on native desert plants (McElroy *et al.* 1966; McElroy and Van Gundy, 1967). This ectoparasitic
6 species reproduces at 30-32.5° C, with 32.5° C being the optimum, to complete a short life cycle
7 of 15-18 days. Almost no reproduction occurs at 20° C and is greatly reduced at 35° C. Van Gundy
8 and Rackham (1961) found reproduction to be greatest in sandy soil and gave experimental
9 evidence of high reproduction in tomato plants. Subsequently, the citrus sheath nematode gained
10 economic importance as a parasite of agricultural crops with the reclamation of Southern
11 California deserts (Maggenti, 1981). In California, citrus is the main host, while other agricultural
12 crops have been experimentally shown to include tomato, blackeye bean, pepper, celery, squash
13 and Tokay grape (Van Gundy, 1959; Van Gundy and Rackham, 1961; McElroy *et al.* 1966;
14 McElroy and Van Gundy, 1967, 1968; Van Gundy and McElroy, 1969). Feeding of *H. arenaria*
15 results in the production of galls at tips of lateral and terminal roots as well as a reduction in the
16 number of feeder roots and top growth. Early studies established the damage potential of this
17 species. The growth of rough lemon seedlings in *H. arenaria* infested soil at 30°C for 5 months
18 was reduced by 36% in comparison to seedlings in non-infested soil. Dry weight of tomato plants
19 was reduced by 28%, and a 10-20% yield reduction in field-grown tomato and squash occurred at
20 the original locality in Mecca, California. Growth of citrus and tomato was reduced from 12% at
21 25°C to 37% at 30°C (McElroy and Van Gundy, 1967, 1968; Van Gundy and Rackham, 1961).

22

23 **21.5.12 Pacific shoot-gall nematode, *Anguina pacifica***

24

25 *Anguina pacifica* was described by Cid del Prado Vera and Maggenti (1984) as a new species
26 from the Northern Pacific Coast of California. This nematode causes stem galls at the base of tillers
27 in annual bluegrass (*Poa annua*), resulting in yellow patches and irregular surfaces on North
28 California golf course putting greens (Fig. 21.8). The disease has been found only along an
29 approximately 20-30-mile-wide coastal corridor from Carmel to Mendocino (McClure *et al.*,
30 2008). Over the years extensive research has been conducted to develop management strategies
31 against *A. pacifica* (Westerdahl *et al.*, 2005). Twenty-nine products were screened in a bioassay

1 for efficacy against the nematode (McClure and Schmitt, 2012). Of those, 8 products showed some
2 degree of control but only 4 were registered for use on golf course greens. McClure and Schmitt
3 (2012) recommended biweekly application of products with the active ingredient azadirachtin that
4 was derived from the Indian Neem tree (*Azadirachta indica*). Recently, Bayer CropScience
5 developed fluopyram as a nematicide with excellent activity against several plant parasitic
6 nematodes. Fluopyram significantly reduced the *A. pacificae* population and associated shoot galls
7 compared to either Neemix or the non-treated control by the end of the study. Two applications of
8 fluopyram at either the low or high rate effectively restored turf health (Baird and Becker 2016)

9 10 **21.5.13 Certain Plant Parasitic Nematodes of Common Occurrence in California**

11
12 Plant parasitic nematodes in this category include species of genera such as *Helicotylenchus*,
13 *Scutellonema* and *Tylenchorhynchus*, that are found frequently and distributed widely in cultivated
14 and non-cultivated region within California. In general, plant damage caused by high populations
15 of these obligate migratory ectoparasitic root feeders may be more significant in small-area
16 production sites and containerized crops in nursery, residential and local situations, than in larger
17 areas and environments such as parks, pastures and cultivated fields. Furthermore, crop damage
18 under field conditions is often difficult to assess since different genera and species are often present
19 in mixed populations (Norton, 1984a).

20 21 **21.5.13.1 Spiral Nematodes of the Genus *Helicotylenchus* spp.**

22
23 In California, *Helicotylenchus* spp. are present in soil around the root zone of a wide range of
24 plants including agricultural crops, fruit trees, ornamentals nursery stock forest trees and shrubs,
25 desert shrubs, grasses and weeds, however, the host status of the associated plants is not always
26 known. Feeding of spiral nematodes results in production of small discolored lesions in the root
27 cortex and other underground parts, on which the nematode feed. Species reproduce mainly by
28 parthenogenesis and high nematode population levels can severely damage roots causing them to
29 become slightly swollen, spongy, discoloured with sloughed-off cortical tissue (Maggenti, 1981).
30 While species of *Helicotylenchus* may not be identified for nematode management in cultivated
31 fields, certain species that have been reported in California include *H. dihystra*, *H. digonicus*, *H.*

1 *pseudorobustus*, *H. erythrinae* and other species (Siddiqui *et al.*, 1973; Dong *et al.*, 2007). Banana
2 spiral nematode, *H. multicinctus*, is not distributed widely in California and was reported in the
3 mid-60s and 70s from Riverside, Los Angeles and San Diego Counties (Sher, 1966; Siddiqui *et*
4 *al.*, 1973). Pathogenicity of *Helicotylenchus* spp. has not studied in California.

6 **21.5.13.2 Spiral Nematodes of the Genus *Scutellonema***

7
8 In California, *Scutellonema* spp., also called spiral nematodes, are common associates of a wide
9 range of agricultural crops, fruit trees, ornamentals, nursery stock, forest trees and shrubs, desert
10 shrubs, grasses, and weeds. Agricultural crops include alfalfa, cotton, potato, corn and several
11 other crops. The host status of associated plants is not always known. *Scutellonema brachyurus*
12 has been reported as wide spread within the state (Siddiqui *et al.*, 1973). General plant damage
13 associated with *Scutellonema* spp. is commonly exhibited as numerous small, brown necrotic root
14 lesion produced as a result of their feeding. Internally, isolated root cavities are produced by the
15 nematodes while above ground symptoms may include leaf stunting and chlorosis, and reduced
16 growth. The shallow root lesions become avenues for secondary invaders, namely bacteria, fungi
17 and mites. Pathogenicity of *Scutellonema* spp. detected on agricultural and ornamental crops in
18 California, has not been studied

20 **21.5.13.3 Stunt Nematodes, *Tylenchorhynchus* spp.**

21
22 *Tylenchorhynchus* spp. are associated with the roots of a wide range of plants including cotton,
23 oats, and corn as well as other agricultural crops, fruit trees, ornamentals, nursery stock, forest
24 trees and shrubs, desert shrubs, grasses, and weeds. The host status of associated plants is not
25 always known. General plant damage associated with *Tylenchorhynchus* spp. includes stunting of
26 the root system which is expressed aboveground by yellowing of foliage, stunted top growth, and
27 sometimes wilt and defoliation (Maggenti, 1981). Generally, *Tylenchorhynchus* spp. are
28 considered mild pathogens of plants and are common associates of several plants (Norton, 1984a;
29 Table 21.2). Pathogenicity of several *Tylenchorhynchus* spp. detected on agricultural and
30 ornamental crops in California has not been studied (McKenry and Roberts, 1985).

1 **21.6 Conclusion and Future Perspectives**

2

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

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

23

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Legends for Figures

Figure 21.1 A: California physical map; B: California county map (Source, A: quazoo.com; B: [picquery](#)).

Figure 21.2 *Meloidogyne* spp. damage A: Carrot; B: Sweet potato (Credit: J. Radewald and University of California, Riverside).

Figure 21.3 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).

Figure 21.4 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).

Figure 21.5 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).

Figure 21.6 A: Sting nematode, *Belonolaimus longicaudatus* feeding on root tip (O. Becker and University of California, Riverside).

Figure 21.7 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).

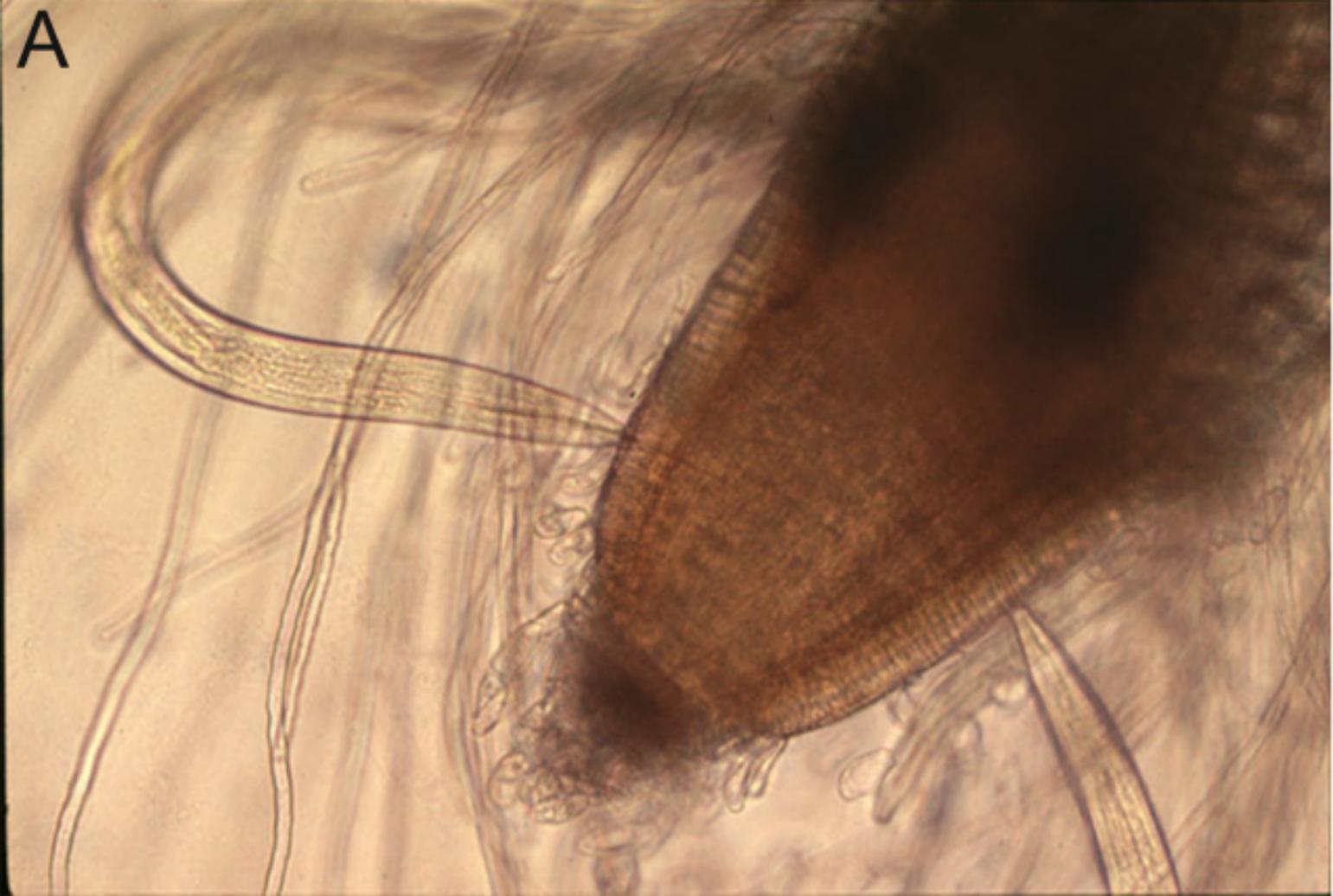
Figure 21.8 *Anguina pacifica*e on *Poa annua*. A: Damaged putting green; B Galls on the crowns of infected plants. (Credit: M. McClure and L. Costello).









A**B**

