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Leaf and Bud Nematodes in Agricultural Crops and Their Management by Biotechnological Approaches

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B. B. Westerdahl and Oluwasesan M. Bello

Abstract

Leaf and bud nematodes in the genus *Aphelenchoides* constitute an important limiting factor in the production of a number of important agricultural crops. The *Aphelenchoides* species which attack aboveground parts of plants cause major economic loss to rice, strawberry, mushrooms, and ornamentals. Losses on rice due to nematode infestation are estimated at 10%. On strawberry, the losses can be as high as 65% in the infested fields. Depending on the level of infestation, losses on mushrooms can be as high as 42%. Important species include *A. besseyi* on rice and strawberry, *A. fragariae* and *A. ritzemabosi* on strawberry, and *A. composticola* on mushrooms. Symptoms of damage are often not recognized because of their similarity to those caused by other pests, diseases, and cultural problems. Molecular methods of identification have been developed to assist with the identification of species. Leaf and bud nematodes can be managed by preventive, physical, cultural, biological, and chemical means. Utilizing certified nematode-free planting materials can prevent infestation. High-temperature treatments can be used to eradicate nematodes from infested planting materials. The use of resistant or tolerant varieties can minimize damage. To help manage *Aphelenchoides*, it is important to have extension personnel to assist growers with recognizing the problem and developing management programs. Because the crops of interest are raised, exported, and imported

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worldwide, it is important to have regulatory programs to minimize the possibility of nematode-infested planting material being exported or imported.

Keywords

Aphelenchoides · Rice · Strawberry · Mushroom · Phytonematodes

16.1 Introduction

Leaf and bud nematodes in the genus *Aphelenchoides* are important limiting factor in the production of agricultural crops. These nematodes attack the aboveground parts of plants causing major economic loss to rice, strawberry, mushrooms, and ornamentals. Rice, *Oryza sativa*, is an important source of food for many people, particularly in Asia, Sub-Saharan Africa, and South America. It is an annual grass that originated in Asia and has been cultivated for thousands of years. It is planted either from seeds or transplants. It grows best with high daytime temperatures and cool nights. It utilizes large amounts of water and is typically planted in a soil type that limits percolation in order to maintain a flooded condition. The ten largest producing countries in order from most to least are China, India, Indonesia, Bangladesh, Vietnam, Thailand, Burma, Philippines, Brazil, and Japan with a total production of 421.3 million metric tons each year. These same countries are also the top ten rice-consuming countries. India, Thailand, Vietnam, Pakistan, the United States, China, Burma, and Cambodia are the largest exporters of rice. Sub-Saharan Africa is the largest importer, followed by the Middle East and Southeast Asia, East Asia, and South Asia (Childs 2022).

The commercial strawberry, *Fragaria* × *ananassa,* was bred in France in the 1700s by crossing plants from eastern North America and from Chile. Commercial strawberries for fruit production are planted from stolons also called “runners” that are horizontal stems arising from a “mother” plant. The runners are produced by the strawberry nursery industry and sold to the fruit production industry. For fruit production, strawberries are grown either as annuals on raised beds that are covered with plastic or as perennials. Annual cropping requires greater initial investment but returns a higher yield (Darrow 1966). The largest producing countries from highest to lowest are China, United States, Egypt, Mexico, Turkey, and Spain with a total production of 8.9 million metric tons. Fruit is produced both for the fresh market and for processing (Tridge 2022). Global exporting of bare root plants is a major market for the nursery industry, and this is a significant concern for the regulatory industry.

Mushrooms are the fruiting body of a fungus known to have been grown in China since 600 AD. The white button mushroom, *Agaricus bisporus*, is the most widely grown variety and was first grown in France beginning in the 1600s (Miles and Chang 1997). Globally, mushroom cultivation has a value in excess of 16.7 billion US dollars. In 2014, China raised more than 30 million metric tons of mushrooms, for an 87% share of the market. Other areas of Asia raised 1.3 million metric tons, while other countries raised 3.1 million metric tons (Taylor 2018). For all of these crops, diseases and pests cause significant loss to the industries. To help manage *Aphelenchoides*, it is important to have extension personnel to assist growers with recognizing the problem and developing management programs. Because the crops of interest are raised, exported, and imported worldwide, it is important to have regulatory programs to minimize the possibility of nematode-infested seeds and plants being exported or imported.

16.2 Plant–Parasitic Nematodes

Plant–parasitic nematodes are microscopic, non-segmented, vermiform aquatic organisms. They utilize a hollow spear or stylet to feed on the cells of plants (Khan 2023). As parasites of plants, they function as either ectoparasites or endoparasites (Khan 2008). As ectoparasites in soil, they live within the film of water that lines the soil pores and feed on roots. As ectoparasites of aboveground parts of plants, they live within protected surfaces of flower and leaf buds or move within a film of water on the surface of stems, leaves, and flowers. As endoparasites, they live either belowground within roots, or aboveground within stems, leaves, and flowers. The life cycle of bud and leaf nematodes is similar to that of other nematodes, consisting of an egg stage, four juvenile or larval stages, and adults (Fig. 16.1). Juveniles and adults have been observed to be active swimmers able to swim up the stems of plants when a film of water is present. Reproduction is thought to be bisexual. The life cycle of bud and leaf nematodes is relatively short lasting approximately 2 weeks. Some species have the ability to become anhydrobiotic during dry conditions and have the ability to survive for several years in this condition. In addition to parasitizing plants, some species are also able to live on fungi (Hesling 1977a, b; Jenkins and Taylor 1967; Siddiqi 1974, 1975).

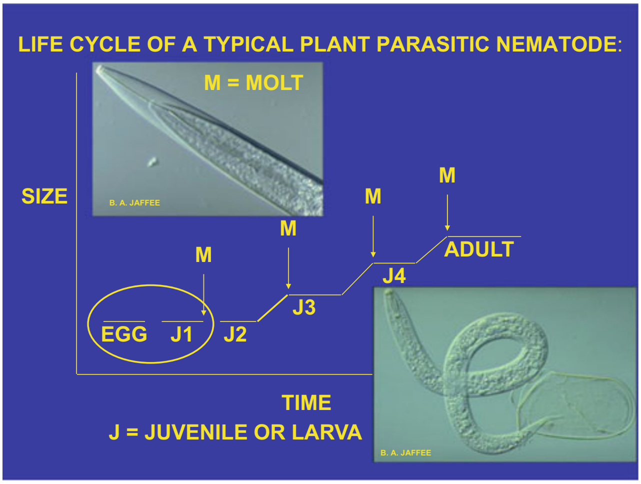

Fig. 16.1 Life cycle of a typical plant parasitic nematode. (Redrawn from Lee 1964)

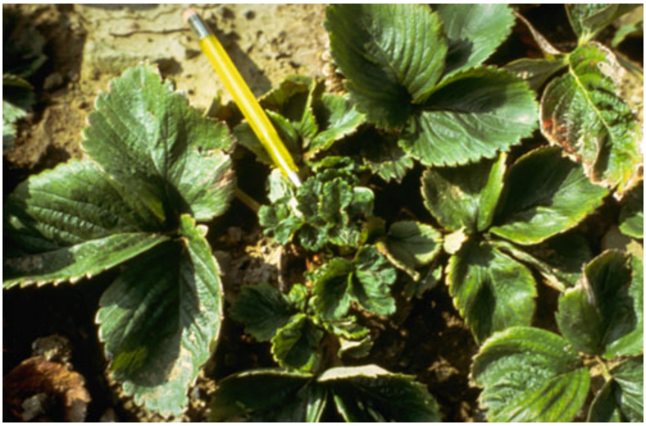

Fig. 16.2 Symptoms of *A. fragariae* on strawberry plant. Department of Entomology and Nematology University of California Davis slide collection

The bud and leaf nematodes are in the Genus *Aphelenchoides*. As suggested by their common name, they generally feed on the aboveground parts of plants. Four nematode clades (groups of organisms that evolved from a common ancestor) have evolved to parasitize plants. *Aphelenchoides* sp. are in Clade 10, the Aphelenchoididae grouped with other species that share similar traits biologically, morphologically, and molecularly. The other clades are the Trichodoridae (Clade 1), Longidoridae (Clade 2), and Tylenchida (Clade 12) (Holterman et al. 2017). Historically, *Aphelenchoides* were placed in a group of nematodes that have the outlet of the dorsal esophageal gland duct orifice located in the metacorpus rather than behind the stylet base as is found in Tylenchida. This grouping has been validated by molecular means. Members of Clade 10 include parasites of plants, parasites of insects, predators of other nematodes, and species that feed on fungi, algae, lichens, and mosses. *Bursaphelenchus xylophilus*, the "pine wood nematode," is another important parasite in Clade 10 that can feed on both plants and fungi (Chap. 25). Also, in Clade 10 is the "red ring nematode" currently known as *Bursaphelenchus cocophilus* (but discussed in older literature as *Bursaphelenchus cocophilus*) that causes "red ring disease of palm."

The important plant parasites of *Aphelenchoides* are typically found aboveground where they are either ectoparasites or endoparasites depending on the species of nematode and of the plant host. *A. fragariae,* for example, is an ectoparasite on strawberries where it feeds on flower and leaf buds causing a disease known as "spring dwarf" (Fig. 16.2), but an endoparasite of ferns (Fig. 16.3) and other ornamental plants where it enters into and feeds within the leaves. *A. ritzemabosi,* a pest of chrysanthemum, enters the leaves through stomata and feeds endoparasitically (Fig. 16.3). For both species, when within the leaves, their movement is initially restricted by the veins of the leaf on which characteristic necrotic lesions form. The necrosis can later spread throughout the leaf. Although not a focus

Fig. 16.3 Symptoms of *Aphelenchoides* on ferns (left) and chrysanthemum (right) illustrating interveinal necrosis. Department of Entomology and Nematology University of California Davis slide collection

Fig. 16.4 Symptoms of *A fragariae* on Easter lily (left) and African violet (**b**) illustrating stunting of infested (left) vs non-infested plants (right). Department of Entomology and Nematology

of this chapter, for management purposes, it is important to consider that leaf and bud nematodes have ornamental plants, aquatic plants, and fungi that can be alternate hosts for the species being covered in detail (Hague 1972; Siddiqi 1975) (Fig. 16.4). *A. besseyi* feeds ectoparasitically both on the growing tips of rice plants where it causes a disease known as "white tip of rice" (Fig. 16.5) and on strawberries where it feeds on young leaves within buds and causes a disease known as "crimp" or "summer dwarf." *A. composticola*, a fungal feeder, is ectoparasitic on mushrooms. *Aphelenchoides* sp. have been able to interact with the bacterium *Corynebacterium fascians* to produce cauliflower disease on strawberry (Hesling 1977a, b; Jenkins and Taylor 1967; Siddiqi 1974, 1975).

Fig. 16.5 Symptoms of *A besseyi* on rice (Khan et al. 2021, p 8). University of California Davis slide collection

Recently, Subbotin et al. (2021) studied several populations that had been previously identified as *A. besseyi*. They determined that morphologically and molecularly *A. besseyi* was a complex of species. They identified a population feeding on strawberries in Florida as matching the characteristics of *A. besseyi*, but a population on rice from Louisiana was identified as being *A. oryzae*, a species that had been previously synonymized with *A. besseyi*. Three populations feeding on ornamental plants in Florida were determined to be different from the two previously described species and were identified as a new species *A. pseudobesseyi*. Several populations from other countries that were previously identified as *A. besseyi* were determined to be *A. pseudobesseyi*. These three species are difficult to distinguish without molecular analysis. These recent findings complicate the situation for regulatory agencies and for the development of non-chemical management programs such as crop rotation and development of nematode-resistant varieties.

16.3 Infestation of Food Crops and Its Management

Leaf and bud nematodes cause serious economic damage to several important crops including rice, strawberry, and mushroom. Reductions are found in both growth and yield. Typical damage symptoms include stunting, wilting, and yellowing of the crop, but these are not diagnostic as such symptoms could be caused by lack of irrigation or fertilization, for example. To diagnose a nematode infestation, samples of infested plant parts and soil need to be taken and sent to a diagnostic laboratory. Nematodes are often irregularly distributed in a field resulting in patches of poor growth.

16.3.1 Rice

Nematodes cause significant economic damage to rice, which is a major source of food in many countries, particularly in Asia. Worldwide, losses from nematodes have been estimated to be 10% (Owen et al. 2023; Sasser and Freckman 1987). This is highly variable from country to country. In the United States, losses due to *A. besseyi* are 1% or less (Koenning et al. 1999). In other locations, losses can be as high as 30–50% (Ichinohe 1972). Variability is affected by variety, the initial level of the nematode population, and cultural practices.

16.3.1.1 White Tip Caused by *Aphelenchoides besseyi*

Aphelenchoides is one of 14 different genera of plant–parasitic nematodes that have been reported to be associated with rice (Ferris 2022a). Depending on where it is found, *A. besseyi* has several common names including rice white tip nematode, crimp nematode, strawberry summer dwarf nematode, strawberry bud nematode, fire-fly blast, heart blight, black grain, and ear blight (Ichinohe 1972; Khan 2010).

A. besseyi is found in at least 71 countries including nine in Europe, 25 in Asia, 27 in Africa, two in North America, five in Central America and Caribbean, three in South America, and five in Oceania (CABI 2021a).

Infection with *Helminthosporium sigmoideum*, a causal agent of stem-rot disease, was less if plants were infected with *A. besseyi*. It was hypothesized that nematode infestation increased the rate of respiration in the plant (CABI 2021a). *A. besseyi* also interacts with *Acrocylindrium oryzae* (previously known as *Sarocladium oryzae*), *Curvularia* spp., and *Fusarium* spp. (Khan 2010).

Leaves and seeds of rice are infected by *A. besseyi* (Jenkins and Taylor 1967). Sixteen days after seeds germinate, white tip disease symptoms become apparent on leaves. The leaf tips first turn pale yellow to white. Later, they may appear shortened and twisted, turn brown, and become necrotic and frayed. Reductions in height, vigor, weight, and number of grains have been reported (CABI 2021a; Khan 2010). Wang et al. (2020) utilized transcriptome sequencing of *A. besseyi* and rice to elucidate their interactions. Their study suggested that *A. besseyi* suppressed the photosynthetic system of rice. In laboratory trials, Liu et al. (2018) determined that hyperspectral reflectance of rice leaves could be utilized to differentiate *A. besseyi* infestation from that of insect and fungal infestations.

Worldwide, it is estimated that three million acres are infested with *A. besseyi* with yield losses of from 2 to 71% (Hollis and Koeboonrueng 1984; Khan et al. 2021).

Management relies on an understanding of the biology of the pest species and begins with an accurate species identification. Molecular techniques are being developed for accurate identification of *A. besseyi,* which is important for breeding programs, certification of seed, and quarantine programs for seed. One method that has been developed is KASP (kompetitive allele-specific PCR) technique using SNP (single-nucleotide polymorphisms) (Devran and Göknur 2020). To detect and quantify *A besseyi* in rice fields in Turkey, Çelik et al. (2019) developed a real-time PCR assay. Rice and fern pathotypes of *A besseyi* can be distinguished by a LAMP (loop-mediated isothermal amplification assay) utilizing the mitochondrial COI (cytochrome oxidase subunit I) gene when as few as five nematodes are present (Yang and Yu 2019).

A besseyi survives in and is disseminated in rice seed where it survives in a quiescent, dehydrated anhydrobiotic stage of reduced metabolism (Hoshino and Togashi 2021). Nematodes become reactivated upon exposure to water. At 25–30 °C, this occurs within 3–4 days (Ichinohe 1972). Nematodes are attracted to rice seedlings and feed ectoparasitically on meristematic tissues (CABI 2021a). As plants grow, nematodes are carried upwards (Christie 1959). They feed ectoparasitically on reproductive tissues and their numbers rapidly increase as plants mature (Christie 1959). At harvest, as rice seeds slowly desiccate, *A. besseyi* aggregate, coil up, and become anhydrobiotic. Up to 64 nematodes, mostly adult females, per seed, have been reported. The economic damage threshold has been reported to be three live nematodes per seed (CABI 2021a). In stored seed, nematode survival was lower at 20–25 °C (3.6 years) than at −5 to 10 °C (18 years) (Hoshino and Togashi 2020).

Reproduction is typically amphimictic but can also be parthenogenetic, and males are common (Huang et al. 1979). The optimum temperature for the development of *A besseyi* is 21–23 °C. A life cycle is reported to take 10 days at 21 °C, 8 days at 23 ° C, and 8–12 days at 30 °C. Development does not occur below 13 °C (CABI 2021a).

In the absence of a host, *A besseyi* is thought to not be able to survive in soil between crops of rice. However, it has been shown that it can be cultured on several species of fungi indicating that it could survive and possibly reproduce in the soil in the absence of rice (Jenkins and Taylor 1967).

Seeding directly into water or irrigating seed beds reactivates nematodes and can reduce subsequent infestation by causing nematodes to use up energy stores prior to germination that typically occurs in 3–5 days (Christie 1959). Low seeding rates and planting in cooler temperatures may reduce levels of infestation (CABI 2021a).

Planting nematode-infected seed is the main route of infestation by *A. besseyi.* Surveys of rice production areas demonstrated that between 2 and 80% of tested seed lots were infested. A number of different hot-water treatments have been developed to eliminate *A. besseyi* from rice seed (Ichinohe 1972). The IRRI (International Rice Research Institute) recommends soaking in cold water for 3 h and then treating in hot water for 15 min at 55 °C (CABI 2021a). Ultrasound and gamma irradiation have also been tested for treatment of seed (CABI 2021a). Exposing seed to a mixture of 97.5% nitrogen and 2.5% oxygen at 25 °C for 10 days has also been utilized to disinfest seed (Khan et al. 2021).

In addition to rice, *A. besseyi* is known to be associated with at least 32 genera of plants. Important crops that are infested include cotton, tobacco, sugarcane, strawberry, soybeans, millet, sorghum, onion, oat, corn, yam, and beans (Ferris 2022a). Ornamental hosts include ferns, gladiolus, chrysanthemum, and tuberose (Ferris 2022a).

Varieties of rice may possess a range of susceptibility. Susceptible varieties may or may not display typical white tip symptoms, while other varieties may be immune to nematode invasion (Ichinohe 1972). It has been observed that nematodes are more attracted to susceptible varieties and that the rate of reproduction is slower in resistant varieties (Jenkins and Taylor 1967). Resistant varieties have been found in studies conducted in Japan, the United States, Italy (Fortuner and Williams 1975), and India (Khan et al. 2021).

Regulations and registrations of pesticides vary with location. Local authorities are consulted to determine those that can be legally used, and product labels are followed. Different methods tested for treating seeds prior to planting include fumigation, or soaking or dusting with various organophosphate and carbamate materials (Jenkins and Taylor 1967). Foliar applications have been less successful than preplant seed treatments.

The supernatant of the bacterial symbiont *Xenorhabdus bovienii*, infective juveniles of the entomopathogenic nematode *Steinernema feltiae*, and the entomopathogenic fungus *Purpureocillium lilacinum* were shown to suppress *A. besseyi* based on observed white tip symptoms and yield (Tülek et al. 2018). Rice utilizes the hormones ethylene, salicylic acid, and jasmonate in defense and immune responses to *A. besseyi* (Xie et al. 2022).

16.3.2 Strawberry

Damage reported to strawberries is serious, but highly variable. In Europe, *Aphelenchoides* was reported to be the seventh most damaging nematode after *Heterodera*, *Globodera*, *Meloidogyne*, *Ditylenchus*, and *Pratylenchus* (Sasser and Freckman, 1987). In Germany, *A. fragariae* reduced yields by 45% and *A. ritzemabosi by 65%* (Blank 1985). *A. fragariae* has also caused significant losses in both France and Italy (Clerfeau et al. 1983; Tacconi 1985). In tests in Poland, on seven strawberry varieties tested, A. *fragariae* and A. *ritzemabosi reduced yields by 32–61%* (McElroy 1972; Szczygiel 1967). In Australia, yields were reduced by 50% by *A. besseyi* (McCulloch 1978). In the United States, losses are infrequent but serious when they occur. For example, in Massachusetts losses as high as 60–70% from *A. fragariae* were reported following the planting of infested planting stock. For *A. besseyi*, infested plants typically yielded 7–10% less than non-infested ones with losses in Louisiana reported at 1–2% and in Florida losses in individual fields were as high as 75% (Brown et al. 1993; Plakidas 1964).

16.3.2.1 Foliar Nematode Disease of Strawberry Caused by *Aphelenchoides* sp.

Three species of *Aphelenchoides* (*A fragariae, A ritzemabosi, and A besseyi*) are aboveground parasites on strawberry (McElroy 1972). Common names for *A fragariae* are spring dwarf (because it is prevalent during cool weather), spring crimp, and red plant (CABI 2022). *A fragariae* is found in eight countries in Asia, 22 in Europe, four in North America, three in Oceania, and one in South America (CABI 2022).

Common names for *A ritzemabosi* are chrysanthemum foliar eelworm, leaf wilt nematode of chrysanthemum, leaf and bud nematode, chrysanthemum foliar nematode, and leaf and bud nematode (CABI 2021b). *A. ritzemabosi* is found in two countries in Africa, seven in Asia, 19 in Europe, three in North America, two in Oceania, and three in South America (CABI 2021b).

Common names for *A. besseyi* are rice white tip nematode, crimp nematode, strawberry summer dwarf nematode (because it is prevalent in warm weather), strawberry bud nematode**,** fire-fly blast, black grain disease, ear blight, and heart blight (CABI 2021a; Khan 2010). *A. besseyi* is found in at least 71 countries including nine in Europe, 25 in Asia, 27 in Africa, two in North America, five in Central America and Caribbean, three in South America, and five in Oceania (CABI 2021a).

Cauliflower disease of strawberry results from the interaction of either *A. fragariae* or *A. ritzemabosi* with the bacterium *Rhodococcus fascians.* In earlier literature, this bacterium is referred to as *Corynebacterium fascians*. In this disease, the flowers of stunted plants look like miniature cauliflowers (Crosse and Pitcher 1952; Pitcher and Crosse 1958).

A. fragariae is most active in cool spring weather when plant growth is beginning. Ectoparasitic feeding activity begins in the crown of the plant from which distorted buds and puckered leaves with short stems emerge. Brown patches may be visible near the mid-rib of leaves. Fruit either fails to develop from the distorted buds or is small and deformed. If runners are allowed to develop, they will likely be infested. During warmer weather, nematodes may become quiescent and symptoms may disappear (McElroy 1972).

A. ritzemabosi and *A. fragariae* may occur separately or together on the same plant (CABI, 2021b). Plants infested with *A. ritzemabosi* are stunted with deformed and crinkled leaves. During warmer weather, symptoms of summer dwarf caused by *A. besseyi* may appear. The symptoms are similar to *A. fragariae* with stunted plants and deformed leaves with short stems. The edges of younger leaves may curl upward, and those of older leaves may curl downward (McElroy 1972).

Yield losses from infestation with *A. fragariae*, *A. ritzemabosi,* and *A. besseyi* can be serious but highly variable. Losses from *A. fragariae* typically occur early in the growing season during cool weather, while losses from *A. besseyi* are seen in warmer weather. Infestations have been shown to reduce the weight of crowns by more than 50%, of fruit yield by more than 80%, and to reduce the number of runners produced by 30% (McElroy 1972).

Management relies on an understanding of the biology of the pest species and begins with an accurate species identification. Sánchez-Monge et al. (2017) utilized the cytochrome oxidase I gene (COI) to distinguish *A. besseyi*, *A. fragariae*, and *A. ritzemabosi*. Wang et al. (2019) utilized a LAMP (loop-mediated isothermal amplification) technique for the identification of individual life stages either alone or in a mixed population of nematode species or in samples of plant tissue.

On strawberry, *Aphelenchoides* species live ectoparasitically on buds and leaves. They move across plant surfaces when a film of water from high humidity, dew, or rain is present (McElroy 1972). Anhydrobiosis permits survival in the absence of moisture (Zhen et al. 2020). *A. fragariae*, *A. ritzemabosi,* and *A. besseyi* are bisexual and reproduce sexually (CABI 2021b). The life cycle of *A fragariae* takes

10–11 days at 18 °C in Lorraine begonia. A female nematode lays about 32 eggs that hatch in 4 days. Juveniles mature into adults in 6–7 days (Strümpel 1967). The life cycle of *A. ritzemabosi* takes 10–13 days and has been studied in chrysanthemum leaves. Female nematodes lay 25–30 eggs that hatch after 3–4 days. It takes 9–10 days for juveniles to mature (Wallace 1960). The life cycle in *Senecio vulgaris* (groundsel) takes 14–15 days (Siddiqi 1974). The life cycle of *A. besseyi* on strawberry takes 2–3 weeks (McElroy 1972).

A. ritzemabosi and *A. fragariae* did not increase in numbers when infested crowns were stored at 14–15 °C, but did increase when stored at 20 °C. They survived at 4 ° C for at least 3 years (French and Barraclough 1962). *A. fragariae, A. besseyi,* and *A. ritzemabosi* can all reproduce on fungi making it possible for them to survive in soil in the absence of a host plant (Hooper and Cowland 1988). De Oliveira et al. (2022) demonstrated that *A. besseyi* can reproduce on pathogenic and non-pathogenic fungi as alternate hosts in the soil**.**

Studies have demonstrated that hot-water treatments of runners prior to planting can effectively control *Aphelenchoides* sp. Treatment of 15 min at 47 °C or 10 min at 46 °C followed by cooling in cold water has been recommended. Qiu et al. (1993) found that exposures of 44.4 °C for 20–30 min, 46.1 °C at 10–15 min, and 47.7 °C at 8–10 min were effective against *A. fragariae*. *A. ritzemabosi was* controlled on strawberry by a 10 min treatment at 46 °C. Strawberry cultivars may have different thermal tolerances, and this should be tested prior to large-scale treatments. Pre-heating runners in warm or room temperature water before treatment and immersing in cold water after treatment are recommended (CABI 2022).

Strawberry plants are propagated vegetatively by means of runners produced from mother plants, and this can lead to the distribution of *Aphelenchoides* species in the planting stock. Worldwide, there are highly effective regulatory programs in place to minimize the spread of *A. fragariae, A besseyi,* and *A. ritzemabosi* on plants (O'Bannon and Esser 1987). Examples of programs to certify that planting stock is nematode-free can be found in EPPO (European and Mediterranean Plant Protection Organization) and CDFA (California Department of Food and Agriculture) documents that provide details for producing nematode-free planting stock and methods to inspect plants and planting sites for strawberry runner plant inspection for both exporting and importing (OEPP/EPPO 2017; CDFA 2009). Studies in Italy conducted over an 8-year time frame have demonstrated the effectiveness of these types of programs (O'Bannon and Esser 1987; Tacconi and Lamberti 1994).

Removing (roguing) and disposal of symptomatic plants as soon as they appear can help to minimize the spread of nematodes to other plants (McElroy 1972). In addition to rogueing of infested plants and propagating from clean mother plants, minimizing surface moisture on plants and contact between plants, planting on ridges, avoiding splashing water from sprinkler irrigation, and rooting runners in containers placed in the row can help to minimize nematode spread in the field (McElroy 1972; Siddiqi 1975).

Over 250 plants in 78 genera in 47 families have been reported to be hosts of *A. fragariae* (CABI 2022; Ferris 2022b). In addition to strawberry, hosts include plants in the families Liliaceae, Primulaceae, and Ranunculaceae and ferns. Wheat has been shown to be a good rotation crop in Japan (CABI 2022).

A fragariae and *A. ritzemabosi* have been reported to occur together in at least 28 hosts. These include strawberry, aster, and begonia. At least 124 genera are alternate hosts of *A. ritzemabosi,* and these are mainly in the Compositae (Ferris 2022c; CABI 2021b). Several weeds including goosegrass, chickweed, buttercup, sowthistle, and speedwell are hosts of *A. ritzemabosi* highlighting that for crop rotation to succeed it is important to control weeds in the alternate crops (CABI 2021b).

In addition to strawberry, *A. besseyi* is known to be associated with at least 32 genera of plants. Important crops that are infested include rice, cotton, tobacco, sugarcane, soybeans, millet, sorghum, onion, oat, corn, yam, and beans (Ferris 2022a). Ornamental hosts include ferns, gladiolus, chrysanthemum, and tuberose (Ferris 2022a).

More than 100 varieties of strawberries grown in various areas of the world have been tested and found to have a range of resistance/tolerance to foliar nematodes, but none have been found that are immune. This indicates the potential for future breeding of varieties with more effective resistance (CABI 2022).

Regulations and registrations of pesticides vary with location. Local authorities are consulted to determine those that can be legally used and follow product labels. Preplant soil fumigation is widely utilized in strawberry fruit production for control of soil-dwelling nematodes, weeds, and fungi and is currently essential for the production of nematode-free planting stock. Because strawberry is a high-value crop, chemical treatments can be cost-effective for improving yields (McElroy 1972).

Various organophosphate and carbamate products have been tested for post-plant treatment of *Aphelenchoides* species on strawberry. Additional chemical tests on ornamentals that have demonstrated efficacy against *A. besseyi* include oxamyl, chlorfenapyr, and spirotetramat (Wheeler et al. 2022), and Rotifa and Evans (2021) tested spirotetramat, abamectin, and azadirachtin alone and in combination with ASM (acibenzolar-*S*-methyl an elicitor of plant defenses) for the management of *A. fragariae* on ornamental plants. All treatments reduced nematode populations compared to an untreated control. In trials on the ornamental plant hosta, Pylon (24% chlorfenapyr) and Nemakill (32% cinnamon oil, 8% clove oil, 15% thyme oil mixture) demonstrated efficacy against *A. fragariae* (Ruisheng et al. 2017).

Thirteen different nematophagous fungi including *Hirsutella rhossiliensis* have been shown to feed on *A. fragariae. H. rhossiliensis* reduced populations of *A. fragariae* by 45–65% (CABI 2022).

16.3.3 Mushroom

Several species of Aphelenchoides are pests of mushroom with A. composticola being the most serious. For example, it is a major factor-limiting mushroom production in India (Richardson and Grewal 1993; Sharma and Seth 1986). Crop loss in Europe, China, Australia, New Zealand, and the United States has also been reported. Infesting mushroom compost with 1, 10, or 50 *A. compostícola* per 100 g compost resulted in yield losses of 26, 40, and 42%, respectively (Arrold and Blake 1968; Richardson and Grewal 1993).

16.3.3.1 Mushroom Disease Caused by *Aphelenchoides composticola*

Worldwide, several species of *Aphelenchoides* have been identified as parasites of commercial mushrooms (*Agaricus bisporus*). Of these, *A. composticola* has been found to cause the most damage. Common names in Germany are Aelchen, Champignon-Blatt (CABI 2019).

An infestation is often not noticeable until patches of the surface of the mushroom bed sink, become foul smelling, and possibly become covered with nematophagous (nematode-eating) fungi (Hesling 1977a, b). Nematodes feed by piercing mycelia with their stylets and sucking out the contents.

In addition to *A. bisporus*, *A. composticola* has been shown to feed on more than ten genera of fungi including several that are plant pathogens (Grewal 1990; Richardson and Grewal 1993), but has not been reported to parasitize plants. Reproduction is bisexual and occurs most rapidly from 23 to 25 °C. The time required to complete a generation is temperature-dependent, requiring 8, 10, and 22 days at 23, 18, and 13 °C, respectively (Arrold and Blake 1967; Cayrol 1967; Okada and Ferris 2001). It can survive without a host for at least 6 weeks and is not killed by freezing or by slow desiccation. From 10,000 to 100,000 nematodes can be found in 1 g of mushroom compost. At high levels, the nematodes can swarm out of the mushroom bed and collect on equipment where they can be easily spread by workers and insects (Hesling 1977a, b).

Good sanitation throughout the growing process is needed to minimize infestation. Pasteurizing wet compost and casing at 60 °C for 2 h is needed to kill nematodes. Dry compost requires temperatures as high as 71 °C to kill nematodes (Sharma and Seth 1986). A number of chemical treatments have been tested to manage *A. composticola* including formulations of neem, dazomet, thiabendazole, and benomyl (Gahukar 2014; Gitanjali 2001; McLeod 1978), but these run the risk of killing the crop or possibly leaving toxic residues. Regulations and registrations of pesticides vary with location. Local authorities are consulted to determine those that can be legally used, and product labels are followed.

16.4 Conclusions and Future Perspectives

Important agricultural species of leaf and bud nematodes include *A. besseyi* on rice and strawberry, *A. fragariae* and *A. ritzemabosi* on strawberry, and *A. composticola* on mushrooms. *Aphelenchoides* species affecting rice, strawberry, and mushrooms feed ectoparasitically on aboveground parts of plants or on fungal mycelia. The major means of nematode dispersal are infested seed for rice, infested runners for strawberry, and infested compost for mushrooms.

Biotechnological approaches are important components of management programs for leaf and bud nematodes. For example, recent advances in molecular identification have determined that *A. besseyi* is a complex of species (Subbotin et al. 2021). This reinforces the need for the accurate identification of species.

When economical and available, crop rotation and use of resistant cultivars are optimum methods for nematode management. Screening of cultivars of rice and strawberry has shown that a range of resistance and tolerance is present in local cultivars. This shows promise for use in breeding programs using biotechnological approaches to develop additional resistant and immune cultivars.

Heat treatment is an effective means for controlling *Aphelenchoides* on rice seed, strawberry runners, and mushroom compost. A cooperative effort involving growers, university research and extension, and government agencies utilizing biotechnological approaches could expand the use of heat treatments by growers for disinfesting planting materials in local cropping systems. Times and temperatures required to kill *A. besseyi*, *A. fragariae, A ritzemabosi,* and *A. composticola* have been experimentally determined. Potential differences in the susceptibility of local rice and strawberry cultivars could be evaluated through university research. Qiu et al. (1993) provided an example of this in which the survival and flowering of local strawberry cultivars not infested with nematodes were evaluated to determine thermal tolerances at predetermined times and temperatures that kill *A. fragariae*. Cooperative programs involving growers, extension, and government agencies could develop equipments from local sources and provide quality control for the treatment of planting materials. These and other cultural and physical methods can reduce the need for using chemical management practices.

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