Entomopathogenic Nematodes for the Management of Subterranean Termites

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Abstract Termites cause economic losses by directly injuring and destroying both living and dead vegetation. They can damage right from sowing the crops till harvest. Billions of dollars are spent annually throughout the world to control and prevent termite infestation. Many bacteria, fungi, and nematodes occurring naturally in soils are known to suppress termite activity. Entomopathogenic nematodes (EPNs) and their associated bacterial symbionts are highly specific in their host range and compatible with many pesticides. EPNs, also called beneficial nematodes, are commercially used to control insect pests. These nematodes offer an environmentally safe alternative to chemical insecticides, and a wide range of EPNs are effective against various termite species. Only a limited number of field studies have been conducted using EPNs as control agents for termites. New isolates of EPNs may prove potential against termite pests in the field. This chapter outlines the potentials of entomopathogenic nematodes in termite management.

Keywords Termite • Biological control • Entomopathogenic nematode

1 Introduction

For many decades organochlorines formed the backbone of termite management worldwide. Synthetic insecticidal compounds became popular due to the long residual action and the wide toxicity spectrum. However, these pesticides were banned or withdrawn from the market for human health and environmental reasons from an increasing number of countries in the late 1980s and the 1990s. Indiscriminate, inadequate, and improper use of these synthetic organic pesticides had caused tremendous damage to the environment. Consequently, negative impacts on soil, groundwater quality, human health, wildlife, and ecological balance within agroecosystems are increasingly becoming a concern. To overcome the hazards associated with chemical pesticides, the use of biopesticides is increasingly being adopted. As a consequence of these developments, the focus in termite management has shifted increasingly to alternative methods in dealing with termite problems.

Biological control constitutes a more environmentally acceptable alternative to traditional chemical control measures. When successfully implemented, it can yield permanent, cost-effective management of pest populations with minimal environmental disturbance. It refers to the application or manipulation of predators, parasitoids, or pathogens in order to suppress and manage insect pest population. The literature contains numerous reports of microorganisms that may have potential to cause the death of termites. Lenz (2005) highlighted the potential of nematodes and fungal pathogens in termite management. A partial review by Myles (2002) lists two viruses, five bacteria, 17 fungi, and five nematodes. The full list of such organisms is no doubt larger. Entomopathogenic nematodes have been found parasitizing species in the orders Hemiptera, Diptera, Hymenoptera, Lepidoptera, Orthoptera, Coleoptera, Thysanoptera, Siphonaptera, as well as Isoptera (Nickle and Welch 1984). These nematodes offer an environmentally safe alternative to chemical insecticides in the management of termites. This chapter outlines the potentials of entomopathogenic nematodes in termite management.

2 Termites

Termites are a group of social insects which are widely distributed throughout the tropical and subtropical regions, with the highest diversity found in tropical forests (Eggleton 2000) while few occur in different temperate areas of the world. They are of paramount importance as pests and belong to the insect order Isoptera, an ancient insect group that dates back more than 100 million years. The Latin name Isoptera means “equal wing” and refers to the fact that the front set of wings on a reproductive termite is similar in size and shape to the hind set. Since the first truly scientific work on termites in 1779, which was carried out in India by J. G. Konig, much work has been done all over the world. The presence of termites is often not readily noticed because of their hidden activities. They act as herbivores as well as decomposers, feeding on a wide range of living, dead, or decaying plant material (Bignell and Eggleton 2000; Traniello and Leuthold 2000). Their feeding habits make them ecosystem engineers, which over long periods of time can modify the physical properties of soil, at various spatial scales (Dangerfield et al. 1998). These termites comprise some 2900 species (Krishna and Grimaldi 2003), of which 300 species are of economic importance as pests in agriculture, forestry, and urban situations worldwide.

Termites present in a locality are pests and do not depend on their species and a number of colonies, more precisely their food habits, whether they are competitors for food resources or not. Based on their habitat, termites can be grouped into three general categories: subterranean, damp-wood, and dry-wood termites (Paul and Rueben 2005). Subterranean termites live in the soil and wood that is in contact with soil. Dry-wood and damp-wood termites live inside wood of varying levels of decay and moisture content. Subterranean termites derived their name because of their association with the soil. These are serious pests of wooden structures causing tremendous amounts of damage (Su and Scheffrahn 1998) and are reported responsible alone for at least 80 % of losses caused by termites (Su and Scheffrahn 1990).

Dry-wood or powder-post termites are primitive termites whose damage often goes unnoticed by homeowners. Dry and powdery pellets, occasionally kicked out by dry-wood termites from infested wood, are very characteristic of their presence. Unlike the subterranean termites, dry-wood termites form colonies within sound dead wood rather than in the soil below. Their ecology and behavior are distinctly different from the subterranean termites, a fact which alters their monitoring and controls procedures from those methods used for standard subterranean termites. They have been reported to cause less than 20 % of damage (Su and Scheffrahn 1990). The pest status of damp-wood termites, however, is minor compared to the other termite groups. The wide distribution, large colonies, cryptobiotic lifestyle, and aggressiveness of subterranean termites make it difficult to manage and control them (Su and Scheffrahn 1988; Culliney and Grace 2000). The annual economic cost of termite damage and prevention worldwide is estimated in billions. Yu et al. (2008) reported damage to wooden structures attributed to termites in the United States can exceed $3 billion annually. Rust and Su (2012) reported global economic impact of termite to be at least $40 billion. Estimates, however, vary considerably by region. High frequency of damage caused by termites and the high losses sustained have resulted in multimillion-dollar pest control industry.

2.1 Biology and Habitat

Termites undergo hemimetabolous (incomplete) metamorphosis. Important biological roles are divided among physically distinct termites, called as castes. Termite colonies contain three principal castes: workers (pseudergates), soldiers, and reproductives (king, queen, alates or swarmers). The worker caste is responsible for the damage that makes termites an economically important pest. They are wingless and sterile and comprise the majority of the population within a colony. Their mouthparts are adapted for chewing through wood or other cellulose materials. Workers do all the physical labor like building nests, foraging, cleaning, feeding all other dependent castes, grooming the queen, etc. Soldiers, however, have only one mission, to defend the colony against invaders with their specialized strong mandibles. They cannot forage for food or feed themselves and depend on the workers to care for them. Soldiers, when disturbed, readily attack approaching object and may secrete a white gluey defensive secretion. Termite queen lays about 3000 eggs a day through its enlarged abdomen (Thompson 2000). The eggs are yellowish-white and hatch after 50–60 days of incubation. The queen lives around 25 years.

Winged reproductives are also called swarmers or alates. Alates are flying form of termites, which fly out in great numbers from mature colonies at certain times of the year. This process is known as swarming. Environmental factors trigger the emergence of swarmers, and they leave the colony in large numbers during spring or early summer in search of new habitats. Following swarming, alates shed their wings, and males and females pair off and seek out a suitable place to establish a new colony. Swarming alates are usually the first sign of infestation noticed. Swarming time, season, and conditions differ among species and locations. Only a small percentage of swarmers survive to develop a new colony. The colony reaches its maximum size in approximately 4–5 years.

The size of a termite colony depends on location, food availability, and environmental conditions. Some colonies remain small; others contain up to several thousand individuals. A mature colony of *Coptotermes formosanus* Shiraki may have 1–4 million termites (Su et al. 1984). While other termites like *Reticulitermes flavipes* (Kollar) may contain ca. 200,000 termites in a colony (Howard et al. 1982) with a foraging range up to 100 m in any direction (King and Spink 1969) (Fig. 1). These data indicated the presence of a large subterranean termite colony beneath an infested structure. A termite mound is the most familiar form of termite nest. Typically, each species builds a characteristic mound, although there may be geographical variation in the size and shape of the mound within species. Apart from grass-eating species, which forage in the open, all termites build tunnels between their nest and source of food through covered runways. These shelter tubes connecting soil with structures are common signs of subterranean termite infestation. Termites construct a variety of tube types as summarized by Ebeling (1978). These covered tunnels provide humidity conditions, thus preventing desiccation, and darkness necessary for their movement and protection against predators. Symbiotic flagellate protozoa are found in the hindgut of lower termites, namely, Kalotermitidae, Rhinotermitidae, Hodotermitidae, Mastotermitidae, Serritermitidae, and Termopsidae. Higher termites, the Termitidae, host no or very few protozoa.

2.2 Distribution and Identification

Many ecological factors influence termite distribution but vegetation and soil type remain the most important. Termites are widely distributed by people who unknowingly transport infested furniture. As a result, many pest termites have very wide distributions. The Formosan subterranean termite *C. formosanus* is the most widely distributed and most economically important. This species of termite is probably endemic to southern China and was apparently transported to Japan prior to the

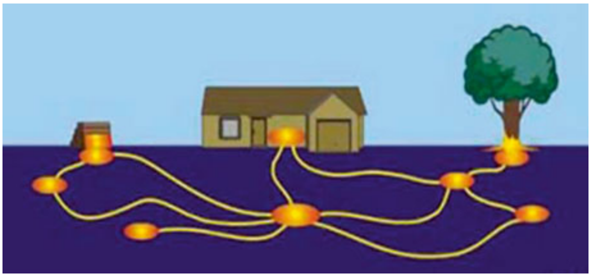

Fig. 1 A single colony of the Formosan subterranean termite *Coptotermes formosanus* Shiraki may contain several million individuals that forage up to 300 ft in soil (*Source*: University of Florida, Publication No. EENY-121)

1600s and to Hawaii in the late 1800s (Su and Tamashiro 1987). Another species of termite, *C. havilandi*, was supposed to have been introduced from Southeast Asia to parts of South and North America and to a number of Caribbean islands, where it became as a serious pest of woodwork in buildings (Scheffrahn et al. 1994; Su et al. 1997a, b). However, in the countries from where it was supposed to have originated, it was never considered a serious pest. Environmental changes can drastically change the species composition, and some rare species in the natural landscape can be more easily detectable in these areas (Dambros et al. 2012). Formosan termites attack a variety of wood products and cause significant damage within a short time period. *C. formosanus*, *R. flavipes*, and *R. hesperus* Banks are the three most important subterranean termite in the United States (Su and Scheffrahn 1990). *C. formosanus* coexists with *Reticulitermes* spp. in some areas of Florida (Scheffrahn et al. 1988a). Termite fauna of Saudi Arabia is predominantly subterranean; however, surveys revealed the presence of dry-wood termites in the Western region, most probably introduced with wood and timber imports from abroad (Faragalla 2002). The majority of the pest species in India are soil inhabiting, either as mound builders or as subterranean nest builders. The major mound-building species are *Odontotermes obesus*, *O. redemanni*, and *O. wallonensis*. The major subterranean species are *Coptotermes ceylonicus*, *C. heimi*, *Heterotermes indicola*, *Odontotermes homi*, *Microtermes obesi*, *Microcerotermes beesoni*, and *Trinervitermes biformis* (Rajagopal 2002) (Table 1).

Soldier termites and alates are the only types of termites that can be accurately identified (Scheffrahn and Su 1994). Soldiers are generally large than the workers, with brownish heads and, in most species, large, toothed mandibles. Unfortunately,

Table 1 Important termite genera in subcontinents

Country	Important termite genera and species
Southern Africa	Anacanthotermes (family Hodotermitidae), Psammotermes and Reticulitermes (family Rhinotermitidae), Amitermes, and Microcerotermes (family Termitidae), and several species of Kalotermitidae
Eastern Africa	Macrotermitidae: Macrotermes (family Termitidae), Hodotermes (family Hodotermitidae), and Schedorhinotermes (family Rhinotermitidae)
Western Africa	Ancistrotermes, Macrotermes, Odontotermes, Microtermes, and Cubitermes (Termitidae)
N. America	Damp-wood termites: (genus *Zootermopsis*,family Termopsidae); dry-wood termites *Incisitermes*, *Neotermes*; subterranean termites *Reticulitermes*, *Heterotermes*, *Amitermes*; and introduced species of *Coptotermes*
S. America	*Cryptotermes* and *Neotermes* (family Kalotermitidae), *Coptotermes* and *Heterotermes* (family Rhinotermitidae), and *Nasutitermes*
China	*Coptotermes, Reticulitermes* (family Rhinotermitidae), *Macrotermes* and *Odontotermes* members of the *Cryptotermes* (Kalotermitidae) and Hodotermitidae
Australia	Subterranean, dry-wood, harvester, and mound builders *Mastotermes*, *Porotemes*, *Stolotemes* (primitive genera)
Europe	*Reticulitermes*

Source: www.chem.unep.ch/pops/termites dry-wood termites do not maintain large number of soldiers in their colonies, and majority of the nest is composed of worker but there is no identification key available for worker individuals. Identification must be done with care, as the alate castes of some dry-wood species found in Alabama were similar in size and color with those of the Formosan subterranean termite. Kirton and Brown (2003) mentioned that *C. gestroi* and *C. havilandi* are, in fact, the same species. *C. gestroi* had been described from the soldier form of the termite by Erich Wasmann in 1896, while *C. havilandi* had been described later by Nils Holmgren in 1911 from the alates of the same species. The difficulty of matching alates to soldiers had led to this situation. If there is taxonomic confusion or the wrong name is applied to the species, then the pest management decisions we make could be based on misleading information. The importance of accurate termite taxonomy in the broader perspective of termite management was highlighted by Kirton (2005). However, Haverty et al. (2005) studied identification of termite species by the hydrocarbons in their feces. They mentioned that hydrocarbons extracted from fecal pellets were qualitatively and quantitatively similar to cuticular extracts and can be used to determine the termite species responsible without the termites present.

2.3 Economic Importance

The economic importance of termites is twofold, extremely beneficial and extremely injurious to man. These small creatures are a part of the natural ecosystem and contribute significantly to most of the world's ecosystems. Their greatest contribution is the role they play in recycling wood and plant material. The breakdown and release of organic matter as termites eat and digest plant material plays an important role in maintaining soil health. Aeration of the soil due to termite burrowing activities helps in maintenance of soil microflora (Wood 1988). Soil fertility improves when termite mounds, rich in minerals, are crushed down and incorporated into the soil. Review by Freymann et al. (2008) on importance of termites for the recycling of herbivore dung highlights the economic importance of termites in tropical ecosystems. Moreover, termites provide a source of protein-rich food for many organisms including ants, guinea fowl, and other mammals including humans. In African countries, use of termites as a protein source for poultry production has been investigated.

Termite species, however, gain pest status when they damage building materials or agronomic and forestry commodities. As the principal food of some of the termite castes is cellulose, they cause economic losses by directly injuring and destroying both living and dead vegetation, buildings, bridges, dams, etc. Termites are among the few forest insects that are able to live in and on both decayed and living plant tissue. They injure living plants originally by attacking from outside but may continue the destruction of living tissues from outside or from within (Fig. 2). Termites also damage man-made fabrics (textile materials), plastics (polytene, polyvinyl chloride), and some metal foils (Howse 1970). Termites ate

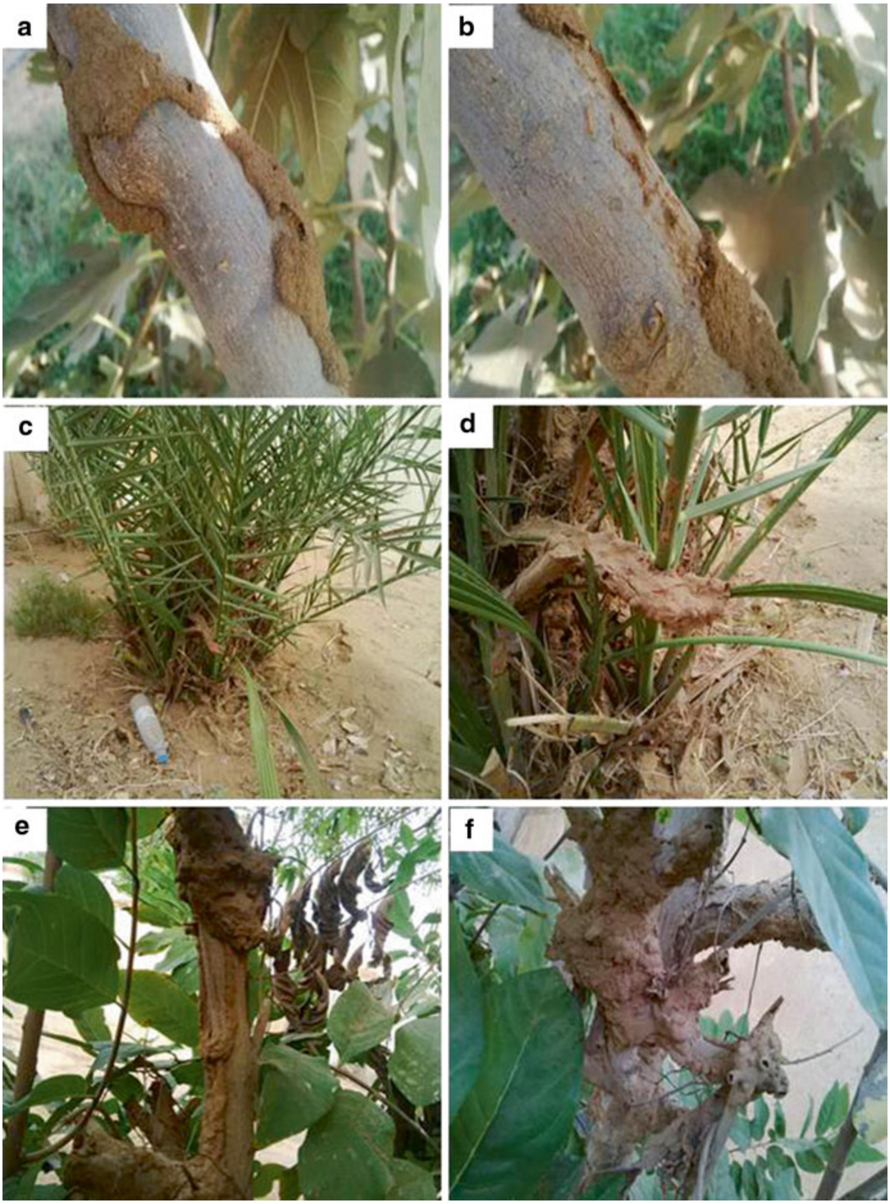

Fig. 2 Termite infestation in various plants

through notes worth Rs. 10 million (about $222,000) stacked in a steel chest inside the State Bank of India, in a northern Indian town (Sacks 2011). The bank was said to be housed in an old building infested with termites. A similar incident happened in Bihar state of India when a trader lost his life savings after termites infested his bank's safe deposit boxes (Tewary 2008). Damage to human habitations by termites varies in its impact. It is estimated that 20 % of Australian homes are infested by termites (Scholz et al. 2010), whereas in China up to 90 % of Chinese homes south of the Yangtze river are affected by termite damage. In what may be the most extreme example of damage by termites, an entire township in India was gradually destroyed by the termite *Heterotermes indicola* and eventually resembled a bombed-out ghost town (Roonwal 1955). Economic losses associated with termite damage in the United States and Japan are around 1000 and 800 million US$ a year, respectively (www.chem.unep.ch/pops/termites), and Japan may be the third largest user of pesticides for structural pest control in the world. Economic losses due to termite in India have been estimated around 35.12 million US$ (Joshi et al. 2005); however, in Malaysia 8–10 million US$ are spent toward termite treatment every year (Lee 2002). Heavy infestation of termite on agricultural crops (field and vegetables) including maize, sorghum, sweet peppers, tomatoes, okra, and millets have also been reported from the western region of Saudi Arabia (Faragalla et al. 1998). Annual economic losses associated with termite activities have also been mentioned by Ghaly and Edwards (2011) (Table 2). Characterization of termite pest problem starts with identification of termite species, knowledge of basic biology and ecology of the species, and evaluation of the magnitude of the economic damage.

2.4 *Losses in Agriculture*

Termites can damage right from sowing the crops till harvest. It is difficult to locate termites and usually it is too late when the typical termite damage symptoms are noticed in field, leading to severe losses. Credible information on the economic losses caused by termites is difficult to obtain. Ground-based monitoring devices, however, have been developed and used experimentally for identification of subterranean termite colony ramifications (Potter 1997). Termites damage was greater in rain-fed than irrigated crops (Sharma et al. 2009). By increasing the number of irrigations, termite damage was reduced (Sharma et al. 2004). Hence, in dry areas where proper facilities for irrigation are not usually

Table 2 Annual economic losses associated with termite activity

Country	Number of termite species	Costs associated with termite activity (US $ 10^6/year)
Malaysia	NA	8–10
India	NA	35.12
Australia	NA	100
China	482	300–375
Japan	21	800
USA	50	1000

available, termite infestation is inimical. In the dryer parts of India, infestation by termite has also been reported by Roonwal (1979) in maize, pearl millet, pulses, sugarcane, cotton, paddy, groundnut, potato, citrus, vegetables, spices, and fruit crops. Annual crops are attacked toward harvest time while perennial crops are attacked most destructively during dry seasons. Severe losses in different regions of India have been recorded on highly susceptible crops such as wheat and sugarcane in North India; maize, groundnuts, and sunflower in South India; cotton in Western India; and tea in Northeast India (Rajagopal 2002). Subterranean termites attack sugarcane crop from its germination through shoot emergence, and finally it affects the quality of canes. At germination stage, the losses up to 90–100 % have been recorded (Salihah et al. 1988). As many as 13 species of termites are reported to cause damage to sugarcane in India. Alam and Miah (1997) reported five species of termites destructive to sugarcane in Bangladesh. Sharma et al. (2004) conducted a survey to determine termite damage on wheat crop covering five mega wheat-growing zones in India. They reported that termites were a real problem in Rajasthan and some parts of Madhya Pradesh. The range of infestation indicated that ~50 % of the fields had low termite damage, ~30 % had medium damage, and ~20 % had severe termite damage. The damage was low in clay and black soils, high in sandy loam soils, and severe in red soils. About 16 species of termite were found to damage the wheat crop in India, of these two species, viz., *Odontotermes obesus* (Rambur) and *Microtermes obesi* Holmgren, were found dominant (Chhillar et al. 2006). Soft wooded tea plants are known to be easily attacked by termites. Live wood-eating termite *Microcerotermes* and dead wood-eating termite *Odontotermes* are tea pest in India (TBI 2014). Ohiagu (1979) reported that termites damage three major cereal crops, maize, millet, and sorghum, in various parts of Northern Nigeria (Table 3).

Table 3 Crop losses and termite genera of different continents

Country	Crop	Losses (%)	Termite species
Africa	Groundnut	Between 10 and 30	*Microtermes* and *Odontotermes*
	Maize	30–60	*Microtermes*, *Ancistrotermes*, *Macrotermes*, *Odontotermes*, *Allodontermes*, and *Pseudacanthotermes*
	Sugarcane	5–10 (Central Africa)	*Amitermes*, *Pseudacanthotermes*, *Macrotermes*, *Odontotermes*, *Microtermes*, and *Ancistrotermes*
		18 (Sudan)	
Southeast Asia	Sugarcane	12 (Pakistan)	*Microtermes*, *Coptotermes*, *Odontotermes*, *Macrotermes*, *Trinervitermes* and *Heterotermes*
Australia	Cashew, mango, and avocado trees	30	*Mastotermes*, *Heterotermes*, *Coptotermes*, *Amitermes*, and *Microcerotermes*

Source: www.chem.unep.ch/pops/termites

3 Entomopathogenic Nematodes

Due to environmental concerns and human safety, efforts have been focused on biological control using entomopathogenic nematodes (EPNs). EPNs are soft-bodied, non-segmented roundworms. They are mobile, highly virulent insect parasites with high reproductive potential. Naturally they occur in soil environments and are capable of parasitizing many economically important insect pests. They locate their host in response to carbon dioxide, vibration, and other chemical cues and in some cases provide a level of insect control equivalent to that of chemical insecticides (Poinar 1986; Georgis 1990). Despite their broad host range and high virulence, these nematodes have shown no mammalian pathogenicity (Gaugler and Boush 1979) and are safe to vertebrates, plants, earthworms, honeybees, and other nontarget organisms (Kaya and Gaugler 1993). In cryptic habitats, EPNs have proven superior to chemicals in controlling the target insect (Gaugler 1981).

The first entomopathogenic nematode was described by Steiner as *Aplectana kraussei* (now *Steinernema kraussei*) in 1923. In 1929, Glaser and Fox (1930) found a nematode, *S. glaseri* (Steiner), infecting grubs of the Japanese beetle *Popillia japonica*, at New Jersey. Jaroslav Weiser described *S. carpocapsae* in 1955. The genus *Heterorhabditis* was described in 1976. The genus *Steinernema* and *Neosteinernema*, family Steinernematidae, and genus *Heterorhabditis*, family Heterorhabditidae (Rhabditida: Nematoda), contain the most important species of entomopathogenic nematodes. Now *Steinernema* contains more than 50 species and *Neosteinernema* only one species, *N. longicurvicauda*. *Heterorhabditis*, however, contains more than a dozen species. Steinernematids and heterorhabditids received great attention as a group of biological control agents in the 1990s. The history of entomopathogenic nematology is briefly reviewed by Poinar and Grewal (2012).

Steinernematids and heterorhabditids are obligate insect parasites (Poinar 1979) and are associated with symbiotic bacteria of the genera *Xenorhabdus* spp. and *Photorhabdus* spp., respectively (Akhurst and Boemare 1990). These *Xenorhabdus* and *Photorhabdus* are motile, gram-negative, facultative, non-spore-forming anaerobic rods in the family Enterobacteriaceae. Together, nematodes and their symbiotic partners form an insecticidal complex that is effective against a wide range of insect hosts (Gaugler and Kaya 1990; Kaya and Gaugler 1993). Symbiotic bacterium of *H. bacteriophora* was earlier characterized as *Xenorhabdus luminescens* in 1979 which was later transferred to the genus *Photorhabdus* (Boemare et al. 1993). Most *Photorhabdus* spp. are luminescent and catalase positive, whereas *Xenorhabdus* spp. have no luminescence and are catalase negative. Studies suggest each *Steinernema* species has an apparent specific natural association with only one *Xenorhabdus* species, though a single *Xenorhabdus* bacterial species may be associated with more than one nematode species (Fischer-Le Saux et al. 1999; Boemare 2002). Poinar (1966) and Poinar and Leutenegger (1968) demonstrated the location of bacteria in the infective-stage juveniles, using light microscopy and later electron microscopy. In *Steinernema* bacterial symbionts are harbored in a specialized structure known as “bacterial receptacle.” In *Heterorhabditis* bacterial symbionts are distributed along a broad stretch of the anterior portion of the nematode intestine. Entomopathogenic nematode species and isolates show substantial variation in behavior, host range, infectivity, reproduction, and environmental tolerances. EPNs find their hosts either actively or passively (Smart 1995). Directional response to electrical fields varies among EPN species which may be used by nematodes for host finding or other aspects of navigation in the soil (Shapiro-Ilan et al. 2012a).

Entomopathogenic nematodes, also called beneficial nematodes, are commercially used to control insect pests. *S. carpocapsae* was the first nematode product marketed while *S. scapterisci* became available commercially only in 1993 and *S. riobravis* in 1994 (Smart 1995). These EPNs offer excellent potential for control of insects in soil habitats but are not well suited for foliar application, as they are sensitive to desiccation and ultraviolet radiation. In laboratory tests, *S. carpocapsae* alone infected more than 250 species of insects from over 75 families in 11 orders (Poinar 1975). The broad host range and high virulence of entomopathogenic nematodes make them suitable for use as augmentative-release biocontrol agents (Hui and Webster 2000). They can be mass produced easily in liquid culture at economically reasonable costs (Ehlers et al. 1998) and are sufficiently small to pass through standard spraying equipment. These nematodes are compatible with many pesticides, can be mass produced and formulated, and have been exempt from registration in many countries. Insects controlled with entomopathogenic nematodes have been reviewed by various researchers (Klein 1990; Georgis and Manweiler 1994; Smart 1995; Hazir et al. 2003; Lacey and Georgis 2012). Several books on the potential use and field techniques of ENPs in various cropping systems has been published (Gaugler and Kaya 1990; Bedding et al. 1993; Lacey and Kaya 2000; Gaugler 2002). Similarly, Lacey and Georgis (2012) highlight EPN development for control of insect pests, above and below ground, including those from foliar, soil surface, cryptic, and subterranean habitats.

Subterranean termites live and forage in habitats that are moist, cool, and without direct sunlight such as soil or wood materials. These environmental conditions are ideal for the survival and movement of steinernematid and heterorhabditid nematodes and, therefore, provide the basis for the interest in their role in control of termites. Research shows that the entomopathogenic nematodes have a potential to use as environmentally safe alternative control tactic for termites (Wang et al. 2002; Yu et al. 2006). The rapid development in the study and commercial application of EPNs in pest control during the last 30 years instigated further interest in finding useful nematodes and better application methods to control subterranean termites. EPNs market continues to grow rapidly with US$14.5 million in 2007 and >US$20 million in 2013 (CPL 2006, 2013a, b).

3.1 Biology

Nematode infective juveniles (IJs) live in soil where they search for susceptible insect hosts. Nonfeeding juveniles invade the body of the susceptible insect by direct penetration either through natural openings (mouth, anus, and spiracles) or, in some cases, through the cuticle. *Heterorhabditis* use an anterior tooth to penetrate directly into the hemocoel. The parasitic cycle of nematodes is initiated by the third-stage infective juveniles (IJs), the only free-living stage. These infective juveniles act as vectors to transport the bacteria (*Xenorhabdus* and *Photorhabdus* spp.) into an insect host within which they can proliferate, as bacteria alone are incapable of penetrating the alimentary tract and cannot independently gain entrance to the host's hemocoel. IJs penetrate the alimentary tract of the host insect and release symbiotic bacteria, which are held in the intestine. At this point in their life cycles, bacteria and nematodes exist separately although in close proximity to one another. The released bacteria cause a lethal septicemia, killing the host within 24–48 h. The bacteria produce extracellular enzymes that break down proteins and lipids in the insect carcass, thereby providing nutrients for bacterial and nematode growth. The bacteria also suppress secondary infection of the host by producing antibiotic substances. Inside the hemocoel, IJs of *Heterorhabditis* release the symbionts by regurgitation, while bacteria are defecated by *Steinernema* spp. (Ciche et al. 2006). Nematode and its symbiotic bacteria act together in overcoming the insect's immune response (Dowds and Peters 2002). *Heterorhabditis* spp., if deprived from their symbionts, are nonpathogenic to insects (Han and Ehlers 1999), whereas symbiont-free *Steinernema* spp. will kill their insect hosts, although it takes them about ten times longer to do so (Ehlers et al. 1997). A review by Stock and Blair (2008) on entomopathogenic nematodes and their bacterial symbionts provides detailed information. Even though the bacterium is primarily responsible for the mortality of most insect hosts, the nematode also produces a toxin that is lethal to the insect (Burman 1982).

Symbiont bacteria create conditions necessary for nematode survival and reproduction within the insect cadaver. The nematode initiates its development, feeding on rapidly multiplying bacterial cells and host tissues that have been metabolized by the bacterium. Nematodes develop through four juvenile stages to the adult and then reproduce. They complete 1–3 generations within the host cadaver, depending on host size. When nematode numbers become high and nutrients become limiting in the insect cadaver, nematode progeny reassociate with bacteria and differentiate into the colonized, nonfeeding IJ form that emerges into the soil to forage for a new host (Kaya and Gaugler 1993). Reproduction differs in heterorhabditid and steinernematid. IJs of heterorhabditid nematodes become hermaphroditic adults, but individuals of the next generation produce both males and females, whereas in steinernematid (with the exception of *Steinernema hermaphroditum* (Griffin et al. 2001)), all generations are produced by males and females (gonochorism) (Grewal et al. 2005).

Infective juveniles do not feed but can live for weeks on stored reserves as active juveniles and for months by entering a near-anhydrobiotic state. The length of time that juveniles survive in the soil in the absence of a host depends upon temperature, humidity, natural enemies, and soil type. Generally, survival is measured in weeks to months and is better in a sandy soil or sandy loam soil at low moisture than in clay soils. The heterorhabditids do not survive as well as do steinernematids (Molyneux 1985). Their survival is better in sterilized soil than in non-sterilized soil. EPN population in non-sterilized soil is reduced by bacteria, fungi, mites, predatory nematodes, tardigrades, and other soil organisms (Smart 1995). Mites appear to be especially voracious nematode feeders.

3.2 Rearing

EPNs in the genera *Steinernema* and *Heterorhabditis* are commercially available for the control of soil-inhabiting insects. Several companies in Asia, Europe, and North America mass-produce EPNs either on a small scale or in large scale using bioreactors (Shapiro-Ilan and Gaugler 2002). EPNs can be reared by different methods either in vivo or in vitro (Bedding 1984; Georgis 1990; Shapiro-Ilan and Gaugler 2002; El-Sadaway 2011). For solid medium culture, a substrate such as beef kidney or liver or chicken offal may be used. The substrate usually is made into a paste that is coated onto a porous substrate such as sponge. The medium is sterilized and inoculated with the bacterium and then nematodes are added 24 h later. Infective juveniles are harvested after about 15 days. This method is labor intensive and is particularly well suited for laboratory use and small-scale field experiments. Production in liquid medium can be done in small containers or in fermentation tanks. Greater numbers of juveniles can be produced per unit area in fermentation tanks, which makes this method especially suited for large-scale commercial production at reasonable quality and cost (Shapiro-Ilan et al. 2012b). Ru (2001) and Sharma et al. (2011) highlight mass production, commercialization, and utilization of EPNs as microbial biopesticides for plant protection.

3.3 Distribution and Dispersal

Steinernematids and heterorhabditids are ubiquitous in distribution and have been recovered from soils throughout the world (Hominick et al. 1996). *S. carpocapsae* and *S. feltiae* are widely distributed in temperate regions, *H. bacteriophora* is common in regions with continental and Mediterranean climates, and *H. indica* is found throughout much of the tropics and subtropics. Other species such as *S. rarum*, *S. kushidai*, *S. ritteri*, and *H. argentinensis* appear to have a much more restricted distribution (Hazir et al. 2003). Juveniles of nematodes can be dispersed at great distances, vertically and horizontally, both actively and passively (Kaya 1990; Parkman et al. 1993). Passively, they may be dispersed by rain, wind, soil, phoresis, infected hosts, or human activity which may, in part, account for their widespread global distribution. Zadji et al. (2014b) observed nematode dispersal occurred by infected termites or phoresis. In addition to jumping for some nematode species, the infective juveniles can disperse in soil up to 90 cm in both the horizontal and vertical directions within 30 days (Kaya 1990). Soil porosity can also affect nematode dispersal with less dispersal occurring as soil pores become smaller. Although some entomopathogenic nematodes have been isolated from insects naturally infected in the field, they are most commonly recovered from soil by baiting with susceptible insects (Bedding and Akhurst 1974). The wax moth larva *Galleria mellonella* (L.) is most commonly used as bait. Molecular techniques have also been applied to measure genetic diversity of the nematodes and provide an initial screen to identify useful strains.

3.4 Genetic Manipulation

A limitation of nematodes for insect control is their susceptibility to environmental stress like extreme temperature, solar radiation, and desiccation, which prevents them from being used to maximum advantage as bio-insecticides under field conditions. The ability of different species to tolerate adverse conditions varies enormously. The potential of genetic engineering to enhance nematode environmental tolerance is being explored. To enhance tolerance of high temperatures, *hsp70A* (heat shock protein genes) from the free-living nematode *Caenorhabditis elegans* was introduced to *H. bacteriophora* juvenile (Hashmi et al. 1995; Wilson et al. 1999). Resulting transgenic strain, however, was not successful at field level. Isolation of natural populations that can survive harsh environments, such as deserts, indicated that some populations have enhanced abilities to survive desiccation. Fodor et al. (2010) isolated a *tps-1* gene from the yeast *Saccharomyces cerevisiae* and transformed it to *H. bacteriophora* which showed increased osmotolerance. In another study, indigenous gut bacteria of the subterranean termite *C. formosanus* were genetically modified with entomopathogenic bacterium *Photorhabdus luminescens* subsp. laumondii TT01, a symbiont of the entomopathogenic nematode *H. bacteriophora*. When termites were fed on filter paper inoculated with these recombinant bacteria, the chromosomal expression of the introduced genes showed that there were insecticidal activities against termite workers and soldiers. Termite mortality was reported 3.3 % at day 5, and it increased from 8.7 % at day 9 to 93.3 % at day 29 (Zhao et al. 2008).

4 Control Measures of Termite

Successful termite management requires many special skills and varies depending on the species causing infestation. An understanding of termite biology and its identification can help to detect problem and methods of control. Subterranean and, less frequently, damp-wood termites can have nests at or near ground level, so control methods for these can be similar. However, dry-wood termites nest above ground; therefore the approach for eliminating them is different. The predominant control strategies for subterranean termite consist of chemical treatment and baiting systems using a matrix containing a slow-acting insecticide or insect growth regulator.

Dry-wood termites, however, must be treated by removing infested wood, using spot treatments or by fumigation. An integrated program to manage termites must be practiced.

4.1 Cultural Practices

Cultural practices regulate termite numbers rather than eliminate them so that the benefits provided by termites are not lost. Removal of the queen or destruction of the nest has frequently been used by farmers as a traditional method for control of mound-building termites. Mounds are physically destroyed, flooded, or burnt with straw to suffocate and kill the colony. Deep plowing exposes termites to desiccation and to predators; therefore repeated plowing and digging of the soil may reduce termite damage. The removal of residues and other debris from the field may reduce potential termite food supplies and hence lead to a reduction in termite numbers and subsequent attack. Wood ash around the base of the trunk of coffee bushes and date palms has been recorded as preventing termite infestations. Intercropping maize and beans is the most effective cultural practice used by small-scale farmers in sub-Saharan Africa. Although termites may damage healthy plants, water-stressed and diseased plants are generally more susceptible to termite attack. Inorganic fertilizers enhance plant vigor and hence the ability to withstand pest damage. Application of nitrogen, phosphorus, and potassium in wheat, barley, and yam has been observed to reduce termite incidence. Sowing of indigenous varieties is recommended. In general, crops susceptible to termites are exotic while resistant crops are indigenous.

4.2 Barrier Control

Barriers can be physical, chemical, or hybrid. Physical barriers are good for prevention of termite damage in buildings and storage structures. As chemical barriers, soil applications of liquid termiticides to form a termite-impermeable barrier are in vogue these days especially for protecting buildings and other structures. The standard measure of acceptable performance is that the chemical barrier must keep termites from penetrating 90 % of the barriers for at least 5 years (Gold et al. 1996).

4.3 Chemical Control

For the last four decades, pest control industry has depended heavily on soil termiticides, and still chemical control is playing a vital role in controlling subterranean termites (Su and Scheffrahn 1998). With cryptic insects such as termites, effective delivery of insecticides to kill the population is particularly challenging. Reproductive and nymphs of subterranean termites are concentrated in nests near or below ground level, out of reach of other control methods. Therefore, common methods for controlling these termites are the application of termiticides or baiting campaigns. Active ingredients in currently available termiticides can be broadly classified as repellent or nonrepellent.

Repellent means that the termites are able to detect the insecticide, which basically serves as a barrier, and termites are repelled by it without receiving a dose that will kill them. Therefore, when using these materials, it is important to make sure there are no gaps remaining in the barrier. Repellent termiticides provide immediate protection for the structure. Currently available repellent termiticides include pyrethroids such as permethrin (Dragnet® FT, Prelude®), cypermethrin (Prevail® FT, Demon® TC), deltamethrin (Suspend® SC), and bifenthrin (Talstar®). Apart from repellent, some termiticides prevent termite invasion by nonrepellent or lethal contact. They include imidacloprid (Premise®), fipronil (Termidor®), chlorfenapyr (Phantom®), etc. Chlorpyrifos, iodofenphos, isofenphos, carbosulfan, and carbofuran have been used as alternatives; however their low persistence often necessitates repeated applications. Environmental factors, viz., soil type, weather, and application techniques, influence the mobility of insecticides in the soil. Use of pesticides containing conventional active ingredients in both agriculture and urban areas had led to increased exposures and unacceptable risks (NRC 1993; Wright et al. 1994). They were also a threat to water quality in many areas (Johnson 2005). Due to increasing concerns about these side effects, there has been great interest in finding other methods of controlling termites and reducing the use of chemicals. Moreover, treatment of soil under the structure may kill only a small portion of the colony. It is very likely that the majority of the colony population will survive to re-infest the structure, either by flying alates or foragers entering through an untreated or an inadequately treated portion of soil.

4.4 Baits

The last decade has seen the rapid development of baiting technology. Termite baits are a promising alternative to soil termiticide treatment. Where liquid termiticides are not normally suitable to apply, termite baits can be used. Bait matrix may contain a slow-acting insecticide or chitin synthesis inhibitor. Foraging termites feed on termite baits and carry the digested cellulose and termiticide back to the colony where they regurgitate their stomach contents to feed other termites, a process known as trophallaxis, leading to the demise of the entire colony population. Effectiveness of these treatment methods varies depending on the skills of the applicator, type and dosage of chemical used, and target species (Rust and Su 2012).

4.5 Trap-Treat-Release

Trap-treat-release (TTR) was developed by Dr. T. G. Myles at the University of Toronto. TTR is a technique for suppressing or killing social insect colonies, particularly subterranean termite colonies. In this technique the toxicant is applied externally to termite bodies as a groomable coating. Coated termites carry effectively larger loads of toxicant than do bait-fed termites. Under laboratory conditions, it is possible to achieve extraordinarily high kill ratios among members of the colony (one treated termite can kill over 1000 untreated termites). Under field conditions, an estimated 50–100 termites are killed for each termite treated.

4.6 Host Plant Resistance

Natural resistance of wood to termite attack is due in part to chemicals deposited during heartwood formation (Kumar 1971; Scheffrahn et al. 1988b). Chemicals in termite-resistant wood may be contact toxic to termites or act as antifeedants, repellents, or protozoacides (Carter et al. 1983). A specific chemical that causes resistance to insects may occur only in one plant species and not in others. Cornelius and Osbrink (2015) evaluated the wood consumption of the subterranean termite *C. formosanus* on ten different species of wood, used as commercial lumber. They reported that teak was the most resistant wood tested, and toxic chemical components of teak hold the most promise as wood preservatives. Indigenous crops are more resistant to termites than exotic crops. In Africa, sorghum and millet are more resistant to termites than maize and cowpea. The indigenous crop bambara nuts are not attacked while groundnuts suffer serious damage.

4.7 Biopesticides

Some plant biomass contains insecticidal activity which can be exploited for termite control. A rich source of new pesticides is plant essential oils. Singh and Kumar (2008) evaluated the anti-termite activity of *Jatropha curcas* Linn. oil and its toxic fraction at 1, 5, 10, and 20 % dilutions against *Microcerotermes beesoni* Snyder. They reported maximum wood protection against termites of both the treatments at 20 % concentration. Orange oil is currently available as an insecticide and has been registered in California under the brand name XT-2000™ for control of dry-wood termites (Mashek and Quarles 2008). Hu et al. (2011) reported anti-termitic properties of *Lantana camara* cultivars against subterranean termite *Reticulitermes flavipes*. Elango et al. (2012) evaluated the anti-termitic activity of crude leaf hexane, ethyl acetate, acetone, and methanol extracts of medicinal plants against *C. formosanus*. All the crude extracts were reported to show anti-termitic activity in a dose-dependent manner and exhibited a significant activity after 24 and 48 h of exposure.

4.8 Biological Control Agents

Natural enemies of insect pests, also known as biological control agents, include predators, parasitoids, and pathogens. Biological control is generally perceived as both providing more permanent insect control and as having less potential damage to the environment or nontarget organisms. Therefore, biocontrol should be considered as a long-range research goal rather than an immediate solution. Brazil has a history of success with biological control projects involving the use of parasitoids, insect pathogenic fungi, and viruses (Campanhola et al. 1995). The shortcomings associated with conventional chemical control methods have prompted policymakers and scientists to evaluate the potential for natural enemies to suppress termite populations. The use of biological control agents to hunt or to infect termites within their hidden galleries is appealing. Reviews by Grace (1997)on biological control strategies for the suppression of termite, by Culliney and Grace (2000) on prospects for the biological control of subterranean termites, and by Verma et al. (2009) on biological alternatives for termite control provide complete knowledge for nonchemical control of termite.

Specialized natural enemies of termites are rather limited in numbers, possibly because of cryptic and protected habitats in which termites live. As termites provide a good source of protein, their predators include spiders, beetles, flies, wasps, and especially ants. Other predators include frogs, reptiles, birds, and mammals such as pangolins, bats, and monkeys. Bushes and trees around farms are a home for many of these useful creatures. Termite predators are both opportunist and specialist, but ants are the greatest predators of termites and may have a considerable local impact on termite populations in some areas of the world. Although ants limit termite numbers under natural conditions, their suitability for use as biological control agents for target termite management has yet to be ascertained. Larvae of *Lomamyia latipennis* (Neuroptera: Berothidae) are carnivorous, live within termite nests, and prey upon damp-wood termites, *Zootermopsis angusticollis* (Hagen) (Tauber and Tauber 1968; Johnson and Hagen 1981). A few parasitoids of termites are known, but their potential for regulating termite populations seems negligible. A larval parasitoid *Verticia fasciventris* Malloch (Diptera: Calliphoridae) was reported to develop in the head of soldier termite in some species of *Macrotermes* (Sze et al. 2008). Parasitized soldiers possess a short and square-shaped head capsule, and these soldiers were statistically less aggressive than healthy soldiers (Neoh and Lee 2011). The use of naturally occurring pathogens of termites offers unique advantages over chemically based termiticides. Characteristics of the colony, such as a protected, underground location, are likely to limit the impact of predators and parasitoids on subterranean termites. The study of pathogens for termite control started as early as 1965 (Yendol and Paschke 1965). Since then there has been renewed interest in using pathogenic organisms, such as bacteria, viruses, nematodes, and most fungi for controlling termites in recent years.

4.8.1 Entomopathogenic Fungi

Fungal diseases are known to cause insect mortality naturally (Vimaladevi and Prasad 2001). Entomopathogenic or disease-causing fungi have received considerable attentions as they are exceptionally virulent and function as lethal parasites of insect pests. These fungi are among the first microorganisms to be used for the biological control of insect pests. They are cosmopolitan organisms, invade their host directly through the cuticle, and have been isolated from soils and infected insects from around the world. More than 700 species of fungi from around 90 genera are pathogenic to insects (Wraight et al. 2007; Hemasree 2013); however, only a few have been thoroughly investigated for their use against insect pests in agriculture. Fungal pathogens for the management of spodopteran pests were reviewed by Khan and Ahmad (2015).

These fungi also offer the best prospect as termite control agents. Conidia of entomopathogenic fungi could be spread through the colony by contact and grooming between contaminated and uncontaminated termites. Investigations with termites have largely focused on two fungal species, *Beauveria bassiana* and *Metarhizium anisopliae*, and recently also *Paecilomyces fumosoroseus*. Green muscardine fungus *M. anisopliae* is especially recommended for practical control of termites as a bio-insecticide and is virulent to all species of termites tested. Conidia from *M. anisopliae* can survive >18 months in termite nests (Milner and Staples 1996). Myles (2002) isolated a virulent strain (pathotype) of *M. anisopliae* from the eastern subterranean termite *Reticulitermes flavipes* in Toronto. Dong et al. (2007) evaluated the efficacy of a new virulent of *M. anisopliae* var. dcjhyium (obtained from *Odontotermes formosanus* in China) against the subterranean termite *O. formosanus* in the laboratory. The new isolate was reported to be highly infectious and virulent against termites and could cause approximately 100 % mortality of termites 3 days post-inoculation at a concentration of 3×10^8 conidia/ml. In the market, there is a bio-control product BioBlast™ containing *M. anisopliae* as active ingredient to be used against subterranean termites. Strains of *M. anisopliae* and *B. bassiana*, when employed in baiting schemes, can be transferred among nest mates and may offer the potential for subterranean termite control (Jones et al. 1996; Wright et al. 2002, 2004). Isolates of *B. bassiana* from soil were as effective as those isolated directly from insect hosts for *Heterotermes tenuis* Snyder (Almeida et al. 1997). *B. bassiana* ATCC 90519 was reported sufficiently pathogenic against subterranean termites (Wright and Lax 2013). Germ tubes of *B. bassiana* can penetrate the integument of *Reticulitermes flavipes* as early as 16 h after application. On the other end antifungal volatile compounds have been identified in *C. formosanus* nests that may contribute to the inability of entomopathogenic fungi to propagate within the colony (Wiltz et al. 1998). Review by Hussain et al. (2012) on the current status of entomopathogenic fungi as mycoinsecticides is worthy to mention.

4.8.2 Bacteria and Viruses

Among the bacteria, *Bacillus thuringiensis* stands out, representing approximately 95 % of microorganisms used in biological control of insect pests in different cultures (Lambert et al. 1992). Castilhos-Fortes et al. (2002) evaluated the effects of *B.*

thuringiensis subspecies against termite *Nasutitermes ehrhardti* under laboratory conditions. They reported that *Bt. kurstaki* registered <72 % mortality at the seventh day after the bacterial application. Singha et al. (2010) evaluated *B. thuringiensis* and *B. thuringiensis* subsp. *israelensis* for their pathogenicity against two species of tea termites, viz., *Microtermes obesi* and *Microcerotermes beesoni*. They reported that *B. thuringiensis* strains caused >80 % mortality in both the termite species. *B. thuringiensis* subsp. *israelensis*, however, was noticed to be more virulent compared to *B. thuringiensis*. Osbrink et al. (2001) isolated *Serratia* from dead termites and reported that three of the *Serratia* isolates were recorded to induce >85 % mortality within 19 days in Petri dish tests. In another study *Pseudomonas fluorescens* CHA0 was reported to kill subterranean termite *Odontotermes obesus* by inhibiting cytochrome c oxidase of the termite respiratory chain (Devi and Kothamasi 2009). Insect viruses can provide safe, effective, and sustainable control of a variety of insect pests. They are highly specific in their host range, usually limited to a single type of insect. Al-Fazairy and Hassan (1988, 1993) reported that nuclear polyhedrosis virus isolated from *Spodoptera littoralis* infects termite castes of *Kalotermes flavicollis*. They mentioned that all tested castes of termites were quite equal in their response to the virus infection and produced over 90 % mortality at 6.4×10^7 polyhedra/ml concentration.

5 Entomopathogenic Nematodes

Majority of the termite control practices are ineffective and ecologically unsustainable and, above all, do not address the root cause of termite infestation and thus merely provide temporary relief to the problem (Mugerwa 2015). Most termite management practices are focused on total elimination of termite population rather than sustaining their population. EPNs are being produced commercially and used as biological control agents in many parts of the world. Because these nematodes are adapted to the soil environment, the principal hosts are soil insects and insects in cryptic habitats. These nematodes have been utilized in classical, conservative, and augmentative biological control programs. *S. scapterisci* originally isolated from Uruguay was successfully introduced into Florida for the classical biological control of mole cricket pests (Parkman and Smart 1996). In the field, however, entomopathogenic nematodes attack a significantly narrower host range than in the laboratory. Indigenous nematodes are exempted from registration in many European countries, Australia, and the United States, while in other countries, they are subject to similar registration procedures as for a chemical pesticide. Use of these nematodes offers a number of advantages and will be useful in countries where alternative control approaches are needed to replace the more toxic insecticides that are currently in use. With the general public becoming increasingly concerned about pesticide usage, the use of nematodes for termite control is a potentially promising market. Current use of *Steinernema* and *Heterorhabditis* nematodes as biological control organisms has been summarized by Shapiro-Ilan and Gaugler (2010) (Table 4).

Table 4 Current use of *Steinernema* and *Heterorhabditis* nematodes as biological control organisms (Shapiro-Ilan and Gaugler 2010)

Crop(s) targeted	Pest common name	Pest scientific name	Efficacious nematodes
Artichokes	Artichoke plume moth	*Platyptilia carduidactyla*	Sc
Vegetables	Armyworm	Lepidoptera: Noctuidae	Sc, Sf, Sr
Ornamentals	Banana moth	*Opogona sachari*	Hb, Sc
Bananas	Banana root borer	*Cosmopolites sordidus*	Sc, Sf, Sg
Turf	Billbug	*Sphenophorus* spp. (Coleoptera: Curculionidae)	Hb, Sc
Turf, vegetables	Black cutworm	*Agrotis ipsilon*	Sc
Berries, ornamentals	Black vine weevil	*Otiorhynchus sulcatus*	Hb, Hd, Hm, Hmeg, Sc, Sg
Fruit trees, ornamentals	Borer	*Synanthedon* spp. and other sesiids	Hb, Sc, Sf
Home yard, turf	Cat flea	*Ctenocephalides felis*	Sc
Citrus, ornamentals	Citrus root weevil	*Pachnaeus* spp. (Coleoptera: Curculionidae)	Sr, Hb
Pome fruit	Codling moth	*Cydia pomonella*	Sc, Sf
Vegetables	Corn earworm	*Helicoverpa zea*	Sc, Sf, Sr
Vegetables	Corn rootworm	*Diabrotica* spp.	Hb, Sc
Cranberries	Cranberry girdler	*Chrysoteuchia topiaria*	Sc
Turf	Crane fly	Diptera: Tipulidae	Sc
Citrus, ornamentals	Diaprepes root weevil	*Diaprepes abbreviatus*	Hb, Sr
Mushrooms	Fungus gnat	Diptera: Sciaridae	Sf, Hb
Grapes	Grape root borer	*Vitacea polistiformis*	Hz, Hb
Iris	Iris borer	*Macronoctua onusta*	Hb, Sc
Forest plantings	Large pine weevil	*Hylobius albietis*	Hd, Sc
Vegetables, ornamentals	Leaf miner	*Liriomyza* spp. (Diptera: Agromyzidae)	Sc, Sf
Turf	Mole cricket	*Scapteriscus* spp.	Sc, Sr, Sscap
Nut and fruit trees	Navel orangeworm	*Amyelois transitella*	Sc
Fruit trees	Plum curculio	*Conotrachelus nenuphar*	Sr
Turf, ornamentals	Scarab grub[3]	*Coleoptera*: *Scarabaeidae*	Hb, Sc, Sg, Ss, Hz
Ornamentals	Shore fly	*Scatella* spp.	Sc, Sf
Berries	Strawberry root weevil	*Otiorhynchus ovatus*	Hm
Beehives	Small hive beetle	*Aethina tumida*	Hi, Sr
Sweet potato	Sweet-potato weevil	*Cylas formicarius*	Hb, Sc, Sf

Nematode species are abbreviated as follows: Hb = *Heterorhabditis bacteriophora*, Hd = *H. downesi*, Hi = *H. indica*, Hm = *H. marelata*, Hmeg = *H. megidis*, Hz = *H. zealandica*, Sc = *Steinernema carpocapsae* Sf = *S. feltiae*, Sg = *S. glaseri*, Sk = *S. kushidai*, Sr = *S. riobrave*, Sscap = *S. scapterisci*, Ss = *S. scarabaei*

5.1 Under Laboratory Conditions

Hundreds of different species from most orders of insects were susceptible to various entomopathogenic nematodes under laboratory conditions. Entomopathogenic nematodes *Steinernema carpocapsae*, *Steinernema riobrave*, *Heterorhabditis bacteriophora*, and *Heterorhabditis indica* were evaluated by Wang et al. (2002) for their activity against *Reticulitermes flavipes* and *Coptotermes formosanus* in the laboratory. All were noticed effective against *C. formosanus* at ≥400 nematodes per termite. *S. riobrave*, however, had no detectable effect against *R. flavipes* even at a rate of 2000 nematodes per termite. They also demonstrated that *H. indica* was more efficacious (*H. indica* > *H. bacteriophora* > *S. carpocapsae* > *S. riobrave*) at $\alpha = 0.10$ level, and nematodes were able to reproduce from *R. flavipes* and *C. formosanus*. In contrast, Manzoor (2012) reported that *S. carpocapsae* and *H. bacteriophora* when applied individually against the eastern subterranean termite *R. flavipes* showed no detrimental effects on workers and nymphs of the termites. These efficacy differences of the same nematode species between two studies may be due to the differences in the strains of nematode species used in each study.

In another study, Yu et al. (2006) evaluated parasitism of subterranean termites by *S. riobrave*, *S. carpocapsae*, *S. feltiae*, and *H. bacteriophora* in laboratory sand assays. They reported that all tested EPNs were capable of infecting and killing termite species *Heterotermes aureus*, *Reticulitermes flavipes*, and *Gnathamitermes perplexus* (Banks). *S. riobrave*, however, was found to be particularly effective in sand assays and caused significant mortality (≥80 %) of worker *H. aureus* and *G. perplexus* at 22 °C. Nematode concentration and incubation time had significant effects on the mortality. Yu et al. (2008) reported that *S. carpocapsae*, *S. riobrave*, and *H. bacteriophora* successfully reproduced in termite *H. aureus* and infective juveniles (IJs) exited the termite cadavers successfully. However, no progeny were produced by *S. feltiae*. However, Yu et al. (2010) compared virulence of three novel strains of *S. riobrave* (3-8b, 7-12, and TP) against subterranean termites *H. aureus*, *R. flavipes*, and *C. formosanus* workers. *H. aureus* was very susceptible to all the *S. riobrave* strains, and termites in all nematode treatments were dead after 4 days. The TP strain of *S. riobrave*, however, caused 75 % and 91 % mortality in *R. flavipes* and *C. formosanus*, respectively, which was more than 300 % and 70 % higher than the mortality caused by other strains. Screening indicated superior virulence in the 355 (=TX) strain of *S. riobrave* to *H. aureus* compared with the virulence of *S. carpocapsae*, *S. feltiae*, and *H. bacteriophora* (Yu et al. 2006). Thus, *S. riobrave* 355 may have substantial potential to be developed as a biocontrol agent for *H. aureus*.

Higher mortalities in subterranean termite *Macrotermes* caused by *S. pakistanense* were reported by Shahina and Tabassum (2010) in a filter paper and sand assay. Mankowski et al. (2005) examined the attachment and infectivity of two entomopathogenic nematode species, *S. carpocapsae* and *H. indica*, on soldiers and workers in two subterranean termite species, *C. formosanus* and *C. vastator*. In attachment tests with *S. carpocapsae*, they noticed that more nematodes attached to soldiers of *C. formosanus* and *C. vastator*. When soldiers alone or workers alone are exposed to the nematodes, there is a differential susceptibility of soldiers and workers to nematode infection with soldiers being more susceptible than workers. The reason for this differential response to nematode infection is that soldiers do not exhibit grooming behavior. El-Bassiouny and El-Rahman (2011) reported the possibility of using entomopathogenic nematodes *H. baujardi* and *H. indica* against the Egyptian subterranean termite *Psammotermes hypostoma* (Desn.) and *Anacanthotermes ochraceus* (Burm.). The bioagent *H. baujardi* was noticed more effective for control of the two tested termites, but *P. hypostoma* was highly susceptible than *A. ochraceus*. Overall, the mortality increased as the nematode concentrations increased and vice versa.

Differential susceptibility of two termite species, *Macrotermes bellicosus* and *Trinervitermes occidentalis*, against EPNs isolates *H. indica* Ayogbe1, *H. sonorensis* Azohoue2, *H. sonorensis* Ze3, and *Steinernema* sp. Bembereke, from Benin (West Africa), was studied by Zadji et al. (2014a). The results at forty-eight hours post-exposure of workers of *M. bellicosus* to 50 IJ of *H. indica* Ayogbe1, *H. sonorensis* Azohoue2, *H. sonorensis* Ze3, and *Steinernema* sp. Bembereke for each termite were 96.3 %, 87.9 %, 94.5 %, and 75.0 % mortality, respectively. In the case of workers of *T. occidentalis*, under the same conditions, these EPN isolates caused 91.7, 98.5, 75.0, and 95.0 % mortality. Based on concentration-mortality data, they reported that isolates *H. indica* Ayogbe1 and *H. sonorensis* Ze3 were more virulent against *M. bellicosus* with LC_{50} values of 11 IJ, whereas *Steinernema* sp. Bembereke was the most virulent against *T. occidentalis* with LC_{50} values of 12 IJ. All tested EPN isolates can be recycled in both *M. bellicosus* and *T. occidentalis* and the soldiers of both termites studied were noticed more susceptible than workers. Twenty-nine Beninese isolates of *H. sonorensis* and one local isolate of *H. indica* were screened by Zadji et al. (2014b) for their pathogenicity against the termite pest *Macrotermes bellicosus*. Most of the isolates (73 %) killed more than 80 % of the insects. Bioassays, however, showed significant differences among isolates of all tested traits. The greatest survival of infective juveniles to heat (8 h), desiccation (8 h), and hypoxia (72 h) was observed with the *H. sonorensis* isolates Kassehlo (72.8 %), Setto1 (72.5 %), and Kissamey (81.5 %, respectively). Sri Lankan isolates of ENPs were compared with two commercial formulations of entomopathogenic nematodes, namely, Biosafe (*S. carpocapsae*) and Nemasys (*S. feltiae*), against the live-wood termite *Postelectrotermes militaris*. Sri Lankan isolate *Heterorhabditis* spp. (HSL 6) and *S. carpocapsae* were reported better controlling agents against *P. militaris* than other isolates tested (Amarasinghe and Hominick 1993a). Wilson-Rich et al. (2007) reported that damp-wood termite *Zootermopsis angusticollis* exhibits a dose-dependent susceptibility to the soil nematode *S. carpocapsae* (Weiser) (Mexican strain).

5.2 Under Field Conditions

Only a limited number of field studies have been conducted using EPNs as control agents for termites. Certain species of nematodes although effective in laboratory control is often quite variable under field conditions. Soil moisture and soil type appear to limit the nematode's ability to move in the soil and locate termites. In the 1930s Glaser and colleagues applied *S. glaseri* to 73 different field plots in New Jersey to control the Japanese beetle, *Popillia japonica* (Glaser 1932; Glaser et al. 1940). They recovered parasitized grubs from 72 plots 2 weeks after application. Parasitism of the grub population by the nematode in the various plots ranged from 0.3 to 81.0 %. A study testing the efficacy of *S. carpocapsae* (Weiser) against foraging workers of *Reticulitermes tibialis* in pastureland was published by Epsky and Capinera (1988). Study showed potential for control of *R. tibialis* in laboratory and field trials. They also established LD_{50} values for specific nematode/termite combinations. Amarasinghe and Hominick (1993b) reported that higher doses of *S. carpocapsae* and *S. feltiae* showed promising control of live-wood termite *Postelectrotermes militaris* in tea plantations. Nguyen and Smart (1994) isolated EPN *Neosteinernema longicurvicauda* Nguyen and Smart from naturally infected subterranean termites, *Reticulitermes flavipes*.

Heterorhabditis sp. have given encouraging results in Australia. Studies indicate that colonies of *Neotermes* attacking in the South Pacific Islands can be eliminated using *Heterorhabditis* sp. from palms and other trees (Dolinski and Lacey 2007). Populations of the damp-wood termite *Glyptotermes dilatatus* that form colonies of only several thousand members have also been successfully managed with *Heterorhabditis* sp. with a dose of 4000 ml and 8000 ml nematode suspension in doses of 40 ml and 30 ml per tea bush, respectively (Danthanarayana and Vitarana 1987).

In contrast, workers reported that EPNs showed effectiveness against subterranean termites in the laboratory but did not cause colony elimination in the field with *C. formosanus* (Fujii 1975; Tamashiro 1976), *R. flavipes* (Mauldin and Beal 1989), or *R. tibialis* (Epsky and Capinera 1988) which have shown to be minimally controlled by nematodes. Nematodes sold commercially in the United States failed to eliminate colonies of *R. flavipes*, in controlled field experiments (Mauldin and Beal 1989). The reasons suggested were termite social behavior like walling-off dead termites and avoiding foraging in nematode infested areas (Fujii 1975; NPCA 1985). Epsky and Capinera (1988) also reported an ability of the subterranean termite *R. tibialis* to detect and avoid *S. feltiae*. Yanagawa et al. (2012) hypothesized that termites can perceive pathogens and this ability plays an important role in effective hygiene behavior. For the successful application of biopesticides to termites in nature, it would be beneficial to identify substances that could disrupt the termite's ability to perceive pathogens. Different isolates or species of entomogenous nematode species that are tolerant to higher temperatures are required for control of subterranean termite in the fields. Insect susceptibility to entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae varies among insect species and is influenced by nematode species, strain, and an assembly of abiotic and biotic factors. Entomopathogenic nematodes also differ in their abilities to survive different environmental conditions.

5.3 Synergism of EPNs

Several previous studies have demonstrated additive or synergistic relationships between the combined use of low-impact insecticides and biological control agents (Kaakeh et al. 1997; Quintela and McCoy 1998; Koppenhofer and Kaya 1998; Nishimatsu and Jackson 1998). Infective juveniles are tolerant of short exposures (2–6 h) to most agrochemicals including insecticides, herbicides, fungicides, and acaricides (Rovesti and Deseo 1990; Ishibashi 1993) and, therefore, can often be tank mixed. However, some pesticides can reduce nematode infectivity and survival (Grewal et al. 1998). Heterorhabditids tend to be more sensitive to physical challenges, including pesticides, than steinernematids (Grewal et al. 2001). Murugan and Vasugi (2011) evaluated bioactivities of *S. glaseri* in combination with neem seed kernel extract (NSKE) against *Reticulitermes flavipes*. On the fourth day 40 % and 70 % mortality were reported at lower (1.0 %) and higher (4.0 %) concentrations of NSKE, respectively. Neem at various concentrations did not affect the survival of nematodes but had considerable impact on the survival of termites which may be due to the presence of bioactive compounds azadirachtins, salanin, etc. Entomopathogenic nematodes and the chloronicotinyl insecticide imidacloprid interact synergistically on termite mortality. The degree of interaction, however, varies with nematode species. Manzoor (2012) reported synergism between imidacloprid and nematodes species *S. carpocapsae* and *H. bacteriophora* that caused more than 50 % mortality of workers and nymphs of *R. flavipes* within all three colonies tested.

6 Survey of New Species/Strains

Screening of entomopathogenic nematode species or strains for the control of specific insect pest, which are adapted to local environmental conditions, could achieve a higher level of efficacy. Therefore, it is important to survey and preserve indigenous entomopathogenic nematode population. Kary et al. (2009) conducted survey in Iran throughout the three provinces in the northwest of the country and concluded that out of the 833 soil samples, 27 (3.2 %) were positive for entomopathogenic nematodes with 17 (2.0 %) containing *Heterorhabditis* and 10 (1.2 %) *Steinernema* isolates. *H. bacteriophora* and *S. feltiae* were the common species. A survey of entomopathogenic nematodes was conducted for the first time in Nepal by Khatri-Chhetri et al. (2010). Of the 276 soil samples studied, 29 (10.50 %) were positive of EPNs containing seven samples of heterorhabditids (24.14 %) and 22 samples

(75.86 %) of steinernematid. To determine the occurrence of EPNs, Zepeda-Jazo et al. (2014) conducted a survey on the Pacific coast of the State of Colima, Mexico. Of the 19 soil samples collected, 14 (73.7 %) were positive for EPNs, containing 12 steinernematid isolates (85.7 %) and two heterorhabditid isolates (14.3 %). Further they reported that most of the isolates were recovered from cultivated habitats, suggesting that there is a higher prevalence of EPNs in cultivated soils. Jawish et al. (2015) conducted a survey of EPNs of the families Steinernematidae and Heterorhabditidae from January 2011 to December 2013 in Damascus countryside of Syria. Of 189 soil samples studied, 17 (9 %) were positive of entomopathogenic nematode with 11 (65 %) samples containing *Heterorhabditis* and six (35 %) *Steinernema* isolates. Therefore survey and evaluation of new species or strains of entomopathogenic nematodes against termite pests may achieve a higher level of management.

7 Conclusion and Future Prospects

EPNs and their associated bacterial symbionts have been proven safe to vertebrates and other nontarget organisms. They are highly specific in their host range and compatible with many pesticides, can be easily produced in vivo and in vitro, can be applied with standard spray equipment, and have been exempt from registration in many countries. A wide range of entomopathogenic nematodes are effective against various termite species. However, limited number of field studies have been conducted against termites using EPNs. New isolates of EPNs from various parts of the world are being studied, which may prove effective against termite pests in the field. Therefore use of EPNs would bring several benefits to sustainable agriculture and develop a better understanding of biodiversity.

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