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REVIEW ARTICLE

Prospects for the biological control of subterranean termites (Isoptera: Rhinotermitidae), with special reference to *Coptotermes formosanus*

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Abstract

Costs associated with subterranean termite damage and control are estimated to approach $2 billion annually in the United States alone. The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, is one of the more economically important subterranean species. In recent years, the shortcomings associated with conventional chemical control methods have prompted policymakers and scientists to evaluate the potential for biological control of subterranean termites (*C. formosanus* in particular), that is, to determine the potential for natural enemies – predators, parasitoids and pathogens – to suppress termite populations. Ants are the greatest predators of termites, and may have a considerable local impact on termite populations in some areas of the world. A few parasitoids of termites are known, but their potential for regulating termite populations seems negligible. Characteristics of the colony, such as a protected, underground location (and, for the *C. formosanus* nest, its modular and dispersed nature), are likely to limit the impact predators and parasitoids have on subterranean termites. Thus, there seems little potential for use of these agents for subterranean termite control. For various reasons, pathogenic organisms, such as viruses, bacteria, Protozoa, nematodes and most fungi, have shown little promise for use in biological termite control. However, research suggests that strains of two well-studied, endoparasitic fungi, *Beauveria bassiana* and *Metarhizium anisopliae*, when employed in baiting schemes, may offer the potential for at least some measure of subterranean termite control, although their successful use is compromised by a number of inherent biological limitations and logistical problems that have yet to be solved. Although not strictly in the realm of classical biological control, recent studies suggest that natural products, such as ant semiochemicals and fungal metabolites (siderophores), or their synthetic analogues, eventually might find a use in termite control programmes as repellents or insecticides in wood treatments or soil applications if stable formulations can be developed.

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Introduction

Of the more than 2700 termite species in the world, only a small minority is of any economic concern. For example, only 70–80 species cause significant damage to structures (Edwards & Mill, 1986). Although the poorer areas of the tropics and subtropics probably suffer more termite damage, it is in the developed countries, with their low action thresholds for urban pests, that the economic impact of termites has received the most attention (Su & Scheffrahn, 1998). For example, the estimated damage to wood and wood products caused by termites annually in the United States exceeds $750 million, 95% of which is contributed by subterranean termites (family Rhinotermitidae) (Mauldin, 1986). Moreover, subterranean termites account for 80% of the approximately $1.5 billion spent annually for termite control in the USA (Su, 1993).

The Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), is one of the more economically important termites in the warmer regions of the world (Su & Tamashiro, 1987). Not only are houses and other buildings attacked by this insect, but also telephone poles, boats, underground electrical and telephone cables, other finished goods (e.g. books, paper, fabric) and at least 48 species of living plants, including valuable crops and ornamentals (Lai *et al.*, 1983; Tamashiro *et al.*, 1987). In China, nesting by the termite has been reported to undermine dykes and cause flooding (Gao, 1987). Although limited in geographic range, in terms of damage potential, *C. formosanus* is the most serious termite pest in that country and Japan (Lin, 1987; Mori, 1987), as well as in the USA.

Control of *C. formosanus* and other subterranean species involves measures to prevent infestation of structures or remedial actions once prevention fails (Su & Tamashiro, 1987; Su & Scheffrahn, 1990; Yates *et al.*, 1997). Prevention of infestations may involve physical means (e.g. sand or steel-mesh barriers beneath foundations) or, more commonly, chemical controls (reviewed by Su & Scheffrahn, 1998). For decades, soil treatment with persistent insecticides has been widely used to protect structures from ground-nesting termites.

Whereas preventive measures can provide an effective, long-term barrier to termite penetration of structures, once an infestation has begun, remedial control of *C. formosanus* is extremely difficult due to the large population size, areal extent and foraging range of the subterranean colony. For example, in the USA, standard practice is to treat the soil beneath and around the structure to halt current invasion and prevent future attack. Usually, no attempt is made to find and destroy the colony, which may be situated anywhere within a volume of soil of hundreds of millions of cubic metres (Su & Tamashiro, 1987). Treatment of soil around the structure therefore kills only a small proportion of the colony, the majority of the population surviving to re-infest the structure, either by flying reproductives or by workers entering through an untreated or inadequately treated portion of soil (Su & Scheffrahn, 1990).

In view of these shortcomings, research efforts have focused on alternative means of termite management. For example, recent studies have demonstrated the efficacy of baiting schemes employing insect growth regulators in eliminating subterranean termite colonies (e.g. Su & Scheffrahn, 1993; Su, 1994; Su *et al.*, 1995; Grace *et al.*, 1996). A need to evaluate the potential for biological control of subterranean termites (*C. formosanus* in particular) also has been recognized (HDOA, 1994; Grace, 1997; USDA, 1999). An earlier review of non-chemical methods of termite control in agriculture and forestry touched upon biological control (Logan *et al.*, 1990). The present paper reviews more specifically and comprehensively the available information concerning termite interaction with the biotic environment to assess the potential for control of subterranean termites through biological means.

Biological control of termites

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. Classical biological control programmes (i.e. the discovery, release, and colonization of natural enemies: arthropod predators and parasitoids, and pathogens) have proved successful against a variety of pests, and knowledge of the role natural enemies play in the ecology of these species has steadily accumulated (Huffaker & Messenger, 1976; DeBach & Rosen, 1991). However, data for termites are relatively scant. Although the influence of predation on termite distribution, abundance and population dynamics may be partially understood in a few cases (Wood & Johnson, 1986), the natural role of termite pathogens is much more obscure (Lee & Wood, 1971).

Predators

Termites have a wide variety of predators, both opportunist and specialist, vertebrate and invertebrate. Attack occurs mainly upon alate reproductives or foraging workers outside the nest (Logan *et al.*, 1990), but a few predators attack termites within the nest (Sheppe, 1970). Among the vertebrates, fish, anurans, lizards, snakes, birds and mammals (including man) are known to take termite prey when available (Nutting, 1969). Insect and other arthropod groups reportedly preying opportunistically on termites include Scorpiones, Solifugae, Acari, Opiliones, Araneae, Chilopoda, Thysanura, Anisoptera, Blattaria, Mantodea, Phasmida, Gryllidae, Reduviidae, Neuroptera, Carabidae, Elateridae, Staphylinidae, Diptera and aculeate Hymenoptera (Pemberton, 1928a; Nutting, 1969; Sheppe, 1970; Phillipsen & Coppel, 1977; Wood & Sands, 1978; Johnson & Hagen, 1981; Pearce, 1997), although all orders of entomophagous insects probably contain at least some species that feed on termites (Deligne *et al.*, 1981).

Ants are the greatest enemies of termites in all regions of the world (Deligne *et al.*, 1981; Hölldobler & Wilson, 1990). A large percentage of ant species, including those from the two largest genera, *Pheidole* Westwood and *Camponotus* Mayr, are opportunistic predators of termites (Hölldobler & Wilson, 1990). Veeresh & Gubbaiah (1984) observed the longlegged ant *Anoplolepis longipes* (Jerdon) (Formicidae), a major agricultural pest in India, to prey facultatively upon termites of an unidentified species. Predation by doryline ants on colonies of *Cubitermes ugandensis* Fuller and *Bellicositermes natalensis* (Haviland) (both Termitidae) was witnessed by Williams (1959) and Bodot (1961), respectively. Yin (1994?) found *Dorylus orientalis* Westwood to be an important natural enemy of *Odontotermes formosanus* (Shiraki) and *Macrotermes barneyi* Light (both Termitidae). Traniello (1981) observed foraging *Nasutitermes costalis* (Holmgren) (Termitidae) to be attacked by workers of the genera *Crematogaster* Lund, *Wasmannia* Forel, *Azteca* Forel, *Pachycondyla* F. Smith, and *Odontomachus* Latreille, as well as *Camponotus*. It is likely that ants account for a significant proportion of the probable near-100% mortality of swarming reproductives (Wood & Sands, 1978).

Termites may comprise a significant portion of the diet in some ant species. For example, Wilson & Oliver (1969) found that the greatest proportion (16.3%) of prey taken by fire ants *Solenopsis richteri* Forel (Formicidae) in cutover pine forest consisted of termites (*Reticulitermes* sp.). Laboratory experiments suggested that *Coptotermes formosanus* might be relatively more resistant to fire ant predation than *Reticulitermes* spp. owing to a higher proportion of soldiers in colonies of the former and their more aggressive response to disturbance (Wells & Henderson, 1993; cf. Cornelius & Grace, 1996, 1997).

Specialized arthropod predators of termites apparently are confined to a few ant species in the subfamilies Ponerinae and Myrmicinae (e.g. Arnold, 1915–1924; Wheeler, 1936; Weber, 1964; Levieux, 1966; Maschwitz & Mühlenberg, 1975; Ohiagu & Wood, 1976; Longhurst *et al.*, 1978, 1979a,b; Longhurst & Howse, 1979; Maschwitz & Schönegge, 1983; Lepage & Darlington, 1984), some of which may serve as important regulators of termite populations in natural ecosystems. For example, *Decamorium uelense* (Sanstchi) (Formicidae) consumed up to 632 *Microtermes* spp. m^{-2} y^{-1}, more than 74% of the *Microtermes* standing crop population and approximately one-eighth of annual production (Longhurst *et al.*, 1979b). *Megaponera foetens* (Fabricius) (Formicidae), a species noted for its organized raids on termites in the Ethiopian region, preyed upon *Macrotermes bellicosus* (Smeathman) (Termitidae) at a rate of 141 termites m^{-2} y^{-1}; other species were consumed at the rate of 52 termites m^{-2} y^{-1} (Longhurst *et al.*, 1978). Predation on *M. bellicosus* was equivalent to slightly more than the annual standing crop and about one-seventh of the total annual production (Collins, 1981). *Megaponera foetens* may make repeated raids on a termite colony until it is destroyed (Sheppe, 1970).

Parasitoids

The main advantage to employing parasitoids for pest control derives from their high degree of host specificity, and parasitoids have been used successfully in biological control programmes worldwide. However, little information is available on parasitoids of termites, and none of it seems to have relevance to biological control. Certain species of the family Phoridae (Diptera) are parasitic on termites (e.g. Schmitz, 1938; Disney, 1988; Disney & Kistner, 1989, 1990), and might play a role in regulating termite densities (Disney, 1986). In other phorids, the association apparently is more facultative, the maggot gaining entry into the host through a wound (Askew, 1971). Bridwell (1920) and Kühne & Becker (1974) reported *Scleroderma* spp. (Hymenoptera: Bethylidae) parasitizing drywood termites (Kalotermitidae), but did not assess their effects on termite population dynamics.

In summary, while a few specialists may have a considerable local impact on termite numbers, most termite predators are opportunistic and exert a low level of mortality that probably is compensated for by colony reproduction (Sheppe, 1970). Moreover, not all termite species are equally vulnerable to predation. Many of the termites attacked by the specialist predators build aboveground nests that are readily located and may be easier to exploit than are subterranean colonies. The well-hidden nest of *C. formosanus*, for example, which may be situated as deeply as 3 m below ground level, comprises an extensive gallery system, in which the main nest is connected by runways with several subnests (Zimmerman, 1948; Su & Tamashiro, 1987). The dispersed and modular nature of the *C. formosanus* colony, as well as its protected, underground location, may limit the impact predation has on this termite species. Similarly, evidence suggests that parasitoids may be of limited value in controlling populations of concealed (including subterranean) pests in general (Gross, 1991). Thus, there would seem to be little potential for use of predators or parasitoids to control *C. formosanus*.

Pathogens

Soil insects have been considered to be good candidates for microbial control (Burges, 1981). The soil environment offers conditions highly favourable for sustaining infection and promoting epizootics: it is humid, protected from ultra-violet radiation and crowded. However, few confirmed pathogens have been isolated from termites (Lund, 1971; Zoberi & Grace, 1990a; Grace, 1994; Zoberi, 1995). Also, whereas many prospective termite pathogens have been tested in the laboratory, relatively few have been given field trials.

Viruses

Viral infection of termites has been little reported. Gibbs *et al.* (1970) isolated a virus infecting *Coptotermes lacteus* (Froggatt) (Rhinotermitidae), which was similar to acute paralysis virus of the honey bee *Apis mellifera* Linnaeus (Hymenoptera: Apidae). A nuclear polyhedrosis virus (NPV), obtained from caterpillars of *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae), was infective to a laboratory colony of *Kalotermes flavicollis* (Fabricius) (Kalotermitidae) (Al Fazairy & Hassan, 1988). Termites died 2–10 days post infection, and, based only on the laboratory results, the authors suggested that control of *K. flavicollis* with NPV might be feasible. However, the potential of viruses for termite control has yet to be evaluated in the field (Al Fazairy & Hassan, 1993).

Accessibility of the pest to be controlled is the prime factor affecting the efficacy of viral pathogens. Insects that feed openly on the foliage of host plants are most easily treated, and the most promising results have been obtained against pests of this type (e.g. caterpillars, sawfly larvae) (Smith, 1967). Insects living in concealed habitats, such as the soil, are more difficult to infect. There are other drawbacks to the use of viruses to suppress pest populations: viruses kill their hosts slowly compared to other pathogens; environmental factors, such as rainfall and solar radiation, may reduce viral persistence in soil; mass production of viruses is hampered by the need for living hosts or tissue culture; lastly, viral formulations have had difficulty competing successfully, on the basis of performance and cost, with other pest control products, such as chemical insecticides or even other microbial agents (Klein, 1988; Fuxa, 1990).

Bacteria

Little research has focused on bacterial infections of termites. Exposure of laboratory colonies of the subterranean species *Reticulitermes flavipes* (Kollar) and *R. hesperus* Banks (Rhinotermitidae) to a mixture of soluble endotoxin, spores and inclusion bodies of *Bacillus thuringiensis* (Berliner) (*Bt*, a bacterium commonly used as a microbial insecticide for control of pest Lepidoptera, Coleoptera and Diptera) resulted in greater than 95% mortality after six days (Smythe & Coppel, 1965). Workers of *Microcerotermes championi* (Snyder) (Termitidae) and *Heterotermes indicola* (Wasmann) (Rhinotermitidae) suffered 100% mortality within 13 days of exposure to two local strains of *B. thuringiensis* in laboratory tests (Khan *et al.*, 1977a). In follow-up studies employing a commercial preparation of *Bt* (Thuricide-HP concentrate), Khan *et al.* (1978, 1985) again found *H. indicola, M. championi* and another termite species, *Bifiditermes beesoni* (Gardner) (Kalotermitidae), to be highly susceptible to infection, exhibiting 100% mortality within six days of exposure.

Laboratory colonies of *M. championi*, *H. indicola* and *B. beesoni* exposed to suspensions of the spore-forming bacterium *Serratia marcescens* Bizio succumbed completely 7–13 days following infection (Khan *et al.*, 1977b). Khan *et al.* (1992) tested the pathogenicity of *Pseudomonas aeruginosa* (Schroeter) against *M. championi*, *H. indicola* and *Coptotermes heimi* (Wasmann) (Rhinotermitidae) in the laboratory. Termite mortality ranged from 25–52% seven days post-inoculation to 84–100% 25 days post-inoculation. The authors concluded from the results that *P. aeruginosa* is 'fairly' pathogenic to the three termite species, although the bacterium's potential as a biological control agent is limited by its occasional status as a plant pathogen.

Despite favourable laboratory results, the potential of bacteria to reduce termite populations has not been demonstrated under field conditions. *Bacillus thuringiensis*, in particular, has limited potential for soil insect control because of its poor survival in soil (Burges, 1981). Moreover, the insects that *B. thuringiensis* strains typically kill in the field are not soil-dwelling, but epigaeic or aquatic (Martin, 1994). However, recent work incorporating recombinant DNA and microencapsulation technologies shows promise for application to termite control strategies employing *Bt* strains that express termite-specific endotoxin (Grace & Ewart, 1996).

Protozoa

Of the four groups of Protozoa containing species parasitic to insects, the Phylum Microspora includes species that are potentially most useful in applied insect control (Henry, 1990). However, the amount of research pertaining to biological control of termites using these agents is negligible. Jafri *et al.* (1976) found microsporidians in the body cavity and proventriculus of *M. championi* collected from the roots of *Saccharum munja* Roxburgh (Poaceae). The organisms apparently are ingested with the food. After passing into the midgut, they attack fat body tissues and cause death. Desportes (1963) described a gregarine (Phylum Apicomplexa) from the haemocoele of the dampwood termite *Zootermopsis nevadensis* (Hagen) (Termopsidae). No assessment of the microbes' potential for termite control was given.

Although Protozoa may be important agents in the natural control of many insects, they have not been used as soil-applied microbial insecticides because they tend to be slow-acting and vulnerable to changes in environmental conditions (Klein, 1988; Henry, 1990).

Nematodes

The roundworms of the Phylum Nematoda play an important role in the natural control of many insect populations. They have been found parasitizing species in the orders Hemiptera, Diptera, Hymenoptera, Lepidoptera, Orthoptera, Coleoptera, Thysanoptera, Siphonaptera, as well as Isoptera (Nickle & Welch, 1984).

Four families of nematodes – the Mermithidae, Allantonematidae, Steinernematidae and Heterorhabditidae – have shown promise for use in insect control programmes (Popiel & Hominick, 1992), with most research focusing on species in the latter two (Kaya & Gaugler, 1993). These entomopathogenic nematodes (so-named because they are vectors of pathogenic bacteria of the genus *Xenorhabdus* Poinar) have a number of characteristics that make them especially suitable for biological control and for commercial production as microbial insecticides: a broad host range, especially among soil-dwelling pests; exemption from registration in the USA; ease of production, storage and application; a high degree of safety to vertebrates, plants and other non-target organisms; and amenability to genetic selection (Kaya & Gaugler, 1993; Kaya *et al.*, 1993).

Few studies have addressed the potential for nematodes to control termites. In an early report, Merrill & Ford (1916) found 77% of colonies, and up to 100% of individuals, of *Reticulitermes lucifugus* (Rossi) (Rhinotermitidae) to be parasitized by *Mikoletzkya aerivora* (Cobb) (Diplogastridae) in field samples. Laboratory exposure of termites to nematodes resulted in successful parasitization (47% at 4 days) and 100% mortality of infected individuals at 12 days. However, no field trials were undertaken. Fujii (1975) obtained 96% mortality in *C. formosanus* within seven days of exposure to infective-stage *Steinernema carpocapsae* (Weiser) (Steinernematidae) in laboratory experiments. Mortality exceeding 95% was recorded by Georgis *et al.* (1982) for both *Zootermopsis* sp. and *Reticulitermes* sp. within three days after laboratory exposure to *S. carpocapsae*; termites also were found to carry infection back to their colonies. Laumond *et al.* (1979) and Trudeau (1989) also reported high rates of infection of *Nasutitermes costalis* and *Reticulitermes flavipes*, respectively, with *S. carpocapsae* under laboratory conditions.

Results of field studies evaluating the efficacy of nematodes in termite control generally have been disappointing. In an early, informal test, Pemberton (1928b) introduced unidentified nematodes from an Indonesian species of *Termes* Linnaeus (Termitidae) into soil around a nest of *C. formosanus*. No evidence of subsequent parasitization was detected. In field trials, in which concentrations of *S. carpocapsae* as high as 10 million individuals m^{-2} were applied to soil beneath wooden baits, Epsky & Capinera (1988) found evidence that *Reticulitermes tibialis* (Banks) (Rhinotermitidae) avoided contact with nematodes and exploited gaps in coverage in nematode-inoculated areas to attack the bait. The field results contrasted with those from their laboratory experiments, in which no avoidance of nematode-infested areas was found.

In a similar study using *Heterorhabditis heliothidis* (Khan, Brooks & Hirschmann) (Heterorhabditidae) as well as *S. carpocapsae* against *Reticulitermes* spp., nematodes applied to plots were not found to reduce feeding damage to wooden bait blocks, and showed no effectiveness in controlling or eliminating the termites (Mauldin & Beal, 1989).

Perhaps the only example of apparently successful biological control of a termite with nematodes involved not a subterranean, but a drywood species, *Glyptotermes dilatatus* (Bugnion & Popoff) (Kalotermitidae), a pest of tea, *Camellia sinensis* (L.) Kuntze (Theaceae). Danthanarayana & Vitarana (1987) showed that a single application of nematodes (*Heterorhabditis* sp.; 4000–8000 ml^{-1} of suspension) to galleries in tea plants eliminated termite colonies within two to three months. Evidence suggested that nematode populations were self-perpetuating in the field, even under extreme environmental conditions. However, at a cost of US$2.39 per 1000 infested bushes, this time-consuming and labour-intensive method is unlikely to be appropriate for use in less valuable crops or in forestry.

Although it may be feasible in limited cases to control crop-infesting termites with nematodes, in general, the utility of nematodes in biological control programmes is compromised by a number of factors that influence their effectiveness. These include soil physical and chemical properties (e.g. moisture, temperature, pore size, compaction, oxygen and carbon dioxide levels, pH, salinity and presence of synthetic chemicals) and biotic factors, such as competitive or predatory interactions with other soil organisms, limited motility and termite behaviours (e.g. isolation of infected individuals from the rest of the colony) that limit the spread of infection (Gaugler, 1988; Kaya, 1990; Popiel & Hominick, 1992).

Protection of structures from subterranean termites involves other considerations. In particular, the low economic threshold for termite damage to homes and other buildings, the immense numbers of nematodes required to kill termites, the presence of secondary reproductives that can rapidly re-establish the old colony or found new ones, and termite avoidance of nematode barriers all combine to limit the use of nematodes for termite control (Klein, 1990).

Although field infections often result from nematode treatments, the impact on target pest populations most often has been modest or negligible, even when billions of nematodes ha^{-1} were applied (Kaya & Gaugler, 1993). Thus, the potential for use of nematodes in biological control may be limited to cases in which chemical insecticides are not practical or appropriate (Nickle & Welch, 1984).

Fungi

Much research interest, especially in recent years, has focused on the use of fungal agents for pest control (Ferron, 1978). At least 22 species of fungi are obligate ectoparasites of termites (Blackwell & Rossi, 1986), although their biological control potential apparently has not been evaluated. Several of the fungi associated with termites appear to be at least facultatively pathogenic (e.g. Thaxter, 1895, 1920; Tate, 1927, 1928; Colla, 1928; Kevorkian, 1937; Stifler, 1941; Altson, 1947; Williams, 1959; Buchli, 1960; Beal & Kais, 1962; Lund & Engelhardt, 1962; Steinhaus & Marsh, 1962; Becker & Kerner-Gang, 1964; Toumanoff, 1965; Yendol & Paschke, 1965; Smythe & Coppel, 1966; Sannasi, 1968; Gouger & Kimbrough, 1969; Kimbrough & Gouger, 1970; Kimbrough *et al*., 1972; Khan & Kimbrough, 1974a,b; Rossi, 1974; Blackwell & Kimbrough, 1976, 1978; Blackwell, 1980; Blackwell & Gilbertson, 1981, 1984; Hänel, 1982b; Ko *et al*., 1982; Preston *et al*., 1982; Zoberi & Grace, 1990b; Yoshimura *et al*., 1992; Ochiel, 1995; Ochiel *et al*., 1997; Sajap *et al*., 1997; Yoshimura & Takahashi, 1998). It is the endoparasitic fungi, however, that have perhaps the greater potential for biological control of termites, and these have received more attention by researchers.

Only two fungal pathogens, *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metschnikoff) Sorokin (Hyphomycetales), have been extensively evaluated for termite control. Rosengaus & Traniello (1997) tested the pathogenicity of *M. anisopliae* on laboratory colonies of *Zootermopsis angusticollis* (Hagen) (Termopsidae). Mortality due to infection was dosage-dependent, LT_{50} (median survival time) values ranging from 2.7 days at a concentration of 7×10^7 conidia (spores) ml^{-1} to more than 10 days at 7×10^1 condia ml^{-1}. Termites directly exposed to the highest concentration were capable of infecting unexposed, healthy nest mates. In a series of laboratory studies, Hänel (1981, 1982a,b) investigated the pathogenicity and biological control potential of *M. anisopliae* on the mound-building species *Nasutitermes exitiosus* (Hill) (Termitidae). There was a clear correlation between conidial concentration and percentage mortality, average mortality exceeding 95% within 11 days at the highest dosages. Termites were observed to segregate cadavers from the rest of the colony, but, in so doing, came into contact with infective conidia.

Subsequent field experiments did not confirm the potential of *M. anisopliae* to give permanent control of *N. exitiosus* colonies (Hänel & Watson, 1983). In five out of seven mounds treated with conidial preparations, termite population densities were significantly reduced. Also, termites exposed to conidia at feeding sites were seen to spread infection back to their colonies, which persisted in some for at least six weeks. Again, densities in the affected colonies were significantly decreased. However, although the fungus persisted for as long as 15 weeks in termite mounds, its incidence declined progressively, as did termite mortality, which was high initially, but decreased over time. The relevance of these results to the control of subterranean termites is unclear.

Several laboratory studies have examined effects of *M. anisopliae* and *B. bassiana* on subterranean termite populations. Results have varied with the termite species and strain of fungus tested, and the concentration of inoculum and its mode of delivery to termite populations. Leong (1966) demonstrated the high pathogenicity of *M. anisopliae* to *C. formosanus*. With short exposures (e.g. 5–35 min), mortality exceeded 86%, and termites succumbed within 3–6 days post treatment. Exposure over 40 min produced 100% mortality; longer exposure times caused death within 24 h. The fungus sporulated only sparsely under conditions of complete darkness, which might limit its utility for biological control of subterranean termites, although pathogenicity was unchanged between dark and light conditions. No significant difference between the pathogenicities of *B. bassiana* and *M. anisopliae* was found. In another study, lengthy exposure (4 h) to sporulating cultures of *B. bassiana* also led to the rapid death of *R. flavipes*, generally in 24–36 h (Bao & Yendol, 1971). Toumanoff & Rombaut (1965) reported 100% mortality in *Reticulitermes* *santonensis* (de Feytaud) (Rhinotermitidae) within 5–6 days of exposure to *B. bassiana* and *M. anisopliae*. Sajap & Kaur (1990) also showed *Coptotermes curvignathus* (Holmgren) (Rhinotermitidae) to be highly susceptible to infection by *M. anisopliae*. Termites died within 36–48 h of exposure to conidia. Another study of *M. anisopliae*, in which termites exposed to conidia were introduced into laboratory colonies, reported 100% mortality in the test colonies within eight days, even when the termite vectors carried low conidial loads (Zoberi, 1995). Spread of the disease through colonies was complete, even though some of the fungus-killed termites were buried by nest mates, impairing growth of the fungus and preventing dispersal of conidia. Results suggested that epizootics within natural subterranean colonies might be initiated by a sufficient number of vector termites contaminated with large doses of inoculum introduced directly into the soil.

Kramm & West (1982) found that conidia of *B. bassiana*, *M. anisopliae* and *Gliocladium virens* Miller, Giddens & Foster remained infective after passage through the intestines of subterranean termites (*Reticulitermes* sp.), a significant finding since mutual grooming, trophallaxis and cannibalism should provide efficient means for spreading the pathogens throughout the colony. Again, strains of *B. bassiana* and *M. anisopliae* were about equally effective, producing complete mortality within 2–5 days. Similarly, Wells *et al*. (1995) concluded that one isolate each of *B. bassiana* and *M. anisopliae*, of all strains tested, showed the greatest potential for control of *C. formosanus* populations, based on LD_{50} (median lethal dose; as conidia per insect), time to death, and conidial production.

However, Lai *et al*. (1982), using other strains of the fungi, found that *M. anisopliae* was more pathogenic than *B. bassiana* in conidial suspensions topically applied to *C. formosanus* colonies. A large increase in conidial concentration (at least 10-fold) was required to increase significantly the rate and extent of infection in the colonies. Grace (1991) also found *M. anisopliae* to cause greater and more rapid mortality than *B. bassiana* in *C. formosanus* at low conidial concentrations. In their evaluation of both pathogens, Jones *et al*. (1996) found the *M. anisopliae* strains to be more virulent, in general, than those of *B. bassiana*. However, although the *M. anisopliae* strains showed lower LT_{50} values, the authors concluded that one strain of *B. bassiana* possessed greater potential as a remedial control for *C. formosanus*, based, in sum, on its lower LC_{50} value (median lethal concentration), moderately low LT_{50}, and transmissibility and survivorship qualities.

Rath & Tidbury (1996) found that *Coptotermes acinaciformis* (Froggatt) (Rhinotermitidae) and *N. exitiosus* were equally susceptible to direct conidial applications of both an Australian and American strain of *M. anisopliae*. They concluded that virulence of *M. anisopliae* is not an essential strain selection criterion, as all isolates are apparently virulent. However, Milner (1992) found that, in general, *C. acinaciformis* and *C. frenchi* (Hill) (Rhinotermitidae) were more susceptible to *M. anisopliae* than *N. exitiosus*. Subsequently, an isolate of the fungus, which was highly pathogenic to all three termite species in the laboratory, reportedly showed some potential to control termite populations in field trials (Milner *et al*., 1996), although few details were provided.

Other work has shown *M. anisopliae* and *B. bassiana* to be ineffective in controlling subterranean termites in the field. In experiments in which conidia of the two fungi were introduced directly into galleries and onto termites subsequently returned to the nest, Lai (1977) failed to initiate an epizootic in colonies of *C. formosanus*, even though the concentration used was sufficient to kill termites within 3–7 days in the laboratory. The negative results were attributed to poor germination of conidia in the nest and elimination of conidia from treated termites through grooming or secretion of a fungistatic agent. Others also have been unable to demonstrate field efficacy of the pathogens despite successful laboratory trials (Suzuki, 1991, 1996; Gitonga, 1996). To date, injection of large quantities of conidia directly into the termite nest has had the greatest success in field studies (Fernandes, 1991; Milner *et al*., 1996).

Beauveria bassiana and *M. anisopliae* may exhibit their greatest potential for subterranean termite control in their use in baiting systems, whereby the termites themselves pick up and introduce infective agents into the colony. Laboratory studies have begun to identify both the promise and problems associated with such techniques. For example, Preston *et al*. (1982) found that baits composed of *M. anisopliae* conidia and culture medium (containing a mixture of conidia, mycelia and metabolites), incorporated in different combinations into paraffin-woodmeal composite blocks, exhibited uniform repellency to termites (*Reticulitermes* sp.), but induced differential mortality. Blocks containing conidia alone produced no detectable mortality, whereas the highest mortalities (but least feeding damage) were associated with blocks containing medium, which remained effective as long as one month. However, the fungus could not be isolated from cadavers. This result, combined with the repellency of the baits, casts some doubt on the system's practical capacity to infect a natural colony. Other studies have reported the conidia (Rath & Tidbury, 1996) and toxins (destruxins; Wahlman & Davidson, 1993; Grace, 1995) produced by *M. anisopliae* to be repellent to termites.

Recent work with a *B. bassiana* strain isolated from *R. flavipes*, and pathogenic to that species (Zoberi & Grace, 1990a) and to *C. formosanus* (Grace, 1991), showed that, although *R. flavipes* workers isolated fungus-killed individuals, there was no avoidance of mycelia or conidia (Zoberi & Grace, 1990a). In a later study, Grace & Zoberi (1992) found that living *R. flavipes* workers exposed to sporulating *B. bassiana* cultures effectively spread infection to unexposed nest mates, whereas introduction of fungus-killed workers did not result in sufficient spore transfer or mycelial growth to cause significant mortality. However, the level of mortality achieved in the laboratory was not considered sufficient to control a termite infestation in the field. Similarly, Kramm *et al*. (1982) showed that active *Reticulitermes* sp. workers exposed to whole cultures of *M. anisopliae* transferred the pathogen to previously healthy termites through grooming. However, termites killed by the fungus were avoided by healthy individuals, and were less effective in spreading the disease to nest mates.

Other laboratory studies of baits have assessed the infectivity of sporulating strains of *B. bassiana* and *M. anisopliae* to *C. formosanus*. In preliminary work, Grace (1993) reported that termites exposed to baits accumulated spore loads (600,000–8 million conidia per individual) that greatly exceeded previously established lethal concentrations (LC_{95}; 490–20,000 conidia per individual), and were capable of transmitting the pathogens to other colony members. Delate *et al*. (1995) achieved complete mortality of termites within 15 days with isolates of both fungi. However, in this case, neither avoidance of fungi by termites nor isolation of infected individuals from the rest of the colony was detected. Results suggested that fungal bait stations might be useful in termite control by providing a continuous and non-repellent source of sporulating cultures for foraging termites to contact, although a self-perpetuating infection within the experimental colonies was not demonstrated.

In summary, of all pathogens tested, the fungi would seem to offer the most potential for at least some measure of termite control. However, the use of fungi in control programmes is compromised by inherent biological limitations and logistical problems. Fungi have a slow mode of action and require high levels of relative humidity; there is also the need for large quantities of infective conidia to contact the target pest population in order to yield an acceptable level of control (McCoy, 1990). It has also been suggested that, because so few of the many strains evaluated for termite control were effective, even under favourable conditions, termites may have evolved a degree of resistance to fungal pathogens (Burges, 1981). However, there is as yet no good evidence to support this speculation.

Perhaps because of the many difficulties involved with their use, there are, at present, few commercial fungal preparations available for pest control in the USA. Further development for biological pest control of *B. bassiana* and *M. anisopliae*, in particular, continues to be hampered by a lack of cost-effective methods for mass production (Federici, 1990).

Fungi may yet find their most effective use in the form of baits, and research in this area is progressing (e.g. Delate *et al*., 1995; Jones *et al*., 1996; Staples & Milner, 1996). Effective baiting schemes for termite control require delivery of sufficient spore inoculum to active termites and subsequent transfer from them to nest mates without stimulating colony defensive behaviours. This will entail both improvement of field techniques for dispensing conidia and identification of new fungal species and strains capable of initiating and sustaining an epizootic once they are introduced into the nest.

Conclusions

Although laboratory studies have hinted at its potential, classical biological control of termites has not yet been convincingly demonstrated. The limited number of field trials that have been attempted largely have failed to establish the permanent, self-sustaining populations of control agents necessary to reduce termite densities below economically damaging levels. This lack of success has resulted from a combination of factors. Intrinsic limitations of natural enemies, such as narrow environmental tolerances, antagonistic interactions with other organisms, limited mobility, or a low level of virulence, diminish their effectiveness as agents of control, whereas natural defensive behaviours of the termite prey, such as avoidance of areas of predator, parasite or pathogen concentration, detection and isolation of infected nest mates, and, in the case of subterranean termites, construction of a cryptic, complex, and largely inaccessible nest, reduce the impact of predation and infection. As Logan *et al*. (1990, p. 324) have remarked, 'Manipulation of predators, either local or introduced, will have little effect if only foraging worker termites are killed, while the possibility of manipulating predators which seek out the king and queen seems remote. Many microorganisms are pathogenic to termites, but few have received more than cursory attention. This, combined with the termites' behavioural mechanisms for combatting infection of the colony, means that successful and widely applicable microbial control is a long way off.' An additional obstacle to progress in microbial termite control relates to the constraints that evolving environmental protection laws place on research, making it increasingly difficult for researchers to import insect pathogens.

A thorough assessment of biological termite control should address the possibility of unintended results. Any pest control programme poses some threat to the environment. Natural enemies introduced for the biological control of specific pests have had negative impacts on populations of nontarget organisms either directly, through predation, parasitism, infection or competition, or indirectly, in their influence on seemingly unconnected species (Howarth, 1991; Secord & Kareiva, 1996). Introduced subterranean termite enemies conceivably might adversely affect nontarget termite species or have secondary effects on other organisms coming into contact with dead or dying termites. To minimize such risks, governments of developed countries, such as Australia and the United States, in recent years have adopted strict quarantine regulations governing the importation of exotic organisms. In the USA, for example, the Department of Agriculture (USDA) and Environmental Protection Agency (EPA) oversee the introduction, host or prey specificity testing and release of biological control agents (Pimentel *et al*., 1984; Secord & Kareiva, 1996). The Environmental Protection Agency is the lead agency responsible for registering and regulating microbial pesticides (Grace, 1994). The testing protocols and other quarantine procedures developed by these agencies are the best compromise between the competing demands of pest control and environmental protection.

However disappointing near-term prospects for successful classical biological termite control would seem to be, research has begun to test promising new parabiological methods to prevent structural infestation by subterranean termites. For example, recent studies have examined the potential for use of ant semiochemicals as termite repellents and toxicants. In laboratory tests conducted by Cornelius & Grace (1994), *C. formosanus* workers avoided contact with filter paper disks treated with extracts of the ant *Ochetellus glaber* (Mayr) (Formicidae); no evidence of termite habituation to the extracts was detected. Extract-treated sand barriers deterred tunnelling completely for 2–4 days at the higher extract concentrations tested, although partial penetration was seen in succeeding days. However, none of these barriers was completely penetrated, even after ten days. Further work showed sand treated with *O. glaber* extracts to be toxic to *C. formosanus* workers, causing 100% mortality after 24 h at the higher concentrations used; median concentrations caused lower mortality, but left survivors immobilized (Cornelius *et al*., 1995). Even at lower concentrations, mortality of extract-exposed termites was three times that of controls after 48 h. Again, treated sand barriers were used, and showed that the repellent components of *O. glaber* extract (identified as two isomers of the monoterpene dolichodial) would significantly reduce the extent of tunnelling as long as 30 days after treatment.

In related work, extracellular metabolites (siderophores) of the brown-rot wood decay fungus *Gloeophyllum trabeum*

(Persoon: Fries) Murrill (Polyporaceae) were found to inhibit feeding by *C. formosanus* (Grace *et al.*, 1992). Siderophore-treated filter paper disks showed negligible feeding, whereas untreated disks were almost completely consumed over a 3-day test period.

Results of these and earlier studies (e.g. Amburgey & Beal, 1977) suggest that natural products, such as ant semiochemicals and fungal metabolites, or their synthetic analogues, might one day be of value in termite control programmes as repellents or insecticides in wood treatments or soil applications. However, the development of more stable formulations, such as microencapsulation, would be necessary to ensure their long-term, residual action.

Future research should establish what role biological methods, particularly the use of pathogens, effectively will play in overall termite management strategies. Biological control may yet come to supplement, but is unlikely any time soon to supplant, other established subterranean termite control technologies.

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