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Perspective

Fifty years of attempted biological control of termites – Analysis of a failure

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ABSTRACT

The use of pathogens as biological control agents has long been considered a promising technology for termite control. Over the past five decades, there has been a large accumulation of scientific literature on the development of control methods using various pathogens. However, despite the evidence that biological control has essentially failed, or failed to be developed, as a method for commercial termite control, this field of research remains very active. In this study, we examined 50 years of research on the microbial control of termites in order to understand why commercial products have failed to be developed and why this field of research remains so active. All (to the extent of our knowledge) of the literature published between 1960 and 2011 was evaluated to investigate any publication bias and to detect false positives in the form of overly optimistic conclusions. This re-interpretation supports the idea that the conclusions frequently expressed have been misleading to some extent, or at least overly optimistic, about the potential for application of biological control to termites. Many results obtained from bioassays with poor biological relevancy have been interpreted as promising, while few results actually support practical application. We also suggest that the failure of termite biological control and the continued research emphasis in this area resulted in part from unrealistic optimism about the potential for development of environmentally friendly methods to control termites, publication bias, and poor understanding of termite biology.

1. Introduction

Termites (Isoptera) include more than 2600 species around the world (Abe et al., 2000), but only a few of them (70–80 species) are considered of economic importance due to their damage to manmade structures and to forestry or agricultural products (Edwards and Mill, 1986; Logan et al., 1990). In recent years, there has been a large increase in the scientific literature concerning termites (Vargo and Husseneder, 2009) which reflects their economic importance and the availability of funding to support termite research. Various preventative and remedial strategies are currently used against pest species in the termite control industry (Su and Scheffrahn, 1998, 2000). Concerning subterranean termites in particular, it has been estimated that 77% of the pest control market share is represented by soil termiticide applications in the United States (Anonymous, 2002). Despite this heavy reliance upon the application of soil insecticides, future termite control technologies may need to conform to higher environmental standards (Su, 2002).

As an alternative to liquid pesticide applications, monitoring-baiting procedures with the use of chitin synthesis inhibitors have been developed (Su, 1994; Grace and Su, 2001), and are commercially available. Botanical insecticides have also been considered (Verma et al., 2009) although their use remains anecdotal. The use of predators as biological control agents has been investigated, but did not reveal any potential for commercial application (Culliney and Grace, 2000).

In developed countries, the market for microbial insecticides for various agricultural pests represents only 1% of the total crop protection market, and mostly represents the sale of *Bacillus thuringiensis* (Berliner) products (Lisansky, 1997; Lacey et al., 2001). Biological control using pathogens has long been considered a promising technology for future termite control options (Grace, 1997) because termites were assumed to live in an environment conducive to entomopathogens (Kramm et al., 1982; Rath, 2000). However, to date, no successful implementation of biological control in the termite control industry has occurred, despite the large body of scientific literature in this particular field (Logan et al., 1990; Culliney and Grace, 2000), suggesting that the effort spent to develop such products has yet to yield concrete results (Grace, 2003).

In the current study, we examined research reports on microbial control of termites for the past 50 years in a narrative review in order to summarize evidence from multiple studies. However, there is an inherent bias in science toward publication of positive

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results (Begg and Berlin, 1988; Hasenboelher et al., 2007), as such results have a much greater chance of reaching publication in peer-reviewed journals than negative results, and as researchers tend to "fish for significance" (Boulesteix, 2010). Thus, an uncritical review of the published studies may lead to an incorrect and usually overly optimistic conclusion (Sutton et al., 2000). In addition, the overall scientific literature suffers from a large accumulation of false (or overly optimistic) positive findings and a dearth of published negative findings (Ioannidis, 2005). Recent advances in the understanding of termite disease resistance mechanisms presented in a companion paper (Chouvenc and Su, 2010) raise questions about the validity and applicability of some of the positive results published within the past 50 years in the field of termite biological control. Some studies may have used protocols with poor biological relevancy and may also have improperly and optimistically interpreted the data provided.

The purpose of our review is to understand why biological control of termites using pathogens has not succeeded despite extensive research efforts and, conversely, why this field of research remains active. We discuss the different protocols used for introduction of pathogens in a termite colony, cover the history of termite biological control, re-interpret all data published since 1960, and discuss some of the biases scientists may have confronted which could contribute to the apparent failure of termite biological control.

1.1. Protocols for introduction of pathogens

Most of the research on termite biological control has followed the concepts of classical biological control of other insect pests using pathogens (Ferron, 1978; Lacey et al., 2001). Due to the cryptic habitat and social organization of termites, however, biological control in termites has had to be modified from strategies used in agricultural crops. An inundative method was used for termite species with a central nest structure, one-piece nesting type, or intermediate nesting type (Abe, 1987). For example, drywood termites, and some dampwood and mound-building termites often, but not always, have a localized central nest where most of the individuals of a colony can be treated (Grace et al., 2009). This method has been used to demonstrate that when most of the termites are accessible for inundative treatment, it is possible to eradicate the colony (Hänel and Watson, 1983; Danthanarayana and Vitharana, 1987; Lenz and Runko, 1992, 1995; Jackson et al., 2010), although some technical limitations can be encountered and colony control can be inconsistent. A colony is defined here as a group of individuals of the same species sharing an interconnected gallery system. Such methods employ pathogens as a bioinsecticide, and transmission among individuals is not necessary.

Unfortunately, the inundative method is not realistic for termite species with a diffuse nest structure (extended nesting type), such as subterranean termites, because only a small fraction of the colony is accessible. Occurrence of an epizootic in subterranean termite species relies upon transmission of the pathogenic agent among all individuals in the colony, which is difficult due to avoidance of the treated areas by healthy individuals (Rath, 2000). Such treatments could use pathogens as a repellent for temporary protection of the treated area, but are not likely to achieve colony-level control. Therefore, alternative protocols have been deemed necessary to introduce pathogens into a subterranean termite colony. A "trap and treat" protocol was mentioned by Milner et al. (1996). This method consists of collecting individuals from a colony, treating them with a virulent entomopathogen, and releasing them back into their original nest in hopes that they will contaminate the rest of the colony. However, it is difficult to inoculate enough individuals simultaneously to trigger an epizootic within the colony (Chouvenc et al., 2008b). A baiting approach has also been considered (Delate et al., 1995; Milner, 2003; Wang and Powell, 2004), but the development of a stable and non-repellent formulation remains problematic. Despite efforts to screen for virulent strains of pathogenic agents, the delivery of sufficient inoculums to a subterranean termite colony remains an unsolved problem (Grace, 2003).

1.2. Brief history of termite biological control

Before 1960, few reports noted the pathogenic effect of microorganisms on termites. Merrill and Ford (1916) and Pemberton (1928) first reported the presence of parasitic "head inhabiting" nematodes in *Reticulitermes lucifugus* (Rossi) and *Coptotermes formosanus* Shiraki respectively, but concluded that such nematodes could not kill termites in soil conditions. De Bach and McOmie (1939) later reported the existence of two bacterial species killing laboratory colonies of *Zootermopsis angusticollis* Hagen and identified them as *Bacterium* sp. and *Serratia marcescens* Bizio. However, these authors did not discuss any potential for using such microorganisms as termite control agents. Both Kevorkian (1937) and Altson (1947) mentioned the presence of the fungus *Conidiobolus* sp. on *Nasutitermes* sp. and *Coptotermes* sp. respectively, also without mentioning any potential as a biological control agent.

In 1958, facing the emergence of *Reticulitermes flavipes* (Kollar) (Syn. *R. santonensis* Feytaud) as a structural pest in the south of France, the *Service de Pathologie des Insectes* from the *Institut Pasteur* in Paris requested a survey of potential disease agents that could be used as biological termiticides. Toumanoff and Toumanoff (1959) conducted the survey and reported that *S. marcescens* could kill termites, but discussed the problem of testing pathogens against laboratory groups of termites with "low vigor". This short report marked the debut of termite biological control research and triggered a series of studies supporting the use of pathogens to kill termites, mainly in the United States. Beal and Kais (1962) identified *Aspergillus flavus* Link as a fungal pathogen of *Reticulitermes* sp. and Lund (1962, 1965b, 1969) suggested that *Serratia* sp. and *Aspergillus* sp. could be used for termite control. Lund (1965a) reported the first field study using *S. marcescens* against *R. flavipes* and stated that termite activity ceased in the treated areas. Smythe and Coppel (1965) showed that *R. flavipes* could be susceptible to a formulation of *B. thuringiensis* and also showed that *Isaria* sp. (syn. *Paecilomyces* sp.) could be pathogenic to *R. flavipes* (Smythe and Coppel, 1966). Page (1966) suggested that *Entomophthora virulenta* Hall and Dunn, in association with *B. thuringiensis*, could be used to control *C. formosanus* in Hawaii. Meanwhile, Toumanoff (1965, 1966) screened several species of entomopathogenic fungi and bacteria, and Toumanoff and Rombaut (1965) concluded that *Metarhizium anisopliae* (Metsch.) Sorokin and *Beauveria bassiana* (Balsamo) Vuill. were the two most virulent entomopathogenic microorganisms against *R. flavipes*. At this time, the potential economic value of termite biological control appeared obvious. Lund (1966) patented formulations of *A. flavus* and *S. marcescens*, and Page (1967) patented the combination of *E. virulenta* and *B. thuringiensis* as biological control agents against termites. However, Lund (1971) concluded in a short report that none of his field studies with various pathogens demonstrated sufficient pathogenicity to termites.

In the late 1960s through early 1970s, interest in the use of pathogens against termites continued to increase (Yendol and Rosario, 1972), as indicated by the growing number of publications in this field (Fig. 1). In Hawaii, Tamashiro (1968) proposed to the US Navy to investigate the effect of various pathogens against *C. formosanus*, including nematodes (*Steinernema* spp.) and fungi (*M. anisopliae* and *B. bassiana*). This project was the beginning of an active program in termite research at the University of Hawaii, and several graduate students focused their studies on