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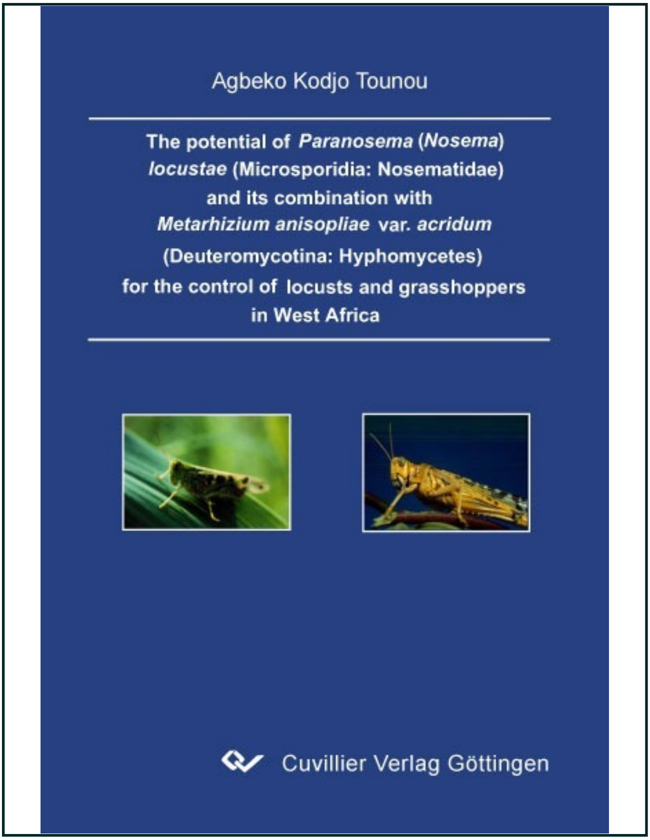
The potential of Paranosema (Nosema) locustae (Microsporidia: Nosematidae) and its combination with Metarhizium anisopliae var. acridum (Deuteromycotina: Hyphomycetes) for the control of locusts and grasshoppers in West Africa



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1 General introduction

1.1 Origin and distribution of grasshoppers and locusts

Grasshoppers and locusts include insects in different families belonging to the super family Acridoidea and the order Orthoptera (Otte, 1981). Grasshoppers and locusts are distinguishable from other orthopterans primarily on the basis of their external morphology. The most obvious and distinctive features of grasshoppers and locusts are their enlarged hind legs and their relatively short and thick antennae. There are more than 350 grasshopper and locust species recorded from the Sahel (Mestre, 1988), of which about 30 are considered to be of regular or irregular pest status (Popov, 1988).

Grasshoppers and locusts occur in a wide variety of habitats, from low-elevation, hot, dry deserts to high-elevation, moist environment. Most species occur in arid and semi-arid environment, and it is in the warm semi-arid and arid desert grasslands that grasshopper and locust species diversity and population densities are the greatest (Otte, 1976). They are relatively large, active insects and require structurally open habitats where they are free to move, and where sunlight levels are high enough to enable them to maintain high metabolic rates. Habitat specificity varies considerably among species of grasshoppers and locusts (Joern, 1979). Some species such as *Schistocerca gregaria* Forskål and *Oedaleus senegalensis* Krauss (Orthoptera: Acrididae) are typically common in desert environments but can be found in a wide variety of habitats over wide geographic and altitude ranges when outbreaks occur. Other species are much more restricted or specific to particular types of habitats. Grasshoppers tend to feed on particular plants that occur in their preferred habitats.

1.2 Biology and ecology of locust and grasshopper

1.2.1 The Senegalese grasshopper *Oedaleus senegalensis*

The Senegalese grasshopper *O. senegalensis* is the most serious periodic grasshopper pest widely distributed throughout the Sahel but also in many other parts of the world (Cheke, 1990; Geddes, 1980). Since the 1970s, deforestation, overgrazing and droughts in Sahel have favoured the development of Kram Kram grasses (*Cenchrus biflorus* Roxb (Cyperales: Poaceae)), suitable habitats for *O. senegalensis* (Cheke et al., 1980). At high population densities, *O. senegalensi*s undergoes a phase change to gregarious morph (Ahluwalia et al., 1976). *Oedaleus senegalensis* has an annual life cycle and is a pest of several subsistence crops. Early instars develop in fallow or grassland. Subsequently, with increase of population densities, late instars and adults can cause economic damage directly to pastures, and also by migrating from pasture into adjacent crops such as millet, maize, beans, sweet potato, cassava and vegetable (Boys, 1978; Popov, 1980; Lobo-Lima and Klien-Koch, 1981; Amatobi et al., 1986).

Under favourable conditions, *O. senegalensis* has a generation time of about 45 days to two months (Popov, 1980; Cheke, 1990), enabling it to complete 3 generations in the short annual rainy season. Depending on the environmental conditions, *O. senegalensis* develops through 5 to 6 nymphal stages. The pest is adapted to dry environments and when conditions are not favourable for its development, it may lay diapausing eggs that can survive underground until the rainy season (Colvin and Cooter, 1995). Hatching in such conditions occurs after 7-8 months (Gehrken and Doumbia, 1996), leading to successive serial hatchings at the beginning of the rainy season. Such a situation makes the egg diapause, an important component of the outbreaks generating mechanism (Fishpool and Cheke, 1983). Both photoperiod and temperature influence the induction of diapause in *O. Senegalensis* eggs. Diop (1993) reported that females, reared under short photoperiod (L:D 10:14 h), produced mostly diapausing eggs, while those reared under long photoperiod (L:D 14:10 h) laid essentially no diapausing eggs. According to Colvin and Cooter (1995), high temperatures (40 °C) and long photoperiods (L:D 14:10 h) which characterize the beginning of the rainy season in the Sahel, cause non-diapausing eggs to be laid while lower temperatures (25 °C) and shorter photoperiods (L:D 12:12 h), which occur at the end of the rains, result in the production of diapausing eggs.

1.2.2 The desert locust *Schistocerca gregaria*

The desert locust, *S. gregaria* is the most commonly Orthopteran known which represents the most complex situation of all the locust pests. During periods of recession the desert locust is usually restricted to the semi-arid and arid deserts of Africa, the Near East and South-West Asia that receive less than 200 mm of rain annually. The insect generally develops from first instar nymphs to adults in about 4-6 weeks. Females lay eggs in an egg pod in sandy soils at a depth of 10-15cm below the surface. A solitary female lays about 95-158 eggs whereas a gregarious female lays usually less than 80 eggs per egg pod (Popov, 1980). Females can oviposit at least three times in their lifetime usually at intervals of about 6-11 days. Hatching occurs during rainy season in response to favourable temperature and moist conditions (Hewitt, 1979).

The most prominent feature of the desert locust is its ability to interconvert between two morphologically, physiologically and behaviourally distinct phases. As desert locusts increase in number and become more crowded, they switch from solitary to gregarious behaviour (Showler and Potter, 1991). Some adult desert locusts are pale gray or beige in the solitary phase, with the males turning pale yellow on maturation. In contrast, an adult from the gregarious (swarming) phase is bright pink when immature and bright yellow when mature. The solitarian phase prevails under endemic conditions in areas of recession, which are characterized generally by dry and warm weather. This phase lives as dispersed individuals in very low densities, feeding on a limited range of desert plants, and reproducing only when environmental conditions are sufficiently favourable. The gregarious phase is characterized by a highly cohesive behaviour, long-distance migratory aptitude, polyphagy, synchronous and accelerated maturation of males and females and mass egg laying by gravid females at common sites.

1.2.3 Other Locusts and Grasshoppers

Other important locust and grasshopper species occur mainly in Africa, but also in the Middle East. They include among others *Zonocerus variegatus* L. and *Kraussaria anguilifera* Krauss (Orthoptera: Pyrgomorphidae); the Egyptian grasshopper *Anacridium aegyptium* L., *Cataloipus fuscocoeruleipes* Sjöstedt, *Diabolocatantops axillaris* Thunberg, *Hieroglyphus daganensis* Krauss, the brown locust *Locustana pardalina* Walk, the red locust *Nomadacris septemfasciata* Serville, *Kraussella amabile* Krauss, *Pyrgomorpha cognata* Krauss (Orthoptera: Acrididae). Some of these locust and grasshopper species may cause severe economic damage to crops while others may occur usually only in small numbers, rarely causing heavy damage and having no economic importance.

1.3 Host plants and economic importance of locusts and grasshoppers

Both grasshoppers and locusts cause direct losses to crops by voraciously devouring vegetation. They feed on several economically important crops among which rice, wheat, cotton, maize and millet are the most important. Some species are host specific to certain plants; others feed on many different species and even families of plants. Total plant loss may occur when attack coincides with vulnerable stages of the crop. Grasshoppers pose damage every year, but become very destructive during outbreak periods. In the Sahel and Sudan savannah zones of West Africa, the Senegalese grasshopper *O. senegalensis* is an important pest of *Pennisetum* (millet), the principal food crop of the region (Cheke et al., 1980). In outbreak years, hopper bands can destroy millet and sorghum seedlings and farmers often have to reseed several times. In 1989, 5.7% of the farmers in northwestern Mali lost 70 to 90% of their millet crop due to grasshoppers (Cheke, 1990; Kremer and Lock, 1992). In Niger, between 10 and 82% damages measured on millet seed heads have been reported to be caused by *O. senegalensis* (Cheke et al., 1980).

1.4 Management options

1.4.1 Chemical control strategies

Control of grasshoppers and locusts has traditionally relied on synthetic insecticides and for emergency situations this is unlikely to change. Large-scale locust and grasshopper outbreaks generally demand immediate attention and significant short-term reduction of the pest populations. To prevent total crop losses following severe outbreaks, chemical controls with conventional pesticides have been the most appropriate strategy in Sahel, Northern United States and Canada, South-eastern Asia, Australia and elsewhere from the 1950s to the mid-1980s (Brader, 1988). The technique of control of locusts and grasshoppers involved the spraying of barriers of persistent organochlorine insecticides across areas infested by hopper bands. For many years, the product of choice was dieldrin, a persistent pesticide well suited for barrier treatment (Brader, 1988). However, concerns about its detrimental impact on the environment resulted in its prohibition in most countries.

Since the withdrawal of dieldrin, locust and grasshopper control has become more difficult and less efficient. In the absence of this product, other less persistent pesticides such as fenitrothion, malathion and fipronil, have been used for acridids control in Africa and in many parts around the world targeting both nymphs and adults (Prior and Street, 1997). They are sprayed or dusted directly onto hopper bands and swarms, or distributed close to them as baits. All of these techniques require much greater effort in locating and treating individual targets than the former barrier technique that had been apparently successful. Most modern pesticides such as fenitrothion that has a half-life of about 24 hours (Sekizawa et al., 1992), are much less persistent and have therefore to be applied more frequently in larger volumes. Hence, even though they are less toxic than dieldrin, their environmental impact may well be worst.

The scale and cost of pesticide application added to the concerns over the environmental and human health implications have triggered a strong interest in international programs for the development of microbial control agents for use in integrated control of acridoid pests.

1.4.2 Biological control as alternative to conventional pesticides

Biological control of acridoid pests has been developed as an alternative to conventional chemical application. At least 200 species of insects, mites, and nematodes attack grasshoppers (Lavigne and Pfadt, 1966; Rees, 1973). Various species of flies and wasps parasitize grasshopper nymphs and eggs while other flies, beetles (including blister beetle larvae in the genus *Epicauta*), birds, and rodents are significant predators. Among diseases that occur naturally in locust and grasshopper populations, the most common are from fungal infections (Lomer et al., 2001; Wraight et al., 1998) and microsporidian, principally *Paranosema locustae* Canning (Microsporidia: Nosematidae) (Brooks, 1988; Lange, 1992, 2001, 2002).

1.5 The entomopathogenic fungi

Entomopathogenic fungi are important pathogens of many insects and other arthropods and frequently cause epizooties that can significantly reduce pest populations all over the world. Approximately 750 species of entomopathogenic fungi are known to infect a number of economically important arthropod pests and have thus received considerable attention as potential microbial control agents (Mulock and Chandler, 2000; Haraprasad et al., 2001). The majority of these entomopathogenic fungi belong to the classes of Zygomycetes, Ascomycetes and Deuteromycetes. Among entomopathogenic fungi that have been considered as alternative to synthetic chemical, species in the genera *Metarhizium* are the most widely used to control grasshoppers and locusts (Bateman, 1997; Jaronski and Goettel, 1997).

Metarhizium anisopliae Metchnikoff (Deuteromycetina: Hyphomycetes) occurs on a wide range of insects in the orders Orthoptera, Coleoptera, Lepidoptera, Hemiptera and Hymenoptera, as well in the class Arachnida. Various studies have shown the potential of *M. anisopliae* as a microbiological control agent of important pests. In Africa, since 1989, the project Lubilosa (French acronym of “Lutte Biologique Contre les Locustes et les Sauteriaux"), a collaborative research programme involving the International Institute of Biological Control (IIBC, Ascot, UK), the International Institute of Tropical Agriculture (IITA, Cotonou, Benin) and the "Département de Formation en Protection des Végétaux" (DPFV, now part of AGRHYMET-CILSS, Niamey, Niger), has worked towards the development of an oil-based formulation of a mycopesticide containing *M. anisopliae* var. *acridum* Driver and Milner, for the control of the desert locusts and grasshoppers (Prior et al., 1992; Prior et al., 1995). Field trials demonstrating the efficacy of *M. anisopliae*, as oil formulation, have been carried out successfully (Lomer et al., 1993; Lomer et al., 2001; Douro-Kpindou *et al.,* 1995; Langewald et al., 1999; Arthurs et al., 2003). The host range of the fungus is narrow and at field application rates it is safe to non-target Hymenoptera, Coleoptera and Homoptera (Ball et al., 1994; Lubilosa unpublished results). The lack of toxicity of *M. anisopliae* to mammals and, consequently to humans (El-Kadi et al., 1983), offers a further advantage over currently used organophosphate pesticides.

1.5.1 Life cycle of entomopathogenic fungi

In general, the life cycle of entomopathogenic fungi begins with the attachment of the spore to the cuticle of the insect followed by germination and active penetration into the cuticle and a rapid proliferation of the fungal cells in the host's body. The fungus rapidly multiplies throughout the body and uses it as a nutrient source. Mortality is due to tissue destruction and occasionally to toxins produced by the fungi (Kershaw et al., 1999). The death of the infested host is followed by the outgrowth of the fungus and the production of infective spores, which can immediately repeat the cycle. The processes of germination of spore and growth on the cuticle are highly dependent on both biotic and abiotic factors. The importance of abiotic factors, such as temperature, relative humidity and light on the infection by entomopathogenic fungi has been intensively investigated (Milner et al., 1997; Estrada et al., 2000). Abiotic factors affect both fungal sporulation and the survival of the conidia (Milner et al., 1997). On the other hand, biotic factors influencing fungal infections include microbial antagonists on the host insect integument, host susceptibility and, most importantly, the varying degree of virulence of the fungal strains.

1.6 The Microsporidian, *Paranosema locustae*

Paranosema locustae is a spore-forming pathogen of the adipose tissue of orthopterans that was isolated, selected, and developed in the USA as a long-term microbial control agent of grasshoppers (Henry, 1978; Henry and Oma, 1981; Johnson, 1997; Lockwood et al., 1999). *Paranosema locustae* belongs to the Microsporidia, a group of unicellular eukaryotes that are obligate intracellular parasites of animals and some protists (Wittner and Weiss, 1999). Microsporidia were historically regarded as Protozoa or Archezoa, but recent studies at the molecular level have shown they are actually related to Fungi (Keeling and Fast 2002).

In North America, Steinhaus (1951) first noticed *P. locustae*, albeit without naming it, in 3 species of grasshoppers of the genus *Melanoplus* from Montana. Soon after, Canning (1955) described *P. locustae* as *Nosema locustae,* using diseased African migratory locusts, *Locusta migratoria migratorioides* Reiche and Fairmaire (Orthoptera: Acrididae), from a rearing colony at the Imperial College Field Station in London. Sokolova et al. (2003), while erecting the new genus *Paranosema* for another microsporidian pathogen of Orthoptera from the cricket *Gryllus bimaculatus*, transferred *N. locustae* to *Paranosema*, based on molecular and ultrastructural grounds, erecting the new combination *P. locustae*. Even more recently, Slamovits et al. (2004) proposed another new combination, *Antonospora locustae*; but Sokolova et al. (2005) provided reasons for favoring the name *P. locustae*.

One of several factors that permitted the selection of *P. locustae* for its development as a microbial control agent is its wide host range among acridomorphs. The pathogen has been extensively field-tested for long-term suppression of locusts and grasshoppers in the United States and Canada (Ewen and Mukerji, 1980; Onsager, 1988; Lockwood et al., 1988; Johnson, 1997). Although infection of *P. locustae* may occasionally result in high levels of mortality among some acridid species (Streett and Henry, 1984), realistic goals of application of this pathogen include reduced feeding by infected insects (Oma and Hewitt, 1984; Johnson and Pavlikova, 1986), delayed development (Schaalje et al., 1992), lower