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Perceptive Role of Fungal Gardens in Colonial Insects

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Abstract

Nature has devised various types of inter relationship between different groups of organisms that enable them to survive or ultimately run in to peril. One of the most beautifully and meticulously articulated relationship among living organisms is symbiosis. About 40-60 million years before the advent of human agriculture, three insect lineages, termites, ants, and beetles, independently evolved the ability to grow fungi for food. The most interesting group of insect known to cultivate some of the most magnificent fungal gardens is perhaps the leaf cutting ants and the mound building termites. These have several adaptations and their life style is suited for nutrition drawn from the fungal associates. The agricultural symbiosis with fungi has allowed both ants and termites to occupy previously inaccessible niches that have abundant resources. Termite, ant, and beetle farmers appear to have made the transition to fungiculture via different evolutionary avenues. In the termites, fungi probably were an important food source before true cultivation, and fungiculture arose when the termites secondarily developed an ability to manipulate fungal growth in their nests.

Key words: *Fungal gardens; Ants;Termites; beetles; Mound ;Fungiculture*

Introduction

Nature has devised various types of inter relationship between different groups of organisms that enable them to survive or ultimately run in to peril. One of the most beautifully and meticulously articulated relationship among living organisms is symbiosis. Symbiosis can be defined as the association between dissimilar organisms in which benefit may accrue to both at least for a period during the association. Associations need not be static. In a few cases, the symbiotic phase may continue to a parasitic or commensal phase.

The mutual and obligate relation is maintained to derive nutrition or other needs like reproduction, shelter etc. Thus in a symbiotic relationship the organisms involved cannot survive without each other. Symbiosis has been observed among different categories of organisms-both higher and lower, plants and animals. This type of relationship has more meaning than just survival and has molded itself through evolutionary history spanning over millions of years. And thus it is obvious that symbiosis has refined with passage of time and has evolved in to a precision interrelationship between the constituent organisms.

As far as animals/ insects feeding on plant materials are considered, there should be a physiological and anatomical mechanism that enables them to digest the high molecular weight and complex biochemical like cellulose and lignin. Specific enzymes are required to digest these plant materials. However, most animals and insects lack this inbuilt mechanism in their body to digest the plant materials. In such an evolutionary situation, they are known to enter in to symbiotic relation with certain microorganism like fungi and bacteria. One of the most important drives that may lead to such a relationship is the inability of animals to digest cellulose. Herbivores, such as horses, sheep, cows, goats, etc. do not have the ability to digest the cellulose from the plant material that they consume. Instead, they have symbiotic bacteria, in their stomach, that have the enzymes that digest the cellulose in the plant material for them. Other animals, such as detritivores, do not carry microorganisms in their gut, but rather consume mycelium in well-decomposed plant material as their food source. Thus, symbiotic relationships between animals and various microorganisms are probably common place. Animals and fungi are heterotrophic. They both require an exogenous source of energy to function. Thus some curious and complex interactions between animals and fungi have evolved. In general, the fungus removes a minute quantity of energy and is thus not a major threat to the animal. However, animals have evolved quite effective immunological responses to deter fungal invasion, indicating fungi have been a severe problem in the pat. The presence of fungal pathogens is unusual. Fungi found associated with animals commonly provide a functional benefit to their host. The benefit is commonly a primary or secondary metabolite. The host is able to exist in harsh and difficult environment because the fungus supplies vitamins or digestive functions, or protection through excretion of toxins.

One such interesting symbiotic relationship in animal kingdom is maintained by several insects with other organisms- mainly the microbial organisms like bacteria, actinomycetes, nematodes, and fungi. Most termite species have symbiotic bacteria in their guts that help in the digestion of lignin and cellulose.

However, the most complex and astonishing association exists between insects and cellulolytic / lignolytic fungi. The insect associates "culture" the fungal counterpart meticulously to satisfy the requirements of fungus and thus ensuring their own nutritional needs. Leaf cutting ants, mound building termites, scolytid beetles, scale insects, ambrosia beetles, bark beetles, sirex wood wasp (*Sirex noctilio)*etc area the few insects that form symbiotic association with fungus mainly to meet nutritional requirements.

Scale insect- fungus symbiosis

The scale insect has formed a well-defined association with the fungus belonging to genus *Septabasidium*. The genus is a member of the Basidiomycota and forms irregular, flattened, colonies that adhere closely to the bark of leaves of living trees, much like the growth of lichens. The colony may be flattened and only a few millimeters in diameter or may grow around the circumference of a branch. The scale insects can be found in the middle layer of the fungus, in chambers that are only slightly larger than the insects, which are connected with numerous tunnels. Some of the insects are parasitized by the fungus, which have inserted haustoria, specialized feeding hyphae, into the insect body. These parasitized individuals are immobile and usually occupy a chamber where they are attached to the plant by their sucking apparatus the suctorial tube. The insect nourishes itself with the plant sap that it obtains through its sucking apparatus, and because the fungus is attached to the insect by haustoria, it is directly being nourished by the plant, with the insect serving as a "pumping" conduit. There are great benefits to the insects as well. A number of scale insects live within the so-call colony of the fungus and are sheltered from the environment and have their food supply beneath them. In addition, they are also protected from predators. Thus, the fungus colony offers the insects shelter resulting in them living longer than their free counter parts. The larval stage of the scale insects that emerges will crawl about the colony, and if it should go to the surface, it will pick up the fungal spores which will adhere to their bodies.

Scolytid beetle- fungus symbiosis

Some scolytid beetles are wood inhabiting insects, and form tunnels in trees that are diseased or have been cut. The tunnels have narrow openings to the outside which widen into a number of caves like chambers where the eggs and larvae will develop. The tunnels and chambers are lined with the ambrosia fungus and is usually a source of food for the adult and is the sole source of food for the larvae. This is a very highly evolved relationship with only certain beetles and fungi occurring together. Neither the fungus nor the beetle species are found free-living in nature. This relationship has also proven to be harmful to a number of economic plants. The European Bark Beetle is responsible for carrying the spores of the Dutch Elm disease that has been having an impact on the *Acacia koa*, a native koa. The adult female beetle carries the fungus with them during their migration and when they are hibernating for the winter. There is a specialized sac, the mycangia, that occur in various locations of the body in different species of insects. When the female finds a suitable plant in which to live, she bores a small hole by which she will have access, which will eventually form a series or gallery of tunnels. It is along the gallery walls that the fungus garden is started. The mycangia produce secretions that prevent the spores from drying and also provides nutrients needed for the germination of the spores. When new tunnels are bored, the beetles prepare a mixture of faces and wood fragments which they smear on the tunnel wall as a substrate for the fungus to grow. This fungus is used as food for both the new larvae that may be borne along the gallery or in special chambers called cradles, and it is responsible for the damage that is done to the tree.

Social insects- fungus symbiosis

The colony forming insects like leaf cutting ants and mound building termites exhibit striking symbiosis with some fungal genes. The insects "culture", nourish and maintain the fungal associates in their nests in well articulated manner that such fungal forms have been beautifully described as "fungal gardens". Martin et al. (1999) have recognized the Leaf cutting ants *Atta* spp. and *Acromermyx* spp. Central and South America and termites in Warmer Asia and Africa as the insects having most complex association with different groups of fungus. Both the leaf cutting ants ant the termites play a major role in the ecosystem by degrading the cellulosic and lignin materials, that otherwise would take longer time for degradation. Thus these organisms have a prominent role in nutrient cycling in the natural and manmade ecosystems, even though these insects are considered to be a major pest in forestry and agricultural production. They have carved out a separate niche for this process in their respective habitats. While the leaf cutting ants occupy the niche in Warmer regions of Central and South America, the niche in Asia is replaced by the termites (Borges, 2001). Such the cultivation of fungi by insects has passed through multiple stages of evolution. This behavioral innovation was a major breakthrough in animal evolution (Moriya et al., 2005). The Attine ants are known to cultivate fungus in their nests for the last 50 million years. Thus the study of this special association would throw out answers to several questions related to evolution of animals especially with respect to nutrition. Due to their complex biological properties, the fungal colonies demand special interest by entomologists and microbiologists. Of late, molecular biologists and evolutionary specialists have taken special interest in the study of fungal gardens and a separate branch of study of fungal gardens "myrmycology" has come in to place. Aanen et al. (2002) have placed the colonies of fungus growing macrotermitinae and attine ants are among the most impressive animal phenomena in the world.

ANTS AND TERMITES

About 40-60 million years before the advent of human agriculture, three insect lineages, termites, ants, and beetles, independently evolved the ability to grow fungi for food. Like humans, the insect farmers became dependent on cultivated crops for food and developed task- partitioned societies co-operating in gigantic agricultural enterprises (Muller and Gerardo, 2002). The way in which these insects cultivate the fungal partners for their own benefit has led several authors to compare this activity with human agriculture. Agricultural life ultimately enabled all of these insect farmers to rise to major ecological importance. Indeed, the fungus-growing termites of the Old World, the fungus- growing ants of the New World, and the cosmopolitan, fungus-growing beetles are not only dominant players in natural ecosystems, but they are also major agriculture, forestry, and household pests. (Wilson, 1971).

The most interesting group of insect known to cultivate some of the most magnificent fungal gardens is perhaps the leaf cutting ants and the mound building termites. These have several adaptations and their life style is suited for nutrition drawn from the fungal associates. The agricultural symbiosis with fungi has allowed both ants and termites to occupy previously inaccessible niches that have abundant resources.

A.FUNGAL GARDENS OF ATTINE ANTS

Ant-fungus mutualism is a verifiable symbiosis seen in certain ant and fungal species, where ants actively cultivate fungus much like humans farm crops as a food source. Interestingly, both ant and fungus are completely dependent on each other for survival. The Leafcutter ant is a well-known example of this symbiosis. Leaf cutter ants are social insects found in warmer regions of Central and South America. These unique ants have evolved an advanced agricultural system based on ant-fungus mutualism. They feed on a specialized fungus that grows only in the underground chambers of the ants' nest. These leaf cutting ants belong to the family

Formicidae and subfamily Myrmicinae. The leaf cutters are put under the tribe Attini and hence are commonly referred to as Attine ants. About 200 species in 12 genera if the attine ants cultivate fungus in their nests in the Nearctic and Neotropical regions (Wilson, 1971). The two major genera are Atta and Acromerymex with a total of 39 species. While about 15 species of Atta are known to cultivate fungus reports put the number of species belonging to Acromerymex to 24. Other prominent leaf cutting ants that cultivate fungus are Trachymerymex and Cyphomerymex (Chapela et al., `1994). Some of the species belonging to these genera have much bearing on agricultural productivity by voraciously destroying the standing crops. For example some *Atta* spp. Are capable of defoliating an entire citrus tree in less than 24 hours (Martin et al., 1999).

Feeding habit

The Attine ants are commonly called leaf-cutting ants because they forage for leaves and cut them into pieces with their mandibles before carrying them back to their colony. The leaf cutting ants have been found to extensively forage up on broad leaved species. They prefer mature leaves, though they often forage on young leaves. However, species like Trachymerymex also prefer collecting fallen litter during lean periods. *Atta texana* can be extremely destructive to landscape plants, gardens and some agricultural crops. These ants damage weeds, grasses, plum and peach trees, blackberry bushes and many other fruit, nut and ornamental plants as well as several cereal and forage crops. Rarely they attack pine trees. They are known to carry forage at least 20 times more than their body weight. Thus the ants deposit a variety of raw materials for the fungus to act up on and indirectly help in ant nutrition. The plant materials brought by the worker ants contain toxins in the form of phenolics and other secondary plant metabolites. These ants carefully select leaves from species that are low in fungistatic compounds, such as phenolics, carry them to underground nests where they are masticated and plant them in soil along with fungal mycelia and glandular secretions containing proteolytic enzymes (Borges, 2001). The fungus not only digests the leaves and plant material for the ants but also detoxify the plant materials. The plant toxins that may be harmful for the fungal companions are detoxified by the worker ants through their oral or anal secretions. As the fungus is provided with food substrate and suitable conditions, it grows well and survives. As the mycelia grow, swollen hyphal tips are formed, called bromatia, which is the part of hyphae that the ants consume. Although a great deal of plant material is brought in to the colony, apparently none of it is consumed by the ants. It is used entirely to feed the fungus and the ants only feed on the fungus (Wilkinson, 2000). Leaf-cutting ants harvest more greenery in South American forests than any other animal. In fact, within the rain forest, leaf-cutter ants consume almost 20% of the annual vegetation growth (Borges, 2002).

The fungus

The leaf cutter ants feed on specialized fungus that grows only in the formers underground chambers of the ant nest, and hence these higher Attine ants cultivate fungal gardens in their colony using leaf material harvested from adjacent living plants. Different species of leaf cutter ants use different species of fungus, but all the fungi the ants use are members of the Lepiotaceae family belonging to the tribe Leucocoprinae. The ants cultivate their fungus, feeding it with freshly cut plant material and maintaining it free from pests and molds.

In studies that have been carried out in excavated nest, it was found that one nest that was four years old contained 1027 subterranean chambers, of which 390 contained fungus gardens. Another, approximately six years old, had 1920 chambers or which 248 contained fungus gardens. Gardens are usually 20-30 cm (8-12 in) in diameter and weight approximately 300g (10.5 oz). It is estimated that these colonies had consumed 6000 kg (13,200 lbs) of vegetation.

In a young colony, the queen and the first workers to hatch from eggs establish the first fungus garden by excavating a chamber and filling it with vegetation brought in by the workers and then inoculating it with the fungus. Different species will utilize different substrate material for their fungus gardens. Once they have returned with the leaf cutting, the workers cut the material into smaller pieces, lick it all over and often deposit anal excreta on it. The excreta, which serve as additional nutrients for the fungus garden, and plant material is then wedged into the garden and inoculated with a fragment of fungus by placing a tuft of mycelium on it. Thus the garden consists of chewed leaf materials surrounded by a dense tuft of mycelium. The mycelium is characterized by the formation of hyphae with swollen tips called staphylae. The staphylae are harvested by the worker ants, held in the gut and subsequently fed to larvae or digested by the adults themselves. Obligate fungal symbionts break down structural carbohydrates in the leaves and produce nutritive protuberances called gongylidia from their hyphae. The ants consume these gongylidia and also prevent the fungi from forming fruiting bodies or sporophores, consequently the fungus is clonally propagated (Borges, 2001). The gardens are sponge-like in appearance and are composed of numerous cavities which the workers walk through. In walking through, the workers probe the mycelium with its antennae, lick it deposit anal droppings on it and also eating hyphae. The lower Attine ants (Trachymerymex) have smaller colonies, commonly among leaf litter. They fed their fungi on the leaves, insects and other organic matter. The fungi of the lower ants appear to be polyphyletic while the association of the higher attine ants with Leucocoprinae is stable and most ancient.

The discovery of the identity of the fungal species involved in these ants were determined by taking pure cultures into the lab and in some cases fruiting bodies have formed. In most instances, they have been determined to be species of the mushroom genera, *Leucoagaricus* and *Lepiota*. Other fungi that have been fruited include *Auricularia*, and *Xylaria*, a member of the Ascomycota. For reasons unknown these species do not form fruiting bodies around or near the colony. *Atta texana* and *Atta cephalotes* the fungus used by these higher species, is believed to be *Attamyces bromafiticus* it is completely dependent on the ants for its propagation and the ants are completely dependent on the fungus for their food. *Leucocoprinus leuteus* and *Lepiota cristatiformis* have been found to be associated with nests of *Atta sexdens* by Herre et al. (1999)

Monoculture

Regardless of the species of ants, the colony only contains one species of fungus. This is difficult condition to maintained since, other fungi and bacteria are everywhere ready to take advantage of whatever organic material that becomes available. The worker ants in probing the mycelium with their antennae are able to distinguish their fungus from alien fungi. When foreign fungi are detected, they are removed by the workers.

Though the exact molecular techniques by which the ants weed out all non-mutualistic fungi and keep the garden free of microbial pathogens and parasites is not properly understood, some biomolecules are believed to be involved in the selective weeding. Phenylacetic acid and β-hydroxydecenoic acid (myrmicacin) produced by the metapleural glands of the ants have antibiotic activity which possible aids in the process. Recently fungus gardens were found to contain antibiotic- producing bacteria of the genus *Streptomyces*, which like the mutualistic fungus inoculums, are also transmitted vertically from colony to colony (Currie et al., 1999a). It has also been reported that the worker ants collect dirt from the garden surface periodically by licking and store it in their infrabuccal cavities, which are special recesses in their mouth. All the waste in the nest, including infrabuccal pellets, spent substrate from gardens and dead ants are carried to the waste chambers in order to avoid contamination. The purpose of these activities is to avoid infection, especially by parasitic fungi. This may lead one to suppose that the ants have the problem of pathogens and parasites well under control.

Some foreign fungi, undoubtedly, are present, but with the far more prevalent, cultured fungus, they are unable to compete and do not make up an appreciable part of the garden. When colonies are abandoned because of disturbance or migration, the fungus garden left behind deteriorates and become contaminated with other fungi and bacteria. Before abandoning their colony, the Attine ants always take some of the fungus garden with then as inoculums to start their new fungus garden.

Other organisms' inhabitating the fungal garden

Even though the ants have the ability to detect foreign organisms like pathogens and parasites, recent studies have shown that the fungus garden is not completely free of other organisms. One of the most prominent pathogen that infects the garden is *Escovopsis.* Although it is thought at present to involve only two symbionts, associated with each other in near isolation from other organisms, the fungal gardens of attine ants are in fact host to a specialized and virulent parasitic fungus of the genus *Escovopsis* (Ascomycotina). *Escovopsis* is known to destroy the entire fungal garden in a very short time and hence is detrimental to the ant-fungus symbiosis. Thus a third mutualism in this symbiosis, a filamentous actinomycete belonging to the genus *Streptomyces,* has been described recently by Currie et al. (1999 b). It produces antibiotics specifically targeted to suppress the growth of the specialized garden parasite *Escovopsis. Streptomyces* has been reported from the gardens cultivated by all attine ants and is also transmitted vertically. The actinomycetes are carried by the ants upon regions of cuticle. It has the capacity to promote the growth of the fungal mutualism, indicating that the association of *Streptomyces* with attine ants is both highly evolved and of ancient origin. Yeasts are frequently isolated from nests of the leaf-cutting ants. The yeasts grow in association with the fungus garden, which consists of mycelium growing on the plant material carried to the nests by the ants. Yeasts are also found in waste deposits, the material discharged by the ants (Carreiro et al., 1997). The role of the yeasts in the symbiosis is not clear, but the ability of many yeast strains to degrade some plant polysaccharides may contribute to the availability of carbon sources for the symbiotic filamentous fungus (Carreiro, 2000). Carreiro et al. (1997) also found several years, among which the dominant species were identified physiologically as *Candida homilentoma, Debaryomyces hansenii* and *Torulaspora delbrueckii* from the nests of *A. sexdens.* Other microorganisms like *Pseudonocardia* have also been recorded to occur in the gardens. A new species of yeast *Sympodiomyces attinorum* sp. nov has been found to be associated with the nest of the leaf cutting ants *Atta sexdens* (Solange et al., 2004).

B. FUNGAL GARDENS OF TERMITES

In civilization, termites are one of the worst pests that we can imagine. However, in nature they play an important role in the decomposition of plant material. Termites (Class Insecta, Order Isoptera), are found mostly in the tropics, some in temperate zones and very few in the cooler climates. With about 2600 species worldwide they are probably dominant organisms in tropical forest environments. Recent studies have broadened our understanding of the evolution of the symbiosis between the attine ants and their fungi considerably but similar large-scale studies of the Macrotermitinae and their *Termitomyces* symbionts have been lacking. About 330 of the more than 2600 species are obligately dependent on the cultivation of the specialized fungus, *Termitomyces*, for food (Abe et al., 2000). About eleven fungi cultivating genera have been so far described worldwide. These termites are distributed in Africa, Madagascar, India and much of Southeast Asia. Symbiotic relationships have had an essential role in termite evolution and involve a range of intestinal microorganisms including protists, methanogenic Archaea, and bacteria. However, only a single Termitidae subfamily, the Macrotermitinae, has evolved a mutualistic ectosymbiosis with fungi of the genus *Termitomyces* (tribe Termitomyceteae, family Tricholomataceae, Basidiomycotina). The fungus helps the termites to degrade the plant-derived material (e.g., wood, dry grass, and leaf litter) on which they live. It grows on a special structure in the nest, the fungus comb, maintained by the termites through continuous addition of predigested plant substrate while the older comb material is consumed.

The termites

The Macrotermitinae have been divided into 11 taxonomically well supported genera and 330 species. Most of the diversity occurs in Africa, where 10 of the 11 genera are found. Five genera occur in Asia (one of these exclusively) and two genera in Madagascar. The genus Macrotermes and Odontotermes are wide spread than others. Macrotermes gilvus is prominent in Southeast Asia. *Odontotermes assmuthi, O. obesus* and *O. wallonensis* are common fungus cultivating termites seen in India and the subcontinent (Roonwal, 1979). *O. bilitoni* and *O.minutus* are seen in Africa. (Aanen et al., 2002). *Macrotermes bellicosus, M. subhyalinus and Microtermes* spp. are distributed well in Africa, though these occur in Asia also.

The termites found in the Old World and parts of Asia consume plant material, construct "combs" with their excreted 'pseudofaeces' and inoculated with the spores of an exosymbiont fungus. *Termitomyces* species, the fungus grows on the combs and produces a nutritious fungal compost containing a variety of energetically expensive nitrogen compounds, that is consumed by the termites. The fungal comb is a kind of extracorporeal digester to which the termites have 'outsourced' cellulose and lignin digestion. The fungus-enriched food allows the termite colony to mobilize energy at faster rates and is not limited by the bacterial endosymbionts of most other species of termite (Gover, 2002).

Feeding habit

The termites forage for several plant materials that are usually rich in cellulose and lignin. Wood, bark, leaves, litter etc. are the preferred materials carried and deposited by the termites. Unlike the attine ants, the termites will eat the plant material where they find it and upon returning to the colony will place their faecal droppings in the fungus garden. Somewhere along the way, perhaps in the digestive tracts of foragers or nest workers, this woody slurry is inoculated with a variety of fungal spores. Once deposited I the comb, the *Termitomyces* spores germinate and begin hyphae through the comb. As these grow, they delignify and digest cellulose, converting it to simple sugars and nitrogen. The termites then consume this enriched fodder for food. Thus unlike attine ants, the termites do not directly feed on the fungi. The slow growth of the fungi ensures that the fungus utilizes only a meager quantity of the food and termites consume the remaining major part (Turner, 2002). The sponge-like fungal garden has spherical structures on its surface composed of conidiophores and conidia. The cellulolytic and pectinolytic enzymes of these wood- rotting fungi help to break down the substrates for termite use. While tending the garden, the workers occasionally nibble on the fungus. The cellulolytic enzymes that are in the mycelium remain active in gut workers. The king, queen, soldiers and nymphs do not eat fungus directly, and live on the salivary secretion of the workers.

Termite fungiculture

Termitomyces is grown on termite feces in subterranean combs that the termites construct within the heart of nest mounds (Batra and Batra, 1979). Combs are supplied with feces of myriads of workers that forage on wood, grass, or leaves. Spores of consumed fungus are mixed with the plant forage in the termite gut and survive the intestinal passage (Batra and Batra, 1979; Wood and Thomas, 1989; Darlington, 1994). The addition of fecal pellet to the comb therefore is functionally equivalent to the sowing of a new fungal crop. Fungus-growing behavior originated only once in termites, involving a single ancestral *Termitomyces* lineage that diversified into several defined cultivar groups, each associated almost exclusively with a similarly defined group of termite farmers. Within each of these termite groups, however, cultivars are exchanged frequently between termite lineages. Termite farmers appear to have evolved adaptations to certain cultivar groups (e.g., specific fertilizing regimes), or cultivars evolved adaptations suitable only for certain farmers e.g., nutrients benefiting only certain termites or both (Rouland- Lefevre, 2000). When the termites nourishes the fungus and provides a safe haven for fungus, latter in turn provides food special chemical metabolites that influence the reproductive dynamics of the termite colonies (Turner, 2002). Since *Termitomyces* is a slow growing fungus it absorbs its digestate slowly. It leaves ample 'leavings' that provide termites a rich food. The fungus enriched food enables the termite to mobilize energy at faster rates than most termites.

Approximately 40 species of *Termitomyces* symbiont have been described. Although additional varieties have been recognized, the low number of fungal species suggests that many of these fungi are shared by different termite species unless morphospecies frequently consist of several sibling species. Mueller and Gerardo (2002) have put the number of taxa under 60 *Termitomyces* as

60 while subsequently Tang et al. (2005) put the number to 68. But reliably only 18 species, collected mainly from West Africa, are reasonably well known, the rest are either synonyms or badly described and difficult to identify. A genus, *Sinotermitomyces* has been reported from China, but species are difficult to classify. Characteristically, *Termitomyces* has been pinkish spores, a cap and stipe at the top of a long 'pseudorhiza' that arises from the comb and the cap has a 'perforatorium' or 'umbo' that assists the mushroom to penetrate the hard ground and there is termite association. Wild fungi parasite the rich store of food in the nest but the evolution of fungistats and diligent weeding ensures that only Termitomyces grows. Abandoned nests are quickly taken over by other fungi, particularly *Xylaria* spp. *Termitomyces robustus, T. letestui, T.microcarpus* are distributed in the Old World regions. *Podaxon pistillaris* is another species that is associated with termite mounds in Africa (Sands, 1969). *Termitomyces titanicus* is the largest of the genus known commonly to reach 1 m cap diameter while *T. microcarpus*, is one of the smallest of the genus has a cap diameter of 2 cm (Gover, 2002). According to reports published by FAO (2004) on the edible mushrooms of the world, *T .titanicus* is the largest of all edible mushrooms. *T. microcarpus* and *T. clypeatus* are well distributed in the continents of Africa and Asia and are seen in Cameroon also (Aanen et al., 20002). Tang et al. (2005) in their review of *Termitomyces* have stated that about 28 new taxa including 20 species and 8 forms from Africa and Asia.

The new taxa described from India are *T. albidolaevis, T. heimii, T. indicus, T. longiradicatus, T. quilonensis, T. poonensis, T. radicatus* and *T. microcarpus* f. *santalensis* (Tang et al., 2005)., *T. longiradicatus* occurs in humid and warm parts of South India. *T .heimii* was originally described from Madras and subsequently was widely reported from South East Asia. *T. eurrhizus* is restricted to Northern India and North East India and South East Asia but is absent from South India.

Monoculture

Macrotermitinae Termites may be considered as small but remarkable 'ecological engineers' that have developed a set of successful agricultural strategies to ensure *Termitomyces* alone 'value-adds' their relatively low grade plant material diet. Success in ensured by propagating fungal clones in huge monocultures, evolving fungistats that appear to co-evolve with pathogens and being intensively vigilant in monitoring the fungal combs to eradicate resistant pathogen mutants before an epidemiological outbreak. Of course, the fungus benefits in having a comfortable home, is well nourished and a variety of species are cultivated that are protected from wild fungal competitors (Gover, 2002).

Although fungus combs are laden with spores of more than two dozen different fungi, including the wood decaying *Xylaria,* it is only the *Termitomyces* spores that germinate and grow. When a comb is removed from the nest, these other spores germinate and grow, quickly overwhelming the *Termitomyces* culture. Fungistatic agents play a major role in maintaining a near axenic condition along with active weeding of fungus combs by termites. A fungus comb removed from the nest with a retinue of termites' delays takeover *Xylaria.* It has been widely suggested that *Termitomyces* competitive edge is provided by some attribute of the nest environment, specifically the high CO_2 concentration there. *Termitomyces* is supposedly more tolerant of high CO_2 concentrations and acidic environments than fungi like *Xylaria.* These are precisely conditions that prevail in the nest. Furthermore, these conditions are reliably provided by the homeostatic tendencies of the termites. By co-opting termites' homeostatic tendencies to provide a favorable environment for themselves, the *Termitomyces* principal fungal competitors are effectively fended off (Turner, 2002).

Mound architecture

The mound architecture of termites is almost to that of the attine ants. It consists of a central royal chamber around which the fungus comb is situated. There are other chambers occupied by the workers and soldiers and the nymphs. A network of tunnels connects these chambers.

An interesting aspect of this complexity is the nests that thermoregulation within the nests that very much essential for the metabolism of the fungal partner. Mound shape is determined by the climate and locality of the mound because it is important that the fungus garden be kept at a comfortable temperature. This is done with a unique array of ventilation in the nests. If it gets too cold, the termites place obstructions in the vents to maintain warmth. When temperatures rise during the day, the vent closures are removed and cooling can commence. The fungus gardens in termite mounds are very similar to those of leaf-cutting ants in that the termites have designed special compartments for the fungi and give special nutritional treatment for colony growth. Turner (2002) is of the opinion that the mushrooms produced by *Termitomyces* may play a major role in mound morphogenesis and social homeostasis. The small moundlets that appear around the main mound originate as repair work built over rotting mushrooms. Shortly after emergence, the mushroom is invaded by numerous beetles and flies that lay eggs. Within a short period of time the mushroom begins to rot. As the mushroom rots, the rotting stems leave a large tunnel for egress by the termites. As with any other breach of the mound, the termites quickly begin to build new mound surface over the mushroom, eventually covering it completely. The covering continues to grow until a new moundlet is formed.

Fungal structure

The structure of the fungal comb is dynamic. Fresh material is continually added to the top, and digested material is consumed from the bottom. Food "flows through" the comb just as silage flows through a silo. A colony amasses a large number of fungus combs, gathered in to a series of galleries atop the neat called fungal garden. Each fungus comb is placed in semi-enclosed space called a gallery. The total mass of the fungal combs typically exceeds the colony's entire mass of termites by about eight fold. A mature colony will have a total of about 40 kg of fungal combs, each combs located in a semi-enclosed gallery around the periphery of the aboveground mound rest. (Gover, 2002; Turner, 2002). Turner (2002) has observed that each year, the fungi produce mushrooms, which eventually emerge from the base of the mound. Prior to mushroom emergence, each fungus comb begins to sprout a number of stems that will penetrate through the hard soil of the mound, coalescing in a mushroom that literally erupts through the mound surface. Several sprouting fungus combs are evident in the fungus garden.

ORIGIN AND ECOLOGY OF ANT AND TERMITE FUNGICULTURE

Fungicultural origins: Termite, ant, and beetle farmers appear to have made the transition to fungiculture via different evolutionary avenues. In the termites, fungi probably were an important food source before true cultivation, and fungiculture arose when the termites secondarily developed an ability to manipulate fungal growth in their nests. Many non-farming termite species are attracted to feed on fungus-infested wood (Batra and Batra, 1979; Rouland- Lefevre, 2000), termite fungiculture therefore may represent an elaboration of such ancestral feeding habits. In contrast, the ancestral insect-fungus association may have been one in which the fungi used insect hosts for dispersal of spores (similar to flowering plants using bees as pollen vectors), and fungus-feeding and fungiculture arose secondarily out of such an ancestral vectoring system. This most likely was the case in the beetles because many nonfungus feeding relatives of the ambrosia beetles are important vectors of fungal spores and because the ambrosia fungi are derived from free-living fungi that depend on arthropods for dispersal (Malloch and Blackwell, 1993). It is unclear whether fungiculture in attine ants arose from ancestral mycophagy or from a system of fungal vectoring by ants (Mueller et al., 2001).

Whereas ant and termite fungiculture originated only once in each group, fungus-growing by ambrosia beetles has arisen at least seven times. Farell (1998) opined that multiple origins of fungiculture in beetles is perhaps not surprising, given the sheer diversity of beetle species and given the importance of feeding specializations in beetle diversification. Multiple origins, however, do not preclude beetle-fungus coevolution within each independently derived system. Indeed, in each of the independently evolved farmer beetle lineages, entire groups of species are specialized on particular groups of cultivars, paralleling not only the specializations already discussed above the termites, but also a series of specializations known for different ant groups each associated with its own cultivar group (Chapela et al., 1994; Mueller et al., 1998; Green et al., 2002). In general, switching of farmers to novel cultivars is possible, but limited almost exclusively to cultivars from within the same cultivar group as the farmers typical cultivar.

Evolutionary reversal back to a non-fungus- farming lifestyle has apparently not occurred in any one of the nine known, independently evolved farmer lineages (one termite, one ant, and seven beetle lineages). This supports the view, formulated first for humans, that the transition to agricultural existence is a drastic and possibly irreversible change that greatly constraints subsequent evolution.

The niche- specialization scenario for fungal gardens of ants and termites

Termitomyces symbiosis implies that many of the evolutionary modifications in this mutualism may be as much "fungus-driven" as "insect-driven". The essentially "symmetrical" symbiosis with *Termitomyces* fungi allowed termites to occupy new food niches, and these diverging niches selected for fungal adaptations to combs built from different plant- derived materials. The roles of the fungal symbionts that were not necessarily obligatory dependent on them. The nutritious role of the fungal symbionts therefore changed rather little until symbiosis became symmetrical in the higher attine ants, a clade characterized by specifically adapted fungi producing unique nutritious structures (gongylidia) for the ant brood (Chapela et al., 1994). In other words, the attine ants primarily evolved specific adaptations to be farmers of rather unspecified fungal crops, and their fungi realized crucial adaptations only in the apical clade of the higher attine ants. The obligate symmetrical interactions that followed allowed the symbiosis to become highly specialized and ultimately produced the leafcutter ants. The Macrotermitinae, on the other hand, specialized on a single group of fungi, which quickly became genetically isolated from its free-living sister group and cospeciated and cospecialized in response to the increasing diversity of fungus- comb substrates across termite species and habitats.

Ecological role

The mound building termite and attine ants turn up the soil and provide opportunities for soil aeration in the deeper layers through the tunnels of the mound/ nest. With the help of the fungal symbionts the plant material is digested and thus the soil is enriched with nutrients. This also helps in the complex nutrient cycling process of the area. Slow degrading materials like lignin are acted upon by the fungal gardens of the termites thus enhancing lignin degradation and release of nutrients. Termite symbionts viz., *Termitomyces* an edible fungus have a major effect on litter degradation in the forest ecosystem. Laboratory studies showed that *Termitomyces* effectively degraded forest litter within 35-45 days after inoculation (Velu et al., 2006). It is estimated that *Atta sexdens* and other leaf cutter ants consume 12-17 percent of leaf mass produced in the Neotropical rain forests, thus performing the role of herbivores. The biomass of termites associated with this fungus is very high and hence they form a food base for other organisms and thus play a significant role in food web.

Economic impact

The attine ants are a serious pests of many agricultural crops in the neotropical region while termites attack a wide range of plants and finished wood furniture, logs etc. termites have been long recognized as a serious pest of forest and agricultural crops across the world and is more problematic in the tropical regions of Africa and Asia.

CONCLUSIONS

Fungus garden opens up huge diversity of uses, which needs to be augumented.

1. Food

The edible and nutritious mushrooms are highly prized as a delicacy and contribute to the local economy. According to Pegler and Vanhaecke (1994) 23 species of *Termitomyces* are eaten as food by various communities. Four edible species are well marketed while 3 have medicinal properties. An FAO report (Anon., 2004) has listed out 20 edible *Termitomyces* from Asia and Africa.

The report states that totally 27 species of *Termitomyces* are consumed in various forms across 35 countries of the world of which 16 countries directly eat the mushroom as delicacy. *T. robustus* mushroom is the favorite species used for food by the Yoruba tribe in Nigeria. A very popular mushroom in China is the jizong mushroom, *Collybia albuminosa*, (Syn. *T. albuminosa*) a shaggy capped fungus that grows in association with 7 different species of termites. It appears in the mountainous areas after torrential rains and for several weeks serves as the dominant food for monkeys in the areas. The indigenous people of Tanzania consume mushroom of *T. singidensis* as regular food and also as a medicinal preparation (Sarimaki et al., 1994). Studies carried at Tamil Nadu Agricultural University, Coimbatore, India showed that *Termitomyces* sp. was rich in nutrients and a major source of proteins. The protein content was found out to be 38.5 to 42.6 mg/ml. It also contains xylanase (28.9-29.6 μmol D-xylose /min) which can also be used as a protein supplement food (Velu et al., 2006).

2. Augmentation of mycorrhizal entity

Studies carried out by Matsuura (2005) revealed that augmentation of soil with mounds of *Macrotermes subhyalinus* enhanced the mycorrhizal performance in *Acacia holosericea*. The results showed that the termite mound amendment significantly increased the ectomycorrhizal expansion. MS mound amendment and ectomycorrhizal inoculation induced strong modifications of the soil functional microbial diversity by promoting the multiplication of carboxylic acid. The occurrence of MS termite mounds could be involved in the expansion of ectomycorrhizal symbiosis and could be implicated in nutrient flow and local diversity.

3. Source of enzymes

The fungal gardens are known for producing several metabolites of which the cellulolytic and lignolytic enzymes are promionent for the degradation of wood and plant parts brought by the ants and termites. Enzymes like cellobiase, several proteases, xylase, β-endo glucanase and β-exo glucanase have been isolated from the fungus gardens (Velu, 2006). These enzymes can be industrially harvested for degrading the biopolymers, delignification process in pulpwood industries and other applications. Termitomyces have been successfully cultured in general soil fungus medium (GSFM). Different lingo-cellulosic substrates were used of which coit pith was found to support best growth (Velu, 2006).

4. Production of antibiotic

The fungal gardens of ants and termites are vulnerable to pathogens and parasites. However, the garden is protected by various mechanisms of which production of antibiotics by the fungus as well as associated organisms like a species of Streptomyces reported from gardens of Attine ants to fend off Escovopsis. Thus the fungal gardens can be utilized for prospecting new antibiotics and then economically exploiting the antibiotic so produced.

5. Detoxification

The leaf cutting ants and termites carry vegetable parts to the nest. In the modern agricultural practice, it is obvious that the plant parts may be adhered with toxic chemicals (pesticides) from agricultural management and also by adsorption of atmospheric pollutants like chloride compounds. Thus the plant material having toxic chemicals may prove fatal for the fungal garden. However, in nature, the fungal gardens remain unaffected by these chlorides and toxins, probably due to detoxification process by either of the symbionts or by both the symbionts. Further research in the mechanism can prove way for devising technology for detoxification of soil and atmosphere loaded with such toxic materials. Also, toxins form a major problem in pharmaceutical industries that depend on plant materials. The leaf cutting ants and their gardens are known to detoxify phenolic plant toxins (Mueller and Gerardo, 2002). This principle or biomolecule used for detoxification of plant feed by the ants, by concentrated R&D, can be used for removing or nullifying the effects of toxic phenolics in traditional systems of health and pharmaceuticals (Borges et al., 2001).

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