Review of Termite Forest Ecology and Opportunities to Investigate the Relationship of Termites to Fire

by

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ABSTRACT

In forests, termites serve as "soil engineers," translocating mineral soil to the surface, constructing macropores to improve water infiltration, increase soil minerals and organic carbon, facilitate the growth of microbes and affect the growth of vegetation. The future productivity of a forest site therefore depends to some degree on termite activity. Termites could reduce the probability of forest fire by reducing fuel loads, either through direct consumption of the wood or through the augmentation of decay fungi. Should a fire adversely affect termite populations in a forest, the decomposition of unburned woody debris will be delayed and nutrient cycling in the forest will be interrupted. For small fires, such as prescribed burning, such interruption is largely a non-issue. Catastrophic or stand-replacing wildfire, however, might affect termite populations in three non-mutually exclusive ways: direct mortality due to the fire itself, through the conversion of cellulose to indigestible materials, and through alterations of the soil. Due to their slow dispersal relative to other soil organisms, termites re-colonize severely burned areas slowly, but can be instrumental in the rehabilitation of waste areas. Termite presence might be augmented to increase the future productivity of a severely burned site. This paper is a review of termite contributions to forest health and fire prevention, the effects of fire on termite populations, the re-colonization of severely burned areas, and the contribution of termites to waste area rehabilitation.

Keywords: Termites, soil engineering, fire, forest productivity, soil rehabilitation

INTRODUCTION

The relationship between forest insects and forest fires is typically discussed in terms of insect attack on fire-weakened trees, or in terms of the susceptibility

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of insect-weakened trees to fire. For a review, see McCullough *et al.* (1998). The relationship between termites, trees and fire, however, is somewhat different. Termites in the United States are not currently pests of living trees, and therefore do not increase a tree's susceptibility to fire. Trees damaged by fire are consumed by termites, but usually not until such extensive damage has occurred that the tree is no longer valuable.

Termites in North American forests have positive effects on forest health, and should help forests recover from fire or other catastrophic disturbance by improving soil structure and nutrient cycling. They might also reduce fire intensity by augmenting the breakdown of fuels. Despite these logical assumptions, very little quantitative research has been conducted. This paper will report the current state of knowledge regarding termites in forest ecosystems, and identify potential avenues for further termite forest ecology research.

Termites in North American Forests

The bulk of the literature regarding termites in the United States relates to their status as structural pests. Much less work has been done on their ecological role in North American forests. The most important species of termites in U.S. forests are in the genus *Reticulitermes* (Rhinotermitidae), and include *R. flavipes* (Kollar), *R. virginicus* (Banks), *R. hageni* Banks, *R. hesperus* Banks and *R. tibialis* (Banks). In the desert southwest and north-central Mexico, *Heterotermes aureus* (Snyder) (Rhinotermitidae), *Gnathamitermes* and *Amitermes* (Termitidae) species are common in many areas. Various species of drywood (Kalotermitidae) and dampwood (Termopsidae) termites can also be found in some locations around the country, but are not widely distributed. Florida has the greatest diversity of termite species, with many genera occurring nowhere else in North American temperate zones. The introduced Formosan subterranean termite *Coptotermes formosanus* Shiraki (Rhinotermitidae) is a significant problem in some southern urban areas, most notably New Orleans, but is not yet known to be established in forests. This species differs from the native subterranean species in that it is able to infest the heartwood of presumably otherwise healthy trees, including several species of oak, beech, dogwood, magnolia, sycamore and poplar (Chambers *et al.* 1988). Should the Formosan subterranean termite become established in forests, not only will stand value decline, but breakage during wind storms

might become significant. This will lead to a higher fuel loading and allow fires of higher intensity to develop. The susceptibility of Formosan subterranean termite-infested trees to fire is an avenue of research that has not yet been pursued. It can be supposed, however, that trees so infested would be more susceptible.

In the most general of terms, termites in North America increase in abundance as one moves south. The risk of termite structural infestation east of the Rocky Mountains is the highest in the southeastern quarter of the United States, from the east coast to about 100° W (roughly Dallas, TX) and south of 35° N (roughly Memphis, TN). A significant risk continues across the entire continent north to 41° N (roughly Chicago, IL), with some lesser risk in Utah. However, some risk exists as far north as 45° N (roughly Duluth, MN). West of the Rocky Mountains, the highest risk occurs in central California, and the risk extends along the West Coast as far north as the southern-most islands of the Alaska panhandle.

In all these areas where termites are common, they likely contribute in some degree to the health and fire cycle of forests. Historically, most research on termite ecology has been conducted in the tropics, particularly Africa, Asia, South America and Australia. Most of the work that has been done in the United States has been in desert ecosystems. The most-studied termites are predominantly mound-builders, which construct conspicuous nests that are much easier to study than are the diffuse subterranean nests and poorly defined foraging areas of subterranean termites. Termites in tropical areas can also be pests of living vegetation, including trees, and so there exists an economic reason to study them, unlike in North American forests where termites are considered beneficial. Exceptions are the grass-feeding termites of the Southwest, which can compete with pasture animals in poor growth years. As we will see later, termite removal of biomass, and therefore reduction of fuel, in North America is much less than is seen in the tropics and subtropics, but nevertheless termites do play a role.

Termites as Soil Engineers

Where they occur, termites are key bioturbators of soil, necessarily moving soil and creating voids underground. They move organic matter from the surface to underground structures, and bring mineral soil to the surface during

the construction of their galleries. The pores created in the soil increase water infiltration, reduce runoff and therefore reduce erosion. In this section, the contribution of termites to soil properties will be discussed. A more detailed review can be found in Holt & Lepage (2000).

Soil Translocation

The workings of mound-building termites are obvious, with large amounts of soil excavated to above-ground structures (Fig. 1) or packed into deadwood once the termites are no longer feeding (Wood 1988). Translocated soil is moist relative to surface soil, therefore translocation serves to maintain the colony's water balance (Turner 2006, Turner *et al.* 2006). This soil is often nutrient rich, initially moist and, in species that mix soil with feces and saliva, high in organic matter. The amounts of soil translocated into mound structures by tropical termites might range from 20 to 4700 kg/ha/year (Lobry de Bruyn & Conacher 1990), and one estimate in Africa claims that over the course of one millennium up to 37 cm of soil might be translocated by the action of termites (Holt & Lepage 2000). In Brazil, translocated
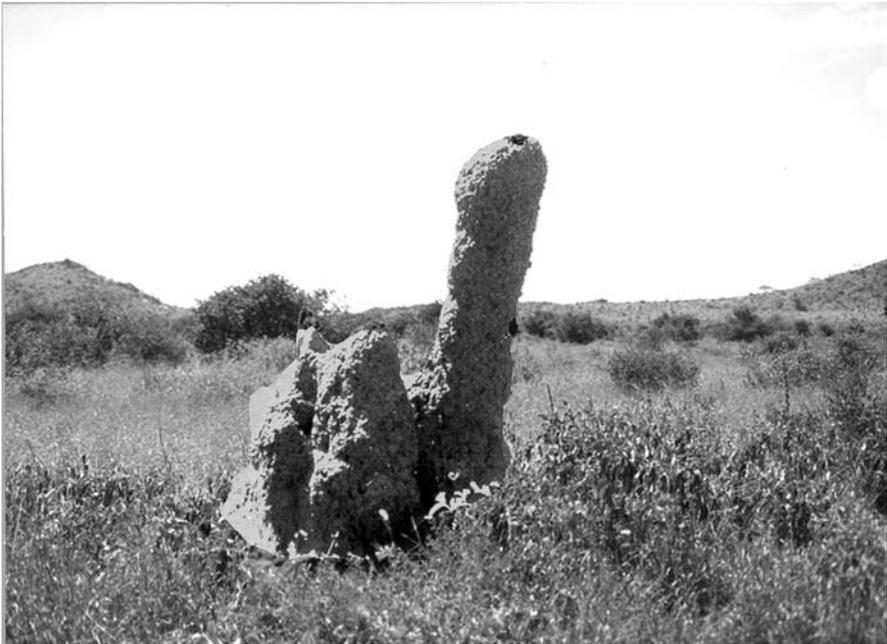

Fig. 1. Termite mound in Kenya, about 1 m diameter at the base and about 2 m in height at the tallest point. Photo by author, May 1993.

soil amounted to between 20.9 and 136.6 m³/ha, with 8.11 to 63.3 m³/ha translocated above the soil surface in mounds (Kaschuk *et al.* 2006). In one study area in Australia termite mounds constituted 21 Mg/ha, about 1% of the total soil in the A1 horizon, and termites turned over 300–400 kg/ha/yr (Coventry *et al.* 1988). In Namibia, mound-building termites in the genus *Macrotermes* can transport on average 3.6 kg (wet) soil/mound/day during the rainy season in open habitats, but this value decreases to 0.9 kg/mound/day in wooded habitats (Turner *et al.* 2006). This reduction was attributed by Turner *et al.* (2006) to the higher soil and air humidity found in wooded habitats, which lessens the need for active movement of moisture (i.e., moist soil) by the termites.

In desert North America, *Heterotermes* turned over 70 kg/ha/yr and *Gnathamitermes* turned over 560 kg/ha/yr, which was generally less than that observed for ants (0.6 to 11 Mg/ha/yr) (Lobry de Bruyn & Conacher 1990). Another study reported that a population of *Gnathamitermes* with a biomass of 1028 individuals in the top 30 cm/m² (or about 3000 individuals/m³) brought 403 g soil/m²/yr (about 4 Mg/ha/yr) to the surface (Spears *et al.* 1975). The soil turnover rate in North American temperate forests, however, has not been examined. North American forest termites do not construct mounds, therefore the question remains of to where these termites move soil in the construction of their subterranean galleries. One interesting possibility is discussed later in this review.

Many mound-building termites not only construct mounds, but also construct protective soil sheeting over the ground to protect themselves from predators and from the effects of sunlight and desiccation (Fig. 2a). Estimates of the amount of soil translocated by termites for use in sheeting range from 675 to 950 kg/ha/yr in Senegal (Lobry de Bruyn & Conacher 1990) to over 1000 kg/ha/yr in Kenya (Holt & Lepage 2000). In Senegal, the total length of soil sheeting constructed by two genera of termites was more than 13 m within about five months in 4 × 4-m plots (Rouland *et al.* 2003). North American termites construct shelter tubes, although on a much smaller scale than in the tropics (Fig. 2b). So far this activity has only been examined in the Sonora and Chihuahua Deserts, where 744 kg/ha/yr soil was translocated in the former case and over 2600 kg/ha/yr in the latter (Nutting *et al.* 1987; MacKay & Whitford 1988), equaling or exceeding the rates in Africa. It is

unknown if this soil comprises the balance of the translocated volume, and a study to be described later indicates that it is not.

As termite mounds and soil sheeting undergo weathering, nutrients leach with the soil water or erode off the mound with soil, making the nutrients available to neighboring vegetation, as will be discussed below. These processes are slowed by the mound-maintenance activities of the termites when the mound is active. Once the mound is abandoned, however, these processes accelerate. Depending on mound size, it might take from three to more than 30 years for a mound to completely erode (Coventry *et al.* 1988), although most of the erosion and leaching takes place in the first few years following mound abandonment (Lobry de Bruyn & Conacher 1990). Ellis (2002) reports that abandoned termite mounds, once fully degraded, might cause the formation of hardpans due to the increased pH and higher concentration of silica and calcium carbonate from previous termite activities. Ellis (2002) cites references that have identified the remains of termite mounds dating back 30,000 years.

Water Infiltration

The effects of termite activity on water infiltration are subjectively obvious, but few studies have examined this quantitatively until recently, and again, these studies are primarily on African mound-building termites. Although the

Fig. 2 Protective soil sheeting over a tree trunk in Mozambique (A), and a wooden ladder in Mississippi (B). Photos by author, April 2007 and March 2004, respectively.

mound surface tends to be much harder than the surrounding soil (presumably to prevent loss of mound moisture to the air) (Turner 2006) and therefore more impervious to rainwater, the construction of foraging galleries and tunnels within and distant from the mound can influence water infiltration rates (Lobry de Bruyn & Conacher 1990, Noguchi *et al.* 1997). An active mound of *Macrotermes* might consist of over 6 km of subterranean galleries (Wood 1988), and abandoned mounds can be quite large, in some cases resulting in a cavity over one meter deep (CJP, personal observation) that could serve as a collection basin for rainwater (Fig. 3). In Africa, some farmers augment termite activity by burying manure (Léonard & Rajot 2001), and in Burkina Faso termite foraging holes (similar to that shown in Fig. 4) increased the water infiltration rate relative to termite-free plots (Mando *et al.* 1996). In Niger, an increase in foraging holes decreased runoff, and the relationship between macropores, runoff and infiltration was mathematically modeled (Léonard & Rajot 2001, Léonard *et al.* 1999, Léonard *et al.* 2004).

Fig. 3. Abandoned termite mound in Mozambique, an extreme example of a soil macropore created by termites. Photo by author, April, 2007.

In the United States, the exact foraging areas of a termite colony are not well studied, but desert termites in Texas have been found excavating as deeply as 124 cm (Ueckert *et al.* 1976). One study in New Mexico demonstrated that water infiltration is higher in lightly vegetated experimental plots containing *Gnathamitermes* than in plots where the termites had been removed (Elkins *et al.* 1986). Interestingly, another study in the Chihuahua Desert in Texas (Spears *et al.* 1975) concluded the opposite. The presence of the same termite genus decreased water infiltration and increased erosion due to the reduction of organic matter, reduced ground cover and decreased capillary (versus non-capillary) pore volume. The fact that in the former study (Elkins *et al.* 1986) the effect was seen mostly in lightly vegetated plots might be the resolution to this inconsistency; the effect of organic matter on water holding capacity might be greater than the effect of termite burrowing on infiltration. Therefore soils with a lower organic matter content (and therefore a lower

Fig. 4. Termite foraging hole, soil sheeting and feeding upon eucalyptus stem in Mozambique. The exit hole is a macropore into which rainwater might enter, the sheeting is rich in nutrients and organic matter, and the removal of above-ground biomass through feeding brings organic matter into the soil. However, this situation is not desirable to forest plantation managers. Photo by author, April 2007.

water holding capacity) might benefit from termite burrowing activity while those soils with higher organic matter might suffer erosion due to termite consumption of the overlying vegetation.

Excavation of a Formosan subterranean termite gallery in Louisiana found that the gallery system of a single nest extended through about 1.4 acres (0.5 ha) and consisted of 1900 feet (580 m) of subterranean tunnels, extending to the water table (King & Spink 1969). For a Formosan subterranean termite colony, the total volume of soil galleries can be greater than 34,000 cm³ (equivalent to nine gallons of soil, which weighs about 45 kg or 100 pounds) (Li & Su 2008).

The Formosan subterranean termite does not build a conspicuous mound although it does construct soil sheeting, and the nest is usually built in subterranean galleries or in voids. The question has been asked how Formosan subterranean termites (and other non-mound builders) construct such large galleries without noticeably translocating the soil elsewhere. It had been supposed for many years that termites compact soil by forcing it aside, but experimental evidence for this is lacking. A recent study suggests that Formosan subterranean termites create space through the consumption of wood volume, as only one-half of the volume of consumed wood was converted to carton nest material (Li & Su 2008). A prior study (Shelton & Appel 2001) reported the evolution of 0.507 and 0.310 ml CO_2/g termite/hr for eastern and Formosan subterranean termites, respectively. Therefore, two hundred Formosan subterranean termites can produce 0.31 to 0.38 g CO_2 in one month, which represented about 50% of the wood volume consumed in one study (Li & Su 2008). Further space can be acquired by excreting fecal matter into soil pores, part of the termites' mechanism for the construction of galleries (Li & Su 2008). This study did not examine the soil volume involved in the construction of sheeting or shelter tubes, nor did it address the possibility of moving soil particles into wood voids created by feeding. The purpose of this aside is to demonstrate the amount of subterranean void space that might be produced by termites in the United States; void space that might produce soil macropores through which water might be transported and stored.

Minerals, Organic Carbon and Nitrogen

The mixing of inorganic soil constituents with plant matter, feces, saliva, fungal combs and the corpses of dead termites alters the chemical charac-

teristics of soil. The interior of termite mounds in Brazil contained higher phosphorous, potassium, calcium, and magnesium than did the surrounding soil, although the content of these minerals at the mound surface was not different (Kaschuk *et al.* 2006). In an Australian study, the 1% of A1 soil incorporated into mounds contained 5–7% of the nutrients and the nutrients in mound material were 2–7 times that of surrounding soil (Coventry *et al.* 1988). Mineral enrichment is often attributed to the termites' translocation of clay and other mineral particles rich in exchangeable cations from deeper in the soil to the surface (Singh *et al.* 1987, Konaté *et al.* 1999, Kaschuk *et al.* 2006). Indeed, it has been suggested that termite saliva and associated microbes might release potassium that was bound to clay (Jouquet *et al.* 2007).

The fungus-growing termites (Macrotermitinae, which are restricted to Africa and Asia) collect plant material from outside the mound and transport it back to the fungal comb, where the plant material serves to grow the fungus. The termites then consume the fungus and decayed plant material rather than directly consuming the plant material at the time of collection (O'Brien & Slaytor 1982). This is not to say that there are not specialists among mound-builders, as many species specialize on grass. In either case, mound builders collect much more biomass than would be required to sustain the colony than if they consumed the plant material itself, increasing the concentration of nutrients and organic matter in the interior of the mounds of fungus growers relative to wood feeders. This will be discussed in more detail below.

Increased organic matter in the mound leads to higher levels of nitrogen and phosphorous (Lobry de Bryun & Conacher 1990), however the degree of enrichment varies depending on the materials chosen for mound construction. Macrotermitinae species, which construct a fungal comb, build their mounds almost entirely out of clay. While this enriches the exchangeable cations relative to the surrounding area (Singh *et al.* 1987), there is minimal organic carbon enrichment as the species in this subfamily use little fecal material or saliva in their mounds. In other termite families and subfamilies, however, a fungal comb is not produced and these mounds are very much richer in organic carbon than is the surrounding soil. On the other hand, some termites can reduce organic matter and nutrients from the surrounding areas by transporting plant material to the mound or to subterranean galleries (see for example Nash & Whitford 1995), although in some cases soil sheeting

can redistribute organic matter and nutrients (Lobry de Bruyn & Conacher 1990). As nutrients are a zero-sum game, enrichment of the mound occurs at the expense of nutrients elsewhere.

Because U.S. forest termites do not construct mounds or even well-defined nests (the Formosan subterranean termite, if it becomes established in forests, will be an exception), it is very difficult to quantify termite contributions to soil fertility. To date, this has only been investigated in the Sonoran Desert by examining the soil translocated into baited areas. *Heterotermes aureus* altered soil to a larger degree than did *Gnathamitermes perplexus* (Nutting *et al.* 1987). These differences were attributed to the differing feeding, shelter tube-building, and other behavioral characteristics of the two species.

Because wood is a nitrogen-poor resource due to its high carbon: nitrogen ratio, termites must obtain their nitrogen from other sources. Nitrogen availability is often considered the limiting factor in carbon cycling and the consumption of plant detritus (Nardi *et al.* 2002). Atmospheric nitrogen N_2 can be converted to NH_3 by some species of bacteria, including those living symbiotically with termites (Nardi *et al.* 2002). The gut protozoa of lower termites (i.e. all termites excluding the family Termitidae) do not fix nitrogen. The nitrogen-fixing ability of termites, both higher and lower, is therefore attributed to symbiotic bacteria, either in the fungal comb or in the gut (O'Brien & Slaytor 1982).

Global nitrogen fixation for forests and woodlands has been estimated as 10 kg/ha/yr (Brady & Weil 1996 in Nardi *et al.* 2002). The relative contributions of arthropods, free-living bacteria, associative nitrogen fixers, symbiotic bacteria and lightning have not been thoroughly examined in any ecosystem, although it is widely assumed that plant symbiotic bacteria (rhizobia) are the most important contributors. Estimates of nitrogen fixation in North American forests vary widely, from 45 to 9200 g N/ha/yr, but it is hypothesized that nitrogen fixation is higher in wetter, more poorly drained soils (Grant & Binkley 1987). In a temperate hardwood forest in New Hampshire, 68% of the nitrogen was derived from nitrogen fixation, but a quantitative mass balance was not conducted on the contribution of different nitrogen fixers (Nardi *et al.* 2002 and references therein). Long-term variation in nitrogen fixation in the northeastern United States was related to the amount of dead wood present; fixation being highest in young forests with significant

slash and in older forests with a significant accumulation of woody detritus. The amount of nitrogen fixation is not accounted for by fixation in wood litter, indicating an additional source of fixed nitrogen elsewhere in the system (Roskoski 1980). Different nitrogenase-encoding genes, *nifH* gene sequences, were found between soil and litter samples from a Douglas fir forest in Oregon, indicating different microbal communities between the two habitats (Widmer *et al.* 1999). Nitrogen fixation by free-living soil bacteria varied seasonally in North Carolina, being higher in the spring and early summer, but was not different based on forest type (Grant & Binkley 1987). A comprehensive review of nitrogen fixation in North American forests, and the factors that contribute to it, is beyond the scope of this review. The nitrogen economy of any forest ecosystem is the result of a complex set of relationships and inputs to which termites contribute both directly and indirectly.

A Costa Rican termite biomass of 1 g/m^2 fixed up to 0.12 kg N/ha/day, or 43.8 kg N/ha/year. Because termite activity is seasonal, at 22% of the maximum rate termites could achieve the global total for nitrogen fixation from woodlands (Nardi *et al.* 2002 and references therein). The North American drywood termite *Cryptotermes brevis* and the dampwood termite *Zootermopsis angusticollis* have low rates at 10 µg N/g wet weight/month (O'Brien & Slaytor 1982). It should be noted that the estimates above are based on several studies from around the world, using a variety of termite species across different habitats. Most of these studies also used the older and indirect measure of nitrogen fixation, the reduction of acetylene. A direct measure of Formosan subterranean termite nitrogen fixation provided by Lilburn *et al.* (2001) by using $^{15}N_2$ fixation and detection of *nifH* in termite guts, found a fixation rate of 4.6 ng N$_2$/termite/ hr, 0.5 ng N$_2$/termite/hr of which was due to symbiotic spirochetes alone. A native *Reticulitermes sp.* (the species was not identified) fixed between 1.5 and 2.75 µg N$_2$/g termite/day (Curtis & Waller 1995), which is much less than that of Formosan subterranean termites (equivalent to 36.8 µg N$_2$/g termite/day) found by Lilburn *et al.* (2001). If we assume that a rather modest-sized termite colony of 200,000 individuals (Su & Scheffrahn 2000) occurs over about 0.5 ha (King & Spink 1969), then a Formosan subterranean termite colony fixes nitrogen at a rate of about 8 g N$_2$/colony/yr or 16 g N$_2$/ha/yr, and a native termite colony of the same size fixes between 219 and 400 mg N$_2$/colony/yr; very much lower than that reported from Costa Rica (Nardi *et al.* 2002).

The fixed nitrogen is converted by the termites into proteins and other nitrogen-containing molecules. Uric acid, a waste product of metabolism, is stored within the bodies of termites, and is neither metabolized nor excreted (Slaytor & Chappell 1994). It might be supposed that this is a nitrogen storage mechanism, but termite tissues lack any enzymes capable of degrading uric acid. Instead, uric acid is degraded by gut bacteria (Potrikus & Breznak 1981) and nitrogen is released in the form of ammonia either from bodily emissions or in the feces (Ji & Brune 2006). Other references in Holt & Lepage (2000) report that most of the nitrogen excreted by termites is in organic forms, such as lignoproteins in feces, and total nitrogen excreted is higher than the total amount ingested. These organic fecal products are mineralized slowly into inorganic NO_3^- and NH_4^+ by microorganisms in the mound or in the soil. Mound soil is higher in inorganic nitrogen than is the surrounding soil (Holt & Lepage 2000). The total nitrogen economy of termites, taking into account fixation, accumulation, metabolism and excretion, is one of the data gaps in our knowledge of the role of termites in forest ecosystems. It seems reasonable to assume that soil nitrogen enrichment is partly caused by the release of accumulated uric acid from the bodies of dead termites, although this has not been examined.

Termite-Microbe Interactions

The relationship between termites and wood-decay fungi is a close one. As mentioned above, fungus-farming termites bring plant material to the mound to a fungal comb were *Termitomyces* fungi degrade the cellulose. These fungi supply the termites with C_1-cellulases (i.e., exocellulases) and it is believed that the termites themselves produce their own C_x-cellulases (i.e., endocellulases). If deprived of the fungal comb, the termites starve, indicating that endogenous C_x-cellulase activity is not sufficient to support life (O'Brien & Slaytor 1982).

The exact succession of wood decay organisms in forests is not known precisely. In an influential paper, Swift (1977) categorized wood decomposition in to three stages: colonization, decomposition and incorporation. Termites are thought to play their biggest role in wood decomposition at the decomposition stage, following the introduction of white and brown rot fungi. However, termites' position in this continuum is debatable. For example,

termites have been shown to consume sterilized wood (Lenz *et al.* 1991). A recent study in South Carolina, however, observed that termite biomass in decaying logs increases only after other invertebrates had already colonized the log (Braccia & Batzer 2008).

North American termites, although they do not construct a fungal comb, have an association with wood decay fungi. It has been known for nearly 50 years that *Gleophyllum trabeum* (formerly *Lenzites trabea*) produces compounds attractive to termites (Esenther *et al.* 1961) and further research into the relationship between termites and fungi continues (for examples, see Cornelius *et al.* 2002, Cornelius *et al.* 2004). Although it has been demonstrated that termites are attracted to wood-decay fungi by some mechanism, it can be assumed that termites carry fungi with them when they infest sound wood. Termites are not known to possess a mycangium (a pocket of enriched symbiotic fungal spores, as do some wood-boring beetles), and the identities of wood-decay fungi carried from one wood source to another by termites have not yet been conclusively determined. Wood decay fungi introduced or augmented by termites will accelerate the rate of wood decay, and therefore reduce the amount of biomass available as fuel. As will be discussed later, decay fungi introduced by termites might have implications for fire prevention and the rehabilitation of a burned waste area.

Termite Effects on Plant Growth

All of the above discussion of termites as soil engineers leads to the hypothesis that termite activity would have a beneficial effect on plant growth. This had been largely unstudied anywhere in the world, let alone in the United States. Although such effects are likely to occur (Fig. 5), there is surprisingly little in the literature. Plant species occurring on termite mounds in Southern Rhodesia (Zimbabwe) have been catalogued, with the observation that termite mounds are often rich in plant species that are rare in the surrounding area (Wild 1952). This study hypothesized that specialized characteristics of mounds (high pH, high water holding capacity, and minerals) allow these species to out compete other vegetation. Similarly, in Australia plant species composition changes as a function of distance from the mound (Spain & McIvor 1988). Increases in the available water content of soil near termite mounds reduced leaf shedding during the dry season in a savanna in Côte

d'Ivoire (Konaté *et al.* 1999), and increased the growth of grass species that are fed upon by termites (Jouquet *et al.* 2004). The effects of nutrient enrichment cannot be discounted in these studies because the same processes that increase the available water content also increase soil nutrients. In one study that observed increased root growth in termite mound soil, the effect was attributed to increased nitrogen content and increased bacterial and fungal activity (Duponnois *et al.* 2006), although spores of mycorrhizal fungi recovered from termitaria in India were not viable (Harinikumar & Bagyaraj 1994). Some studies report the potential of using termite mound material as a fertilizer (Brossard *et al.* 2007). Incorporation of termite nest material and NPK fertilizer increased the growth of eggplant beyond the use of NPK alone, but the growth of okra and andiroba were not improved by amendment with nest material without added NPK (Batalha *et al.* 1995). The authors of that study hypothesized that the amount of nest material used was insufficient to produce measurable effects. It is commonly observed that

Fig. 5. Increased growth of eucalyptus trees near termite mound in Mozambique, caused by soil enrichment. Smaller trees farther from the mound can be seen to the left of the larger trees. Photo by author, April 2007.

the surfaces of occupied mounds are relatively free of vegetation (Spain & McIvor 1988). This effect has been attributed to the hardness of the mound, but termite maintenance activities (repair of cracks) and removal of growing plant material likely contribute (Rogers *et al.* 1999).

The effect in North America is theoretically similar but probably much less in degree due to the smaller termite biomass. The effect should also decrease as one moves north due to declining termite abundance. Termite contributions to nutrient enrichment and the consequent benefit to plant life have not been investigated in the United States. If above-ground wood can be likened to a termite mound, termites colonizing a tree stump or a standing snag carry soil material upwards into the wood and organic matter downwards into the soil. This might be in the form of shelter tubes or by movement of soil and deposition of feces into interior wood galleries. The Formosan subterranean termite can also build carton nests above ground. In either case, as the wood continues to degrade, the soil and nutrients deposited by the termites, in addition to the nutrients released from the wood by fungal decay or in the termite feces, become available to the surrounding plant life. The contribution of termites to these processes in the United States and Canada would be hard to separate from the contributions of fungi, bacteria and other wood-destroying invertebrates. Consequently little work, if any, has been done.

Termites can be a significant pest of living vegetation in the tropics, including trees such as eucalyptus (Fig. 4). For reviews, see Wood (1996), Constantino (2002) or Mitchell (2002). This discussion is beyond the scope of this review, unless the Formosan subterranean termite becomes established in North American forests (which it has not yet done).

Termite Contribution to the Prevention of Fires

Because termites consume dead wood, they theoretically contribute to the reduction of fuel loading, thereby lessening fire potential. Although this is widely believed, the hypothesis has not been scientifically tested and is debatable (see below). The studies reviewed here discuss the biomass reduced by termites, and the effects on fire potential (if any) are discussed at the end of the section.

Plant biomass in tropical rainforests can be more than 500 Mg/ha, compared with 400 Mg/ha in temperate deciduous forests and less than 300 Mg/ha in

northern coniferous forests, 75% of which consists of above-ground woody biomass. Annually, about 30% of forest primary production is converted to wood (Swift 1977). As wood is relatively recalcitrant to decomposition (compared with other plant materials), this can lead to a significant accumulation of dead wood over the course of years. In a Panama rainforest, dead wood might constitute 6.2 Mg/ha (Swift 1977). In Arizona, one study found that a desert forest ecosystem had a standing crop of dead wood of 2 Mg/ha and a dead wood accumulation of 0.45 Mg/ha/yr (Haverty & Nutting 1975). Below-ground root biomass, which is usually estimated at about 20 to 25% of the above-ground biomass (Swift 1977), does not contribute to fuel loading but is available to termites as food. Logically, a high below-ground biomass should be correlated to a high above-ground biomass.

The rates of biomass turnover by termites have been examined to some degree. A population of *Macrotermes* in Nigeria that had a biomass of 134 kg/ha fresh weight consumed 1300 to 1500 kg/ha/yr of plant material. This probably represents a high contribution, however, perhaps as much as five or six times that of other termites (Bignell & Eggelton 2000). This overestimate might stem from the large size of *Macrotermes* relative to other termites, as well as the fact that these termites do not directly consume the plant material itself, but bring it to a fungal comb and the termites feed on the fungal hyphae and decayed plant material (i.e., they bring more plant material to the mound than they consume). More conservative estimates from Côte D'Ivoire indicate that wood-feeding termites turn over 20 to 30 kg/ha/year, and grass-feeding termites turn over 50 to 100 kg/ha/year (Bignell & Eggelton 2000 and references therein). A study in Botswana found that the abundance of fungus-growing termites was significantly related to increased wood decomposition rates (Schuurman 2005). An Australian colony of grass-feeding termites can consume up to 300 kg/ha/yr (Coventry *et al.* 1988). In a recent study of wood degradation in South Carolina, termites were cited as a substantial contributor (along with click beetle larvae, midge larvae and mites) to the invertebrate biomass in decaying logs (Braccia & Batzer 2008). In total there was a 10 to 30% loss of log mass, depending on habitat, from all sources of degradation (fungi, termites and other invertebrates) in 960 days, but the contribution by invertebrates alone was not reported in that study. The authors did note, however, that termite biomass was highest during a

time when the rate of wood mass loss was also at its highest (Braccia & Batzer 2008). In Arizona, a correlation between the termite foraging population and food availability was observed. The total termite biomass of two of the four species identified generally increased with increasing standing dead wood, increasing annual production, or both, however biomass turnover was not measured in that study (Haverty & Nutting 1975).

In the desert United States the termite contribution to biomass turnover is larger in arid and semi-arid areas due to loss of the contribution of decay fungi (Neary *et al.* 1999). It is estimated that in the Sonoran Desert termites consume up to 60% of all dead wood, but termites overall only contribute about 1 to 2 percent of total carbon mineralization in the United States (Bignell & Eggelton 2000). Competition with wood-decay fungi is responsible for this low average, as well as the large portions of the country that have low termite abundance. In localized areas, the contribution of termites is likely to be much larger.

Another way to estimate biomass turnover is to measure the amount of carbon mineralization. Because a termite's only source of carbon is vegetable biomass, through endogenous cellulases, via cellulases acquired from symbiotic fungi or through the acetate and butyrate products provided by symbiotic protozoa, any CO_2 produced represents fuel biomass that has been removed from the system. Forest termites in Africa produce 105 to 568 kg CO_2/ha/yr, those in neotropical regions produce 52 to 313 kg CO_2/ha/yr and those in oriental regions produce 30 to 122 kg CO_2/ha/yr (Bignell & Eggelton 2000, from references therein). In semi-arid woodlands, up to 20% of the CO_2 produced can be from the action of termites (Lobry de Bruyn & Conacher 1990). In Côte d'Ivoire, the termite-related CO_2 production rate of 272 kg CO_2/ha/yr represented nearly 5% of the total above-ground primary production and 11% of the CO_2 generated from sources other than fire (Konaté *et al.* 2003).

Direct measurement of CO_2 emission rates in North American termites showed that the native eastern subterranean termite emitted 0.507 ml CO_2/g termite/hr, which was higher on a per-gram termite basis than that of the Formosan subterranean termite at 0.310 ml CO_2/g termite/hr (Shelton & Appel 2001). From these data, Li & Su (2008) calculated that 200 termites produce 0.31 to 0.38 g CO_2/month. If we assume, as we did above, a colony

of 200,000 individuals (Su & Scheffrahn 2000) occurring over about 0.5 ha (King & Spink 1969), then this colony produces 620 to 760 g CO_2/ha/month for an overall rate of approximately 7.4 to 9.1 kg CO_2/ha/yr; much lower than that produced in the tropics.

It is unknown if, but logical to assume that, termites can introduce decay fungi into sound wood. Decay rates augmented by the introduction and spread of decay fungi by termites could further affect fuel loads in forests. However, because termites are less abundant in colder areas, eliminating the effects of climate on both termites and fungi would be necessary to examine this relationship.

There are several lines of reasoning that argue against termites' ability to reduce the overall severity of a fire. The first argument concerns the amount of biomass consumed by termites. If a heavy fuel load is considered to be > 400 Mg/ha, and if, at most, termites turn over 1.3 to 1.5 Mg/ha/yr, then it would take 267 years for termites to completely mineralize a heavy fuel load to nothing. This argument is countered by the observation that termites seem to be able to remove about one-fourth or more of the cross sectional area of a pine log within a couple years, and the combined action of termites and fungi caused a 30% reduction in sweet gum log mass within 2.7 years (Braccia & Batzer 2008). Termite modification of wood, such as increasing the total surface area for the establishment of decay microbes and the termite-mediated transport of these microbes might lead to a synergistic and non-linear total biomass reduction. Although one study reported that the per-weight caloric value of degraded wood was actually 40% higher than sound wood (Knoll *et al.* 1993), there should be a net reduction in total caloric value due to reductions in wood volume and density, leading to a reduction of flammable mass, as a result of decay. The second argument is that fire potential is gauged by such broad measures that the biomass removed by termites, with or without a synergistic contribution by decay fungi, is too small to change the overall severity and effects of a fire. A third argument is that the woody material preferred by termites, logs and large branches, constitutes only a portion of the material that burns in a fire; finer debris contribute more to fire severity. Non-woody fuels and smaller pieces of wood burn more readily than do larger pieces due to the increased surface area to volume ratio of smaller pieces, as well as to smaller pieces' inability to retain moisture. Larger pieces are more

resistant to ignition, and therefore do not contribute to fire intensity in any but the more-intense fires (Pyne *et al.* 1996). Until controlled experiments on the matter are conducted, however, the issue will remain unresolved.

EFFECTS OF FIRE ON TERMITES

Fire Characteristics and Effects

A comprehensive review of forest fire characteristics, physics and impacts is beyond the scope of this review. For an earlier in-depth discussion of fires, see Pyne *et al.* (1996). Fire severity is based on several characteristics, including duration (length of time of active burning), intensity (production of thermal energy and release of heat) and rate of spread (initiation of combustion in adjacent areas). Many other factors, such as topography, climate, wind, time since last burn, and so forth, contribute to fire severity, but their effects are largely through their effect on one or more of the three characteristics mentioned. Forest fires vary in their temperature, with ground temperatures in light fuel (< 1 Mg/ha) fires typically 200–300 °C (similar to grass fires), but in fires with heavy fuels, such as slash (> 400 Mg/ha), temperatures are usually 500–700 °C, but 1500 °C is possible (Neary *et al.* 1999).

The most important variable affecting soil organisms during a fire is the magnitude and duration of the heat transfer to the soil. The amount of heat transferred depends mostly on fire duration, but fire intensity, soil moisture, soil texture, soil organic matter, climate and topography also play secondary and non-mutually exclusive roles. Slower-moving and larger fires tend to transfer more heat, but this is not an absolute. A low-intensity fire (such as a smoldering peat fire) that is moving slowly will transfer more heat to the soil than will a fire of greater intensity that is moving rapidly; in this case fire duration is the important factor (Neary *et al.* 1999). In one experimental burn in Colorado, soil temperatures increased less at a heavier fuel site (a meadow with 8.8 Mg/ha) than in a low-fuel forest site (1.4 Mg/ha) because the meadow fire was much briefer than the forest fire (Massman *et al.* 2003).

The mechanisms of heat transfer to the soil depend on several factors. In light fuels, radiation is the primary mechanism, whereas conduction occurs with heavy fuels (Neary *et al.* 1999). Once the soil has absorbed heat, the heat can be transferred within the soil by the process of evaporation and

condensation of water. In this process soil water absorbs heat, evaporating to become steam. The vapor can travel rapidly through soil pores to cooler soil, where the steam condenses back to a liquid, transferring its heat energy to the soil as it does so. This raises the temperature of the soil, thus propagating the fire's thermal energy over a greater area. Not surprisingly, this process is more efficient in moist soil (Neary *et al.* 1999).

The depth of soil heating varies depending on the transfer of heat to the soil, as mentioned above. The increase in soil temperatures at varying soil depths has been examined in experimental burns in Colorado. Beneath a burning slash pile (560 Mg/ha, duration = several hours), increased soil temperatures were observed down to about 70 cm. The soil reached 50 °C at 50 cm and nearly 400 °C at 2 cm (Massman *et al.* 2003). In the same study, soil temperatures at all depths during experimental forest fires increased with an increase in fuel loading, with no increase in soil temperature at 2 cm at the low-fuel site (1.4 Mg/ha, duration = 25 minutes), significant increases in soil temperature to between 10 and 15 cm at the medium- and high-fuel sites (15 Mg/ha, duration = 30 minutes and 32 Mg/ha, duration = 30 minutes, respectively) (Massman *et al.* 2003). These results are consistent with studies in Australia that found only slight soil temperature increases below 2-cm in low- and moderate-intensity fires (Bradstock & Auld 1995).

Recent reviews of the effects of fire on soil have been provided by Certini (2005) and Knicker (2007). Not surprisingly, the extent of alterations to the soil depends on fire intensity and duration, and can be short term, long term or permanent (Certini 2005). Low- to moderate-intensity fire has few, if any, deleterious effects on soil. However, water repellency, which results from fires of 176 to 288 °C (Neary *et al.* 1999), might be observed for time following the fire (Certini 2005). An increase in water repellency would cause lower soil moisture and higher soil erosion. More severe fires result in increased soil erosion, loss of soil minerals in ash plumes, loss of organic matter and loss of microbial activity (Neary *et al.* 1999).

Loss of organic matter in soils begins at about 200 °C, with complete oxidation of organic matter at about 460 °C, and structural changes in organic matter are observed at intermediate temperatures. Oxygen-containing compounds (such as carbohydrates and cellulose) are degraded before lipids and waxes (Certini 2005, Fernádez *et al.* 1997). The catastrophic 2002 Biscuit

fire in southwestern Oregon interrupted an on-going long-term ecosystem productivity study, and allowed the direct measurement of a catastrophic fire's effects on soil, which are reported in Bormann *et al.* (2008). The fire burned at > 700 °C over large areas and was much more intense than most wildfires reported in the literature. There was an increase in near-surface rocks, indicating the combustion, convective erosion or post-fire wind and water erosion of a substantial amount of mineral soil. Researchers noted a total loss from all mechanisms of 127 Mg/ha loss of soil, with a loss of 23 Mg C/ha and 0.69 Mg N/ha, around 60% of which was lost from the mineral (i.e., non-organic) horizons (Bormann *et al.* 2008). Losses from less-intense wildfires are expected to be more modest.

Despite the immediate loss of carbon and nitrogen in extreme fires, nitrogen levels sometimes increase for a time following the fire. Ammonium is formed by combustion in lower-intensity fires (Certini 2005), and the loss of competition for ammonium with plants (Neary *et al.* 1999) and other nitrogen sinks (Grant & Binkley 1987) allows nitrogen accumulation. The rates of nitrogen fixation were 45 g/ha in an unburned site and 950 g/ha in a burned site (Jorgensen & Wells 1971 in Grant & Binkley 1987). Similarly, a long-term increase in organic carbon was observed in a site burned ten years previously, presumably due to improved growing conditions caused by the fire (Certini 2005). Phosphorous has also been observed to increase following a fire (Certini 2005 and references therein).

Soil cations, including potassium, calcium and magnesium, generally increase in soil following lower-intensity fires (Certini 2005). In high-intensity fires, however, these cations might be lost in the ash plume or through consequent soil erosion (Neary *et al.* 1999). The increase in soil pH caused by high-temperature fire (> 450 °C) can either positively or negatively affect the availability and solubility of these macronutrients (Certini *et al.* 2005). There are few studies on changes to micronutrients, such as iron, manganese, copper, zinc, boron and molybdenum, but these can be presumed to change through the same processes that change the macronutrients.

Soil porosity is often reduced by fire, resulting in more compacted soil with higher bulk density through the collapse of soil aggregates and the closing of soil pores by ash or clay (Certini 2005 and references therein).

The immediate effects of fire are a reduction in microorganism diversity

and abundance. Microorganisms are generally more tolerant to heat than are soil animals, including invertebrates (Neary *et al.* 1999). However, most microorganisms occur in the top 2.5 cm of soil, which experiences the highest temperatures during fires (Knicker 2007). Microbial mortality in fires is higher in soils with higher soil moisture, possibly due to the greater heat-conducting capability of water or due to evaporation and condensation (Certini 2005). Complete sterilization of the soil occurs only in extreme cases (Knicker 2007). One recent study found that immediately following a fire, overall microbial biomass was not different between sites experiencing low- and high-severity fires, although the soil respiration rate was lower in burned sites relative to non-burned sites, and there was a decrease in fungal biomarkers in the burned sites (Hamman *et al.* 2007). In the short term (about 30 days), nutrients re-leased by the fire increased microbial numbers, followed by a decline as the nutrients leached or were depleted (Knicker 2007). Secondary mortality of microorganisms can result from toxic combustion products, such as dioxins, dibenzofurans and polyaromatic hydrocarbons (Certini 2005). Negative ef-fects of burning on microbe populations may persist for some years following a fire (Fritze *et al.* 1993).

The best way to assess the effects of catastrophic fires on termites would be to conduct a study that monitored termite presence and activity for several years before an intense fire and for several years afterward, compared to un-burned control plots. Because catastrophic fires cannot be set experimentally, inferential data must be collected by either extrapolating results obtained from smaller, controlled fires or by observing catastrophically burned areas after the fact and then making assumptions about termite conditions before the fire. Unfortunately, the work of Bormann *et al.* (2008), which serendipitously was able to compare soil conditions before and after a stand-replacing fire, did not record soil invertebrates.

Direct Mortality

Most studies of direct invertebrate mortality during fires have been con-ducted on species other than termites, including earthworms and nematodes (Certini 2005). One study demonstrated that prescribed burning had no effect on soil insect populations (Siemann *et al.* 1997), but the sampling conducted in that study would not have detected termites. In a Swedish study, insect

mortality during a fire depended on the amount of organic matter consumed, which would indicate the intensity of the fire. Those insect species occurring deeper in the soil profile were less affected, and survival increased with increased body hardness and mobility (Wikars 2001). Termites are soft bodied, but are relatively mobile in pre-existing tunnels and galleries. However, it is unlikely that termites would be able to construct new tunnels quickly enough to escape heating of the soil during a fire.

The construction of mounds has been credited for the ability of mound builders to survive fires in Brazil, western Africa and Australia (DeSouza *et al.* 2003, Bignell & Eggleton 2000, Ewart 1991, Abensperg-Traun & Milewski 1995). These mounds have hard clay shells, which are relatively dry and insulate the colony from the heat of the fire. Because fire intensity varies between areas even within the same fire, a localized colony might be able to escape a fire through random chance. There is the reverse possibility, however, that a colony might be completely eliminated by a fire if the fire becomes too intense in a localized area.

The literature is varied when discussing the direct effects of fire on termites. In one study, termites were among the most severely affected species, although there was some protection in mounds, and the largest effect was the result of the loss of food and microhabitats (Mathieu *et al.* 2005). A light fire in Brazil caused no change in termite generic richness or abundance (DeSouza *et al.* 2003). Following a fire of 260–816 °C but which caused little heating of the soil, reduced termite foraging was observed immediately after the fire, but it quickly recovered to previous levels (Gander 1982). In an Australian study, Abensperg-Traun & Milewski (1995) concluded that direct mortality and not depletion of food was responsible for lowered wood-eating termite diversity and abundance two years after a fire. On the other hand, in a different Australian study, during which soil heating was limited to the top 7.5 cm of soil, termites were the most commonly observed insects following the fire, followed by ants and beetles (French & Keirle 1969). These results might be reconciled by the observations of Dawes-Gromadzki (2007), who determined that termites were the most abundant macroinvertebrates both before and after low-intensity fires, but that the fire reduced the abundance of all of the collected taxa. The termites were therefore the most affected due to their high relative abundance. Because most of the other taxa in that study

were absent two weeks following the fire, it is impossible to determine if all taxa were affected to the same degree by the fire, or if more mobile taxa might have escaped the fire and subsequently left the study area in search of food.

Because North American forest termites do not construct mounds, they are afforded no protection beyond the insulating properties of the soil itself. From the work of Massman *et al.* (2003) reviewed above, and by assuming that all termites are killed at soil temperatures above 50 °C (Hu & Appel 2004), low-fuel fires of short duration in forests should not kill any termites in the soil, however fires at sites with higher fuel loads should kill termites to the depth to which the soil surpasses 50 °C: 15 cm in medium- to high-fuel sites, and 50 cm under extremely heavy fuels, such as slash piles (Massman *et al.* 2003).

The depth of termite foraging is known in a relative sense with desert termites in North America, but not with any certainty in temperate forests. The majority of termite foraging in deserts is in the top 10 to 20 cm of soil, and in Nevada there was an exponential relationship between soil depth and the likelihood of encountering a termite nest: 75% chance in the top 0.5 m, 90% chance in the top 1 m, 94% in the top 2 m, 97% in the top 4 m, and 99% in the top 8 m (Myles & Hooten 2000). If this relationship generally holds true then a catastrophic wildfire would kill about 75% of the termites (i.e., those in the top 0.5 m) in the area. Any termites or colonies below the depth of lethal temperature during a fire will escape the effects, and will likely move back into the heated soil once it has cooled.

Termites are relatively mobile in pre-existing galleries and tunnels, and might have a good chance of escaping soil heating during a fire. However, if no tunnels, galleries or soil voids currently exist when the fire takes place, the termites will be unable to escape as they would not be able to dig quickly enough to escape the heating of the soil profile. It is unknown if termites in temperate environments occur more or less deeply in the soil than they do in deserts because in areas where water is more plentiful it might not be necessary to tunnel as deeply. Formosan subterranean termite carton nests in Louisiana have been found from between 2 to 46 inches (5 to 115 cm) below the soil surface, with tunnels extended to the water table (King & Spink 1969). Just as mound-building termites might by chance escape direct mortality from fire in areas of low fire intensity, North American forest termite colonies, which

are dispersed throughout the soil and might contain several reproductive pairs (a situation known as polygyny (Thorne *et al.* 1999, Higashi *et al.* 2000)), might survive in a localized area.

Depletion and Alteration of Food Resources

Logic holds that if a significant portion of an area's food resources are depleted by some means, such as fire, then the communities relying upon that food resource will suffer. In the tropics, this has been demonstrated (for example, in Mathieu *et al.* 2005).

Alteration of habitat is intimately linked to the depletion of food resources. In Cameroon, termite species abundance and termite biomass were reduced in plots experimentally cleared by mechanical removal of dead wood and vegetation, although more modest disturbances had little or no effects (Eggleton *et al.* 1996). In that study, it was concluded that the termites left the area due to lack of food, altered habitat and loss of soil moisture. Similar results were obtained in another study in Indonesia, where agricultural production of cassava and plantation monoculture caused reductions in termite abundance (Gathorne-Hardy *et al.* 2002). Clearance by a catastrophic fire would have a similar effect, perhaps aggravated by direct termite mortality as well as alteration of soil properties and of microorganism communities.

When wood burns it undergoes chemical and structural changes that might make it no longer desirable or useful as a food source. In the production of char, the incomplete burning of wood that occurs between 250 and 500°C, cellulose and hemicellulose are converted to a heterogeneous mixture of aromatic, phenolic or *O*-furan compounds (Baldock & Smernik 2002, Czimczik *et al.* 2002, Knicker 2007). If wood were altered in such a way that termites no longer recognize it as food, or were unable to digest it, then fire would result in a large portion of woody biomass becoming unavailable to termites, which might have an effect similar to the complete combustion to ash. Support for this hypothesis comes from the popular and scientific observation that char is biologically inert, and is only sparingly metabolized by microorganisms (Baldock & Smernik 2002), especially in oxygen-poor environments (Knicker 2007). In fact, many archeological sites are identified and dated by char deposited millennia before. This partial charring of wood did not deter termites from feeding upon wood blocks or bolts. A

non-statistical trend was observed that charred wood might be attacked more readily (Peterson *et al.* 2008), an observation also noted by Bernklau *et al.* (2005). The mechanism of such an effect has not been examined. In the 2008 study of Peterson *et al.* when the termites were forced to feed upon char to the exclusion of wood there was a significant decline in the number of termite gut protozoa, an effect often ascribed to starvation. However, starved termites lost their protozoa more rapidly than did char-fed termites, which lost their protozoa more rapidly than did termites fed pine shavings (pine-fed termites saw no reduction in protozoa numbers) (Peterson *et al.* 2008). In short, it seems that termites were able to derive some nutritional benefit from the consumption of char, but declining protozoa numbers would have led to the eventual starvation of the termites and the termites could not have fed on char exclusively for an indefinite period. Termites fed surface-charred pine blocks had black abdomens within three days of feeding, indicating that they were consuming the char.

Changes in Soil Properties and Microorganisms

It is unclear what soil conditions need to be present to ensure termite survival. In the most general sense, it is known that the soil must be moist enough to prevent desiccation, warm enough to prevent freezing and include sufficient sources of food. The wide variety of habitats infested by termites speaks to the insects' ability to tolerate a wide range of conditions. The effect of fire-altered soil properties on termites has not been investigated in North America or in the tropics. Termite presence, as far as anyone knows, is more dependent upon climate than it is on soil conditions.

As a consequence of soil compaction, the rate, but not the extent, of termite tunneling will be slowed. Termites build into soil of different compaction at different rates; up to 221 cm/day in loose soil versus 96 cm/day in more compacted soil (Tucker *et al.* 2004). Although compaction affects the rate of tunneling, it did not affect the number or diameter of primary tunnels, but did reduce the number of secondary exploratory tunnels (Tucker *et al.* 2004). The lower water holding capacity of compacted soil could also affect the suitability of the soil habitat for termites.

Cellulolytic protozoa that are required for the digestion of cellulose in the termite gut cannot live outside of the termite, and termites pass the protozoa

to one another rather than acquire them from the environment (Lewis & Forschler 2006). In other words, fire will have no affect on cellulolytic protozoa. The relationship of termites to wood decay fungi is still a matter of research, and it is unclear to what degree termites require the presence of decay fungi in order to find wood. A study by Lenz *et al.* (1991) demonstrated that all termite species examined fed upon sterilized wood blocks, but it should be noted that the termites were not surface-sterilized in that study and it is possible that the termites brought fungal spores with them and fed upon the wood once the spores had an opportunity to attack the wood. It is also not clear how rapidly decay fungi will recolonize an area after a burn, or by what exact mechanism this occurs. It is almost a certainty, however, that microbial recovery in a burned area will occur more rapidly than will recovery of the termite population.

Termite Recolonization Following a Fire

Termites will begin exploring burned areas once the soil has cooled. The length of time for a burned area to return to a normal daily temperature cycle (recovery time) depends on the intensity and duration of the fire. In experimental burns in Colorado, the recovery times ranged from about two hours at low fuel sites to 16 to 20 hours at heavier fuel sites and about two weeks under a burned slash pile (Massman *et al.* 2003).

Termites that survived the fire in existing subterranean structures (nests, galleries and tunnels) could simply move back into the existing structures that were affected by the fire, provided that the structures did not collapse or become otherwise unusable. Reproductive individuals, if they survived, would continue to produce offspring.

If all the termites in an area were killed by a fire, then recolonization would necessarily occur from surrounding areas. The rate at which this happens will depend on several factors, including the rate of termite colony dispersal, the availability of food in the burned area, and the suitability of the habitat (soil properties, etc.). The latter two have been discussed above, and will not be elaborated upon here because factors that affect the subsequent survival of termites that survived the fire will similarly affect pioneer populations in a burned area.

The area-to-perimeter ratio is important in recolonization (Bell *et al.* 1997), and smaller areas will be recolonized more quickly than will larger ones (see

French & Keirle 1969). Climate also affects a termite colony's potential to expand. In wet years, termite population density depends mostly on temperature, while in dry years it depends mostly on soil moisture (Ueckert *et al.* 1976). In the Chihuahuan Desert, soil moisture, and not temperature, was the determining factor describing termite foraging, with termites significantly less active in dry soil, such as that exposed by loss of ground cover (MacKay *et al.* 1986). Of course, exposed soil will absorb more sunlight and reach a higher temperature, resulting in higher water evaporation, although there should be no effect due to temperature alone.

There are few studies on the dispersal rate of termites. A plot of 100 coconut trees on 0.7 ha that was devoid of *Microcerotermes biroi*, a tree-nesting termite in New Guinea, had 10% of its trees infested with this species within 18 months, and 63% of the trees were infested within four years (Leponce *et al.* 1996).

It can be assumed that the rate of termite recolonization is slower than for other insect species of similar size and population density. This is for many reasons. First, termite workers are flightless, have soft bodies and are susceptible to desiccation. For this reason, termites only rarely forage in the open, and must either tunnel through the soil or construct shelter tubes to explore new areas, both of which are relatively slow processes. Second, unlike non-social insects, the foraging individuals of a termite colony are not reproductive without undergoing significant physiological changes, so although workers might explore a new area and utilize any food resources found there, a colony cannot be established until a reproductive pair arrives. The third reason, related to the second, is that reproductive termites are not strong fliers. Winged adult termites only fly once in their lives, losing their wings shortly after the nuptial flight. Marked Formosan subterranean termites in New Orleans have been collected up to 900 m from the point of marking, moving with the wind at low wind speeds of less than 1 m/sec (Messenger & Mullins 2005). In flight mill studies, Shelton *et al.* (2006) determined that the maximum flight distance of a male eastern subterranean termite was 265 m, while that of a female termite of the same species was nearly 460 m, but the average flight distance (not reported in that study) was likely much lower. Once a mating pair establishes a colony, it takes no less than a few years for that colony to begin producing more reproductive individuals. Therefore, the

rate of recolonization of a waste area by termites is limited largely by the dispersal rate of reproductive pairs, which is very low compared to other insects. Dispersal by colony budding, during which secondary reproductives develop and begin to reproduce without a nuptial flight (see Thorne *et al.* 1999 for a review), is likely to be very slow, as the budded colony occurs within the established foraging area of the existing colony.

The classic example of recolonization of waste areas is Krakatau Island, which was completely defaunated by volcanic eruptions in 1883. Recolonization of these islands by termites was examined by Gathorne-Hardy *et al.* (2000). Even after 113 years, termite species richness was lower on Krakatau Island than on neighboring Sumatra and Java. Of the three termite families found on the neighboring islands, all three are found on Krakatau, but the number of subfamilies of Termitidae are reduced from four to one. All of the termite species currently found on Krakatau are wood-feeders while soil-nesting species are common on neighboring islands. This indicates that floating infested wood (or perhaps inadvertent introduction in wood products by humans) is the primary mode of termite recolonization (Gathorne-Hardy *et al.* 2000).

If a fire were not overly severe, termites might find a higher amount of available food following a fire, due to the increased above- and below-ground biomass of trees killed by the fire. Termite infestation of bolts or wood blocks was not affected by the presence of char and the observation that termites consuming charred wood had black abdomens indicate that the char is ingested (Peterson *et al.* 2008). Again, because North American termites do not commonly attack healthy trees, significant tree kill caused by the fire might provide a food resource previously unavailable.

Termite Rehabilitation of Waste Areas

In a review of methods that can be used to improve the future productivity and health of production forests, termites are noted for their contribution to wood decomposition in the tropics, but their role in the southeastern United States was not examined (Johnston & Crossley 2002). However, many of the recommendations for soil restoration in that review (stem-only harvest, longer rotations, minimizing soil disturbance) would augment termite populations and activity.

Much of the earlier discussion on the role of termites as soil engineers is relevant to the use of termites for soil rehabilitation. Termites are recognized

for their role in the recovery of disturbed soil (Gathorne-Hardy *et al.* 2002). Desert reclamation experiments have been conducted in the Sahel of western Africa, and termites have been cited as an important contributor to this process. The approach is simple; augment termite presence and activity to increase desirable soil properties (Mando *et al.* 2002). The formation of soil crusts in degraded soil in Burkina Faso is thought to be partly due to the loss of termite activity (Mando & Miedema 1997). The presence of termites in crusted soil increased water infiltration amounts, infiltration rate, soil water content and soil porosity and reduced soil bulk density compared with termite-excluded plots (Mando *et al.* 1996). Mulching (as opposed to disking or plowing) increased termite activity in crusted soil, resulting in the opening of pores in the crust and increased the number and size of soil pores, improved soil aggregation and increased the amount of soil material brought to the surface (Mando & Miedema 1997). In Australia, water storage was about 20% higher in mulched plots that included invertebrates, of which termites comprised a major component, than in mulched plots were invertebrates had been excluded through the use of insecticides (Dawes-Gromadzki 2005).

Many studies have suggested the use of termite mound material to enrich soil due to the accumulation of nutrients and organic matter (see Brossard *et al.* 2007 for discussion and references). Such uses, however, are limited by the availability of mounds and their slow rate of regeneration (Brossard *et al.* 2007).

Due to the large amount of disturbance to forests caused by fire, rehabilitation of these areas is important in the site's future productivity. Based on the results of the African experiments in the Sahel and in Australia, it seems reasonable that augmentation of termite activity, or even the reintroduction of native termite species from neighboring areas, in severely burned forests might improve soil characteristics by reducing water runoff and increasing soil pore volume, nitrogen fixation, macro- and micro-nutrient translocation, and other beneficial effects. The diversity of invertebrates in good sites is higher than it is in poor sites (Dawes-Gromadzki 2005), therefore as the health of the system improves invertebrate diversity would increase, allowing the establishment of beneficial insects. This approach has been wholly unexamined in the United States. Such an approach might be best seen on poor or marginal sites.

Despite successful results in Africa, this approach is controversial. Logical reasoning, backed by scientific evidence (Spears *et al.* 1975, Nash & Whitford 1995, Narayanan 2004), indicates that termite consumption and sequestration of organic matter might increase the rate of desertification by removal of surface organic matter, especially living plant material, and through increased soil exposure and consequent loss of soil water. Competition with domestic cattle for grass, especially during dry years, has also been mentioned as a negative consequence of termite activity (Narayanan 2004). An experiment conducted in New Mexico found an increased percentage of grass cover, but a decreased percentage of shrub cover, in areas of animal-caused (including termite-caused) soil disturbance, but it was not clear if the presence of grass augmented animal populations or if the animal populations augmented the grass growth (Jackson *et al.* 2003).

Obviously, research must be conducted before large-scale termite-based reclamation projects can be undertaken, especially in areas prone to desertification. As the termite genera studied by the cited studies, *Gnathamitermes*, feeds largely on grass and not wood (Narayanan 2004), the negative effects caused by depletion of ground cover cannot be discounted. Wood-feeding termite genera, such as the native *Reticulitermes*, might not cause these harmful effects. On the other hand, introduction of wood-feeding species into areas with low woody biomass might not allow the termites to become established. That being said, *Reticulitermes* can consume dead grass, as the author has kept termite populations alive for up to six months in the laboratory with only straw for food, until they succumbed to desiccation (CJP, personal observation).

CONCLUSION

There is much that can still be learned regarding the relationship between termites, trees and fire. The benefits to forest health of termite activities can only be supposed at this point as scant hard research exists. Improved tree health as a result of termite-mediated soil enrichment, more favorable hydrological properties and an increased pace of carbon cycling should result in areas where termites are abundant and active. This should improve tree growth characteristics as well as tree resistance to fires, diseases and attack by other insects. Reduction of fuel loads in termite-active areas, either through

direct consumption of woody biomass by termites or through synergism with termite-associated wood decay fungi, will contribute to the reduction of fire severity.

Following a fire, the future productivity of the site will depend partly on the contribution of termites and their symbionts to site rehabilitation. The ability of termites to recolonize a burned area and the contribution termites will have on the productivity of the burned area need to be examined.

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