Chapter 8
Cues Used by Subterranean Termites During Foraging and Food Assessment

Timothy M. Judd

Contents

Abstract Subterranean termites tunnel through soil to locate new food sources, an energetically expensive process. The use of efficient search patterns and food location cues reduce the cost of foraging. Once arriving at a potential food source, termites assess its quality using a different set of cues. These types of cues could affect recruitment and colony health and survival. This chapter reviews what is known about the foraging process of subterranean wood-feeding termites, a group that con-

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T.M. Judd (✉)
Department of Biology, Southeast Missouri State University, Cape Girardeau, MO, USA
e-mail: tjudd@semo.edu

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tains a number of economically important pests. It summarizes what is known about search patterns used by these termites and the role of food location cues to effectively reach a viable food source. This chapter also discusses what is known about wood preference and how different components of wood such as density, secondary metabolites, nutrients, and other factors affect food selection in subterranean wood-feeding termites.

Keywords Subterranean termite • Foraging • Food selection • Wood preference • Foraging cues

8.1 Introduction

Termites have been traditionally grouped according to their feeding ecology including one-piece termites (those that live in and feed on wood), arboreal termites, and subterranean termites (Abe 1987). Subterranean termites include soil feeders, litter feeders, and wood feeders (Abe 1987; Donovan et al. 2001; Eggleton and Tayasu 2001). There are several reviews of termite nutritional ecology and foraging behavior that include all feeding types of termites (Wood 1978; Waller and La Fage 1987; Traniello and Leuthold 2000). This chapter will instead focus on the location and selection of food in one feeding group, the subterranean, wood-feeding termites (hereafter just referred to as subterranean termites). Due to the economic importance of many of them, there have been a number of studies that have examined the types of cues used during foraging and selection of food. This review discusses what is known about the cues used by subterranean, wood-feeding termites during different stages of foraging, including search patterns, localization cues, and assessing food quality. Understanding the search patterns and cues used during the foraging process could improve methods for controlling termites and possibly lead to methods that prevent termite infestations.

8.1.1 Nutrition and the Role of Wood in the Termite Diet

Wood contains high levels of carbohydrates that are accessible by termites especially with the aid of symbionts (Brune 2014). The primary carbohydrates found in wood, cellulose and hemicelluloses, are broken down in the termite gut (Esenther and Kirk 1974; Inoue et al. 1997; Slaytor 2000). Starches may also be found in wood especially in the sapwood, and their amount in wood depends on the tree species (Buchanan 1963). The large amount of accessible polysaccharides means that wood provides an excellent energy source for termites (Traniello and Leuthold 2000). Nitrogen is very limiting in wood as are other nutrients (Waller and La Fage 1987). Ash makes up 0.2–0.9% of the total wood dry mass (Buchanan 1963), creating possible limitations in acquiring adequate amounts of vitamins and minerals.

The primary minerals that make up the ash are calcium, potassium, magnesium, and iron, with calcium and potassium making up the bulk of that minor mineral component (Buchanan 1963). Termites have other means of accessing limiting nutrients. It has been known for some time that termites have nitrogen-fixing bacteria in their gut (Breznak et al. 1973; Bentley 1984; Slaytor and Chappell 1994; Ohkuma et al. 1999; Yamada et al. 2006). Other symbionts help manufacture vitamins such as vitamin B_{12} (Wakayama et al. 1984). Recently, it has been found that *Reticulitermes flavipes* will acquire minerals directly from the soil (Janzow and Judd 2015). It is likely that other species of subterranean termites can obtain minerals from the soil as well. Although wood can supply some of the other nutrients termites need (La Fage and Nutting 1978), it may primarily represent an energy source for subterranean termite colonies.

8.2 Locating Food

Foraging can be described as a three-stage process: (1) search patterns, (2) response to food location cues, and (3) assessing a food source (Kennedy 1965; Bernays and Chapman 1994). The first stage occurs in the absence of cues that indicate the location of a food source. Central-place foragers, those animals foraging from a central nest, need to maximize the search area but minimize the energy expenditure in doing so (Bell 1990). At the second stage, the forager identifies a potential target. In general, cues will allow foragers to determine the location of a food source and potentially some indication of its quality. The final stage occurs at the food source itself. It is at this stage that phagostimulants and other cues allow the forager to determine the palatability of the food source. Subterranean termites are central-place foragers, and based on the research so far, it appears they apply strategies based on these three stages when foraging for food.

8.2.1 Search Patterns

Burrowing is an expensive endeavor, and measurements taken from burrowing arthropods have found their energetic costs to be similar to those of burrowing vertebrates (White 2001; Xu et al. 2014). The energetic cost of burrowing also depends on the composition and moisture level of the substrate (White 2001) and on the metabolic level of the organism (Xu et al. 2014). Given the energetic cost of burrowing, subterranean termites should use strategies and search patterns that minimize energetic costs (Su 2005). Several studies have shown that tunneling patterns are nonrandom and minimize overlap (Lee et al. 2007, 2009; Lee and Su 2010a, b). Although different species have different tunneling patterns (Puche and Su 2001; Grace et al. 2004), they all maximize the search area and minimize energetic costs (Lee et al. 2008; Hapukotuwa and Grace 2012). However, soil is not homogenous, and a number of soil characteristics will influence the termite tunneling behavior (Su and Puche 2003; Grace and Campora 2005). Moisture level (Su and Puche 2003; Green et al. 2005; Cornelius and Osbrink 2010, 2011b), gaps in the soil, structural guides (Lima and Costa-Leonardo 2012), and soil type (Haverty 1979; Houseman and Gold 2003; Su 2005; Hua and Kirton 2007) can all alter termite tunneling patterns. Gaps may reduce the energetic cost of tunneling, and moisture may increase the chance of encountering chemical cues. Substrates such as sand have larger particles which may reduce tunneling costs (Houseman and Gold 2003). However, the sand cannot retain water and other charged particles as well as other soil types (Brady and Weil 1996) which may reduce the availability of localization cues to foraging termites.

8.2.2 Localization Cues

An airborne forager can use a number of cues when searching for a food source. Color, visual patterns and chemical odor gradients provide cues to locations of food sources (Bernays and Chapman 1994). These types of cues are not mutually exclusive and would benefit a forager to be able to rely on several cues to locate a food source. Likewise, a subterranean forager would also have to rely on multiple cues to increase the likelihood of detecting suitable food sources. Subterranean termites are more likely to feed on food sources located at the surface than on those that are buried (Ettershank et al. 1980). Thus, it can be inferred that the termites are expecting cues from the surface to determine the location of a food source. The local cues discovered thus far include thermal shadows and chemical gradients.

8.2.2.1 Thermal Cues

Ettershank et al. (1980) measured the temperature of the soil under food sources and compared the measurements to those of exposed soil. They found that the soil temperature was lower under food sources and proposed that the food sources created thermal shadows, temperature gradients that could act like cues for the subterranean forager. In a laboratory study, Swoboda and Miller (2005) tested the hypothesis that *Reticulitermes* would respond to thermal shadows. They confirmed that termites were more likely to move under a food source if the temperature was cooler under the food than the surrounding soil. Furthermore, when they created a scenario in which the soil was warmer under the food source, the termites did not respond. Organic substrates contain more water and would be greater heat sinks than mineralized substrates such as rocks (Swoboda et al. 2004). Thus, it is possible for a subterranean forager to distinguish a potential food source from a non-food source item on the surface.

8.2.2.2 Chemical Cues

In the natural environment, wood will go through several stages of decomposition. During this process, chemicals from the wood leech into the soil (Fukasawa et al. 2014). It has been shown that termites prefer wood that is decomposing to wood that has been freshly cut (Su 2005; Gazal et al. 2012). Interestingly, termites have been found to be attracted to wood or sawdust that is being decomposed by certain fungi (Esenther et al. 1961; Cornelius et al. 2002, 2014). Even extracts from wood or sawdust will attract termites or increase tunneling behavior (Reinhard et al. 1997; Cornelius et al. 2014). The exact nature of the attractants was not examined by these studies. Su (2005) found that laboratory colonies of *Reticulitermes flavipes* and *Coptotermes formosanus* were attracted to decaying wood disks in a laboratory setting. He proposed that the termites were attracted to small particles that leeched from the wood into the soil. Several possible candidates that match the prediction made by Su (2005) have been found to attract termites.

One molecule in particular that is given off during decomposition is the gas carbon dioxide. It is used by other subterranean insects such as the corn rootworm to locate food sources (Bernklau and Bjostad 1998a, b). Damp wood gives off CO_2, and this gas is a metabolic by-product of some wood degraders. A number of termite species were found to be attracted to higher levels of CO_2 and followed CO_2 gradients to their source in the field and laboratory settings (Bernklau et al. 2005; Broadbent et al. 2006). Waller et al. (1999) simulated the by-products of wood degradation by fungi by drenching soil with sucrose and yeast or urea and tested the effects of these treatments on termite foraging behavior. Laboratory experiments showed that *Reticulitermes flavipes* and *R. virginicus* preferred soil drenched with sucrose plus yeast or soil drenched with a urea solution over soil drenched with water. Field trials showed weaker responses to both cues, but they were higher than the controls. It is possible that the yeast and sucrose combination was producing CO_2, but this was outside the scope of that study.

Ions represent another small chemical that could leech through the soil. Rotting logs release a number of ions into the soil (Fukasawa et al. 2014). Botch and Judd (2011) examined the levels of ions at different soil depths and found that potassium was the only ion examined that formed gradients under the soil. When tested in the lab, the presence of potassium caused *Reticulitermes flavipes* workers to tunnel more than in its absence. Thus, there are a number of small chemicals that could act as potential cues for subterranean termites that are near decomposing wood.

Based on the work so far, we can now conclude that subterranean termites are not digging blindly to locate food sources but that there are a number of cues available to them. Subterranean termites are searching for food that is at the surface, and the cues they are using, thermal shadows and chemical gradients, originate from the surface. Thermal shadows indicate to foraging termites that an object is above them. Organic materials will produce different thermal shadows than inorganic substrates (Fig. 8.1); however, termites may not be able to use thermal shadows to determine the state of wood decomposition. The decomposition process of wood releases many particles, some of which can readily travel through the soil and form gradients. CO_2, potassium

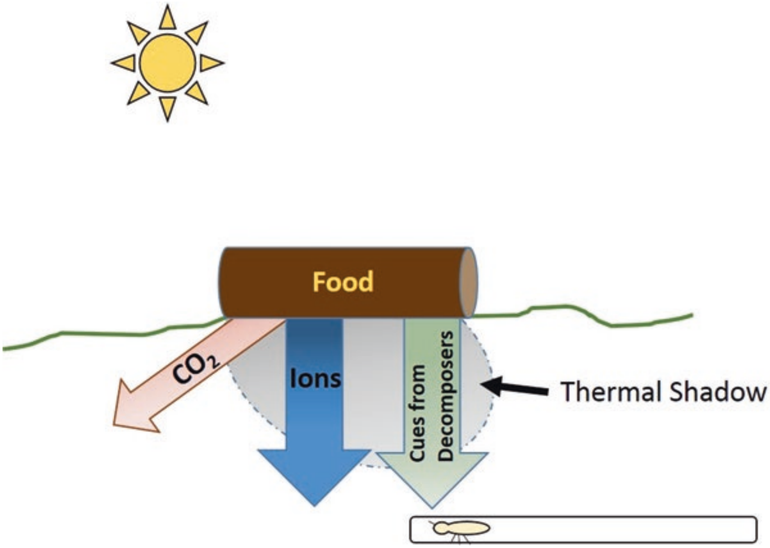

Fig. 8.1 Localization cues that can allow subterranean foragers to locate a food source include thermal shadows, CO$_2$, ions, and volatile produces from decomposers

ions, and urea fit this description (Fig. 8.1), and all three increase termite foraging behavior. Additional molecules released from the decomposers may play a role as well (Cornelius et al. 2002, 2014). Thus, termites would be able to detect a piece of wood on the surface and determine if it is in the correct stage of composition.

8.3 Cues Used at the Food Source

Once the forager reaches a food source, the individual must determine if the food item is palatable. These cues should indicate the level of decay, the nutrients available to the termites, and the presence of secondary metabolites that would affect survival.

8.3.1 Wood Preference

A number of studies have tested the preference of wood in subterranean termites. Many of those workers compared wood commonly used in construction, while others compared common wood to exotic ones that are not commonly used. A number of studies used wooden blocks in choice and no-choice tests to determine the relative palatability of wood from different tree species. Results from many of the laboratory assays are summarized in Table 8.1. Although differences in methodology can produce different results (Haverty and Nutting 1974; Su and La Fage 1984; Lee and Forschler 2016), overall some trends can be seen from comparing these studies.

Table 8.1 Results of several laboratory studies investigating the relative level of feeding on different wood species

Termite species	Order of wood preference (most eaten to less eaten)	Source
Coptotermes curvignathus	*Hevea brasiliensis* > *Alstonia angustifolia* > *Cinnamomum scortechinii* > *Khaya ivorensis* = *Dialium kunstleri trifoliolatum* > *Fagraea fragrans* = *Dipterocarpus grandiflorus* = *Pometia pinnata* > *Madhuca utilis* = *Neobalanocarpus heimii* = *Cotylelobium lanceolatum* = *Shorea curtisii*	Kadir and Hale (2012)
Coptotermes Formosanus	*Picea* sp. = *Pseudotsuga menziesii* > *Betula alleghaniensis* = *Quercus rubra* = *Juglans boliviana* > *Sequoia sempervirens* > *Hymenaea courbaril* > *Swietenia macrophylla* > *Chamaecyparis nootkatensis* > *Tectona grandis*	Cornelius and Osbrink (2015)
	Pseudotsuga menziesii > *Sequoia sempervirens* > *Chamaecyparis Nootkatensis*	Grace and Yamamoto (1994)
	Pinus sp. = *Pseudotsuga menziesii* = *Cardwellia sublimis* = *Eucalyptus deglupta* > *Eucalyptus robusta* = *Metrosideros polymorpha* = *Acacia koa* > *Pandanus tectorius* > *Thespesia populnea* = *Cryptomeria japonica* > *Cordia subcordata* > *Calophyllum inophyllum*	Grace et al. (1996)
	Albizia falcataria = *Acacia mangium* = *Pinus sylvestris* = *Pinus caribaea* = *Hevea brasiliensis* = *Araucaria cunninghamii* > *Azadirachta excelsa* = *Tectona grandis* (Malaysia) > *Koompassia malaccensis* = *Casuarina equisetifolia* = *Tectona grandis* (Burma)	Grace et al. (1998)
	Pseudotsuga menziesii > *Intsia palembanica*	Grace and Tome (2005)
	Pseudotsuga menziesii > *Shorea laevis*	Grace and Tome (2005)
	Pseudotsuga menziesii = *Pinus* sp. > *Sequoia sempervirens*	Hapukotuwa and Grace (2011)
	Pseudotsuga menziesii > *Pinus Palustris*	Hapukotuwa and Grace (2010)
	Betula alleghaniensis > *Liquidambar styraciflua* > *Araucaria angustifolia* > *Acer saccharum* > *Carya illinoensis* > *Quercus rubra* = *Liriodendron tulipifera* = *Fraxinus americana* = *Pseudotsuga menziesii* = *Pinus taeda* > *Pinus ponderosa* = *Thuja plicata* > *Taxodium distichum* > *Gleditsia triacanthos* = *Tilia americana* = *Sequoia sempervirens* = *Chamaecyparis nootkatensis* = *Prunus serotina* > *Juniperus virginiana* = *Juglans nigra* = *Sassafras albidum* = *Quercus alba* = *Maclura pomifera* = *Dalbergia latifolia* = *Dalbergia stevensonii* = *Machaerium* sp. = *Cedrela odorata* = *Swietenia macrophylla* = *Ochroma lagopus*	Morales-Ramos and Rojas (2001)

(continued)

Table 8.1 (continued)

Termite species	Order of wood preference (most eaten to less eaten)	Source
	Acer saccharum > *Pinus taeda* > *Pinus elliottii elliottii* > *Larix occidentalis* > *Pseudotsuga menziesii* > *Juglans nigra* > *Sequoia sempervirens* > *Quercus* sp. > *Pinus ponderosa* > *Taxodium distichum* > *Prunus serotine*	Smythe and Carter (1970a)
Coptotermes Gestroi	*Pseudotsuga menziesii* = *Pinus* sp. > *Sequoia sempervirens*	Hapukotuwa and Grace (2011)
	Pinus palustris > *Pseudotsuga menziesii*	Hapukotuwa and Grace (2010)
	Hevea brasiliensis > *Alstonia angustifolia* > *Diallium kunstleri trifoliolatum* > *Dipterocarpus grandiflorus* = *Khaya ivorensis* = *Cinnamomum scortechinii* > *Madhuca utilis* = *Pometia pinnata* = *Shorea curtisii* = *Fagraea fragrans* > *Neobalanocarpus heimii* = *Cotylelobium lanceolatum*	Kadir and Hale (2012)
	Pseudotsuga menziesii = *Pinus ponderosa* = *Picea engelmannii* = *Tsuga heterophylla* > *Thuja plicata* = *Sequoia sempervirens*	Su and Tamashiro (1986)
Coptotermes Heimi	*Populus deltoides* > *Mangifera indica* > *Erythrina suberosa* > *Betula utilis* > *Elaeis guineensis* > *Ficus religiosa* > *Heterophragma adenophyllum* > *Terminalia arjuna* > *Moringa oleifera* > *Putranjiva roxburghii* > *Syzygium cumini* > *Zizyphus jujube* > *Melia azedarach* > *Abies pindrow* > *Acacia arabica* > *Eucalyptus citriodora* > *Azadirachta indica* > *Alstonia scholaris* > *Cordia obliqua* > *Albizia lebbeck* > *Pinus roxburghii* > *Cedrus deodara* > *Pinus wallichiana* > *Dalbergia sissoo*	Manzoor et al. (2015)
Heterotermes Aureus	*Cercidium floridum* > *Opuntia fulgida* > *Prosopis juliflora velutina* > *Acacia greggii*	Haverty and Nutting (1974)
Heterotermes Indicola	*Populus deltoides* > *Mangifera indica* > *Betula utilis* > *Erythrina suberosa* > *Moringa oleifera* > *Eucalyptus citriodora* > *Syzygium cumini* > *Elaeis guineensis* > *Ficus religiosa* > *Zizyphus jujube* > *Abies pindrow* > *Melia azedarach* > *Heterophragma adenophyllum* > *Terminalia arjuna* > *Putranjiva roxburghii* > *Acacia arabica* > *Cordia obliqua* > *Pinus wallichiana* > *Albizia lebbeck* > *Alstonia scholaris* > Cedrus deodara > *Pinus roxburghii* > *Azadirachta indica* > *Dalbergia sissoo*	Manzoor et al. (2015)
Reticulitermes Flavipes	*Ochroma pyramidale* > *Pinus* sp. = *Ceiba pentandra* > *Pseudotsuga menziesii* = *Poulsenia armata* = *Tsuga heterophylla* = *Chamaecyparis nootkatensis* = *Qualea* sp. > *Juniperus* sp. = *Erisma* sp. = *Tabebuia* sp. = *Chamaecyparis thyoides*	Arango et al. (2006)

(continued)

Table 8.1 (continued)

Termite species	Order of wood preference (most eaten to less eaten)	Source
	Pinus elliottii elliottii > *Pinus taeda* > *Prunus sertina* > *Pinus ponderosa* > *Larix occidentalis* > *Acer saccharum* > *Pseudotsuga menziesii* > *Juglans nigra* > *Quercus* sp. > *Taxodium distichum* > *Sequoia sempervirens*	Smythe and Carter (1969)
	Pinus taeda > *Pinus elliottii elliottii* > *Acer saccharum* > *Larix occidentalis* > *Juglans nigra* > *Sequoia sempervirens* > *Quercus* sp. > *Prunus sertina* > *Taxodium distichum* > *Pinus ponderosa* > *Pseudotsuga menziesii*	Smythe and Carter (1970a)
Reticulitermes Virginicus	*Pinus elliottii elliottii* > *Pinus taeda* > *Larix occidentalis* > *Sequoia sempervirens* > *Acer saccharum* > *Juglans nigra* > *Pseudotsuga menziesii* > *Pinus ponderosa* > *Taxodium distichum* > *Quercus* sp. > *Prunus sertina*	Smythe and Carter (1970a)
	Pinus sp. > *Quercus* sp. > *Sequoia* sp. > *Populus* sp.	Lee and Forschler (2016)

Orders are list from highest to lowest preference from termites, according to the authors' results. Tree species separated by ">" indicates the species on the left has a higher level of palatability. Species separated by "=" indicates no difference in palatability

One general trend is that yellow pine (*Pinus*) and Douglas fir (*Pseudotsuga menziesii*) are generally among the more susceptible woods to attacks by most termite species tested. Many of the studies found that teak (*Tectona grandis*) and tropical species in the genus *Shorea* are resistant to attacks by termites of the genus *Coptotermes*. It also appears that exotic and tropical woods seem to resist to attacks by the commonly studied subterranean termites (Table 8.1). Smythe and Carter (1969) and Morales-Ramos and Rojas (2003) noted that there was a correlation between wood preference and survivorship. For this review, a combined analysis of the relationship between level of feeding and survivorship was examined across studies and found that the relationship between wood selection and survivorship seems to exist for many of the studies shown in Table 8.1. For those laboratory studies that reported mass of food consumed and percent mortality or survivorship, the mean weight loss was converted to milligrams of wood consumed per day, and percent mortality was converted to percent survivorship, based on the data provided in the published papers. When the date were combined, there was a significant positive correlation between the amount of wood consumed per day and the percent survivorship (arcsine transformed for the analysis) (regression $F = 48.8$, $p < 0.001$, Fig. 8.2). Thus, the general pattern is that termites are avoiding wood that reduces survivorship.

It should be noted that despite the general trends, it is also evident that different termite species have different preferences (Wood 1978; Ngee et al. 2004; Kadir and Hale 2012; Li et al. 2015; Manzoor et al. 2015) and that intraspecific variation also occurs (Ngee et al. 2004). Field studies on naturally occurring wood species also showed that different species of termites in the same habitat have different wood preferences (Haverty and Nutting 1975; Ravan et al. 2015).

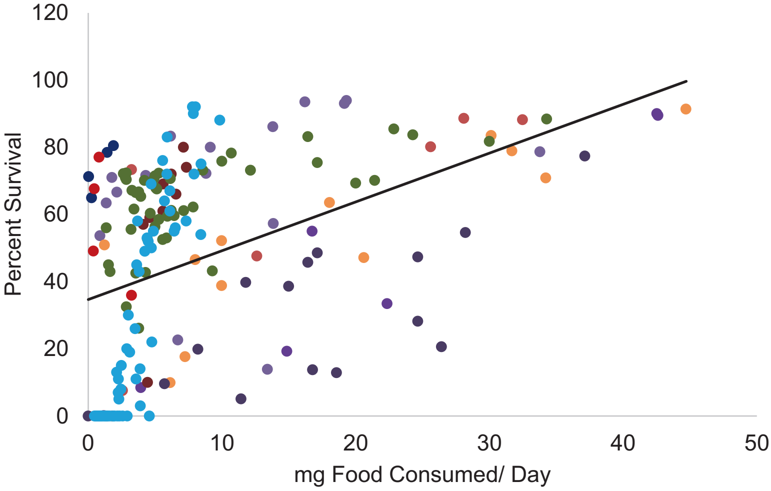

Fig. 8.2 Mean percent survival of termites vs. mean food consumed per day from laboratory studies which tested wood preference using wood blocks from several different tree species. Combined data show a significant positive correlation between the amount of food consumed and the percent survivorship in the colony (F = 46.5, $p < 0.001$). Different colored dots indicate data from different studies: orange (Cornelius and Osbrink 2015), yellow (Grace et al. 1996), dark blue (Grace and Tome 2005), green (Grace et al. 1998), purple (Grace and Yamamoto 1994), brown (Smythe and Carter 1969), light blue (Smythe and Carter 1970a), red (Hapukotuwa and Grace 2010), gray (Manzoor et al. 2015), red (Arango et al. 2006)

8.3.2 Properties of Wood Affecting Preference

There are a number of factors that could explain the differences in wood selectivity, including (1) secondary metabolites, (2) hardness (or density), (3) composition, and (4) nutritional value (Fig. 8.3). These properties are not mutually exclusive (Bultman and Southwell 1976; Shanbhag and Sundararaj 2013). Wood can change its properties depending on the soil it grows in (Buchanan 1963). For example, Grace et al. (1998) noted that teak (*Tectona grandis*) from Burma was more resistant to termite attack than the same species from Malaysia (Table 8.1).

8.3.2.1 Secondary Metabolites

One obvious difference between wood species is the secondary metabolites that are present. Several lines of evidence suggest that these are important factors. Earlier studies have shown that extracts taken from sawdust of wood that are not favored by termites will repel them as well and lower their survival in a laboratory setting (Smythe and Carter 1970b; Carter and Smythe 1974; Carter and de Camargo 1983; Grace et al. 1989; Sattar et al. 2015). If secondary metabolites are extracted from wood, it can become more palatable to termites (Kirker et al. 2013). Adding extracts

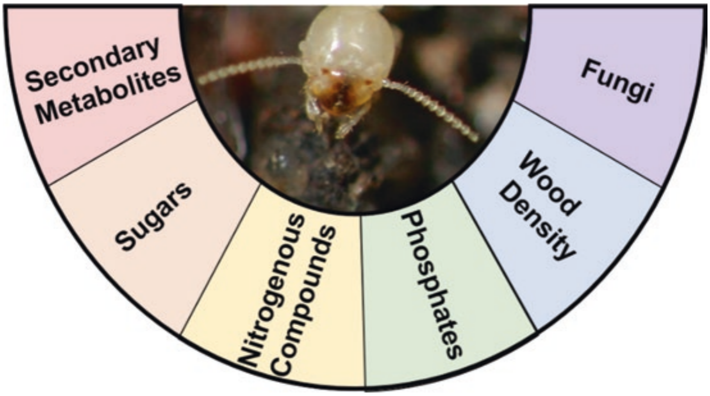

Fig. 8.3 Properties and components of wood that termites use to assess food quality

to normally favored food can also reduce palatability (Carter and de Camargo 1983; McDaniel 1992). In addition to other components mentioned above, Shanbhag and Sundararaj (2013) also found, in field studies, that wood with higher levels of phenols had lower levels of termite attacks. Thus, secondary metabolites effectively play an important role in termite food selection and survival.

8.3.2.2 Hardness or Density of Wood

A number of studies have examined the influence of density or hardness of wood on termite preference. Laboratory (Behr et al. 1972; Arango et al. 2006) and field studies (Bultman and Southwell 1976; Wood 1978; Souza et al. 2009; Owoyemi and Olaniran 2014) have found that harder wood is generally more resistant to termite attack than softer wood. However, this is not always the case (Mustafa 2011). Waller et al. (1990) compared the feeding levels of *Coptotermes formosanus* when given pine (*Pinus* sp.) or mahogany (*Swietenia macrophylla*) that were compressed or uncompressed. They found that the termites ate more of the uncompressed wood vs. the compressed one, for the same species. However, when the amount of biomass removed from each block was calculated, the biomass consumed from a compressed or uncompressed block of wood from the same species did not differ. Thus, in studies that use percent mass consumed as an indicator of preference, it may be considered that the same amount of biomass is consumed if one wood species is denser than another.

One aspect that relates to density is the concentration of cellulose and lignin in wood. *Reticulitermes flavipes* prefers artificial food sources that have higher concentrations of cellulose (Judd and Corbin 2009). Higher ratios of cellulose to lignin are also preferred. This preference has also been confirmed in the field. Shanbhag and Sundararaj (2013) found that wood preferred by subterranean termites had higher levels of cellulose and lower levels of lignin than non-preferred wood. One interesting question is how termites assess the amount of cellulose. One possible mechanism is that termites break down the cellulose into its components, then tasting the sugars. Subterranean termites have cellulase in their saliva (Inoue et al. 1997), thus higher concentrations of cellulose would produce higher concentrations of sugar in the mouth. Cypret and Judd (2015) tested this concept using starch and glucose. When *R. flavipes* was presented with a choice between food enriched with equal levels of glucose and starch, they found that there was no preference. When the same experiment was run with an amylase inhibitor in each food source, the termites preferred the food enriched with glucose. When given a choice between food enriched with xylose and xylan, *R. flavipes* preferred food with xylose. *Reticulitermes flavipes* lacks xylanase in its saliva (Inoue et al. 1997). Thus, termites are only capable of detecting polysaccharides when there is an enzyme in their saliva to break these molecules down.

8.3.2.3 Simple Sugars

A number of studies have examined the effect of sugars on the feeding preferences of termites. Glucose, xylose, sucrose, and fructose were the most common sugars examined across all studies. Results for trials testing the preference of food enriched with one of these four sugars, compared to an unenriched control, are summarized in Table 8.2. The results for each of these sugars were not consistent across termite species. The genera *Heterotermes* and *Coptotermes* seemed to have a low response to the four sugars compared. Castillo et al. (2013) found that *Coptotermes curvignathus* responded positively to disks soaked in 3% glucose, while *C. gestroi* only responded to xylose. However, Haifig et al. (2010) found that *C. gestroi* did not respond significantly more to food enriched with xylose than to unenriched food. Similarly, responses to different sugars were not consistent in the genus *Reticulitermes*. The two species found in the eastern United States, *R. flavipes* and *R. virginicus* [Swoboda et al. (2004) collected their termites in the Eastern United States], seemed to prefer food enriched with 1–3% glucose (0.1 M is about 1.8%) and 1–3% sucrose. *Reticulitermes hesperus* showed a positive response to 2% xylose and 2% fructose (Saran and Rust 2005). Wallace and Judd (2010) noted these discrepancies and proposed that there may be seasonal and population differences. They tested the sugar preferences of *R. flavipes* collected from four populations in the spring, summer, and fall and found that populations differed in their response to food enriched with glucose, xylose, and sucrose. There were also seasonal shifts in preferences for food enriched with xylose and sucrose within populations.

Other sugars were tested in some of the aforementioned studies as well, and they showed mixed results between species as well. Saran and Rust (2005) found that *R. hesperus* preferentially fed on filter paper enriched with 2% maltose or 2% arabinose. Arabinose is found in some hemicellulases in wood (Buchanan 1963). They also found that *R. hesperus* fed on filter paper enriched with 5%, but not 2%, ribose. Interestingly, *C. curvignathus* did not prefer food enriched with ribose at levels

Table 8.2 Summary of experiments that tested the potential preference between sugar-enriched substrate and a control substrate in single-choice tests

Species	Media	Glucose (%/ Y/N)	Xylose (%/ Y/N)	Sucrose (%/ Y/N)	Fructose (%/ Y/N)	Source
Coptotermes curvignathus	Filter paper	3%/Y	3%/N			Castillo et al. (2013)
	Filter paper	6,9,12,15%/N	6,9,12,15%/N			Castillo et al. (2013)
Coptotermes Gestroi	Filter paper	3%/N	3%/Y			Castillo et al. (2013)
	Filter paper	6,9,12,15%/N	6,9,12,15%/N			Castillo et al. (2013)
	Filter paper	3, 5%/N	3, 5%/N	3%/N	5%/ml/N	Haifig et al. (2010)
Heterotermes Tenuis	Filter paper	3, 5%/N	3, 5%/N	3%/N	5%/ml/N	Haifig et al. (2008)
Microtermes traegardhi	Millet stem disks	20%/Y		20%/Y	20%/Y	Abushama and Kamal (1977)
Microtermes obesi	Filter paper	0.1,1,2,3,4,5,6,7%/Y				Sattar et al. (2015)
Reticulitermes sp.	Brown paper towel	0.1 M/Y	0.1 M/N	0.1 M/Y	0.1 M/N	Swoboda et al. (2004)
	Brown paper towel	0.01 M/N	0.01 M/N	0.01 M/N	0.01 M/Y	Swoboda et al. (2004)
	Brown paper towel	0.001 M/N	0.001 M/N	0.001 M/N	0.001 M/N	Swoboda et al. (2004)
Reticulitermes flavipes and *R. virginicus*	Filter paper	1%/Y	1%/N	1%/Y		Waller and Curtis (2003)
	Filter paper	3%/Y	3%/Y	3%/Y		Waller and Curtis (2003)
Reticulitermes Flavipes	Cellulose agar	3.5%/Y^{P}	3.5%/Y^{P,S}	3.5%/Y^{P,S}		Wallace and Judd (2010)
Reticulitermes Hesperus	Paper disks	2%/N	3%/Y	2%/N	2%/Y	Saran and Rust (2005)

Only the results for glucose, xylose, sucrose, and fructose are shown. For each sugar "Y" indicates a significant preference for the enriched food, "N" indicates no significant preference as reported by the authors of the paper.^{P} indicates only certain populations showed a preference,^{S} indicates the preference varied between seasons equal or higher than 5%, when tested (Castillo et al. 2013). Galactose-enriched food was preferred over controls by *Reticulitermes* sp. (Swoboda et al. 2004), but this was not the case for *C. gestroi* (Haifig et al. 2010) or *Heterotermes tenuis* (Haifig et al. 2008). A similar result was found with raffinose at very low levels (Swoboda et al. 2004; Haifig et al. 2008, 2010). However, food enriched with trehalose was preferred by all of the termites tested (Swoboda et al. 2004; Haifig et al. 2008, 2010). The overall conclusion that can be drawn is that not all species respond to sugars in the same way, and population and seasonal differences should also be taken into account when performing these studies.

8.3.2.4 Nitrogenous Compounds

Due to the fact that the nitrogen content in wood is low, nitrogenous compounds seem like potential phagostimulants for termites. Unlike sugars, there has been less overlap among the nitrogenous compounds examined in different studies, but some comparisons can be made. Like sugars, studies using amino acids have also produced mixed results. Mauldin and Rich (1975) found that casein and egg albumin are toxic to *Reticulitermes flavipes* and *Coptotermes formosanus* at concentrations greater than 0.5%. In a choice test, Castillo et al. (2013) found that *C. curvignathus* and *C. gestroi* preferred filter disks soaked in 3% casein solution, compared to a control. Higher concentrations (6%, 9%, 12%, 15%) were not preferred. Survival was not affected by concentrations as high as 9% for *C. curvignathus* or 12% for *C. gestroi*. A few studies have tested the effect of food preference by individual amino acids. *Coptotermes formosanus* preferred filter paper enriched with either D-aspartic acid or L-glutamic acid, over controls (Chen and Henderson 1996). L-proline, L-lysine, and L-isoleucine increased feeding rates in no-choice tests (Henderson et al. 1994; Chen and Henderson 1996). Swoboda et al. (2004) tested the effectiveness of eight amino acids (L-arginine, L-aspartic acid, L-cysteine, L-isoleucine, L-lysine, L-methionine, L-phenylalanine, and L-proline) on influencing the feeding preference and feeding rates of *Reticulitermes* sp. None of the amino acids tested showed any positive effects, and several (L-arginine, L-aspartic acid, L-isoleucine, L-phenylalanine, and L-proline) actually reduced the feeding rates. L-alanine showed similar effects on the feeding behavior of *C. curvignathus* and *C. gestroi* (Castillo et al. 2013). The results from amino acids differed from species to species and in some cases caused a negative feeding response. Consistent patterns of selectivity, at the genus level, do not even seem to be present.

The effects of urea and uric acid on termite feeding behavior have also been tested. Urea was found to increase feeding rates in *C. formosanus* (Henderson et al. 1994), *Microtermes obesi* (Sattar et al. 2015), and *Heterotermes tenuis* (Haifig et al. 2008), but it did not appear to act as phagostimulant for *C. gestroi* (Haifig et al. 2010). Uric acid was only found to be attractive to *Reticulitermes* sp. at very low concentrations, while higher concentrations had no effect (Swoboda et al. 2004).

Coptotermes formosanus did not respond to uric acid differently than controls (Morales-Ramos et al. 2009). Morales-Ramos et al. (2009) also tested the effect of glucosamine and salicylic acid on termite feeding at concentrations of 50, 225, 450, and 675 ppm. They found that food enriched with 450 ppm of glucosamine and that food enriched with 50 ppm of salicylic acid were preferred over their controls. Other concentrations showed no effect.

One possible reason for the variation in response to nitrogenous compounds by termites is the changes in the need for nitrogen during the year. There is evidence that the need for dietary nitrogen fluctuates during the year. Curtis and Waller (1998) found that levels of nitrogen fixation fluctuated during the year in *R. flavipes* and *R. virginicus*, with rates that were not the same for all castes. Thus, the need for dietary nitrogen may also vary during the year and may affect the influence of nitrogenous compounds on feeding rates. This is a research area yet to be fully explored.

8.3.2.5 Phosphates

Phosphates represent another limiting nutrient in wood. Phosphates are important for the production of ATP and mRNA. Limitations in phosphates can reduce the production of protein even if nitrogen is readily available (Elser et al. 2000). Botch et al. (2010) examined the role of phosphates in food preference of *R. flavipes* and found that food enriched with phosphates was preferred over controls during the fall but not in the spring and summer.

8.4 Fungi and Other Decomposers

Termites have had a long association with fungi, and it is becoming increasingly clear that fungi can influence the foraging and food selection of subterranean termites. A number of species of fungi have been found to attract termites (Esenther et al. 1961) or make the wood more palatable (Waller et al. 1987; Getty and Haverty 1998; Little et al. 2012a, b; Cornelius et al. 2014). There are a number of reasons for these associations. Fungi offer a potential source of nitrogen and other nutrients if consumed (Sands 1969). Both *Reticulitermes flavipes* and *Coptotermes formosanus* will consume the fruiting bodies of white-rot fungi (Waller et al. 1987). As mentioned earlier, fungi can begin the decomposition process on wood and release some of the cues the termites need to locate a food source (Cornelius et al. 2002). Also, in the process fungi can potentially break down some of the secondary metabolites that might repel or harm termites (Waller et al. 1987). Thus, fungi may increase the palatability of the wood as they degrade it or act as phagostimulants themselves (Fig. 8.3).

8.5 Conclusion

The foraging process of subterranean termites is a three-step process. During the searching phase, the termites produce tunnel patterns that minimize overlap and energetic costs. Subterranean termites are expecting local cues that originate from the surface. Thermal shadows and chemical gradients of small particles such as CO_2, ions, and urea allow termites to locate a food source that is in the correct stage of decay. Finally, a number of cues will help determine palatability of wood including density, cellulose concentration, sugars, nitrogenous compounds, phosphates, secondary metabolites, and the presence of some fungi. There is a level of redundancy in the termite foraging system which is important, due to the energetic cost of burrowing and the fact that some types of wood can increase mortality.

One conclusion that can be reached by comparing multiple studies is that there is interspecific and even intraspecific variation on the types of cues used to determine palatability. There are a number of factors that could cause this variation, in addition to differences among species. The composition of wood from a tree species is not constant and can be influenced by soil, moisture levels, and other environmental factors (Buchanan 1963). In addition, feeding preferences change during the year, as the termite colony composition is not static. Colonies reproduce (produce winged alates) annually or biannually (Higa and Tamashiro 1983; Scheffrahn et al. 1988; Lax and Wiltz 2010; Mullins et al. 2015), and thus, they will show variations in their nutritional needs. In addition, termites in temperate climates or high altitudes may experience periods of time where foraging is not possible due to low temperatures. Termites in these climates need to prepare for winter. Seasonal changes in foraging activity have been observed in subterranean termites (Haverty et al. 1974; Cornelius and Osbrink 2011a), and studies have found seasonal effects in food preference (Botch et al. 2010; Wallace and Judd 2010) and nitrogen fixation (Curtis and Waller 1998). Understanding the nutritional changes in a termite colony throughout the season may help understand what might increase palatability of food sources.

Finally, termite food preference is affected by previous feeding experience (McMahan 1966). This was mentioned in a review by Waller and La Fage (1987) as an understudied topic and appears to remain so even today. Understanding the foraging behavior and food selectivity of a population of subterranean termites might require an understanding of the influence of soil on the wood, of the foraging cues used by that population, and of the seasonal patterns of termite nutritional needs.

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