Chapter 7
Trail Pheromones in Termites

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Contents

Abstract Termites use a range of semiochemicals to maintain the organization and integrity in their colonies. Among these semiochemicals, the trail pheromone is responsible for the orientation and recruitment of nestmates from the nest to the food sources. Trail pheromones in termites are secreted by a unique exocrine gland source, the sternal gland present in the abdominal sternites of all termite castes. In the majority of termite species, trail pheromone comprises a single compound. However, in the most advanced species, trail pheromone comprises two or, in one exception case, a blend of three compounds. In general, there is a clear difference between composition of trail pheromone in termite species from basal families and from those of more advanced families. Distinct responses of workers and soldiers to trail pheromone are observed as well as the response to trail pheromone from neighbouring colonies. The present chapter outlines the current states of knowledge of trail pheromones in termites.

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7.1 Introduction

Insect societies (termites, ants, some bees and wasps) have been calling attention over years due to their ecological role, social evolution, collective behaviour and the efficient and spectacular ways of communication. Most of the activities in social insects are chemically mediated, which allow to maintain the organization and integrity in their colonies. Chemical communication is even more evident in termite species since they are blind, and semiochemicals are involved in almost all activities of their life. Among these activities, it is the exploration of environment in search of food resources (e.g. foraging process). Such collective behaviour is coordinated by trail pheromones, and in some termite species, for example, *Constrictotermes cyphergaster* (Termitidae: Nasutitermitinae), it is responsible for the establishment of impressive columns with thousand individuals (Fig. 7.1). The ecology and behavioural aspects of foraging in termites have been reviewed by Traniello and Robson (1995) and Traniello and Leuthold (2000). Recently, Almeida et al. (2016) have showed a new behavioural repertoire of foraging in termites.

Trail pheromone is secreted by sternal glands and is deposited when a termite presses its abdomen against the substrate (Fig. 7.2). Such pheromone stimulates foragers to leave the nest and orient them to the food source (Stuart 1961, 1981). Foraging seems to begin with an explanatory phase of searching for food, proceed-

Fig. 7.1 Foraging in the open-air termite *Constrictotermes cyphergaster* (Termitidae, Nasutitermitinae). Sergipe, Brazil

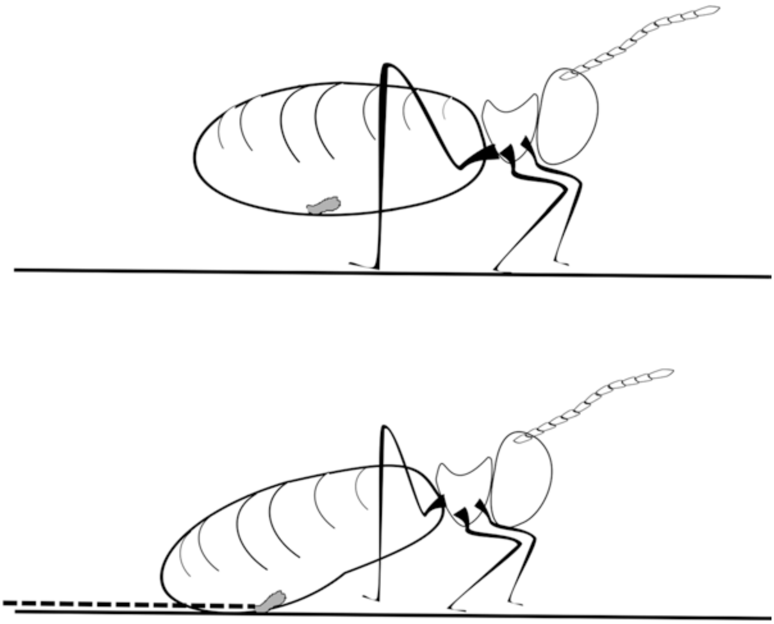


Fig. 7.2 A schematic drawing of termite worker depositing trail pheromone in the substrate

ing by the recruitment of the nestmate to the food source. In the explanatory phase, trail pheromone deposited appears less attractive than that deposited in the recruitment and foraging trails (Reinhard and Kaib 2001). Trail pheromone is responsible to trail-following behaviour. It is a decisive communication channel to those termite species that acquire their food resource outside of their nests (“separate” life type; Hodotermitidae, some Rhinotermitidae and almost all Termitidae) and also for species that consume a resource in which they nest or also those that move from one nesting site to another (“intermediate” life type; e.g. Mastotermitidae, Rhinotermitidae and some Termitidae). However, in “one-piece” termite species (e.g. Termopsidae and Kalotermitidae), trail pheromone is used to locate areas of disturbance and to colonize new food sources (Traniello and Leuthold 2000), because such species does not need orientation mechanisms to foraging.

According to Sillam-Dusses (2010), trail pheromone in “one-piece” termite species may be involved in the alarm communication, in which a trail laid by an alarmed termite from the point of disturbance leads the nestmates to defend and repair the disturbance point. Recently, Cristaldo et al. (2014) suggested that the obligatory inquiline *Inquilinitermes microcerus* (Termitidae, Termitinae) should use trail pheromone in similar way that in “one-piece” termite species, because such species seems not to forage outside from their host nest (Florencio et al. 2013; Barbosa-Silva et al. 2016). In this species, trail pheromone must be used to avoid contact with host colonies, inside the shared nest (Cristaldo et al. 2014).

In the last decades, numerous studies have shown the chemical nature of trail pheromones in different termites (see Costa-Leonardo et al. 2009; Sillam-Dusses 2010; Bordereau and Pasteels 2011). This chapter outlines the current status of knowledge of termite trail pheromones.

7.2 The Glandular Source of Trail Pheromone: The Sternal Gland

The sternal gland located in the abdominal sternites is the sole glandular source of trail pheromone in termites (Noirot 1969) (Fig. 7.2). The sternal gland has been observed in all castes and secretes not only the trail pheromone but also the sex pheromone (Noirot 1969; Bordereau and Pasteels 2011).

The number and position of sternal glands are variables across termite families (see Noirot 1995; Quennedey et al. 2008). In Mastotermitidae (*Mastotermes darwiniensis*), the most basal termite family, three separate sternal glands are present in the middle of the 3rd, 4th and 5th abdominal sternites. Although *M. darwiniensis* have three active sternal glands, their efficiency varies considerably. According to Sillam-Dusses et al. (2007), the trail pheromone secreted by the sternal gland present in the 4th abdominal sternites induces a higher activity, compared to that of the sternal gland present in the 3rd abdominal sternites. However, the trail pheromone produced by sternal glands from 5th abdominal sternites was almost inactive.

In other termite families, a single sternal gland is observed. In Termopsidae and Hodotermitidae species, the sternal gland is found in the margin of the 4th abdominal sternites. In Kalotermitidae, Rhinotermitidae, Serritermitidae and Termitidae, a single sternal gland is observed in the margin of the 5th abdominal sternite (Noirot 1995; Quennedey et al. 2008).

A decrease in the size of sternal glands is also observed among termite families, varying from the large one found in Mastotermitidae (200/300 μm × 450/800 μm × 15/25 μm) (length × width × height) to the very small sternal gland of Nasutitermitinae species (100 μm × 195 μm × 25 μm) (Quennedey et al. 2008).

Another interesting point is the presence of different cell classes in the sternal glands across termite families: class 1 and 2 cells are found in all termite species, while class 3 cells are found only in Termopsidae, Serritermitidae and Rhinotermitidae species (see details in Quennedey et al. 2008). The presence of different class cells can be related with semiochemicals secreted in the sternal glands that can have another role than the trail-following behaviour. In the dampwood termite *Zootermopsis angusticollis* (Archotermopsidae), for example, sternal gland secretions have been reported to have fungistatic properties (Rosengaus et al. 2004).

7.3 Chemistry of Trail Pheromones in Termites

7.3.1 *Composition*

The trail pheromones have been identified in 66 species across 7 termite families (Table 7.1). Their chemical diversity is very low, with only nine compounds identified (Fig. 7.3; Table 7.1), belonging to four chemical classes (alcohols, aldehydes,

Table 7.1 Chemical compounds acting as trail pheromones across termite families

Family/Subfamily	Genus	Trail pheromone	References
Mastotermitidae	*Mastotermes*	(*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol	Sillam-Dussès et al. (2007)
Archotermopsidae	*Hodotermopsis*	*syn* 4,6-dimethyldodecanal + traces of 4,6-dimethylundecan-1-ol	Lacey et al. (2011)
	Zootermopsis	*syn* 4,6-dimethyldodecanal	Bordereau et al. (2010)
Stolotermitidae	*Porotermes*	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol	Sillam-Dussès et al. (2007)
	Stolotermes	(E)-2,6,10-trimethyl-5,9-undecadien-1-ol	Sillam-Dussès et al. (2007)
Kalotermitidae	*Cryptotermes*	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Incisitermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Kalotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Neotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Postelectrotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
	Procryptotermes	(Z)-dodec-3-en-1-ol	Sillam-Dussès et al. (2009b)
Rhinotermitidae	*Coptotermes*	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Tokoro et al. (1989) and Sillam-Dussès et al. (2006)
	Heterotermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Reticulitermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Matsumura et al. (1968), Tai et al. (1969), Tokoro et al. (1991), Laduguie et al. (1994) and Wobst et al. (1999)

(continued)

Table 7.1 (continued)

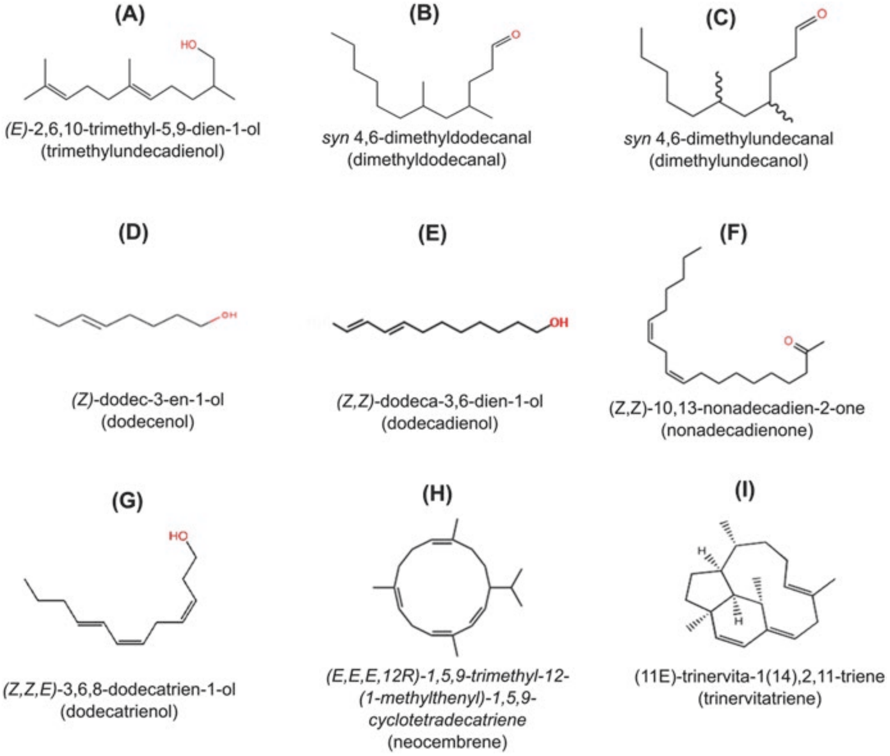
Family/Subfamily	Genus	Trail pheromone	References
	Prorhinotermes	Neocembrene	Sillam-Dussès et al. (2005)
		Neocembrene + dodecatrienol	Sillam-Dussès et al. (2009a)
	Rhinotermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Schedorhinotermes	(3*Z*,6*Z*,8*E*)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
Serritermitidae			
	Glossotermes	(10Z,13Z)-nonadeca-10,13-dien-2-one	Hanus et al. (2012)
Termitidae			
Macrotermitinae	*Ancistrotermes*	(Z,Z)-dodeca-3,6-dien-1-ol	Robert et al. (2004)
	Macrotermes	(Z)-dodec-3-en-1-ol	Peppuy et al. (2001a)
	Odontotermes	(Z)-dodec-3-en-1-ol	Peppuy et al. (2001b)
		(Z,Z)-dodeca-3,6-dien-1-ol	Deng et al. (2002)
		(3Z)-dodec-3-en-1-ol + (3Z,6Z)-dodeca-3,6-dien-1-ol	Wen et al. (2014)
	Psammotermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2011)
	Pseudacanthotermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Bordereau et al. (1993)
Termitinae	*Amitermes*	Dodecatrienol + neocembrene	Kotoklo et al. (2010)
	Cubitermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Drepanotermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Inquilinitermes	Dodecatrienol +neocembrene*	Cristaldo et al. (2014)
	Termes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
Syntermitinae	*Silvestritermes*	Dodecatrienol + neocembrene	Bordereau and Pasteels (2011)
	Cornitermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)
	Embiratermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Bordereau and Pasteels (2011)
	Syntermes	(3Z, 6Z, 8E)-dodeca-3,6,8-trien-1-ol	Sillam-Dussès et al. (2006)

(continued)

Table 7.1 (continued)

Family/Subfamily	Genus	Trail pheromone	References
Nasutitermitinae	*Constrictotermes*	Dodecatrienol +neocembrene	Sillam-Dussès et al. (2010) and Cristaldo et al. (2014)
	Nasutitermes	Neocembrene	Moore (1966) and Birch et al. (1972)
		Neocembrene + dodecatrienol	Sillam-Dussès et al. (2010)
	Nasutitermes	Dodecatrienol +neocembrene + trinervitatriene	Sillam-Dussès et al. (2010)
	Trinervitermes	Neocembrene	McDowell and Oloo (1984)
		Neocembrene + dodecatrienol	Sillam-Dussès et al. (2010)

*Trail pheromone identity was inferred by results obtained by behavioural bioassays; no compounds were found in the sternal glands of workers (see more details in Cristaldo et al. 2014)



(A) *(E)*-2,6,10-trimethyl-5,9-dien-1-ol (trimethylundecadienol)

(B) *syn* 4,6-dimethyldodecanal (dimethyldodecanal)

(C) *syn* 4,6-dimethylundecanal (dimethylundecanol)

(D) *(Z)*-dodec-3-en-1-ol (dodecenol)

(E) *(Z,Z)*-dodeca-3,6-dien-1-ol (dodecadienol)

(F) (Z,Z)-10,13-nonadecadien-2-one (nonadecadienone)

(G) *(Z,Z,E)*-3,6,8-dodecatrien-1-ol (dodecatrienol)

(H) *(E,E,E,12R)-1,5,9-trimethyl-12-(1-methylthenyl)-1,5,9-cyclotetradecatriene* (neocembrene)

(I) (11E)-trinervita-1(14),2,11-triene (trinervitatriene)

Fig. 7.3 Compounds identified as trail pheromone in termite species hydrocarbons and ketones). In most of the termite species, the trail pheromone is made of a single compound while in others, particularly in Nasutitermitinae species, it is made of two compounds. The presence of three compounds acting as trail pheromone was described only in *Nasutitermes corniger* (see Sillam-Dusses et al. 2010).

The trail pheromone seems to be very conserved across termite families. The (*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol (trimethylundecadienol; Fig. 7.3a) is the compound acting as trail pheromone in *Mastotermes darwiniensis* (Mastotermitidae) and also in two species of Termopsidae, *Porotermes adamsoni* (Porotermitinae) and *Stolotermes victoriensis* (Stolotermitinae) (Sillam-Dusses et al. 2007). In the family Archotermopsidae, *syn* 4,6-dimethyldodecanal (dimethyldodecanal; Fig. 7.3b) is the trail pheromone in *Zootermopsis angusticollis* and *Z. nevadensis* (Bordereau et al. 2010). However, in *Hodotermopsis sjoestedti*, the trail pheromone is composed of *syn* 4,6-dimethylundecan-1-ol (dimethylundecanol; Fig. 7.3c) and traces of dimethyldodecanal (Lacey et al. 2011). In Kalotermitidae, all species studied so far have (Z)-dodec-3-en-1-ol (dodecenol; Fig. 7.3d) as trail pheromone (Sillam-Dusses et al. 2009b). The (3*Z,6Z,8E*)-dodeca-3,6,8-trien-1-ol (dodecatrienol; Fig. 7.3g) is the trail pheromone in almost all species from Rhinotermitidae family (see Table 7.1 for references). The exception is the *Prorhinotermes* sp. that has (1E,5E,9E,12R)-1,5,9-trimethyl-12-(1-methylethenyl)-1,5,9-cyclotetradecatriene (neocembrene; Fig. 7.3h) or the mixture of neocembrene and dodecatrienol as trail pheromone (Sillam-Dusses et al. 2005, 2009a). In Serritermitidae family, it has been identified the (10Z,13Z)-nonadeca-10,13-dien-2-one (nonadecadienone; Fig. 7.3f) as trail pheromone of *Glossotermes oculatus* (Hanus et al. 2012).

In the advanced termite species (Termitidae), trail pheromone differs among subfamilies. Dodecenol (Fig. 7.3d) was identified in Macrotermitinae as trail pheromone of *Macrotermes* sp., *Odontotermes hainanensis* and *O. maesodensis* (Peppuy et al. 2001a), while dodecadienol (Fig. 7.3e) was identified as trail pheromone of *Ancistrotermes pakistanicus* (Robert et al. 2004) and *O. formosanus* (Deng et al. 2002). Dodecatrienol was identified as trail pheromone for *Pseudacanthotermes militaris* and *P. spiniger* (Bordereau et al. 1993).

Among Termitinae sp., dodecatrienol was identified as trail pheromone in *Cubitermes* sp., *Drepanotermes perniger* and *Termes hispaniolae* (Sillam-Dusses et al. 2006). The mixture of dodecatrienol and neocembrene was identified as trail pheromone in *Amitermes evuncifer* (Kotoklo et al. 2010) and *Inquilinitermes microcerus* (Cristaldo et al. 2014). Dodecatrienol is the trail pheromone in almost all species of Syntermitinae studied so far (Sillam-Dusses et al. 2006; Bordereau and Pasteels 2011). However, the mixture of dodecatrienol and neocembrene was identified as trail pheromone in *Silvestritermes euamignatus* (Bordereau and Pasteels 2011). In Nasutitermitinae species, the mixture of dodecatrienol and neocembrene was identified as trail pheromone in *Constrictotermes cyphergaster* (Sillam-Dusses et al. 2010; Cristaldo et al. 2014), some species of *Nasutitermes* genus and also in *Trinervitermes geminatus* and *T. trinervoides* (Sillam-Dusses et al. 2010). In *N. corniger*, the compound trinervitatriene (Fig. 7.3i) was also identified as trail pheromone, additionally to the mixture of dodecatrienol and neocembrene (Sillam-Dusses et al. 2010). Neocembrene was reported as single component of trail pheromones in

N. exitiosus, *N. graveolus*, *N. walker* (Moore 1966; Birch et al. 1972) and in *T. bettonianus* (McDowell and Oloo 1984). The trail pheromone of termites from Apicotermitonae subfamily remains unidentified.

In general, there is a clear difference between trail pheromone from species of basal termites (from Mastotermitidae to Stolotermitidae) and those from more advanced families (from Kalotermitidae to Termitidae): basal termite species have trail pheromone made of C14 alcohol or a C14 or C18 aldehyde, while advanced termite species have trail pheromones made of C12 alcohols or C20 diterpenes. Such distinction seems to be related to their ecology and life style (Sillam-Dusses 2010).

7.3.2 *Activity Threshold of Trail Pheromones*

The trail pheromone activity threshold varies from 1 ng/cm in the most basal termite *M. darwiniensis* (Sillam-Dusses et al. 2007) to 10^{-8} ng/cm in *Reticulitermes hesperus* (Saran et al. 2007). Optimal activity threshold ranges, in most species, between 10^{-2} and 1 ng of pheromone per cm of trail (Bordereau and Pasteels 2011). Above 1 ng of trail pheromone, trail-following behaviour is generally reduced once chemoreceptors are saturated and termite is unable to follow the trails.

7.4 Responses of Workers and Soldiers to Trail Pheromone Signals

Different responses of termite castes (workers and soldiers) to the trail pheromone have been reported in the literature. In almost all termite species studied, the trail pheromone seems to be deposited only by workers during the recruitment phase (Costa-Leonardo et al. 2009). However, soldiers have been shown to be responsible for the initial exploration of foraging area, proceeded by the recruitment of workers in some Rhinotermitidae (*R. santonensis* (Reinhard and Kaib 2001), *Heterotermes tenuis* (Casarin et al. 2008) and *Coptotermes intermedius* (Olugbemi 2011)) and also in Nasutitermitinae species (*N. corniger* (Traniello 1981; Traniello and Busher 1985), *Longipeditermes longipes* (Miura and Matsumoto 1998), *Constrictotermes cyphergaster* (Moura et al. 2006) and *N.* aff. *coxipoensis* (Almeida et al. 2016)). In *Coptotermes gestroi*, workers initiate the foraging, but soldiers are recruited after discovery of the food source (Arab et al. 2012). Workers and soldiers have been reported to initiate the exploration of new areas in *Velocitermes heteropterus* (Haifig et al. 2015). According to Almeida et al. (2016), the participation of soldiers in the initial exploration of areas, with continued participation in trail construction and escorting services during tunnel construction, must be common among the Nasutitermitinae species.

The precise role of emission of trail pheromone and responses to these signals by the termite soldiers are still poorly explored. However, in *Nasutitermes* species, soldiers have been shown to deposit trails more attractive than those deposited by workers (see Arab et al. 2006; Almeida et al. 2016). In *N. corniger*, trails laid by soldiers were observed to recruit only soldiers, but those laid by workers recruited both workers and soldiers (Traniello 1981). These observed differences in the responses of castes to trail pheromone must be related to qualitative or quantitative differences between workers and soldiers, as already hypothesized by Arab et al. (2006) and Almeida et al. (2016).

Different responses to pheromone trails was also observed among small workers in *M. bellicosus*, preferentially following trails established by small workers than those established by large ones (Gessner and Leuthold 2001).

7.5 Detection of Trail Pheromones by Neighbouring Colonies

Although the ecological success of any organism depends on the specificity of its communication channels, perception of heterospecific signals by other individuals is widely observed in nature (Danchin et al. 2004; Valone 2007; Evans et al. 2009; Cristaldo et al. 2016b). The ability to perceive and respond to trail pheromones from neighbouring colonies can benefit the exploiter about food source location.

In termites, perception and response to trail pheromone from neighbouring colonies have been observed among neighbouring colonies of the same as well as of different species. Oloo (1981) observed that workers of *Trinervitermes bettonianus* do not show a significant preference to trails from their own colony compared with those from neighbouring colonies of the same species. However, *T. bettonianus* as well as the sympatric species *M. michaelseni* and *Odontotermes* sp. was not able to follow trail from neighbouring colonies of sympatric species. In another study, allopatric populations of *T. bettonianus* were able to follow alien as well as their own trails (Oloo and McDowell 1982). Similar results were also reported for *R. grassei* and *R. santonensis* (Wobst et al. 1999) and in *P. spiniger* and *P. militaris* (Bordereau and Pasteels 2011). According to Peppuy et al. (2001b), specific signals of trail pheromone must be more marked among species from different genera than among species from the same ones.

Recently, Cristaldo et al. (2016a) have shown that resource availability can modulate the perception and response of neighbouring colonies in *Nasutitermes* aff. *coxipoensis*. Workers from colonies reared under low and intermediate resource availability followed the same distance on trails with extracts from their own colonies, compared to extracts from neighbouring colonies. However, workers from colonies reared with high resource availability avoided the following chemical cues from neighbouring colonies. Such results indicate that chemical cues from neighbouring colonies can be detected by termites and may influence colony foraging choice.

The perception and response of chemical cues from neighbouring colonies should have a strong impact on termite community structure, including the spatial distribution of foraging areas, species co-occurrence and species coexistence in a single nest (termite inquilinism) (see details in Cristaldo et al. 2016a; Araújo et al. 2017). In fact, the perception and avoidance of trail cues from host nest by inquilines seem to ease the cohabitation among different termite species, in a single nest (see Cristaldo et al. 2014).

7.6 Conclusion

The study of trail pheromone in termites has been increased in the last decades; however, its composition in species of Apicotermitinae subfamily has not been studied yet. In general, the termite trail pheromone seems to be very conserved among families, with only nine compounds identified as trail pheromone. There is a clear difference between trail pheromone from basal termite species and that from more advanced families. Such distinction seems to be related with their ecological life style. In Nasutitermitinae species, trail pheromone deposited by soldiers plays a key role in the recruitment of workers, from the nest to the food source. Although few studies have reported the ability of termites to follow chemical cues from neighbouring colonies, such behaviour possibly has a strong impact on termite community structure.

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