

Chemical Communicators in Nematodes

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Abstract: Chemical signals released by one organism and perceived by another organism are classified as semiochemicals. Semiochemicals are divided into pheromones, which elicit intraspecific responses, and allelochemicals, which elicit interspecific responses. Nematodes utilize and (or) recognize signals from both categories of semiochemicals. The existence of pheromones, specifically sex and aggregation pheromones, has been demonstrated in numerous plant and animal parasitic and free-living nematodes. Sex pheromones have been isolated and purified from *Nippostrongylus brasiliensis* and *Heterodera glycines*, and epidietic pheromones have been shown to be responsible for initiation of dauer juvenile formation in *Caenorhabditis elegans*. Allelochemicals cause interspecific responses in insects and other invertebrates but are only postulated to occur in nematodes. Food-finding behavior of nematodes is almost certainly caused by host-released allelochemical messengers. Understanding of the behavioral responses and the chemical messengers that affect bioregulation of various processes in nematodes will influence future management strategies.

Key words: allelochemicals, allomones, behavior, nematodes, pheromones, semiochemicals, synomones.

Recognition by one member of a species of another member of the same species, of a specific host, or of a deterrent factor in the environment is often due to chemical cues. The response of organisms to various chemical stimuli have been well documented in the literature (13,43).

Random finding of a mate or a food source would often be detrimental to an organism's ability to survive because of unnecessary energy expenditures. This effect on survival is especially important in organisms like nematodes with low vagility (mean distance between the point where an individual is born and where it dies) (53). Chemical cues and behavioral responses to these cues, therefore, probably play a major role in all aspects of nematode survival.

Perception of the environment by nematodes is generally thought to be due to chemosensory interactions. Chemotaxis has long been recognized as a major factor in response of nematodes to stimuli (54); however, other factors, such as an internal passive response, might also result in a specific behavior. For example, *Nippostrongylus brasiliensis* juveniles emerge from pulmonary capillaries as a result of an internal gustatory stimulus from feeding; this is de-

scribed as a "non-oriented phenomenon" of behavior (11,12). Even though such passive responses must occur in certain circumstances, this review will deal mainly with stimuli externally perceived by nematodes.

Recognition of chemotaxis of plant parasitic nematodes to their hosts began to receive attention in nematode research as early as 1925 (55). The occurrence of sex attractants in nematodes was discovered in the late 1960s (19). To date, however, no specific compounds that are the actual stimuli for either sex-oriented or feeding-oriented behavior have been chemically identified.

Removal from use of the most economical and effective soil fumigants for control of plant parasitic nematodes and the potential banning of other nematicides by regulatory agencies have made the search for naturally occurring behavior modifying bioregulators of great importance. The potential use of naturally occurring or modified bioregulators in plant parasitic nematodes to disrupt mating, host-finding, or development is perhaps the future direction of plant parasitic nematode management.

Understanding and manipulating bioregulators of insects has introduced new pest management strategies into entomology. Even though the use of synthesized sex pheromones has not eliminated certain pests, these compounds have altered pesticide application (1) and introduced monitoring techniques that have allowed for a reduction in the amount of insecticides ap-

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TABLE 1. Definitions of semiochemicals* that cause interactions to occur between organisms.

Terms	Definitions	Subcategories of chemical cues
Pheromone	A chemical that causes a physiological or behavioral response between members of the same species (intraspecific)	<ul style="list-style-type: none"> a. <i>Sex</i>—(attractive and aggregation) cause a behavior response between or within sexes b. <i>Epidietic</i>—produced by members of a species to regulate population densities c. <i>Alarm</i>—warning or protective responses produced by members of a species
Allelochemic	A chemical that causes a physiological or behavioral response between members of different species (interspecific)	<ul style="list-style-type: none"> a. <i>Allomone</i>—evolves a negative response to the receiver b. <i>Kairomone</i>—evolves a favorable response to the receiver c. <i>Synomone</i>—evolves a favorable response to both the emitter and receiver d. <i>Apneumone</i>—a response emitted by a nonliving material

* See Norlund et al. (30) for a review of all terminology.

plied in certain management programs (32,40). In order to begin to utilize such approaches in nematology, interdisciplinary cooperation is essential. Techniques for gas chromatography (GC), high performance liquid chromatography (HPLC), mass spectrometry (MS), and nuclear magnetic resonance spectroscopy (NMR) have been successfully utilized for the identification of insect pheromones, neurotransmitters, hormones, and steroids and can be applied to nematology.

For nematology to benefit from chemical ecology, it is important to employ the concepts and terms currently used in other behavioral disciplines to define and describe the various chemotaxes (30). Law and Regnier proposed a classification system describing known groups of chemical-releasing stimuli (28). They used the term "semiochemicals" for the group of chemicals that mediate interactions between organisms. This term is derived from the greek word "semeon" which means signal or mark. Semiochemicals are further divided into two major groups: pheromones and allelochemicals (Table 1).

The term "pheromone" was coined by Karlson and Butenandt (26) and Karlson and Luscher (27) from the greek "phereum," to carry, and "hormon," to excite or stimulate. Pheromones generally are considered intraspecific, affecting members of the species. They are further subdivided into sex pheromones, alarm pheromones, and epidietic pheromones.

The second major class of semiochemicals is called "allelochemic," a term introduced by Whittaker (54) to describe chemicals involved in interspecific interactions. Allelochemicals are further defined as chemical cues that are interspecific and involved with the host recognition response. Allelochemicals are divided into four subgroups: allomones, kairomones, synomones, and apneumones. All of these terms except alarm pheromones and apneumones, which have not yet been demonstrated in nematodes, are discussed as they relate to current studies in nematology.

PHEROMONES

Sex pheromones: Of the three groups of pheromones, sex pheromones have received the most attention (3,19). Sex pheromones, which are intraspecific, are divided into attractive pheromones which occur between sexes and aggregating pheromones which occur within the same sex or in juveniles (4,41). These types of pheromones have the greatest potential for altering bioregulation through disruption of mating.

Greet (21) in 1964 observed the first sex attractants in the free-living nematode, *Pangrolaimus rigidus*. Two years later Green (18) reported a sex attractant in *Globodera rostochiensis* and *Heterodera schachtii*. In the same year Roche (39) reported a sex attractant from parasitic nematode, *Ancylostoma caninum*. Since then more than 30 species of free-living and plant and animal

parasitic nematodes have been studied for sexual behavior influenced by pheromones. The most extensive studies have been on the cyst nematodes (Heteroderinae) and the animal parasite, *N. brasiliensis*. Aggregating pheromones have been described for *N. brasiliensis*, and the active fraction has been isolated and partially identified (4-8). When all possible combinations of sexes were observed in bioassay (23), no aggregating pheromones were detected in *Radopholus* spp.

Bioassay is the basic tool for the initial detection and quantification of biological activity. Most behavioral bioassays developed for sex pheromones have used dose-responses of males to determine the optimum number of females necessary to establish an attractive pheromone gradient (8,20,23,33), but establishment of threshold levels for male response is necessary to ensure that complete behavioral activity is measured. Bioassays have demonstrated that oversaturation of the males by pheromone lowers or eliminates their response, and using too few females fails to establish a gradient that males can follow (8,24,34).

Many types of bioassays have been developed for rapid pheromonal screening. Huettel and Rebois (24) compared different types of bioassays (i.e., sand slide and agar plate) and found that all previously developed methods required at least 36 hours of exposure for maximum attraction. At least 2 hours are required for *N. brasiliensis* females (8) and 12-24 hours for cyst nematodes to establish an attraction gradient (20,24,34). The most rapid bioassay is based solely on copulatory behavior patterns. These behavior patterns have been described for *Heterodera glycines* based on in vitro observation in root explant culture and on isolated crude pheromone (24,25). Behavioral observations have been used also to distinguish closely related species of *Radopholus* spp. (23). Most bioassays used only observations of male movement in response to a pheromone source either established from entire females or from agar discs that have absorbed the attractant from females.

Robert and Thorson (37) were the first to isolate pheromonally active lipid fractions by thin layer chromatography (TLC) from nematode homogenates of female *N.*

brasiliensis. Recently, it was determined, based on TLC, HPLC, and gel filtration, that pheromone from female *N. brasiliensis* contains two components, one water soluble and the other organic soluble (3). Huettel et al. (25) isolated a water soluble pheromone from whole female *H. glycines*, and this close range pheromone has been purified by HPLC, but the exact structure has not yet been determined.

Epidietic pheromones: Epidietic pheromones are defined as chemical cues produced by members of a species that regulate of their population density. These compounds are released by stimuli such as overcrowding or a reduction in the food supply (10,31). These pheromones generally promote insect dispersal when population densities are high or feeding sites are occupied by other members of the same species (34). Epidietic pheromones are also associated with reduction in fecundity (35). In the flour moth, *Ephestia kuekniella*, pupation is retarded by a secretion from the mandibular glands of the last instar larva when overcrowding occurs (10). Similar chemical population regulation has been reported in *Caenorhabditis elegans* (14).

Golden and Riddle (14) isolated and tentatively identified a hydroxylated short chain fatty acid-like substance that is responsible for dauer juvenile formation in *C. elegans*. This pheromone is produced by juveniles in response to depletion in the food supply. The pheromone can be extracted from spent liquid culture medium containing starved *C. elegans*. A bioassay based on dose-response to the isolated pheromone was developed, and it was shown that the pheromone can cause dauer formation in *C. elegans* after only 4 hours incubation. An antagonistic food signal, however, can reverse the dauer stage and allow development to continue (15,16). These two environmental cues, the pheromone and the food signal, in response to a third cue, temperature, appear responsible for optimum survival of this nematode.

Population changes in response to food stimuli, especially in sexual differentiation in *Meloidogyne* sp., have been reported to occur (47,48). Unfavorable conditions, such as overcrowding, cause high proportions of males to develop in these parthenoge-

netic populations (2,46). It has been proposed that developing females, which have two gonads, change sex and become males with two testes rather than normal males with a single testis. This sex reversal is thought to occur as a survival mechanism since males do not feed; only nematodes that continue developing as females use the available food source (22). No studies have attempted to isolate compounds that may be responsible for this sex shift; however, if epidietic pheromones were implicated, they could be valuable in management programs by altering the sex ratio of the nematode population and thus relieving the feeding pressure on the host crop.

ALLELOCHEMICS

Allomones: Some organisms can either produce or acquire substances that can result in a behavioral or physiological response detrimental to an invader (9,29). The role of allomones has been well characterized in plant defense mechanisms against herbivores (36). Allomones are not only involved in defense mechanisms but can be important cues in complex host interactions.

The nature of plant response to nematodes has received considerable attention (17). Nematicidal compounds produced by many different species of plants have been investigated since resistance to root-knot nematodes in marigolds, *Tagetes* sp., was first reported in 1938 (49). Extensive studies of *Tagetes* spp. have been conducted subsequently and the naturally occurring nematicide, α -terthienyl, isolated and identified (50), but unfortunately α -terthienyl and synthesized analogues have been inactive in soil. *Asparagus officinalis* also reduces population densities in certain nematodes in the soil (42). The natural nematicide, asparagusic acid, was identified by Takagusi et al. (44). Other plants have been shown to contain alkaloids, diterpenes, and phenolics that protect them from nematode attacks (17).

Synomones: Nordlund and Lewis (29) proposed the term "synomone" for chemicals that mediate mutualistic interactions. These chemicals are further defined as cues that benefit both the receiver and the emitter, with the behavioral or physiological response being adaptively favorable. Symbiotic relationships are probably often me-

diated by cues that promote synchronized behavior. An interesting relationship in nematodes has been demonstrated in the animal parasite *Dictyocaulus viviparus* and the fungus *Pilobolus kleinii*. Nematode eggs are passed in the feces where they hatch. First-stage and second-stage juveniles feed on bacteria in the feces. Third-stage infective juveniles (J3) become inactive. To complete its life cycle, the nematode must be ingested by cattle; however, cattle avoid grass immediately adjacent to dung piles. Interestingly, the *Pilobolus* fungus which begins its life cycle in dung also requires digestion by an herbivore for spore germination. As the fungus produces sporangiophores, the nematode J3 becomes active and migrates up the sporangiophores to the sporangium. When the sporangium explodes, both spores and J3 nematodes are shot 3–4 meters out from the dung pile. A chemical cue from the sporangium appears necessary to activate the nematodes and direct them to migrate to sporangium for dispersal to grass that will be grazed on by cattle (38).

Kairomones: Kairomones are chemical cues (e.g., hormones, pheromones, or even allomones) that induce a favorable behavioral and physiological response in the receiver (9). In nematodes, these might be in the form of host-parasite recognition mediated by lectin-carbohydrate interactions (55). Kairomones are very common in bio-control relationships where a parasitoid must recognize its parasite host. For instance, an insect predator on bark beetles, *Thanasimus dubius*, uses the beetles' sex pheromone to locate the beetle (51).

Free-living plant and animal parasitic nematodes all use kairomones in some form. Juveniles of the hookworm, *Ancylostoma caninum*, are attracted to a low molecular weight component in dog serum. Recognition of the serum component, and attraction to it, is thought to play a role in the well-defined migration exhibited by juveniles after entering the host, which allows them to immediately find a vein and enter the bloodstream (52).

Recent studies have been conducted on the attraction of *Bursaphelenchus xylophilus* to oleyl compounds (55). Of this group, the terpene β -myrcene was found to be highly attractive to this nematode (45). This compound, as well as other oleyl group ter-

penes, is highly attractive to some insects as well. For instance, ipsenol, which is structurally related to β -myrcene, is the aggregation pheromone of the bark beetle, *Ips proconfusus*. It is possible that some entomophilic nematodes use the pheromones of their insect hosts to find the galleries in the trees where the insects are feeding.

CONCLUSION

The terminology introduced in this review to describe semiochemicals is not generally used in nematology; however, it is both appropriate and descriptive of chemically mediated responses occurring within and between nematodes and their hosts. The use of these concepts and terms will enable nematologists to better relate to other behavioral disciplines.

As more chemical cues are described and the chemicals subsequently isolated and identified, new approaches to nematode management through bioregulation can be investigated. Natural bioregulators may be useful tools for determining population dynamics of parasites and for predicting population cycles of nematodes. Innovative approaches to the use of more target specific environmentally safe nematicides are necessary in all aspects of parasitic nematode control.

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