

Ecology and Evolution of Soil Nematode Chemotaxis

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Abstract Plants influence the behavior of and modify community composition of soil-dwelling organisms through the exudation of organic molecules. Given the chemical complexity of the soil matrix, soil-dwelling organisms have evolved the ability to detect and respond to these cues for successful foraging. A key question is how specific these responses are and how they may evolve. Here, we review and discuss the ecology and evolution of chemotaxis of soil nematodes. Soil nematodes are a group of diverse functional and taxonomic types, which may reveal a variety of responses. We predicted that nematodes of different feeding guilds use host-specific cues for chemotaxis. However, the examination of a comprehensive nematode phylogeny revealed that distantly related nematodes, and nematodes from different feeding guilds, can exploit the same signals for positive orientation. Carbon dioxide (CO₂), which is

ubiquitous in soil and indicates biological activity, is widely used as such a cue. The use of the same signals by a variety of species and species groups suggests that parts of the chemo-sensory machinery have remained highly conserved during the radiation of nematodes. However, besides CO₂, many other chemical compounds, belonging to different chemical classes, have been shown to induce chemotaxis in nematodes. Plants surrounded by a complex nematode community, including beneficial entomopathogenic nematodes, plant-parasitic nematodes, as well as microbial feeders, are thus under diffuse selection for producing specific molecules in the rhizosphere that maximize their fitness. However, it is largely unknown how selection may operate and how belowground signaling may evolve. Given the paucity of data for certain groups of nematodes, future work is needed to better understand the evolutionary mechanisms of communication between plant roots and soil biota.

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Introduction

All animals depend on green plants, either directly or indirectly, as their primary source of energy. Primary consumers need plants for nourishment, whereas secondary consumers, such as predators or parasites may use plant cues to locate their herbivore hosts. Several decades of work have shown that animals use plant-derived physical (visual, tactile), and/or chemical (olfactory, gustatory) cues to locate and accept their food source (Schoonhoven et al., 2005). Most of these multitrophic interactions studies have been done using

aboveground communities (Price et al., 1980; Vet and Dicke, 1992; Tschamtkke and Hawkins, 2002). However, the last decade has shown a marked increase in exploring interactions between plants and soil animals (e.g., Strong et al., 1999; Gange and Brown, 2002; De Deyn et al., 2003; Van der Putten, 2003; de la Peña et al., 2006; Rasmann and Agrawal, 2008; Bonkowski et al., 2009), and how plants mediate interactions between aboveground and belowground communities (Van der Putten et al., 2001; Wardle, 2002; Bezemer and van Dam, 2005; Erb et al., 2008; Kaplan et al., 2008; van Dam, 2009). Indeed, roots often are the storage site for nutrients and metabolites, are a place where energy from photosynthesis can be stored, and can act as a shelter for soil-dwelling organisms (Hunter, 2001). Therefore, roots are a hub for ecological interactions that ultimately influence almost all groups of soil inhabitants (Coleman, 1976; Fogel, 1985; Walker et al., 2003; Whittaker, 2003).

General patterns and theories for chemically-mediated interactions that structure aboveground communities (Price et al., 1980; Vet and Dicke, 1992; Karban and Baldwin, 1997) also can be applied belowground (Strong et al., 1999; van Tol et al., 2001; van der Putten et al., 2009; Rasmann et al., 2011a). In fact, as aboveground, plants can influence the behavior, abundance, and composition of soil animal communities (e.g., Yeates, 1999; Buyer et al., 2002; Vikeftoft et al., 2009), and can mediate indirect interactions between organisms of different trophic levels (Coleman, 1976; Strong et al., 1999). However, striking differences exist between above- and belowground subsystems (see also Erb et al., 2012, this issue).

The soil matrix is composed of all three phases (gas, liquid, and solid), which can impact mobility, behavior, signaling, and interaction between organisms in a different manner than when living aboveground. This will influence the mobility of organisms belowground, often not surpassing more than 1 m² in their lifetime, whereas aboveground, vertebrates can explore more than 1 ha per day (Hedlund et al., 2004). Moreover, the physico-chemical legacy of the soil, shaped by high metabolic retention capacity, slow turnover of chemical metabolites, slower diffusion, and higher heterogeneity suggests a slower rate for ecological interactions to occur (Coleman et al., 2004). Roots themselves also have a very different physiology, which may lead to distinct patterns of interactions belowground compared to aboveground (see Erb et al., 2012, this issue). All this together should impose selection for particular stimuli to be perceived by soil organisms. For example, soil inhabitants are strongly limited in their use of visual information, but rather use chemical and tactile cues to communicate and behave (Jones, 2002). Roots can produce and exude into the rhizosphere a great variety of compounds ranging from amino acids, complex polysaccharides, and proteins, to smaller, more volatile lipophilic molecules, all of which also

have been shown to directly or indirectly influence the soil community of organisms (Bais et al., 2006). The aim of our review is to list and discuss published information on how plant chemical exudates can influence the ecology and evolution of host-searching and foraging strategies of soil-borne nematodes (but see also Johnson and Nielsen (2012), this issue for discussion on belowground herbivorous insects).

We particularly focus on soil nematodes because they are among the most diverse groups of soil organisms. Each square meter of soil may contain millions of individual nematodes belonging to over 400 species (Gaugler and Bilgrami, 2004). There are at least seven functional types, including: plant feeding nematodes (e.g., the genera *Pratylenchus*, *Heterodera*, *Meloidogyne*, *Helicotylenchus*, *Aphelenchoides*), plant-associated nematodes (e.g., the genera *Tylenchus*, *Dorylaimellus*), fungal hyphae-feeding nematodes (e.g., the genera *Aphelenchus*, *Aphelenchoides*, *Leptonchus*, *Diphtherophora*), bacterial feeding nematodes (e.g., the genera *Rhabditis*, *Plectus*, *Cephalobus*, *Caenorhabditis*), nematodes that feed on unicellular eukaryotes, animal-parasitic nematodes (e.g., the genera *Heterorhabditis*, *Steinernema*), and omnivorous nematodes (e.g., the order *Dorylaimida*) (Yeates, 1999). These functional types are taxonomically heterogeneous, and most likely the result of convergent evolution (e.g., Blaxter et al., 1998; Holterman et al., 2006). Additionally, it is worth noting that more than one feeding habit can occur within a genus (e.g., the genus *Aphelenchoides* harbors fungivorous and plant-parasitic species), or even within a single individual (Yeates, 1999).

Because of their abundance, systematic and functional diversity, and their representation in multiple trophic levels in the soil food web, nematodes have strong influences on ecosystem dynamics and functioning (Yeates et al., 2009). They have been shown to influence soil nutrient cycling, growth rate, health, and yield of plants as well as populations of other soil inhabitants. For example, herbivores influence plant yield (Chitwood, 2002), plant community composition (De Deyn et al., 2004), and successional dynamics (Mortimer et al., 1999; De Deyn et al., 2003). Microbial feeders can stimulate nutrient cycling and plant yield (Ingham et al., 1985; Fu et al., 2005). Detritivorous nematodes can contribute up to 40 % of total organic matter mineralization (De Ruiter et al., 1993), and predators and parasites can reduce arthropod populations (e.g., Kaya and Gaugler, 1993), which in turn can have cascading effects on plant performance (Strong et al., 1999; Rasmann et al., 2011b).

Below, we review literature of nematode sensory machinery and chemically-mediated orientation toward organic molecules. Little is known of how chemotaxis has evolved during the radiation of nematodes. Chemotaxis is the directed orientation of the nematode toward or away from the source of stimulation (in our case the plants). Using a

comprehensive phylogeny of nematodes, we map chemical compounds that have been proven to produce taxis. This will lead to preliminary conclusions on how chemotaxis can evolve in soil nematodes. Finally, we discuss how plants can structure communities of nematodes through root exudation and how this may operate to their own benefit.

The Sensory Apparatus of Soil Nematodes

As in all animals, nematode behavior is the coordinate integration of several external stimuli leading to responses (e.g., locomotion, movement, feeding, mating, penetration) (Gaugler and Bilgrami, 2004). Nematodes' sensory apparatus allows them to use chemical, electrical, light, mechanical, and temperature stimuli (Jones, 2002) to orientate, move, and locate a sexual partner, as well as energy sources (food) in the soil (Lee, 2002).

Nematode sense organs basically can be subdivided into cuticular and internal sense organs. Cuticular sense organs generally are composed of a sheath cell, a socket cell, and a variable number of dendritic processes, and are responsible for detecting chemical, mechanical and temperature related stimuli. Internal sense organs are more diverse, mainly responsible for detecting mechanical stimuli as well as light stimuli (Jones, 2002). Invariably, the largest and most complex of the nematode sense organs are the amphids, which are exposed to the external environment by a pore in the cuticle, primarily functioning as chemoreceptors. In *Caenorhabditis elegans*, the tail bilateral sensory organs called phasmids also are shown to function as chemoreceptors and help the nematode orientate towards or away from the chemical stimuli (Hilliard et al., 2002). Numerous nematode taxa do not have phasmids (e.g., members of Clade 1–6 according to Holterman et al. (2006)). Because of the complexity and abundance of soil chemicals compared to other physical stimuli, chemoreception is undoubtedly the most important source of stimulus to nematodes (Jones, 2002).

Responses by nematodes to chemical stimuli have been extensively studied in the bacteriophagous nematode *C. elegans*, some plant-parasitic (e.g., *Meloidogyne* and *Globodera* spp.), and in an increasing number of animal-parasitic nematodes (e.g., *Heterorhabditis* and *Steinernema* spp.). Among the genera mentioned above, *C. elegans* has an uncommon ecology: it is present only in nutritionally very rich habitats (e.g., mature compost heaps), and is seldom found in 'normal' soils. Hence, some restraint in the extrapolation of *C. elegans* data to other genera would be justified.

Chemotaxis in Nematodes

In sections below and in Table 1, we summarize major chemo-attractants for soil nematodes. The high occurrences

of a wide variety of compounds known to mediate changes in nematode behavior for particular species (e.g., *C. elegans*) are likely due to research bias towards model species. For example, because of the ability to map gene-level responses with behavior, studies of attraction/repulsion to/from allelochemicals in *C. elegans* comprise most of the work done on all nematodes (Bargmann and Mori, 1997). Although some compounds have been identified as potent nematode repellents, such as, D-tryptophan, α -terthienyl, high levels of CO₂, copper and zinc ions, and inositol (Balanova and Balan, 1991; Ward, 1978), we focused on plant produced kairomones, which stimulate positive orientation, and also because most studies assess positive orientation in nematode bioassays. This will set the stage for discussing evolutionary ecology of plant-nematode interactions.

Chemotaxis of Plant-Parasitic Nematodes Plant-parasitic nematodes can be divided into broad groups based on the plant parts they infest. Foliar nematodes (*Aphelenchoides* sp.) move into shoots and invade leaf buds causing necrosis and deformation of plant leaves. The stem nematodes (*Ditylenchus dipsaci*) cause malformations, decline in growth, and dry rot in above- and belowground parts of stems. Other nematodes infect roots and cause growth reduction in whole plants and malformations in underground plant parts (*Meloidogyne* spp., *Rotylenchus uniformis*), root necrosis, and growth reduction (*Pratylenchus penetrans*, *Tylenchulus semipenetrans*), or growth reduction without any obvious or typical symptoms (*Globodera rostochiensis*, *G. pallida*, and *Tylenchorhynchus dubius*). Here, we limit our analysis of allelochemicals that affect soil-dwelling plant-parasitic nematodes, which mainly exploit plant roots as their only source of nutrients. Species of plant-parasitic nematodes may spend their whole life cycle outside the plant, feeding from the surface or deeper tissues, while others have the capacity to invade the root and feed from cortical cells. In many cases, feeding cells are transformed into highly specialized feeding structures to support nematode development and reproduction such as for cyst (e.g., *Heterodera* and *Globodera* spp.) and root-knot nematodes (*Meloidogyne* spp.) (Wyss, 2002). Both these so-called sedentary endoparasites are economically important because of their ability to cause damage to major crop species.

Different control mechanisms underlie the hatching of cyst and root knot nematodes. Root knot nematodes in general have a far broader host range than cyst nematodes. Because of their specificity, it is essential for cyst nematodes to hatch in the direct vicinity of a suitable host plant, instead of near any plant species. Cyst nematode hatching is triggered by a complex mixture of components released by the roots of host plants in a species-dependent manner (Prot, 1980). There is a variable degree of dependence of cyst

Table 1 Attractive chemical compounds for different trophic guilds of soil nematodes. Shown are nematodes species grouped in three different guilds (bacteriophagous, entomopathogenic, and plant-parasitic) and their corresponding chemical attractant. Choice of the references is based on whether the study correlated actual nematode behavior with individual chemical compounds present. We excluded all compounds

that stimulated repulsion, but we acknowledge that different concentrations of the same compounds can be either attractive or repulsive (see text). Note that entomopathogenic nematodes are functionally bacteriophagous, but cannot grow and reproduce outside the arthropod protective shell, making them unique in regard of their guild

Feeding guilds and nematode species	Attractive compounds	Compounds' type	References	
Bacterivorous				
<i>Caenorhabditis elegans</i>	2,3 butanedione	ketone	(Hallem et al., 2011)	
	2-butanone		(Hallem et al., 2011)	
	2-pentanone		(Hallem et al., 2011)	
	3-carene	terpenes	(Hallem et al., 2011)	
	4,5 dimethylthiazole	thiazoles	(Hallem et al., 2011)	
	α -humulene	terpenes	(Hallem et al., 2011)	
	α -pinene		(Hallem et al., 2011)	
	benzothiazole	thiazoles	(Hallem et al., 2011)	
	cAMP	cAMP	(Bird, 1960)	
	carbon dioxide	atmospheric gaz	(Bird, 1960)	
	ethylacetate	acids	(Hallem et al., 2011)	
	ions	ions	(Ward, 1978)	
	linalool	terpenes	(Hallem et al., 2011)	
	methyl acetate	acids	(Hallem et al., 2011)	
	octadecanoid acid		(Hallem et al., 2011)	
	propanol	alchools	(Hallem et al., 2011)	
	trimethylamine	amines	(Hallem et al., 2011)	
Entomopathogen				
<i>Heterorhabditis bacteriophora</i>	(<i>E</i>)- β -caryophyllene	terpenes	(Rasmann et al., 2005)	
	1-heptanol	alcohols	(O'Halloran and Burnell, 2003)	
	1-hexanol		(O'Halloran and Burnell, 2003)	
	1-nonanol		(O'Halloran and Burnell, 2003)	
	1-octanol		(O'Halloran and Burnell, 2003)	
	1-pentanol		(O'Halloran and Burnell, 2003)	
	2-acetylthiazole	thiazoles	(O'Halloran and Burnell, 2003)	
	2-heptanol	alcohols	(O'Halloran and Burnell, 2003)	
	2-isobutylthiazole	thiazoles	(O'Halloran and Burnell, 2003)	
	2-methylpyrazine	pyrazines	(O'Halloran and Burnell, 2003)	
	2-nonanol	alcohols	(O'Halloran and Burnell, 2003)	
	2-octanol		(O'Halloran and Burnell, 2003)	
	3-nonanol		(O'Halloran and Burnell, 2003)	
	4,5 dimethylthiazole	thiazoles	(Hallem et al., 2011)	
	4,5-dimethylthiazole	thiazoles	(O'Halloran and Burnell, 2003)	
	benzothiazole	thiazoles	(O'Halloran and Burnell, 2003)	
	caproic acid	acids	(O'Halloran and Burnell, 2003)	
	caprylic acid		(O'Halloran and Burnell, 2003)	
	carbon dioxide	atmospheric gaz	(O'Halloran and Burnell, 2003)	
	methyl salicilate	aromatic compound	(Hallem et al., 2011)	
	methylvaleric acid	acids	(O'Halloran and Burnell, 2003)	
	p-cymene	terpenes	(Hallem et al., 2011)	
	propanol	alcohols	(Hallem et al., 2011)	
	undecyl acetate	acids	(Hallem et al., 2011)	
	<i>H. indica</i>	geijerene	terpenes	(Ali et al., 2011)
		pregeijerene		(Ali et al., 2011)

Table 1 (continued)

Feeding guilds and nematode species	Attractive compounds	Compounds' type	References
<i>H. megidis</i>	(<i>E</i>)- β -farnesene		(Kollner et al., 2008)
	(<i>E</i>)-nerolidol		(Kollner et al., 2008)
<i>Steinernema carpocapsae</i>	2-nonanone	ketone	(Hallem et al., 2011)
	4,5 dimethylthiazole	thiazoles	(Hallem et al., 2011)
	carbon dioxide	gaz	Gaugler et al. 1980
	heptanol	alcohol	(Hallem et al., 2011)
	hexanol		(Hallem et al., 2011)
	nonanol		(Hallem et al., 2011)
	octanol		(Hallem et al., 2011)
	octyl acetate	acids	(Hallem et al., 2011)
	pentanol	alcohols	(Hallem et al., 2011)
<i>S. diaprepsi</i>	α -santalene	terpenes	(Ali et al., 2011)
<i>S. feltiae</i>	α -santalene		(Ali et al., 2011)
<i>S. glaseri</i>	carbon dioxide	gaz	(Robinson, 1995)
<i>S. riobrave</i>	α -santalene	terpenes	(Ali et al., 2011)
Plant-parasite			
<i>Aphelenchoides fragariae</i>	carbon dioxide	gaz	(Bird, 1960)
<i>A. ritzemabosi</i>	carbon dioxide		(Klinger, 1970)
<i>Ditylenchus dipsaci</i>	carbon dioxide		(Pline and Dusenbery, 1987)
<i>Globodera pallida</i>	g-aminobutyric acid	acids	(Riga, 2004)
	L-glutamic acid		(Riga, 2004)
<i>G. rostochiensis</i>	a-aminobutiric acid		(Riga, 2004)
	L-glutamic acid		(Riga, 2004)
<i>Heterodera schachtii</i>	carbon dioxide	gaz	(Bird, 1960)
<i>Meloidogyne incognita</i>	carbon dioxide		(McCallum and Dusenbery, 1992)
<i>M. javanica</i>	carbon dioxide		(Pline and Dusenbery, 1987)
<i>Panagrellus silusiae</i>	carbon dioxide		(Viglierchio, 1990)
<i>Rotylenchus reniformis</i>	cAMP	cAMP	(Riddle and Bird, 1985)
	ions	ions	(Riddle and Bird, 1985)
<i>Tylenchulus semipenetrans</i>	geijerene	terpenes	(Ali et al., 2011)
	ions	ions	(Abou-Setta and Duncan, 1998)
	limonene	terpenes	(Ali et al., 2011)
	pregeijerene		(Ali et al., 2011)

nematodes on these plant cues: whereas exposure to root diffusates is almost a prerequisite for the hatching of potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*), the hatching of soybean and beet cyst nematodes (*Heterodera glycines* and *H. schachtii*) is merely stimulated by such compounds. In contrast, the hatching of root knot nematodes is mainly temperature driven (Perry and Wesemael, 2008).

One of the remarkable characteristics of root diffusate-based hatching of cyst nematodes is the high activity of host plant-derived hatching stimuli (“eclepins”). The water-soluble glycinoclepins A, B, and C (pentanor- (A) or nortriterpenes (B and C)) isolated from the roots of kidney bean are active at concentrations as low as 10^{-11} – 10^{-12} g per ml (Masamune et al., 1982). The tetranortriterpene solanoclepin A released by

the roots of potato are active in the same concentration range (Schenk et al., 1999). Interestingly, glycinoclepins and solanoclepins are chemically closely related triterpenes.

Diffusion in the liquid phase is the main mechanism responsible for spreading eclepins in soil, and eclepin-dependent cyst nematode species will hatch only in the close vicinity of a host root (cm range). It is conceivable that the freshly hatched pre-parasitic juveniles can follow relatively unspecific cues, such as CO₂ to reach the root of a host plant. Such a general signaling compound would not work for root knot nematodes, as their hatching is mainly triggered by a very general signal (*viz.* soil temperature). However, root knot nematodes are highly polyphagous. This applies especially to the most abundant species in

agro-ecosystems, such as *M. incognita*, *M. javanica*, and *M. arenaria*. For these nematodes, following a steep (plant-derived) CO₂ gradient would imply a reasonable chance to reach a suitable plant root. The attraction of *M. incognita* by CO₂ has been shown in several studies (Dusenbery, 1987; Pline and Dusenbery, 1987). A related, alternative mechanism for host finding by root knot nematodes was proposed by Wang et al. (2009). Juveniles of *Meloidogyne hapla* had a strong preference for pH between 4.5 and 5.4, and the authors proposed root knot nematodes to be attracted by dissolved CO₂, resulting in local acidification, rather than by CO₂ itself.

For plant-parasitic nematodes other than cyst or polyphagous root knot nematodes, it is critical to exploit chemical gradients in soil that relate to the presence of a suitable host plant. For these nematodes, olfactory and other sensory organs of the nematode are essential (Huang et al., 2003). It has been acknowledged for long that plant-parasitic nematodes can locate roots of host plants in the soil (Prot, 1980) by using allelochemicals produced by the plants, as well as other soil-borne chemical compounds (Perry and Aumann, 1998). However, besides the general signal furnished by carbon dioxide (CO₂) emissions, the factors that trigger plant-parasitic nematode attraction and direction are still largely unexplored (Table 1). Carbon dioxide was shown to attract *Ditylenchus dipsaci* (Klinger, 1963; Dusenbery, 1980). Increased CO₂ levels in *Fusarium oxysporum* infested lucerne (*Medicago sativa*) roots, attracted *P. penetrans* to infected roots (Edmunds and Mai, 1967). Other, non-identified diffusates from the roots of potato increased the activity and also attracted the infective second stage juveniles of the potato cyst nematode (*G. rostochiensis*) to the roots (Perry, 1997; Devine and Jones, 2003). Similarly, *M. javanica* and *G. rostochiensis* juveniles may respond to tomato (Prot, 1980) and potato (Rolfe et al., 2000) root diffusates, respectively (reviewed in Curtis et al., 2009). The use of these attractive plant properties has been a proposed method for luring nematode pests to non-host trap crops (Franco et al., 1999). Exudates from *Asparagus officinalis* and *Tagetes erecta* are attractive to a wide range of nematodes, however, once lured in they are killed by the plants' defensive compounds (glycosides and thiophene from *A. officinalis* and *T. erecta*, respectively) (Bilgrami, 1997). Although the orientation of endoparasitic nematodes to preferred invasion sites is well established, the exact compounds in the diffusate responsible for attraction are not known (Curtis et al., 2009).

Besides CO₂, other volatile organic molecules have also been shown to serve as attractants (Table 1) or repellents for plant-parasitic nematodes, such as *M. incognita*, (McCallum and Dusenbery, 1992). Castro et al. (1989) demonstrated that volatiles from cucumber roots were attractive to *M. incognita*. Only very recently, however, it was shown that

plant-parasitic nematodes can follow gradients of herbivore-induced terpenoid volatile organic compounds; *Tylenchulus semipenetrans* were more attracted to *Citrus* spp. roots infested by weevil larvae compared to uninfested plants (Ali et al., 2010, 2011). A series of terpene compounds were identified, including α -pinene, β -pinene, limonene, geijerene, and pregeijerene (Ali et al., 2011).

Chemical Ecology of Entomopathogenic Nematodes Soil-dwelling entomopathogenic nematodes comprise two families: Steinernematidae (genus *Steinernema* and *Neosteinernema*) and Heterorhabditidae (genus *Heterorhabditis*). They only grow and reproduce inside arthropod hosts, and third instar infective juveniles leave the cadaver. The infective juvenile (dauer juvenile) is the only stage that can survive without food for long periods while searching for alternative hosts in the soil (Gaugler, 2002). All members of both these families are actually bacteriophagous, having evolved the ability to carry and introduce symbiotic bacteria into the body cavities of insects. Bacteria then reproduce in the insect, thus furnishing the food for the nematodes to complete their life-cycle (Poinar, 1990). Because of their ability to kill the majority of insect orders and families in the soil, and the relative ease of large-scale culturing in artificial solid or liquid media, they have been promoted as exceptionally good candidates for the biological control of insect pests of roots in crop fields (Gaugler and Kaya, 1990). In general, foraging strategies of entomopathogenic nematodes can be divided into two broad categories; a cruiser form, which is highly mobile, and an ambusher form (sit-and-wait) (Campbell and Gaugler, 1997). Cruising foragers have a higher probability of finding sedentary and cryptic resources than ambushers, and ambush foragers are more effective at encountering resources with high mobility (Lewis, 2002). However, direct evidence suggests that foraging strategies used by different infective juveniles species to find a host vary along a continuum between ambush and cruise foragers (Campbell and Gaugler, 1993; Campbell and Gaugler, 1997; Lewis et al., 1992, 1993), and this behavior is plastic depending on the habitat type (Ennis et al., 2010).

Entomopathogenic nematode attraction to a suitable host can integrate different possible cues such as temperature, electric potential, carbon dioxide, and various organic and inorganic substances. However, no specific compound has been put forward for entomopathogenic nematode attraction toward the insect host (Kaya and Gaugler, 1993; Boff et al., 2001). It is generally assumed that nematode orientation and aggregation is due to unspecific signaling, such as CO₂ emissions. For example, Lewis et al. (1993) found that *S. glaseri* responded positively to volatiles cues from an insect host, and that this response was eliminated if CO₂ were removed. A similar response was later found by Grewal et al. (1994) for other cruiser *Steinernema* spp. and for two species of *Heterorhabditis*. This general response to

unspecified volatile cues has been extended to many other *Steinernema* spp. (Campbell et al., 2003). On the other hand, it has been argued that CO₂ should function mainly as a short-range attractant, playing a role in host penetration through the spiracles (Ishibashi and Kondo, 1990). It also seems unlikely that such a general signal could be unambiguously exploited by foraging nematodes looking for a specific arthropod host feeding on roots. Indeed, Bilgrami et al. (2001b) found that *S. glaseri* was attracted to plant tissue from roots and leaves from *A. officinalis* and *T. erecta*, but not to nitrogenous insect products (Bilgrami et al., 2001a). Moreover, it was proposed simultaneously that entomopathogenic nematodes can use arthropod herbivore-induced plant cues to locate the site of wounding, which would automatically reveal the host (Boff et al., 2001, 2002; van Tol et al., 2001).

To date, few tritrophic interactions implying below-ground herbivore-induced volatile compounds have been described, but examples include both agricultural (Rasmann et al., 2005; Ali et al., 2010, 2011) and (semi-) natural systems (Rasmann et al., 2011b). Nematodes *H. megidis*, and *H. bacteriophora* have been shown to be attracted to the sesquiterpene (*E*)- β -caryophyllene emitted by insect-damaged corn (*Zea mays*) plants (Rasmann et al., 2005; Rasmann and Turlings, 2008). Ali et al. (2010) demonstrated that citrus roots upon feeding by the root weevil *Diaprepes abbreviatus* emit several terpenes including α -pinene, β -pinene, limonene, geijerene, and pregeijerene, which attracted *S. carpocapsae*, *S. diaprepesi*, *S. riobrave*, and *H. indica* from the surrounding soil. Further studies demonstrated that application of isolated HIPV pregeijerene increased larval mortality in citrus and blueberry agroecosystems by attracting naturally occurring EPN species (Ali et al. 2012 *In press*). Recently, Hallem et al. (2011) reported positive chemotaxis of *H. bacteriophora* and *S. carpocapsae* nematodes to several volatiles such as methyl salicylate, hexanol, heptanol, undecyl acetate, or 4,5-dimethylthiazole. Interestingly, they also showed that several volatiles repelled the same nematodes.

Chemotaxis and *C. elegans* In the bacteriophagous *C. elegans*, attraction can be mediated by a wide variety of compounds, including anions, cations, amino acids, nucleotides, variation in pH, vitamins, bacteria derived cyclic AMP, or various volatile organic compounds including the well-studied CO₂ (reviewed in Lee, 2002). Single chemosensory neurons are able to detect high and low concentrations of a single odorous compound (Sengupta et al., 1993). Also, odorant responses can adapt to various concentrations, which is reversible (Sengupta et al., 1993). Generally, responses to chemicals are dependent on developmental stage or, likely, other unknown environmental factors (Goode and Dusenbery, 1985; Riddle and Bird, 1985).

Chemotaxis and Other Nematodes Based on current systematic, ecological, and physiological knowledge, only a small fraction of nematodes are parasites of plants or animals. In fact, most nematode diversity is represented by species that are free-living in fresh water, marine, or soil systems (Baldwin et al., 2004). Free-living nematodes forage on a wide variety of substrates including bacteria, fungi, or plants. Little is known of the exact allomones that drive behavior and attraction of all other nematodes. It has been shown that secretions from fungal mycelia can attract the fungal feeder *Paurodontoides linfordi* (Klink, 1969). The free-living nematode *Panagrellus redivivus* was strongly attracted to cell-free filtrates of culture media of certain yeast and fungi, suggesting that material released by the microorganisms, such as esters or fatty acids serve as chemo-attractants (Balanova and Balan, 1991). Similarly, the free-living nematodes *Acrobelloides* sp. and *Pristionchus lheritieri* are attracted to kairomones emitted by suitable bacterial food in culture (Anderson and Coleman, 1981).

Ecology and Evolution of Soil Nematode Chemotaxis

In the complex soil matrix, in which gaseous, liquid, and solid phases can co-exist, nematodes have been shown to rely on both volatile, as well as water-soluble molecules for foraging (Bargmann and Horvitz, 1991). Indeed, it has been argued that *C. elegans* nematodes can rely on both water-soluble molecules (i.e., taste) and volatile molecules (i.e., smell) for different chemotaxis behaviors. Bargmann and Mori (1997) suggested that as volatile molecules travel quickly through diffusion and turbulence in the air, they may be used for longer-range chemotaxis, whereas water-soluble molecules are mainly used for short-range chemotaxis. For example, *H. megidis* nematodes, attracted to the corn-produced sesquiterpene (*E*)- β -caryophyllene, have been recaptured at 0.5 m distance from the release point after 2 weeks (Rasmann et al., 2005, 2011b). Proportionally, to equate a nematode, humans would need to travel at 1,500 km h⁻¹ to cover the same distance!

Evidence gathered in this review would suggest that both short- and long-range chemotaxis are widespread among different nematode taxa. Nematodes from different feeding guilds and from different branches of the phylogeny, indeed, utilize various, often similar, volatile, and non-volatile compounds in the soil to locate their food sources (Table 1). Undoubtedly, nematodes have evolved to sense compounds originating from a relatively long distance. However, the question is if the trait for smelling particular and possibly specific compounds may have evolved independently several times during nematode radiation. Alternatively, all nematodes may be able to smell the same molecules. In that

case, the “smell” trait may be general and may have been conserved during the radiation of nematodes.

We mapped the nematode phylogeny and chemical compounds that stimulate attraction in different nematodes feeding groups in combination (Fig. 1). Such mapping showed that: 1) different feeding guilds of nematodes have repeatedly and independently evolved several times during the radiation of the group (Baldwin et al., 2004; Bert et al., 2011). This implies convergent evolution of feeding habits among soil nematodes. 2) Although we acknowledge the paucity of data, preliminary results suggest that some compounds such as CO₂ or some ions can be detected and used by a wide variety of different feeding guilds. This implies phylogenetic conservatism in chemical compound use. In other words, if traits responsible for recognition of particular compounds are conserved during the radiation of nematodes into different feeding guilds, we should then expect a broad distribution of similar compounds that can initiate a chemotaxis response, which is what we can see in Table 1, and Fig. 1.

Although respiratory emissions of CO₂ remain the most widely studied mechanism for nematode and soil-dwelling arthropod attraction (Johnson and Nielsen, 2012, this issue), this might not be the most effective mean for root location (Johnson and Gregory, 2006). In particular, in mixed stands or for specialized plant parasites, CO₂ cannot provide reliable information. Furthermore, orientation toward CO₂ gradients by the European cockchafer, *Melolontha melolontha*, disappeared when other plant-derived signals were present (Reinecke et al., 2008).

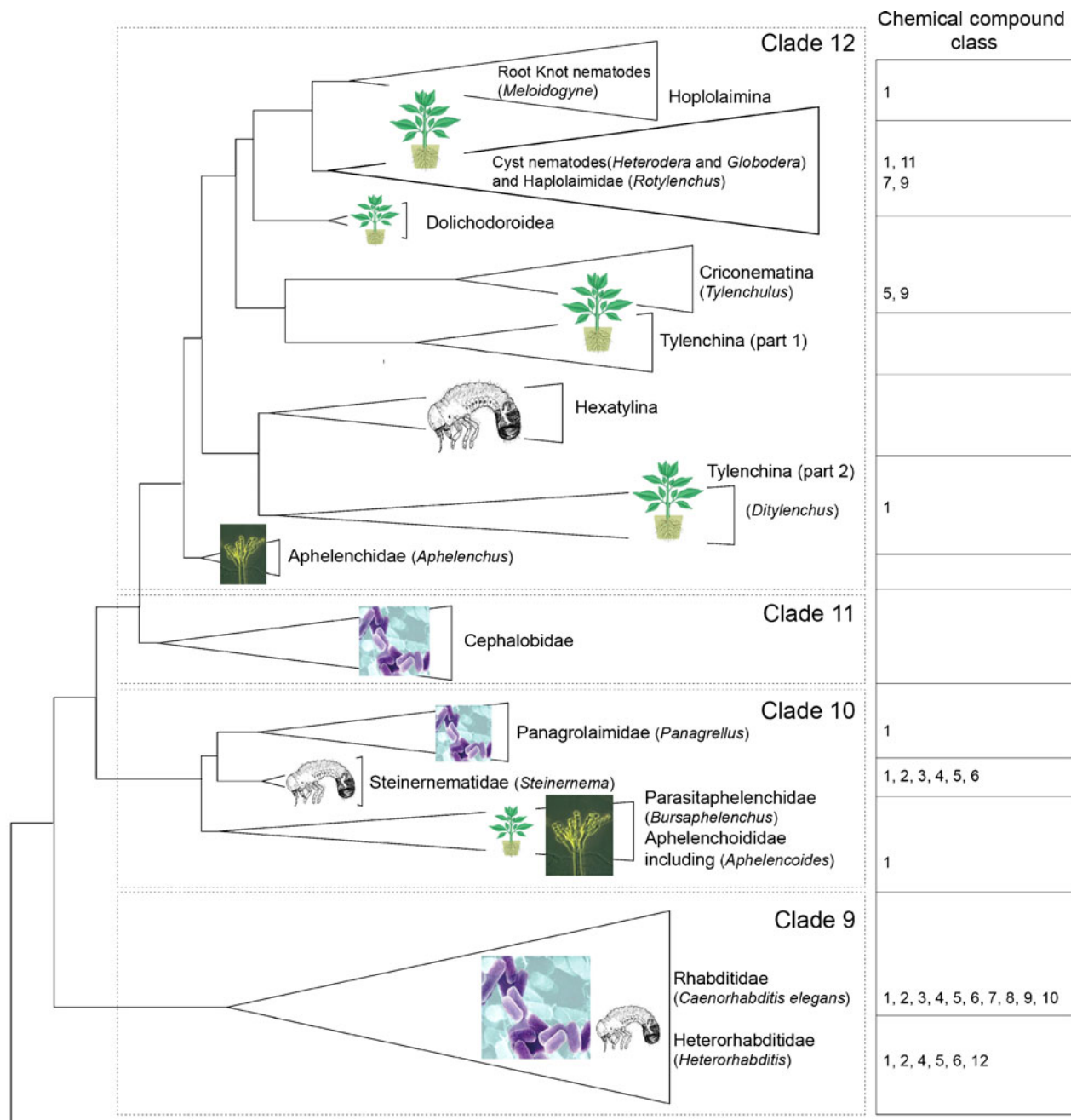
Indeed, besides CO₂, other recently discovered compounds involved in nematode attraction include plant-produced sesquiterpene molecules that can trigger attraction for phylogenetically and functionally different nematodes. Ali et al. (2011) showed that insect-induced citrus root chemicals (geijerene and pregeijerene) can attract the phytopathogenic nematode *T. semipenetrans*, as well as entomopathogenic nematodes *S. carpocapsae*, *S. riobrave*, and *H. indica*. Other compounds found to be triggering chemotaxis in various nematodes include various ions, salts, and amino-acids, again arguing for conserved chemo-sensory machinery across nematode species.

Given this striking conservatism in nematode sensory behavioral responses, can we still expect the evolution of the ability to sense particular chemical compounds in the soil? High levels of specificity would be strongly suggestive of such a relationship. For example, four closely related marine bacteriophagous nematodes have partially overlapping microhabitat preferences. These nematodes were found to have species-specific differences in their responses to three different strains of bacteria. This suggests that the least some level of food specialization may have occurred in conjunction with a specialized chemotaxis response (Moens et al., 1999).

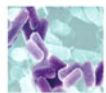
Fig. 1 Evolution of chemotaxis in nematodes. Shown is the schematic SSU rDNA-based phylogenetic relationship between nematodes belonging to Clades 9–12 (based on Holterman et al., 2006). *Right table* shows identity of chemical compounds that have been associated with nematode attraction toward odor sources. 1) atmospheric gas (CO₂), 2) alcohols, 3) ketones, 4) organic acids, 5) terpenoids, 6) thiazoles/pyrazidines, 7) cAMP, 8) esters, 9) ions, 10) amines, 11) amino acids, 12) aromatic compounds. See Table 1 for specific compounds. Overall, the figure shows the overwhelming presence of CO₂ as nematode attractant across different nematode taxa and feeding guilds. It also shows the paucity of data for many groups of nematodes (see text for details)

Similar to other adaptive traits, different nematode chemical receptors may evolve if there is heritable variation in their production and effect, which in turn affects fitness. To our knowledge, measurement of genetic variation in nematode chemotaxis for specific compounds, and how this affects nematode fitness has not yet been attempted. We do, however, have evidence that different strains of nematodes can be recruited by different chemical compounds (Hiltpold et al., 2010; Moens et al., 1999). As various plant-parasitic nematode strains can differentially infect a given host plant, recognition and attraction might indeed be under selection (Perry et al., 2009). Hiltpold et al. (2010) have shown that only few cycles of selection are sufficient to increase *H. bacteriophora* attraction toward corn emitting (*E*)-β-caryophyllene. It is likely that strong directional selection of nematode attraction in corn fields will enhance the efficacy of entomopathogenic nematodes.

Still, there remains a gap in our interpretation of how insect-parasitic nematodes would have become sensitive to indirect cues of host location, such as herbivore induced plant volatiles. Answers may be provided when considering the life histories of closely related nematode taxa, along with their associated bacteria. For example, the insect-parasitic nematode genus *Heterorhabditis* most closely resembles a genus of marine nematodes, *Pellioiditis* (Dougherty and Nigon, 1949). Species from *Pellioiditis* are selective bacterial feeders that occur in intertidal and coastal regions (Poinar, 1993). There is evidence that the heterorhabditids evolved in a coastal habitat from free-living microbiotrophic marine nematodes (Hara et al., 1991; Poinar, 1993). The bioluminescent bacterium that is responsible for the pathogenic effects of *Heterorhabditis* on invertebrates is *Photorhabdus*. These bacteria are believed to have originated from a marine shore habitat, where there are many reports of living and dead marine invertebrates containing luminescent bacteria (Harvey, 1952). *Pellioiditis marina*, a candidate for a pellioiditid that could have evolved into an insect-parasitic heterorhabditid, can survive on a luminescent bacteria (Tietjen et al., 1970). This may reveal a scenario that could permit a free-living bacterial feeder like *P. marina* to have evolved into an insect-parasitic nematode, where an injective juvenile came in contact with and retained bacteria



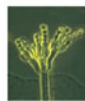
Clades 1-8



bacterivore



insect parasite



fungivore



plant parasite

lethal to invertebrates. This early heterorhabditid need only to parasitize a littoral and beach dwelling crustacean, and a shift from crustacean to an insect would not have been

difficult. Possible hosts would be root-feeding weevils (*Otiorynchus* spp., Curculionidae) that are found along seacoasts on the roots of beach grasses (e.g., *Ammophila*

arenaria or seashore wormwood, *Artemisia maritima*) or scarabid larvae of *Aegialia arenaria* (Scarabidae) along coastal dwelling and beach grass root feeders (Von Lengerken, 1929). Interestingly, scarabs and curculionids currently are known to be among the most susceptible soil insects to *Heterorhabditis* nematodes (Poinar and Georgis, 1990). If sensitivity to a volatile signal is as inheritable as demonstrated by studies of Hiltpold et al. (2010), entomopathogenic nematode sensitivity to herbivore induced plant volatiles becomes likely. Future work could evaluate this potential relationship by examining herbivore-induced compounds released by plant roots in sandy coastal regions, along with entomopathogenic nematode bioassays.

Ecological Impacts of Root Exudates

Different scenarios of root-exuded allomones to benefit overall plant fitness can be envisaged. For example, 1) plants can indirectly benefit from emissions of kairomones that attract bacterial or fungal feeders, which in turn can benefit plants by stimulating microbial community turnover and organic matter recycling (e.g., Luscher et al., 2004; Chapman et al., 2006). 2) Plants can emit molecules that can be defensive towards antagonists, such as the plant-parasitic nematodes (direct defense). For example, the roots of the french marigolds (*Tagetes patula* and *T. erecta*) contain α -terthienyl and other derivatives of bithienyl, both of which can inhibit populations of *Meloidogyne* and *Pratylenchus* (Giebel, 1982). Roots of

nematode-resistant banana plants were found to contain high levels of flavonoids, dopamine, caffeic esters, and ferrulic acids (Valette et al., 1998). Ferrulic acid molecules bound to cell walls of banana plants then were speculated to reduce the activity of cell wall-degrading enzymes in *Radopholus similis* nematodes (Wuyts et al., 2007). 3) Exudation of damaged roots can attract entomopathogenic nematodes to their arthropod hosts (indirect defenses). Based on evidence gathered here, different scenarios of root-exuded allomones to benefit overall plant fitness can be envisaged. For example, the common milkweed *Asclepias syriaca* is generally fed by the specialist root herbivore larvae of the cerambycid beetle *Tetraopes tetraophthalmus*. Emissions of volatile organic compounds by common milkweed in the soil can increase after insect damage. In lab experiments, this increased emission was correlated with increased entomopathogenic nematodes *H. bacteriophora* attraction. Subsequent field trials demonstrated that soil inoculation of entomopathogenic nematodes benefitted the plants by restoring plant biomass to control levels (Rasmann et al., 2011b). This, with previous work on bush lupine (Strong et al., 1996, 1999), is probably the best evidence of a natural subterranean trophic cascade that may result into enhanced plant performance. Whether or not this is correlated with higher levels of particular volatile emissions has not been assessed. Roots of *A. syriaca* plants emit a very complex mixture of >30 compounds of which only few are described as being in the terpene family (Rasmann et al., 2011b). Such a complex blend by itself

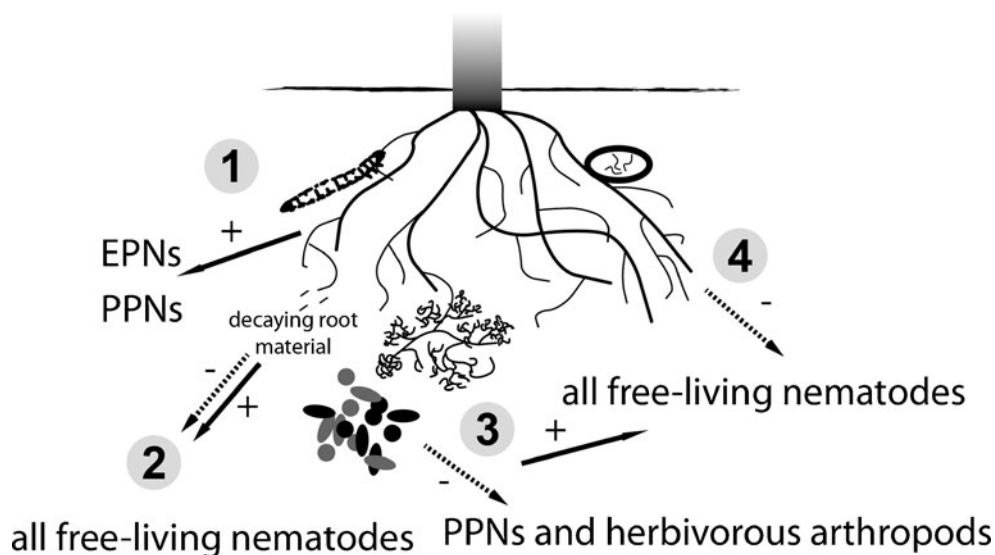


Fig. 2 Belowground plant chemically-derived nematode community structuring. Because of generalized and widespread detection of similar compounds across different nematode groups as shown in Fig. 1, we propose that 1) herbivorous arthropods or plant-parasitic nematodes (PPNs) can induce plants to release chemical organic compounds in the soil matrix, which can attract other herbivores (PPNs) as well as entomopathogenic nematodes (EPNs). 2) Root leachates and root-based detritus can become information cues for all free living

nematodes in the rhizosphere. 3) Root symbiotic fungi and bacteria can stimulate root respiration (CO_2) and exudation to attract plant-parasitic nematodes as well as root-feeding arthropods. Fungi and bacteria not directly associated with roots by living in the rhizosphere can increase CO_2 levels to attract free-living soil nematodes. 4) Plants can counteract nematode attack by producing repelling compounds, which can simultaneously repel other free-living nematodes

already impedes the assessment of which particular compounds are responsible for the attraction. A problem similar to one found in above-ground systems (Hare, 2011), where the emerging picture is that volatile production in plants is the result of diffuse selection due to multiple players interacting with the plant.

The emission of organic molecules can have unintended effects on non-target organisms in addition to nematodes. For example, increased CO₂ levels or other exudates have been shown to attract herbivorous arthropods, which can further decrease plant fitness (see Johnson and Nielsen, 2012, this issue). Therefore, nematode-induced changes in soil chemical characteristics may contribute to the structuring of specific communities around roots. These complex interactions may limit the development of optimal soil management practices. For example, the insect herbivore-induced emissions of terpenes by citrus plants have been shown to attract entomopathogenic nematodes (Ali et al., 2010; 2011). These compounds also may attract plant-parasitic nematodes *T. semipenetrans* (Ali et al., 2011). Therefore, unless rootstocks are not otherwise resistant to *T. semipenetrans*, this co-attraction may hamper the exploitation of citrus-induced volatile emission in biological control strategies that target the root weevil *Diaprepes abbreviatus*. In Fig. 2 we have outlined possible direct and indirect chemically-mediated effects on different nematode feeding guilds. Undoubtedly, future work is needed to complement the paucity of literature on the exact nature of compounds driving nematode foraging behavior.

Conclusions

Nematodes from different feeding guilds can ‘smell’ and ‘taste’ a variety of diverse compounds in soil. The sensory capacity of different nematode feeding guilds is remarkably similar, and there appears to be a key role for some general compounds, such as CO₂, to be ubiquitous nematode attractants. Plant-borne soil chemical signatures can attract nematodes, thus structuring nematode communities in the rhizosphere. Different nematode species will in turn impose specific selective pressure on plants to produce a unique blend of chemical exudates. Of course, this only plays a role in wild plants that are not under artificial selection by plant breeders. The fitness benefits for plants to produce specific root exudates in soil is then the net outcome of diffuse co-evolution imposed by all soil organism in the rhizosphere, including nematodes from all trophic levels (Fig. 2).

The relative simple laboratory settings in which most bioassays described above were done undoubtedly have produced a highly simplified version of the complex chemical profile of natural soils, where thousands of similar molecules co-exist. Interestingly, however, chemical complexity seems

to facilitate nematode foraging behavior. A recent report shows that CO₂ interacts synergistically with (*E*)- β -caryophyllene and dimethyl disulfide to increase *H. megidis* nematode attraction (Turlings et al., 2012). Future work should, therefore, aim at measuring single but also interactive effects of organic molecules that drive nematode behavior. Chemical characterization of agricultural soils might be a better starting point, not only for applied reasons of improving biological control of crop pests, but also from the fundamental point of view of understanding ecological mechanisms driving nematode foraging behavior. However, complementary studies in natural soils are needed in order to understand evolutionary mechanisms that drive nematode foraging behavior. For example, most of the volatile and non-volatile cues involved in belowground defense and resistance against herbivores remain unknown. Understanding more of these complex mechanisms that drive plant-nematode interactions would not only allow a better understanding of ecological interactions in the rhizosphere, but also offer ecologically sound alternatives in pest management in agricultural systems, such as breeding more attractive plants, intercropping attractive pest-resistant plants, or genetically modify crop plants for increased resistance (see Hiltbold and Turlings, 2012, this issue).

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