

An evaluation of types of attractants enabling plant-parasitic nematodes to locate plant roots

Roland N. Perry

*Plant Pathogen Interactions Division, Rothamsted Research, Harpenden, Herts. AL5 2JQ, UK, e-mail: roland.perry@bbsrc.ac.uk

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Summary. The ability of plant-parasitic nematodes to orientate towards stimuli from plant roots enhances the chances of host location. This brief review examines the attractants involved in terms of their spatial attributes. Several gradients exist around physiologically active roots and it is probable that some constitute 'long distance attractants' that enable nematodes to migrate to the root area. Attractants that cause nematodes to move to individual roots may be termed 'short distance attractants' and there is evidence that, in some instances, the attractiveness of a host to the pest species is correlated with its efficiency as a host. The orientation of second-stage juveniles of endoparasitic nematodes to the preferred invasion site, the root tip, is well established but the cues that constitute the associated 'local attractants' are unknown. The types of attractants are discussed briefly in the context of plant physiology and the root environment.

Key words: attractants, root attraction, root diffusates, semiochemicals, sensory responses.

Attraction to roots

The orientation of plant-parasitic nematode to the roots of their host plants is an important area of research as disruption of this aspect of the host-parasite interaction may lead to novel control strategies. This brief review, based on an invited plenary paper given by the author at the Meeting of the Russian Society of Nematologists (Moscow, June, 2005), discusses the type of signals that may be involved in attracting nematodes to the root area and to specific host roots. The review will examine critically the reality of some proposed attractant gradients in the context of work by plant physiologists.

While in the soil, plant-parasitic nematodes are dependent on their food reserves and need to locate a host rapidly in order to feed and develop. The ability to orientate towards stimuli from plant roots enhances the chances of host location (Perry, 1997). Several gradients are thought to exist around physiologically active roots and it is probable that some of these gradients constitute '**long distance attractants**' that enable nematodes to migrate to the root area. Attractants that cause nematodes to move to individual host roots may be termed '**short distance attractants**' and the orientation of second-stage juveniles (J2) of endoparasitic nematodes to the preferred invasion site, the root tip, is likely to be mediated by '**local attractants**'. Most plant-parasitic nematodes in soil

will require some, or all, of these types of attractants. The exceptions are those species, such as *Globodera rostochensis* and *G. pallida*, that are unlikely to utilise long distance attractants as they hatch near the root in response to chemicals from the host roots, and endoparasitic species that do not have a preferred invasion site on the root and, thus, may not need local attractants.

Gradients around roots are thought to include pH, CO₂, temperature and ions (Perry & Aumann, 1998); in addition, a range of carbon compounds, including amino acids and sugars, are excreted by roots (Rovira, 1969; Jaeger *et al.*, 1999). Some, or all, of these gradients may act as long distance attractants. However, it is worth examining further the likelihood that such gradients are constant or extensive enough to serve as orientation stimuli for nematodes. It is difficult to generalise about the chemical gradients directly attributable to roots. There will be enormous differences, depending, amongst other variables, on the soil type and plant. Other factors, such as age of the root or presence of microorganisms, also condition the root's attractiveness. In addition, *in vivo* experimental demonstration of gradients is extremely difficult and much of the information from plant physiology and soil biology derives from *in vitro* experiments, where a variety of analytical methods are used. It is equally difficult to generalise about nematode responses to putative attractants. Although, in *in vitro* experiments,

nematodes may show preferences to a given concentration or may respond to a gradient, it cannot be assumed that such gradients exist in the soil or are sufficiently stable and constant to provide a consistent attractant for nematodes. Examination of data on pH, CO₂ and temperature as putative long distance attractants provides contrasting examples.

pH as an attractant

The pH of soil is typically buffered by ammonium, carbonates, sulphates and phosphates often bound to or comprising soil particles. Their concentrations are changed by plant roots and the soil microflora and vary markedly with depth and distance from roots. Thus, pH and any substance whose concentration is pH dependent might establish concentration gradients in the soil providing information to nematodes about depth, vertical orientation and the location of roots (Robinson & Perry, 2006). However, the establishment of pH gradients around roots and their use by nematodes for orientation is far from clear. Plants require nitrogen and acquisition of nitrogen by roots alters rhizosphere pH and redox potential (Bloom *et al.*, 2002). Roots change the pH of soil around them by releasing H⁺ or OH⁻ charges in order to balance cation-anion uptake at the root surface (Vetterlein & Jahn, 2004) and by a build-up of CO₂ forming carbonic acid that may contribute to a pH decrease (Hinsinger *et al.*, 2003). However, soil pH itself and the pH buffering capacity of soil, mentioned above, will dampen root-mediated changes (Hinsinger *et al.*, 2003) and, thus, any pH gradient around the root may only be localised and not be temporally or spatially constant. There is evidence from work on cowpea, that the root can only influence pH to a distance of under 1 mm in soil (Rao *et al.*, 2002). The type of plant will also affect rhizosphere pH changes. For example, in contrast to cereals or other crops, legumes are known to acidify the rhizosphere (Roa *et al.*, 2002). Thus, pH is unlikely to be responsible for long distance attraction to roots. It may only be involved in specific host-nematode interactions as a local attractant.

Carbon dioxide as an attractant

By contrast to pH, there is more evidence to support CO₂ as a long distance attractant. *In vitro* experiments, principally using agar plate bioassays, have demonstrated that CO₂ strongly attracts a number of species of plant-parasitic nematodes, including *Ditylenchus dipsaci*, *Heterodera schachtii* and species of *Meloidogyne* and *Pratylenchus* (Robinson, 2002). Concentrations of CO₂ ex-

ceeding 5% suppress nematode activity and failure by early workers to detect attraction of nematodes to CO₂ may have been because CO₂ flow rates and, therefore, concentrations were too high. The ideal assay system to test the reality of gradients and attraction is a three-dimensional matrix that equates to the soil conditions much more closely than agar plate assays. Such assays are very difficult and time consuming to undertake but the leading worker in this area of research, Forest Robinson, has conducted elegant experiments to demonstrate the role of CO₂. He used infusion pumps to deliver small amounts of CO₂ over extended periods of time through needles positioned within tubes of moist sand (Robinson, 1995) and found the optimal release rate for attracting *Meloidogyne incognita* and *Rotylenchulus reniformis* to a point source was extremely small at 15 µl min⁻¹, and long periods of 40 and 29 h, respectively, were needed to attract most of the nematodes from 52 mm of the source. The total amount of gas released was calculated to be equivalent to that released by a germinating sunflower seed.

Pline & Dusenbery (1987) elegantly showed that the threshold at which *M. incognita* responds to CO₂ varies with ambient concentration, meaning that nematodes can detect about the same relative change at any ambient concentration. In the soil, this ability enables the nematodes to detect gradients at far greater distances from the source than would be possible with a fixed concentration differential threshold. Robinson (1995) found that *M. incognita* and *R. reniformis* were strongly attracted to CO₂, migrating up a 0.2% per cm gradient at a mean ambient CO₂ concentration of 1.2%, which was a 16% per cm relative change.

Although the current consensus is that CO₂ attracts nematodes to roots and that either dissolved CO₂ or carbonic acid is the attractive species (Robinson & Perry, 2006), there are other factors that complicated the picture. CO₂ released by roots also affects gradients of redox potential, pH, carbonic acid, bicarbonate and carbonate in the soil. CO₂ is released by living and decaying plant and animal tissues and soil-dwelling stages of plant-parasitic nematodes have to distinguish their food source, live roots, from decaying material. *Meloidogyne incognita* is repelled by ammonia and several nitrogenous salts released by decaying material so it is possible that the negative response to these compounds overrides the response of nematodes to CO₂ from decaying material. Plant roots can produce the gas ethylene, especially when soil conditions are anaerobic. Nematodes may be sensitive to a decreased O₂ content around roots and it is possible that CO₂/O₂ ratios are important.

Temperature as an attractant

It is well established that plant-parasitic nematodes migrate in response to temperature. Several species of plant-parasitic nematodes exhibit a 'preferred temperature' to which they migrate when placed on a temperature gradient *in vitro*. In most cases where tested, the preferred temperature is shifted partly or completely in the direction of a new adaptation temperature within several hours. The threshold ambient temperature change eliciting a detectable change in the rate of movement of J2 of *M. incognita* is less than 0.001°C (Robinson, 2004). In migration experiments, gradients sufficient to achieve a maximal response by *M. incognita* and other species, including *G. rostochiensis*, *D. dipsaci* and *Tylenchulus semipenetrans*, are between 0.01 and 0.1°C per cm. This extremely sensitive response to temperature may enable nematodes to orientate to and be attracted by metabolic heat from roots, and nematodes have been shown to be attracted to heat released by germinating alfalfa seedlings in Petri dishes (El-Sherif & Mai, 1969). However, root metabolism is a small heat source and it is unlikely that temperature would act as a long distance attractant, although it may play a role as a short distance attractant or, more likely, as a local attractant (see below).

By contrast, solar radiation has a marked effect on soil temperatures and diurnal surface heating and cooling sends a heat wave down through the soil every day. The wave characteristically starts with maximum amplitude at the surface during the afternoon, dampening as it moves downward 2-3 cm per h. Robinson (1994) found behaviourally effective gradients of temperature extended deep into the soil of a cotton field in Texas. In addition, hourly collection of temperature data at 2.5 cm increments down to 60 cm across most months of the year clearly showed gradient inversions and other perturbations indicative of rainy periods, cold fronts and other weather patterns throughout most of the root growth zone.

Since soil temperatures change constantly and gradients invert daily while nematodes are constantly adapting and migrating in response to gradients, it is exceedingly complex to predict the net result. Robinson (1994) subjected two root parasites, *M. incognita* and *Rotylenchulus reniformis*, and one foliar parasite, *D. phyllobius*, in the laboratory to gradient fluctuations in soil that precisely mimicked those measured previously in cotton fields. The two root parasites consistently moved in opposite directions; moreover, movement of *R. reniformis* was down and *M. incognita* was up, consistent with their known vertical distributions

in cotton fields. The foliar parasite appeared to move toward cool regions regardless, consistent with previous observations on agar, and consistent with its need to be attracted to the soil surface during rainy periods to ascend cool, moist foliage.

It seems that temperature might be the most consistent cue for a nematode to differentiate up from down within soil where gravitational effects are minuscule compared to surface tension (Robinson & Perry, 2006). Temperature may serve as a collimating stimulus, providing a vertical directional reference, and thus may not be an attractant *per se*, except perhaps for local orientation to a preferred invasion site (see below).

Short distance attractants

Long distance attractants enable a nematode to move to a root area. Volatile or non-volatile chemicals that cause nematodes to move to individual host roots may be termed 'short distance attractants'. Studies on attraction of nematodes to host roots have used a variety of experimental conditions and it is often difficult to compare results. In general, the attraction is non-specific but there are notable exceptions and these will be examined in more detail in this section.

Roots modify local soil conditions by respiring, releasing various organic compounds, and taking up salts and water. The leaves of a plant in the sun will quickly warm and the heat can be transferred down the stem to the root. On a sunny day this heat transfer may be sufficient to alter the temperature of the root. With increasing closeness to a root, among other changes, O₂, K⁺ and NO₃⁻ decrease, and CO₂, amino acids and sugars increase. These changes will be greatest just behind the root tip at the site of maximal uptake. By modifying local conditions around a root, gradients may be established along which a nematode can move. There is a paucity of research on specific attractants and what has been done is often difficult to interpret; for example, much of the early work on the responses to salts was undertaken using unbalanced salt solutions on agar plates, a situation far removed from soil conditions.

Ditylenchus phyllobius, a foliar parasite of certain *Solanum* spp., is attracted to an unknown compound that appears to be unique to the host (Robinson *et al.*, 1979). The attractant accumulates in leaves and is leached out during rainy weather to accumulate at the base of stems, establishing a gradient in the surrounding soil. The infective fourth-stage juvenile of *D. phyllobius* utilizes these gradients to locate stems; it then moves up them to the foliar buds. The attractant is freely

soluble in water and retains activity after freeze drying and is an excellent example of a short distance attractant eliciting chemotactic responses by the nematode to maximise its chances of invading a host.

The general terms, root diffusates or root exudates, are used by nematologists to denote chemicals released by roots that have an effect on root parasitic nematodes, either by inducing hatching of certain species or by attracting nematodes to the roots. Among the first to demonstrate the latter role of root diffusates were Luc *et al.* (1969), who used radioactive phosphorus to track nematodes in soil and demonstrated that diffusates were attractants and stimulated nematode activity. Potato root diffusate (PRD) stimulated movement of hatched J2 of *G. rostochiensis* (Clarke & Hennessy, 1984) and may aid in host location. Electrophysiological analysis of sensory responses demonstrated that spike activity of J2 of *G. rostochiensis* increased on exposure to host root diffusate, PRD, but not to root diffusate from the non-host sugar beet, thus indicating that responses to diffusates may be host-specific (Rolfe *et al.*, 2000). PRD is required to stimulate hatching of the majority of J2 of the potato cyst nematodes *G. rostochiensis* and *G. pallida* (Perry, 2002) but the chemicals in PRD responsible for hatching differ from those responsible for attracting the J2 to the root (Devine & Jones, 2002). Both species were attracted to several chemical fractions of PRD but there were differences between the two species in their chemotactic responses to the chemicals. The nature of these chemicals awaits elucidation. There is other evidence that indicates that, in some instances, the attractiveness of a host to the pest species is correlated with its efficiency as a host. The numbers of J2 of *M. naasi* attracted to a resistant species of grass were fewer than were attracted to susceptible plants and Balhadère & Evans (1994) considered that this may be associated with a less acidic pH produced by roots of the resistant cultivar. Thus, with this species of nematode, pH may be one factor acting as a local attractant.

There has been little attempt either to analyse the chemoattractants in root diffusates or to link work on nematode responses with information from plant biologists on root physiology. Work on the attractiveness of ions, for example, needs now to be related more closely to the ionic dynamics of roots and the likelihood of establishing gradients. One example will illustrate this. Phytosiderophores of oat roots are secreted into the soil water under iron deficiency conditions. After binding of Fe_2^+ , the phytosiderophores re-enter the root cells and

release Fe^{2+} ions, which are then assimilated by the oat plants. Oat siderophores, such as avenic acids and mutagenic acid, have been shown to attract J2 of *Heterodera avenae* (Lung, 1993). However, it is not clear whether such compounds can establish gradients in soil around the root. In addition, these siderophores are secreted under conditions of iron deficiency, whereas *H. avenae* parasitizes roots independently of the availability of iron in the soil.

Amino acids are known to be among the many plant compounds that cause a feeding response in insects and it has been suggested that amino acids establish gradients around physiologically active roots, although it is unclear how extensive these gradients might be. Exposure of J2 of *G. rostochiensis* to glycine elicited no response in electrophysiological tests (Rolfe *et al.*, 2000) and this may correlate with low levels of glycine around the roots. Thus, orientation of J2 may not be mediated by glycine. Exposure to D-glutamic acid resulted in a significant increase in spike activity but exposure to the L-isomer gave no response (Rolfe *et al.*, 2000). In insects, the D isomers of many amino acids usually elicit a phagostimulatory response, whilst many L-amino acids are feeding deterrents (Mullin *et al.*, 1994).

Local attractants

J2 of endoparasitic nematodes, such as *Globodera* and *Meloidogyne* species, orientate to the preferred invasion site, the root tip (von Mende *et al.*, 1998) but the active factors that constitute the 'local attractants' around the root tip are unknown. Cells at the root tip of potato plants produced a more active diffusate than cells located elsewhere but diffusate appeared to be produced along the entire root (Rawsthorne & Brodie, 1986). Henriksen *et al.* (1992) point out that because a progression of root cell maturation occurs as one moves away from the apical meristem, it is reasonable to expect that cellular biochemistry and metabolic requirements may also vary with position along the root axis. Such activity may provide cues for the nematode. At the root surface, temperature may be a cue as there is likely to be a temperature gradient along the root from the metabolically highly active root tips to the more mature parts of the root. It has been demonstrated that longitudinal gradients of respiratory activity and nitrate assimilatory enzyme activity occur along the root axis of barley and maize, respectively. However, in studies of the transport of inorganic nitrogen into barley roots, Henriksen *et al.* (1992) found that fluxes of NH_4^+ and NO_3^- varied with position along the root and

with time. Moreover, different roots showed unique temporal and spatial patterns of uptake. Clearly, these types of variations obviate ammonium and nitrate fluxes as local attractants for nematodes requiring to invade a specific root area.

It is possible that allelochemicals are responsible but it is also possible that the nematodes orient to an electrical potential gradient at the elongation zone of the root tip. Bird (1959) was the first to suggest that plant-parasitic nematodes may orientate along a gradient produced by lower redox potential at the root surface. However, differences in root cell resting membrane potential between resistant and susceptible potato cultivars did not affect the numbers of J2 of *G. rostochiensis* invading (Sheridan *et al.*, 2004). Thus, the relative importance of electrical and chemical attractants for location of root tips is unknown.

CONCLUSION

Advances in analytical and behavioural techniques should now enable investigation of the temporal and spatial attributes of gradients of putative attractants in the soil environment. In addition, more detailed investigation of nematode responses is necessary. This should be based on a two-fold approach, with analysis of movement in three-dimensional environments augmented by information on the responses to set concentrations of attractants. In the soil, nematodes are exposed to a mixture of behaviour-modifying factors; tests on single compounds provide useful information but tests on combinations of factors are necessary to examine possible synergistic effects.

This brief review has indicated the types of cues that may be responsible for attracting nematodes to the roots but has not examined other aspects, such as inhibitors and repellents, and changes in the roots induced by feeding and/or invading nematodes, which themselves may alter the attractiveness of roots to other nematodes. Analysis of the information available on location of roots by plant-parasitic nematodes clearly demonstrates the need for a closer research link between nematologists, plant physiologists and soil biochemists to enhance our understanding of the host-nematode interactions in the soil.

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Perry R. N. Различные типы аттрактантов, обеспечивающих обнаружение корней растений нематодами – паразитами растений.

Резюме. Способность паразитирующих в растениях нематод ориентироваться при движении на стимулы, исходящие от корней растений, существенно увеличивает их шансы обнаружить подходящего хозяина. В обзоре кратко анализируются различные аттрактанты, типизированные по дистанционности их действия. Различные типы градиентов присутствуют в пространстве, окружающем живые корни растений, и, возможно, что некоторые из этих градиентов представляют собой «аттрактанты дальнего действия», обеспечивающие нематодам возможность миграции к прикорневую зону. Аттрактанты, побуждающие нематод двигаться к отдельному корню могут быть названы «аттрактантами ближнего действия». Имеются свидетельства, показывающие, что привлекательность корней для вредителей зачастую коррелирует с общей пригодностью этого растения как хозяина для данного вида нематод. Способность личинок 2-й стадии эндопаразитических нематод определять предпочтительное место внедрения в оконечности корней хорошо известна, но природа факторов, ассоциированных с этими «локальными аттрактантами», пока неизвестна. Эти типы аттрактантов рассматриваются в связи с физиологией растений и экологическими особенностями прикорневой зоны растений.