Feeding Behavior of *Criconemella xenoplax* in Monoxenic Cultures

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ABSTRACT

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Criconemella xenoplax was grown in monoxenic cultures on crimson clover, carnation, tomato, and western sand cherry. Nematode population densities increased on crimson clover, and second-stage juveniles did not accumulate in cultures. Some second-stage juveniles did not feed or develop further on carnation and tomato, resulting in accumulation of this stage in cultures. All stages of the nematode fed on the western sand cherry, but roots remained viable for only 4–5 wk. Feeding behavior was studied in most detail on tomato, but it appeared to be similar on all hosts. Stylet penetration of root tissue was deliberate and lasted up to 80 min. After penetration, the stylet became stationary and a 1- to 3-h secretion phase followed. Secretion was accomplished by intermittent twitching of the posterior of the metacorpus and apparent slight opening of the pump chamber. Globular secretions accumulated around the stylet tip in parasitized cells. Ingestion was characterized by maximum dilation of the pump chamber and was continuous for up to 8 days. Ingestion ceased and the stylet was retracted when adults became gravid. Juveniles often molted after a single feeding episode. *C. xenoplax* fed as an ectoparasite for prolonged periods on a single-root cortical cell without destroying the cell.

Additional keywords: Dianthus caryophyllus, Mesocriconema xenoplax, Lycopersicon esculentum, Prunus besseyi, Trifolium incarnatum.

Criconemella xenoplax (Raski) Luc and Raski (=*Mesocriconema xenoplax* (Raski) Loof & de Grisse) has a broad host range (28,29) but has been documented as a pathogen on only a few of its recorded hosts. The nematode has been implicated as a component of the peach disease syndrome that results in premature tree mortality (14) and enhanced susceptibility to bacterial canker (11). At high population densities, *C. xenoplax* injured roots and stunted growth of peach, plum, and prune (*Prunus* spp.) seedlings in greenhouse studies (1,12,13). *C. xenoplax* caused root injury and retarded growth and flower production in carnation (*Dianthus caryophyllus* L.) (20) and injured *Vitis vinifera* L. 'Blauburgunder' (10), but it caused no notable injury to Thompson seedless grapes (15). This inconsistency in injury to different hosts remains unexplained.

Few details of the feeding behavior of *C. xenoplax* have been reported. Feeding is required for juveniles to molt and for maturation of oocytes in adult females (19). Stylet insertion was characterized as slow and deliberate, and the metacorpus reportedly pumped regularly during feeding (23). Feeding at a single site lasted 18 h in one case, and longer feeding episodes were presumed likely. On carnation, *C. xenoplax* has been observed with the anterior embedded in root tissues (20). Observations of other species of *Criconemella* have indicated similar feeding behavior (9,16,21). Feeding activities of *Criconemoides* (gen. dub. in Criconematinae) are regarded to destroy root cells by removing the cytoplasm (5). Other than being grouped with other ectoparasitic nematodes, little evidence supports this description for the feeding behavior of *Criconemella.*

Previous studies have been limited by the difficulties of observing nematode behavior in soil environments. With the recent establishment of *C. xenoplax* in monoxenic cultures in an agar medium, examination of feeding behavior in a transparent medium became possible (24). The objective of this study was to describe the feeding behavior in detail of *C. xenoplax* in monoxenic cultures. Four different hosts were included to establish the general nature of nematode behavior. This information will enhance our understanding of the interactions between the nematode and its hosts and help clarify the extent and nature of root damage. Abstracts of this work have been published (24,25).

MATERIALS AND METHODS

Plant materials. Root-explant cultures were established for carnation (*D. caryophyllus* 'Double Grenadin'), crimson clover (*Trifolium incarnatum* L. var. *elatius* Gibbelli & Belli 'Dixie'), and tomato (*Lycopersicon esculentum* Mill. 'Rutgers') on Gamborg's B-5 medium containing vitamins (6), sucrose (20 g L^{-1}), and Bacto agar (10 g L^{-1}, Difco Co., Detroit, MI). Each species was originally established in culture from sterile seedlings. Seeds were immersed in 0.05% (w/v) sodium hypochlorite for 20 min, rinsed three times for 15 s in sterile water, placed in sterile glass petri dishes on moist paper or on water agar (15 g L^{-1}), and incubated at approximately 26 C for germination. When apices of the radicles were 1–2 cm long, they were excised and placed in plastic petri dishes (10 cm in diameter) containing Gamborg's medium. Petri dishes were sealed with laboratory film (Parafilm, American Can Co., Greenwich, CT), and three holes were made in the film with a needle for air exchange. Root-explant cultures were incubated at 24–27 C in the dark. A single-root clone that grew well in culture was selected for each species and perpetuated by transfer of root tips to fresh media every 2–4 wk.

Whole-plant cultures of western sand cherry (*P. besseyi* L. H. Bailey) also were established on Gamborg's medium. Seeds were disinfested and germinated as described above except that seed coats were removed before incubation on water agar. Removal of seed coats eliminated the need for stratification of seed and improved the chances of obtaining sterile plants. Single clones of western sand cherry were maintained by transfer of shoots from sterile plants to fresh media. Shoots developed roots without hormone treatment. Petri dishes were sealed with laboratory film as described above. Cultures were incubated under fluorescent lights 14 h per day at 21–29 C.

Nematode cultures. Cultures of *C. xenoplax* were established in a greenhouse (15–37 C) from collections made at the Sandhill Research and Education Center near Elgin, SC. Nematodes were cultured on *P. persica* (L.) Batsch 'Nemaguard' seedlings in sand

and were periodically subcultured by transfer of extracted nematodes to 2-wk-old seedlings. Plants were fertilized weekly with half-strength Hoagland's solution containing K_2NO_3 and $CaNO_3$ as the sources of nitrogen (7).

For initial monoxenic cultures, nematodes were disinfested by incubation in 2-methoxyethyl mercuric chloride (16 $\mu g\ ml^{-1}$) for 5 h before transfer to sterile plant cultures. Ten to 30 nematodes were transferred individually from the disinfestant solution to the sterile plant cultures. Subcultures were established by transfer of agar blocks containing nematodes and roots to fresh media. Cultures with herbaceous hosts were commonly divided into four to eight pieces for transfer to fresh Gamborg's medium, depending on subjective evaluation of population density at the time of subculture. Crimson clover and tomato root tips were transferred to fresh media and allowed to become established before inoculation with nematodes. Nematodes for western sand cherry were commonly derived from crimson clover cultures, and nematodes for all other hosts were commonly derived from cultures on the respective host. All cultures with nematodes were incubated under conditions described above for the plant cultures.

Nematode observation procedures. Nematode behavior was observed in petri dishes with an inverted microscope (model IMT-2, Olympus Optical Co., Tokyo, Japan) and a Hoffman modulation contrast system (Modulation Optics Inc., Greenvale, NY) or in inverted dishes with a stereoscope or compound microscope with standard optics. Video recordings of nematode activities were used to establish behavioral patterns. Recordings were made with a color camera (Reichert-Jung model JE3362, Javelin Electronics Inc., Torrance, CA) and a video cassette recorder (model VCR754, Emerson Radio Corp., North Berger, NJ) or with a black-and-white camera (model KP-140, Hitachi Denshi, Ltd., Tokyo, Japan) and a time-lapse video recorder (model AG-6020, Panasonic Industrial Video, Secaucus, NJ) attached to a high-contrast picture monitor (model PM-910A, Ikegami Tsushinki Co., Tokyo, Japan). Observations under the time-lapse mode were recorded at 2-s intervals.

Complete recordings of all events from stylet insertion to stylet withdrawal were made for three adult nematodes feeding on tomato roots. One additional recording of the sequence of events during stylet insertion on tomato was completed. For at least 10 nematodes on each host, short observations (1–10 min) were made once daily on individual nematodes to establish stylet placement and rate of pulsation of the metacorpus over the period of days that nematodes fed. Observations for each selected nematode were continued on a daily basis until that nematode stopped feeding. Black-and-white photographs were used to document position of the stylet for these daily observations. Rates of pulsation of the metacorpus of feeding nematodes were determined by timing the period in which 30 beats occurred.

RESULTS

The general behavior of *C. xenoplax* in cultures with the different plant species varied only slightly. Crimson clover was a good root-explant host and nematodes remained active in crimson clover cultures 15–20 wk after establishment, even though roots had stopped growing by approximately week 12. Eggs were deposited and second-stage juveniles did not accumulate in culture, indicating that they developed to the next stage. All stages readily fed without obvious preference for any site along the length of young roots. Second-stage juveniles accumulated in cultures on roots of tomato and carnation, indicating that they did not feed on roots. Without feeding, these juveniles cannot continue to develop. This arrested development of second-stage juveniles was most severe in tomato cultures, in which inactive second-stage juveniles composed up to 89% of the population in one set of 12-wk-old cultures as compared with 17% for crimson clover cultures of similar age. Adult nematodes were viable in tomato cultures 25 wk after establishment. Carnation was suitable for growth of nematodes for only 7–8 wk. After 8 wk, when the roots densely covered the culture plate, the nematodes became inactive and usually were unsuitable for establishing new cultures. Nematodes fed on roots of young, actively growing western sand cherry plants, but roots normally stopped growing after 4–5 wk. Soon thereafter nematode activity ceased and many nematodes died.

In all cultures, females and juveniles of *C. xenoplax* moved on and through the agar medium to feed on roots. Nematodes spent a considerable amount of time moving through the medium. Immediately preceding feeding periods, nematodes explored the root surface with their heads. The stylet was not used during this exploration, but the head prodded and the lips moved over the root surface. On four occasions, exploration occurred in the vicinity of another nematode that was feeding. The nematode bumped the feeding nematode with its head and rubbed the root surface near the feeding site. Usually nematodes in a culture were dispersed over the roots, with only an occasional group of two to four nematodes feeding within one body width of each other. After selection of a site to initiate feeding, the head was pressed against the root epidermis, resulting in compression of the cuticle annules at the head. The head soon became stationary, and the stylet insertion phase was initiated. Most nematodes remained entirely outside of root tissues during feeding. However, nematodes occasionally embedded their anterior in natural cracks associated with lateral root emergence and in splits in the epidermis and cortex that resulted from secondary growth of roots.

The following observations were derived from three nematodes feeding on tomato roots that were videotaped for the duration of feeding (3–5 days). Intermittent observations of nematodes on the other hosts are mentioned and confirm the general nature of this behavior. Aspects of the behaviors that were apparently consistent across all hosts observed were specified.

Stylet insertion involved no rapid motion, was directed at a single point, and required 80 min in one case (Fig. 1). During the first phase, the stylet was thrust a short distance into the tissue once or twice per minute. After a time, deeper penetration occurred, and the stylet was retracted less frequently. During the final phase (about 30 min), no stylet retractions were observed other than a very slight back-and-forth movement (not shown) that occurred intermittently during the remainder of the insertion phase. The general pattern for stylet insertion included an initial phase of slow stylet thrusting followed by a phase of slow insertion to the final depth for feeding. The stylet was inserted usually to about half of its length into the root tissue. Variations among the insertion sequences may have occurred in the duration of the two phases, but measurement of this variation was impossible because candidate nematodes could not be identified before stylet insertion had begun.

Immediately after stylet insertion, a secretion phase was initiated that lasted 1–3 h. The posterior portion of the metacorpus periodically twitched, and the pump chamber slightly opened intermittently during this phase. Carnation and tomato roots were sufficiently clear for visualization of the tip of the stylet in a cortical cell. Globular secretions accumulated around the stylet tip in cortical cells of both hosts. However, the origin of these secretions within the nematode could not be ascertained.

After secretion, the ingestion phase began. The stylet remained stationary throughout the feeding episodes recorded for the three nematodes on tomato, indicating that feeding involved a single cortical cell. During short daily observations of individual nematodes on the other hosts, no change in the position of the stylet was ever detected during feeding episodes (Fig. 2). The position of the stylet was precisely documented each day with a photograph. The cytoplasm of parasitized tomato cells appeared aggregated around the stylet tip. The feeding period lasted for 4–5 days and the metacorpus pumped continuously in the three videotaped nematodes. On the basis of the short daily observations on all hosts, feeding periods lasted 1–8 days. The metacorpus was pumping during every observation period. Two additional adults were videotaped for continuous periods to confirm that pumping was continuous for at least 7 h during feeding episodes. In carnation and tomato roots, the tonoplast in the parasitized cell pulsed with the pumping of the metacorpus. The rate of pulsation by the pump chamber varied for nematodes feeding on the different

plant hosts; it tended to be slowest for nematodes feeding on western sand cherry (1.3 pulsations per second) and most rapid for those feeding on herbaceous hosts (1.5 pulsations per second). The significance of this variation is not known. The anus was monitored for 4 h during the feeding period of one nematode. Flexing by muscles near the anus appeared to indicate that defecation was occurring.

During feeding, nematodes increased in diameter and lengthened slightly, and in adult females ovaries developed (Fig. 2). Once the metacorpus stopped pumping, the stylet was slowly and smoothly withdrawn in 1–5 min. On one occasion, the stylet became stuck in the parasitized tomato cell. The nematode moved back and forth for over 1.5 h before the stylet was freed. Retraction of the stylet occurred after the stylet was completely removed from host tissues by movement of the head. If a nematode was dislodged by a mechanical disturbance before feeding stopped, metacorpal pumping continued for 5–10 min and then, after pumping stopped, the stylet was slowly retracted.

Gravid females stopped feeding, moved through the agar, and deposited eggs (10–20 per female). Eggs deposited in or on the agar medium hatched in 8–10 days. For starved nematodes, the intestine appeared empty initially and then was densely packed with dark material after 1–3 days of feeding. Molting of juveniles was initiated soon after the feeding episode. Necrosis was not observed in cortical cells at feeding sites while the nematodes were feeding or for the next 2 days after feeding ceased and nematodes departed. Although necrotic cells were observed on some roots, these could not be associated with known feeding sites. In general, necrosis was not a common occurrence associated with feeding by this nematode under these cultural conditions.

One to four males of *C. xenoplax* were observed in four different cultures on western sand cherry. Males moved in a serpentine fashion and migrated more rapidly through the agar than females. The distinctive male morphology was first evident in fourth-stage juveniles.

DISCUSSION

As an ectoparasite, *C. xenoplax* appears to behave differently from some other ectoparasitic nematodes in that it feeds continuously from a single-root cortical cell for 1–8 days. No necrosis was associated with feeding sites for individual nematodes, and necrotic tissue was not a common symptom on parasitized roots. The details of this behavior were not anticipated nor reported previously. The feeding relationship developed through the five phases described by Wyss (27), but each phase lasted considerably longer than those described for most other ectoparasitic nematodes. This type of feeding behavior appears to be more highly evolved than that exhibited by nematodes that feed from a cell for very short times before moving to a new host cell. Other species of *Criconemella* and species of *Paratylenchus* have patterns of feeding behavior similar to that of *C. xenoplax* with respect to the duration of feeding at a single site, and they may develop

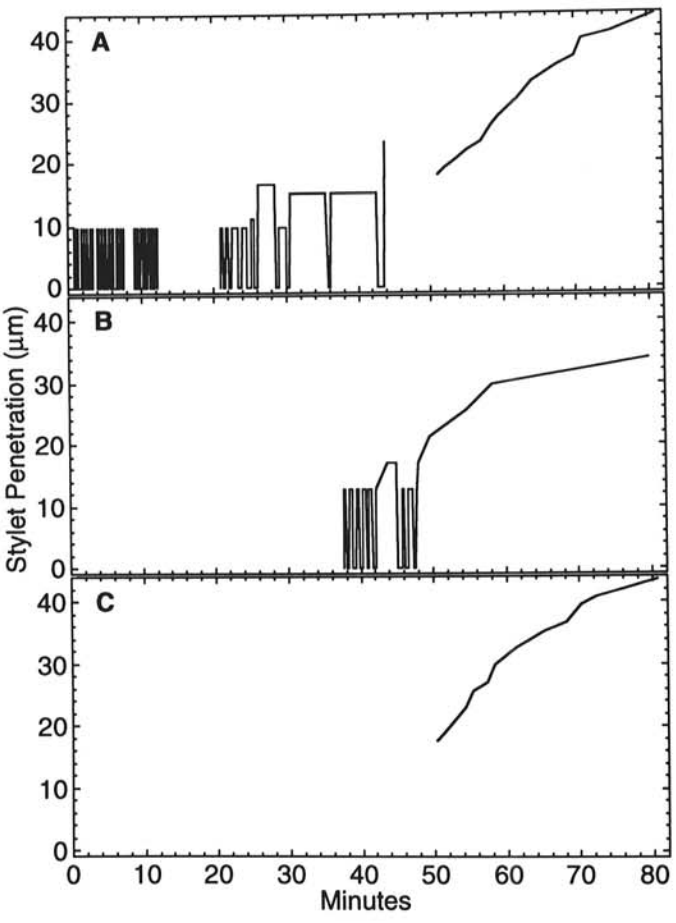

Fig. 1. Depth of insertion of the stylet tip by *Criconemella xenoplax* adults into tomato roots over time. **A–C,** Three nematode traces aligned according to the end of the insertion event (the initiation of stylet insertion was not observed). Stylet insertion involved two phases, slow stylet thrusting (1–2 thrusts per minute) followed by slow insertion to the final depth. Stylets were about 86 µm long. Periods in which observations were not recorded are indicated by the absence of a trace line.

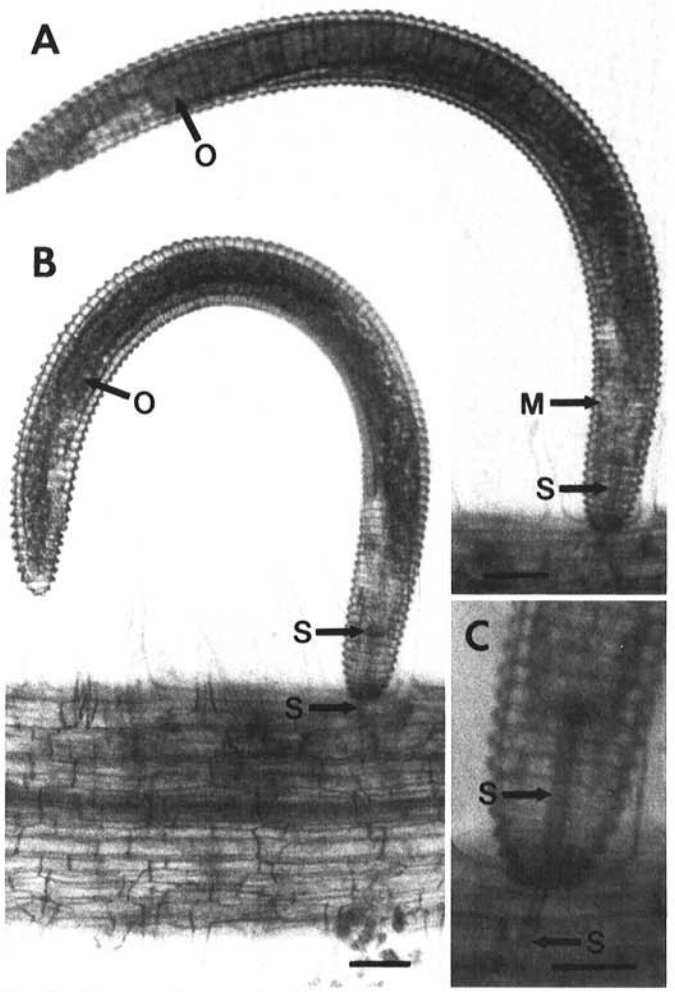

Fig. 2. *Criconemella xenoplax* feeding on root of tomato in monoxenic culture. During the feeding episode oocytes matured. **A,** This adult female had been feeding for at least 5 days. Oocytes were mature when the nematode left the root and egg deposition soon followed. **B,** The same nematode as in **A,** but 4 days earlier. Note the developing oocytes and the position of the stylet. **C,** An enlarged view of the nematode head illustrating the position of the stylet, which was unchanged at each daily observation during the feeding episode. M, metacorpus; O, oocyte; S, stylet. Bars = 50, 50, and 25 µm for **A–C,** respectively.

feeding relationships similar to those described here (9,16–18,21).

Our observations suggest that nutrients were continuously supplied by a single host cell during the prolonged ingestion phase of the feeding cycle. Doncaster (3) speculated that enhanced intercellular movement of nutrients from adjacent cells is likely when nematodes feed from a single cell for long periods. In an ultrastructural study of plant cells parasitized by *C. xenoplax,* single-root cortical cells were modified extensively during the feeding episode (8). Most host cell organelles accumulate around thestylet tip. The plasma membrane of the food cell is invaginated by the stylet and remains intact except for an opening created at the stylet orifice. When nematodes feed near root tips, plasmodesmata that connect the cytoplasm of the parasitized cell with the cytoplasm of neighboring cells are extensively modified. Modifications include enlargement of plasmodesmatal channels and, therefore, may allow an increased flow of solutes from the neighboring cells into the food cell to support sustained ingestion of nutrients by the nematode.

A calloselike material was deposited around stylets where they passed through host cells (8). The deposit was readily apparent in electron micrographs of cells fixed after stylet withdrawal. This material may have caused the stylet of one of the observed nematodes to become lodged in the cell.

All plant species used in this study are reported as suitable hosts for *C. xenoplax.* Nematode population densities increased 7.5-fold on tomato in 3 mo (19) and 120-fold on Alenius carnation in 3 mo (20), but no measurements were made with peach. Population densities increased 6.6-fold on Dixie crimson clover and 8.8-fold on Nemaguard peach in 90 days (29). Selections of western sand cherry were less suitable as hosts than Nemaguard peach (26). Although tomato and carnation appear to be good hosts in monoxenic cultures on the basis of our ability to sustain populations on these hosts through subcultures, many second-stage juveniles failed to develop, which indicated that they had not fed on roots. This same phenomenon has not been reported in soil environments, but the proportion of second-stage juveniles in populations resulting from short-term studies in soil may need to be quantified to accurately portray host suitability. Nematode population densities may increase substantially because of egg deposition by feeding adults, but high population densities will not reflect root injury if only a few of the resulting second-stage juveniles feed.

Several authors referred to observations of *Criconemella* spp. embedded in root tissues and speculated that these nematodes should be considered semiendoparasites (16,20,21). In this study, we saw no evidence of the type of nematode behavior that has been associated with rupture of plant cells (2–4). When the anterior of *C. xenoplax* was observed within root tissue, natural cracks in the epidermis and cortex were always detected as access points. None of the previous reports provided evidence that the embedded nematodes of this or other species of *Criconemella* had penetrated intact root tissue. We believe that embedded nematodes pictured in other reports on *Criconemella* spp. could have entered tissues through natural openings in every case. Our observations support a general concept that this nematode feeds exclusively as an ectoparasite.

Although females and juveniles of *C. xenoplax* moved through the agar by alternately elongating and shortening the body as previously described (21–23), the males observed moved in a serpentine fashion that is typical of most other soilborne nematodes. This pattern of movement for males has not been mentioned to our knowledge in published reports.

Ectoparasitic nematodes are considered to have a primitive mode of parasitism (27). However, the feeding behavior and the cellular phenotype (8) indicate that *C. xenoplax* has a rather highly evolved feeding relationship with its hosts. Furthermore, the nature of the feeding relationship of this species with host plants appears to be relatively nondestructive in that the parasitized cell is not killed. Most reports concerning direct observations of parasitized roots indicate that high densities of this nematode are required for root injury (10,21). Nematode population densities in our cultures were relatively low and never resulted in simultaneous feeding by a large number of nematodes on a contiguous segment of root, as has been depicted in some reports (21). Root injury most likely is caused by extreme physiological stress resulting from the simultaneous feeding activity of many nematodes rather than by direct physical damage associated with feeding by this nematode. Other species in the genus *Criconemella* and perhaps species in other genera in the Criconematoidae probably share many of the behavioral characteristics described here for *C. xenoplax.*

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