Host Response to *Sarisodera hydrophila* Wouts and Sher, 1971

M. Mundo-Ocampo and J. G. Baldwin[1]

Abstract: The histopathology of two populations of *Sarisodera hydrophila* Wouts and Sher, 1971 was examined on *Salix lasiolepis* Benth. (willow), *Populus fremontii* Wats. (cottonwood), and *Lyonothamnus floribundus* Gray (ironwood) using light microscopy as well as scanning and transmission electron microscopy. *Sarisodera hydrophila* induces formation of a single uninucleate hypertrophied cell (giant cell) which varies only slightly among the three hosts. The giant cell is enclosed by the root stele and contacts phloem, vascular cambium, and xylem. The single hypertrophied nucleus of the giant cell is ameboid or lobulate in shape, generally with a single nucleolus. The cell is characterized by a wall which is separated into two distinct regions about 2 μm and 13 μm thick; the thicker region occurs adjacent to the nematode head. Cell wall ingrowths, such as those associated with host responses to certain other plant-parasitic nematodes, were not observed in giant cells induced by *S. hydrophila*. However, a high frequency of pit fields with plasmodesmata occurred in the thinner portion of the cell wall which is adjacent to vascular elements. Roots of the three hosts simultaneously infected with S. *hydrophila* and *Meloidogyne* sp. resulted in adjacent responses characteristic of each nematode, supporting the view that the specific type of host response is a function of the nematode rather than the host. The varying expressions of host responses among Heteroderoidea may be useful in testing congruency with existing interpretations of phylogeny. *Key words:* Heteroderoidea, histopathology, syncytium, uninucleate giant cell.

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Heteroderoidea, specifically *Heterodera* Schmidt, 1871 *sensu lato* and *Meloidogyne* Goldi, 1892 have been considered to have the most complex host-parasite relationship among plant parasitic nematodes. They induce specialized cells which sustain sedentary feeding parasitic stages (1,9,10,13,16, 20,41). These responses to *Heterodera* and *Meloidogyne* have been examined on numerous host species (5,6,10,15,16,21,31,41). However, the basic histopathology is similar among plant species but varies among nematode genera.

Terminology to refer to host reactions induced by members of Heteroderoidea generally has been inconsistent, but we have selected to use the nomenclature described by Bird (6). Thus, *Heterodera* induces formation of a *syncytium* which is defined as a multinucleate mass of protoplasm formed by fusion of uninucleate cells; usually this is accompanied by cell wall dissolution. On the other hand, *Meloidogyne* typically induces the formation of a *coenocyte* which is a multinucleate mass of protoplasm formed by repeated nuclear division, without formation or dissolution of cell walls (17,20). Some researchers have suggested that cell wall dissolution and cell fusion are also induced by *Meloidogyne* (3,4,7, 11), resulting in a combination coenocyte-syncytium. Host responses for both *Meloidogyne* and *Heterodera* have been considered to be nematode-induced transfer cells, because of the presence of cell wall ingrowths involved in short distance solute transport (22,23,24). *Hylonema ivorense* Luc et al., 1978 induces the formation of a single uninucleate hypertrophied cortical cell which may be termed *giant cell,* according to the definition by Bird (6). However, no information regarding the possible presence of cell wall ingrowths in the single uninucleate giant cell of Heteroderoidea is yet available.

The variation in histopathology among genera of Heteroderoidea emphasizes the need to characterize the type of host response induced by members of genera which have not yet been examined; these characterizations are also needed to determine if the pattern exhibited by histological responses among Heteroderoidea is congruent with existing interpretations of phylogeny. We selected to first examine responses of *Sarisodera hydrophila* Wouts and Sher, 1971 from the type locality on one host, as well as a population from Santa Cruz Island, California, on two hosts.

MATERIALS AND METHODS

Roots of *Salix lasiolepis Benth.* (willow), and *Populus fremontii* Wats. (cottonwood) infected with various development stages

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[1]Graduate student and Assistant Professor, respectively, Department of Nematology, University of California, Riverside, CA 92521. This represents a portion of the senior author's Ph.D. thesis.

of *S. hydrophila* were collected at the type locality, 12 miles east of Temecula, California. In addition, infected roots of *Lyonothamnus floribundus* Gray (ironwood) were collected at Santa Cruz Island. Roots of each of the three hosts also had galled regions infected with *Meloidogyne* spp., and these were collected to process for comparison. (Preliminary observations of these populations of *Meloidogyne* suggest that they may be undescribed new species.) The roots were processed for histological examination, including bright field and Nomarski interference light microscopy (LM) as well as scanning (SEM) and transmission (TEM) electron microscopy.

Root pieces for bright field LM were fixed in 3.0% formaldehyde for 24 h, followed by rinsing in distilled water and dehydration in a graduated ethanol and N-butyl alcohol series (19). Root pieces were oriented and embedded in Paraplast-Plus tissue embedding medium. Sections about 10 μm thick were cut, mounted on glass slides, and stained with safranin and fast green (2).

Root pieces were fixed for Nomarski interference LM in 3.0% glutaraldehyde in 0.025 M phosphate buffer at pH 7.2. After rinsing in buffer, the pieces were dehydrated in a graduated acetone series and embedded in Spurr's resin (38). Sections (2 μm) were cut with glass knives using a Porter Blum MT-2B ultramicrotome. They were mounted on glass slides coated with Haupt's solution, and observed with Normarski interference optics; some slides were stained with 1.0% toluidine blue in 1.0% sodium borate.

Root pieces were fixed for SEM in 2.0% glutaraldehyde in 0.025 M phosphate buffer at pH 7.2 for at least 12 h. Specimens were then washed in buffer and postfixed in 2.0%osmium tetroxide (OsO_4) for 2 h. After rinsing in distilled water, the tissue was dehydrated in a graduated acetone series. Roots were split in longitudinal and cross sections with a clean sharp razor blade under the dissecting microscope to expose feeding sites of the nematodes. Additional segments were treated to reveal inner cell wall structure by using cytoplasm digestion techniques modified from Kinden and Brown (29) and Jones and Dropkin (27). Following postfixation in osmium tetroxide and rinsing, specimens were placed in 1.0% aqueous periodic acid for 2 min and rinsed five times in distilled water during a 10-min period. The specimens were then placed in aqueous 4.0% potassium hydroxide (KOH) for about 30 min at 55 C, washed in distilled water, and transferred to 1.0% acetic acid for 5 min. After rinsing with distilled water for 10 min, the samples were returned to osmium tetroxide for 3 h for further hardening. Nondigested and digested specimens were critical point dried using carbon dioxide; sputter-coated with 20 nm gold-palladium and examined with a JEOL JSM-35C scanning electron microscope at 15 KV.

Tissue was prepared for transmission electron microscopy (TEM) as for Nomarski interference LM except that following fixation in glutaraldehyde tissue was postfixed in 2% osmium tetroxide as for SEM. Thin sections were mounted on fomvar coated grids, stained with uranyl acetate and lead citrate (40), and examined with a Hitachi H-600 transmission electron microscope.

RESULTS

Sarisodera hydrophila induces formation of a single uninucleate hypertrophied cell (giant cell) with similar responses between populations examined and among willow, cottonwood, and ironwood (Figs. 1, 2, 3). The following description of the host re-

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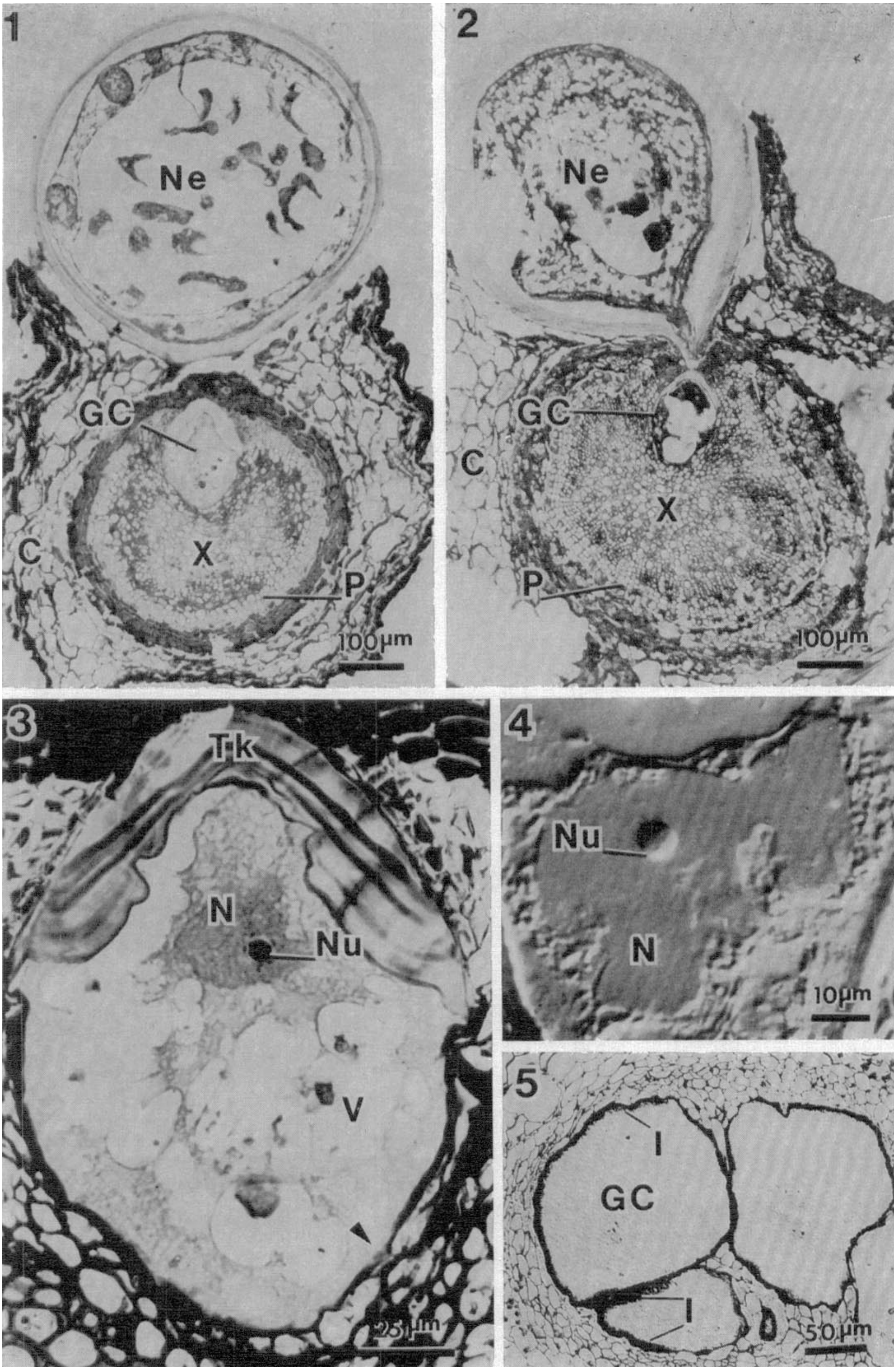
Fig. 1–5. Transverse sections through roots infected with *Sarisodera hydrophila* (unless indicated otherwise) and *Meloidogyne* sp. 1) Bright field LM of willow showing giant cell (GC) and adjacent nematode (Ne). C = cortex, P = phloem, X = xylem. 2) Bright field LM of ironwood showing a giant cell (GC) with adjacent nematode (Ne). C = cortex, P = phloem, X = xylem. 3) Enlargement of giant cell from section adjacent to that in Figure 1, including large nucleus (N) with single nucleolus (Nu) adjacent to thick portion of the cell wall (Tk). Arrowhead indicates minute interruption in cell wall. V = vacuole. 4) Nomarski interference LM of nucleus (N) including an enlarged nucleolus (Nu). 5) Nomarski interference LM stained with toluidine blue, of willow showing cluster of giant cells (GC) induced by *Meloidogyne* sp. I = ingrowths.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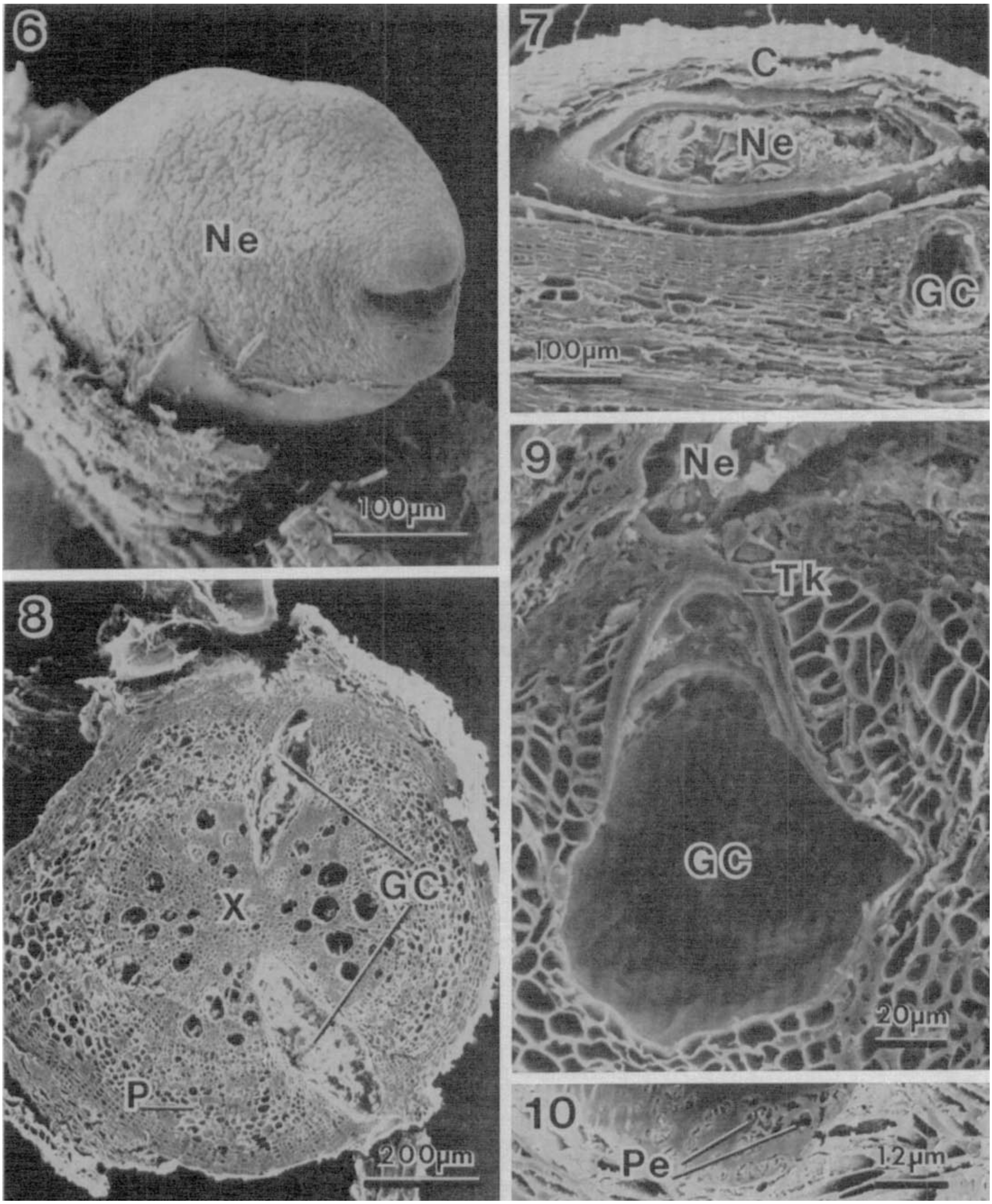
sponse focuses on willow but applies to all responses with exceptions being noted.

Surface observations of roots infected with *S. hydrophila* showed yellowish-white sedentary females partially embedded within the roots (Fig. 6). In some cases, the nematodes occurred under the cortex and were not noticeable unless the cortex was removed (Fig. 7). No external symptoms, such as galls and/or necrotic lesions, were



Figs. 6–10. SEM of *Sarisodera hydrophila* and infected willow roots. 6) Female (Ne) embedded in root. 7) Longitudinal section of root with female (Ne) under cortex (C) and adjacent to giant cell (GC). 8) Transverse section of root, with two giant cells (GC) adjacent to xylem (X) and phloem (P). 9) Giant cell (GC) with thick cell wall (Tk) adjacent to nematode head (Ne). 10) Internal surface of giant cell wall showing perforations (Pe).

evident. In contrast, roots infected with *Meloidogyne* spp. had galls and egg masses typical of root-knot infection.

Sections revealed that *S. hydrophila* establishes a feeding site at the internal boundary of the cortex; as the cell where it initiates the giant cell expands radially it becomes enclosed by the root stele and contacts phloem and xylem (Figs. 1, 2, 8). Adjacent cells are compressed and distorted as a result of enlargement of the giant cell; however, no hyperplasia or hypertrophy in surrounding tissues was observed. Only one giant cell occurs per female, although two or more adjacent females may result in giant cells close to each other (Fig. 8). Giant cells vary in size from approximately 100 to 300 μm long and 70 to 200 μm wide and are shaped from ovoid to irregular. Some variations may be host specific; for example, cottonwood has a tendency to have larger and more irregularly shaped giant cells.

The most conspicuous feature of the giant cell is the cell wall. Two distinct regions occur, one of which has extreme thickening (TkCW) and varies from 12 to 15 μm wide (Figs. 3, 9) and another more internal region which is about 2 μm wide. The TkCW contacts phloem and cork cells and occurs on the side of the cell adjacent to the nematode (Figs. 1, 2, 3, 9, 11). The internal surface of the TkCW is irregularly thickened (Fig. 3); however, no cell wall protuberances or boundary formations were observed with LM, SEM, or TEM (Figs. 3, 9, 10, 12, 13, 14). The TkCW is composed of microfibrils and is continuous with walls of adjacent dead cork cells (Fig. 11). The thinner part of the wall generally includes an inner layer of microfibrils similar to those of the TkCW (Fig. 14). Transverse sections indicate interruptions in the wall and connections between cytoplasm of the giant cell and adjacent vascular tissue (Fig. 3). These interruptions appear as perforations with SEM and are elucidated with TEM to be primary pit fields with numerous plasmodesmata which connect cytoplasm of giant cells with adjacent xylem and phloem elements (Figs. 12, 13, 15, 16); these pit fields do not appear to differ from those between adjacent phloem cells.

During the first stages of giant cell development, cytoplasm is optically dense and granular. As the nematode and cell mature, small vacuoles, plastids, mitochondria, and rough endoplasmic reticulum are abundant (Figs. 14, 17, 19, 20, 21). Eventually the cell is dominated by a large central vacuole and other organelles are restricted to the periphery. Plastids are particularly abundant around the nucleus; they are electron dense and may contain lipid (Figs. 17, 21). Mitochondria and rough endoplasmic reticulum appear normal and are distributed throughout the cytoplasm (Figs. 14, 19, 20). The nucleus of the giant cell is about 30–60 μm in diameter and is ameboid or lobulate in shape (Figs. 4, 17). Generally, a given nucleus includes one enlarged electron-dense nucleolus, but in some cases two or more nucleoli are present (Figs. 17, 18). Nucleoli may be either adjacent or separated, and frequently they include small electron-lucent regions (Figs. 17. 18).

Root sections of willow, ironwood, and cottonwood infected with *Meloidogyne* spp. showed a host response typical for the nematode genus, including a cluster of multinucleate cells. Toluidine blue stained a "fringe" on the internal surface of the cell walls indicating typical wall ingrowths (Fig. 5).

DISCUSSION

Sarisodera and *Heterodera sensu lato* are considered by some taxonomists to comprise Heteroderinae, primarily because they share the ability to form cysts (37,42). However, the present study suggests striking differences regarding the means by which each group subjugates its host to sustain feeding. That is, *Sarisodera* sp. induces a single uninucleate giant cell (SUGC) whereas *Heterodera sensu lato* results in a syncytium (32). The distinct response induced by *Sarisodera* sp. is consistent on the three hosts examined. Similarly, *Heterodera sensu lato* invariably is associated with a syncytium throughout its host range (12,13,20, 25,31,33,36). Thus, the specific type of host response apparently is a function of the nematode rather than the host. This view is further supported by observations of a consistent host response among three hosts infected with *Hylonema ivorense* (39). Jones and Dropkin (26) observed that species of *Meloidogyne, Heterodera,* and *Rotylenchulus* induce distinct responses on the same host and proposed that initiation of each response is determined by the nematode through introduction of specific compound(s) and withdrawal of cytoplasm. Similarly, we have shown that plant roots simultaneously infected with *Sarisodera* sp. and *Meloidogyne* sp. resulted in adjacent responses characteristic of each nematode. These observations support the view that cell modifications induced by *Sarisodera* sp. are nematode specific.

The induction of a SUGC is not unique to *Sarisodera* but occurs among other Heteroderidae including *Hylonema* (39), as well as *Meloidodera and Cryphodera* (Mundo-Ocampo and Baldwin, unpublished observations). Whereas these cells are fundamentally similar with respect to the uninucleate condition, they differ in details. For example, the SUGC of *Sarisodera,* unlike *Hylonema,* is characterized by the TkCW, and the giant cell of *Sarisodera* is not associated with adjacent necrotic tissue.

Studies of host responses to sedentary nonheteroderids, including *Nacobbus* spp. and *Rotylenchulus* spp., allow for additional comparisons with *Sarisodera* sp. Although *Nacobbus* spp. induce a syncytium in the several hosts examined (28), it resembles the SUGC of *Sarisodera* sp. in certain respects. For example, wall ingrowths are absent, but pit fields with numerous plasmodesmata occur between the syncytium and adjacent vascular elements. *Rotylenchulus macrodoratus* Dasgupta et al., 1968 induces in soybean and oak a SUGC which resembles that of a *Sarisodera* but differs by the absence of a thickened portion of the cell wall (TkCW) and the presence of wall ingrowths (8). On the other hand, *Rotylenchulus reniformis* Linford and Oliveira, 1940 induces a syncytium in the same hosts (35).

The most conspicuous feature of the SUGC induced by *Sarisodera* sp. is the remarkable deposition of wall material (TkCW) adjacent to the nematode head. The material is fibrous and its chemical structure probably includes pectins and hemicellulose (25,34). The position of the material suggests that it is a defense response to stylet penetration. The remaining portion of the cell wall has periodic regions which are particularly thin (i.e., pit fields); wall ingrowths are absent. This is in contrast to the abundant ingrowths for increased transport of solutes in transfer cells associated with other nematodes (20,25). The presence of ingrowths in cells modified by *Meloidogyne* on willow, cottonwood, and ironwood and their absence in the same hosts in cells modified by *Sarisodera* suggests that occurrence of ingrowths is determined by the nematode rather than the host. The pit fields in SUGC of *Sarisodera* have a high frequency of plasmodesmata which are adjacent to vascular tissues. Jones (21) notes that this arrangement provides a pathway for transport of solutes from vascular tissue to giant cells.

Cytoplasmic modifications observed in the SUGC of *Sarisodera* sp. are similar to those observed for host responses of other sedentary nematodes, including the presence of numerous plastids, mitochondria, and rough endoplasmic reticulum (16,20, 21). The enlarged single nucleus in the SUGC of *Sarisodera* sp. resembles that of *Hylonema* sp. and *R. macrodoratus.* No information is available regarding the mechanism of enlargement of the nucleus, although Cohn and Mordechai (8) suggest that mitotic stimulation is absent in the SUGC induced by *R. macrodoratus.*

Hypotheses of phylogeny of Heteroderidae can be tested by the discovery of new characters that occur in varying states among members of the group. We have considered that the character "host response" is expressed as a SUGC, cluster of

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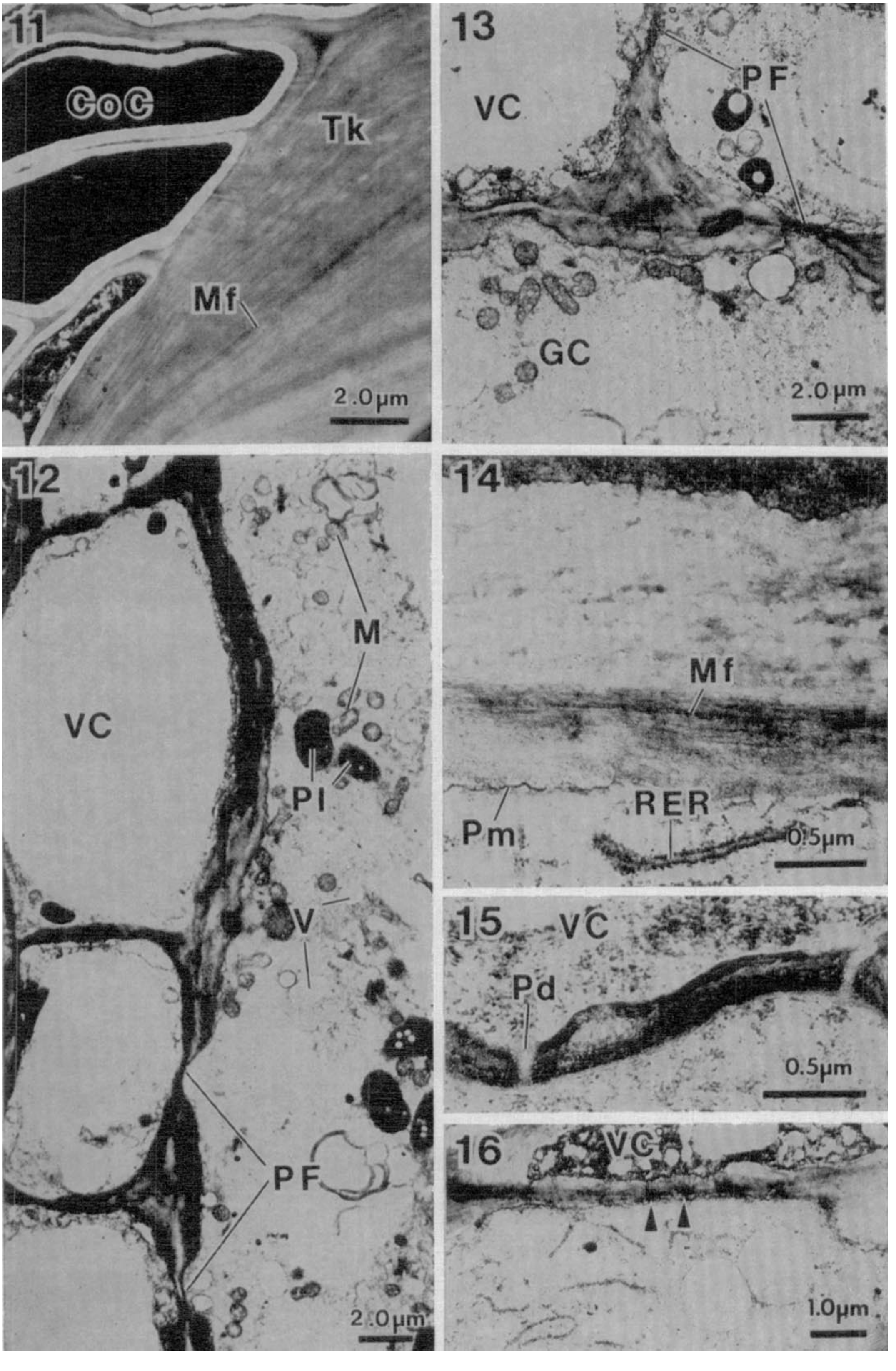
Figs. 11–16. TEM of giant cell wall in willow roots infected with *Sarisodera hydrophila.* 11) Thick cell wall (Tk) composed of microfibrils (Mf). CoC = cork cells. 12) Thin part of wall adjacent to vascular cells (VC) showing pit fields (PF). M = mitochondria, V = vacuoles, Pl = plastids. 13) Thin part of wall of giant cell (GC) and wall between two vascular cells (VC) showing pit fields (PF). 14) Thin part of cell wall with layer of microfibrils (Mf) adjacent to giant cell plasmalemma (Pm). RER = rough endoplasmic reticulum. 15) Enlargement of plasmodesmata (Pd) in pit field. 16) Pit field between giant cell and vascular cell (VC). Arrowheads indicate sites of plasmodesmata.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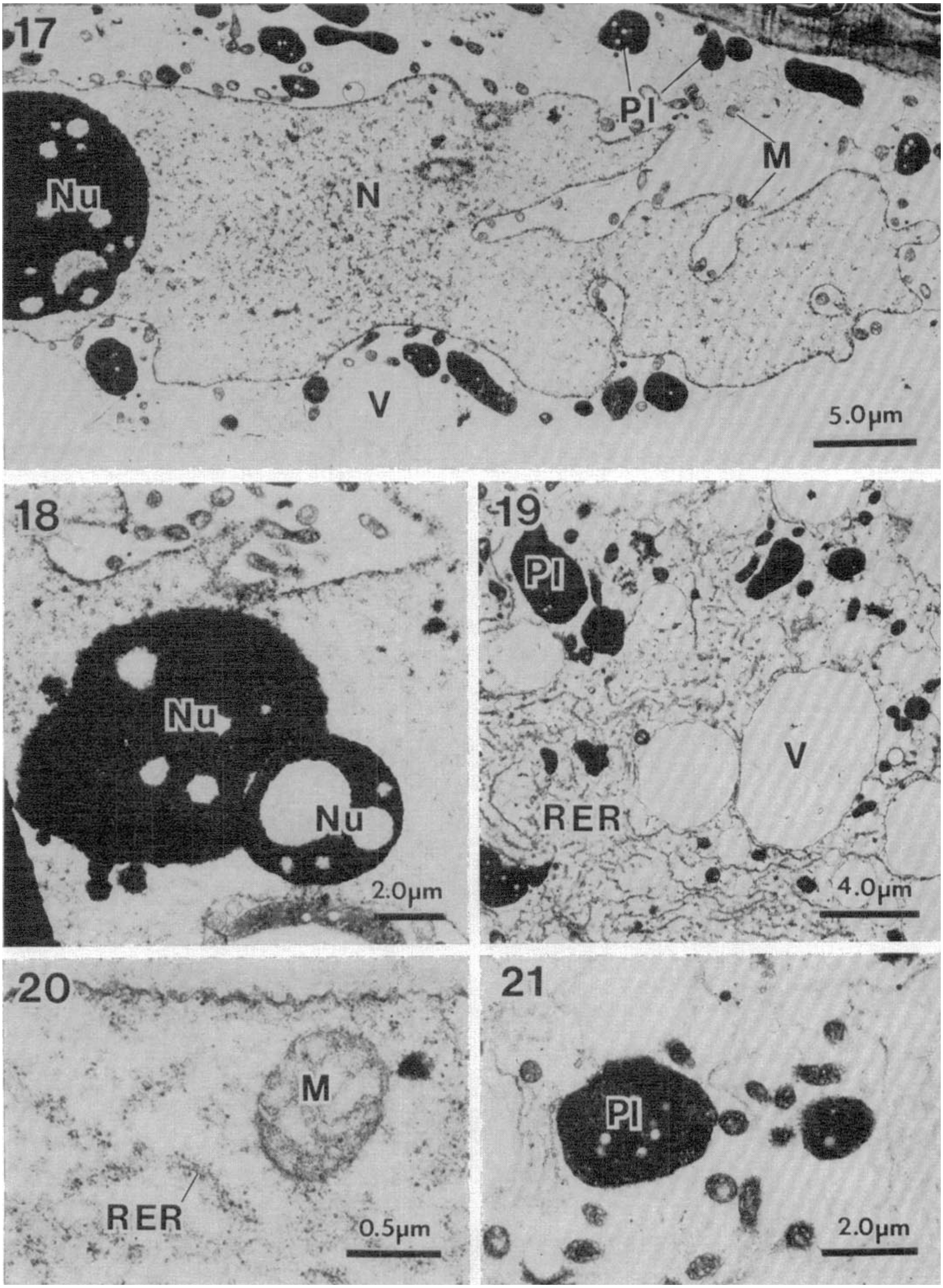

Figs. 17–21. TEM of organelles of giant cell induced by *Sarisodera hydrophila* in willow roots. 17) Portion of enlarged nucleus (N) with electron dense nucleolus (Nu). M = mitochondria, Pl = plastids, V = vacuoles. 18) Pair of adjacent nucleoli (Nu). 19) Cytoplasm including vacuoles (V), plastids (Pl), and rough endoplasmic reticulum (RER). 20) Mitochondria (M) and rough endoplasmic reticulum (RER) adjacent to plasmalemma (Pm). 21) Enlargement of plastid (Pl).

multinucleate giant cells, or syncytium. Utilization of these three character states in interpreting phylogeny requires that they each be a function of the nematode (i.e., not altered with the host); we have noted evidences in support of this hypothesis. The expression of a uninucleate giant cell by *Meloidodera* spp., *Cryphodera* sp. (Mundo-Ocampo and Baldwin, unpublished observations), *Hylonema* sp. (39), and *Sarisodera* sp. versus a syncytium in *Heterodera* spp. *sensu lato* is not incongruent with the hypothesis of phylogeny of Heteroderidae indicated by a cladogram proposed by Ferris (14). However, congruency assumes the capacity to form a syncytium, to be the derived state. Evidence for or against this assumption might be gained through nematode-host development studies or outgroup comparisons. The cladogram indicates *Sarisodera* and *Heterodera sensu lato* as derived from a common ancestor, primarily because they share the ability to form cysts (14). Although some investigators (18,30, 42), suggest that cysts of the two groups arose independently, evidence comparing the specific nature of the two cysts is not yet available. If additional shared derived characters are discovered, a common ancestry would be supported; on this basis we suspected prior to this study that *Sarisodera* would produce a syncytium similar to that of *Heterodera sensu lato*. However, the host response to *S. africana* also needs to be examined, particularly since relative to *S. hydrophila*, it shares a number of characteristics with certain *Heterodera* spp. Examination of host responses of species of additional genera, including *Ataloderа*, *Thecavermiculatus*, *Dolichodera*, and *Verutus*, will further elucidate the usefulness of host responses in conjunction with other characters for interpretating phylogeny of Heteroderoidea and, specifically, the relationship between *Sarisodera* and *Heterodera sensu lato*.

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