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Anatomical Changes Induced by *Punctodera chalcoensis* in Corn Roots

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Punctodera chalcoensis Stone et al. is a cyst nematode parasitizing corn (*Zea mays* L.) and teosinte (*Zea mexicana* (Schrad.) Kuntz) in Mexico (7). This nematode damages corn severely in Tlaxcala and Puebla states of Mexico (7). Pathogenic studies of *P. chalcoensis* on corn have been conducted in the greenhouse (2). Mundo-Ocampo and Baldwin (6) reported that *P. chalcoensis* induces a syncytium in roots. These authors suggested that *Globodera*, *Heterodera*, and *Punctodera* evolved from a common ancestor, in part because species in these genera induce similar syncytia. However, no description is given of the anatomical changes induced by *P. chalcoensis*, nor is the plant host mentioned.

We studied the anatomical alterations induced by *P. chalcoensis* on corn (*Zea mays* cv. Criollo Chalqueño) roots. Corn roots infected with *P. chalcoensis* were collected from a field in Amecameca, Mexico. Roots were gently washed free of soil, cut in 4–5-mm-long segments, fixed in Craf III (chromic acid, acetic acid, formalin, distilled water), dehydrated in a tertiary butyl alcohol series, and embedded in paraffin. Embedded roots were cut in 10–15-μm sections which were stained with safranin, crystal violet, fast-green, and orange G; mounted in Canada balsam; and examined under a compound microscope (3).

Punctodera chalcoensis females were usually observed with the posterior portion of the body protruding from the root surface. However, many females were observed with the entire body embedded in the root tissues (Fig. 1A). Nematodes penetrated the cortex, damaging cortical cells. They established permanent feeding sites in the endodermis by modifying endodermal and adjacent pericycle cells to form a syncytium (Fig. 1A, B). Pericycle cells enlarged, and the cytoplasm became very dense (Fig. 1B). Phloem and vascular parenchyma cells were also incorporated into the syncytium (Fig. 1B). Metaxylem elements sometimes fused with syncytium but more often were compressed by the syncytium expansion (Fig. 1B, C). During cell fusions, walls of adjacent cells dissolved, leaving only wall segments inside the syncytium (Fig. 1C). Syncytial nuclei were usually hypertrophied, deeply indented, and with prominent nucleoli (Fig. 1D); they averaged 13 μm wide × 18 μm long, whereas normal pericycle cell nuclei averaged 2.5 μm wide × 3.5 μm long. There was no evidence of mitotic activity inside the syncytia.

Punctodera chalcoensis commonly initiated

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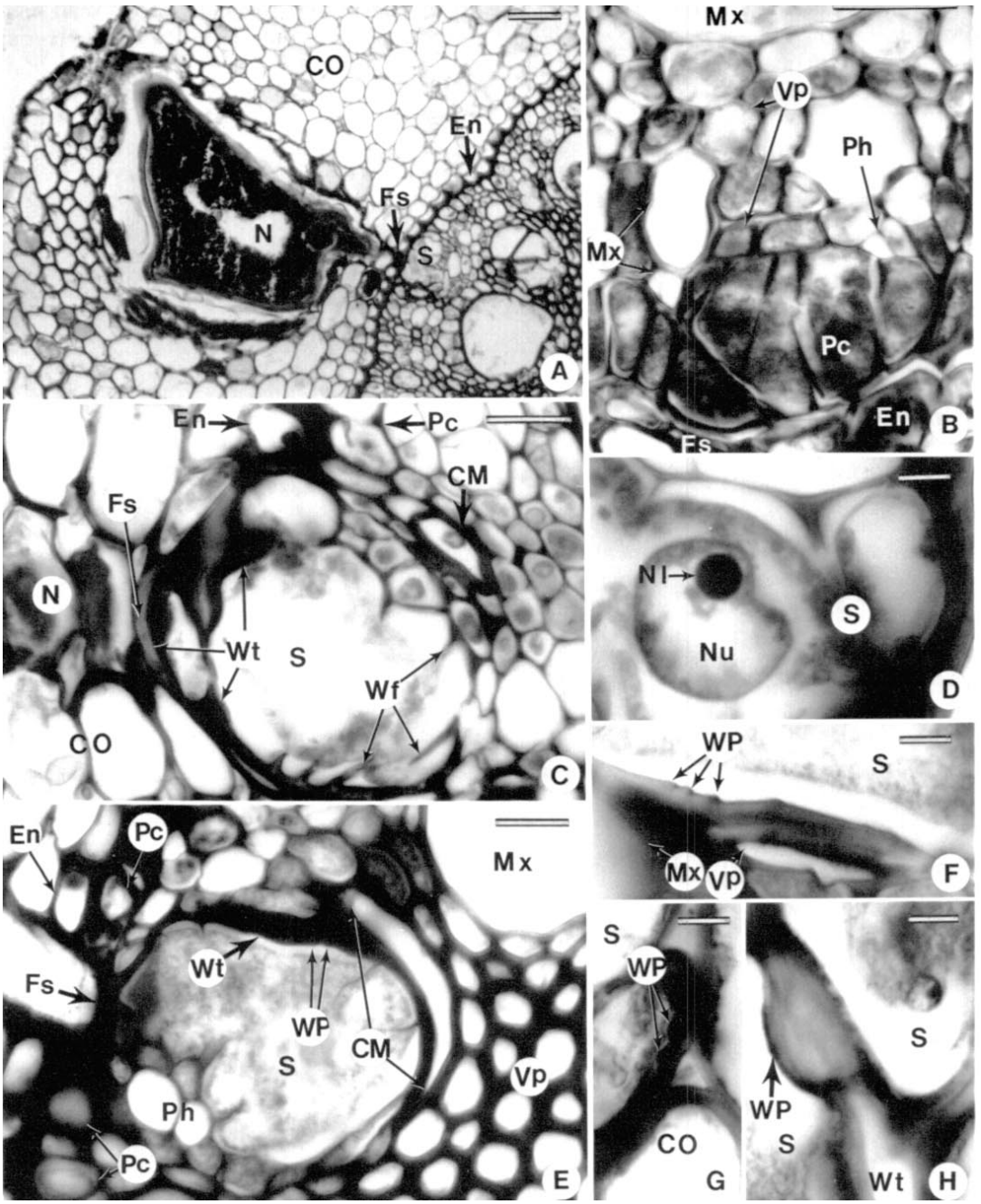
FIG. 1. Anatomical alterations caused by *Punctodera chalcoensis* in corn roots. A) Cross sections showing a female nematode (N) embedded in the cortex (CO) and feeding on a syncytium (S) originating from an endodermal cell (En). Note deeply stained cortical cells adjacent to nematode body. Fs = nematode feeding site. Scale bar = 50 μm. B) Cross section showing large and partially fused pericycle cells (Pc) in proximity to nematode feeding site (Fs) in the endodermis (En). Note compressed metaxylem elements (Mx) by syncytial cells. Ph = phloem, Vp = vascular parenchyma. Scale bar = 31 μm. C) Cross section showing a syncytium (S) originating from cortical parenchyma (CO). Syncytial wall thickenings (Wt) are visible at nematode feeding →



site (Fs), inside the syncytium and adjacent to normal cortical cells (CO). Syncytial wall segments (Wf) are present inside the syncytium. CM = compressed metaxylem, En = endodermis, Pc = pericycle. Scale bar = 21 μm. D) Cross section showing a hypertrophied nucleus (Nu) with prominent nucleolus (Nl) and deep indentation in a syncytium (S). Scale bar = 5.3 μm. E) Cross section showing a syncytium (S) originating from a pericycle cell (Pc). Syncytial wall thickenings are evident at nematode feeding site (Fs) and in proximity to a compressed metaxylem element (CM). En = endodermis, Ph = phloem, Vp = sclerenchymatous vascular parenchyma, WP = wall protuberances. Scale bar = 18 μm. F) Thickened wall of the same syncytium (S) of E at higher magnification showing protuberances (WP) in proximity of metaxylem (Mx) and vascular parenchyma (Vp) elements. Scale bar = 5.3 μm. G) Cross section showing a syncytium (S) originating from cortical parenchyma (CO) with wall protuberances (WP) in proximity to a normal cortical cell (CO). Scale bar = 5.3 μm. H) Cross section showing a syncytium (S) originating in the cortex with wall thickening (Wt) and a large wall protuberance (WP). Scale bar = 5.3 μm.

a feeding site in an endodermal cell (Fig. 1A), but in some cases it established a feeding site in a cortical or pericycle cell (Fig. 1C, E). Syncytia originating from endodermis and pericycle expanded deeply into the stele (Fig. 1E), whereas those originating from a cortical cell expanded into the cortex and adjacent portions of the stele (Fig. 1C).

The outer walls of mature syncytia were irregularly thick at nematode feeding sites and adjacent to vascular elements (Fig. 1C, E). Syncytial walls were up to 10 μm thick vs. 2.2 μm for normal metaxylem cells. Syncytia originating from cortical parenchyma cells also had thick walls adjacent to normal cortical cells (Fig. 1C). Thick wall remnants from cell fusions also occurred inside syncytia (Fig. 1C).

The syncytium outer walls contained protuberances, especially adjacent to vascular elements (Fig. 1E, F) and cortical cells (Fig. 1G). Very large wall protuberances extending up to 4–5 μm occurred in syncytia originating from cortical parenchyma cells (Fig. 1H). The irregular-shaped syncytia were about 80 μm wide × 95 μm long.

Only *Atalodera, Globodera, Heterodera, Punctodera,* and *Thecavermiculatus* species in the family Heteroderidae have so far been found to induce syncytia (6). *P. chalcoensis* syncytia are more similar to those of *Globodera* and *Heterodera* spp. (1,4) than those of *Atalodera* spp. (5). *P. chalcoensis* syncytia showed thickened walls, not only at nematode feeding sites, as those caused by *Atalodera* spp., but also in proximity to vascular and cortical cells, as those caused by *Globodera* and *Heterodera* spp. Wall protuberances, absent in *Atalodera* syncytia, were present in *P. chalcoensis, Globodera,* and *Heterodera* syncytia. These wall structures are reminiscent of transfer cell walls in normal plants, which increase the membrane area (4). *P. chalcoensis* syncytia in corn roots were smaller than those of *Atalodera* spp. (80 μm wide × 95 μm long vs. 150 μm wide × 400 μm long). Our observations agreed with those of Mundo-Ocampo and Baldwin (6) that *Globodera, Heterodera,* and *Punctodera* species induce similar syncytia.

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