STRUCTURE OF SYNCYTIA INDUCED BY *HETERODERA SCHACHTII* SCHMIDT IN ROOTS OF SUSCEPTIBLE AND RESISTANT RADISH (*RAPHANUS SATIVUS* L. VAR. *OLEIFORMIS*)

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ABSTRACT

The structure of syncytia induced by *Heterodera schachtii* Schmidt in roots of susceptible *Raphanus sativus* L. cv. "Siletina" and resistant radish cv. "Pegletta" was investigated. In the radish cultivar "Siletina" the syncytia most often appeared in the elongation zone of lateral roots. They were initiated in the procambium and pericycle but also included the parenchyma cells of vascular cylinder. In the susceptible cultivar "Siletina" the cells forming the female's syncytia were subject to hypertrophy. Their cytoplasmic density increased. The cytoplasm contained numerous organelles. The proliferation of the smooth endoplasmic reticulum took place. Branched cell wall ingrowths were formed next to the vessels. In the male's syncytia the cells were only slightly increased. Their protoplasts contained few organelles. The cell wall ingrowths were poorly developed. In the syncytia of the resistant cultivar "Pegletta" there was only a slight increase of the cell volume. A well developed system of rough endoplasmic reticulum was observed in the protoplast. Distended ER cisterns contained fine fibrillar material. Material of similar structure also appeared in numerous small vacuoles. In resistant plants only some, not numerous, syncytia spreading in procambium fully developed and functioned long enough for the parasite females to mature. At an advanced stage of infection a well developed system of a rough ER was observed also in those syncytia and numerous vacuoles appeared.

KEY WORDS: *Heterodera schachtii*, *Raphanus sativus*, syncytium, ultrastructure.

INTRODUCTION

The invasive nematode larvae of the genera *Heterodera* and *Globodera* infect the roots of susceptible and resistant plants. They affect morphogenesis of the root cells leading to the appearance of syncytium, through which the parasite obtains nutrients from the vascular tissues of the host (Jones and Northcote 1972). The investigations carried out on many plants belonging to the families such as *Brassicaceae* (Wyss et al. 1984, Golinowski and Magnusson 1991), *Fabaceae* (Endo 1965, 1991, Gipson et al. 1971), *Poaceae* (Grymaszewska and Golinowski 1987, Bleve-Zacheo et al. 1995), *Chenopodiaceae* (Yu and Steele 1981, Steele 1971, Bleve-Zacheo et al. 1987) and *Solanaceae* (Hoopes et al. 1978, Rice et al. 1985, 1987) have revealed that the syncytia initiated in the resistant plants develop less intensively than in the susceptible plants and early die. The action of defense mechanisms limiting the development of syncytia and thus the development of nematodes expresses itself in a various way depending on the plant resource of the resistance genes. In the resistant radish infected with *Heterodera schachtii* the degenerative changes in the syncytium protoplast observed already in 4-5 days after

the infection are connected with the activity of the rough endoplasmic reticulum (Wyss et al. 1984). The early dying syncytia in those plants allow the maturation of only the male parasites. Taking into consideration the results obtained in the recent years on the model plant *Arabidopsis thaliana* (Golinowski et al. 1996a, Sobczak et al. 1996) revealing that the syncytia of a male and a female *Heterodera schachtii* have different ultrastructure the attempt was made to compare the syncytia formed as a result of that nematode action in a susceptible and resistant radish.

MATERIAL AND METHODS

Roots of radish (*Raphanus sativus* L. var. *oleiformis*) cv. "Siletina" (susceptible to *Heterodera schachtii*) and cv. "Pegletta" (resistant) were investigated. The radish seeds were surface sterilized with 3.5% calcium hypochlorite and grown in agar medium in Petri dishes. Three day old seedlings were transferred to the nutrient medium on the base of 0.7% Dai-chin agar with a modified 0.2 concentrated Knopp's mineral composition with 0.1% Gamborg's B5 vitamin solution and

2% sucrose (Sijmons et al. 1991). In 7 days after placing seedlings to the nutrient medium, the cysts containing nematode invasive larvae of beetroot eelworm were placed on the roots. Material for the investigation was collected at times corresponding to the nematode developmental stages: second-stage juvenile (J2), third-stage juvenile (J3), fourth-stage juvenile (J4), mature parasites (Golinowski and Grymaszewska 1991). Root segments containing syncytia were pre-fixed for 2-3 h in a mixture of glutaraldehyde (3%) and paraformaldehyde (4%) in 0.1 M sodium cacodylate buffer at pH 7.2-7.3 and post-fixed for 2 h in 1% osmium tetroxide at 4°C. Samples were dehydrated in ethanol and propylene oxide and embedded in Epon 812. Series of transverse sections were made with the ultramicrotome (Reichert), stained with azure and toluidine blue and analysed under light microscope; ultrathin sections contrasted with uranyl acetate and lead citrate were examined with the electron microscope JEM 100C.

RESULTS

The structure of syncytia in the roots of the susceptible radish cultivar "Siletina"

In a susceptible radish cultivar syncytia most often appeared in the elongation zone of the lateral roots. They were initiated in the procambium cells next to the protoxylem vessels. From that site they spread in the vascular cylinder by means of an intensive dissolution of walls and fusions of protoplasts of the successive cells of procambium, neighbouring parenchymatic cells and cells of the pericycle. They also included the not yet differentiated mother cells of the central vessels of the metaxylem. At the same time, still preserving contact with the vessels syncytia developed along the root in an acro- and basipetal direction. At an advanced stage of the infection they included the whole central part of the vascular cylinder (Fig. 1). The cells incorporated into syncytia were subject to hypertrophy (Fig. 1, 3). The volume and density of

their cytoplasm increased. Central vacuole became disintegrated. Numerous plastids, mitochondria and dictyosomes in the cytoplasm were distributed in the peripheral parts of the cells (Fig. 5). In the protoplast of the active syncytia a system of rough and smooth endoplasmic reticulum was well developed (Fig. 3, 4, 5, 6). There appeared some small, at first not numerous, vacuoles. They contained fine fibrillar material (Fig. 4). Some cell wall ingrowths were formed on the walls of cells neighbouring the tracheary elements of the root (Fig. 6). At the advanced stage of infection, proliferation of the smooth ER took place in the syncytia. Apart from numerous organelles the cytoplasm contained large lipid bodies. The shape of nuclei present in the syncytia was irregular. Small vacuoles filled with fibrillar material were very numerous in older syncytia (Fig. 4). They were mainly distributed closely to the outer syncytial wall, cell wall ingrowths and fragments of the dissolved cell walls were preserved in the syncytia. The strongly branched cell wall ingrowths were situated next to the vessels (Fig. 6). The stimulation of the divisions of the vascular cylinder cells took place in the vicinity of the widespread syncytia. Some of the newly formed cells differentiated into the tracheary elements (Fig. 1).

Some of the syncytia formed in the roots of the susceptible cultivar developed less intensively (Fig. 2). These syncytia were initiated in the elongation zone, in the pericycle. The pericycle cells incorporated to the syncytia increased in size. Despite of that the syncytia had not become large; the remaining incorporated cells (procambium cells and stelar parenchyma cells) enlarged to a small degree. At the beginning their cytoplasm was dense, however, it contained few organelles (Fig. 7). In the protoplast a large number of small vacuoles could be seen containing some fibrillar material (Fig. 8). There were no cell wall ingrowths in the young syncytia at the border with the vessels (Fig. 7). When the nematode larvae reached the third stage of their development the cytoplasm in the syncytia was diluted. It mainly contained some free ribosomes, smooth endoplasmic reticulum, lipid

Fig. 1 and 2. Cross sections through the roots of *Raphanus sativus* cv. "Siletina" infected with *Heterodera schachtii*.

Fig. 1. Large female's syncytium (S) takes up the centre of the vascular cylinder. The surrounding tissues are subject to cellular divisions. Some of the new cells differentiate into vessels (arrows). N – nematode. Bar=64.1 μ m.

Fig. 2. Male's syncytium (S) is situated close to the edge of the vascular cylinder. The syncytium cells adjoining the tracheal elements have the cell wall continuity preserved. The linear arrangement of cells next to the syncytium indicates their divisions. N – nematode. Bar=64.1 μ m.

Fig. 3 and 4. Ultrastructure of the female's syncytium in the root of *Raphanus sativus* cv. "Siletina" infected with *Heterodera schachtii*.
Fig. 3. Cell wall ingrowths formed in the enlarged procambium cell (arrows). The system of endoplasmic reticulum (ER) is developed. Nu – nucleus, Ga – dictyosome, Pa – plastid. Bar=4.71 μ m.
Fig. 4. Fragment of a pericycle cell incorporated to the syncytium. The developed system of endoplasmic reticulum (ER) is seen in the protoplast. Numerous small vacuoles (V) contain fine fibrillar material. CW – thickened external tangential cell wall. Bar=0.98 μ m.

bodies and large compact arrangements of membranes (myelin structures) (Fig. 9). The nuclei in the syncytia were irregular in shape. The lately formed cell wall ingrowths were poorly developed (Fig. 9, 10). Sometimes they appeared on the radial and tangential walls in the cells which had no direct contact with the vessels. The cells situated next to the vessels only slightly increased in their volume and the continuity of their walls was preserved (Fig. 10).

In the susceptible cultivar some not numerous syncytia also appeared which, however, did not reach their full development and early died (Fig. 11). In such syncytia the cells enlarged only slightly. They had small, not numerous, openings in their walls. The development of the cell wall ingrowths was not far advanced. No development of the ER in the protoplast was observed. Early, some very numerous vacuoles appeared. The inside of the vacuoles was electron-lucent. There were no degenerative changes in the cells surrounding the dying syncytia.

The structure of the syncytia in the roots of the resistant radish cultivar "Pegletta"

In the resistant plants syncytia were formed in the lateral roots. Similarly as in susceptible cultivar they were initiated in the elongation zone, in the procambium and pericycle. They also included the parenchymal cells of the vascular cy-

linder. The contribution of particular cell types to the syncytium structure varied. Some syncytia developed mainly in the pericycle (Fig. 12). In such cases the cells of that tissue significantly increased in size. They did not contain the central vacuole. As compared to them the cells situated deeper in the vascular cylinder increased in size only to a small degree (Fig. 13). Their cytoplasm was less dense. There were few mitochondria and plastids in the syncytium cells in the resistant plants. The system of a rough endoplasmic reticulum was poorly developed. The ER cisterns were irregularly distended in many places. They contained material of fibrillar structure (Fig. 12, 13). Numerous small vacuoles were formed from the distended ER cisterns as a result of fragmentation. These vacuoles participated in the protoplast lysis in the syncytium cells. Through the invagination of the vacuole enveloping membrane the protoplast fragments were introduced inside the vacuole and degraded there. Various stages of the protoplast lysis in the syncytium cells are presented in Fig. 15 and 16. Large electron-lucent zones filled only with the fine fibrillar material (Figs 15, 16) appeared in the cytoplasm, after the tonoplast degradation, as the result of ingesting of the protoplast components present in the vacuoles. In the terminal segments of syncytia the process of protoplast degradation was usually more advanced than in parts close to the nematode's head. The cells had strongly diluted cytoplasm, which

Fig. 5 and 6. Ultrastructure of the female's syncytium in the root of *Raphanus sativus* cv. "Siletina" infected with *Heterodera schachtii*.

Fig. 5. Enlarged cells of a young syncytium have dense protoplast containing numerous mitochondria (Mi) and plastids (Pa) situated next to the cell wall. Ga – dictyosome, ER – endoplasmic reticulum, V – vacuole. Bar=3.92 μ m.

Fig. 6. The cell wall ingrowths (WI) are strongly branched in the cells of an older syncytium. The syncytium nuclei (Nu) are irregular in shape. X – metaxylem vessel. Bar=2.45 μ m.

contained some, not numerous, organelles and large aggregations of membranes. Cell wall ingrowths formed in the syncytia of the resistant cultivar were poorly developed. Sometimes they appeared one by one, irregularly spaced on the whole surface of the cell wall (Fig. 13).

Some syncytia, initiated in the resistant cultivar, developed mainly on the basis of non-differentiated mother cells of the central metaxylem vessels (Fig. 14). These syncytia included a small number of cells which increased in size only slightly. In most of them the continuity of the walls was preserved. Poorly developed cell wall ingrowths were formed only on the walls included in the syncytia of the mother cells of the metaxylem vessels (Figs 15, 16). At the advanced stage of the infection, the protoplast degradation took place also in the syncytia with vacuoles filled with fibrillar material.

In the resistant radish cultivar the full development was reached only by a few syncytia. They were formed on the basis of procambium cells (Fig. 17). In such cases the cells incorporated into the syncytia enlarged only slightly but they contained numerous organelles such as plastids, mitochondria and dictyosomes and a well developed system of endoplasmic reticulum. Some lipid bodies could be observed in them. The protoplast contained few small vacuoles (Fig. 18). Most of them were electron-lucent inside. The proliferation of RER

took place in the older syncytia (Fig. 19). Small agglomerations of osmiophilic homogeneous substance were formed in the ER cisterns (Fig. 19). Osmiophilic thickenings were formed on the plasmalemma. Small vacuoles, numerous in the older syncytia, contained small protoplast fragments, which indicated the beginning of the degenerative changes (Fig. 19). In tissues surrounding the syncytia, in the resistant radish cultivar no degenerative changes were observed. Only some single cells adjoining the vessels had very dense protoplast which was detached from the cell wall (Fig. 15).

DISCUSSION

In the susceptible radish cultivar "Siletina" the best place for the formation and development of syncytium is the elongation zone in the lateral roots, where the differentiation of the metaxylem central vessels has not yet taken place. The initial cells of the syncytia were the procambium cells or the pericycle cells similarly as in *Arabidopsis thaliana* infected with *Heterodera schachtii* (Golinowski et al. 1996a, Sobczak et al. 1996). Syncytia initiated in the procambium, on the basis of the successive cells of that tissue, were strongly developed. They spread in the central part of the vascular cylinder. The

Fig. 7 and 8. Ultrastructure of the male's syncytium in the root of *Raphanus sativus* cv. "Siletina" infected with *Heterodera schachtii*.

Fig. 7. Procambium cells incorporated into the syncytium have the cell walls dissolved (CW). The syncytium protoplast contains some, not numerous, organelles. Nu – nucleus, V – vacuole, Pa – plastid, Mi – mitochondrion, RER – rough endoplasmic reticulum. X – metaxylem vessel. Bar=3.92 μ m.

Fig. 8. Enlarged fragment of syncytium. Small vacuoles (V) present in the protoplast are filled with fibrillar material. My – myelin structure, CW – cell wall. Bar=2.35 μ m.

cells incorporated into syncytia form an effective transfer system and the nematode larvae feeding through them mature as females (Golinowski et al. 1996a). The cells incorporated into the syncytium were subject to hypertrophy. Their cytoplasm density and volume increased. The number of organelles also increased. The proliferation of endoplasmic reticulum was observed. Changes in the apoplast were expressed by an intensive degradation of the cell walls which led to the fusion of protoplasts and the formation of strongly developed cell wall ingrowths on the segments of the walls adjoining the vessels. These observations agree with the results of earlier investigations performed on *Arabidopsis thaliana* (Golinowski et al. 1996a) and *Brassica napus* var. *oleifera* (Magnusson and Golinowski 1991) infected with *Heterodera schachtii*.

Syncytia initiated in the susceptible radish cultivar in the pericycle developed less than the syncytia initiated in the procambium. The cells of the syncytia, especially those situated next to the vessels increased slightly in size. Their cytoplasm was less dense and they contained fewer organelles. The process of changes in wall structure was not advanced in them. The cell wall ingrowths appeared late and were poorly developed. The ultrastructure of those syncytia was similar to the ultrastructure of the syncytia in *Arabidopsis thaliana* from

which the larvae maturing into males obtained their food (Sobczak et al. 1996).

Apart from syncytia, which enable the nematode males and females to mature in the susceptible plants, there were also such syncytia initiated which were subject to vacuolation and early death thus not producing the transfer system of a standard value. Similar situation was also observed in *Arabidopsis thaliana* (Golinowski et al. 1996b). The causes of the syncytium early degradation are not known.

In the resistant radish cultivar syncytia were also initiated in young parts of the roots. However, they developed poorly not reaching the large sizes. Only in rare cases they increased by incorporating the pericycle cells which were subject to hypertrophy. Most often the cells incorporated in the syncytia increased only slightly in size and had the continuity of the cell walls preserved. Their cytoplasm density and the number of organelles did not increase. There was no proliferation of the smooth ER as it was observed in the susceptible cultivar. The cell wall ingrowths, which were formed next to the vessels, were scattered and poorly developed. The distinguishing trait of those syncytia was an intensive dilation of the rough endoplasmic reticulum cisterns containing some osmiophilic fine fibrillar material, which led to the formation of numerous

Fig. 9 and 10. Ultrastructure of the male's syncytium in the root of *Raphanus sativus* cv. "Siletina" infected with *Heterodera schachtii*.

Fig. 9. The diluted syncytium cytoplasm contains plastids (Pa), mitochondria (Mi) and lipid bodies (Li). Cell wall ingrowths situated next to the vessels (X) are marked with an arrow. My – myelin structure. Bar=3.27 μ m.

Fig. 10. The developed system of the endoplasmic reticulum (ER) is visible in the syncytium protoplast. Mi – mitochondrium, Pa – plastid, Nu – nucleus, Li – lipid body. Cell wall ingrowths are marked with an arrow. MVB – multivesicular body, X – metaxylem vessel. Bar=3.92 μ m.

vacuoles. Starting with that stage of development, the process of protoplast degradation had began. In view of the lack of other changes in the syncytia and surrounding tissues it can be accepted that the vacuoles filled with fibrillar contents functioned as the digestive vacuoles. The appearance of these

vacuoles could result from the action of the plant defensive mechanisms which, by means of the disintegration of structure and functioning of the syncytia, limited the nematode development and reproduction. Poorly developed, early dying syncytia probably supply only such an amount of food that

Fig. 11. Ultrastructure of dying syncytium in the root of *Raphanus sativus* cv. "Siletina". The syncytium protoplast contains numerous vacuoles (V). Cell wall ingrowths (arrow) are poorly developed. CW – fragments of dissolved cell wall, X – vessel. Bar=3.92 μ m.

Fig. 12 and 13. Ultrastructure of syncytium in the root of *Raphanus sativus* cv. "Pegletta" infected with *Heterodera schachtii*.

Fig. 12. Pericycle cells (Pe) incorporated into the syncytium are very strongly enlarged. They have dissolved wall fragments (CW). The protoplast contains a developed system of the rough endoplasmic reticulum (RER). The distended ER cisterns contain fibrillar material (arrows). Bar = 3,92 μ m.

Fig. 13. The cell wall ingrowths in the syncytium cells situated next to the vessels (X) are marked with arrows. Bar = 2,45 μ m.

allows the maturation of males which are less demanding than the females (Müller et al. 1981).

In the resistant radish cultivar only single syncytia developed on the basis of the procambium cells and only those functioned for a period of time long enough to allow the ma-

turation of also the female forms of the nematode. It is proved by the small amount of cysts on the roots of the resistant cultivar. The results pointing to the participation of the rough endoplasmic reticulum in the defensive reaction of the resistant radish cultivar infected with *Heterodera schachtii*

Fig. 14. Cross section through the root of *Raphanus sativus* cv. "Pegletta" infected with *Heterodera schachtii*. Small syncytium includes still non-differentiated mother cells of the metaxylem central vessels (arrow). N – nematode. Bar=64.1 μ m.

Fig. 15 and 16. Ultrastructure of syncytium in the root of *Raphanus sativus* cv. "Pegletta" infected with *Heterodera schachtii*.

Fig. 15. Small vacuoles (V) present in the syncytium cells contain fine fibrillar material and protoplast fragments (arrows). The protoplast in the procambium cell (PC) adjacent to the vessel (X) is subject to degradation. Bar=1.96 μ m.

Fig. 16. Cell wall ingrowths (WI) are formed in the mother cell of the metaxylem vessel incorporated into the syncytium. Numerous small vacuoles (V) are seen in the protoplast. Li – lipid body, X – differentiated metaxylem vessel. Bar=2.45 μ m.

agree with the earlier observations by Wyss et al. (1984) who suggest that the RER cisterns transport the hydrolytic enzymes synthesized on the ribosomes and release them to the vacuoles. After the enzyme degradation of the tonoplast

there is the disintegration of the syncytium cytoplasm and organelles. The RER accumulation was also observed in the syncytia of the resistant soybean cultivars infected with *Heterodera glycines* (Endo 1991).

Fig. 17. Cross section of the root of *Raphanus sativus* cv. "Pegletta" infected with *Heterodera schachtii*. Syncytium (S) contains numerous procambium cells situated in the direct neighbourhood of the vessels (X). N – nematode. Bar=64.1 μ m.

Fig. 18 and 19. Ultrastructure of syncytium in the root of *Raphanus sativus* cv. "Pegletta" infected with *Heterodera schachtii*.

Fig. 18. Cell wall ingrowths (arrows) are situated in the syncytium cells next to the vessels (X). Nu – nucleus, V – vacuole. Bar=6.54 μ m.

Fig. 19. Numerous small vacuoles (V) in the syncytium which contain protoplast fragments (arrows). Osmiophilic substance present in the cisterns of endoplasmic reticulum is marked with the arrow heads. WI – cell wall ingrowths, X – vessel. Bar=2.45 μ m.

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STRUKTURA SYNCYTIÓW W KORZENIACH WRAŻLIWEJ I ODPORNEJ RZODKWI
(*RAPHANUS SATIVUS* L. VAR. *OLEIFORMIS*) PORĄŻONEJ MĄTWIKIEM BURAKOWYM
(*HETERODERA SCHACHTII*)

STRESZCZENIE

Badano strukturę syncytiów indukowanych przez *Heterodera schachtii* Schmidt w korzeniach *Raphanus sativus* L. cv. „Siletina” (wrażliwa) i cv. „Pegletta” (odporna). U rzodkwi odmiany „Siletina” syncytia najczęściej powstawały w korzeniach bocznych w strefie elongacji. Były inicjowane w prokambium i w perycyklu. Obejmowały również komórki parenchymatyczne walca osiowego. U wrażliwych roślin (cv. „Siletina”) komórki budujące syncytia samic podlegały hipertrofii. Wzrastała w nich gęstość cytoplazmy. W cytoplazmie były zawarte liczne organelle. Następowła proliferacja agranularnego endoplazmatycznego retikulum. Przy naczyniach tworzyły się rozgałęzione wyrostki transferowe. W syncytiach samców komórki powiększały się w małym stopniu. W protoplaście występowało niewiele organelli. Wyrostki transferowe były słabo rozwinięte. U odpornej odmiany „Pegletta” w syncytiach następował tylko nieznaczny wzrost objętości komórek. W protoplaście rozbudowany był system granularnego endoplazmatycznego retikulum. Rozdęte cysterny ER zawierały drobnowłóknisty materiał. Materiał o podobnej strukturze występował też w licznych małych wakuolach. W odmianie odpornej tylko nieliczne syncytia rozprzestrzeniające się w prokambium osiągały pełnię rozwoju i funkcjonowały dostatecznie długo aby dojrzałość osiągnęły samice pasażysty. W zaawansowanym stadium infekcji również w tych syncytiach rozbudowany był system granularnego ER i powstawały liczne wakuole.

SŁOWA KLUCZOWE: *Heterodera schachtii*, *Raphanus sativus*, histologia, syncytium, ultrastruktura.