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Histopathogenesis of susceptible and resistant responses of wheat, barley and wild grasses to *Meloidogyne naasi*

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Summary – The highly resistant responses of the wild grasses *Aegilops variabilis* and *Hordeum chilense* infected by the root-knot nematode *Meloidogyne naasi*, were studied using light microscopy, in comparison with the susceptible responses in two cereal cultivars, *Triticum aestivum* cv. Chinese Spring and *Hordeum vulgare* cv. Doublet, together with the partially resistant response of barley cv. Morocco. Both full resistances involve early induced hypersensitive-type responses, with a range of necrotic sites in the endodermis, thus preventing most nematodes from migrating into the stele. Such necrosis is not lethal to juveniles, but impedes any feeding and development. Differences between the resistant species were seen in the changes in the cortical and endodermal cells close to nematodes : callose deposition by *A. variabilis*, lignin deposition by *H. chilense*. The partial resistance of cv. Morocco appeared to be associated with a lower efficiency of the giant-cells as a source of nutrients. The induction of the resistance mechanisms in the three resistant hosts is discussed.

Résumé – ***Histopathologie des réactions de sensibilité et de résistance du blé, de l'orge et de graminées sauvages à* Meloidogyne naasi** – Les réactions des graminées sauvages *Aegilops variabilis* et *Hordeum chilense*, plantes totalement résistantes au nématode à galles *Meloidogyne naasi*, sont comparées en microscopie optique aux réactions de deux variétés sensibles de céréales, *Triticum aestivum* cv. Chinese Spring et *Hordeum vulgare* cv. Doublet, ainsi qu'à la réaction du cv. d'orge partiellement résistant, Morocco. Dans ces deux premiers cas, la résistance totale fait intervenir de façon très précoce des réactions de type hypersensible où la présence de sites nécrotiques au niveau de l'endoderme empêche la plupart des nématodes de migrer vers la stèle. De telles nécroses ne paraissent pas être létales pour les nématodes même si elles s'opposent à leur nutrition et à leur développement. Les deux espèces diffèrent cependant dans la nature des changements précoces induits dans les parois des cellules du cortex et de l'endoderme au contact des nématodes : callose chez *A. variabilis*, lignine chez *H. chilense*. La résistance partielle du cv. Morocco est probablement associée à une plus faible efficacité des cellules géantes dans leur rôle nutritionnel. Les mécanismes des réactions induites chez les trois hôtes sont discutés de façon détaillée.

Key-words : *Meloidogyne naasi*, light microscopy, *Aegilops variabilis, Hordeum chilense.*

Two sources of full resistance to the cereal root-knot nematode *Meloidogyne naasi* have been found in some wild grasses closely related to wheat : *Hordeum chilense* accessions (Cook & York, 1981; Miller *et al.*, 1981; Person-Dedryver *et al.*, 1990) and the accession n° 1 of *Aegilops variabilis* (Person-Dedryver & Jahier, 1985; Yu *et al.*, 1990). These resistances, each governed by one dominant gene, have been studied at the Plant Breeding Station of the INRA (35650 Le Rheu, France) to be introgressed into wheat accessions.

In the case of *A. variabilis* n° 1, resistance is characterized by a low invasion rate by the infective second-stage juveniles (J2), an arrested growth of the root tip with slight swellings of the tips (Yu, 1990), and usually no nematode development, although very seldom, some males, small females or immature females can be found after 30 days of culture of whole plants at 20 °C on 2 % water agar (Balhadère, 1993). In the case of *H. chilense*, some galls are found in the field. The numbers of invading J2 seem to be limited by the occurrence of an extensive necrotic reaction, which depends on temperature (more at 27 than at 20 °C). Therefore, little penetration is observed under controlled conditions, i.e. with temperatures above 20 °C (Balhadère, 1993), compared with the soil temperatures found in the field.

Since the work of Siddiqui on histopathogenesis of the susceptible and partially resistant responses in cereals to *M. naasi* (Siddiqui & Taylor, 1970; Siddiqui, 1971), little has been done on this subject. It was thus of interest to compare the structural and physiological characterization of the two full resistances with the susceptible responses in wheat and barley cultivars, using light microscopy. By observing the development of the two resistances, it was hoped to see whether different mechanisms could be implied as had been suggested by Person-Dedryver *et al.* (1990), based on differences in gall formation. The partially resistant barley cv. Morocco, which presents a slower development rate of nematodes and a reduced formation of females (Loos & Person-Dedryver, 1990) was also investigated.

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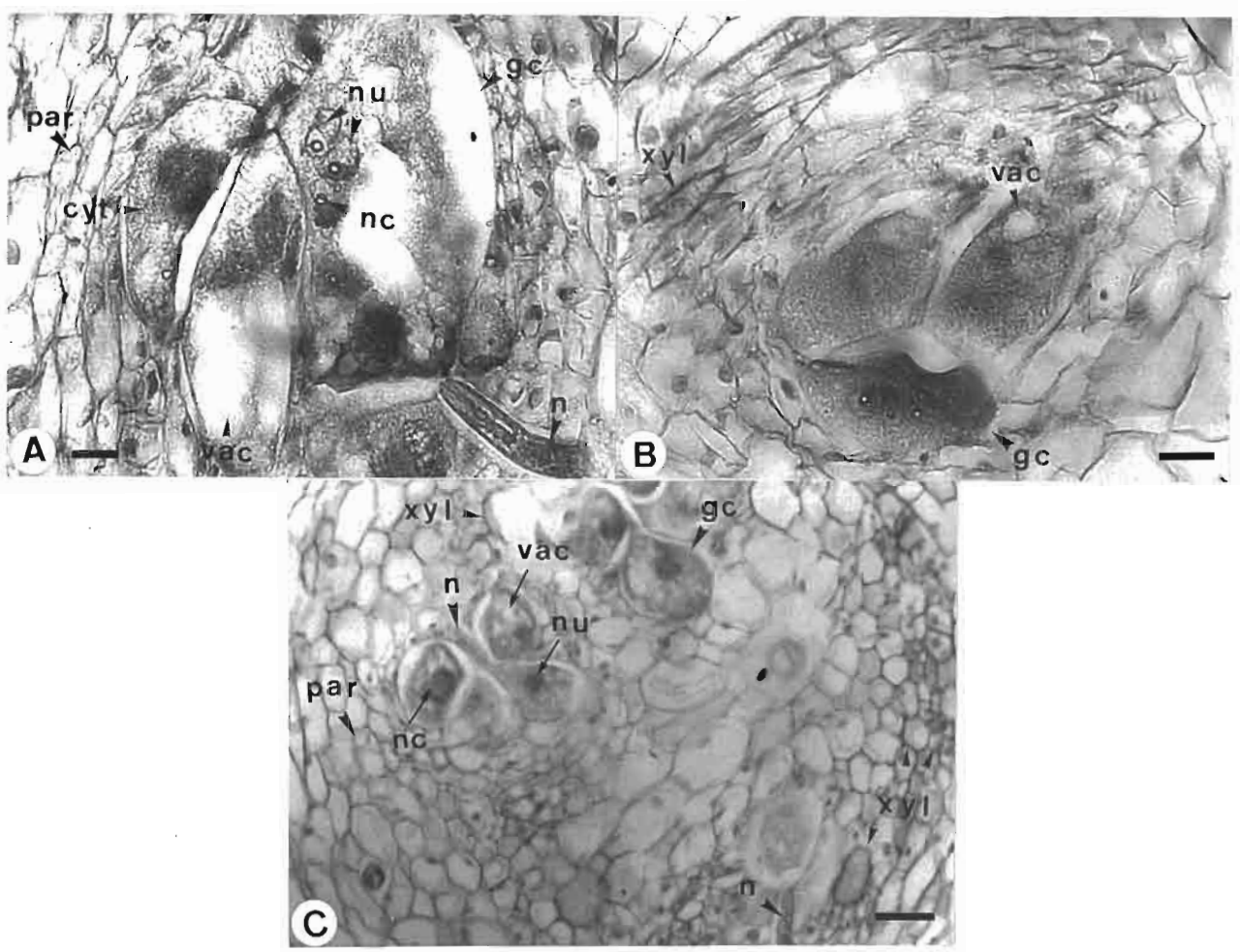

Fig. 1. *Transverse sections through roots of barley cvs Doublet and Morocco, showing susceptible and partially resistant responses to invasion by the Welsh population of* Meloidogyne naasi. *A : Cv. Doublet, 10 days after inoculation, showing one nematode near its feeding site. (Note the presence of many nucleoli); B : Cv. Doublet, 30 days after inoculation, showing one feeding site, surrounded by several layers of parenchymatic cells and some xylem cells. (Note the small size of vacuoles inside the giant cells); C : Cv. Morocco, 10 days after inoculation, showing the formation of several feeding sites inside the stele and the presence of many xylem vessels near the giant cells.*
(Cyt = cytoplasm; gc = giant cell; n = nematode; nc = nucleolus; nu = nucleus; par = parenchyma; vac = vacuole; xyl = xylem. Bar equivalents : A = 5 µm; B = 10 µm; C = 25 µm.)

Materials and methods

Fresh J2 from a Welsh population of *M. naasi* were collected after extraction in water at 20 °C from infested soil obtained at the Institute of Grassland and Animal Production, Aberystwyth.

Roots from the following plants were studied : susceptible barley cv. Doublet and wheat cv. Chinese Spring, resistant barley cv. Morocco, resistant accessions of *H. chilense* " PI283375 ", *A. variabilis* n° 1 and wheat " x^8 " (a recombinant accession, bearing the dominant gene of resistance " Rkn-mn1 " from *A. variabilis*) together with some amphiploids obtained from the cross between *H. chilense* and cv. Chinese Spring.

After treatment in a 5 % NaOCl solution for 5 minutes, the seeds of the plants were germinated on 2 % water agar in Petri dishes at 20 °C. Three to four day-old seedlings were individually transferred onto blocks of 2 % water agar in sterile dishes. For root infection, each tip was inoculated with 30 J2, then covered with a layer of 2 % water agar and incubated in a 20 °C constant temperature for 24 hours. Some of the plants were then examined while others were transferred onto a fresh 1 % water agar plate and left at constant 20 °C for 2, 4, 9, or 29 days. For examination, infested roots were excised and fixed in formalin-aceto-alcohol (FAA) for a minimum period of 24 hours.

Roots were dehydrated through an alcohol series (10 to 100 %), allowing 1 hour for each step, then infiltrated with xylene and embedded in Paraffin wax (Paraplast®, melting point : 56-57 °C). Sections, 10 to 15 µm thick, were cut with a rotary microtome and left overnight on a hot plate to dry. The safranin O and fast-green procedure as described by Daykin and Hussey (1985) was followed for staining. Slides were observed under a Dialux 20 ER light microscope and photographed.

Results

The susceptible response in cvs Doublet and Chinese Spring

In the susceptible barley cv. Doublet, the first J2 were seen within 24 hours in the cortical tissue in the region of root elongation. After 3 days, nematodes were found in the cortex and often in the stele with some cortical damage. No sign of cellular hypertrophy was detected at this stage.

At 5 days, in cv. Chinese Spring, most nematodes had settled in the stele, having initiated a giant cell response : i.e. cytoplasmic and nuclear enlargement, metabolically active cytoplasm (dense and granular) with two or four actively dividing nuclei, each with several hypertrophied nucleoli (stained bright-red). The few J2 still in the cortex had failed to induce any hypertrophy of surrounding cells at this stage.

At 10 days, the cytoplasm of giant cells in both susceptible cultivars appeared dense and granular while the nuclei were hypertrophied. The multinucleolate state of the nuclei, although poorly evident (Fig. 1 A) was also observed. Much cortical proliferation was seen around the feeding site beyond the two or three layers of compacted parenchyma cells. Abnormal xylem cells (recognizable due to the characteristic wall thickening pattern) were also seen around giant cells.

At 30 days, the previously mentioned features remained visible in cv. Doublet. There was an increase in the number of abnormal xylem reticulate cells in vicinity of the giant cells, together with an increase in the cytoplasm/vacuole ratio but no increase in size of either giant cells or galls (Fig. 1 B).

The partially resistant response of cv. Morocco

At 10 days, galls on cv. Morocco often contained several feeding sites, all composed of several multinucleate giant cells (Fig. 1 C). Some differences from susceptible cultivars were detected, such as a smaller size of giant cells, a more intense coloration of nuclei and the presence of many small vacuoles. The gap observed between the cell walls and the protoplasts was obviously an artefact due to the fixation procedure.

The fully resistant response of *A. variabilis* (accessions *A. variabilitis* N° 1 and " x^8 ")

After 1 day, the J2 had already penetrated and were found in the root cap (Fig. 2 A), in the zones of root elongation (Fig. 2 B) and differentiation (Fig. 2 C), both inter- and intra-cellularly. On one sample, the first signs of cellular reaction could be seen in the differentiated endodermal cells with the presence of bright-green stained callose (by fast-green) in the cell walls and a dark diffuse cellular content (stained purple-green; Fig. 2 D).

At 3 days, this reaction was more extensive, mainly affecting the cortical cells, although very seldom some cells in the stele (Fig. 2 E, F, G). A few cells on the track of the nematode or in contact with their bodies presented the same green coloration and a degenerating cytoplasm.

At 5 days, two types of root reactions were seen. First, in the cortex no further increase in the size of the reacting zone was detected, neither were there any signs of giant cell induction. Secondly, in the stele, some small cells, possibly corresponding to protophloem poles, gave evidence of one or two divisions, whereas adjacent bigger cells (possibly parenchymatic cells) showed a dark nuclear mass spread all through the cell, without any sign of successful nuclear division.

At 10 days, as previously reported, reactions were mainly dispersed in the cortex, roughly located next to the endodermis (Fig. 3 B), indicated by the presence of brightly stained red walls (suberin) in this tissue. Inside the reacting cells, the nucleus appeared as a purple-red mass distributed throughout the cell while the cytoplasmic contents stained green and were disorganised (Fig. 3 A). Nematodes, still unswollen, were seen within the tissue both intra- and extra-cellularly.

At 30 days, the same features could still be observed : red thickned walls, disorganized cytoplasm and remnants of J2, but it was clear that disturbance to the root structure remained very localized. After dissection of infected roots 30 days after inoculation, these few J2 found inside localized necrotic parts of cortex were still alive, although depleted of body reserves.

The fully resistant response of *H. chilense* (accession" PI283375 " and amphiploïds)

By 24 hours after inoculation, the first nematodes had penetrated into the cortex, both inter- and intra-cellularly. In the zone of differentiation, cortical cells containing several nematode bodies appeared enlarged, showing thickened, stained walls (lignin) in contact with both the endodermis and adjacent cells (Fig. 4 A). No such reaction was observed in cells at the meristematic or elongating stages (Fig. 4 B).

After 10 days, resistance-related responses were located in the endodermis (Fig. 4 C, D) and involved groups of 4-5 cells with the presence of thickened red

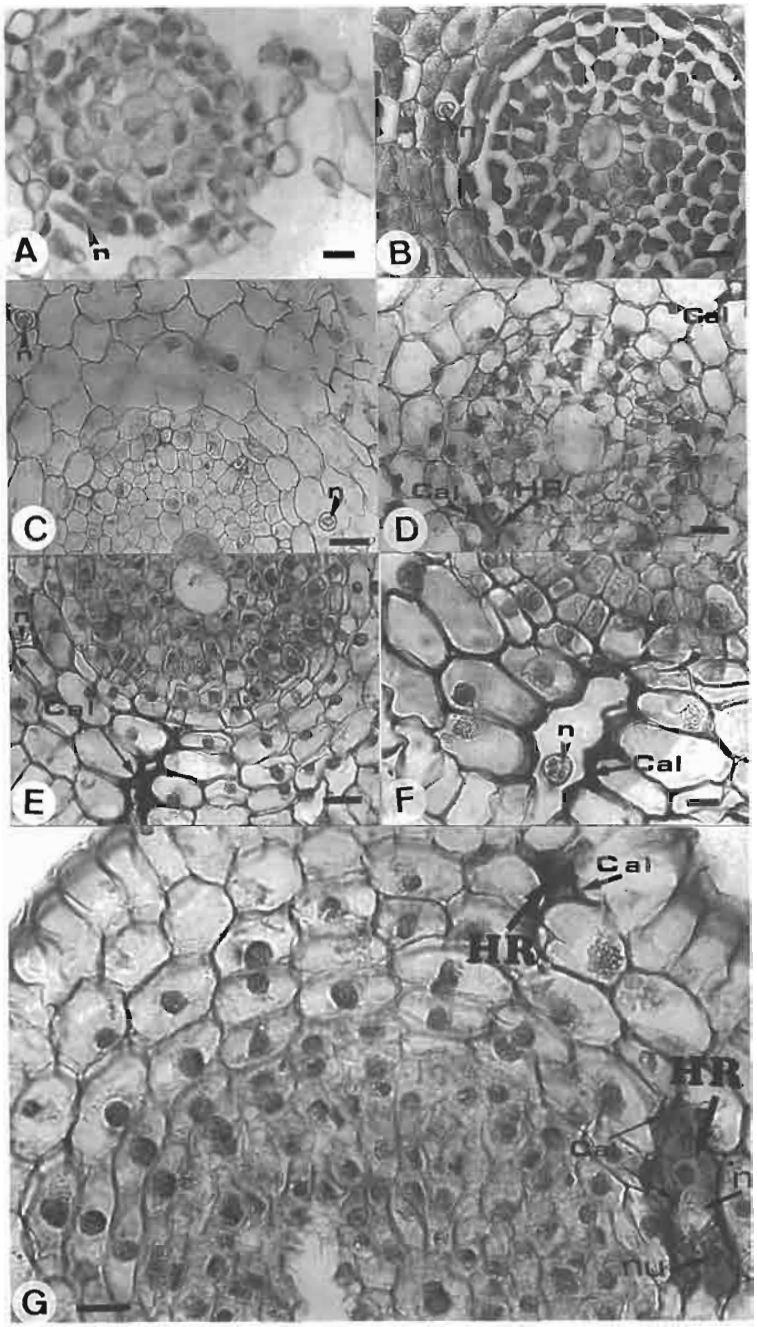

Fig. 2. *Transverse sections through roots of accession* Aegilops variabilis *n° 1, showing resistant response to invasion by the Welsh population of* M. naasi. *A : Root cap, one day after inoculation; B : Zone of root elongation, one day after inoculation; C, D : Differentiated zone, one day after inoculation. (Note the deposition of material stained green by fast-green – probably callose – in the walls of the hypersensitive cell in D); E : Three days after inoculation. (Note the deposition of callose along the track of the nematode's migration); F : Three days after inoculation. (Note the extensive cortical disruption); G : Three days after inoculation. Note the development of the hypersensitive reaction around nematodes in the cortex and endodermis.*
(Cal = callose; HR = hypersensitive cell (cell in which hypersensitive reaction has occurred); n = nematode; nu = nucleus. Bar equivalents : A, F = 5 μm; B, C, D, E, G = 10 μm.)

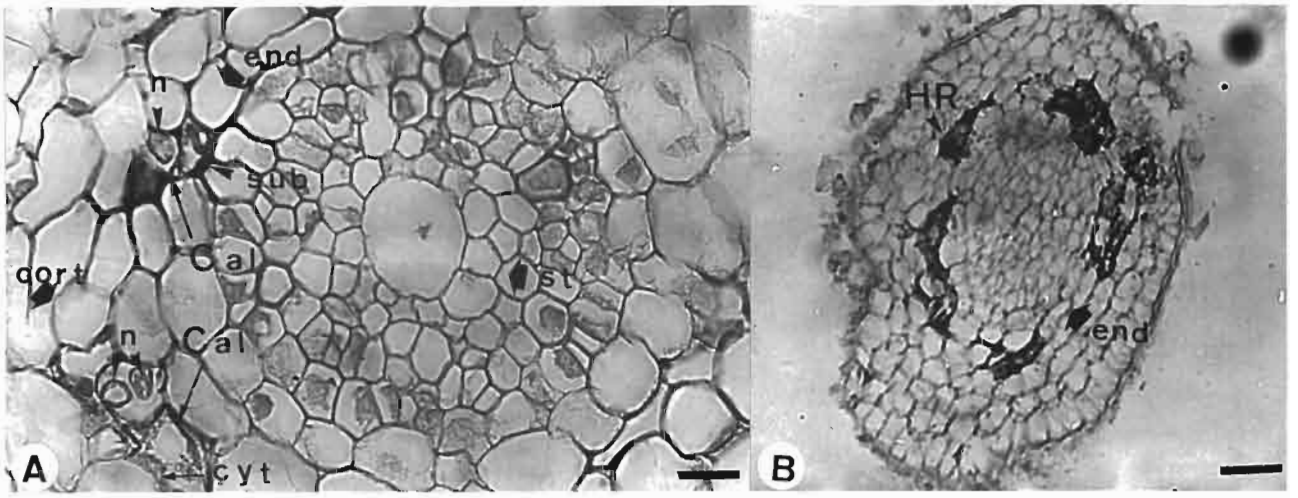

Fig. 3. *Transverse sections through roots of* Aegilops variabilis *n° 1, showing resistant response to invasion by the Welsh population of* M. naasi *(all sections are in the differentiated zone). A : Ten days after inoculation, showing the deposition of suberin in reacting endodermal cells in contact with nematodes; B : Ten days after inoculation. (Note the location of the hypersensitive reactions on a circle corresponding to the endodermis.)* (Cal = callose; cort = cortex; cyt = cytoplasm; end = endodermis; HR = hypersensitive cell; n = nematode; st = stele; sub = suberin. Bar equivalents : A = 25 μm; B = 10 μm.)

walls (suberin, lignin) both longitudinally and transversally in contact with unaffected neighbouring cells. Reacting cells showed no sign of giant cell induction, but had a dark-red content, often necrotic (brown) or with disorganized green contents scattered next to the walls and eventually an occasional sign of " disruption " of the walls between them (Fig. 4 D).

Discussion

The susceptible response in cvs Doublet and Chinese Spring

Both cultivars showed a typical susceptible response, as described by Siddiqui and Taylor (1970). The presence of abnormal xylem vessels (wound xylem) at 10 days after inoculation agreed with the idea of a giant cell induction and maintenance mediated through plant growth factors, possibly involving auxin (Jones, 1981) and ethylene (Glazer *et al.,* 1985). Appearance of xylem after only 5 days is supported by the suggestion that three rounds of DNA synthesis are needed to activate genes for tracheary element differentiation (Comer, 1978) and by the state of nuclear replication at that date. The presence of nematodes trapped in cortex, with no successful feeding relationship established, was also noticed by Siddiqui and Taylor (1970). This could originate from a nematode entering the root too close to the differentiation zone, and finding increasing difficulties for progressing intracellularly either forward or backward, due to the increased resistance to the deformation by the walls of differentiated cells (Wyss *et al.,* 1992).

The partially resistant response of cv. Morocco

Giant cells were formed, capable to sustain the feeding and the development of nematodes. However their small size and the great number of feeding sites within a root section could account for a limited food supply and an increased competition between nematodes, resulting in a slower development. It is yet difficult to determine the reasons underlying this formation of numerous small feeding sites and to ascertain the causal link between this observation and the existence of a slow development rate.

The fully resistant responses

The reaction which may be responsible for resistance of *A. variabilis* acted quickly (as soon as one day) and locally (near the nematode), with effects on all cellular components. Walls in direct contact with nematodes were quickly covered by a non-lignified material stained by fast-green – probably callose as it is commonly implicated in wound response and in resistant responses to fungi (Beckman *et al.,* 1982). Later accumulation of lignified material (stained in red by safranin), was probably suberin, as it is a commonly synthesized compound in endodermis in response to pathogen invasion (Van Fleet, 1972).

The rapid degeneration in the cytoplasm of involved cells and the limitation of this reaction to the close vicinity of nematodes were consistent with the structural and ultrastructural characterization of hypersensitive response to root-knot nematode infection (Dropkin, 1969; Paulson & Webster, 1972).

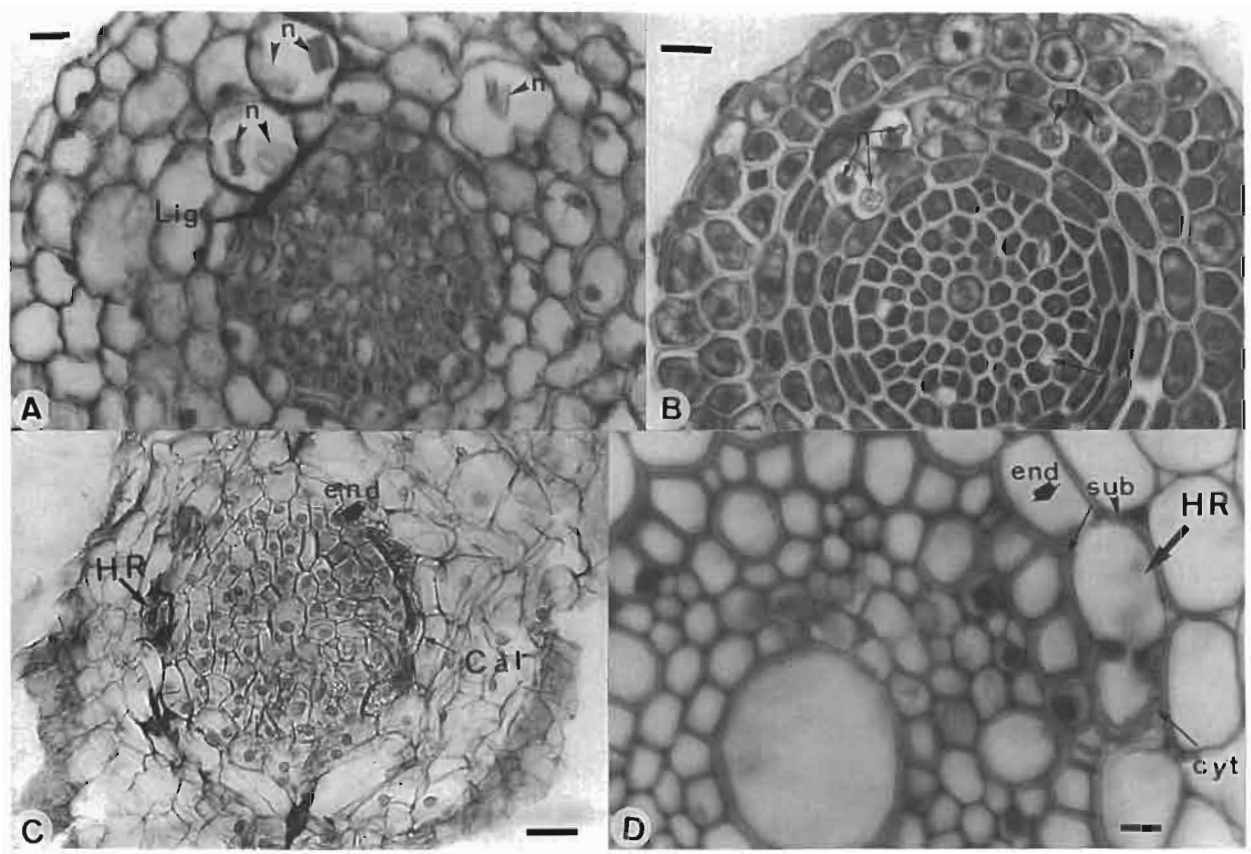

Fig. 4. *Transverse sections through roots of* Hordeum chilense *" PI283375 " and amphiploïd plants, showing resistant responses to invasion by the Welsh population of* M. naasi. *A :* H. chilense *" PI283375 ", one day after inoculation (differentiated zone). (Note the accumulation of lignin – darkly stained red – in cell walls surrounding nematodes); B :* H. chilense *" PI283375 ", one day after inoculation (meristematic zone). Note the absence of any reaction; C :* H. chilense *" PI283375 ", 10 days after inoculation (differentiated zone), showing the development of hypersensitive reactions at the endodermis limit; D : Amphiploïd plant, 10 days after inoculation, showing the deposition of suberin (brightly stained red) in walls of hypersensitive endodermal cells. No nematode is seen in this root section.*

(Cal = callose; cyt = cytoplasm; end = endodermis; HR = hypersensitive cell; Lig = lignin; n = nematode; sub = suberin. Bar equivalents : A, D = 5 µm; B, C = 10 µm.)

These mechanisms appear very efficient as they quickly restrict the nematodes in the cortex region where successful giant cell induction is impossible. Furthermore they limit nematode feeding while causing little histopathology of surrounding cells or the conductive tissues without killing the nematode.

However, even when the nematode successfully settled in the stele, the giant cell induction apparently stopped after the first two rounds of nuclear division. One possible interpretation is that although J2 are capable of inducing divisions in small cells still at an early stage in their differentiation, a counteracting hypersensitive reaction of the cell subsequently arrests this response. When larger cells were initially fed on, the attempted modification failed as soon as it started, leading to a distorted nucleus. However these limited responses in the stele appear to provide the J2 with both a small amount of nutrients and suitable conditions to occasionally go beyond the J4 stage and become males or even very small females.

The recent observations of Wyss *et al.* (1992) showed that during root invasion by *Meloidogyne,* a complex inter-cellular migration first towards, and then away from the root tip to the differentiation zone, allows the J2 to reach the vascular vessels by avoiding the endodermis, which they cannot penetrate directly. Thus, one major factor underlying resistance of *A. variabilis* could be the relative speed of cell differentiation in roots compared with the rate of nematode progression into tissue. This could result in :

(i) the trapping of nematodes in the cortex and endodermis by a rapid hypersensitive reaction;

(ii) the early expression of the resistance gene inside the first differentiated cells (cortical and stelar parenchy-

ma) which are in contact with the nematode before a giant cell induction site is reached);

(iii) the low attractiveness of roots to the juveniles in soil (Balhadère & Evans, 1994).

H. chilense also showed an early hypersensitive-type response, with autolysis of a few endodermal and cortical cells in contact with nematodes. One difference observed with *A. variabilis* is the early development of wall thickening, possibly here through synthesis and mobilisation of lignified material instead of callose in differentiating cortical cells in contact with nematodes; however callose also seems to be accumulated later in endodermal reacting cells.

In the Graminae, active lignification provides an effective mechanical barrier against microbial degradation and " seems to be of special importance for induced resistance mechanisms " (Moerschbacher, 1989). As there is an almost complete absence of phytoalexin in this family, lignification appears to be a causal factor in hypersensitive death, elicited in particular by oligosaccharides from fungi walls (Moerschbacher, 1989).

Evidence in support of the hypotheses concerning enzymes and cellular compounds involved in resistance will be given through cytochemical localization of these substances (Balhadère & Evans, 1995). However observations on longitudinal root sections will be useful to study the progress of nematodes with time inside the root tissues (Berthou, pers. comm.).

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