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Fungal pathogens of *Arabidopsis thaliana* (L.) Heyhn.

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Abstract

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An isolate of *Erysiphe cruciferarum* (which causes powdery mildew of crucifers), originally observed growing on *Brassica napus* (oilseed rape), was found to be pathogenic on plants of *Arabidopsis thaliana* collected from a Zürich suburb called Weiningen. Observations on the infection process on the Weiningen strain of *Arabidopsis* are reported here.

Two other pathogenic fungi, *Rhizoctonia solani* and *Botrytis cinerea,* were isolated from naturally infected plants of *A. thaliana* strain RLD grown from mutagenised seed.

The importance of these observations, in terms of developing model systems to investigate host-pathogen interactions, is discussed.

Introduction

The small crucifer *Arabidopsis thaliana* has long been recognised as a suitable subject for classical plant genetic studies (Laibach 1943). With the explosive development of plant molecular biology in recent years, its small genome (70,000 kb) and low amount of repetitive DNA, have made *Arabidopsis* an attractive subject for a whole variety of molecular genetic investigations (see Meyerowitz 1987 for a recent review). Traditionally, although plant geneticists could observe mutations which altered phenotype, it was difficult to identify the genetic lesion unless it occurred in a well characterised biochemical pathway, or was tagged with a transposable element. With *Arabidopsis* it is theoretically quite easy to isolate clones of the mutated gene by coupling chromosome walking with co-segregation of the mutation with known genetic or RFLP markers (Somerville 1989). Thus, genes marked by mutation can now be identified and characterised at the molecular level. In this sense *Arabidopsis* is becoming the *"E. coli"* of the plant world. Studies on development, metabolism and cell biology have made rapid progress but the use of *Arabidopsis* to gain an insight into the molecular biology of plant-pathogen interactions has been hindered by the lack of well characterised pathogens. Thus, although several fungal pathogens of *Arabidopsis* have been mentioned briefly in the literature (see for example Brandenburger 1985), detailed descriptions of host-parasite relationships of *Arabidopsis* do not exist. Therefore, more knowledge about *Arabidopsis* pathogens is needed urgently.

Obligate fungal plant pathogens tend to be highly specialised with respect to the hosts they can colonise. Among the obligate fungal parasites of *Arabidopsis, Puccinia thlaspeos* (Gäumann 1959, Brandenburger 1985), *Albugo candida* (syn. *Cystopus candidus*) (Lindau 1901, Brandenburger 1985), *Plasmodiophora brassicae* (Colhoun 1958, Brandenburger 1985, E. Koch and P. H. Williams, unpublished) and *Peronospora parasitica* (syn. *P. arabidopsidis*) (Lindau 1901, Gäumann 1918, Brandenburger 1985, Koch and Slusarenko 1990) have been reported.

Little is known about the susceptibility of *Arabidopsis* towards less specialised, non-obligate pathogens. Based on artificial inoculations, Sjödin and Glimelius (1988) concluded that *Arabidopsis* was highly susceptible to *Leptosphaeria maculans*. Several non-obligate pathogenic fungi infect a wide range of host plants, and it must be strongly suspected that *Arabidopsis* is susceptible to at least some members of this group. However, the only report of which we are aware is the isolation of *Sclerotinia* sp. from *Arabidopsis* by Morgan (1971).

The isolation of two rather unspecialised pathogenic fungi, *Rhizoctonia solani* (sclerotial state of *Thanatephorus cucumeris*) and *Botrytis cinerea* (conidial state of *Sclerotinia fuckeliana*) from *Arabidopsis* is described in the present paper. Furthermore, we report the successful development of the obligate pathogen *Erysiphe cruciferarum* on *Arabidopsis* following inoculation with conidia obtained from infected oilseed rape (*B. napus*). *E. cruciferarum* causes the major powdery mildew of crucifers. The collective name *E. poligoni* DC. was used by Salmon (1900) for the pathogen on swede (U.S. = rutabaga), turnip and other crop hosts. This species was reclassified by Blumer (1933) who used the name *E. communis* for those forms whose morphology was indistinctly known and where cleistothecia seldom developed. Further revision was proposed by Junell (1967), who regarded *E. communis* as a *nomen ambiguum* and used *E. cruciferarum* for the powdery mildew pathogen of a wide range of wild and cultivated crucifers (Dixon 1988).

Materials and methods

Plant and fungal material

Seed of *Arabidopsis* strain RLD was kindly supplied by Werner Bernhard (this institute). *Arabidopsis* strain Landsberg erecta was obtained from the Crucifer Genetics Cooperative, University of Wisconsin, Madison, USA. Strain Weiningen is the progeny of a group of 5–10 *Arabidopsis* plants collected recently near Zürich (Koch and Slusarenko 1990).

Powdery mildew infected leaf material was collected from an oilseed rape plant (*B. napus* ssp. *oleifera*) in the Botanical Garden, Zürich. *Rhizoctonia solani* and *Botrytis cinerea* were isolated from naturally infected *Arabidopsis* strain RLD grown from seeds which had been treated with the mutagenic agent ethyl methane sulphonate (EMS). These plants were growing in the winter months in a glasshouse and had been sown densely in seedling trays (60 × 40 × 5 cm). The glasshouse had high humidity, daily temperatures fluctuating between 10–25 °C over a three week period, and no supplementary lighting. *R. solani* was isolated from surface sterilised (1% sodium hypochlorite for 30 seconds, followed by rising with sterile distilled water) infected leaves by incubation on potato dextrose agar (PDA) containing 100 μg ml^{-1} streptomycin. *B. cinerea* was isolated by stroking aerial conidiophores with an inoculation needle and streaking onto streptomycin-containing PDA. After the initial isolation, both fungi were subcultured on PDA without antibiotic.

Cultivation and inoculation of plants

Arabidopsis plants for test inoculations were raised in potting compost in 12 cm diameter plastic pots in a glasshouse under controlled temperature conditions of 23 ± 3 °C with 16 h supplementary

lighting per day (Koch and Slusarenko 1990). Plants at the 3–5 leaf stage were inoculated with *E. cruciferarum* by rubbing pieces of *B. napus* leaves bearing conidiophores against individual leaves of *Arabidopsis* strain Weiningen. Pots containing inoculated plants were placed in plastic bags overnight and subsequently, without bags, on the window sill in the laboratory.

Three pots with plants of each *Arabidopsis* strain (RLD, Landsberg erecta and Weiningen) were inoculated with 1 × 1 cm squares cut from potato dextrose agar cultures of *R. solani*. Three squares per pot were placed on *Arabidopsis* plants at the early rosette stage. Uninoculated plants served as controls. Pots were placed in plastic bags, transferred to the glasshouse and kept under the controlled conditions described above. The plastic bags were removed after four days.

Light microscopy of whole-leaf mounts

Whole leaves were boiled for approximately one minute in the lactophenol-trypan blue stain solution (10 ml lactic acid, 10 ml glycerol, 10 g phenol, 10 mg trypan blue, dissolved in 10 ml distilled water) and then decolourised in chloral hydrate (2.5 g chloral hydrate dissolved in 1 ml distilled water) for at least 30 minutes. They were mounted in chloral hydrate and viewed under a compound microscope equiped with interference or phase contrast optics.

Scanning electron microscopy

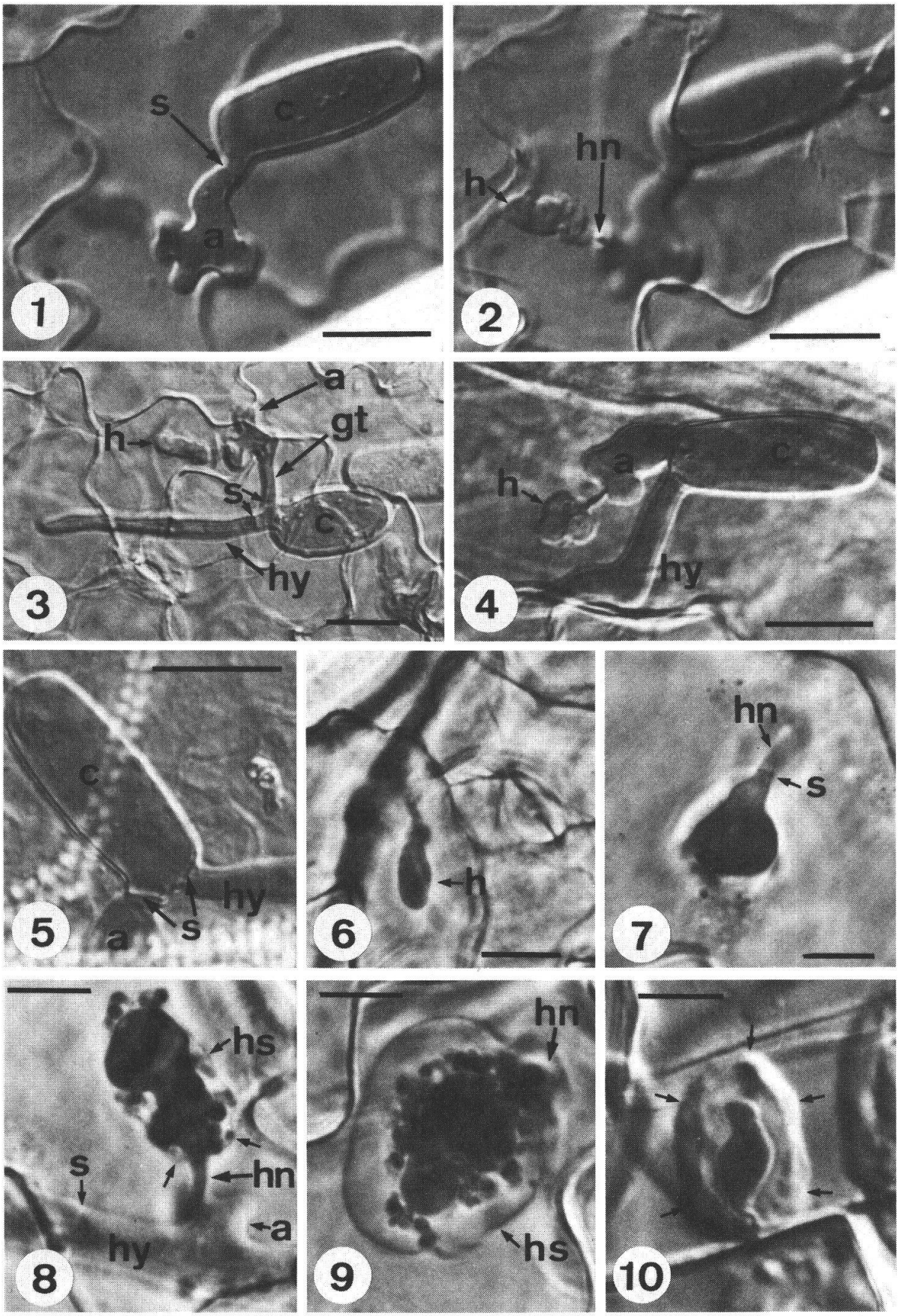
Infected leaves were fixed in the vapour of a 4% (w/v) aqueous solution of osmium tetroxide for three hours at room temperature, dehydrated in a graded series of acetone, and critical point dried. After mounting on specimen stubs with conductive silver paint, and sputter-coating with an 80:20% alloy of gold and palladium, the samples were examined in a Cambridge S-4 Stereoscan electron microscope.

Results

Development of E. cruciferarum

Light microscopy of whole-leaf mounts showed that by 18 hours after inoculation of *Arabidopsis* strain Weiningen, powdery mildew conidia had germinated and formed large, irregularly lobed appressoria. Appressoria were produced directly from conidia (Figs. 1 and 4), or, less frequently, they developed at the apices of well defined germ tubes (Fig. 3). Typically, the first haustorium was inserted into the underlying epidermal cell (Fig. 2). Formation of the appressorium was generally accompanied by the formation of a hypha which originated from the same (proximal) end of the conidium as the appressorium or appressorial germ tube, respectively (Figs. 3 and 4). In few cases, this hypha emerged from the opposite (distal) end of the conidium. Appressoria, appressorial germ tubes and hyphae were always separated from the conidium by a septum (Figs. 1, 3 and 5). By three days after inoculation these hyphae had grown 3–4 spore lengths, were septate, and had produced 2–3 haustoria. By this time, additional hyphae had grown from the distal ends of conidia, so that often, two hyphae were present at the distal end of the conidium and one hypha and the appressorium at the proximal end.

Young haustoria were globose but later became elongated-pyriform to irregular-shaped (Figs. 6 and 7). In specimens stained 5 days after inoculation, haustorial bodies could be clearly seen to be surrounded by a sac-like structure which terminated in the region of the haustorial neck (Figs. 8 and 9). This appears to be the "haustorial sac" described by Bushnell and Gay (1978), composed of the extrahaustorial membrane, the vacuolar membrane of the host cell and a thin layer of host cytoplasm which appear as one entity in the light microscope. Granular structures were observed in the extrahaustorial matrix, i.e. the space between the haustorial sac and the haustorium (Figs. 8 and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9). These structures appeared to be haustorial lobes which extended from the haustorial body into the matrix. Hirata (1967) described two types of powdery mildew haustoria, those of *Erysiphe graminis* and those of other mildews as represented by *Sphaerotheca fuligena*. In the latter, haustorial lobes extend convolutely over the surface of the haustorial body, giving the entire structure a compact form and granular appearance (Hirata 1967). Lobed haustoria were observed in various members of the *Erysiphaceae* (Bushnell and Gay 1978), including *E. polygoni* (Stavely et al. 1969).

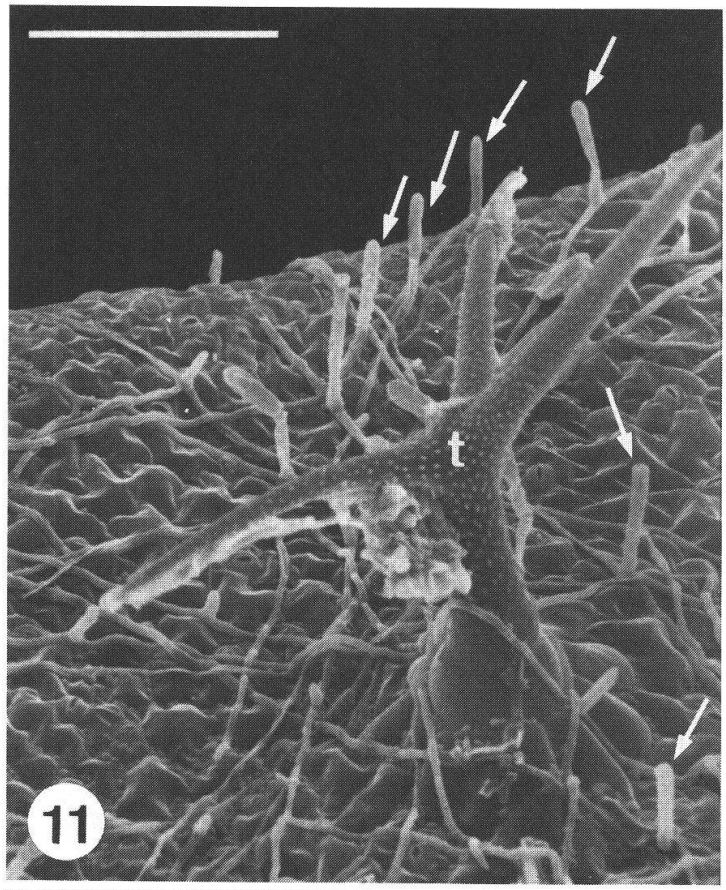
In a few cases, the complete encapsulation of haustoria in host cells of *Arabidopsis* was observed (Fig. 10). Similar encasements were observed surrounding some haustoria formed by *Peronospora parasitica* in cells of *Arabidopsis* (Koch and Slusarenko 1990). This phenomenon could represent an attempt by the host to limit infection. Other potential resistance reactions were the deposition of granular material adjacent to haustoria, the formation of large papilla-like structures underneath the appressoria (seemingly preventing haustorium formation), and in a few cases, necrosis of host cells invaded by haustoria (not shown).

Microscopic observation of whole-leaf mounts five days after inoculation revealed the formation of the asexual conidial stage of *E. cruciferarum* on *A. thaliana*. Conidiophores were erect and consisted of a few, more or less straight, cylindrical cells to which a maturing conidium was attached (Fig. 12). According to Boesewinkel (1980) and Braun (1987), *E. cruciferarum* belongs to those members of the Erysiphaceae in which the conidia are formed singly. Hyphal growth of *E. cruciferarum* on *Arabidopsis* was comparatively thin, and conidiophore formation remained sparse (Fig. 11). The leaves were symptomless to the unaided eye. Infections remained restricted to the inoculated leaves, which may reflect a rather low degree of compatibility between host and pathogen, but could also be due to unfavourable environmental conditions.

Abbreviations used in figures:
a, appressorium; c, conidium; gt, germ tube; h, haustorium; hn, haustorial neck; hs, haustorial sac; hy, hypha; s, septum; t, trichome

Figures 1–10. Infection process and haustorium formation by *Erysiphe cruciferarum* on *Arabidopsis thaliana* strain Weiningen.

Fig. 1. A germinated conidium with a multi-lobed appressorium. Bar = 25 µm.
Fig. 2. The same infection site as in Fig. 1, but focussed through to the primary haustorium in the epidermal cell. The haustorial neck extends from one of the appressorial lobes. Bar = 25 µm.
Fig. 3. A germinated conidium. The appressorium is positioned at the apex of a short germ tube. Bar = 25 µm.
Fig. 4. A germinated conidium. The appressorium developed directly from the conidium. Bar = 25 µm.
Fig. 5. Septation between conidium and appressorium and conidium and hypha. Bar = 25 µm.
Fig. 6. A young elongated-pyriform haustorium. Bar = 10 µm.
Fig. 7. Haustorium showing a septum in the region of the haustorial neck. Bar = 5 µm.
Fig. 8. Superficial hypha with a appressorium and mature haustorium. The haustorial neck extends from one of the appressorial lobes. The haustorial sac surrounds the haustorial body and appears connected to the haustorial neck (arrows). Bar = 5 µm.
Fig. 9. A mature haustorium. The haustorial sac appears expanded. Numerous granular structures surround the haustorial body. Bar = 5 µm.
Fig. 10. A haustorium surrounded by a thick capsule (arrows), in an epidermal cell over a leaf vein. Bar = 10 µm.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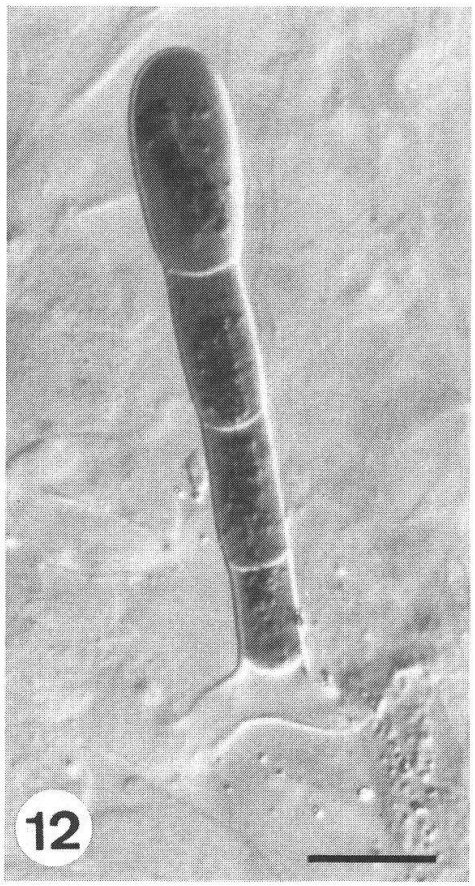
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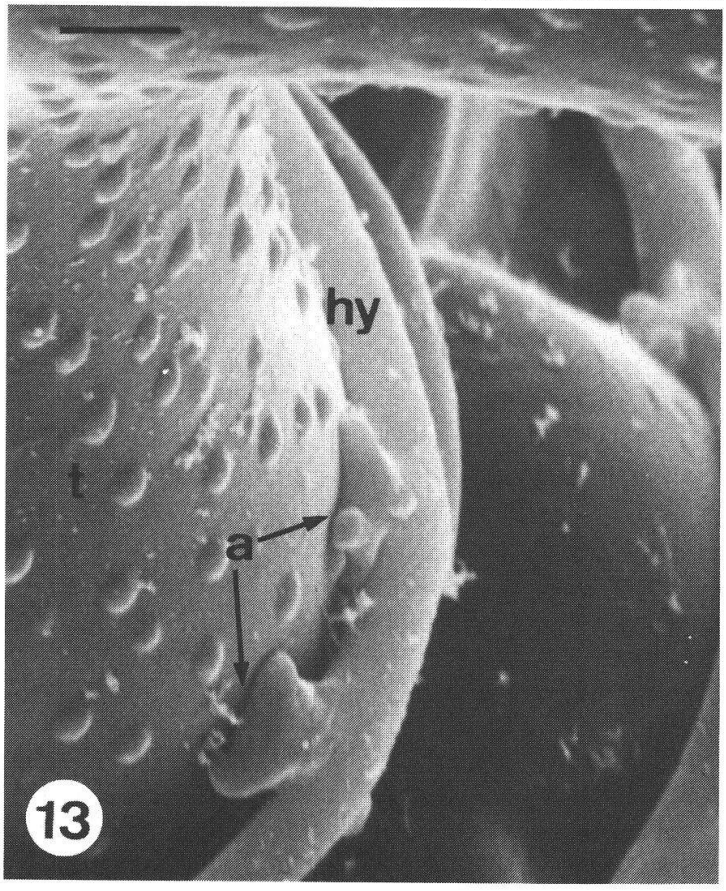
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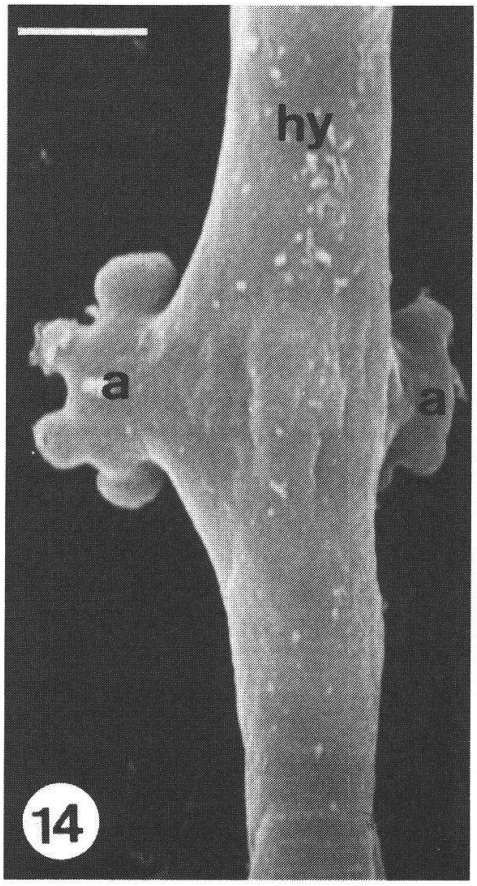
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In powdery mildews, appressoria are formed either at the end of conidial germ tubes or as lateral outgrows of superficial hyphae. They function as structures which both attach the mycelium to the host surface and form haustoria (Braun 1987). Considerable variation in the morphology of appressoria exists between different species of powdery mildews (Neger 1902, Zaracovitis 1965, Boesewinkel 1980, Braun 1987). Boesewinkel (1980) grouped *E. cruciferarum* among those *Erysiphaceae* with "multilobed haustoria". In our study, appressoria on hyphae of *E. cruciferarum* frequently had 2–4 lobes (Figs. 8, 13 and 14). Haustoria did not extend from the centre of appressoria but from one of the appressorial lobes (Figs. 2 and 8). Appressoria were formed singly (Fig. 8) or on opposite sides of hyphae (Fig. 14). The shape of appressoria on hyphae corresponded closely with the hyphal appressoria of *E. cruciferarum* depicted by Boesewinkel (1980) and Braun (1987), but the shape of appressoria formed on germ tubes differed from those shown by both authors. Apparently, the appressoria on germ tubes of *E. cruciferarum* are variable, because the shape of these structures also differs considerably between the reports of Boesewinkel (1980) and Braun (1987).

Isolation of Rhizoctonia solani

In an experiment aimed at obtaining M2 seed, plants grown in seedling trays in a glasshouse under high humidity and low light were completely overwhelmed by a natural infection (Figs. 15 and 16). Infected plants showed pale to dark brown lesions of different sizes (Fig. 17), which quickly developed into a soft rot of the affected plant parts. Threads of mycelium were visible on the soil and the rotting plant material. When affected seed trays were incubated at room temperature in a plastic bag, the disease spread rapidly to adjacent plants and the patches of overwhelmed seedlings grew quickly in diameter. On the abaxial side of leaves showing lesions, greyish spots were visible which were identified under the microscope as thick layers of fungal mycelium. When isolated and cultured on PDA, a rapid growth of brown mycelium was produced. Based on morphological characters, the fungal isolate was identified as *Rhizoctonia solani.*

In order to test the susceptibility of different strains of *Arabidopsis* to *R. solani,* and to eliminate any possible effects of the mutagenic treatment, the three strains of *Arabidopsis* were grown from untreated seed, inoculated with *R. solani,* and covered with plastic bags. Four days after inoculation, a web of mycelial threads extended from the squares of agar inoculum onto the leaves. After removal of the plastic bags, the plants appeared dark green in colour and quickly collapsed, developing into a slimy mass. A few plants at the periphery of the pots remained unaffected. In contrast, uninoculated control plants showed no disease symptoms. No differences in susceptibility were noticed between the three *Arabidopsis* strains tested.

Figures 11–14. Formation of conidiophores and lobed appressoria by *Erysiphe cruciferarum* on *Arabidopsis thaliana.*

Fig. 11. Hyphae and conidiophores (arrows) on the leaf surface. Bar = 100 μm.
Fig. 12. A conidiophore of *E. cruciferarum.* Note the three cylindrical cells bearing a single, maturing conidium. Bar = 25 μm.
Fig. 13. Lobed appressoria (arrows) on hypha growing along the base of a trichome. Bar = 5 μm.
Fig. 14. Hypha with four-lobed appressorium. A second appressorium is present on the opposite side of the hypha. Bar = 2.5 μm.


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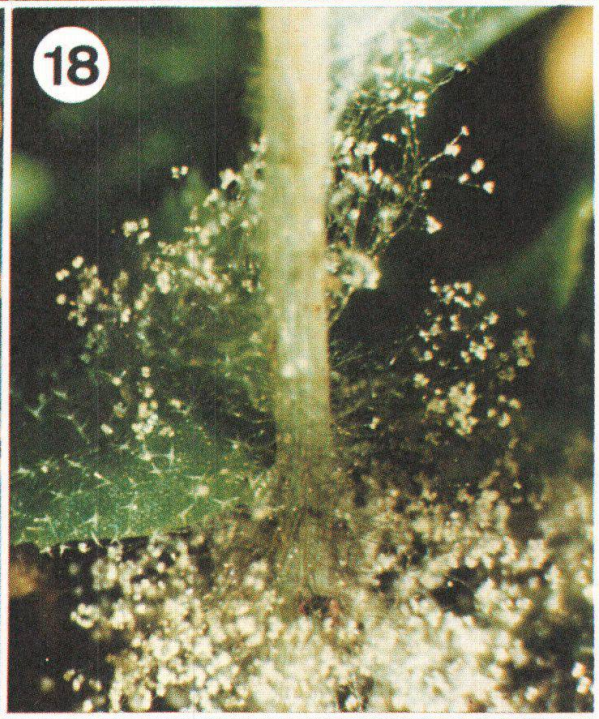
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Isolation of Botrytis cinerea

In seedling trays belonging to the same experiment as those from which *R. solani* had been isolated, grey mould was observed on a few plants at the rosette stage. The incidence of disease increased greatly following shoot formation and flowering, which could be due simply to a spread of infection, but may indicate a higher susceptibility of the senescing plant tissue, especially since *Botrytis* does occur typically on older, senescent tissues (Jarvis 1980). The disease was very severe, necessitating fungicidal treatment. Sporulation occurred on rosette leaves and on the lower portion of shoots (Fig. 17). The fungus was isolated, cultured on PDA and identified as belonging to the *Botrytis cinerea* group.

Artificial inoculations of plants grown from untreated seed were not made. Therefore, an effect of the mutagenic treatment cannot be ruled out completely. However, the observation that virtually every plant was affected rather suggested a general susceptibility of *Arabidopsis* strain RLD to *B. cinerea.*

Discussion

Two strategies have been employed to find pathogenic fungi capable of colonising *Arabidopsis.* Firstly, natural infections have been looked for in the field and glasshouse. In this way *Arabidopsis* plants infected with downey mildew caused by *Peronospora parasitica* were found (Koch and Slusarenko 1990), and further testing has shown that both resistant and susceptible *Arabidopsis* strains exist; opening up the possibility of studying the molecular basis of these differential interactions in a host very amenable to such investigations. *Sclerotinia* sp. has also been isolated from naturally infected *Arabidopsis* by Morgan (1971). The second strategy has involved trying to infect *Arabidopsis* with pathogens from related crucifers. In this way *Plasmodiophora brassicae* (E. Koch and P. H. Williams) which causes clubroot, *Leptosphaeria maculans* (Sjödin and Glimelius 1988) which causes stem canker, *Xanthomonas campestris* pv. *campestris* which causes blackrot (M. Daniels, personal communication) and turnip yellows mosaic virus (TYMV) (Martinez, cited by Somerville 1989) have been shown to infect *Arabidopsis* successfully. In the present study we report the susceptibility, in artificial inoculations, of *A. thaliana* to an *E. cruciferarum* isolate from oilseed rape, and we describe the isolation of *R. solani* and *B. cinerea* from naturally infected material and, in the case of *R. solani,* infection of the host with an axenic culture. To our knowledge, none of these fungi has previously been reported as a pathogen of *Arabidopsis.* Thus, the potential for using *Arabidopsis* to study host-pathogen interactions is growing steadily.

Susceptibility of *Arabidopsis* to a powdery mildew was also observed recently by E. Koch and P. H. Williams (unpublished). In this case, the inoculum was suspected to have

Fig. 15. *R. solani.* The fungus is spreading towards the plants in the upper part of the picture which are still unaffected. Infected plants are completely overwhelmed.

Fig. 16. Close-up view of the center of Fig. 15 showing discolouration and rotting of plants.

Fig. 17. *R. solani.* Disease leaves showing, from left to right, increasing degrees of infection, with a healthy leaf (extreme right) for comparison.

Fig. 18. *B. cinerea.* Conidiophores growing from a shoot of *A. thaliana.*

derived from powdery mildew infections of other crucifers grown in the same glasshouse, and formation of powdery mildew conidia occurred on maturing *Arabidopsis* plants. In the present study, very young leaves of *Arabidopsis* were inoculated with conidia of *E. cruciferarum*. Generally, young plant tissue is more susceptible than aging tissue to infection by biotrophic fungi. Sporulation of *E. cruciferarum* on *Arabidopsis* was sparse, and macroscopically visible disease symptoms were absent. However, from a qualitative point of view it was evident that the inoculated plants were suceptible to this pathogen. *E. cruciferarum* was able to infect the inoculated plants, the vegatative development was identical to colonisation of other host plants by this fungus, and most importantly, sporulation occurred within a short period after inoculation. The observation that the development of the fungus appeared restricted is in agreement with the description of *E. cruciferarum* by Junell (1967) who stated that the conidial state is "often thin and rather inconspicuous". In other cases, however, the fungus totally covers the host and conidia are formed in abundance (Junell 1967). Supposedly, these differences result primarily from differing degrees of compatibility between host and parasite, but may also be due to environmental factors and age of the host plant. To date, very little is known about the host-parasite relationships of *E. cruciferarum*. In *Erysiphe graminis,* pathogen races can be differentiated by their interactions with host genotypes carrying different resistance genes, and host and parasite interact in a manner typical for a gene-for-gene relationship (Ellingboe 1978). Clearly, it would be very interesting to characterise the pathogenic specialisation of *E. cruciferarum* with respect to different strains of *A. thaliana*.

The susceptibility of *Arabidopsis* to *B. cinerea* and *R. solani* is not surprising since both these fungi have a very wide host range (Ellis and Waller 1974, Mordue 1974). Among the Crucifereae, *Botrytis* infections occur on *B. oleracea* (Crüger 1983) and on oilseed rape (*B. napus*). Damp conditions and cool temperatures (7–16 °C) favour spore germination and infection of plant tissues by *Botrytis* (Maude 1980). In the present study, infection of *Arabidopsis* by *B. cinerea* may have arisen via soilborne sclerotia or, perhaps more likely, from conidia disseminated from infected debris of other plants grown in the same glasshouse.

Infection of *Arabidopsis* by *R. solani* was most probably from soilborne inoculum. *R. solani* survives almost exclusively in the form of sterile mycelium (hyphae or sclerotia) associated with organic debris in soil (Boozalis and Scharen 1959). The collective species *R. solani* is divided into several anastomosis groups (AG). Different races of the fungus are probably equivalent to the anastomosis groups, but variation also exists within each anastomosis group; different members showing preferences as to host range, temperature optimum, and so on (Agrios 1988). In our study, no attempt was made to identify the anastomosis group of *R. solani* isolated from *Arabidopsis*. In previous studies, isolates from cruciferous hosts were identified as belonging to AG2 (Ogoshi 1976) or AG1 and AG2 (Parmeter et al. 1969).

Systematic testing of a number of *Arabidopsis* ecotypes and mutants available from a central international seed collection (Kerchheim and Kranz 1985) might reveal graded, or completely differential responses towards these pathogens. This would be of great interest for developing model systems for the investigation of host-pathogen interactions.

Thanks are due to Rosemarie Honegger for the scanning electron microscopy, and to Werner Bernhard for donating infected plant material from his M2 experiment.

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