A Comparative Study of the Haustorial Development of *Striga asiatica* (L.) Kuntze on Sorghum Cultivars

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ABSTRACT

Ten sorghum cultivars were studied for their mode of *Striga* parasitization, and the factors conferring resistance. In resistant cultivars most of the *Striga* haustoria failed to penetrate beyond the endodermis, whereas in susceptible cultivars the haustoria penetrated the endodermis and became established.

Resistant cultivars showed marked endodermal and pericyclic thickening and the deposition of silica in their endodermal cells, which were lacking in the susceptible cultivars. Extra thickening in pericyclic cells as a response to the entrance of haustorium was observed in cultivars N-13 and IS-4202.

Ten cultivars studied showed differential haustorial reactions. These reactions included: extra thickening in the pericycle in response to haustorial infestation, haustorial collapse, tylosis-like occlusions in the xylem vessels, and the deposition of dark-staining materials in the cortex. Although no definite conclusion could be drawn regarding the relationship between the degree of mechanical tissue development and field resistance, there was evidence that some field-resistant cultivars have strong mechanical tissues. There could, however, be other factors governing resistance to *Striga* in the field.

Key words: *Striga asiatica*, sorghum, haustorium, anatomy, endodermis, pot test, host resistance mechanism, parasitization, susceptibility.

INTRODUCTION

Striga, belonging to the family Scrophulariaceae, is a serious root parasite of several food crops such as sorghum, pearl millet, maize and cowpea. A severe attack by this parasite sometimes causes total crop failure. In India, sorghum is predominantly attacked by *Striga asiatica* (L.) Kuntze. Ramaiah and Parker (1982) reviewed control measures for *Striga* eradication and concluded that measures for the effective control of *Striga* should include an integrated approach involving resistant cultivars and simple agronomic practices.

Three different host resistance mechanisms to *Striga* have been reported by previous workers, i.e. resistance due to low stimulant production (Kumar, 1940; Williams, 1959), mechanical barriers (Saunders, 1933), and antibiosis or physiological obstruction (Saunders, 1942). However, studies on the latter two mechanisms are limited.

The infestation of its host by *Striga* depends on the successful penetration of *Striga* haustoria into the vascular tissue of the host root. The present investigation was undertaken to study the mode of haustorial development and penetration and to learn more about the nature of mechanical barriers in some sorghum cultivars.

MATERIALS AND METHODS

Ten sorghum cultivars were included in the present investigation (Table 2). All these lines were field tested for resistance to *Striga asiatica* in India, at Akola in 1976, and Dharwar

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in 1978. The Akola experiment was replicated four times and a susceptible check cultivar CSH-1 was planted after each set of 10 cultivars to establish the general infestation level in the field. In Dharwar, five susceptible checks were randomized throughout the trial plot. The results were reported as percentages of the susceptible check infestation. Cultivars having less than 10 per cent of the susceptible check were considered as resistant and others as susceptible.

Striga asiatica seeds collected on the ICRISAT farm in March 1975 were mixed with sterilized coarse sand in 200 ml paper cups. Twenty sorghum seeds were sown in each cup and 3 d after emergence the seedlings were thinned to five per cup. The seedlings were grown under artificial light and watered with 10 per cent Hoagland's solution. After 4 weeks (by which time *Striga* was well established on the roots of the susceptible cultivars), the seedlings were carefully removed from the cups. The roots were gently washed and the root regions with *Striga* attachments were fixed in a FPA mixture (40 per cent formalin, propionic acid, 70 per cent ethyl alcohol in the proportion of 5:5:90 by volume). After fixation, the materials were passed through absolute alcohol and a tertiary butanol series and finally processed for microtome sectioning following Johansen's technique (Johansen, 1940). The sections were cut through the root regions which had a *Striga* attachment, processed and stained for permanent slide preparation.

Three to five attachments for each sorghum cultivar were studied for *Striga* parasitization. Microscope observations were made on the degree of thickening of the inner endodermal cell walls, the presence of silica in the endodermal cells, and the degree of thickening of the pericycle walls (Table 1) on lateral roots of comparable age. The endodermal cell wall thickness was measured using an ocular and stage micrometer and the endodermal cell wall and pericycle scored as high (1) intermediate (2) or low (3) on the basis of the thickness of either one or both. Photomicrographs were taken using a Nikon Aphophot microscope camera with PX-135-36 film.

In order to understand whether the development of mechanical tissue differed between resistant and susceptible cultivars, a time-course study of the changes in root anatomy was made on the susceptible CSH-1, an All India Coordinated Sorghum Improvement Project hybrid, and N-13, Nandyal Local, a resistant cultivar. For the root anatomy studies plants were grown in pots in the absence of *Striga* and examined 7, 14, 21 and 28 d after emergence. Tests for lignification were carried out with staining reactions with safranin/toluidine blue (Feder and O'Brian, 1968).

RESULTS

Parasitization of susceptible cultivars

The process of penetration by the *Striga* haustorium into the root of susceptible cultures has been described by several workers (Saunders, 1933; Musselman, 1980).

The germinating *Striga* seed, the attachment to the host, and the invasion of the host root by a haustorium are depicted in Figs 1–4. The seed of *Striga asiatica* has a very thick seed coat with reticulation (Fig. 1). The epidermal cells of the seed coat are large and sub-cubical, and the outer layer of the seed coat contains considerable tannin as indicated by the staining reaction of toluidine blue.

Germination began with the radicle making its way out through the seed coat (Fig. 2). The plumule grew very slowly at this stage, and still remained within the seed coat until the haustorium established its vascular contact with the host root. The plumular axis was visible within the arch of the two cotyledonary leaves (Fig. 2).

A bulbous haustorium, formed at the tip of the radicle, made contact with the endodermis of the host root and pressed against cortical cells which became distorted as the haustorium penetrated into the cortex and ultimately came into contact with the endodermis (Fig. 3). At this stage the outer tangential wall of the endodermis became

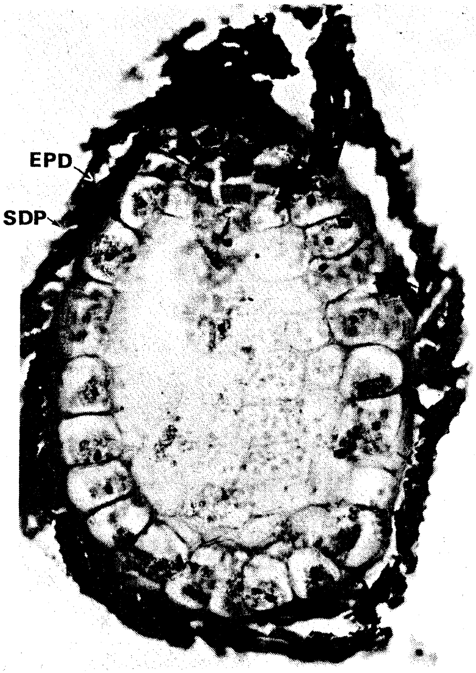


FIG. 1. Longitudinal section of *Striga* seed showing fringe-like outgrowth on seed coat and cubical cells in the epidermis. 240 × . SDC, seed coat; EPD, epidermis.

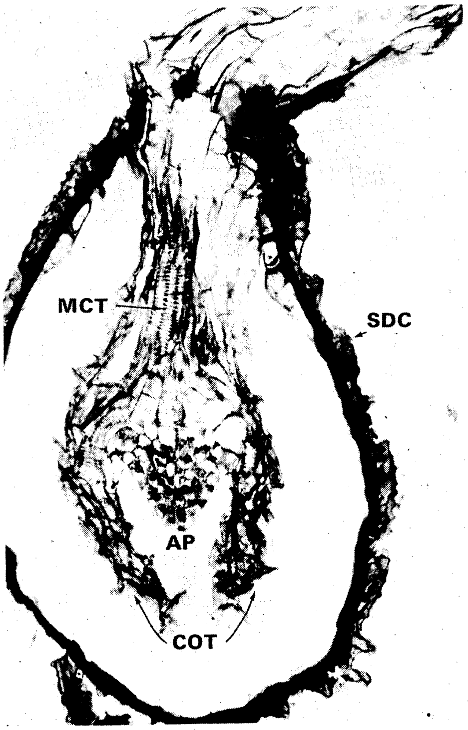


FIG. 2. Longitudinal section of germinating *Striga* seed showing plumule with two cotyledons still covered by the seed coat. 256 × . SDC, seed coat; MCT, mesocotyl; COT, cotyledon; AP, plumular apex.

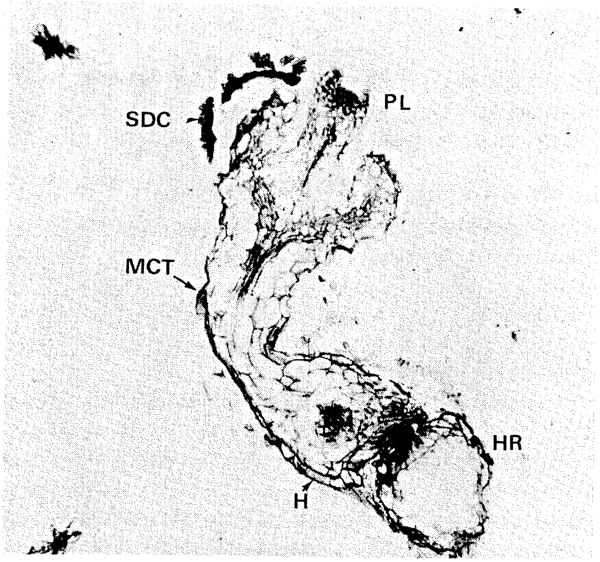


FIG. 3. Longitudinal section of germinating *Striga* seed showing emergence of the *Striga* seedling and the bulbous haustorium establishing connection with host stele. 75 ×. SDC, seed coat; PL, plumule; MCT, mesocotyl; H, haustorium; HR, host root.

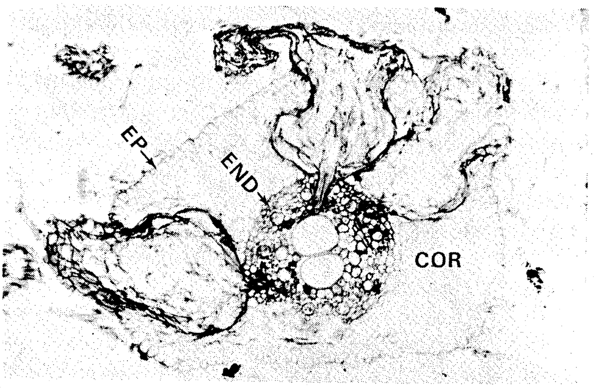


FIG. 4. Transverse section of a susceptible cultivar root, Swarna, showing three bulbous haustoria, one of which has already established connection with the host stele. 75 ×. END, endodermis; EP, epidermis; COR, cortex.

disrupted, allowing the haustorium to penetrate the stele of the host and to establish a connection with the host vascular bundle (Figs 3–4). In some cases the presence of a substance which stained dark green with toluidine blue was noticed when the haustorium was in contact with the endodermis (Fig. 5). This may be an enzyme secreted by the haustorium to dissolve the cell wall.

The invasion of the host stele was completed by the development of tracheids from the axis of the young haustorium. These tracheids were characterized by the spiral thickenings as described by Rogers and Nelson (1962) and penetrated the xylem elements either by dissolving the cell walls or by mechanically disrupting them, making the host–parasite vascular connections complete. At this stage the haustorium was almost double the size of the host stele (Fig. 4).

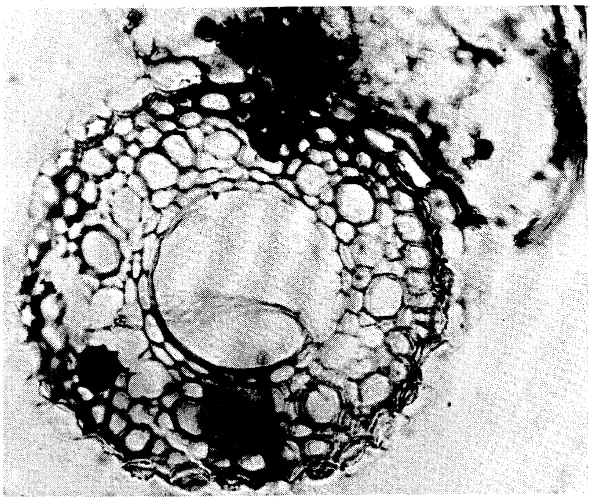


FIG. 5. Transverse section of the root of a susceptible cultivar CSH-1 showing dark-staining materials derived from the haustorium and distortion of tissue at the point of contact of the haustorium with the host endodermis. 320 ×.

Haustorial development in resistant roots

In the resistant cultivars the attachment to the root, and the penetration of the cortex by the haustorium, followed the same process as in the susceptible cultivars. However, in the resistant cultivars most of the haustoria failed to penetrate the endodermis, in contrast with the susceptible cultivars, in which most of the haustoria were successful in establishing the vascular connection with the host root (contrast Figs 6–8 with Figs 3–5).

Some resistant cultivars were found to have thickening in the endodermal and pericycle cell walls; and the endodermal cells in some of the cultivars were found to contain silica. These were observed in the resistant cultivar N-13, Nandyal Local (Fig. 10) in contrast to the susceptible CSH-1 (Fig. 9). The course of development of these thickenings in the absence of *Striga* was followed in these two cultivars in a separate study. Cell wall thickening in these two tissues as well as the presence of silica was observed in N-13 as early as 7 d after germination (Fig. 10). CSH-1, in contrast, showed only insignificant thickening in the endodermis and contained no silica as late as 14 d after germination (Fig. 9). By 28 d, there was only a small increase in thickening in the endodermis and pericycle in CSH-1, whereas N-13 had accumulated considerable thickening materials, especially in the pericycle, by that time.

In addition, several apparent responses to the invasion by the *Striga* haustorium were observed in certain resistant cultivars. One of these reactions appeared to be extra lignification in the pericycle cells at the point of contact of the haustorium with the endodermis in N-13 and IS-4202 (Figs 6 and 8). As a result, the haustorium appeared to become distorted and failed to penetrate into the stele (Fig. 6). In another resistant cultivar, SRN-4841, a few haustoria did penetrate through the suberized endodermis but, on reaching the xylem, tylosis-like occlusions were formed in the cavity of the xylem vessels (Fig. 11).

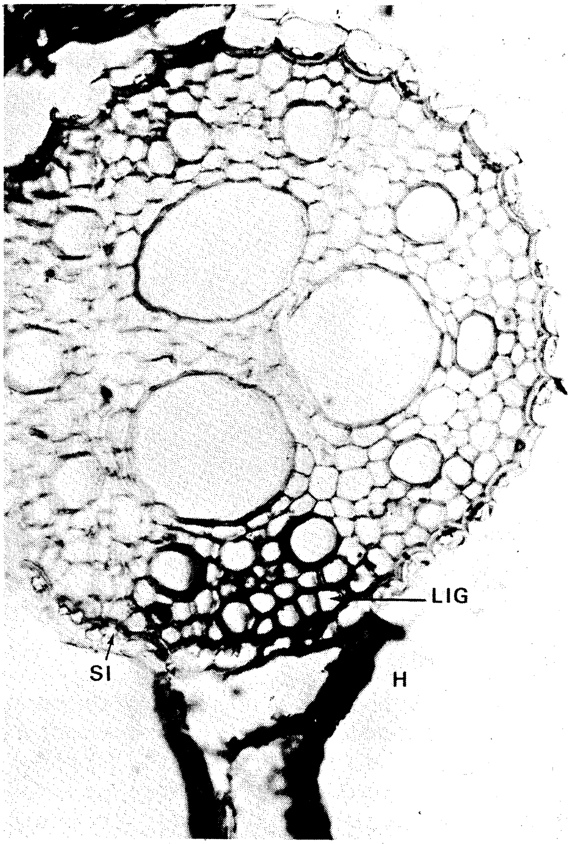


FIG. 6. Transverse section of the root of a resistant cultivar IS-4202 showing collapsing of the haustorium and extra lignification just below the hood of the haustorium. 320 ×. H, haustorium; LIG, extra lignification; SI, silica body.

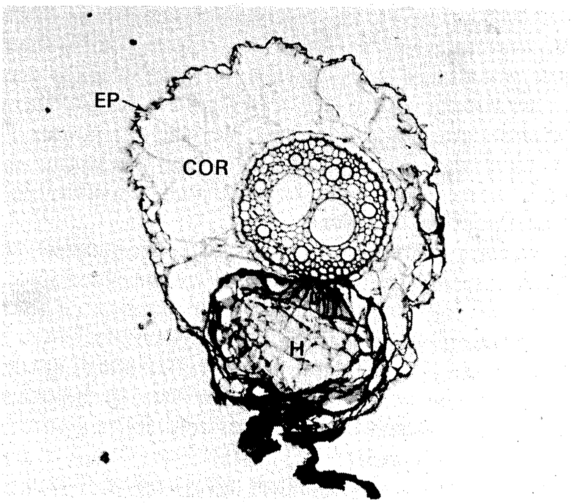
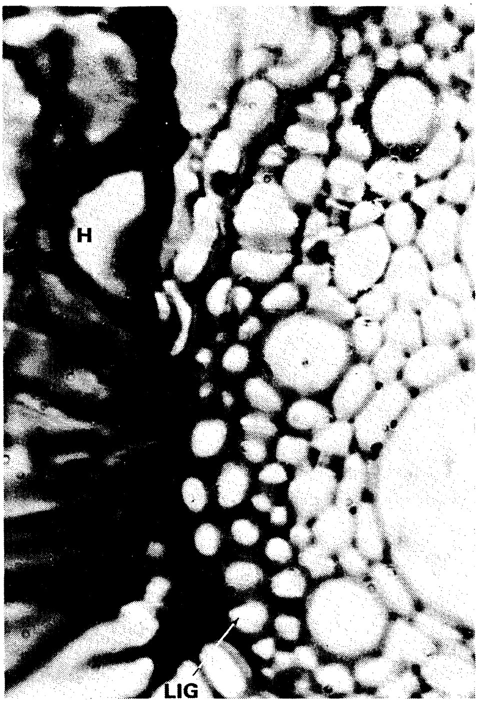


FIG. 7. Transverse section of the root of a resistant cultivar N-13 showing failure of establishment of the haustorium to xylem vessel. 75 ×. EP, epidermis; COR, cortex; H, haustorium.



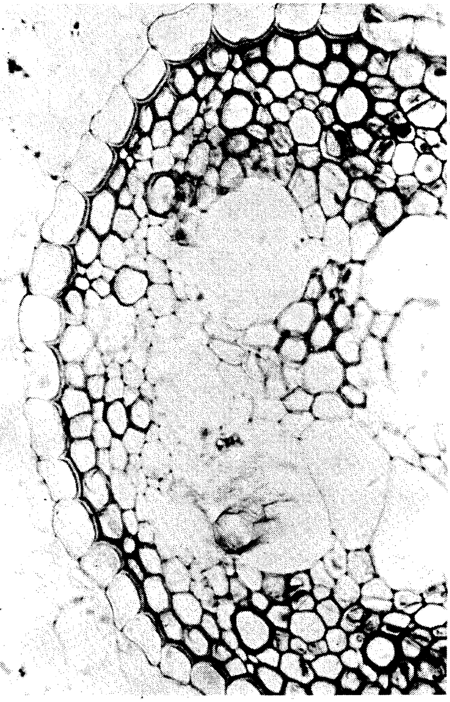


FIG. 8. Transverse section of the root of a resistant cultivar showing extra lignification in the pericycle below the hood of the haustorium at higher magnification. 256 ×. H, haustorium; LIG, extra lignification.

FIG. 9. Top side of root of CSH-1 showing insignificant thickening and absence of silica at 14 d. 256 ×.

Relationship of host root anatomy and resistance to Striga

The root anatomy of 10 selected cultivars was examined for the thickness of the inner tangential wall of the endodermis, the degree of lignification of the pericycle, and the frequency of occurrence and size of silica in the endodermal cells. Each genotype was scored as high (1), intermediate (2) or low (3) for each of these characteristics. The genotype with the low score (1) representing the maximum expression of the character was associated with resistance. A detailed description of the meaning of each category is presented in Table 1, and the score for all the 10 genotypes including the check CSH-1 in Table 2. The range in these characters is not great and the classifications are not distinct in all cases.

In the overall scoring more weight was given to the intensity of mechanical tissue (sclerenchyma) in the pericycle and size of silica in the endodermis. This mechanical tissue was assumed to resist the invading haustorium. Based on the overall score, it appeared that all the cultivars showing field resistance have a high or intermediate rating for all the three characters. In the cases of IS-4202 and IS-5218, all the three characters were rated as intermediate, but collectively might be regarded as strong in restricting haustorial penetration.

This study indicated that there was substantial variability in the mode of haustorial development, as well as in the intensity of mechanical barriers in the host root resisting the haustorial growth. There are six cultivars belonging to resistant and moderately resistant groups showing predominant mechanical barriers (i.e. N-13, SRN-4841, IS-4202,

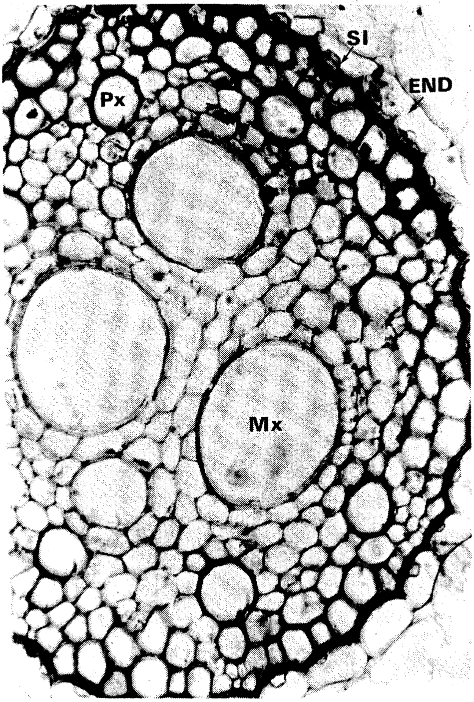


FIG. 10. Transverse section of root of N-13 showing much more thickening in the endodermal cell wall and pericycle even at 7 d. 256 × . END, endodermal thickening; Px, protoxylem; Mx, metaxylem; SI, silica body.

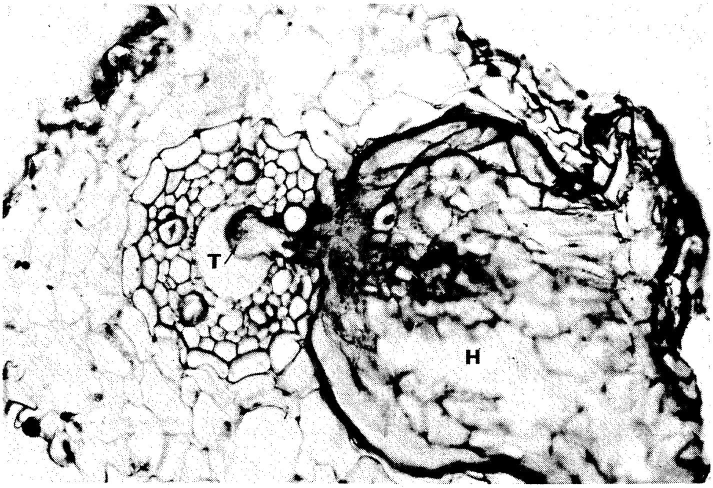


FIG. 11. Transverse section of root of a resistant cultivar, SRN-4882, showing tylosis type of occlusion in the xylem vessels from the haustorium. 256 × . T, tylosis; H, haustorium.

TABLE 1. *Description of three classes of sorghum root anatomical characters*

Character	Score* 1	2	3
Inner tangential wall of endodermis	4·68±0·69 μm	3·53±0·28 μm	2·35±0·11 μm
Pericycle	Two or more layers of very thick lignified cells	Moderately thickened and generally unilayered	Thin-walled and unilayered
Silica	Always present, large, occupying 0·50–0·75 of the lumen in endodermal cell	Generally present, but smaller than those in the high class	Generally absent or when present, very small, occupying less than 0·25 of the lumen

* Score: 1 = high; 2 = intermediate; 3 = low.

TABLE 2. *Field resistance and root anatomical traits of sorghum cultivars in scores (1 = high, 2 = intermediate, 3 = low)*

Cultivars	Field test* Akola, 1976	Dharwar, 1978	Mean	Root anatomy characters Endodermis	Pericycle	Silica	Overall
Resistant							
IS-5218	1	2	1·5	2	2	2	2
N-13	0	6	3·0	1	1	1	1
NJ-1515	2	4	3·0	2	1	2	1·9
IS-4202	3	5	4·0	2	2	2	2
SRN-4841	0	11	5·5	2	1	2	2
23-4	—	10	10·0	1	1	2	1
IS-5106	1	8	4·5	3	3	3	3
Susceptible							
CS-3541	25	—	25	3	3	3	3
IS-2162	124	—	124	3	3	2	3
CSH-1	100	100	100	3	3	3	3

* Expressed as percentage of susceptible check – CSH-1.

IS-5218, NJ-1515, 23-4). There was only one cultivar, IS-5106, which had a low score for mechanical tissue but showed good resistance. It was assumed that some other undefined mechanisms were operating to confer resistance to this genotype.

DISCUSSION

A comprehensive review dealing with the physiological concepts of the association between parasitic angiosperms and their hosts has been provided by Tsivion (1978). Several studies have previously been made to investigate the mode of parasitization of a susceptible host by *Striga* (Musselman, 1980). The present study with Indian *Striga asiatica* corroborates with the findings of the previous authors regarding the mode of parasitization of the host root. There are very few studies that compare the haustorial development processes in resistant and susceptible cultivars.

Saunders (1933) identified three resistant cultivars in South Africa and made particular reference to *Striga lutea*, which was found to have different resistance mechanisms. In the first cultivar the obstruction of haustorium was by cortical cells with very little resistance from the endodermis and vascular cylinder; in the second cultivar, the inner walls of the endodermis and vascular cylinder both obstructed the penetration of haustoria fairly effectively; and in the third cultivar, the serious impediment to haustorial penetration was the vascular cylinder itself rather than the endodermis.

In the present investigation cultivar N-13 was found to have resistance associated with highly thickened endodermis and pericycle tissue and SRN-4841 was found to have resistance from suberized endodermal cell walls and silica deposition, a highly lignified pericycle and presence of silica (Table 1). Extra lignification in pericycle cells at the point of contact of the haustorium was observed in N-13 and IS-4202 resulting in failure of *Striga* haustoria to enter the stele (Figs 8 and 10).

The role of lignification in parasite resistance is well recognized in wheat (Ride, 1975), sunflower (Panchenko and Antonova, 1974) and cucumber (Hijwegen, 1963).

In the present study the collapse of haustoria in the cortex and the deposition of dark-staining materials could be the impact of a physiological obstruction (or antibiosis) as reported by Saunders (1942). The deposition of material stained dark green with toluidine blue could be a substance reported to be produced by the advancing haustorial cells in *Striga asiatica* (Saunders, 1933) and *S. gesnerioides* (Okonkwo and Nwoko, 1978). They reported that this substance softened or dissolved the cell wall of host tissue. The chemical concerned has not been identified, but tests for cellulase were reported to be negative (Rogers and Nelson, 1962).

In the present study no direct comparison has been made to relate the presence of mechanical tissue with field resistance, but studies were undertaken with an objective of investigating haustorial development on some sorghum genotypes. The field resistance of some of these genotypes was known. Although no clear-cut conclusion could be made regarding either field or mechanical resistance, there are indications that some of the resistant lines such as N-13 and IS-4202 produced more mechanical tissue, while susceptible lines produced less mechanical tissue. There are exceptions (IS-5106) where some other mechanisms may be playing a role in conferring resistance. It may be that, in addition to these mechanical barriers, the resistant cultivars have some unknown factor, such as enzymes or hormones, which confer field resistance. However, this study contributes some evidence that mechanical resistance does seem to be an important, but not the exclusive, mechanism of host plant resistance to *Striga asiatica*.

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