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An *in vitro* technique for studying specific *Striga* resistance mechanisms in sorghum

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Witchweed (*Striga* sp.) is a noxious parasitic weed of many cereals, that causes considerable crop damage in the semi-arid tropics. Although, a number of control measures have been suggested, breeding crops which are resistant to the attack is the most feasible and effective way of control. However, breeding efforts have been hampered by the lack of adequate laboratory techniques that uncover critical host-parasite interactions, that occur naturally beneath the soil. Germination stimulant production is the sole *Striga* resistance mechanism in sorghum [*Sorghum bicolor* (L) Moench] that has been extensively studied and exploited for breeding purposes. Other *Striga* resistance mechanisms have not been effectively characterized and used. The purpose of this study was to develop an *in vitro* screening technique for evaluation of sorghum germplasm for specific *Striga* resistance mechanisms. We hereby report the development of a reliable screening technique, the Extended Agar Gel Assay (EAGA). Using the technique, we screened seven sorghum genotypes with known reactions to *Striga* parasitsm, SRN39, Framida, IS9830, 555, N13, Dobbs, Serena , CK60B, Shanqui Red, IS-4225, and two wild sorghum accessions, P78, and P47121, and we were able to characterize specific host defense reactions (mechanisms). These reactions indicate the potential existence of at least four separate mechanisms of *Striga* resistance in sorghum: 1) low production of *Striga* seed germination stimulants; 2) evidence of germination inhibitors; 3) low production of the signal required for haustoria initiation and 4) a hypersensitive response (characterized by a distinct necrotic area on the host root at the attachment site that discourage parasitic establishment. The development of this laboratory assay enabled us to identify and characterize distinct resistance mechanisms. These mechanisms can be exploited through conventional plant breeding programs. Additionally, the resistance genes can be pyramided into one background for more durable *Striga* resistance.

Key words: Witchweed, *Striga* resistance, host parasite interaction, germination, haustoria.

INTRODUCTION

The witchweed (*Striga* sp.), a parasitic weed of various crops, is the most limiting biotic factor in the production of sorghum by small farmers in rainfed agricultural areas of the semi-arid tropics (Ejeta et al., 2007). The parasite also attacks other crops including, millet (*Pennisetum glaucum* L.), maize (*Zea mays* L.), and cowpea (*Vigna unguiculata* Walp), (Parker and Reid, 1979).

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Abbreviations: EAGA, Extended Agar Gel Assay; **ddH_2O,** doubled distilled water; **NaOCl,** sodium hypochloride.

Although a number of control measures have been suggested, breeding crops which are resistant to the attack is the most feasible and effective way of *Striga* control. Great efforts have been devoted in the last few decades to identifying germplasm with resistance to *Striga* parasitism. Much of these effort were directed to empirical selection in field tests where unpredictable environmental factors influence *Striga* infestation. Nevertheless, some cultivars with good level of *Striga* resistance have been identified in sorghum (Ejeta, 1995), maize (*Z. mays*) (Kim et al., 1998), rice (*Oriza sativa*) (Johnson et al., 1997), and cowpea (*Vigna sinensis*) (Atokple et al., 1995). These breeding efforts have, however, been slowed by the lack of simple, reliable

screening methods, which have also limited our knowledge of host parasite interactions and host defense mechanisms.

Several host resistance mechanisms have also been proposed in the literature including low germination stimulant production, low production of the haustorial initiation factor, avoidance mechanisms, presence of physical barriers, and antibiosis (Ejeta et al., 1999). Low germination stimulant production is the only mechanism that has been studied and exploited for breeding purposes (Hess et al., 1992; Ejeta et al., 1999). Few studies and scattered hypotheses in literature relate to the other mechanisms. Most of these hypotheses are based on cytological studies, with poor field correlation, or field and pot experiments where inoculums uniformity and other environmental factors are a problem. Identification of host resistance mechanisms and candidate resistance genes that act pre- and post-infection. *Striga*-host associations rely on the ability to observe those events naturally hidden beneath the soil. This requires controlled culture on artificial media. The cultural conditions should be simple and reproducible for large scale screening of germplasm.

Several artificial growth systems have been tried to study host parasite interactions (Visser and Kollman, 1981; Lane et al., 1991). Most of these investigations were hampered by the difficulty in initiating infection or in obtaining enough infection sites. The most successful of these systems was developed by Lane et al. (1991). Yet even this procedure has not been used for routine screening largely because of problems with reproducibility. To date, little is known about the actual host defenses that discourage parasitic growth and establishment. Therefore, there is a great need to develop simple reproducible *in vitro* systems to carry out biological studies on parasitic associations and for use in breeding programs.

In this study, we report on the development of an *in vitro* bio-assays, the extended agar gel assay (EAGA) which we have employed to evaluate selected sorghum genotypes and wild sorghum accessions for specific *Striga* resistance mechaisms.

MATERIALS AND METHODS

Source of seeds

Striga asiatica seeds were obtained from USDA/APHIS, Whiteville Methods Development Center, Whiteville, NC. The seeds were stored and handled under quarantine restrictions approved by the USDA/APHIS and the Indiana Department of Natural Resources. Seeds of sorghum genotypes, SRN39 (low- stimulant-producer), Framida (low-stimulant-producer), IS9830 (low-stimulant-producer), 555 (low-stimulant-producer), N13 (high-stimulant-producer), Dobbs (high-stimulant-producer), Serena (high-stimulant-producer), CK60B (high-stimulant-producer), Shanqui Red (high-stimulant-producer), IS-4225 (high-stimulant-producer), and two wild sorghum species, P78 (*Sorghum drummondii*) and P47121 (*Sorghum arundinaceum*) were screened using EAGA.

Surface sterilization of sorghum seeds

Sorghum seeds were soaked in 10 ml 2.62% sodium hypochloride (NaOCl) solution (50% commercial bleach) for 30 - 60 min and rinsed three times with double distilled water (ddH2O). They were then soaked in 0.5% solution of N- [(trichloromethyl) thio]- 4-cyclohexene-1, 2-dicarbomixide (Captan 50-W) for 24 h, washed three times in sterile ddH2O, transferred to petri dishes that contained moist filter paper and incubated in the dark at 28°C for 24 h. Only healthy germinated seeds were selected for the extended agar gel assay.

Surface sterilization and conditioning of *Striga* seeds

Striga seed surface sterilization and conditioning was performed using the procedure described by Mohamed et al. (1998). Briefly, seeds were added to 10 mL in a 50-mL flask containing 3 - 5 drops of Tween 20, followed by removal of as much sand and debris as possible with a pipette, and sonicating the seeds for 2 min with occasional swirling. After sonication, the remaining sand/debris and water were removed with a pipette. The seeds were rinsed-3 times with H_2O depending on their cleanliness. Seeds were allowed to settle before pipetting to reduce loss. Seeds were sonicated and swirled 3 - 4 times a minute in a flask containing Metricide diluted 10 times. The seeds were then rinsed 3 times in 10 mL ddH_2O. 4 mL of ddH_2O and 1.5 mL of a 0.015% Benomyl [methyl-1-(butylcarbomyl)-2-benzimidazolecarbamate] solution were then added to each flask followed by 10 mL of sterile water. The flasks were then placed in a 28°C incubator to begin conditioning. Every 3 - 4 days, under a laminar air hood, seeds were pipetted into fresh sterile flasks containing 15.5 mL of the Benomyl solution and returned to the incubator.

The assay (EAGA)

The assay is a modification of the agar gel assay described by Hess et al. (1992). In the EAGA, large petri dishes with a thick agar layer were used so as to support growth of sorghum seedlings for a longer period of time. Around 1500 *Striga* seeds (4 drops of settled seeds) conditioned for 8 - 22 days were pipetted using a sterile 150 mm petri dish. A 0.7% agar solution was autoclaved for 15 min, then cooled to 50°C for at least one hour. The 50°C agar was poured into the petri dish containing conditioned *Striga* seeds, which produced an even distribution of seeds. Four pre-germinated sorghum seeds were placed at even intervals along the edges of each dish so that the radicles just penetrated the gel. The dishes were then covered and placed in an incubator at 28°C. The EAGA is used to establish genotypic differences in inducing *Striga* germination, haustoria initiation, as well as to detect differences in hypersensitive response.

Three days following inoculation, each dish was observed for germination, parasitic attachment and host root development, and then treated with ethylene to remove any difference in host roots for inducing *Striga* seed germination. Ethylene treatment was done in a dosing chamber located in a bio-safety cabinet in order to prevent ethylene contamination of the room. Little ethylene is needed, a 30-s burst inside the sealed chamber is sufficient to germinate all viable *Striga* seeds. Plates were left in this chamber for two days. After 48 h in the dosing chamber (5 days following inoculation), plates were vented in front of the bio-safety to remove any residual ethylene before placing them under grow light for 12 h. Data were collected under the microscope where the entire length of the host seedling root is scanned under a magnification of at least ×25. The dishes were observed at 2, 5, and 7 days following ethylene dosing and 5, 7, and 10 days after pouring plates for *Striga* attachment, and number of attachment sites was recorded. Sites of attached

Table 1. Mean *Striga* seed germination of selected set of sorghum genotypes with reported field reactions at 27 and 30°C.

Sorghum genotype	Field reaction to *Striga*	Germination distance at 27°C (mm)	Germination distance at 30°C (mm)	*Striga* germination index at 27°C
P78	N/T	0.00 [c]	0.00 [g]	0.58 [d]
P47121	N/T	19.16 [a]	28.67 [a]	1.04 [c]
SRN-39	R	0.00 [c]	0.58 [f]	1.21 [b]
555	R	0.45 [c]	0.75 [f]	1.09 [b]
Framida	R	1.15 [c]	2.95 [f]	1.05 [c]
IS9830	R	0.75 [c]	1.95 [f]	0.97 [c]
N13	R	20.00 [a]	27057 [a]	1.21 [b]
Dobbs	R	10.79 [b]	17.75 [d]	1.12 [b]
Serena	R	18.24 [a]	20.94 [c]	1.56 [a]
CK60B	S	16.83 [a]	26.33 [b]	1.14 [b]
Shanqui-Red	S	19.36 [a]	29.00 [a]	1.38 [a]
IS4225	S	18.36[a]	28.63 [a]	1.48 [a]

R= Resistant, S, Susceptible, N/T= Not tested.

Striga were circled on the petri dish for future observation of necrosis and parasitic discouragement. A *Striga* seedling is counted as having a haustorium only if hairlike projections (tubercles) are present on the radicle. The three most distant *Striga* (with haustoria) from the seedling root was identified and the shortest distance to the primary host was measured to the nearest 0.5 mm. HR was observed when a well defined necrotic lesion develops around the attachment site. The reaction normally starts a few hours after attachment and the lesion becomes more intense in 24 h. *Striga* seedling discouragement was observed for 3 days following the attachment. Whereas *Striga* seedling attached on susceptible host roots penetrate and develop, those on resistant roots are discouraged and penetrate or develop beyond attachment. Data were collected on total number of *Striga* seedlings that were attached, penetrated, caused necrosis, or those discouraged from further development. The percent of *Striga* seedlings with necrosis and with discouraged attachment relative to total attachments in each of four sorghum roots was subjected to statistical analysis.

To examine *Striga* seed germination, the agar petri dishes were incubated at two temperature regimes, 27 and 30°C. The agar petri dishes were checked 3 days after incubation for *Striga* seed germination. *Striga* seed germination was clearly observed through the bottom of the petri dish using a dissecting microscope. The furthest germinated *Striga* seed from the host root was marked and the maximum distance between the host root and the most distant germinated *Striga* seed was recorded. The total distance for each of the four seedlings in three petri dishes was recorded and used for statistical analysis.

After the maximum germination distance was recorded, the petri dishes were then treated with ethylene to promote *Striga* seed germination at 30°C. The petri dishes were observed under a dissecting microscope 48 h after ethylene treatment (5 days after incubation). Germination rates of *Striga* seeds in agar were measured in areas of the agar in close proximity to the host root and far away from the host root. A germination index was assigned representing the ratio of proximal and distal *Striga* germination rates. The germination indexes of four seedlings in three petri dishes were recorded and numbers used for statistical analysis. After the germination index was recorded, the petri dishes were observed under a dissecting microscope for haustoria initiation "the appearance of hairlike projections (tubercles)". The furthest haustorium formed from the host root was marked and the maximum distance between the host root and the most distant haustorium were recorded. The total number of haustoria formed within 4 cm along the root was recorded as a percentage of total germinated *Striga*. The maximum distances and percentages of haustoria formed for each of the four seedlings in four petri dishes were observed. The maximum haustoria distance for each of the four seedlings in three dishes was recorded and used for statistical analysis.

To test the effect of high doses of ethylene treatment on haustoria observation, two sorghum genotypes, P78 and SRN39 were used. After the maximum germination distance was recorded, the agar petri dishes were treated with ethylene "for nine seconds". 48 h after ethylene treatment (5 days after incubation), it was observed under a dissecting microscope for haustoria initiation.

To examine the effect of incubation time on haustoria formation, the petri dishes were observed 5 and 7 days following the infection. The total distance for each of the four seedlings in three dishes was recorded and used for statistical analysis.

To test the utility of the extended agar gel to measure haustoria initiation distance, three sorghum genotypes, SRN-39, P78 and Shanqui Red, were used. Four seedlings from each genotype were replicated eight times at 27°C. The experiment was repeated three different times. The mean maximum haustoria initiation distance, for each of the seedlings, in eight petri dishes were recorded and numbers used for statistical analysis.

RESULTS

Striga germination

Stimulation of *Striga* seed germination by exudates produced by selected sorghum genotypes was evaluated using the assay. Among sorghum genotypes tested, five, namely 555, Framida, IS9830, SRN39 and P78 (*S. drummondii*) were classified by this assay as low germination stimulators (Table 1). Wild sorghum accession P78 produced no *Striga* germination. However, wild sorghum accession, P47121, had the highest germination distance (Table 1). Germination distance increases with temperature in most genotypes (Table 1). P78 had no *Striga* seed germination even at 30°C, while all other

Figure 1. *Striga* seed germination after ethylene treatment. No germination around P78root even after ethylene treatment (a) and normal seed germination after ethylene treatment around SRN-39root (b) using the EAGA.

Table 2. Mean *Striga* haustoria distance of a selected sorghum genotypes using the extended agar gel assay.

Sorghum accession	Haustoria initiation distance 5-days	Haustoria initiation distance 7-days
P78	0.35[c]	0.63[d]
P47121	5.25[a]	17.61[a]
SRN-39	5.22[b]	12.43[b]
555	4.29[a]	09.17[c]
Framida	5.45[a]	16.79[a]
IS9830	5.88[a]	16.95[a]
N13	5.86[a]	16.79[a]
Dobbs	5.28[a]	16.18[a]
Serena	5.78[a]	16.44[a]
CK60B	5.63[a]	17.92[a]
Shanqui-Red	5.87[a]	18.45[a]
IS4225	5.81[a]	15.95[a]

Mean in each column followed by the same letter are not significantly different at P = 0.05.

genotypes including the low germination stimulant check, SRN39, showed some increase in germination as temperature increased from 27 to 30°C.

A germination index was assigned representing the ratio of proximal and distal *Striga* germination rates. A germination index of one, means the artificially stimulated *Striga* germination rate in agar near the host root equaled that away from the root. Most lines assayed had a germination index greater than one, suggesting more germination events proximal to the root (Table 1). *Striga* seed near the roots of P78 consistently showed lower germination rates after ethylene treatment of seeds further out on the petri dish, which suggests inhibition of germination proximal to the root (Table 1 and Figure 1).

Haustorial initiation

Two days after treatment of *Striga* seeds with ethylene to induce uniform germination, haustorial distance was measured on the same petri dishes used to evaluate germination distance and germination index. The proportion of germinated *Striga* with haustoria was recorded. Little variation was observed among the cultivars in their haustorial initiating properties. P78 showed the lowest value among the cultivars and accession tested. Germinated *Striga* rarely developed haustoria on petri dishes with P78 (Table 2). Haustorial formation increased with time, as each genotype showed more haustorial formation after seven days than they did at five days (Table 2).

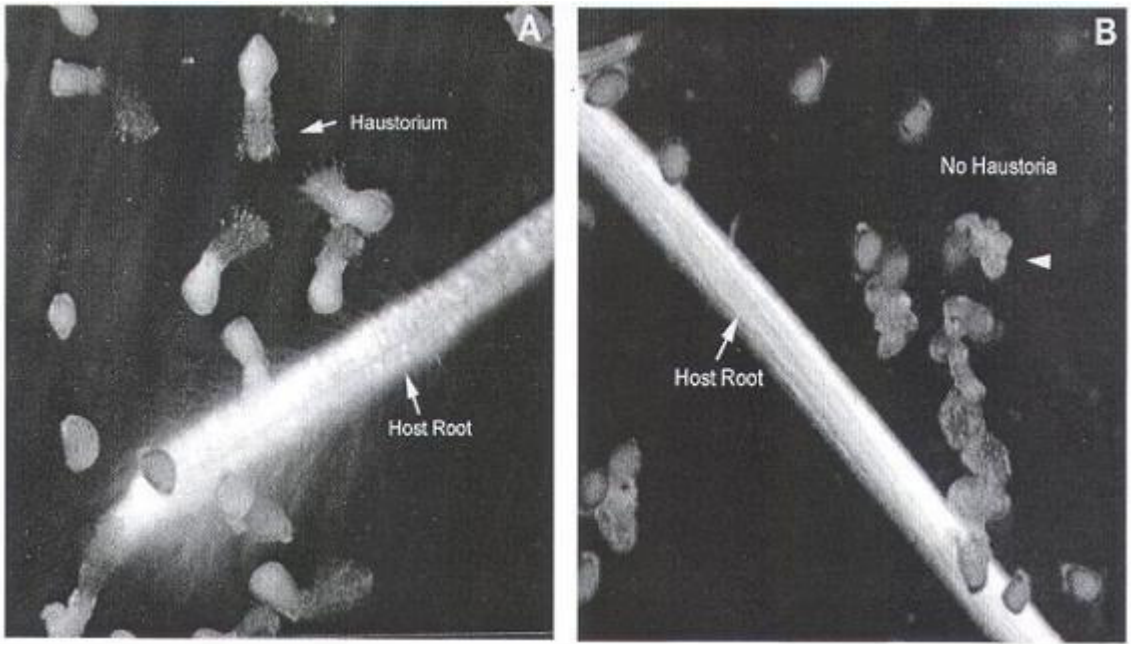

Figure 2. Root of sorghum cultivar SRN-39 causes nearby *Striga* radicles to differentiate into haustoria (A), whereas sorghum mutant P78 dose not initiate haustoria (B) even with Striga seed pre-germinated with high dose of ethylene.

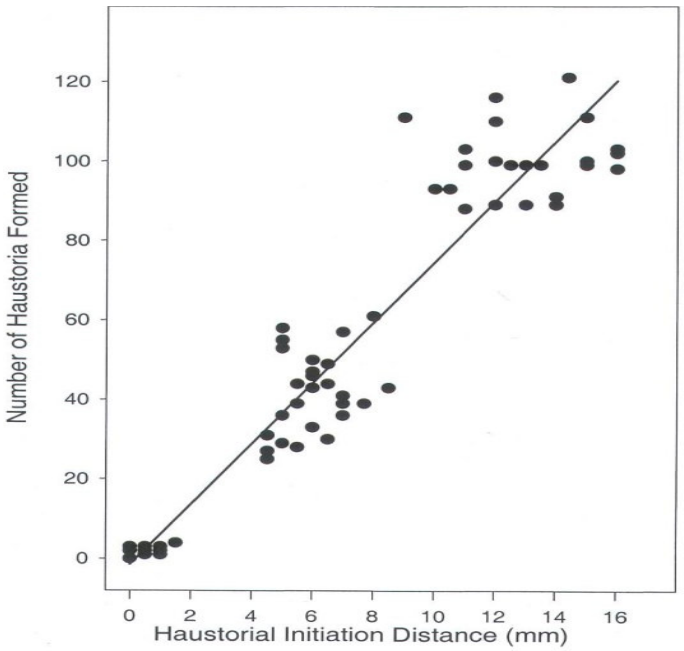

Figure 3. Correlation between number of haustoria formed and maximum distance from the host root and the further *Striga* seedling with haustoria.

Petri dishes treated with high ethylene dose "for nine seconds" caused formation of a coiled *Striga* radicle. This coil in the radicle was released when haustorial signal was received. Release of the coil made it easier to observe haustorial formation and to measure the haustorial distance. In P78, however, most of the radicles around the root remained coiled (Figure 2). Sorghum genotypes that caused the formation of many haustoria also stimulated haustorial formation in seeds that were farthest away from the host root, while genotypes that caused fewer haustoria to be formed exhibited a closer distance to the host root. A positive correlation (r = 0.91) was observed between the total number of haustoria formed and the distance from the root to the furthermost haustorium formed (Figure 3). The same correlation (r = 0.91) was found 2 and 4 days after ethylene treatment. We chose 2 days to minimize the error due to cultivar differences, which might come from the development of more root hairs and lateral roots, making the measuring distance less accurate (Table 2).

To test the utility of the extended agar gel assay in measuring the haustoria initiation factor production, three sorghum genotypes were assayed repeatedly. Among genotypes, differences were consistently clearer, and within genotype variations were small which is shown by the small standard error within and between runs (Table 3). P78 consistently showed low haustoria initiation distances (less than 0.4 mm) while SRN-39, and S. Red, showed consistently large haustrial initiation distances (more than 4.00 mm) (Table 3).

Parasitic attachment and penetration events were also observed in agar. Genotypes whose roots develop necrotic areas upon infection are quite clear in agar (Table 4). Necrotic areas were evident from the reddening of host cells around the point of haustoria attachment and

Table 3. Variation in haustoria initiation distance within- genotypes and among replications using the EAGA.

Haustoria initiation distance (mm) among replications			
Sorghum genotypes	**Replications**	**Mean**	**SE**
P78	8	0.345	0.119
SRN-39	8	5.219	0.556
S. Red	8	5.875	0.755

Haustoria initiation distance (mm) across runs				
Sorghum genotypes	**Run 1**	**Run 2**	**Run 3**	**SE**
P78	0.45	0.35	0.58	0.056
SRN-39	5.66	4.99	5.98	0.277
S. Red	5.76	5.15	6.34	0.630

Table 4. HR in *Striga* parasitism for selected set of sorghum genotypes as determined by EAGA.

Sorghum genotype	*Striga* seedlings attached to sorghum roots	*Striga* seedlings attached with necrotic lesions	*Striga* seedling discouraged from penetration
No.			
SRN-39	6.3^{c}	0.0^{c}	0.0^{c}
Framida	9.6^{b}	6.5^{b}	5.8^{b}
IS9830	9.9^{b}	0.0^{c}	0.0^{c}
555	9.7^{b}	0.0^{c}	0.0^{c}
N13	11.5^{ab}	1.1^{c}	0.0^{c}
Dobbs	10.3	7.1^{b}	6.7^{b}
Serena	13.1^{a}	6.7^{b}	6.0^{b}
CK60B	11.1^{b}	1.2^{c}	0.0^{c}
IS4225	13.0^{a}	0.0^{c}	0.0^{c}
Shanqui-Red	11.2^{b}	0.0^{c}	0.0^{c}
P47121	14.3^{a}	12.3^{a}	11.9^{a}

Mean in each column followed by the same letter are not significantly different at P = 0.05.

penetration (Figure 4). With time these sites turned dark brown later in the reaction. Parasite development at these sites was usually arrested at the stage of cotyledon emergence from the seed coat. However, some parasitic associations in which the surrounding host cells exhibited necrosis developed normally (Table 4).

DISCUSSION

The extended agar gel assay is a potential useful tool for screening sorghum germplasm for *Striga* germination stimulation, haustorial initiation activity and for post-infection reactions. In the last few decades, several artificial growth systems have been used to study host parasite signal exchange and host defense reactions (Visser, 1981; Ramaiah, 1990). Low germination stimulant production is the only host-derived signal that has been studied *in vitro* and exploited for breeding purposes (Hess et al., 1992; Ejeta et al., 1999). Most investigations for signals and post infection defense reactions have been hampered by the difficulty of initiation infections. Ramaiah (1990) concluded that *in vitro* attachment is generally low and less than 9% of those attached *Striga* seedlings that eventually penetrate. The most successful of these systems was developed by Lane et al. (1991), where pre-germinated *Striga* seeds were placed on the host root to increase the attachment. However, this procedure has not been used for routine screening largely because of reproducibility problems.

The assay, like the agar gel assay developed by Hess et al. (1992) can distinguish between gentotypes for high and low stimulatory influence on *Striga* germination. This assay can also detect differences in haustoria initiation and establish genotypic differences for early host post-infection reactions. The longer period of growth and development of *Striga* on roots is more easily followed when supported by the thicker agar layer in the petri dishes.

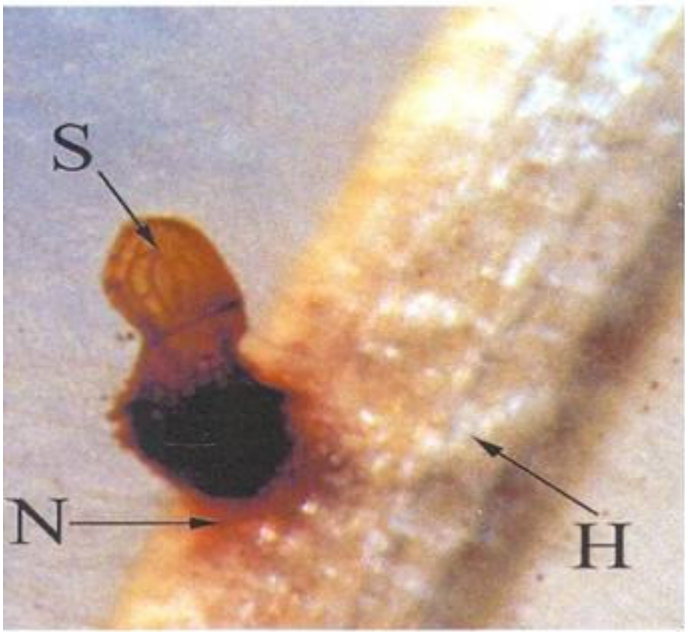

Figure 4. Hypersensitive responses in sorghum where necrotic area on the host root (H).

Using this assay a new source of resistance to *Striga* was discovered, where *Striga* rarely germinated near the roots, even in the presence of ethylene.

The assay is relatively quick, easy and reliable for monitoring pre-infection influences on *Striga*. These characteristics give the assay utility as a screening tool for *Striga* resistance mechanisms in sorghum germplasm. The assay has many advantages over other assays developed. It can be used to screen for more than one mechanism of resistance and allow screening of a large number of genotypes. The assay is simple, reproducible and non-destructive, which makes it possible to screen and monitor host-parasite signal exchanges and early host defense reactions. Currently all reported sources of low germination stimulant production, including the cultivars in this study, appear to be conferred by a single recessive gene (Volgler et al., 1996; Ramaiah, 1990). Whether this resistance gene is the same in all sources is not yet known. Sorghum cultivar 555 (also known as IS18475) is present in the pedigree of several *Striga* resistant varieties, including SAR1 and Framida has been reported in the pedigree of SRN39 (Doggett, 1988). From these data it appears that resistance due to a low germination stimulant production mechanism rests on a narrow genetic base.

The influence of wild sorghum P78 on *Striga* germination appears to be quite different from that of other sources. In the EAGA, *Striga* seed did not germinate in P78 until petri dishes were treated with ethylene, unlike the low stimulant producing genotypes, where a few *Striga* seeds germinated near the host root. Even given a powerful artificial signal in the form of ethylene, very few *Striga* seeds germinated near the roots of P78 giving it lower *Striga* germination index than any other cultivar.

Such low germination could be due to some inhibitory compounds .produced by this accession thus blocking the germination or interfering with the response sequence of conditioned *Striga* seed. We know that germination is inhibited but the causal agent remains unknown.

Although the haustoria initiation signal is very important for parasitism, the actual haustoria initiation factor remains unknown. The extended agar gel assay measures the distance of farthest haustorium initiated from the host root but do not measure the amount of haustoria initiation factor that is produced. This assay measures only initiation as a component of host-parasite signal exchange.

Generally, there are no significant differences in haustoria initiation distance in cultivated sorghum varieties (Weerasuriya et al., 1993). The only identified genotype that has low haustoria initiation distance is P78; in fact, the distance is less than 10% of that found in all the other cultivars and accessions tested. If the difference in haustoria initiation detected by the extended agar gel assay correlate with field resistance, it will help in depleting *Striga* seed reserves in soils. Low *Striga* haustorial initiation with high germination stimulant producers could deplete the *Striga* seed banks. The initiation of haustoria takes place after *Striga* seeds germinate. As a result, the germinated seeds either receive the signal to start the parasitic life cycle or they die. Consequently, using low haustorial initiation germplasm will reduce the seed reserve and reduce the possibility of more virulent strain development. Furthermore, the few *Striga* seeds able to survive can easily be destroyed before seed setting.

The development of these laboratory assays enabled us to identify and characterize distinct resistance mechanisms. These mechanisms can be exploited through conventional plant breeding programs. The resistance genes can be pyramided into one background for more durable *Striga* resistance.

The assay can also be used to identify DNA markers having close linkage to specific resistance mechanisms. This should permit an accurate assignment of chromosome localization for important resistance factors. These in turn may allow more accurate selection of favorable resistance genes in breeding programs. Map-based cloning of individual genes will also be possible, thus enhancing the prospects for transferring and pyramiding of resistance genes into elite germplasm backgrounds of sorghum and other *Striga* host.

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