

# Striga Research and Control

## A Perspective from Africa

*Striga* (Scrophulariaceae) is a genus of obligate root-parasitic flowering plants. Within the genus, there are 30 to 35 species, over 80% of which are found in Africa (28,30,35). Over two-thirds of the species of *Striga* occur in West and Central Africa, and over half of the *Striga* species occur in East and South Africa (35). Nine species occur outside of Africa, and three of these species are endemic to Australia (28,35). Two species, *Striga asiatica* (L.) Kuntze and *S. gesnerioides* (Willd.) Vatke, have been introduced to the eastern coast of the United States (20,36). An extensive eradication program for *S. asiatica* began in North and South Carolina in the 1950s, with a targeted eradication date later in the 1990s (37).

Most species of *Striga* are of no agricultural importance, but those that parasitize crop plants can be extremely damaging (Fig. 1). In sub-Saharan Africa, the damage caused by these parasites can be devastating to resource-poor farmers, whose lives can be threatened by complete yield loss of both cereal and legume crops. All of the cultivated food-crop grasses in Africa, e.g., fonio (*Digitaria exilis* L.), maize (*Zea mays* L.), millet (*Pennisetum americanum* (L.) K. Schum.), rice (*Oryza sativa* L.), sorghum (*Sorghum bicolor* (L.) Moench), and sugarcane (*Saccharum officinarum* L.), are parasitized by one or more *Striga* spp. The species of particular economic importance are *Striga hermonthica* (Del.) Benth. (Fig. 1) and *Striga asiatica* (L.) Kuntze (Fig. 2). Of secondary importance are *Striga aspera* (Willd.) Benth. (Figs. 3 and 4) and *Striga forbesii* Benth. Yield losses on cereals attributable to infection by these parasites may reach

100%, and levels of infestation are frequently so great that continued cereal production becomes impossible and farmers abandon these fields in search of less infested areas (14,24). In West Africa alone, it is estimated that about 40 million hectares in cereal production are severely infested by *Striga* spp., while nearly 70 million hectares have moderate levels of infestation (24). As a result, FAO estimates that annual yield losses due to *Striga* spp. in the savannah regions alone account for \$7 billion and are detrimental to the lives of over 100 million African people (27). Unfortunately, control options are limited.

The *Striga* problem in Africa is intimately associated with human population growth. Traditional African cropping systems included prolonged fallow, rotations, and intercropping, which were common practices that kept *Striga* spp. infestations at tolerable levels (14,24). As population pressure and demand for food production increased, land use intensified. With greater use of monocropping and little or

no fallow, populations of these parasites have gradually increased and become threats to food production (14,30). At the same time, farmers shifted their preference in cereal crops away from local cultivars of crops like sorghum and millet, which produced relatively low but sustainable yield, toward "improved" high-yielding cultivars and high-yielding crops like maize. Unfortunately, these new cultivars did not evolve under *Striga* pressure and frequently have little or no resistance to *Striga* spp.

*Striga* spp. also parasitize dicotyledonous plants, of which cowpea, *Vigna unguiculata* (L.) Walp, is an important example. This crop is widely grown in the savannah and Sahel regions of Africa, is used for both food and forage, and is traditionally intercropped with cereals. The relatively high protein content and quality of cowpea make it an important dietary supplement in Africa. Rotations and crop mixes with cowpea are beneficial in maintaining soil fertility and tilth, and in the control of some *Striga* spp. on cereals



Fig. 1. Sorghum plants showing droughtlike symptoms resulting from severe infection by *Striga hermonthica*, which is flowering at the base of the sorghum.

Dr. Berner's address is: International Institute of Tropical Agriculture, PMB 5320, Oyo Road, Ibadan, Nigeria. E-mail: IITA@CGNET.COM

This article is in the public domain and not copyrightable. It may be freely reprinted with customary crediting of the source. The American Phytopathological Society, 1995.

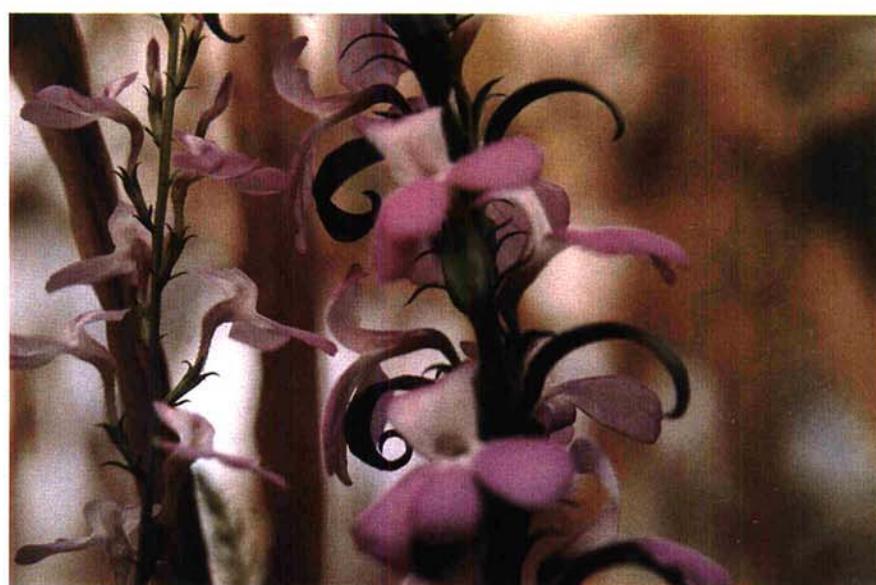


**Fig. 2.** *Striga asiatica* parasitizing maize in Nigeria. The red flower morphotype of this species is also common in West Africa.

(31). A major obstacle to cowpea production is parasitism by *S. gesnerioides* (Fig. 5). Yield reductions due to *S. gesnerioides* on susceptible cultivars are reported to range from 41 to 83% (2). Because cowpea and cereals are often intercropped in Africa, it is common to find several species of *Striga* on different crops in the same field. This complexity makes control more difficult. Multiple control options are needed to provide flexible and sustainable control over a wide range of conditions and for different strains and races of *Striga* spp. To do this, scientists from the International Institute of Tropical Agriculture (IITA) have organized *Striga* research around themes of epidemiology, host-parasite interactions, host-plant resistance, biological control, agronomic control, and socioeconomic adaptation of control options. Some of the outcomes of this research and implications for *Striga* control in Africa are discussed in the following sections.

### Life Cycle

*Striga* spp. seeds are extremely small, each weighing about 7 µg (Fig. 6). Germination of seeds requires exposure to an exogenous germination stimulant after an environmental conditioning period in which the seeds imbibe water (44). Usually this stimulant is a host-root exudate (19,44), but some non-host-root exudates and synthetic compounds can also stimulate germination (13,30). After germination, endosperm nutrients can sustain the seedlings for 3 to 7 days in the absence of a host (32,44). If the seedling does not attach to a host and successfully establish a parasitic link within this period, the seedling dies. If a host root is in close proximity (2 to 3 mm) to the germinated *Striga* seedling, chemical signals are exchanged that direct the *Striga* radicle to the host root, initiate haustorium induction, and result in successful attachment and establishment of xylem-to-xylem connections between the parasite and host (38,41). One of the better documented of these chemical signals is 2,6-dimethoxy-p-benzoquinone (2,6-DMBQ), which is suggested as the product of enzymatic degradation of the host root responsible for



**Fig. 3.** Inflorescences of *Striga aspera* (left) and *Striga hermonthica* (right) showing relatively longer extension of the corolla neck over the calyx and glandular hairs on the corolla neck of *S. aspera* compared to the abrupt corolla bend over the calyx and the glabrous appearance of the corolla neck of *S. hermonthica*. Both are allogamous species, which can be cross-fertilized by insect pollinators, thus permitting the exchange of virulence genes between species. All other species are autogamous.

stimulating formation of the parasite haustorium (12). Haustoria of parasitic angiosperms are specialized organs developed from parasite radicles prior to penetration; they differ anatomically from fungal haustoria (43).

*Striga* spp. are obligate root parasites wholly dependent on a host from germination through flowering and reproduction. After successful attachment, developing *Striga* plants grow underground for 4 to 7 weeks prior to emergence. Numerous parasitic attachments usually occur on the same plant. Most of the damage to the host plant occurs during this stage. Symptoms of parasitism are often dramatic but nondescript, resembling drought stress, nutrient deficiency, and vascular disease (Fig. 7). Severe plant stunting often results. Following emergence, *Striga* plants form chlorophyll and begin to photosynthesize, but they are still unable to survive in the absence of host attachment (32,38). Flowering time is species and environment dependent. *S. gesnerioides* begins to flower as it emerges (16,30). *S. asiatica*, *S. aspera*, and *S. hermonthica* begin to flower about 4 weeks after emergence. Flowering begins basally on the raceme, and seeds are mature about 4 weeks after flowering (38). Each *Striga* plant is capable of producing from 50,000 to 500,000 seeds, which may remain viable for 14 years in soil (6,38). Only a fraction of these seeds germinate in any season in the presence of a host.

### Constraints for *Striga* Control

Practices that were developed for *S. asiatica* control in the United States are generally unsuitable in Africa because



**Fig. 4.** Field of fonio (*Digitaria exilis*) severely damaged by *Striga aspera* infection. No grain was harvested from this field.

they require chemical inputs and application equipment (17,37) that are not available or are prohibitively expensive for African farmers. To put effective *Striga* control within the reach of African farmers, simple, inexpensive measures need to be developed that are tailored to the diversity of African cropping systems. The diversity of both the crop species in these systems and the parasites themselves necessitates employment of an assortment of



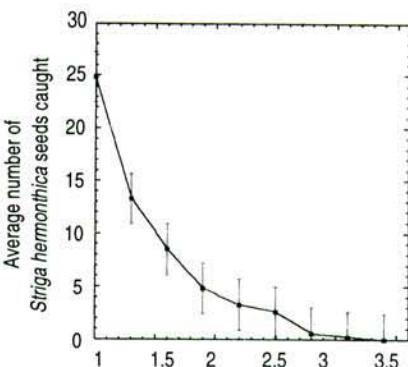
**Fig. 5.** Cowpea plants severely damaged by *Striga gesnerioides* parasitism. Numerous erect flowering *S. gesnerioides* plants have emerged around the infected cowpea plants.



**Fig. 6.** *Striga hermonthica* seeds (0.2 to 0.5 mm long) interspersed with seeds of cowpea, maize, millet, and sorghum.



**Fig. 7.** Symptoms of *Striga hermonthica* infection on maize leaves. Symptoms begin as interveinal chlorosis and flecking and progress to leaf necrosis. Plants are usually severely stunted.



**Fig. 8.** Mean number of *Striga hermonthica* seeds caught on coated microscope slides placed at distances ranging from 10 to 2,560 cm from mature *S. hermonthica* plants in fields in Nigeria and Republic of Benin during the harmattan season in 1991 and 1992. (Data points are means of both years.)

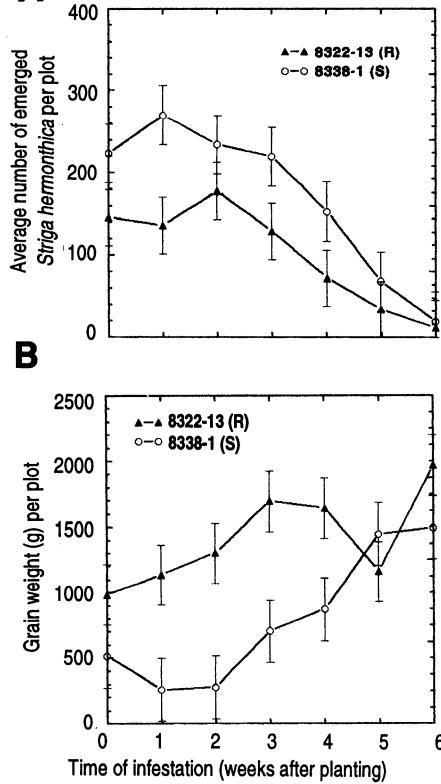
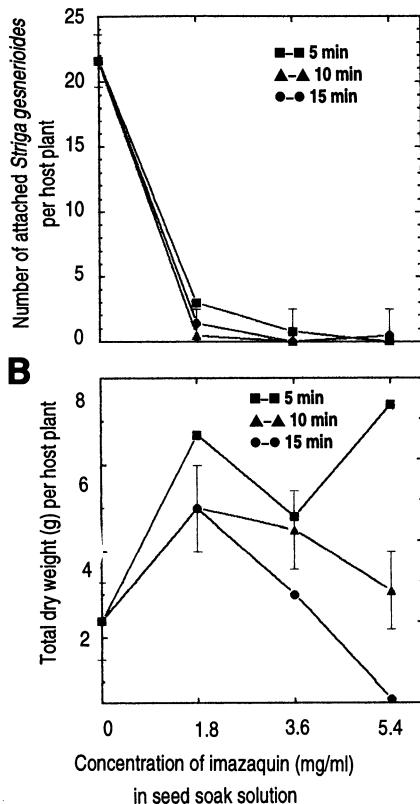
control inputs. *Striga* diversity is reflected in species differences and also in distinct morphotypes, physiological strains, and races of the species. For example, *S. gesnerioides* parasitizes tobacco, *Ipomoea* spp., and *Tephrosia* spp. as well as cowpea (28), but *S. gesnerioides* isolates from one host will often fail to parasitize a different host species (30). In addition, cowpea cultivar-specific races of *S. gesnerioides* have been reported (25). Differential interspecific virulence of *S. hermonthica* on maize, millet, and sorghum has been well-documented (23,30,32) and is evidenced by the failure of *S. hermonthica* isolates collected from either of these hosts in one location to parasitize one of the other hosts from another location.

### Research and Control Options

**Striga epidemiology and population dynamics.** In order to develop *Striga* control strategies in Africa, it was necessary to ascertain the primary modes of dispersal of the parasites. One of the main mechanisms of *Striga* seed dispersal was previously thought to be wind (32). This assumption implies annual influxes of windblown *Striga* seeds from infested areas into farmers' fields and suggests that methods to reduce yield loss should receive greater attention than in-field eradication. To clarify the situation, the relative importance of wind, cattle (through seed ingestion and deposition), and man (through contamination of planting materials) in seed dispersal was examined (9). Wind was found to be relatively ineffective in long-distance seed dispersal (Fig. 8) and is probably not responsible for annual influxes of *Striga* seed into farmers' fields. Only about 8% of *Striga* spp. seeds ingested by cattle remained viable, and these were not deposited far ( $\leq 0.5$  km) from the site of ingestion.

This indicates that cattle are also relatively ineffective in long-distance *Striga* spp. seed dispersal. The amount of *Striga*-seed contamination of cowpea, maize, millet, and sorghum seeds sold in local Nigerian markets was found to range from 62.5 to 85.4% of the samples contaminated, with average contamination ranging from 29.8 to 64.3 *Striga* seeds per sample (9). Because crop seeds for planting are purchased from these markets by farmers often living many kilometers away, *Striga*-seed contamination can quickly lead to dispersal over great distances and introduction of *Striga* into previously uninfested areas. Crop seeds are likely to be contaminated as a result of harvesting, threshing, and drying processes in *Striga*-infested areas (9). After processing, seeds are taken to market (not necessarily the same market from which the planting material was purchased) for sale. Thus, newly infested sites can quickly become new foci for *Striga* spread through contamination, sale, and redistribution of crop seeds. The use of *Striga*-free planting material is thus the first step in control and can be ensured by purchasing seeds from reputable seed companies, planting seeds harvested only from *Striga*-free fields, and drying and threshing harvested seeds only in *Striga*-free areas. Through the use of *Striga*-free planting material, the spread of *Striga* can be reduced, making eradication in individual fields feasible.

The effect of time of *S. hermonthica* infection on host yield loss and reproductive capability of the parasite was studied (11). *S. hermonthica* seeds were used to infest maize and sorghum plants at different growth stages to simulate different times of infection. Delaying infection of *S. hermonthica* on both maize and sorghum until 4 to 6 weeks after planting significantly reduced emergence and reproduction of

**A****B****A**

**Fig. 9.** Effects of delaying *Striga hermonthica* seed infestation, and subsequent infection, on *S. hermonthica* emergence (A) and grain yield (B) on two field-grown maize cultivars, 8322-13, a resistant maize hybrid, and 8338-1, a susceptible maize hybrid.

the parasite, and significantly increased host yield (11). For maize, a resistant hybrid showed no yield advantage over a susceptible hybrid when *S. hermonthica* infestation occurred later than 5 weeks after planting (Fig. 9). Studies with several host crops showed that ability to stimulate *S. hermonthica* seed germination declined when host roots were older than 4 weeks, but that factors such as root peridermal thickening may also prevent parasitism on older roots. These studies indicate that control measures that protect hosts from *S. hermonthica* infection for 4 to 6 weeks after planting should reduce parasite reproduction and increase host yield.

**Striga-host interactions.** *Striga* has been shown to cause disease in the host by inducing enzyme and plant hormone changes, disrupting host-water relations, and reducing carbon fixation below that expected purely by competition (41). Preattachment and early postattachment stages of *Striga*-host interactions are of particular relevance to host protection. For example, host genotypes that produce little or no *Striga* seed germination stimulant can avoid parasitism (33). Hosts lacking inducible 2,6-DMBQ production may similarly avoid parasitism by failing to stimulate *Striga* haustoria development.

**Fig. 10.** Mean numbers of *Striga gesnerioides* attached (above- and below-ground) to cowpea plants (A) and total dry weight of those plants (B) from seeds soaked for 5, 10, or 15 min in aqueous imazaquin solutions and planted in soil infested with 3,000 germinable *S. gesnerioides* seeds.

Deposition of cellulose-containing materials in roots of resistant hosts may act as mechanical barriers to prevent parasite penetration (29), while postattachment hypersensitivity functions as a resistance mechanism in *S. gesnerioides*-cowpea systems (16,25,39).

One potential protection practice that is applicable for use in African farming systems is host-seed treatment. The seed treatments that we tested were chosen for potential to selectively interfere with parasitism through inhibition of amino acid biosynthesis by the parasite (26). One such material, the acetolactate synthase (ALS) inhibitor imazaquin, had previously shown efficacy in control of a soilborne pathogen of soybean (8) and control of two parasitic plants, *Cuscuta* sp. (26) and *Orobanche crenata* Forsk. (18).

Results of tests with imazaquin for the control of *S. gesnerioides* on cowpea (7) showed that a simple aqueous seed soak solution with low amounts of imazaquin gave excellent protection against the parasite and improved plant yields (Fig. 10). With the seed treatment, parasite seed germination occurred and protection was achieved by postattachment mortality of the parasite. An additional control benefit

**Table 1.** Number of plants of different cowpea cultivars infected by *Striga gesnerioides* at Zakpota (Republic of Benin)

Cultivar	1990	1991	1992
IT82D-847	0.5 <sup>a</sup>	15.5	...
B301	2.8	6.0	28.0
IT86D-371	32.5	25.8	...
TVu 3236	22.5	22.3	41.0
IT86D-534	22.5	20.0	...
IT84D-472	19.3	26.8	...
IT84D-666	14.3	13.8	...
IT81D-985	1.8	1.5	8.0
IT81D-994	0.0	0.0	0.0
SUVITA-2	0.8	0.0	1.0

<sup>a</sup> Data are averages of four plots of 6 m<sup>2</sup> each.

<sup>b</sup> ... = Not tested.

was obtained by reducing parasite seed density in the soil (7). In early field tests, some cowpea cultivars were severely damaged by imazaquin phytotoxicity. In subsequent field tests with cowpea cultivars selected in the laboratory for tolerance to imazaquin, the seed treatment has shown promise in protecting from *S. gesnerioides* parasitism and improving yield. More work at the local level is necessary to optimize components of the technology for local conditions. Estimates of cost of the imazaquin seed treatment on cowpea ranged from \$3.00 to \$10.00 per hectare based on seeding rates of 30 kg ha<sup>-1</sup> and variable imazaquin costs (7). We recently began to test other ALS inhibitors for use as seed treatments for *S. hermonthica* control on maize. Problems with phytotoxicity of the ALS inhibitors on some maize lines occurred, but excellent *S. hermonthica* protection has been achieved.

**Host-plant resistance: cowpea.** IITA's crop-breeding mandate includes cowpea and maize. Two cowpea cultivars, Gorom Local (SUVITA-2) from Burkina Faso and 58-57 from Senegal, were identified as resistant to *S. gesnerioides* in 1981 (16). These cultivars and other breeding lines were then evaluated in multiple locations in Burkina Faso, Cameroon, Niger, Nigeria, and Mali from 1983 to 1986. Both SUVITA-2 and 58-57 were found resistant to *S. gesnerioides* in Burkina Faso but were susceptible in all other countries, indicating the presence of different *S. gesnerioides* races (16). Two cowpea cultivars, B301 (a traditional cultivar from Botswana) and IT82D-849 (an improved breeding line from IITA), were identified as *S. gesnerioides* resistant in 1987 (16). Both B301 and IT82D-849 showed stable resistance to *S. gesnerioides* across Burkina Faso, Mali, Republic of Niger, and Nigeria (2,16). A number of other resistant lines have since been identified.

In 1990, a few plants of IT82D-849 and B301 were found infected by *S. gesnerioides*.

des at Zakpota, Republic of Benin. Further studies at this site showed that there was some level of susceptibility in B301 and in IT82D-849, indicating another new race at Zakpota (Table 1). This has recently been independently confirmed (25). Both IT81D-994 and SUVITA-2, which are resistant to the *S. gesnerioides* race in Burkina Faso, are resistant to the new race at Zakpota, suggesting that the Zakpota race may be related to the Burkina Faso race. Lines listed in Table 1 are being tested at different locations and are being crossed to B301 and IT82D-849 to ascertain whether they have the same or different genes for resistance.

Different mechanisms of *S. gesnerioides* resistance in cowpea have been observed (39). Cultivar B301 stimulates germination of *S. gesnerioides* seeds and permits attachment, but further growth is inhibited by a hypersensitive reaction that results in necrosis of host tissue around the point of infection, causing death of the parasite. In attachments where hypersensitivity does not take place and the initial infection is successful in establishing a connection to the host vascular system, small tubercles 1 to 2 mm long develop, but no further growth takes place. The biochemical basis of these mechanisms is not known. Expression of resistance to *S. gesnerioides* in IT82D-849 is slightly different from B301. This cultivar stimulates *S. gesnerioides* seed germination and attachment and inhibits parasite development like B301, but about 10% of the plants show some development and support limited *S. gesnerioides* growth. Occasional emergence of one or two *S. gesnerioides* plants has also been noticed on IT82D-849 plants, but the

emerged *S. gesnerioides* plants are very weak and die before reproductive maturity (16,39). Another cultivar, IT81D-994, permits establishment of a few *S. gesnerioides* (three to five per cowpea plant) but delays parasite emergence. The emerged parasites cause little damage.

Genetic studies revealed a single dominant gene for *S. gesnerioides* resistance in B301 (16). Other studies have shown that *S. gesnerioides* resistance in IT82D-849 and in SUVITA-2 are controlled by single dominant genes different from that of B301 (39,40). The single dominant gene possessed by SUVITA-2 against the race of *S. gesnerioides* from Burkina Faso is nonallelic to the single dominant genes in B301 and IT82D-849.

A systematic breeding program to develop cowpea cultivars resistant to *S. gesnerioides* was undertaken in 1987. The source of resistance was B301, which was crossed to a high-yielding cultivar with resistance to aphids, bruchids, thrips, and several diseases. Progenies were selected under disease, insect, and *S. gesnerioides* pressures, leading to development of a number of *S. gesnerioides*-resistant breeding lines with combined pest resistance (16) and a mean yield improvement of 56% over the *S. gesnerioides*-susceptible parent. These lines were distributed to various national programs in Africa, and further breeding continues using these lines as parents. To develop a range of cultivars with combined resistance to different races of *S. gesnerioides*, our breeding program now involves both local cultivars and other selected parents, including IT81D-994, SUVITA-2, and 58-57.

**Host-plant resistance: maize.** To be

acceptable to African farmers, maize cultivars must possess resistance to multiple pests and diseases, including *Striga* strains, and have good yield potential, agronomic, and storage characteristics in the absence of pest and disease constraints. Although most farmers grow open-pollinated cultivars (OPs), hybrids are in demand in some areas. To develop acceptable OP and hybrid maize cultivars with *S. hermonthica* resistance, IITA's breeding program relied primarily on field evaluation. *S. hermonthica* resistance screening began in 1982 under natural infestations (21). Significant variation in resistance to *S. hermonthica* was observed among IITA inbred lines and hybrids in 1983. Resistance was first identified in lines derived from temperate-zone germ plasm and later in tropical germ plasm (15,21). Due to the difficulty of reliably assessing resistance in segregating materials under highly variable field conditions, screening was initially carried out on genetically uniform inbreds and hybrids. To reduce field variability and permit screening of segregating materials, artificial infestation with *S. hermonthica* seeds was initiated in 1985. Infestation is carried out by placing about 3,000 germinable (viable and nondormant) *S. hermonthica* seeds in each planting hole immediately prior to planting maize (22). Genotypes are evaluated under infested and noninfested conditions in adjacent strips of the same field. To ensure that selected materials have resistance to potentially different biotypes of *S. hermonthica*, two sites in Nigeria and one site in northern Côte d'Ivoire are used for screening.

Progress in developing inbreds and hybrids with reduced damage under *S. hermonthica* infestation was made using a rating scale based on *S. hermonthica* symptom severity (22). Some of the hybrids developed using the symptom rating scale have also shown resistance to *S. asiatica* (22,34). Open-pollinated synthetics have been formed by recombining resistant inbred lines. In developing broad-based open-pollinated populations with

**Table 2.** Evaluation of early-maturing maize cultivars under *Striga hermonthica* infestation in Mokwa, Nigeria, in 1994<sup>a</sup>

Cultivar <sup>b</sup>	Maize damage rating <sup>c</sup>	<i>Striga</i> count <sup>d</sup>	Yield		
			Infested (t ha <sup>-1</sup> )	Noninfested (t ha <sup>-1</sup> )	Index <sup>e</sup>
1. ACR 92 TZE Comp. <sup>f</sup> 5	3.5	45	3.3	6.5	16.1
2. Pool 16-DT STR	5.1	50	1.9	4.5	4.0
3. TZE Comp. 4 C2	5.1	48	1.8	4.9	3.7
4. TZE Comp. 5 C4	4.9	102	2.2	4.8	1.1
5. TZE Comp. 5 C3	5.3	109	1.6	5.3	-2.5
6. Maka-SR BC3	6.4	116	0.8	4.5	-11.2
Mean (15 entries)	5.4	66.8	1.6	4.7	0.0
Prob. > F	0.005	0.011	0.008	0.002	0.000
LSD (0.05)	1.13	36.6	0.86	0.76	8.44

<sup>a</sup> Trial was conducted using 5 m of infested and 5 m of noninfested rows with four replicates.

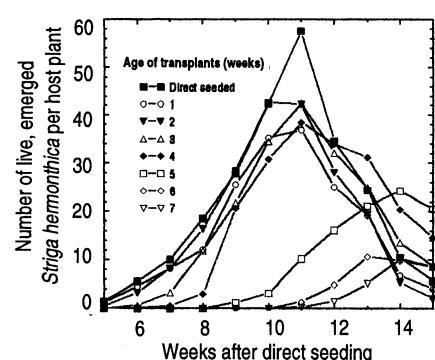
<sup>b</sup> Entries 1-4 were evaluated for the first time in 1994; entries 1 and 4 are improved selections from entry 5.

<sup>c</sup> Ratings (1-9), where 1 = no damage and 9 = severe damage, based on average symptom severity at 8 and 10 weeks after planting.

<sup>d</sup> Number of emerged *Striga* at 8 weeks after planting.

<sup>e</sup> Calculated by standardizing values, multiplying by assigned weights, and summing across variables. Larger values indicate better performance. Additional variables included in the index (not shown) were *Striga* counts at 10 weeks after planting, ratings of symptom severity at harvest, and ratings of plant and ear appearance in noninfested rows.

<sup>f</sup> Comp. = composite.



**Fig. 11.** Effects of direct sorghum seeding and transplanting of 1- to 7-week-old sorghum seedlings on *Striga hermonthica* emergence.

resistance to *S. hermonthica*, selection is based on an index that includes assessment of plant damage, number of emerged *S. hermonthica* plants, and yield under infested conditions, as well as agronomic characteristics of noninfested plants. The response to selection in both early (90 days to maturity) (Table 2) and late (120 days to maturity) populations and synthetics is encouraging.

The inheritance of resistance to *S. hermonthica* reported in maize appears to be quantitative (22). General combining ability (GCA) and specific combining ability (SCA) were found to be significant for host-plant damage ratings and *S. hermonthica* emergence in a diallel cross of 10 inbred lines, but GCA was of greater magnitude for host-plant damage and SCA was more important for *S. hermonthica* emergence. Other experiments confirmed the relative importance of additive genetic effects for host-plant damage and nonadditive effects for *S. hermonthica* emergence. Heritabilities of host damage and yield loss due to *S. hermonthica* are moderate (generally 0.3 to 0.5), but heritabilities for *S. hermonthica* emergence are low (generally <0.1) (J. G. Kling, unpublished). Accumulating evidence that genetic correlations between *S. hermonthica* emergence and levels of plant damage are low suggests that different genes control *S. hermonthica* emergence and levels of host-plant damage in maize. Although reduced emergence of *S. hermonthica* was included in our selection index, it is now recognized that a more concerted effort is needed to improve this trait in our resistant populations and hybrids. As part of this effort, traditional African maize cultivars, improved IITA maize inbreds and hybrids, and wild relatives of *Zea mays*, which support significantly fewer *S. hermonthica* plants, are presently being incorporated into a low-emergence pool for further selection in the laboratory and field.

By screening segregating families and pyramiding resistance genes through recurrent selection procedures, we should incrementally develop resistance that is durable over time and widely effective against a highly variable and rapidly changing parasite. One disadvantage in the use of quantitatively inherited resistance is the difficulty in transferring the resistance to locally adapted cultivars through back-crossing. International agricultural research centers (IARCs) and national breeding programs must develop populations and synthetics with good agronomic characteristics and acceptable grain quality in addition to good levels of *Striga* resistance. These improved materials can then be selected further at a national level for field tolerance and local adaptation.

**Agronomic control.** Considerable research has been done on simple agronomic modifications that farmers can make to control *Striga*. The most frequently used

control is hand weeding. But hand weeding is only practical in preventing buildup of parasite seeds in lightly infested soil. Under high levels of infestation and infection, hand weeding may not be worthwhile, since substantial damage to the current crop has already occurred and there still remains a substantial reservoir of seeds in the soil for infection the next season.

A complication of the use of herbicides is that most herbicides available for *Striga* control in Africa are applied postemergence, by which time substantial *Striga* damage to the crop has already occurred. This damage is discouraging to resource-poor farmers who have invested in the herbicide and expect an immediate return.

There are numerous literature references, many conflicting, on the control of *Striga* through management of soil fertility, particularly nitrogen fertility (32). We have seen no direct beneficial effect of increased nitrogen fertility on *Striga* control (D. K. Berner, unpublished). Systematic studies are needed to determine if nitrogen may have an indirect role in *Striga* control through its influence on soil biota or other factors. From a practical standpoint, nitrogenous fertilizers are difficult for many African farmers to obtain and are generally too expensive to apply at levels suggested in the literature for *Striga* control (32).

A host protection practice other than host-seed treatment that can be acceptable to African farmers is transplanting from *Striga*-free nursery beds. Since maize is not amenable to transplanting, this practice is applicable only to millet and sorghum. For these crops, transplanting is an established local practice to adjust time of crop establishment to coincide with periods of labor availability. Studies with local sorghum cultivars (10,11) showed significant reduction in emerged *S. hermonthica* plants on transplanted 5-, 6-, and 7-week-old sorghum seedlings compared to direct-seeded sorghum (Fig. 11). Sorghum yield was influenced both by *S. hermonthica* parasitism and by transplanting shock on older seedlings. Studies with 80 farmers (42) showed that, when using traditional transplanting techniques, there were highly significant reductions in emerged *S. hermonthica* on mature plants from 5- and 6-week-old sorghum transplants compared with direct-seeded sorghum. In heavily infested fields, there were net yield gains from transplanting sorghum (42). In lightly infested fields, the yield increase due to reduced parasitism could not compensate for the yield loss due to transplanting shock (42). Further research is needed to improve nursery bed management and optimize yield of sorghum transplants in combination with *S. hermonthica* control. It may also be possible to select sorghum and millet cultivars that show minimal yield loss from transplanting.

To reduce the amount of *Striga* seed in soil, effective and acceptable replacements of traditional fallow rotation are needed. A well-known means of reducing densities of *Striga* seeds in the soil is through the use of nonhost crops that stimulate *Striga* seed germination. Since the germinated seeds cannot survive without a host, the seedlings die. Rotating these nonhosts with cereal hosts can be an effective means of reducing densities of *Striga* seeds in the soil while maintaining agriculturally productive land. But there is considerable variability within nonhost species in ability to stimulate *Striga* seed germination (3,31). The task of characterizing this variation is compounded by the variability within and between *Striga* spp. To ensure that the most effective nonhosts are placed in rotation systems, cultivars of these crops should be screened for efficacy at the local level with the particular *Striga* spp. and strain present in the area. Screening can be done in the field, but the amount of material that can be screened is limited by land and labor availability. At least 2 years is required—one for growth of the nonhost and another for evaluation of the nonhost effects by host cultivation, and in-field variability in *Striga* infestation makes accurate selection of the best materials difficult. To overcome these constraints, we have developed a simple laboratory assay that uses cut roots of test cultivars to stimulate *Striga* seed germination and statistically adjusts for root weight and distance from the source of stimulant (3). Environmentally conditioned *Striga* spp. seeds are placed on glass-fiber disks around a central well containing 1.0 g of cut roots of the test plant. Germinated and ungerminated seeds on each disk are counted after 48 h. Although the assay is subject to chemical artifacts from root destruction, efficacy rankings of cultivars evaluated by the assay (Table 3) correlate significantly with *S. hermonthica* parasit-

**Table 3.** Range of variability typically observed within soybean for stimulation of *Striga hermonthica* seed germination by cut roots<sup>a</sup> of different cultivars

Cultivar	Relative germination (%) <sup>b</sup>	Standard error
TGX1649-11F	63.4	2.75
TGX1707-4E	53.6	2.43
TGX1660-15F	52.4	2.58
TGX1485-1D	20.9	4.21
TGX1648-3F	20.0	3.65
TGX1660-18F	17.5	2.76
Deionized water	17.2	4.21

<sup>a</sup> One gram of cut roots of each cultivar was used in analysis.

<sup>b</sup> Mean germination relative to germination induced by 10 ppm of a synthetic germination stimulant. n = 16.

ism of sorghum and sorghum yield in the field; after a 1-year rotation,  $r = -0.96$  and 0.96 between germination in the laboratory and number of emerged *S. hermonthica* and sorghum yield, respectively (D. K. Berner, *unpublished*). The assay is simple and inexpensive and could be readily adopted by national programs for routine testing of promising cultivars.

**Biological control.** Because the economically important *Striga* spp. are endemic to Africa, there is little opportunity for classical biological control through introduction of pests and pathogens of *Striga* from areas outside Africa. Biological control through inundation with locally occurring pests and pathogens may be feasible. One widely occurring insect pest of several *Striga* spp. in Africa, *Smicronyx* sp., has been examined extensively as a biological control agent (5). However, natural enemies and pathogens of the insect limit its efficacy unless inundation is regularly repeated (5). Numerous fungal pathogens of *Striga* plants have been described (5), and two species of *Fusarium* are being tested for postemergence *Striga* control (1,4). However, the problems with postemergence mycoherbicides (fungi pathogenic to weeds) in Africa are the same as for chemical herbicides: the cost of applying the herbicides and the lack of immediate yield loss abatement. An alternative may be the use of bacteria pathogenic to *Striga* seeds. Several bacteria have been isolated and show promise in destroying *Striga* seeds and reducing parasitism without detrimental effects on the host (D. K. Berner, *unpublished*). Because bacteria can be formulated into inoculants, expensive application equipment is not required. Bacteria could be routinely applied when planting a selected nonhost rotation crop and produce a dual benefit as the rotation crop stimulates fatal germination of *Striga* seeds while the bacteria parasitize ungerminated seeds.

**Integrated control.** While single control options may lead to increases in crop

yield and decreases in density of *Striga* seeds in soil, none of the controls known is completely effective in eliminating *Striga* infestations. Because of the longevity of *Striga* seeds in the soil and the variability within and between *Striga* species, there is a tremendous potential for the parasites to adapt to individual controls, e.g., host-plant resistance and host-seed treatments. In addition, African farming systems are so diverse that not all control options will be universally acceptable or universally effective. Sustainable *Striga* control therefore requires rigorous and unremitting implementation of integrated systems of control. To achieve an effective integrated control program in Africa, four objectives adapted from the witchweed control program in the United States (17,37) need to be met: i) prevent influx of *Striga* seeds, ii) reduce amount of *Striga* seeds in the soil, iii) prevent *Striga* reproduction, and iv) reduce crop losses. To accomplish these objectives, we have endorsed an integrated *Striga* control scheme shown in Figure 12. The starting point of control, which addresses objective i), is the use of *Striga*-free planting material to avoid infestation in *Striga*-free areas or areas under active control. The central focus of the control program, which addresses objective ii), is crop rotation with selected non-host cultivars efficacious in germinating *Striga* spp. seeds. This focus is analogous both to the traditional fallow system that controlled *Striga* spp. in the past and to the successful U.S. control effort that uses ethylene gas to stimulate *S. asiatica* seed germination (37). Host-plant resistance, host-seed treatments, transplanting, and biological control reduce the amount of *Striga* seeds in the soil, stop *Striga* reproduction, and reduce crop losses. As appropriate, one or more of these options should be fitted into the control program to augment control by crop rotation.

### Delivery of Control Options to the African Farmer

Current systems of delivery of *Striga* control options are handled primarily by national agricultural research and extension services (NARES) in each country. Other contributors to this process are non-governmental organizations (NGOs), e.g., farmers' cooperatives, Cooperative for Assistance and Relief Everywhere (CARE), United States Peace Corps, and seed companies. Delivery through these systems has been piecemeal primarily due to poor communication; lack of coordinated research, training, and extension efforts; and lack of donor commitment to a unified and comprehensive *Striga* control campaign. To improve research coordination and communication, the Pan African *Striga* Control Network (PASCON) was formed in 1988 in Banjul, Gambia, through an Organization of African Unity resolution. Currently, 27 African countries

and several IARCs and overseas research laboratories are members of this network. PASCON has provided a forum for information exchange and has conducted workshops on current *Striga* research. It has not been able to establish a coordinated and functional *Striga* research, training, and extension effort, primarily because of lack of funding.

Given the variability within and between *Striga* spp. and the diversity of African farming systems, testing and adaptation of control options developed by IARCs and other laboratories must be done at the local level by NARES and must be followed by implementation through local extension services. This should be accompanied by direct development of control options by NARES. To accomplish this, local research facilities will have to be improved and staffed with trained research and extension workers. Given the current state of many national economies in Africa, local support for development of facilities and training of personnel will probably remain inadequate. NARES research and extension grants need to be encouraged and funded. Regional research, training, and extension centers should be developed and expanded through NARES and IARCs to obtain the greatest benefit from resources invested in *Striga* control. Coordination of these centers and their personnel should be housed in a continent-wide project administered by PASCON and supported by both public and private sector funds. Funds from various sources should be combined to support a single coordinated control effort rather than a multitude of ineffective, often competing, projects. A modest 1% annual improvement in *Striga* control in Africa would net crop yield increases worth \$70 million annually (27).

### Literature Cited

- Abbasher, A. A., and Sauerborn, J. 1992. *Fusarium ngamai*, a potential bioherbicide for *Striga hermonthica* control in sorghum. *Biocontrol* 2:291-296.
- Aggarwal, V. D., and Ouedraogo, J. T. 1989. Estimation of cowpea yield loss from *Striga* infestation. *Trop. Agric.* 66:91-92.
- Alabi, M. O., Berner, D. K., and Olaniyan, G. O. 1994. Characterization of soybean cultivars for *Striga hermonthica* control. *Phytopathology* 84:1151.
- Anonymous. 1994. Controlling parasitic weed by fungus. *Spore* 53:10.
- Bashir, M. O. 1987. The potential for biocontrol of witchweeds. Pages 183-206 in: *Parasitic Weeds in Agriculture*. Vol. 1, *Striga*. L. J. Musselman, ed. CRC Press, Boca Raton, FL.
- Bebawi, F. F., Eplee, R. E., Harris, C. E., and Norris, R. S. 1984. Longevity of witchweed (*Striga asiatica*) seed. *Weed Sci.* 32:494-507.
- Berner, D. K., Awad, A. E., and Aigbokhan, E. I. 1994. Potential of imazaquin seed treatment for control of *Striga gesnerioides* and *Alectra vogelii* in cowpea (*Vigna unguiculata*). *Plant Dis.* 78:18-23.
- Berner, D. K., Berggren, G. T., and Snow, J. P. 1992. Method for protecting plants against soil-borne fungi using glyphosate

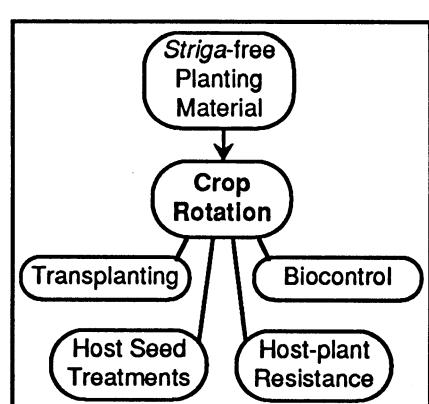


Fig. 12. An integrated *Striga*-control scheme. The central focus involves crop rotation with selected nonhost cultivars that are highly effective in germinating *Striga* spp. seeds.

- and imazaquin compositions. U.S. patent 5,110,805.
9. Berner, D. K., Cardwell, K. F., Fatuoti, B. O., Ikie, F. O., and Williams, O. A. 1994. Relative roles of wind, crop seeds, and cattle in dispersal of *Striga* spp. *Plant Dis.* 78: 402-406.
  10. Berner, D. K., and Ikie, F. O. 1994. Transplanting for control of *Striga hermonthica* in Africa. *Phytopathology* 84:1104.
  11. Berner, D. K., Ikie, F. O., and Aigbokhan, E. I. 1994. Some control measures for *Striga hermonthica* utilizing critical infection period on maize and sorghum. *Proc. East. South. Afr. Maize Conf. Maize Res. Stress Environ.*, 4th, CIMMYT, Harare, Zimbabwe.
  12. Chang, M., and Lynn, D. G. 1986. The haustorium and the chemistry of host recognition in parasitic angiosperms. *J. Chem. Ecol.* 12:571-579.
  13. Cook, C. E., Wichard, L. P., Wall, E. E., Egley, G. H., Goggon, P., Luhun, P. A., and McPhail, A. T. 1972. Germination stimulants. II. The structure of strigol - a potent seed germination stimulant for witchweed (*Striga lutea* Lour.). *J. Am. Chem. Soc.* 94:6198.
  14. Doggett, H. 1984. *Striga*: Its biology and control - an overview. Pages 27-36 in: *Striga Biology and Control*. E. S. Ayensu, H. Doggett, R. D. Keynes, J. Marton-Lefevre, L. J. Musselman, C. Parker, and A. Pickering, eds. Int. Counc. Sci. Union, Paris, France, and Int. Dev. Res. Ctr., Ottawa, Canada.
  15. Efron, Y. 1993. Screening maize for tolerance to *Striga hermonthica*. *Plant Breed.* 110:192-200.
  16. Emechebe, A. M., Singh, B. B., Leleji, O. I., Atokple, I. D. K., and Adu, J. K. 1991. Cowpea-*Striga* problems and research in Nigeria. Pages 18-28 in: *Combating Striga in Africa*. Proc., Int. Workshop Org. IITA, ICRISAT, and IDRC. S. K. Kim, ed. IITA, Ibadan, Nigeria.
  17. Eplee, R. E. 1981. *Striga*'s status as a plant parasite in the United States. *Plant Dis.* 65:951-954.
  18. Garcia-Torres, L., and Lopez-Granados, F. 1991. Control of broomrape (*Orobanche crenata* Forsk.) in broad bean (*Vicia faba* L.) with imidazolinones and other herbicides. *Weed Res.* 31:227-235.
  19. Hauck, C., Muller, S., and Schildknecht, H. 1992. A germination stimulant for parasitic flowering plants from *Sorghum bicolor*, a gen-



**D. K. Berner**

Dr. Berner is a *Striga* biologist in the plant health management division of the International Institute of Tropical Agriculture (IITA), in Ibadan, Nigeria. He earned his B.S. degree in biology from Illinois State University and his M.S. degree in rice genetics and Ph.D. degree in soybean pathology from Louisiana State University. Prior to obtaining his advanced degrees, he worked from 1975 to 1980 in Sierra Leone and Mauritania in rice development and management. He returned to Africa in his current position with IITA in 1991. At IITA, he is currently leader of the host-plant resistance program and coordinator of the *Striga* research group. His responsibilities include developing, through research, sustainable control measures for *Striga* and related genera that are adoptable by African farmers, working with African national agricultural research and extension systems in the development and implementation of control measures, training national program personnel, and supervising students in *Striga* research. His research program on *Striga* spp. encompasses epidemiology, host-parasite interactions, host-plant resistance, physiology, and biological control.



**J. G. Kling**

Dr. Kling is a maize breeder in the crop improvement division of the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria. She came to IITA in 1988 as a postdoctoral fellow to work on methods for improving nitrogen use efficiency in maize. In 1991, she assumed responsibility for developing improved maize populations for the lowland ecologies of West and Central Africa. Her present research includes breeding for resistance to *Striga hermonthica*, downy mildew (*Peronosclerospora sorghi*), stem borers (*Eldana saccharina* and *Sesamia calamistis*), and other disease and insect pests of maize. She is involved in a collaborative project with the University of Hannover, funded by Gesellschaft für Technische Zusammenarbeit (GTZ) to investigate possible relationships between root morphology and nitrogen use efficiency. She conducts research on postharvest utilization of maize in collaboration with food technologists and national program scientists in Benin, Mali, and Nigeria. She earned her Ph.D. in genetics at North Carolina State University in 1988 and her M.S. in agronomy at the University of Nebraska in 1984. Her thesis research for both degrees involved quantitative genetic studies in maize. Her undergraduate degree was in crop science at Oregon State University.



**B. B. Singh**

Dr. Singh is a cowpea breeder in the crop improvement division of the International Institute of Tropical Agriculture (IITA) in Kano, Nigeria. He earned his B.S. degree in agriculture from G. B. Pant University of Agriculture and Technology, Pantnagar, India, and his M.S. and Ph.D. degrees in plant breeding and genetics from the University of Illinois. Prior to coming to IITA, he was an associate professor of breeding and a senior research officer at the G. B. Pant University of Agriculture and Technology, Pantnagar, India. He came to IITA in 1979 as a legume breeder in a joint IITA/USAID/Tanzania project. In 1981, he became the principal cowpea breeder at IITA, Ibadan, Nigeria. From 1989 to the present he has been a cowpea breeder and officer in charge of IITA's station in Kano. He has developed numerous cultivars of cowpea with multiple disease and insect resistance that have been released by many national programs in Africa, Latin America, and Asia. His current research agenda includes the development of high-yielding cowpea cultivars with multiple pest resistance for cropping systems of the dry savannas of Africa.

- uine host plant. J. Plant Physiol. 139:474-478.
20. Herbaugh, L., Upton, N. P., and Eplee, R. E. 1980. *Striga gesnerioides* in the United States of America. Proc. South. Weed Sci. Soc. 33:187-190.
  21. Kim, S. K. 1991. Breeding maize for *Striga* tolerance and the development of a field infestation technique. Pages 96-108 in: Combating *Striga* in Africa. S. K. Kim, ed. Proc. Int. Workshop Org. IITA, ICRISAT, and IDRC. IITA, Ibadan, Nigeria.
  22. Kim, S. K. 1994. Genetics of maize tolerance of *Striga hermonthica*. Crop Sci. 34:900-907.
  23. King, S. B., and Zummo, N. 1977. Physiologic specialization in *Striga hermonthica* in West Africa. Plant Dis. Rep. 61:770-773.
  24. Lagoke, S. T. O., Parkinson, V., and Agunbiade, R. M. 1991. Parasitic weeds and control methods in Africa. Pages 3-14 in: Combating *Striga* in Africa. Proc. Int. Workshop Org. IITA, ICRISAT, and IDRC. S. K. Kim, ed. IITA, Ibadan, Nigeria.
  25. Lane, J. A., Moore, I. H. M., Child, D. V., Cardwell, K. F., Singh, B. B., and Bailey, J. A. 1994. Virulence characteristics of a new race of the parasitic angiosperm *Striga gesnerioides* from southern Benin on cowpea. Euphytica 72:183-188.
  26. Liu, Z. Q., Fer, A., and Lecocq, F. M. 1991. L'imazaquine: un herbicide prometteur pour la lutte curative contre la cuscute (*Cuscuta* spp.) dans les cultures de soja (*Glycine max*). Weed Res. 31:33-40.
  27. Mboob, S. S. 1986. A regional programme for West and Central Africa. Pages 190-194 in: Proc. FAO/OAU All-Afr. Gov. Consult. *Striga* Control. Maroua, Cameroon.
  28. Musselman, L. J. 1987. Taxonomy of witch weeds. Pages 3-12 in: Parasitic Weeds in Agriculture. Vol. 1, *Striga*. L. J. Musselman, ed. CRC Press, Boca Raton, FL.
  29. Olivier, A., Benhamou, N., and Leroux, G. D. 1990. Cell surface interactions between sorghum roots and the parasitic weed *Striga hermonthica*: cytochemical aspects of cellulose distribution in resistant and susceptible host tissues. Can. J. Bot. 69:1679-1690.
  30. Parker, C., and Riches, C. R. 1993. Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK.
  31. Parkinson, V., Efron, Y., Bello, L., and Dashiel, K. 1987. Trap crops as a cultural measure in *Striga* control in Africa. FAO Plant Prot. Bull. 35:51-54.
  32. Pieterse, A. H., and Pesch, C. J. 1983. The witchweeds (*Striga* spp.) - a review. Abstr. Trop. Agric. 9:9-35.
  33. Ramaiah, K. V. 1987. Breeding cereal grains for resistance to witchweed. Pages 227-242 in: L. J. Musselman, ed. Parasitic Weeds in Agriculture. Vol. 1, *Striga*. CRC Press, Boca Raton, FL.
  34. Ransom, J. K., Eplee, R. E., and Langston, M. A. 1990. Genetic variability for resistance to *Striga asiatica* in maize. Cereal Res. Commun. 18:329-333.
  35. Raynal-Roques, A. 1991. Diversification in the genus *Striga*. Pages 251-261 in: Proc. Int. Symp. Parasitic Weeds, Nairobi, 5th. J. K. Ransom, L. J. Musselman, A. D. Worsham, and C. Parker, eds. CIMMYT, Nairobi.
  36. Sand, P. F. 1990. Discovery of witchweed in the United States. Pages 1-6 in: Witchweed Research and Control in the United States. P. F. Sand, R. E. Eplee, and R. G. Westerbrooks, eds. Weed Sci. Soc. Am., Champaign, IL.
  37. Sand, P. F., and Manley, J. D. 1990. The witchweed eradication program survey, regulatory and control. Pages 141-151 in: Witchweed Research and Control in the United States. P. F. Sand, R. E. Eplee, and R. G. Westerbrooks, eds. Weed Sci. Soc. Am., Champaign, IL.
  38. Saunders, A. R. 1933. Studies in phanerogamic parasitism, with particular reference to *Striga lutea* Lour. South Afr. Dep. Agric. Sci. Bull. 128.
  39. Singh, B. B., and Emechebe, A. M. 1990. Inheritance of *Striga* resistance in cowpea genotype B301. Crop Sci. 30:879-881.
  40. Singh, B. B., Emechebe, A. M., and Atokple, I. D. K. 1993. Inheritance of *Alectra* resistance in cowpea genotype B301. Crop Sci. 33:70-72.
  41. Stewart, G. R., and Press, M. C. 1990. The physiology and biochemistry of parasitic angiosperms. Annu. Rev. Plant Physiol. Plant Mol. Biol. 41:127-151.
  42. Versteeg, M., Adanguidi, J., Djenotin, J., and Nonfon, R. 1994. Recherche participative efficace entre paysans, ONG, SNRA et IITA pour contrôler *Striga hermonthica* au Nord du Benin. Pages 413-433 in: Proc. Region. Conf. Syst. Agraires Agric. Durable Afr. Sub-Saharienne, Int. Found. Sci., Cotonou, Benin.
  43. Visser, J., and Dorr, I. 1987. The haustorium. Pages 91-106 in: Parasitic Weeds in Agriculture. Vol. 1, *Striga*. L. J. Musselman, ed. CRC Press, Boca Raton, FL.
  44. Worsham, A. D. 1987. Germination of witchweed seeds. Pages 45-61 in: Parasitic Weeds in Agriculture. Vol. 1, *Striga*. L. J. Musselman, ed. CRC Press, Boca Raton, FL.