# Relative Roles of Wind, Crop Seeds, and Cattle in Dispersal of Striga spp.

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#### **ABSTRACT**

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Parasitic flowering plants of the genus Striga cause extensive damage to cereal and legume crops in Africa, but factors affecting seed dispersal have not been well understood. Petrolatum-coated microscope slides placed at regular intervals from Striga hermonthica plants and suspended at 1-, 2-, and 3-m heights from trees within and around S. hermonthica-infested fields indicated that distribution of seeds by wind was not extensive. The maximum horizontal distance that seeds were caught was 12 m and the maximum vertical distance was 2 m. Samples of local market supplies of cowpea, maize, millet, and sorghum from six areas of Nigeria over 2 yr contained an average of 20.9, 32.4, 24.2, and 27.3 Striga seeds, respectively. Cattle dung was sampled intensively for parasite seeds in and around two S. hermonthica-infested fields and from 45 locations (88 fields) in S. hermonthica-infested areas of Nigeria. Cattle dung was of minor importance in seed dispersal. Implications of dispersal mechanisms in control are discussed.

A diverse number of parasitic seed plants in the savannah zone of Africa pose serious threats to both cereal and legume production (1,2,6-8). The most devastating of these are species in the genus *Striga*, family Scrophulariaceae (16). The most common and devastating

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species in the savannah zone is S. hermonthica (Del.) Benth., a parasite of millet (Pennisetum americanum (L.) K. Schum.), sorghum (Sorghum bicolor (L.) Moench), maize (Zea mays L.), rice (Oryza sativa L.), and sugarcane (Saccharum officinarum L.) (2,15,18,19). Cowpea (Vigna unguiculata (L.) Walp.) is frequently intercropped with cereals in this zone and is a host of S. gesnerioides (Willd.) Vatke, the second most common species of Striga (1,15). These species have coevolved with their respective hosts and have been pests in traditional cropping systems for many years (15,18,

19). Because the traditional cropping systems involved prolonged fallow, rotations, and mixed cropping, populations of Striga spp. were kept in check at tolerable levels (18). However, with increasing population pressure, the demand for increased food production, monocropping, and the intensification of land use, with little or no fallow, populations of these parasites have gradually increased and become threats to food production (18,19). Yield losses due to these pests are augmented when plants are already in poor health because of drought and low soil fertility. Expensive fertilizers, lack of viable control opportunities, and paucity of resistant cultivars make alleviation of the problem difficult for the African farmer (2,3,18). Estimates in the literature indicate frequent yield losses above 50% attributable to Striga spp. on all of the host crops (1,2,7,19). Arable fields are often abandoned because of prohibitive parasite populations (2,15). Equally alarming are the field reports indicating that the range of these parasitic plants appears to be increasing (2,15).

Species of *Striga* reproduce prodigiously and are capable, in a single crop season, of producing 50,000-500,000

seeds per parasite plant (19). Sorghum fields heavily infested with *S. hermonthica* have been reported to yield more than 900,000 flowering *S. hermonthica* plants per hectare (7). Given the above reproduction, this would result in  $4.5 \times 10^{10}$  parasite seeds per hectare. These seeds are viable for 7-14 yr (5,23).

Despite the seriousness of these parasites and their capacity for reproduction, little is known about mechanisms governing their seed dispersal. Because of the small size of these seeds (0.20-0.50 mm long) (17,19), wind has been assumed to be a major dispersal mechanism (13,19). However, S. asiatica (L.) Kuntze has never moved, as wind-dispersed seed would be expected to do, from the original areas of infestation in the United States (9,22). There have been no studies on wind dispersal of Striga spp. seeds in Africa.

Contamination of crop seeds with weed seeds is well known and is a measure of seed purity (14). Although Striga spp. seeds are listed in the United States Federal Noxious Weed Act (12), they have not been documented as being a crop seed contaminant. The possible importance of this mechanism of dispersal in Africa is unkown.

Incubation of S. hermonthica seeds in sheep rumen liquor was shown to generally result in reduced seed viability (4). However, in another study, maize grown in dung from cattle fed with Striga spp. plants became severely infected (11). Under natural conditions, there are no reports on dispersal of Striga spp. seeds through dung or on viability of Striga spp. seeds extracted, after prolonged exposure, from dung.

To slow or stop the spread of *Striga* spp., the mechanisms of dispersal need to be better understood. With this knowledge, control strategies could be more effectively structured. The objectives of this study were to examine the roles of wind, host crop seeds, and cattle in *Striga* spp. seed dissemination.

### MATERIALS AND METHODS

Dissemination by wind. These studies were conducted in the southern Guinea savannah zone of West Africa. In 1991 in Nigeria, a 1-ha field in Mokwa (lat. 9.35° N, long. 5.11° E) and a 0.5-ha field in Abuja (lat. 9.12° N, long. 7.20° E) were artificially infested with S. hermonthica by placing 1,500 germinable parasite seeds in each planting hole 7 days prior to host planting (20). In the Mokwa field, two susceptible maize cultivars (8321-21 and 8425-8) and two susceptible sorghum cultivars (Mokwa Local and CK60B) were planted on 3 July in the infested holes in four-row  $\times$  10-m plots. Crop planting density was 53,333 plants per hectare, with a  $75 \times 25$  cm spacing. Five plots of each crop per cultivar were planted in a completely randomized design. In the Abuja field, only the susceptible maize cultivars were used. Planting was done on 30 July. Other conditions were the same as for the Mokwa trial. Growth duration of the maize cultivars was 115 days and that of the sorghum cultivars was 90 days for CK60B and 150 days for Mokwa Local. A swath of 40 m around each field was kept free from vegetation that could have impeded the free movement of parasite seeds. Plots were situated so that no trees were in this 40-m swath. Any trees within the fields were left standing, according to local farming practices, and the crops were established around them.

To assay the horizontal extent of wind dispersal of S. hermonthica seeds, petrolatum-coated microscope slides were placed in vegetation-free areas outside the fields at intervals of 10, 20, 40, 80, 160, 320, 640, 1,280, and 2,560 cm away from stands of mature S. hermonthica plants on the field borders. Ten radii of slides spaced at these intervals (10-2,560 cm) were placed around each field at the time of S. hermonthica flowering. Thus, there were 10 replications of each distance at each sampling time for each field. The slides were tied to bamboo stakes at 30 cm above the ground. A 1-cm-diameter wooden stick was placed behind the lower edge of the slide to tilt it upward at a 45° angle. The entire exposed face of each slide was coated with petrolatum, but only seeds on the center 6.5 cm<sup>2</sup> of the slide were counted. To assay vertical dispersal, slides were hung at 1-, 2-, and 3-m heights from trees within the fields and from trees within a 0.25-km radius of the fields. Five replications of each height in each area (within and outside the field) in each location were used. Both faces of the slides hung from trees were coated with petrolatum, and seeds on the center 6.5 cm<sup>2</sup> of each face were counted. All slides were changed weekly for 8 wk, and numbers of captured seeds were counted. Deployment of slides began 116 days after planting (DAP) and continued through 175 DAP. Because S. hermonthica seed maturity and release coincide with the onset of the dry season in Nigeria, rain had no effect on the quality of data collected.

In 1992, this dispersal study was repeated at Hadagon (lat. 7.00° N, long. 2.10° E), Republic of Benin. A 0.5-ha field was infested as described above with 1,000 germinable S. hermonthica seeds per hill and planted on 21 September during the second rainy season. The 115-day susceptible maize cultivar 8338-1 was used. Deployment of slides began 63 DAP and continued through 98 DAP. S. hermonthica seeds were counted as described above. As in 1991, maturity and release of parasite seeds coincided with the onset of the dry season and rain had no effect on data quality.

Dissemination with crop seeds. During the postharvest (December to January) seasons of 1991 and 1992, seeds of cowpea, maize, millet, and sorghum were collected from local markets in Abuja, Bida, Kaduna, Kano, Mokwa, and Zaria, Nigeria; these areas are representative of the *Striga*-infested savannah of Nigeria. In local markets, crop seeds, whether for consumption or planting, are displayed and sold from large pans. To ensure that the small *Striga* seeds could be detected in the grain samples, the upper portion of grain in the pan was removed and only the bottom 1–3 kg of seeds (where small particles settle) were sampled. Sample sizes varied according to seed availability from the sellers. One randomly chosen sample was purchased from each of eight markets in each location.

After collection, seed samples were taken to the laboratory at the International Institute of Tropical Agriculture, Ibadan, Nigeria, and Striga spp. seeds in the samples were isolated. Initially, seeds were separated by turbulent, flowing water in a cabinet-top elutriator (10) and particles the size of Striga seeds were collected on a 90-µm mesh sieve. Particles on the sieve were then backwashed with water into a separatory column containing K<sub>2</sub>CO<sub>3</sub> of specific gravity 1.4. Particles of approximately the same weight as an intact Striga spp. seed (5  $\times$  10<sup>-6</sup> g) were suspended around the H<sub>2</sub>O-K<sub>2</sub>CO<sub>3</sub> interface, while empty Striga spp. seed coats and other lightweight particles were suspended at the surface of the water layer. After the sieve contents were backwashed into the separatory column, particles were allowed to settle for 20 min. The column was then emptied, without disturbing the suspended layers, through a stopcock at the bottom. Particles were collected on 60- $\mu$ m mesh sieves, and *Striga* spp. seeds were then counted under a dissecting microscope. Seeds were differentiated only at the genus level; no attempt was made to differentiate the seeds into species.

Statistical comparisons were made only for average number of seeds per sample between the 2 yr of collection. Statistical comparisons between locations were not made because a general inference was desired only for the *Striga*-endemic area of Nigeria. Comparison of locations, without data on the large number of associated variables that could affect seed lot contamination, would have had little practical value.

Dissemination by cattle. After harvest of maize and sorghum in the 1991 study, cattle (Bos sp.) managed by local farmers were allowed to graze in and around the S. hermonthica-infested fields. Fields used in these studies were isolated from other S. hermonthica-infested fields, so there was no overlap in grazing between infested areas. Two weeks after grazing, 30 samples of 10 dung droppings each were collected from within each infested field and another 30 samples were collected from a radius of 0.5 km around the fields.

After harvest in 1992, cattle dung was collected from 45 random locations in the savannah zone of northern Nigeria.

Within these locations, one sample consisting of 10 droppings was collected from within a S. hermonthica-infested field (38 samples from 45 locations) and one was collected from uninfested fields in the same area (50 samples from 45 locations).

In both years, the samples were taken to the laboratory at the International Institute of Tropical Agriculture in Ibadan, where Striga spp. seeds were isoseeds and seed coats were counted. Via-

lated. No attempt was made to differentiate species of Striga based on seed morphology. To isolate Striga spp. seeds, samples were dissolved in water for 1 day, then seeds were separated by elutriation and K<sub>2</sub>CO<sub>3</sub> as previously described. Particles were collected separately on 60μm mesh sieves, and intact Striga spp.

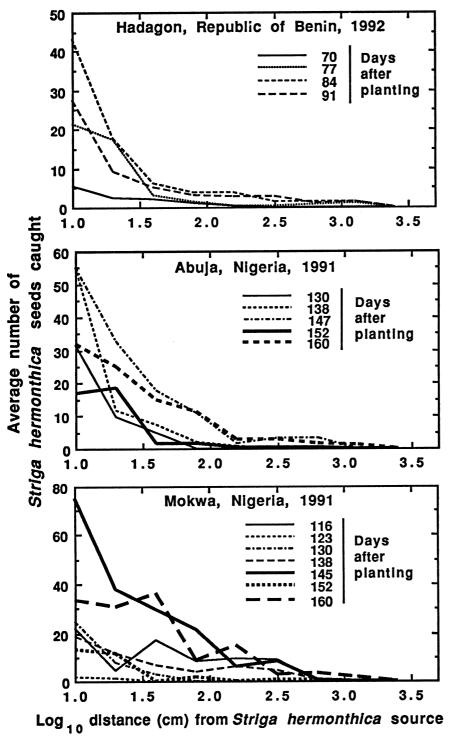


Fig. 1. Average number of Striga hermonthica seeds caught on coated microscope slides placed 10, 20, 40, 80, 160, 320, 640, 1,280, and 2,560 cm from mature S. hermonthica plants. Data were collected from a mix-planted sorghum and maize field in Mokwa, Nigeria, and from a maize field in Abuja, Nigeria, in the early dry season of 1991 and from a maize field in Hadagon, Republic of Benin, in the early dry season of 1992. Data points are averages of 10 samples taken at the indicated times after planting.

bility of intact seeds was determined by the tetrazolium chloride embryo staining technique (5).

## RESULTS

Dissemination by wind. In all locations, seed catches declined sharply with increasing distance from the seed source. Seed catches at distances greater than 80 cm ( $log_{10} = 1.9$ ) declined to less than one-half of those at 10 cm. In all locations, maximum extent of dispersal was  $1,280 \text{ cm } (\log_{10} = 3.10) \text{ at a height of}$ 

In Mokwa, the greatest number of seeds caught per slide at 1,280 cm was 1.5 at 160 DAP. At 640 cm ( $\log_{10} = 2.8$ ), the greatest number of seeds caught per slide was 3.5 at 160 DAP (Fig. 1). The largest seed catch, averaged over all slides, was at 145 DAP. A few seeds were caught as early as 116 DAP, but the bulk of seed dispersal appeared to be between 145 and 160 DAP.

In Abuja, the greatest number of seeds caught per slide at 1,280 cm was 1.3 at 160 DAP (Fig. 1). At 640 cm, the greatest number caught per slide was 3.3 at 147 DAP. The largest seed catch was at 147 DAP. Only small amounts of seeds were caught at any distance before 130 DAP and after 160 DAP, and the period of maximum dispersal was between 138 and 147 DAP.

In Hadagon in 1992, the greatest number of seeds caught per slide at 1,280 cm was 1.2 at 91 DAP (Fig. 1). At 640 cm, the greatest number caught per slide was 1.3 at 84 DAP. The period of substantial seed catches was between 77 and 91 DAP. Outside this range, few seeds were caught at any distance.

The period of maximum seed dispersal in all locations was from 25 November through 6 January, which is the middle of the annual harmattan season.

The maximum vertical distance at which S. hermonthica seeds were caught was 2 m. A maximum of 10 seeds were caught at this height and only from traps in the 15 trees within infested fields. No seeds were caught on any of the 45 treehung traps outside the infested areas.

Dissemination with crop seeds. Striga spp. seeds were found in all grain samples. The amounts found in the different crop seed samples varied each year. The overall contamination of crop seeds was 19.4% (42/216 samples) in 1991. An average of 16.6% (9/54) of cowpea samples, 33.3% (18/54) of millet samples, 14.8% (8/54) of sorghum samples, and 13.0%(7/54) of maize samples (Table 1) were contaminated with Striga seeds. In 1991, the largest amounts of Striga seeds were found in millet and sorghum samples from the Kano market, with over 300 and 200 seeds, respectively, in a single sample (Table 1). The greatest frequency of contamination in 1991 was also found in Kano in all of the crop seeds except cowpea. Contamination of maize seeds in 1991 was found only in Kano and

Kaduna, the latter being the principal maize-growing region of Nigeria.

In 1992, seed samples of all crops from all sites contained Striga seeds. Relatively few market samples did not contain parasite seeds. The overall Striga seed contamination of crop seeds was 63.9% (138/216) of all the samples collected. An average of 61.1% (33/54) of the cowpea samples, 55.5% (30/54) of the millet samples, 62.9% (34/54) of the sorghum samples, and 75.9% (41/54) of the maize samples were contaminated with Striga seeds (Table 1). These numbers were much higher in 1992 than in 1991, particularly for cowpea and maize. Maximum and average numbers of Striga seeds in the samples were also much higher for all crops (Table 1) but were particularly high for cowpea and maize.

Dissemination by cattle. Few Striga spp. seeds were found in dung samples from areas outside infested fields in the 1991 study (Table 2). Approximately twice the number of Striga spp. seed coats as intact seeds-638 vs. 387-were found in the dung samples. Considering the total number ingested, this results in 37.7% intact seeds after passage through the cow gut. The average number of intact Striga spp. seeds per sample from within infested fields was seven (range 0-98). As 30 samples were taken from each field, this would yield a reinfestation of 210 intact seeds per preinfested field. Viability of intact seeds was 22.0%, leaving a reinfestation of 46 viable seeds per infested field, or, overall, 8.3% of the total ingested (22% viability of 37.7% intact seeds). Viability of freshly harvested seeds from the same fields averaged 80.5%. The average number of intact Striga spp. seeds collected from dung samples outside infested fields was 0 (range 0-2).

Sampling from 45 locations (88 fields) in 1992 showed there were nearly equal numbers of intact *Striga* spp. seeds recovered from dung within and outside infested fields. The average number of seeds recovered was 23 per infested field and 15 per uninfested area. Viability was 21.6%, leaving infestations of five and three seeds per infested and uninfested areas, respectively.

### **DISCUSSION**

The results of these studies show that Striga spp. seeds are not efficiently or widely dispersed by wind. Supporting evidence for this conclusion comes from the S. asiatica-infested areas of the United States. The parasite was accidentally introduced to maize-growing areas of North and South Carolina sometime in the 1950s (22). Since that time, the parasite has not appeared in other maize-producing areas of the United States. This has been due to strict quarantine of infested areas (9), but had wind been a primary dispersal agent, S. asiatica would have appeared in other areas de-

spite quarantine procedures. The frequency and force of hurricanes along the eastern coast of the United States since 1950 would surely have provided sufficient wind for dispersal of *S. asiatica* to areas far from those in quarantine.

The relative unimportance of wind as a dispersal agent is particularly significant when control options are being considered. Had this study shown widespread wind dispersal of *Striga* spp. seeds, the option of localized eradication would not be feasible and control efforts would be best directed to limiting host damage by host plant resistance or crop protection. As it is, localized eradication

should be possible by combining exclusion of new influxes of the parasite, crop rotations to reduce soil levels of parasite seeds, and methods to stop parasite reproduction.

The prevalence of *Striga* spp. seeds in market samples of crop seeds indicates the importance of this mechanism of dispersal when seeds are used as planting materials. Although differences in crop seed contamination were observed both years, it is not clear whether these differences reflect increasing amounts of contamination or increased proficiency of sampling and seed isolation processes. However, the overall levels of contam-

Table 1. Presence of Striga spp. seeds in samples of cowpea (Vigna unguiculata), maize (Zea mays), millet (Pennisetum americanum), and sorghum (Sorghum bicolor) seeds collected from eight markets in each of six locations in Nigeria during 1991 and 1992 postharvest seasons

Location Crop	No. of samples with seeds		of s	ium no. eeds sample	Av. no. of seeds per sample <sup>b</sup>	
	1991	1992	1991	1992	1991	1992
Abuja						
Cowpea	1	8	12	227	2	88* c
Maize	0	8	0	148	0	84 <b>*</b>
Millet	3	7	2	88	1	42 <b>*</b>
Sorghum	0	7	0	116	0	48
Bida						
Cowpea	1	6	4	89	1	36 <b>*</b>
Maize	0	8	0	222	0	108*
Millet	4	1	1	1	0	0
Sorghum	2	3	2	25	0	5
Kaduna						
Cowpea	0	6	0	98	0	29
Maize	3	8	9	162	1	54 <b>°</b>
Millet	0	6	0	101	0	30
Sorghum	0	7	0	71	0	31
Kano						
Cowpea	0	6	0	200	0	45°
Maize	4	6	14	250	2	56°
Millet	8	5	321	74	109	19*
Sorghum	5	7	230	388	64	86
Mokwa						
Cowpea	4	5	36	90	11	30
Maize	0	6	0	178	0	74°
Millet	3	3	3	38	1	8
Sorghum	1	8	3	345	0	92*
Zaria						
Cowpea	3	2	30	15	6	3
Maize	0		0	36	0	10
Millet	0	5 8 3	0	202	0	80°
Sorghum	0	3	0	2	0	1

<sup>&</sup>lt;sup>a</sup> Samples were clean, market-quality seed and sizes ranged from 1 to 3 kg, depending on quantity available from the seller.

**Table 2.** Presence of *Striga* spp. seeds in cattle dung samples collected within *Striga hermonthica*-infested fields and within a 0.5-km radius of infested fields during December 1991 and December 1992<sup>a</sup>

	No. of samples		No. of intact seeds		No. of seed coats		Av. no. of intact seeds/ sample/field	
Sample sites	1991	1992	1991	1992	1991	1992	1991	1992
Within infested fields Within 0.5-km radius	60	38	387	857	638	24	7	23
of infested fields	60	50	5	730	10	35	0	15

<sup>&</sup>lt;sup>a</sup> During 1991, 30 samples of 10 droppings each were taken from each site in two fields. During 1992, individual samples of 10 droppings were taken from each field in 45 randomly selected locations in northern Nigeria.

<sup>&</sup>lt;sup>b</sup> All averages rounded to nearest integer.

c \* = Significant difference between years ( $P \le 0.05$ ).

ination indicate that this mechanism may well account for most new establishments of these parasites. In this study, crop seeds were sampled between December and January soon after crops had been harvested. Local seed purchases for planting materials later in the year (May–July) might be expected to contain even greater amounts of parasite seeds, as these small seeds settle to the bottom of crop seed containers and the uppermost contents of the containers would have been gradually sold or consumed since harvest the previous season.

Because S. hermonthica is obligately allogamous (21), at least two viable plants would have to survive to cross and establish a new infestation focus. Many samples contained over 50 seeds. However, with autogamous Striga spp. such as S. gesnerioides and S. asiatica (16), only one seed is sufficient to establish a new focus of infestation. Contaminated imported seed stocks may have been the source of the initial S. asiatica infestation in the United States, which subsequently developed into a serious long-term agricultural problem.

Of significance is the source of the samples in these studies. All were marketquality seeds that had been thoroughly winnowed and contained little, if any, visible field trash, such as leaves, husks, and panicle or pod fragments. Seeds saved by farmers for planting in the following season are not of this market quality and probably contain even greater amounts of Striga spp. seeds. The reason for this amount of contamination is probably the method of harvest of these crops. Stalks of cereal crops are cut at the base and laid in rows in the field to dry. After drying, the grains are threshed and stalks are used as building materials. In Striga-infested fields, Striga plants are frequently intermixed with the drying grain crop and parasite seeds become intermixed with crop seeds upon threshing. Since cowpea is often intercropped with cereals, harvest of cowpea incorporates not only the cowpea parasite S. gesnerioides but also the cereal parasite S. hermonthica.

The best solution to contamination of crop seeds with lightweight Striga spp. seeds is field sanitation. Farmers need to be made aware of the ease with which their planting materials can become contaminated and must avoid laying crops in the vicinity of these parasites. Plant quarantine services and seed industries also need to be aware of potential crop seed contamination with Striga spp. Unaided sieving of crops seeds is inadequate to remove the lightweight Striga spp. seeds, which do not pass readily through sieves without external pressure. Cleaning of contaminated seeds by washing or vacuum (D. K. Berner, unpublished) is feasible at the plant garantine or seed industry level, but the current procedures are too time-consuming and labor-intensive to be carried out on-farm.

Dung samples collected from outside S. hermonthica-infested fields contained relatively few parasite seeds in either year of the study. After the 1991 study, it was felt that because passage of green matter through the cattle gut may take more than 1 or 2 days, our survey area may not have been wide enough to adequately sample material ingested in the field and deposited farther away. However, the relatively high numbers of Striga spp. seeds found in dung samples within infested fields in 1991 seemed to indicate that greater amounts should have been found in the surrounding area if this was an important dispersal mechanism. The low percentages of intact viable seeds in dung samples from within infested fields in the 1991 study indicated that animal ingestion and deposition may be only a short distance and relatively minor dispersal mechanism. The results of the 1992 study confirmed this, as an average of only three viable seeds per uninfested area were found. If these were S. hermonthica seeds, the probability of only three seeds establishing a new focus of parasite infestation is low, since this species is obligately allogamous.

The importance of dispersal of seeds on animal hooves and fur, however, was not addressed in this study. Because animal herds roam widely across the savannah zone of Africa, this possible mechanism needs to be examined in more detail. There have been no reports of *Striga* spp. seed dispersal by birds.

A mechanism that may account for widespread parasite seed dispersal is the transportation (and often sale) of cowpea fodder from infested fields to areas deficient in animal feed during the dry season. Depending on location, inspection of the contents of any bundle of fodder could reveal the presence of seed bearing S. hermonthica, S. aspera (Willd.) Benth., S. gesnerioides, and Alectra vogelii Benth., either individually or collectively, since all of these parasites can be found within a single field. Control of this means of dispersal in Africa will be very difficult during times of critical need for animal feed. The means of reducing spread by fodder can only be the localized reduction of parasite populations from fodder-producing areas.

The overall results of these studies indicate that man, through agricultural produce and animal movement, is the primary factor in dispersal of *Striga* spp. Although disconcerting, this mechanism can be controlled through farmer education and plant quarantine service awareness. Because annual influxes of *Striga* spp. seed by wind do not appear to occur in farmers' fields, localized eradication could be made effective by stopping recontamination of fields by man and through appropriate control measures aimed at existing *Striga* spp. populations.

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