Assessment of Different Legumes for the Control of *Striga hermonthica* in Maize and Sorghum

Zeyaur R. Khan,* Charles A. O. Midega, Ahmed Hassanali, John A. Pickett, and Lester J. Wadhams

ABSTRACT

The witchweed, Striga hermonthica (Del.) Benth., is a major constraint to maize (Zea mays L.) and sorghum [Sorghum bicolor (L.) Moench] production in sub-Saharan Africa. Intercropping maize and sorghum with desmodium (Desmodium spp.) effectively controls Striga and enhances grain yields. Studies were thus conducted to assess the potential role of intercropping maize and sorghum with different food legumes for control of Striga. Seasonal Striga counts in the intercrops, other than greenleaf desmodium where the counts consistently remained close to zero, were generally not significantly different from those in the control in both crops. A pooled analysis across seasons, however, showed that intercropping sorghum with cowpea [Vigna unguiculata (L.) Walp.], greengram [Vigna radiata (L.) Wilczek], and crotalaria (Crotalaria ochroleuca G. Don), and maize with crotalaria significantly reduced Striga populations. Within-season analysis showed that it was only the greenleaf desmodium intercrop that maintained significantly enhanced grain yields relative to the control. On the other hand, multiseason analysis showed that it was only the crotalaria, cowpea, and greenleaf desmodium intercrops in maize and greenleaf desmodium intercrop in sorghum that significantly enhanced grain yields. These results indicate that intercropping sorghum with cowpea, greengram, or crotalaria and maize with crotalaria could be combined with other cultural methods for a sustainable control of S. hermonthica.

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MAIZE AND SORGHUM are the two most important cereal crops in sub-Saharan Africa. One of the most important biotic constraints of both crops are parasitic weeds in the genus *Striga* (Scrophulariaceae) (Oswald and Ransom, 2001), of which *S. hermonthica* is by far the most important, infesting an estimated 158 000 ha of maize and sorghum in the Lake Victoria basin alone (Hassan et al., 1995). Infestations of cereal crops by *Striga* result in severe grain losses, estimated at US\$7 billion annually (Berner et al., 1995), and the most affected are the resource-poor subsistence farmers (Gurney et al., 2006).

Striga weakens the host, wounding its outer root tissues and absorbing its supply of moisture, photosynthates, and minerals (Tenebe and Kamara, 2002), and is so ingeniously adapted to its environment (Bebawi and Metwali, 1991) and integrated with the host that it will only germinate in response to specific chemical cues present in root exudates of its hosts or certain nonhost plants (Yoder, 1999; Parker and Riches, 1993). It also causes "phytotoxic" effects within days of attachment to its hosts (Frost et al., 1997; Gurney et al., 1999), whose underlying mechanism has not yet been elucidated (Gurney et al., 2006). These effects result in a large reduction in host plant height, biomass, and eventual grain yield (Gurney et al., 1999). Various control strategies have been tried, some with partial or local success, but all have limitations and none has provided a complete solution (Oswald, 2005). It has also been complicated by the abundant seed production by Striga plants, longevity of the seed bank (Bebawi et al., 1984), and a complicated mode of parasitism.

Published in Crop Sci 47:728–734 (2007). doi: 10.2135/cropsci2006.07.0487 © Crop Science Society of America 677 S. Segoe R.d., Madison, WI 53711 USA Traditional African cropping systems, which included prolonged fallow, rotation, and intercropping, besides maintaining or improving soil fertility, exert some control of *Striga* (Kureh et al., 2000). However, increasing human population has resulted in intensive land use comprising intensive cultivation of small pieces of land, with shortened or no fallow (Webb et al., 1993), and in some areas continuous cereal cropping with little or no fertilizer or manure application (van Ast et al., 2005). These changes in cropping systems have resulted in the depletion of soil fertility and a general decrease in *Striga* control (Berner et al., 1996), coupled with a build-up of *Striga* seed in the soil seed bank, resulting in serious losses in crop yields (Parker and Riches, 1993).

Striga seedlings must attach to a host root within 3 to 5 d after germination or they die (Worsham, 1987). Hence, a sustainable Striga control option for the African resource-poor farmers is the use of trap crops, particularly legumes, that stimulate germination of the parasite's seeds but are nonhosts, in rotation with cereals (Berner et al., 1996) or in suitable intercropping arrangements (Khan et al., 2002; Oswald et al., 2002, Khan and Pickett, 2004). It has been shown in various studies that intercropping cereals with legumes can reduce the number of Striga plants that mature in an infested field (Saunders, 1933; Carson, 1989; Webb et al., 1993; Babiker and Hamdoun, 1994; Carsky et al., 1994; Khan et al., 2000, 2001, 2002; Tenebe and Kamara, 2002; Khan et al., 2006a, 2006b). However, apart from desmodium, a fodder legume whose species have been shown to uniformly control Striga (Khan et al., 2006a, 2006b), there is a wide variation in the ability of different other legumes and their cultivars in suppression of Striga (Emechebe and Ahonsi, 2003).

Apart from its use in *Striga* suppression, *Desmodium* spp. form part of a wider cropping system for the control of cereal stemborers involving a diversionary mechanism where stemborer moths are repelled from the main crop and subsequently attracted to a trap crop ("push–pull" strategy) planted as a perimeter crop (Khan et al., 2000, 2001; Khan and Pickett, 2004). The objective of the current studies was therefore to compare the effects of different legumes with greenleaf desmodium on the control of *Striga* in areas where farmers do not have livestock and would want to intercrop cereals with a food legume.

MATERIALS AND METHODS Study Site

Field trials were conducted during the long (March–August) and short (October–January) rainy seasons of 2003 and 2004 at the International Centre of Insect Physiology and Ecology (ICIPE), Thomas Odhiambo Campus, Mbita Point (0°25' S, 34°12' E), on the eastern shores of Lake Victoria in the Suba District of western Kenya, where *S. hermonthica* is a serious limitation to maize and sorghum cultivation (Watt, 1936; Oswald, 2005). The field station is infested with *S. hermonthica* (average 100 *S. hermonthica* seeds per 250 g soil). It receives approximately 900 mm of rainfall per annum, has a mean annual temperature of 27°C and is located at an altitude of approximately 1200 m above sea level.

Plot Layout and Data Collection

Maize was intercropped with one of the six different species of legumes: cowpea (Var. ICV2), crotalaria, greengram (Var. Local), groundnut (Arachis hypogaea L.) (Var. Homabay), greenleaf desmodium [Desmodium intortum (Mill.) Urb.] and beans (Phaseolus vulgaris L.) (Var. Local 'Nyayo') (all Fabaceae). Maize was planted at 75 cm between and 30 cm within rows, while greenleaf desmodium was planted through a drilling system in furrows between the rows of maize. A control plot of maize monocrop was included. The seven treatments were laid out in a completely randomized design in four replications. Treatment plots measured 5 by 6 m each and were separated by a 2-m buffer strip. Additionally, the six legumes were intercropped with sorghum in similar plots, in a separate field, and were laid out in a completely randomized design in four replications as above. A control plot of sorghum monocrop was similarly included. Sorghum was planted at a spacing of 60 by 30 cm. Two weeks after germination, sorghum and maize plants were thinned to one plant per hill. Greenleaf desmodium, being a perennial legume was planted only once, at the beginning of the study, and only cut back at the beginning of subsequent cropping seasons while the other legumes were planted together with both maize and sorghum at the beginning of every cropping season. The maize variety used was a Striga-susceptible, medium maturing, commercial hybrid 513, while the sorghum variety was similarly a Striga-susceptible, early-maturing hybrid Gadam Hamam. Both are recommended for midaltitude regions with moderate rainfall. Plots were kept weed free by hand-weeding, except for S. hermonthica throughout the growing season. During the 8th and 12th weeks after maize and sorghum emergence, 54 maize and sorghum plants were randomly sampled in each treatment plot and the number of emerged S. hermonthica plants counted from within a radius of 15 cm of each plant. At physiological maturity of both crops, height of each of 54 randomly selected maize and sorghum plants was measured in each plot. All the maize and sorghum plants in each experimental plot were then harvested and grain yields converted into megagrams per hectare.

Statistical Analysis

Seasonal and multiseasonal data were averaged for each treatment and subjected to a one-way (treatment) and two-way (treatment and season) analyses of variance (ANOVA) (SAS Institute, 2001) procedures respectively, using a generalized linear model. These were employed to test for any significant differences among treatments and seasons, with regards to S. hermonthica infestation, plant (maize and sorghum) height, and grain yields. Seasonal S. hermonthica data were analyzed for each sampling occasion (8 and 12 wk after crop emergence) while counts at the 12th week after crop emergence were used for the multiseasonal analyses. Because of the high variability observed for the actual Striga counts, both within and among treatments, $\log_{10}(n + 1)$ transformations of the original data were performed, which stabilized the variance for the analyses. Similarly, the data on plant height were subjected to square root transformation and conformed to the assumptions of ANOVA as indicated by tests of normality in the univariate procedure and modified Levene's test of homogeneity of variance (Brown and

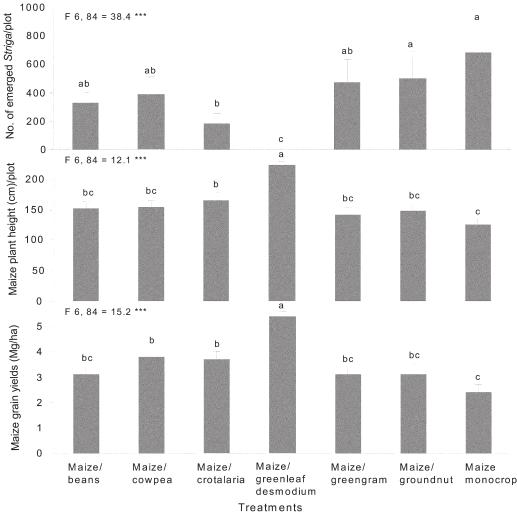


Figure 1. Average (±SE) multiseason *Striga* counts and maize plant height (centimeters) per plot, and grain yields (Mg ha⁻¹) in different maize–legume intercrops. Means represent data averages of four cropping seasons. Within a parameter, means (bars) marked with different letters are significantly different (*** differences significant at 0.001 probability level).

Forsythe, 1974; SAS Institute, 2001) before analysis. Thereafter, Tukey's studentized range test was used to separate the means at P < 0.05. Untransformed means are presented in tables and figures.

RESULTS AND DISCUSSION

Striga counts were generally lower in the intercrops than in the control plots of maize. However, it was only in the greenleaf desmodium intercrop where the seasonal differences in Striga counts were significant throughout the study period. Striga counts were also significantly lower in the crotalaria intercrop than in the control in the short rainy season of 2004 (Table 1). Similar observations were made in sorghum where seasonal Striga counts were generally lower in the intercrops than in the control plots, although it was only in the greenleaf desmodium (and crotalaria during the 12th week after emergence) intercrops that these counts were consistently and significantly lower than in the control plots (Table 2). Multiseason analyses showed significant differences between treatments, with no interactions between treatments and seasons in both crops. In maize, only greenleaf desmodium and crotalaria

intercrops had significantly lower *Striga* counts than the control (Fig. 1). However, in sorghum all intercrops except bean and groundnut had significantly lower *Striga* counts (Fig. 2), indicating that the effect of most of the legumes was more pronounced in sorghum than in maize.

These results corroborate the findings of Oswald et al. (2002) who assessed *Striga* control potential of different legumes (cowpea, soybean [*Glycine max* (L.) Merr.], yellow gram [*Cicer arietinum* L.], bambara [*Vigna subterranean* (L.) Verdc.], bean, groundnut, and greengram) in western Kenya in different planting arrangements with maize and concluded that although *Striga* numbers were reduced to an extent by the intercrops, if *Striga* was not uprooted before seed dispersal in a cropping season, the season to season reduction in *Striga* populations was not significantly observable. Similarly, Reda et al. (2005) found no significant control of *Striga* through intercropping sorghum with 10 legumes and oilseed crops in northern Ethiopia.

The mechanisms by which *Desmodium* spp. control *Striga* have been elucidated and involve, in addition to the benefits derived from increased availability of N and soil

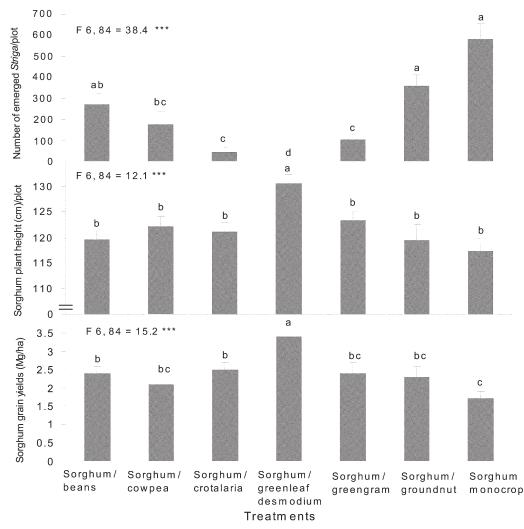


Figure 2. Average (±SE) multiseasonal *Striga* counts and sorghum plant height (centimeters) per plot, and grain yields (Mg ha⁻¹) in different sorghum–legume intercrops. Means represent data averages of four cropping seasons. Within a parameter, means (bars) marked with different letters are significantly different (*** differences significant at 0.001 probability level).

shading, an allelopathic effect of the root exudates of the legume, produced independently of the presence of Striga (Khan et al., 2002). The root exudates contain blends of secondary metabolites with Striga seed germination stimulatory and postgermination inhibitory activities (Tsanuo et al., 2003). This combination provides a novel means of in situ reduction of the Striga seed bank in the soil through efficient suicidal germination even in the presence of graminaceous host plants in the proximity (Khan et al., 2002). Additionally, because greenleaf desmodium is a perennial crop, it is able to exert its Striga control effect even when the host crop is out of season, an attribute that makes it a more superior trap crop than the other legumes. Some varieties of cowpea, soybean, and groundnut have also been shown to control Striga through a combination of mechanisms ranging from induction of suicidal germination of Striga seeds, N fixation, and smothering effect (Oswald et al., 2002; Emechebe and Ahonsi, 2003; Gbèhounou and Adango, 2003; Kuchinda et al., 2003; Olupot et al., 2003). The latter is more effective in cultivars that develop dense canopies (Oswald et al., 2002), which reduce light penetration, increase humidity, and reduce soil temperatures (Khan et al., 2002; Oswald et al., 2002). These negatively affect growth and development of the emerged *Striga* plants, resulting in reduced reproduction of the parasite. In the current study however, except for greenleaf desmodium, these mechanisms did not consistently reduce seasonal *Striga* populations.

These observations were associated with significantly taller maize and sorghum plants in the greenleaf desmodium intercrops than in the associated control plots (Tables 3 and 4), except during the long rainy season of 2003 and short rainy season of 2004, when sorghum plants did not differ in height between treatments (Table 4). Overall, it was only the greenleaf desmodium intercrops that significantly enhanced plant height in both maize and sorghum (by 95.6 and 11.8% respectively) (Fig. 1 and 2). Crotalaria intercrop also had significantly taller maize plants than those in the control plots (Fig. 1). Although the grain yields were generally higher in the intercrops than in the control plots during most of

Table 1. Mean (±SE) Striga counts per plot of maize planted in sole stands or intercropped with a legume during the long and short rainy seasons of 2003 and 2004.

Cropping season [†]	Treatments										
	WAE [‡]	Maize monocrop	Maize/ groundnut	Maize/ greengram	Maize/ desmodium§	Maize/ crotalaria	Maize/ cowpea	Maize/ beans	F P)	
LR 2003	8	876.7(301.7)a¶	781.0(299.1)a	814.0(280.9)a	4.2(3.6)b	387.7(193)a	693.2(247)a	235.7(121)a	11 ***		
	12	1660.7(415)a	1342.5(582)a	1149.5(510)a	9.5(6.7)b	525.0(204)a	943.7(324)a	455.0(242)a	8.4 ***		
SD 2002	8	473.7(95.6)a	369.7(109)a	242.2(87.0)a	0.0(0.0)b	94.0(33.9)a	154.5(91.9)a	178.5(90.3)a	25.9 **		
SR 2003	12	512.0(186)a	476.7(155)a	374.2(165)a	0.0(0.0)b	119.2(33.2)a	204.5(132)a	215.7(154)a	7.8 ***		
LR 2004	8	236.5(138)a	117.2(48.4)a	232.7(73.5)a	0.0(0.0)b	57.7(42.9)a	309.2(150)a	252.7(71.9)a	14.4 ***		
	12	310.0(194)a	109.2(34.4)a	249.0(102)a	0.2(0.2)b	70.7(46.3)a	236.7(174)a	412.2(118)a	13.9 ***		
00.0004	8	243.0(104)a	58.5(3.3)ab	138.7(68.2)ab	0.5(0.5)c	28.2(16.1)b	180.2(53.6)a	213.5(58.9)a	20.4 ***		
SR 2004	12	210.0(106.5)a	40.2(8.8)ab	93.0(38.7)ab	0.0(0.0)c	10.0(3.4)b	120.7(61.9)a	197.7(60.7)a	17.7 ***		

**Significant at 0.01 probability level.

***Significant at 0.001 probability level.

[†]LR, long rainy season; SR, short rainy season. [‡]WAE, weeks after crop emergence.

[§]Desmodium, greenleaf desmodium.

Within a sampling occasion (weeks after crop emergence) in a cropping season (rows) the means marked by different letters are significantly different.

Table 2. Mean (±SE) Striga counts per plot of sorghum planted in sole stands or intercropped with a legume during the long and short rainy seasons of 2003 and 2004.

Cropping season [†]	Treatments									
	WAE‡	Sorghum monocrop	Sorghum/ groundnut	Sorghum/ greengram	Sorghum/ desmodium [§]	Sorghum/ crotalaria	Sorghum/ cowpea	Sorghum/ beans	F P	
	8	194.2(59.9)a [¶]	133.2(46.5)a	23.0(6.7)a	0.0(0.0)b	42.0(27.8)a	91.0(71.7)a	58.7(31.6)a	12.7 ***	
LR 2003	12	873.5(172.5)a	518.7(114.2)ab	57.0(12.9)bc	1.2(1.2)d	102.2(76.1)c	196.7(149.9)abc	287.2(163)abc	14.3 **	
SR 2003	8	219.7(61.6)a	276.7(164.9)a	18.2(8.3)a	0.0(0.0)b	26.7(13.9)a	86.0(64.8)a	57.7(29.9)a	8.3 **	
Sh 2003	12	535.2(85.6)a	410.2(155.2)ab	38.5(15.3)bc	0.0(0.0)d	20.0(7.40)c	247.2(183.8)abc	182.0(87.7)abc	11.5 ***	
	8	251.0(78.0)a	278.2(33.1)a	55.0(13.1)ab	0.0(0.0)c	31.5(18.6)b	172.7(123.4)ab	269.2(66.4)a	13.9 ***	
LR 2004	12	504.0(74.2)a	272.2(18.9)ab	78.7(13.3)ab	0.7(0.7)c	53.0(23.6)b	101.2(76.9)b	416.7(75.2)a	15.3 **	
00.0004	8	216.2(100.1)a	169.2(37.4)a	103.7(26.4)a	2.0(1.1)b	24.2(5.9)a	139.5(91.8)a	169.5(40.0)a	9.6 **	
SR 2004	12	404.5(168.3)a	231.2(13.1)a	243.2(66.9)a	1.0(1.0)c	14.2(2.5)b	153.2(96.4)ab	196.7(42.5)a	17 ***	

**Significant at 0.01 probability level.

***Significant at 0.001 probability level.

[†]LR, long rainy season; SR, short rainy season.

[‡]WAE, Weeks after crop emergence.

SDesmodium, greenleaf desmodium.

[®]Within a sampling occasion (weeks after crop emergence) in a cropping season (rows) the means marked by different letters are significantly different.

the seasons, it was only greenleaf desmodium intercrops that consistently yielded significantly higher grains than the associated control plots in both crops (Tables 3 and 4). The differences in grain yields in both crops intercropped with greenleaf desmodium and the other legumes within seasons were, however, not consistently significant, although grain yields were consistently higher in the former. Except for crotalaria and cowpea intercrops in the long rainy seasons of 2003 and 2004, respectively, when maize grain yields were significantly higher in the intercrops than in the control, intercropping maize and sorghum with the legumes, except greenleaf desmodium, did not significantly enhance seasonal grain yields in both crops. Multiseason analysis however, showed that overall, cowpea, crotalaria, and greenleaf desmodium significantly enhanced maize grain yields by 58.3, 54.2, and 125% respectively (Fig. 1). On the other hand, only greenleaf desmodium intercrop significantly enhanced (by

100%) overall grain yields of sorghum (Fig. 2). These results corroborate those of Oswald et al. (2002) who observed that intercropping maize with cowpea, soybean, yellow gram, bambara, bean, groundnut, and greengram did not significantly enhance or reduce maize grain yields in western Kenya. Similarly, Khan et al. (2001, 2002, 2006a, 2006b) showed that intercropping maize with *Desmodium* spp. significantly enhanced both plant height and grain yields in maize and sorghum. The current studies therefore confirm that except for greenleaf desmodium, the other intercrops did not significantly enhance seasonal grain yields.

In conclusion, intercropping maize and sorghum with the legumes other than greenleaf desmodium did not consistently provide significant seasonal control of *Striga* and enhanced grain yields. The overall effect however showed that intercropping maize with cowpea, crotalaria, and greenleaf desmodium led to a reduction in *Striga* infesTable 3. Average (±SE) height of maize plants, planted in sole stands or intercropped with a legume, per plot at harvest and grain yields during the long and short rainy seasons of 2003 and 2004.

a .				Treatments						
Cropping season [†]	Maize monocrop	Maize/ groundnut	Maize/ greengram	Maize/ desmodium [‡]	Maize/ crotalaria	Maize/ cowpea	Maize/ beans	F P		
			Plan	t height, cm						
LR 2003	156.5(10.6)b§	193.4(30.5)ab	186.2(24.6)ab	261.5(4.9)a	205.2(19.7)ab	180.3(21.9)ab	202.9(26.9)ab	2.2 *		
SR 2003	83.8(13.9)b	110.0(16.1)b	99.1(9.9)b	208.5(3.3)a	129.0(13.9)b	126.4(19.9)b	118.8(19.8)b	7.3 ***		
LR 2004	123.2(10.8)b	138.7(5.8)ab	134.4(14.4)ab	200.3(22.6)a	163.4(31.1)ab	153.0(25.6)ab	135.2(19.3)ab	2.6 *		
SR 2004	137.7(18.2)b	150.9(13.8)ab	149.6(18.8)ab	207.9(9.6)a	166.9(15.1)ab	156.4(13.8)ab	148.9(14.9)ab	2.3 *		
Grain yields, Mg ha⁻¹										
LR 2003	1.9(0.2)c	2.5(0.4)bc	2.8(0.2)bc	4.6(0.2)a	4.2(0.4)ab	3.4(0.7)abc	3.0(0.1)abc	6.1 ***		
SR 2003	3.4(0.3)b	4.6(0.3)ab	4.1(0.6)ab	5.6(0.2)a	5.0(0.3)ab	4.7(0.3)ab	4.3(0.6)ab	2.9 *		
LR 2004	0.7(0.3)c	1.6(0.6)bc	2.5(0.9)bc	5.6(0.2)a	2.5(0.6)bc	3.5(0.8)b	2.4(0.4)bc	6.8 ***		
SR 2004	3.4(0.7)b	3.7(0.6)ab	3.0(0.8)b	5.9(0.2)a	3.2(0.4)b	3.7(0.7)ab	2.9(0.4)b	2.6 *		

*Significant at 0.05 probability level.

***Significant at 0.001 probability level.

[†]LR, long rainy season; SR, short rainy season.

[‡]Desmodium, greenleaf desmodium.

[®]Within a parameter in a cropping season (rows) the means marked by different letters are significantly different.

Table 4. Average (±SE) height of sorghum plants, planted in sole stands or intercropped with a legume, per plot at harvest and grain yields during the long and short rainy seasons of 2003 and 2004.

. .				Treatments								
Cropping season [†]	Sorghum monocrop	Sorghum/ groundnut	Sorghum/ greengram	Sorghum/ desmodium [‡]	Sorghum/ crotalaria	Sorghum/ cowpea	Sorghum/ beans	F	Ρ			
			P	Plant height, cm								
LR 2003	129.2(2.7)a§	126.7(0.8)a	130.8(1.8)a	135.8(0.7)a	128.1(2.7)a	127.9(2.9)a	126.4(6.3)a	1.2 N	1S¶			
SR 2003	108.3(1.3)d	113.9(1.3)cd	119.2(0.8)bc	133.0(1.4)a	117.1(1.9)c	123.8(2.0)b	117.0(0.7)c	29.8 *	**			
LR 2004	111.8(0.8)c	116.7(1.7)bc	124.0(3.9)ab	127.7(2.9)a	124.4(1.8)ab	120.5(2.5)abc	117.9(1.8)abc	5.2 *	*			
SR 2004	120.3(6.0)a	120.8(12.4)a	119.4(4.7)a	126.2(5.0)a	115.1(2.3)a	116.5(6.2)a	117.2(2.7)a	0.3 N	1S			
			Gra	in yields, Mg ha-1								
LR 2003	2.1(0.2)b	3.0(0.3)ab	3.2(0.4)ab	3.7(0.3)a	2.9(0.2)ab	2.5(0.4)ab	3.0(0.4)ab	2.3 *				
SR 2003	2.4(0.1)b	3.0(0.3)ab	2.9(0.4)ab	3.9(0.3)a	3.0(0.3)ab	2.6(0.3)b	2.9(0.2)ab	2.9 *				
LR 2004	0.5(0.2)b	1.1(0.4)b	0.9(0.4)b	2.7(0.3)a	1.6(0.1)ab	1.6(0.2)ab	1.3(0.2)b	5.2 *	*			
SR 2004	2.0(0.1)b	2.1(0.7)ab	2.6(0.3)ab	3.4(0.1)a	2.7(0.2)ab	1.8(0.3)b	2.6(0.1)ab	2.6 *				

*Significant at 0.05 probability level.

**Significant at 0.01 probability level.

***Significant at 0.001 probability level.

[†]LR, long rainy season; SR, short rainy season.

[‡]Desmodium, greenleaf desmodium.

[®]Within a parameter in a cropping season (rows) the means marked by different letters are significantly different.

¹NS, not significantly different.

tation (although insignificant in the cowpea intercrop) whose effect was realized in significant yield increases. However in sorghum, although all intercrops except beans and groundnut significantly controlled *Striga*, it was only in the bean, crotalaria, and greenleaf desmodium intercrops where yield increases were significant. Intercropping with these legumes therefore shows some promise as a suitable component of an integrated *Striga* management approach for the small holder farmers, but this would need to be combined with other cultural methods such as handweeding of emerged *Striga* to avoid replenishment of *Striga* seed bank in the soil. Similar studies are also desirable in

different environments to assess the performance of the legumes in an array of soil types under different *Striga* densities and moisture levels.

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References

- Ast, A. van, L. Bastiaans, and S. Katile. 2005. Cultural control measures to diminish sorghum yield losses and parasite success under *Striga hermonthica* infestation. Crop Prot. 24:1023–1034.
- Babiker, A.G.T., and M. Hamdoun. 1994. Striga in the Sudan: Research activities. p. 126–130. In S.T.O. Lagoke et al. (ed.) Improving Striga management in Africa. Proc. of the Second General Workshop of the Pan-African Striga Control Network (PASCON), Nairobi, Kenya. 23–29 June 1991. FAO, Accra, Ghana.
- Bebawi, F.F., R.E. Eplee, C.E. Harris, and R.S. Norris. 1984. Longevity of witchweed (*Striga asiatica*) seed. Weed Sci. 32:494–507.
- Bebawi, F.F., and E.M. Metwali. 1991. Witch-weed management by sorghum–Sudan grass seed size and stage of harvest. Agron. J. 83:781–785.
- Berner, D.K., R. Carsky, K. Dashiell, J. Kling, and V. Manyong. 1996. A land management based approach to integrated *Striga hermon-thica* control in sub-Saharan Africa. Outlook Agric. 25:157–164.
- Berner, D.K., J.G. Kling, and B.B. Singh. 1995. *Striga* research and control—A perspective from Africa. Plant Dis. 79:652–660.
- Brown, M.B., and A.B. Forsythe. 1974. Robust tests for equality of variances. J. Am. Stat. Assoc. 69:364–367.
- Carsky, R.J., L. Singh, and R. Ndikawa. 1994. Suppression of *Striga hermonthica* on sorghum using a cowpea intercrop. Exp. Agric. 30:349–358.
- Carson, A.G. 1989. Effect on intercropping sorghum and groundnut on density of *Striga hermonthica* in the Gambia. Trop. Pest Manage. 35:130–132.
- Emechebe, A.M., and M.O. Ahonsi. 2003. Ability of excised root and stem pieces of maize, cowpea and soybean to cause germination of *Striga hermonthica* seeds. Crop Prot. 22:347–353.
- Frost, D.L., A.L. Gurney, M.C. Press, and J.D. Scholes. 1997. Striga hermonthica reduces photosynthesis in sorghum: The importance of stomatal limitations and a potential role for ABA? Plant Cell Environ. 20:483–492.
- Gbèhounou, G., and E. Adango. 2003. Trap crops of Striga hermonthica: In vitro identification and effectiveness in situ. Crop Prot. 22:395–404.
- Gurney, A.L., M.C. Press, and J.D. Scholes. 1999. Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*. New Phytol. 143:573–580.
- Gurney, A.L., J. Slate, M.C. Press, and J.D. Scholes. 2006. A novel form of resistance in rice to the angiosperm parasite *Striga hermonthica*. New Phytol. 169:199–208.
- Hassan, R., J.K. Ranson, and J. Ojeim. 1995. The spatial distribution and farmers' strategies to control *Striga* in maize: Survey results from Kenya. *In* D. Jewell, et al. (ed.) Proc. of the Fourth Eastern and Southern Africa Regional Maize Conference, Harare, Zimbabwe. 28 Mar.–1 Apr. 1994. CIMMYT, Harare, Zimbabwe.
- Khan, Z.R., A. Hassanali, W. Overholt, T.M. Khamis, A.M. Hooper, J.A. Pickett, L.J. Wadhams, and C.M. Woodcock. 2002. Control of witchweed *Striga hermonthica* by intercropping with *Desmodium* spp., and the mechanism defined as allelopathic. J. Chem. Ecol. 28:1871–1885.
- Khan, Z.R., C.A.O. Midega, J.A. Pickett, L.J. Wadhams, A. Hassanali, and A. Wanjoya. 2006a. Management of witchweed, *Striga hermonthica*, and stemborers in sorghum, *Sorghum bicolor*, through intercropping with greenleaf desmodium, *Desmodium intortum*. Int. J. Pest Manage. 52:297–302.
- Khan, Z.R., and J.A. Pickett. 2004. The 'push-pull' strategy for stemborer management: A case study in exploiting biodiver-

sity and chemical ecology. *In* G.M. Gurr et al. (ed.) Ecological engineering for pest management: Advances in habitat manipulation for arthropods. CABI publishing, CABI, Wallingford, Oxon, UK.

- Khan, Z.R., J.A. Pickett, J. van den Berg, L.J. Wadhams, and C.M. Woodcock. 2000. Exploiting chemical ecology and species diversity: Stemborer and *Striga* control for maize and sorghum in Africa. Pest Manage. Sci. 56:957–962.
- Khan, Z.R., J.A. Pickett, L.J. Wadhams, A. Hassanali, and C.A.O. Midega. 2006b. Combined control of *Striga* and stemborers by maize–*Desmodium* spp. intercrops. Crop Prot. 25:989–995.

Khan, Z.R., J.A. Pickett, L.J. Wadhams, and F. Muyekho. 2001. Habitat management strategies for the control of cereal stemborers and *Striga* in maize in Kenya. Insect Sci. Applic. 21:375–380.

- Kuchinda, N.C., I. Kureh, B.D. Tarfa, C. Shinggu, and R. Omolehin. 2003. On farm evaluation of improved maize varieties intercropped with some legumes in the control of *Striga* in the northern Guinea savanna of Nigeria. Crop Prot. 22:533–538.
- Kureh, I., U.F. Chiezey, and B.D. Tarfa. 2000. On-station verification of the use of soybean trap crop for the control of *Striga* in maize. Afr. Crop Sci. J. 8:295–300.
- Olupot, J.R., D.S.O. Osiru, J. Oryokot, and B. Gebrekidan. 2003. The effectiveness of *Celosia argentia* (*Striga* 'chaser') to control *Striga* on sorghum in Uganda. Crop Prot. 22:463–468.
- Oswald, A. 2005. *Striga* control—Technologies and their dissemination. Crop Prot. 24:333-342.
- Oswald, A., and J.K. Ransom. 2001. *Striga* control and improved farm productivity using crop rotation. Crop Prot. 20:113–120.
- Oswald, A., J.K. Ransom, J. Kroschel, and J. Sauerborn. 2002. Intercropping controls *Striga* in maize based farming systems. Crop Prot. 21:367–374.
- Parker, C., and C.R. Riches. 1993. Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK.
- Reda, F., J.A.C. Verkleij, and W.H.O. Ernst. 2005. Intercropping for the improvement of sorghum yield, soil fertility and *Striga* control in the subsistence agriculture region of Tigray (northern Ethiopia). J. Agron. Crop Sci. 191:10–19.
- SAS Institute. 2001. SAS user's guide. Statistics, version 8.2 ed. SAS Institute, Cary, NC.
- Saunders, A.R. 1933. Studies in phanerogamic parasitism, with particular reference to *Striga lutea* Lour. Science Bulletin 128. South Africa Department of Agriculture, Pretoria, South Africa.
- Tenebe, V.A., and H.M. Kamara. 2002. Effect of *Striga hermonthica* on the growth characteristics of sorghum intercropped with groundnut varieties. J. Agron. Crop Sci. 188:376–381.
- Tsanuo, M.K., A. Hassanali, A.M. Hooper, Z.R. Khan, F. Kaberia, J.A. Pickett, and L.J. Wadhams. 2003. Isoflavanones from the allelopathic acqueous root exudates of *Desmodium uncinatum*. Phytochemistry 64:265–273.
- Watt, W.L. 1936. Control of *Striga* weed in Nyanza Province, Kenya. East Afr. Agric. J. 1:320–322.
- Webb, M., C. Conroy, D. Baguma, and R. Kabanyoro. 1993. Survey of the socio-economics of weed control on smallholder farms in three districts of Uganda. Report R2014(S). Natural Resources Institute, Chatham, UK.
- Worsham, A.D. 1987. Germination of witchweed seeds. p. 45–61. In L.J. Musselman (ed.) Parasitic weeds in agriculture. Vol. 1: Striga. CRC Press, Boca Raton, FL.
- Yoder, J.I. 1999. Parasitic plant responses to host plant signals: A model for subterranean plant-plant interactions. Curr. Opin. Plant Biol. 2:65–70.