The Biology and Control of Striga: a Review

***Fasil Reda*[1] *and J.A.C. Verkleij*[2]**
[1]*Melkassa Research Center,E thiopian Agricultural Research Organization,*
P.O. Box, 2003, Addis Ababa, Ethiopia
[2]*Free University, Faculty of Biology, Department of Ecology and Eco-toxicology of Plants,*
De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands

Abstract

Striga is one of the major biological constraints of subsistence agriculture in Sub-Saharan Africa. It is a major problem in 59 countries accounting for an average crop loss of 40%. There are about 40 species of Striga, but the most wide-spread and damaging of all is *Striga hermonthica*. The species is known to have originated in the bordering areas of Ethiopia and Sudan along with its main cereal host — sorghum. It is in this part of the continent that the species shows great diversity in behaviour, i.e., attacking non-traditional cereal host crops such as tef and barley and occurring in highland plateaus of up to 2450 m. The intent of the paper is to highlight relevant points on the origin, distribution and importance of the noxious pest, and review what is known so far of its biology and control with more emphasis to recent advances made in research.

Key words: Striga, biology, control

Distribution and Importance

In the plant kingdom parasitism evolved independently, occurring in at least 17 different plant families. But the families which include species of importance as weeds number not more than eight (Parker and Riches 1993). Two families that contain parasitic members are traditionally defined: Scrophulariaceae and Orobanchaceae. These families contain more than 45 genera and 1650 parasitic species and also exhibit the entire range of trophic conditions found in parasitic plants — hemiparasites to holoparasites (Nickrent and Duff 1996). There are 40 taxa in the genus Striga Lour., 82.5% of which occur in Africa. The number of species decreases gradually through Asia, from Arabia to Indo-Malaysia and Australia (Raynal-Roques 1991).

The probable center of origin and spread of the main weedy Striga species was first proposed by Rao and Musselman (1987). The authors suggested that with the introduction of agriculture and domestication of native grasses as cereal crops, the cereal- Striga species associated with these grasses became domesticated. Sorghum (*Sorghum bicolor* L. Moench) is the crop with which Striga is probably associated in its evolutionary history. At least Striga *hermonthica* (Del.) Benth. appeared to have originated in the same area where sorghum originated, the Sudano-Ethiopian region (Musselman 1980), and moved along the routes of introduction of its host to different parts of Africa and Arabia. This hypothesis is based on the fact that it is in sorghum, among the various hosts of witchweeds, that resistance mechanisms are best known and that the indicated region is where *S. hermonthica* is known to occur in more diverse forms and in the wild. Striga represents the greatest biological constraint for food production in Africa with greatest diversity in the savannas and grasslands north of the equator, and it is an economically important problem in 59 countries (Mboob 1989). Of the more than 30 known species, three cause the greatest damage to crops in sub-Saharan Africa, namely, *S. hermonthica*,.*S. asiatica* (L.) Kuntze and *S. gesnerioides* (Willd.) Vatke *S. hermonthica* mainly attacks sorghum, millet (*Eleusine caracana* L. Gaertn.), and maize (*Zea mays* L.) in tropical and sub-tropical regions spreading across from West Africa to Ethiopia. *S. hermonthica* is the most important pest in crops throughout its geographical range, but in native vegetation, it seems to be restricted to the Ethiopian region (Raynal-Roques 1996). *S. asiatica*, parasitizes sorghum, millet and maize in South Africa, and *S. gesnerioides* is a parasite of broad-leaved dicotyledonous plants including cowpea (*Vigna unguiculata* (L.) Walp) in West Africa and tobacco (*Nicotiana tabacum* L.) in East Africa.

Mboob (1989) estimated that Striga threatens the lives of over 100 million people in Africa. Two-thirds of the 73 million ha devoted to cereal crop production in Africa is seriously affected. Many authors have attempted to put an approximate figure to the economic consequences of the parasitic weed problem. Mboob (1989) presented a conservative estimate of 40% crop loss due to Striga in Africa, representing an annual loss of cereals worth US $7 billion. The overall loss in grain production, according to Sauerborn (1991), amounts to 4.1 million t. He further pointed out that another 44 million ha grain-producing area could be at risk. In East Africa, the parasite is a serious pest that threatens subsistence cereal production. Yield losses are estimated to range between 65 and 100% (Ejeta et al. 1991). Striga has recently been reported to extend to areas where it had not previously been present (Fasil and Parker 1994).

Biology

Striga species have normal green foliage but are parasitic on the roots of other plants. They are among the most specialized of all root-parasitic Scrophulariaceae. Striga combines life styles of both a holoparasite at the seedling stage and a hemiparasite as a green, chlorophyll-containing emergent plant. *S. hermonthica* is the largest of the species occurring commonly as weeds, usually at least 30–40 cm high and sometimes 100 cm and more (Parker and Riches 1993). Due to its obligate out-crossing nature, *S. hermonthica* is a highly variable species, even within localities. Morphological variability is demonstrated in a wide range of shape and color, and less obvious variation in leaf size and shape. Physiological variation is seen in differences of host range. There is evidence for distinct host preference in many areas. For instance, there are localities in West Africa where only pearl millet (*Pennisetum glaucum* L. R. Br.) is attacked and sorghum is quite immune. Elsewhere, sorghum is attacked and millet very little or not at all. In Ethiopia pearl millet is not attacked, but many non-traditional cereal host crops like tef (*Eragrostis tef* [Zucc.] Trotter), barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) are parasitized.

Striga has extremely small seeds (0.1 to 0.4 mm long), and a single plant can produce up to 200000 seeds (Parker and Riches 1993). Striga seeds can remain viable in the soil for many years (14 years and more) provided they are stored under dry conditions (Okonkwo 1991). Prerequisites for Striga seed germination comprise three main stages: after-ripening period, conditioning period under moist conditions, and exposure of seeds to a chemical stimulant that triggers germination. The seeds require conditioning under warm and moist conditions for a period of 10–21 days before they could germinate in response to stimulants exuded from host root (Okonkwo 1991). Studies aimed at elucidating the physiological basis for conditioning and factors affecting germination suggested that there could be various mechanisms involved. These include: leaching of chemical germination inhibitors from the seeds, synthesis of germination stimulant in the seed, and increased permeability within the seed (Okonkwo 1991).

Research efforts aimed at determining the number and type of the natural germination stimulants have spanned many years. Since the 1940s, many investigations have been carried out to extract, purify, and characterize the compounds in host and non-host root exudates that stimulate germination of Striga seeds. Cook et al. (1972) finally succeeded in characterizing a *S. asiatica* seed germination stimulant (strigol) from root exudates of cotton (*Gossypium hirsutum* L.), a non-host. Efforts to identify germination stimulants from host plant roots have gone unsuccessful for a long time. Then in the early 1980s, Netzly and Butler (1986) isolated the first host-produced germination stimulant for Striga termed sorgoleone. However, no correlation was found between sorgoleone production of sorghum varieties and their susceptibility to Striga. Later, a further natural stimulant substance (sorgolactone), closely related to strigol was identified from sorghum (Hauck et al. 1992). Eventually, the major Striga germination stimulant produced by maize and proso-millet (*Panicum miliaceum*) was found to be strigol (Siame et al. 1993). Sorgolactone is a close analog of strigol, and Striga hosts produce more than one of these strigolactones (Butler 1995).

There is a continuous exchange of signals between host and parasite throughout the developmental stages (Ejeta and Butler 1996). Further studies on host-parasite association revealed that phenolic substances produced by hosts signal the formation of the attachment organ of the parasite — the haustorium. The first such chemical to be recognized and characterized was xenognosin A (Riopel and Baird 1987), and later 2,6-demethoxy-p-benzoquinone (2,6-DMBQ) was isolated from sorghum root extracts (Chang and Lynn 1986). Recent studies show that the xenognostic chemicals that trigger haustorium development were commonly quinones, phenolic acids, or flavonoids derived from the phenylpropanoid pathway (Albrecht et al. 1999). Recent investigations suggest that host roots naturally release several factors that induce haustoria (Yoder et al. 2001).

The process of haustoria development is similar in *S. hermonthica* and *S. asiatica* (Ramaiah et al. 1991). Sticky hairs develop on the young haustorium, which help it to adhere to any surface. After attachment by these hairs, intrusive cells develop at the root tip which penetrates the cortex of the host root, apparently producing enzymatic secretions so that host cells are separated rather than intra-cellularly penetrated (Parker and Riches 1993). Once the haustorium is inside the host stele there is rapid development of direct links between parasite and host xylem systems. The haustorium is a key organ in parasitic plants, forming the bridge between the parasite and the host, both physically and physiologically. Through the haustorium, nutrients and water are transferred from the conductive system of the host into that of the parasite, and all hormonal interactions between the two organisms are facilitated. Furthermore, complex biochemical transformations seem to occur inside the haustorium. For instance, while the source of sugars in the host root is normally a combination of glucose, fructose and sucrose, the sugar in the xylem exudates of *S. hermonthica* was found to be largely mannitol (which is barely present in the host), suggesting transformations that must take place in the haustorium (Press et al. 1989).

The parasite is known to depend on the host for many of its growth requirements. A series of studies have shown that chlorophyll content is lower in the parasite and its efficiency is only 20–30% that of non-parasitic plants (Stewart and Press 1990). It has further been shown that Striga has a high rate of photorespiration, and there is little or no net gain from its photosynthesis. Subsequently, other studies showed that about 35% of the organic carbon, in the parasite, is derived from the host (Graves et al. 1990). Stewart et al. (1984) suggested that nitrogen acquired by the parasite from the host was likely to be in the form of amino acids and amides. However, recent research showed that Striga acquires the bulk of the nitrogen in non-transformed form as nitrate (Pageau et al. 2001). Although Striga absorbs nitrogen compounds from the host, it synthesizes amino acids by itself (Press et al. 1986). The ability of the parasite to draw the necessary amounts of carbon and nitrogen from the host almost certainly depends on the maximum flux of sap across the xylem bridge. This may be achieved to some degree by differential osmotic pressure, which is generally much higher in the parasite than in the host. Striga damages the host by depriving it of its nutrients and by influencing the growth and carbohydrate partitioning. Furthermore, the parasite affects host photosynthesis, and causes impaired growth through ways which are not yet fully understood (Rousset et al. 2001). The effect of Striga on photosynthesis and phenological development could vary depending on the degree of susceptibility of the host (Van Ast et al. 2001).

Control

The various measures available to date for the control of parasitic weeds, particularly Striga, have been comprehensively reviewed in the past. Some of the highly valuable references in this area include: proceedings of past international parasitic weeds symposia (seven such symposia have been held so far, the latest in June 2001, in Nantes, France) and books (Musselman 1987, Parker and Riches 1993, Press and Graves 1995). Here below, an account is given of the more recent advances in Striga management. Some of the conventional control methods are also briefly reviewed to highlight strategies relevant to subsistence agriculture systems.

Hand weeding

This is the most practical of all available control measures to resource-poor farmers in developing countries. It can eventually lead to significant reduction in Striga infestation, but the function and limitations have to be recognized from the outset. The potential benefits of such an operation may not be realized until after 4–5 years, and timing is critical to ensure effectiveness. Early weeding was reported to have resulted in improved crop yield, but the return from such an exercise in practical terms is usually low and leads to re-sprouting of the parasite and, ultimately, to increased frustration of farmers. The optimum time for hand pulling Striga is 2–3 weeks after flowering and repeating the operation at 3–4 weeks interval until and beyond harvest (Parker and Riches 1993). In western Kenya pulling out Striga plants by hand before seed-set was as effective as trap cropping in restoring the productivity of land infested with Striga (Odhiambo and Ransom 1994). Uprooted Striga plants have to be carried out of the field and dried and burned to minimize the risk of re-infestation. It is vital that any economic assessment of hand pulling be made on a long-term basis, which not only takes account of the benefits of reduced infestation on future cereal crops but also the detrimental effects of increased infestation in untreated crops (Parker and Riches 1993). It is worth noting that individual efforts of farmers may not prove effective in the end, as long as infestation persists in neighboring fields as a source of seed that could be potentially blown in by wind. Approaching the problem on community basis is pertinent for a more complete impact on Striga. Such farmers' campaigns organized every year, several times in a season, are showing signs of declining infestation in northern Ethiopia.

Cropping systems

1. Rotation

Rotation of infested land into non-susceptible crops or fallow is theoretically one of the simplest solutions, but also one that is very rarely at all simple or acceptable (Parker and Riches 1993). Rotation using non-host crops interrupts production of Striga seed and allows the seed population in the soil to decline. Crops vary in their effectiveness in a rotation system. Some so-called trap-crops are known to produce Striga - germinating stimulants, but are not susceptible to attack. Cowpea was particularly effective in this regard among a range of crops in recently conducted laboratory assays (Fasil Reda, Melkassa Research Center, 2002, unpubl. data). Some varieties were more effective than others. Effectiveness is also known to vary across Striga populations, necessitating site-specific recommendations. A five-year rotation experiment in northern Ethiopia, which involved sorghum/cowpea and sorghum/haricot bean (*Phaseolus vulgaris* L.) alternate cropping resulted in significantly higher cereal yields but failed to lead to concomitant reduction in Striga infestation (Fasil and Wondimu 2001). Results on *S. asiatica* have sometimes been more encouraging. Eplee and Norris (1990) compared the performance of many potential trap-crops and reported cotton to be capable of providing up to 90% reduction of *S. asiatica* in a single season in USA. The fact that four or more years of rotation are likely to be needed emphasizes the practical limitations of the technique. Few farmers will be willing to give up growing cereal for a long time but this method may find application in badly infested areas where growing of cereal grains is no longer possible.

2. Intercropping

Intercropping is a potentially viable, low-cost technology, which would enable to address the two important and interrelated problems of low soil fertility and Striga. Since the 1980s, many encouraging results were reported on the control of Striga through intercropping sorghum; for instance, sorghum with cowpea (Carsky et al. 1994), and cowpea and haricot bean (Fasil et al. 1997). Identifying the optimal spatial and temporal arrangements, and selecting effective, compatible and adapted legume crops, depending on the natural endowments of localities and existing populations of Striga, could be an important prerequisite. Carsky et al. (1994) showed that there was a reduction in Striga from intercropping sorghum with cowpea in the same row. However, studies in Kenya indicated that intercropping with cowpeas between the rows of maize instead of within the maize rows

Table 1. Labour requirement for hand pulling of Striga

Time of pulling	No shoots pulled (no/ha)	Labor (man hr/ha)	No shoots pulled (no/ha)	Labor (man hr/ha)
	Lower Bir		Beles	
Early, vegetative stage	585000	310	646000	491
Late, after flowering	187000	86	198000	221

Source: Fasil 2002

Table 2. Effect of intercropping on Striga and sorghum yield

Treatment	Striga count shoots/plot	Grain yield (kg/ha)	Biomass yield (kg/ha)
Intercropping (I)			
Sole sorghum (+)[1]	97	321	5066
Sole sorghum (-)[2]	95	444	5067
Sorghum/soybean	636	360	4867
Sorghum/cowpea	41	443	5517
Sorghum/h. bean	77	466	5783
LSD (0.05) (I)	29	NS	845
Planting arrangement (A)			
BC[3]/30 DAS[4]	72	402	5600
BC/0 DAS	79	474	5889
AR5/30 DAS	45	383	4800
EOR[6]/0 DAS	44	435	5267
LSD (0.05) (A)	34	NS	975
LSD (0.05) (I X A)	59	NS	NS
CV (%)	45	24	14

[1] With fertilizer
[3] Broadcast sowing
[5] Alternate row planting
[2] Without fertilizer
[4] Days after sowing
[6] Legume planted every two rows of sorghum

Source: Fasil (2002)

significantly reduced Striga (Odhiambo and Ransom 1994). In Ethiopia, one row of legume every two rows of sorghum was an optimum arrangement both in terms of reduction in parasitic weed incidence and increase in cereal yield (Table 2). In another environment alternate row planting of sorghum and legumes, with staggered planting of the crops (sowing of legume intercrops 3–4 weeks after the cereal), was found more productive and led to an overall reduction in infestation over two seasons (Fasil 2002). The findings showed the need for developing site-specific recommendations on intercropping.

3. Relay cropping and improved fallows

Relay cropping — sequential planting of legumes and cereals in the same field — and improved fallow systems, which involve use of perennial legume shrubs are receiving a growing research attention as a promising method for resource poor farming communities. The system increased cereal yield and was found to be effective against Striga (Rao and Mathuva 2000). Improved fallowing implies putting land out of cereal production, which may not be favorably accepted by small farmers. On the other hand, relay cropping could be an attractive option especially in areas affected by natural resource degradation.

Experience in Ethiopia with *Sesbania sesban* Merill and *Cajanus cajan* showed that the outcome from such an intervention could depend on the environment, i.e., rainfall and inherent soil fertility. Transplanting of the legume shrubs into sorghum fields one month later led to consistent increase in cereal yield and decline in parasitic weed incidence at a site endowed with better weather and edaphic conditions (Table 3). In a dry highland location, under moisture stress and non-fertilized conditions, the system in some cases resulted in significantly lower sorghum yield (Table 4).

Nitrogen fertilizers

Generally, the Striga problem is most severe in areas with low inherent soil fertility. The critical element among nutrients is widely believed to be nitrogen. In vitro studies showed that high nitrogen concentration leads to reduced germination stimulant production in cereals (Cechin and Press 1993), and ammonium-nitrogen and urea may exert direct toxic effects on the parasite (Pieterse 1991). However, results from field experimentation are less clear. Abayo and Rioba (1991) reported that up to 140 N kg/ha^{-1} had no significant effect on maize yield, but it reduced Striga population in partitioning in favor of the ear and increased maize grain yield by 64%. On the other hand, several other studies conducted in Africa indicated that application of mineral fertilizers or farmyard manure did not reduce Striga infestation (Babiker & Fasil 1991, Smaling et al. 1991). Therefore, results of field trials with fertilizers from many countries have never been consistent (Parker & Riches 1993). The effect of nitrogen fertilizer is not always apparent. But experience from Ethiopia, in recent years, showed that the outcome from the use of such an input depends on weather patterns and inherent fertility (Fasil 2002). The effect of nitrogen was consistent and positive in the northwestern lowlands of Ethiopia where were adequate rainfall and less impoverished soils. Mixed results were obtained in the degraded dry highlands in the northeast. There was relatively better crop response to nitrogen in good seasons, which led to significantly improved yields despite the apparent increase in Striga infestation. However, the best yields were obtained from half of the recommended rate of fertilizer

Table 3. Relay cropping and fertilizer effect on sorghum yield and Striga *hermonthica* infestation at Sheraro, northern Ethiopia 1998–2000.

Treatment	1998			1999			2000		
	Grain yield (kg/ha)	Biomass yield (t/ha)	Striga count (n/plot)	Grain yield (kg/ha)	Biomass yield (t/ha)	Striga count (n/plot)	Grain yield (kg/ha)	Biomass yield (t/ha)	Striga count (n/plot)
Shrubs									
Control (no tree)	343	1.94	4530	547	7.70	162	1330	8.11	556
Sesbania	394	1.88	4190	584	7.82	92	1920	7.89	261
Cajanus	330	1.87	4380	558	8.00	110	1760	7.36	330
P>0.05	NS	NS	NS	NS	NS	NS	NS	NS	*
Fertilizer									
Control (no fertilizer)	106	1.40	3940	166	5.16	110	907	5.44	503
20.5 N/23 P_2O_5 kg.ha^{-1}	287	1.90	4730	618	7.63	87	1760	8.32	360
41 N/46 P_2O_5 kg.ha^{-1}	674	2.39	4430	904	10.75	52	2450	9.60	284
P>0.05	**	**	NS	**	**	NS	**	**	NS

Source: Fasil 2002

* = $p > 0.05$

** = $p > 0.01$

NS, not significant

Table 4. Relay cropping and fertilizer effect on sorghum yield and Striga *hermonthica* infestation at Adibakel, Northern Ethiopia, 1998 – 2000.

Source: Fasil 2002

Treatment	1998			1999			2000		
	Grain yield (kg/ha)	Biomas-s yield (t/ha)	Striga count (n/plot)	Grain yield (kg/ha)	Bioma-ss yield (t/ha)	Striga count (n/plot)	Grain yield (kg/ha)	Biomas s yield (t/ha)	Striga count (n/plot)
Shrubs									
Control (no-shrub)	148	2.47	278	639	5.28	206	693	6.1	148
Sesbania	86	2.12	316	396	4.29	379	453	4.6	158
Cajanus	131	2.30	417	444	4.16	319	533	5.6	152
P>0.05	NS	NS	NS	*	NS	NS	NS	NS	NS
Fertilizer									
Control (no-fertiliser)	91	2.04	284	352	3.33	134	464	4.1	123
20.5 N/23 P_2O_5 $kg.ha^{-1}$	145	2.28	385	535	4.57	332	640	5.8	186
41 N/46 P_2O_5 $kg.ha^{-1}$	131	2.57	343	593	5.83	439	587	6.5	151
P>0.05	NS	NS	NS	*	**	*	NS	**	NS

* = p > 0.05; ** = p > 0.01; NS, not significant

for the area, suggesting possible detrimental effects of high doses of mineral fertilizers in drought years. Therefore, the fertility maintenance strategy in the dry highlands should aim at a gradual improvement of soil conditions to enhance crop performance possibly under continued heavy presence of the parasite. The use of mineral fertilizer may not show visible effect on Striga, at least in the short-run until the fertility level reaches a threshold that could create a non-conducive soil environment to the pest.

Host plant resistance

The use of resistant crop cultivars is viewed as the most reliable and economically feasible means of Striga control. Unfortunately, despite many years of work, there are few available varieties with durable and broad-based resistance. Nevertheless, there are relatively more promising leads in sorghum compared to other crops, although the tremendous variability of the pest, particularly *S. hermonthica*, casts doubt on the stability of any identified resistance source. SRN-39, a resistant sorghum variety, was released in the early 1990s in the Sudan for commercial production. SRN-39 was used in a crossing program to produce varieties with good agronomic background and adaptation to various Striga -prone environments in the tropics (Ejeta and Butler 1996). Some promising crosses from this program have undergone wide-scale testing in many African countries. SRN-39 and its progenies (P-9401 and P-9403) were locally released in northern Ethiopia with satisfactory results in dry seasons. Those varieties, unfortunately, seem to fail to out-yield local varieties in good years and under less Striga pressure. Work on the development of resistance varieties against *S. asiatica* has been going on with some more visible success since the early twentieth century. Subsequently, many useful materials have come out over the years from this effort, which involved a wide range of scientists and institutions. The most notable varieties that were developed were: Framida, N-13 and the SAR series sorghums. Most of those varieties have also shown some level of resistance to *S. hermonthica*. SAR-24, ICSV- 1006 and ICSV-1007 were the three superior sorghum varieties identified from field trials in Ethiopia (Babiker and Fasil 1991, Fasil et al. 1997). Recent efforts using wild relatives of sorghum as basis for creating genotypes with elevated level of resistance yielded encouraging results (Gurney et al. 2001). New state-of-the-art molecular techniques may enable to better understand the genetic and physiological basis of resistance and provide a rapid means for the identification of varieties with durable resistance. Creating superior varieties through the introduction of resistant genes and pyramiding of various genes, conditioning for the different forms of resistance, in elite crop varieties, seems to be a realistic objective for the near future. Introgression of genes controlling various control mechanisms into improved sorghum germplasm is underway in USA (Ejeta et al. 2001). Significant advances are being made towards developing marker-assisted selection procedures for resistance to *S. hermonthica* (Ejeta et al. 2001, Haussmann et al. 2001).

Biological control

The gall-forming weevil (*Smicronyx* spp.) was found promising with some level of host specificity a long time ago. But it was never used on a large scale against the parasitic weed. The only practical attempt that was made on biological control was in Ethiopia, where *Smicronyx albovariegatus* and *Eulocastra argentisparsa* were introduced from India in 1974 and 1978. No systematic assessment and follow-up was made at the time because of the prevailing political unrest in the area of release but none of them has apparently established. Indigenous insect species cause various levels of damage to Striga in many parts of the country (Fasil Reda, personal observation) and could potentially be multiplied and used locally. Biological control of Striga with pathogens is far more advanced due to the huge amount of research devoted to it in recent times. Many findings showed that *Fusarium* spp. were able to reduce Striga emergence (Abbasher et al. 1996). Granule formulation of *F. oxysporium* at a rate of 0.5 g. $kg^{-1}$of soil reduced the emergence of Striga by 78% in pots (Elzein et al. 2001).

A number of soil-borne bacterial isolates such as *Pseudomonas* spp. (Ahonsi et al. 2001) and *Azospirillum brasilense* (Bally et al. 2001) were found effective in inhibiting *S. hermonthica* seed germination in vitro. But their impact is known to vary across crop cultivars, potentially limiting the practical value of this technique.

The other newly emerging aspect of biological control is on the role of arbuscular mycorrhizal fungi, which form symbiotic relationship with crop roots and Striga. Most recently, Lendzemo and Kuiper (2001) reported that mycorrhizal fungi significantly reduced *S. hermonthica* infestation on a tolerant, but not on a susceptible sorghum variety. There is paucity of information in this area of research. Therefore, it is too early to judge the potential contribution of this type of fungi for Striga management. Despite many promising results, particularly on the use of pathogenic fungi, there is still a long way to go to refine methods of fermentation, formulation and application to come up with a cost-effective biological control product (Sauerborn 2001). The main reason for the unlikely prospect of this control method receiving worldwide acceptance is the reluctance of many governments and authorities to allow the introduction and use of exotic organisms. Hence, the use of biological control agents will be limited, and will continue to have local application in the foreseeable future.

Integrated control

In this section it would be worthwhile to pinpoint not only the integration of the various control techniques but also the integration of disciplines and other issues facing research on parasitic weeds, particularly Striga at present. No single method has so far provided solution to the Striga problem. The tremendous variability within the main species, *S. hermonthica,* i.e., the existence of strains, which behave in different ways, makes the problem highly complex. Furthermore, Striga affects the subsistence, resource-poor farming community, beset by other multiple production constraints such as recurrent drought, loss of soil fertility and an overall natural resources degradation. The lack of appreciation of the complexity of the issue and the lop-sided efforts of addressing the pest as a single and simple biological constraint prevented the scientific community from making headway in the fight against Striga. No matter what kind of "innovative" and "novel" strategies are developed, Striga was one step ahead and the scientific community was mercilessly beaten time and again, in the past. It is long overdue, therefore, that all stakeholders start realizing that Striga is a socio-economic problem, a natural resource problem and a biological problem all in one. Therefore, all the three aspects should be considered and a broader new outlook developed to increase the chances of arriving at a comprehensive and lasting solution to the scourge.

Integration is highly pertinent in the area of research. Integrated methods, which are developed taking stock of the opportunities and limitations of subsistence farming, and address all or part of the diverse but highly interrelated constraints should be sought. Molecular genetics is a welcome addition to the more conventional approaches, which dominated parasitic weed research in the previous decades, and may help to unravel the complex nature of Striga and elucidate the intricate host–parasite interactions. Scientists working in this area should, however, resist various temptations and focus on the type of research that could be translated into practical application to help people hard-hit by the problem.

Intensive effort should continue to sensitize and encourage communities and government authorities natural resources rehabilitation and conservation aimed at restoring the fertility of soils. Such an effort will ultimately lead to increased farm output and improved farmers' living standards, which would in turn create the impetus and motivation on the part of farmers, who are the key players in the whole scenario, for an all-rounded approach to the problem. As far as integrated Striga management is concerned there is no single and ideal prescription that could be readily handed out to work in all kinds of environments. Farmers should always be encouraged to use a combination of methods with proven effectiveness under their circumstances.

References

Abayo GO and AO Rioba. 1991. Response of maize to different nitrogen rates. Kakamega Research Center Annual Report. Pp. 51-59. Kenya Agricultural Research Institute, Nairobi.

Abbasher AA, DE Hess, J Sauerborn and J Kroschel. 1996. Effect of different *Fusarium* spp. on seed germination of *Striga hermonthica* (sorghum and millet strains), *Striga asiatica* and *Striga gesnerioides*. **In**: Moreno MT, JI Cubero, D Berner, D Joel, LJ Musselman and C Parker (Eds). Pp. 879-887. Proceedings (Advances in Parasitic Plant Research) of the 6th Parasitic Weed Symposium. Junta de Andalucia, Cordoba, Spain.

Ahonsi MO, AM Emechebe, DK Berner and STO Lagoke. 2001. Selection of seed germination inhibiting rhizobacteria for *Striga hermonthica* biocontrol. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (Eds). Pp. 266-269. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Albrecht H, JI Yoder and DA Phillips. 1999. Flavonoids promote haustoria formation in the root parasite *Triphysaria. Plant Physiology* 119: 585-591.

Babiker AGT and Fasil Reda. 1991. Recent advances in Striga research in Sudan and Ethiopia. In: Ransom JK, LJ Musselman, AD Worsham and C Parker. (eds). Pp. 180-189. Proceedings of the 5th International Symposium on Parasitic Weeds. CIMMYT, Nairobi, Kenya.

Bally R, L Miche, ML Bouillant, R Rohr, G Diamantidis and G Salle. 2001. Inhibition of Striga seed germination by soil bacteria of the genus *Azospirillum. In:* Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 295. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Butler LG. 1995. Chemical communication between the parasitic weed Striga and its host crop. American Crop Science Symposium Series 582: 158-168.

Carsky RJ, L. Singh and R Ndikawa. 1994. Suppression of *Striga hermonthica* on sorghum using a cowpea intercrop. *Experimental Agriculture* 30:349-358.

Cechin I, and MC Press. 1993. Nitrogen relations of the sorghum-*Striga hermonthica* host-parasite association: Germination, attachment and early growth. *New Phytologist* 124: 681-687.

Chang M and DG Lynn. 1986. Haustoria and the chemistry of host recognition in parasitic plants. *Journal of Chemical Ecology* 12: 561-579.

Cook CE, LP Whichard, B Turner, ME Wall, GH Egley, P Coggon, PA Luhan and AT Mcphail. 1972. Germination stimulants II. The structure of strigol – a potent seed germination stimulant for witchweed (*Striga lutea* Lour.). *Journal of the American Chemical Society* 94: 6198-6199.

Ejeta G, AGT Babiker, K Belete, P Bramel, C Grenier, A Ellicott, T Housley, I Kapran, A Mohamed, P Rich, C Shaner and A Toure. 2001. Breeding for durable resistance in sorghum. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 166-169. Nantes, France. Proceedings of the 7th International Parasitic Weed Symposium.

Ejeta G and LG Butler. 1996. Biotechnological approaches for understanding mechanisms of resistance to Striga. In: Moreno MT, JI Cubero, D Berner, D Joel, LJ Musselman and C Parker. (eds). Pp. 567-572. Proceedings (Advances in Parasitic Plant Research) of the 6th Parasitic Weed Symposium. Junta de Andalucia, Cordoba, Spain.

Ejeta G, LG Butler, DE Hess and RK Vogler. 1991. Genetic and breeding strategies for Striga resistance in sorghum. In: Ransom JK, LJ Musselman, AD Worsham and C Parker (eds). Pp. 539-544. Proceedings of the 5th International Symposium on Parasitic Weeds. CIMMYT, Nairobi, Kenya.

Elzein A, J Kroschel and J Sauerborn. 2001. Host specificity assessments of *Fusarium oxysporium* (Foxy2), a potential antagonist of *Striga hermonthica*: implications for its use as an acceptable mycoherbicide. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 301. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Eplee RE and RS Norris. 1990. Soil sampling equipment and equipment to separate seeds from the soil. In: Sand PF, RE Eplee and RG Westbrooks (eds). Pp. 136-140.Witchweed Research and Control in the United States. Weed Science Society of America. Champaign, Illinois.

Fasil Reda. 2002. *Striga hermonthica* in Tigray (Northern Ethiopia): Prospects for control and improvement of crop productivity through mixed cropping. PhD Thesis. Free University. Amsterdam, The Netherlands.

Fasil Reda, Gebremedhin Woldewahid, Beyenesh Zemichael and Wondimu Bayou. 1997. An integrated approach to the control of Striga in sorghum. Pest Management Journal of Ethiopia **1**: 43-49.

Fasil Reda and C Parker. 1994. Distribution and importance of Striga and related parasitic weeds in Ethiopia. In: Lagoke STO, R Hoevers, SS Mboob and R Traboulsi (eds). Pp. 157-163. Proceedings (Improving Striga Management in Africa) of the 2nd General Workshop of the Pan-African Striga Control Network. Nairobi, Kenya.

Fasil Reda and Wondimu Bayou. 2001. *Striga hermonthica* control through long-term crop rotation in sorghum-based cropping system in Northern Ethiopia. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 304. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Graves JD, A Wylde, MC Press and GR Stewart. 1990. Growth and carbon allocation in *Pennisetum typhoides* infected with the parasitic angiosperm *Striga hermonthica*. *Plant, Cell and Environment* 13: 367-373.

Gurney AL, D Grimanelli, FK Kanampiu, DA Hoisington, JD Scholes and MC Press. 2001. Can wild relatives of cereal provide new sources of resistance to the parasitic angiosperm Striga? In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 247. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Hauck C, S Muller and H Schildknecht. 1992. A germination stimulant for parasitic flowering plants from *Sorghum bicolor*, a genuine host plant. *Journal of Plant Physiology* 139: 474-478.

Haussman BIG, DE Hess, GO Omanya, BVS Reddy, N Seetharama, SZ Mukuru, M Kayentao, FG Welz and HH Geiger. 2001. Towards marker-assisted selection for Striga resistance in sorghum. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 212-215. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Lendzemo VW and TW Kuiper. 2001. Effects of arbuscular mycorrhizal fungi on damage by Striga *hermonthica* on two contrasting cultivars of sorghum. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 299. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Mboob SS. 1989. A regional program for Striga control in West and Central Africa. In: Robson TO and HR Broab (eds). Pp. 190-194. Proceedings (*Striga* – Improved Management for Africa) of the FAO/OAU all-African Government Consultation on Striga Control. FAO. Maroua, Cameroon.

Mumera LM and FE BELOW. 1993. Role of nitrogen in resistance to Striga parasitism of maize. *Crop Science* 33: 758-763.

Musselman LJ. 1980. The biology of Striga, Orobanche, and other root parasitic weeds. *Annual Review of Phytopathology* 18: 463-489.

Musselman LJ. 1987. Parasitic Weeds in Agriculture. Volume I. – Striga. CRC Press, Boca Raton, Florida.

Netzly DH and LG Butler. 1986. Roots of sorghum exude hydrophobic droplets containing biologically active components. *Crop Science* 26: 775-778.

Nickrent DL and RJ Duff. 1996. Molecular studies of parasitic plants using ribosomal RNA. In: Moreno MT, JI Cubero, D Berner, D Joel, LJ Musselman and C Parker (eds). Pp. 27-52. Proceedings (Advances in Parasitic Plant Research) of the 6th Parasitic Weed Symposium. Junta de Andalucia, Cordoba, Spain.

Odhiambo GD and JK Ransom. 1994. Preliminary evaluation of long-term effects of trap-cropping and maize management on Striga. In: Pieterse AH, JAC Verkleij and SJ ter Borg (eds). Pp. 505-512. Proceedings (Biology and Management of Orobanche) of the third International Workshop on Orobanche and Striga Research. Royal Tropical Institute. Amsterdam, The Netherlands.

Okonkwo SNC. 1991. The germination of Striga – a review. *In:* Ransom JK, Musselman LJ, Worsham AD and Parker C (eds). Pp. 144-154. Proceedings of the 5th International Symposium on Parasitic Weeds. CIMMYT, Nairobi, Kenya.

Pageau K, Simier P, Robins R and Fer A. 2001. Nitrogen uptake and metabolism in *Striga hermonthica* growing on sorghum. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 157. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Parker C and CR Riches. 1993. *Parasitic Weeds of the World: Biology and Control.* CAB International. Wallingford.

Pieterse AH. 1991. The effect of nitrogen fertilizers on the germination of seeds of *Striga hermonthica* and *Orobanche crenata*. *In:* Wegmann K and Musselman LJ (eds). Proceedings (Progress in Orobanche Research) International Workshop on Orobanche Research. Obermarchatal, Eberhard-Karls-Universität, Tübingen, Germany.

Press MC and Graves JD. 1995. *Parasitic Plants*. Chapman and Hall. London.

Press MC, JJ Nour, FF Bebawi and GR Stewart. 1989. Antitranspirant-induced heat stress in the parasitic plant *Striga hermonthica* – a novel method of control. *Journal of Experimental Botany* 40: 585-591.

Press MC, N Shan and GR Stewart. 1986. The parasitic habit: Trends in metabolic reductionism. In: ter Borg SJ (ed). Pp. 96-106. Proceedings of the Workshop on Biology and Control of Orobanche. Wageningen, The Netherlands.

Ramaiah KV, VL Childley and LR House. 1991. A time-course study of early establishment stages of the parasitic angiosperm *Striga asiatica* on susceptible sorghum roots. *Annals of Applied Botany* 118: 403-410.

Rao MJV and LJ Musselman. 1987. Host specificity in *Striga* spp. and physiological "strains". In: Musselman LJ (ed). Pp 12-26. Parasitic Weeds in Agriculture. CRC Press, Boca Raton, Florida.

Rao MR and MN Mathuva. 2000. Legumes for improving maize yields and income in semi-arid Kenya. *Agriculture Ecosystems and Environment* 78: 123-137.

Rayanal-Roques A. 1991. Diversification in the genus Striga. *In:* Ransom JK, Musselman LJ, Worsham AD and Parker C (eds). Pp. 251-261. Proceedings of the 5th International Symposium on Parasitic Weeds. CIMMYT, Nairobi, Kenya.

Raynal-Roques A. 1996. A hypothetic history of Striga. In: Moreno MT, JI Cubero, D Berner, D Joel, LJ Musselman and C Parker (eds). Pp. 105-111. Proceedings (Advances in Parasitic Plant Research) of the 6th Parasitic Weed Symposium. Junta de Andalucia, Cordoba, Spain.

Riopel JL and Baird WV. 1987. Morphogenesis of the early development of primary haustoria in *Striga asiatica*. In: Musselman LJ (ed). Pp. 108-125. Parasitic Weeds in Agriculture. CRS Press. Boca Raton, Florida.

Rousset A, Simier P and Fer A. 2001. Phytotoxicity of xenobiotics in *Striga hermonthica*. In: Fer A, Thalouarn P, Joel DM, Musselman LJ, Parker C and Verkleij JAC (eds). Pp. 159. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Sauerborn J. 1991. The economic importance of the phytoparasites Orobanche and Striga. In: Ransom JK, LJ Musselman, AD Worsham and C Parker (eds). Pp. 137-143. *Proceedings of the 5th International Symposium on Parasitic Weeds*. CIMMYT, Nairobi, Kenya.

Sauerborn J. 2001. Angiospermous root parasites and fungi as natural antagonists. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 248-251. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Siame BA, Y Weerasuriya, K Wood, G Ejeta and LG Butler. 1993. Isolation of strigol, a germination stimulant for *Striga asiatica,* from host plants. *Journal of Agriculture and Food Chemistry* 41: 1486-1496.

Smaling EMA, A Stein and PHM Sloot. 1991. A statistical analysis of the influence of *Striga hermonthica* on maize yields in fertilizer trials in Southwestern Kenya. *Plant and Soil* 138: 1-8.

Stewart GR, Nour J, Macqueen M and Shah N. 1984. Aspects of the biochemistry of Striga. In: Ayensu E, Doggett SH, Keynes RD, Marton-Lefevre J, Musselman LJ, Parker C and Pickering A. (eds). Pp. 161-178. Striga Biology and Control. International Council of Scientific Unions Press. Paris, France.

Stewart GR and Press MC. 1990. The physiology and biochemistry of parasitic angiosperms. Annual Review of Plant Physiology and Plant Molecular Biology 41: 127-151.

Van Ast A, Bastiaans L and Kropff MJ. 2001. Effects of *Striga hermonthica* on photosynthesis and carbon allocation in sensitive and tolerant sorghum. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and Verkleij JAC (eds). Pp. 151-154. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.

Yoder JI, M Matvienko, D Jamison, M Torres, Q Ngo, AJ Nava, A Nava, Y Goldwasser, A Wojtowicz and R Wrobel. 2001. Early parasite responses to host root factors. In: Fer A, P Thalouarn, DM Joel, LJ Musselman, C Parker and JAC Verkleij (eds). Pp. 5-10. Proceedings of the 7th International Parasitic Weed Symposium. Nantes, France.