Striga hermonthica seed bank dynamics

process quantification and modelling

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“Doonin doonin, kononi be nyaga da”
“Little by little, the bird makes its’ nest”
Bambara wisdom

Dedicated to my parents, Loes and Huib

Abstract

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This thesis presents a study on the quantification of seed bank dynamics of the parasitic weed *Striga hermonthica*. The main objectives were to quantify transition rates between different stages of the life cycle, determine these under different conditions and control strategies and to develop and use a population model to project long-term seed bank dynamics. To this end, field experiments were performed in Mali, with sorghum in 2002, 2003 and 2004, and Niger, with millet in 2004. Three demographic processes behind *Striga hermonthica* seed bank replenishment were determined and quantified, namely (1) recruitment of Striga plants, (2) survival of emerged Striga plants to maturity and (3) fecundity (number of seeds produced per mature plant). Striga seed production was highly variable between years and sites, because of high variability in recruitment. Different control strategies reduced Striga at different stages in the life cycle. Intercropping the host cereal with non-host trap crops mainly reduced recruitment and survival while late weeding acted almost solely on survival to maturity. A critical re-assessment of the seed bag method used to determine Striga seed mortality in the soil, led to the conclusion that the method overestimates seed mortality. It was suggested to adapt the seed bag method in order to measure seed mortality more accurately. An adapted seed bag burial method and a soil sampling method were used simultaneously to determine processes and rates of seed bank depletion under bare soil, fallow and different crop covers. Results suggested that the main cause of seed bank depletion was germination of seeds. Both methods yielded similar seed bank depletion percentages and most germination was found in soil under host crops, sorghum and millet, followed by intercrops of a host and a non-host trap crop, non-host crops, fallow and bare soil. The information and insights obtained were used to develop a spatially explicit, stochastic Striga population model, with which long-term effects of crop systems and control was modelled. The spatial patterns of emerged Striga plants after point inoculation with stochasticity in the attachment stage of Striga resembled spatial distribution of Striga that is typically observed in farmers' fields. Sensitivity analysis showed that only two slope parameters for the dispersal curve of seeds and seed death other than germination in response to millet roots were of minor importance for population growth. The model indicated that intercrops of host cereals and non-host crops showed higher potential to reduce the Striga seed bank than did rotations of these. The implications of the findings are discussed in the context of integrated Striga management and participatory research.

Key words: Weed control, integrated management, parasitic weed, population, sorghum, millet.

Preface

After counting thousands of plants and seed capsules and millions of seeds, seemingly endless analysis, writing and re-writing we are finally there. Now is the time to thank the people who, directly or indirectly helped me to complete this thesis.

This thesis could never have come to a good end without my many supervisors, although supervisors have come and gone and there were some changes in the composition over time. Prof. Dr. Martin Kropff, my promotor, Dr. Tjeerd Jan Stomph and Dr. Wopke van der Werf, my co-promotors gave me guidance, but let me free to make my own decisions and mistakes, which is essential in the process of doing a PhD. Martin Kropff has always been supportive and enthusiastic even though his time became more and more limiting as time went by. When I was in The Netherlands, Tjeerd Jan always made time for me and we met twice in Mali and once in Niger to assess the experiments together in the field. There, his true nature of researcher shined, giving me energy and motivation. Wopke van der Werf, with his critical analytical and editorial skills, helped a lot in writing and with the modelling.

I started my PhD with about four daily supervisors in Wageningen, which was a bit too much. Aad van Ast and Lammert Bastiaans decided that too many cooks would spoil the broth and so, they retreated from the supervision. They were, however, always available for advise and discussions and Aad has helped me by advice and assistance in the editing of the thesis. He is for me, a Striga veteran and I am glad to have him by my side as a paranymph. Paula Westerman (my daily supervisor for the modelling part) unfortunately had to leave to work in the US, but Felix Bianchi took over this job with an open mind and result-oriented attitude. I would like to thank them both for helping me in the difficult task of conceptualization and construction of the population model. Alistair Murdoch gave me very good advice and comments on the different chapters.

I would like to thank the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), my current employer, for collaboration during my PhD work. ICRISAT also gave me the opportunity to continue working on this thesis in addition to my work as an Associate Professional Officer in 2006 and 2007. My supervisors Eva Weltzien and Ramadjita Tabo have been very committed to the collaboration and finishing of the thesis. Other people who have helped improve this thesis were Mitch Tuinstra, Paul Goedhart, and Wampie van Schouwenburg.

There were many people who made my life pleasant during my stay in Wageningen as well as in Mali. Jonne Rodenburg has been a friend with whom I shared many happy moments in Holland and Mali and a colleague with whom I have

had many fruitful discussions on Striga, although I believe our work could have been more complementary. I also want to thank Rik Schuiling for his friendship and for always letting me stay with him, making me feel at home and welcome in his house in Wageningen. There were many friends in Wageningen of which most (like me) came and went again, which is sometimes sad but exciting as well. I would especially like to thank Santiago Ridaura Lopez, Coen Elemans, Claudia Cangemi, Pablo Tittonell, Michiel van Breugel, Christine Chizana and Jessica Milgroom for friendships and fun.

Furthermore, I have enjoyed the company of my fellow PhD students at the Haarweg as well as the valuable discussions we had. Thank you Nick den Hollander, Jochem Evers, Paul Belder, Harm Smit, Marjolein Kruidhof, Pytrik Reidsma, Bart Timmermans, Sanne Heijting, Wim Westerhuis, Ilse Geijzendorffer, Shibu Muhammed Ebrahim, Venasius Lendzemo and Gideon Ayongwa for laughter and a good atmosphere.

In Mali and Niger, I had a great stay and was able to work thanks to many people. I know there will be some names spelled out wrong and some forgotten but here we go…. the late Idrissa Sangare, Bakary Sidibe, Moussa and Lasine Keita, Ibrahim Sissoko, Boubabcar Cisse, Badara Diallo, Abdoulaye Bah, Samuel Guindo, Almouner Yattara, Ana Dolo, Abibatta Ouattara (ICRISAT-Mali), Seriba Katile, Siaka Dembele (IER-Mali), Harouna Dodo and Ibrahim Maikano (ICRISAT-Niger). Then there were friends outside work like Tahirou Santara (Koke) and the family Santara, Kalifa Dembele, Aminata Sangare, Fatoumata Nomoko, Nienke Muurling and Bouba Djabate with whom I had fun and learnt so much about Africa and Mali in particular. Furthermore, Bintu (mama) Doucoure and the family I lived with for almost a year, treated me as one of their own although our genetic, phenotypic and cultural differences could not have been greater.

Emma, you stimulated me to deepen my studies, explore more of the world and have a lot of fun in doing just that!! I will always stay thankful. When travelling abroad it is often difficult to keep in contact with friends. Fortunately, we always find ways to retrieve contact with a couple of friends like Oscar Mangiapane, Bart de Knegt, Pieter Bas Glas, Quint Blom, Sanne Groot, Ruud Jansen and Ingrid van Welie.

My family has always supported me, stayed interested and stuck with me when I was abroad, even though I did not always keep in contact as often as they would have liked. So, Loes, Huib, Margot and Tjarko……. This thesis may be terrible to read but you better read a couple of pages because it took me and colleagues some blood, litres of sweat but fortunately no tears to finish. To anybody else who has helped me one way or another.

Bedankt, thank you, merci, ini tse, Tom

Bamako, May 2007

Contents

CHAPTER 1

General introduction

This thesis describes experimental and modelling work that aims at unravelling and quantifying the life cycle of a parasitic weed, *Striga hermonthica* (Del.) Benth. This weed causes significant yield losses in cereal crops in sub-Saharan Africa, adding to poverty and human suffering. The analysis made here is with a view towards finding ways of effective management of the weed problem by means of a long-term management approach that targets the seed bank.

This introduction starts with a description of the genus *Striga* and, in particular, the species *Striga hermonthica* and why the genus *Striga* has become such a problem in sub-Saharan Africa. Next, the life cycle of *Striga hermonthica* is described in detail because a quantitative understanding of the life cycle is the key to understanding how the seed bank, and with it the weed problem, can be managed. Finally, gaps in the quantitative knowledge of the seed bank are identified and objectives of the research are explained. The introduction concludes with a short overview of each of the chapters of this thesis.

The genus *Striga*

Striga spp. are hemi-parasitic plants that parasitize the root systems of their hosts. All *Striga* species except *Striga angustifolia* [Don.] Saldanha are dependent on a host to establish themselves, which makes them obligate parasites (see below). Most *Striga* species are annuals but some are perennials (Parker & Riches, 1993).

The genus *Striga*, family *Orobanchacecae*, contains about 41 species that are found on the African continent and parts of Asia; Africa is the presumed region of origin (Wolfe *et al*., 2005). By parasitizing crop species, they can cause substantial yield losses and are therefore considered agricultural pests. The literature to date cites three species as having a significant impact on agriculture in tropical and subtropical areas. These are *S. hermonthica* (Del.) Benth., *S. asiatica* (L.) Kuntze and *S. gesneroides* (Willd.) Vatke. The first two species parasitize cereal crops and wild grasses while the third parasitizes broadleaved plants including the crop species cowpea (*Vigna unguiculata* (L.) Walp.) and tobacco (*Nicotiana tabacum* L.) (Mohamed *et al*., 2001). *S. asiatica* occurs throughout Africa, Arabia, and Asia. *S. gesneroides* is found in the same region although its distribution is concentrated in sub-Saharan Africa. *S. asiatica* and *S. gesneroides* both have a self compatible reproduction system. *S. hermonthica* is an obligate outcrosser, occurs only on the

African continent, and has the greatest agricultural impact of all *Striga* spp. This thesis focuses on *Striga hermonthica.* Wherever possible, the shorthand name "Striga" is used instead of the full species name *Striga hermonthica*.

Striga hermonthica

Striga hermonthica is a green erect herb with bright pink flowers and a height of around 30–40 cm at flowering. *S. hermonthica* is suggested to originate from the same area as sorghum (*Sorghum bicolor* [L.] Moench). It is thought to have co-evolved with wild relatives of sorghum during domestication in the Sudano-Ethiopian region of Africa (Mohamed *et al*., 1998). With the introduction of sorghum into new regions in Africa, it may have spread by crop seed contamination. It is thought that new areas and fields are still being colonized by contaminated crop seeds (Berner *et al*., 1994). *Striga hermonthica* parasitizes, not only, on sorghum but also on other cereals, e.g., maize (*Zea mays* [L.]) and millet (*Pennisetum glaucum* [L.] R. Br.) (Parker & Riches, 1993). *Striga hermonthica* has been reported to parasitize rice (*Oryza glaberrima* [Steudel] and *O. sativa* [L.]), finger millet (*Eleusine coracana* [L.] Gaertn.) and sugarcane (*Saccharum officinarum* [L.]) (Gurney *et al*., 1995) and recently, tef (*Eragrostis tef* [Zucc.] Trotter) and barley (*Hordeum vulgare* L.; Hussien, 2006).

Striga hermonthica is one of the most important biological constraints to the production of millet, sorghum and maize in sub-Saharan Africa despite more than 50 years of research. Some fields have become so badly infested with Striga that farmers are forced to abandon the field or grow other crops (Hussien, 2006). *Striga hermonthica* occurs in sub-tropical areas with an annual rainfall ranging from 300–1200 mm. However, it may be able to adapt to agro-climatic conditions outside its current distribution range and to other crop species (Mohamed *et al*., 2006).

The Striga problem: control options and integrated control

Semi-arid tropical farming in sub-Saharan Africa suffers from increasing land pressure due to human population growth. This leads to continuous monocropping of (cereal) hosts in the same field for long periods (>10 years). Where previously the seed bank would decrease to tolerable levels of *Striga hermonthica* after a fallow period, a reduction in length of fallow periods has favoured the development of high levels of infestation (Samaké *et al*., 2005, 2006; Weber *et al*., 1995). Parallel to this development, insufficient application of organic and inorganic fertilizers has, in many places, led to a depletion of soil organic carbon and nutrients (Yamoah *et al*., 2002). The combination of reduced fallow periods and insufficient nurture of the soil leads to higher Striga infestation levels, poorer soils and ultimately, declines in cereal yield (Emechebe *et al*., 2004). *Striga* spp. are estimated to affect the livelihoods of about

300 million people living in sub-Saharan Africa (Mboob, 1989). In this area, 26 million hectares of cereal fields (maize, sorghum and millet) are infested with *S. hermonthica* and *S. asiatica* and annual yield losses are estimated at about 10.7 million tons (Gressel *et al*., 2004). Oswald (2005) summed up many of the control options proposed in the reviewed literature. Many researchers suggest that a so-called integrated Striga control or management (ISC or ISM) approach would be the best strategy for short and long-term Striga control and crop yield improvement. However, the concept of integrated Striga management, like integrated pest management also implies that choices of control options must be based on a sound knowledge of the biology and population dynamics of the pest (Ehler, 2006). The life cycles of the economically important *Striga* species are very closely linked to the growing seasons of their hosts (Fig. 1). As the Striga seed bank plays an important role in population dynamics, it is important to know the effects of available control options on Striga seed bank dynamics.

The *Striga hermonthica* life cycle

To understand the population dynamics of *Striga hermonthica* it is necessary to take a closer look at its most important life cycle stages and transitions (Fig. 1).

Seeds

Striga hermonthica seeds are very small (0.2 × 0.3 mm), light weight (0.4–0.5 × 10^{-2} mg) and one plant can produce up to 200,000 seeds (Parker & Riches, 1993). Seeds have long life expectancies under both laboratory and field conditions (Samaké *et al*., 2006), and a persistent seed bank can build up within one or two years of flowering Striga plants occurring in a field (Webb & Smith, 1996). However, there is much controversy on the longevity of seeds in the soil and on the causes of seed mortality.

Primary dormancy

Until recently, it was thought that freshly produced seeds were dormant (primary dormancy) and needed a post-ripening period of about six months before being able to germinate (Vallance, 1950). It was also suggested that this was a mechanism that prevented germination of seeds during unfavourable conditions in the dry season when the host is not present (Doggett, 1965). Recent research has challenged this point of view as germination of fresh seeds was induced as early as 28 days after pollination of the flowers (Aigbokhan *et al*., 1998). In either case, seeds surviving the dry season are expected to be non-dormant at the start of the rainy season.

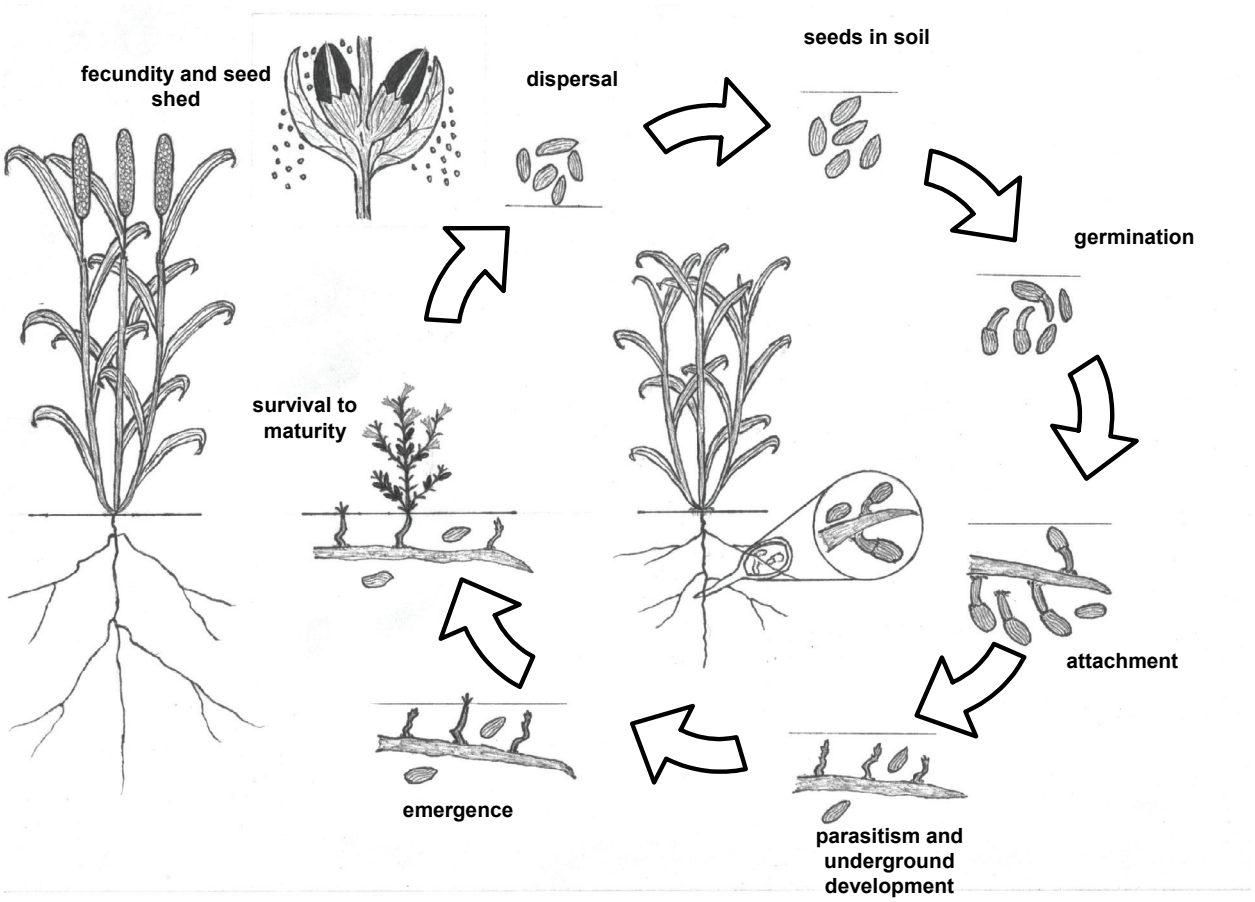

Fig. 1. The *Striga hermonthica* life cycle on millet (by S. Guindo & T.A. Van Mourik).

Germination

Seed exposure to moist conditions in combination with a temperature of between 25–45 °C for a minimum of four days (by the first rains of the rainy season) makes seeds responsive to germination stimulants (Muller *et al*., 1992). This period is referred to as (pre)conditioning (Fig. 1). Germination of *Striga hermonthica* seeds is triggered by the presence of sesquiterpenes or strigolactones, which are exuded by host and non-host roots (Cook *et al*., 1972). These sesquiterpenes are chemically similar to the signal that induces hyphal branching of mycorrhiza, the first step towards a mutualistic, symbiotic association between plants and mycorrhiza (Akiyama *et al*., 2005). When a host or a non-host root exudes trace amounts of germination stimulants, a chemical gradient is created (Bouwmeester *et al*., 2003; Fate & Lynn, 1996). It is suggested that this gradient is used by Striga seeds to (1) increase the chance of germinating only in the vicinity of potential host roots (Fate *et al*., 1990), and (2) to find the host root by growth of the radicle "up" the concentration gradient, in a process called chemotropism (Williams, 1960, 1961).

The germinated seed needs to find, and attach itself, to the host root within three to five days, before seed reserves are depleted and host root penetration is no longer possible (Chang & Lynn, 1986). Furthermore, the radicle is only able to grow to a maximum of about 5 mm and so, optimally, the seed should only germinate if the root is less than 3–4 mm away (Ramaiah *et al*., 1991).

Attachment and underground development

Contact between the tip of the radicle and the host root initiates an attachment process that leads to the formation of a root structure called the haustorium. The haustorium links the xylem sap flow of the host root with that of the parasite and connects the parenchyma tissues of the host and the parasite (Kuijt, 1969). This connection allows *Striga hermonthica* to withdraw water, nutrients and carbon assimilates from the host (Cechin & Press, 1994; Pageau *et al*., 1998). Host recognition and haustorium development are mediated by chemicals, such as phenolic acids, quinones and flavanoids (Yoder, 2001). Phenolics and allelopathic quinones are plant defence chemicals, which suggests that *Striga* spp., such as herbivorous insects, uses these defence chemicals as recognition cues (Atsatt, 1977).

The attached seedling causes damage to its host in two ways. The first direct negative effect on host growth originates from simple competition for water, nutrients, assimilates and amino acids between the host (shoot) and the attached Striga seedling (Cechin & Press, 1994). The second, more indirect "pathogenic" effect from the attached seedling, is a disruption of the host's hormonal balance (Frost *et al*., 1997; Taylor *et al*., 1996) and a reduction of the host's photosynthesis process (Graves *et al*., 1989; Gurney *et al*., 1995; Smith *et al*., 1995; Watling & Press, 2001). This effect becomes evident several days after establishment of the haustorium. The attached seedling forms a sprout which grows towards the soil surface. From the time of attachment until emergence, Striga is fully dependent on the host for water, nutrients and assimilates, making it a holo-parasite during this stage of its life cycle.

Emergence

The time between attachment and emergence can vary from three to six weeks (Olivier *et al*., 1991; Parker, 1965). Upon emergence, the leaves and stems turn green and start to photosynthesize. There is evidence for density dependent feedback mechanisms that regulate the maximum number of plants that can emerge and survive to maturity per host (Doggett, 1965; Van Delft *et al*., 1997; Webb & Smith, 1996). Andrews (1945) and Doggett (1965) suggest that about 10–30% of the attached seedlings reach the soil surface.

Survival to maturity

Striga plants start flowering between one to two months after emergence (Parker & Riches, 1993). Some studies have observed premature mortality of emerged plants but this process has only been quantified in one study (Webb & Smith, 1996). Flowering *S. hermonthica* plants are pollinated by bee-flies (Bombyliidae, Diptera) and butterflies (Lepidoptera). After pollination, a green capsule with seeds is formed within seven to ten days. A flowering Striga plant can bear from one to about 30 flower branches with flowers that are each 1 to 2 cm large. Flowers appear and open in sequence from the bottom of the flower branch upwards. Flowering is a continuous process and all stages, from flower buds to capsules that are already shedding seed, can be found simultaneously on one plant or flower stalk. Senescence sets in from the tip of the capsule downwards. Eventually, the capsule turns black and opens, shedding its seed.

Fecundity

Estimates of fecundity (number of seeds produced per mature Striga plant) vary widely and may depend on growing conditions, host species and host variety (Andrews, 1945; Parker & Riches, 1993; Rodenburg *et al*., 2006b). Estimates of average fecundity range from 5,000 to 84,000 seeds per plant, while maximum fecundity is in the order of 200,000 seeds per plant. Seed production, or a proxy indicator for seed production, has only recently been related to control options (Rodenburg *et al*., 2006b; Van Ast & Bastiaans, 2006).

Seed shed and dispersal

The time between capsule formation and its opening when ripe is about one week (Webb & Smith, 1996). Galling weevils (Smicronyx spp.) predate seed capsules (Pronier *et al*., 1998). No information is available on seed predation on the soil surface. Wind, runoff water, cattle, harvested plant material, agricultural implements and infested crop seed lots may vector the *Striga hermonthica* seeds. Wind, (water and tillage) are probably responsible for short distance dispersal (<1 km within fields or between neighbouring fields), whereas harvested plant material, infested crop seeds and grazing cattle may facilitate long distance dispersal (>1 km, between villages and regions) (Berner *et al*., 1994).

Striga seed bank dynamics, knowledge gaps

Densities of *Striga* spp. seeds found in field soils are highly variable and can be as large as 882,000 seeds per square metre (Table 1). The highest densities of *Striga hermonthica* were reported in Kenya in bimodal climate zones with two cropping

Table 1. Densities of *Striga* spp. found in soils in Africa and the United States.

Country	Depth	Seeds per 100 g [a]		Seeds per m^2 [b]		Remarks	Source
	(cm)	Mean	Maximum	Mean	Maximum		
USA	0-15	284	459	639,000	1,032,750	*S.asiatica*, exotic weed on maize (ca 21% viable)	Robinson & Kust, 1962
South Africa	0-20	32	-	96,000	-	*S. asiatica, S. gesneroides*	Visser & Wentzel, 1980
Nigeria	0-10	8	75	12,300	112,500	*S. hermonthica, S.gesneroides, S. asiatica*	Hartman & Tanimonure, 1991
Cameroon	0-10	127	-	190,500	-	During seed shedding, after 2 year host cropping	Carsky *et al*., 1996
Mali	0-15	18	91.2	40,275	205,200	Only viable seeds considered (30 % of all)	Smith & Webb, 1996
Kenya	0-5	44	-	32,600	-	KFF [c], during seed shedding (1995)	Van Delft *et al*., 1997
Kenya	0-5	13	-	9,380	-	KFF, after 1 year fallow (1996)	Van Delft *et al*., 1997
Kenya	0-5	22	-	16,500	-	KFF, before seed shedding (1996)	Van Delft *et al*., 1997
Kenya	0-10	22	-	33,000	-	KFF, before seed shedding (1996)	Van Delft *et al*., 1997
Kenya	0-10	163	-	243,800	-	KFF, after seed shedding (1996)	Van Delft *et al*., 1997
Kenya	0-20	138	294	414,600	882,000	Added 60,000 seeds m^{-2}	Oswald & Ransom, 2001
Ghana	0-30	-	-	1,800	-	Compound field [d], C_{org}(%) = 1.27	Sauerborn *et al*., 2003
Ghana	0-30	5	-	20,700	-	Middle field [d]	Sauerborn *et al*., 2003
Ghana	0-30	11	54	48,150	243,000	Bush field [d], C_{org}(%) = 0.71	Sauerborn *et al*., 2003
Nigeria	0-15	-	-	26,000	-	After 2 years farmer practice (FP) (2000) [e]	Schulz *et al*., 2003
Nigeria	0-15	-	-	15,500	-	After 2 years Integrated *Striga* Control (ISC) (2000) [f]	Schulz *et al*., 2003
Ghana	0-15	-	-	9,400	-	Before experimentation cereal plots (1997) [g]	Abunyewa & Padi, 2003
Ghana	0-15	-	-	16,700	-	After 2 years of cereals (millet or sorghum)	Abunyewa & Padi, 2003
Ghana	0-15	-	-	28,200	-	Before experimentation legume plots (1997)	Abunyewa & Padi, 2003
Ghana	0-15	-	-	8,200	-	After 2 years of legumes (bambara nut or soyabean)	Abunyewa & Padi, 2003
Nigeria	0-15	-	-	9,710	-	Before experimentation (2002)	Franke *et al*., 2006
Nigeria	0-15	-	-	14,400	-	After 2 years farmer practice (2004)	Franke *et al*., 2006
Nigeria	0-15	-	-	5,200	-	After 2 years of ISC (2004) [g]	Franke *et al*., 2006

[a] Air dry soil, [b] Assuming a depth of 10 cm, soil bulk density 1.5 g cm^{-3}, unless otherwise mentioned, [c] Kibos farm field,
[d] Compound, middle and bush fields located 0.22, 0.32 and 1.65 km from farm, [e] FP; a cereal, intercrop or fallow, followed by a local (susceptible) maize,
[f] ISC; a soya bean or cowpea trap crop followed by a resistant maize, [g] average seed density of two sites (Gotulis and Terudig).

seasons in which hosts are cultivated two times per year (Oswald & Ransom, 2001). Recent studies have tried to explain the variability in the size of seed banks and determine, to what extent, densities can be reduced by control options (Van Delft *et al*., 1997; Abunyewa & Padi, 2003; Sauerborn *et al*., 2003; Schulz *et al*., 2003; Franke *et al*., 2006).

The dynamics of the Striga seed bank are the result of two processes, namely seed bank replenishment and seed bank depletion. Seed bank replenishment can further be broken down into seed production of mature plants and arrival of seeds from external sources. Three main processes preceding seed production are recruitment (the number of emerged Striga plants divided by the number of seeds in the soil), survival of emerged plants and fecundity of mature plants. Seed bank depletion may be caused by germination, pathogens, seed ageing, seed predation, and export of seeds to other fields. Most field studies on *Striga* spp. and control options have focused on host yield aspects rather than seed bank dynamics. Observations on Striga population dynamics were often limited to plant counts or measurement of the dry weights of the emerged plants. The success of a control option is generally assessed by measuring the reduction in the number of emerged Striga shoots compared to a control treatment. This measure does not necessarily reflect seed bank replenishment or depletion. Individual steps in the Striga life cycle have rarely been quantified.

Striga seed production is an essential part of the Striga life cycle but has been determined in only a few studies (Weber *et al*., 1995; Webb & Smith, 1996; Rodenburg *et al*., 2006b). The different processes leading up to seed production (recruitment, survival and fecundity) need separate quantification in order to understand at what stages in the Striga life cycle control options intervene.

Little information is available on seed bank depletion under field conditions and the processes underlying seed bank depletion. There is great controversy on the rate and causes of Striga seed death with some studies suggesting attack of seeds by pathogens or microbial activity as the main cause of seed bank depletion (Pieterse *et al*., 1996; Gbèhounou *et al*., 2003) and others suggesting seed germination in response to host and non-host roots as the main course of depletion (Oswald & Ransom, 2001; Khan *et al*., 2002). The controversy and conflicting results may be explained by the use of different methods to measure seed death, namely the seed or Eplee bag method (Eplee, 1975) and the soil sampling method (Hartman & Tanimonure, 1991). The seed bag method appears to yield extremely high mortality rates of Striga seeds compared to the soil sampling technique. The methods for measuring seed bank depletion need a critical assessment and the rates and causes of seed death need to be determined.

Determination of seed bank replenishment and depletion will allow for construction and parameterization of a model that simulates seed bank dynamics. Such

a model can generate plausible long-term projections of control options on the seed bank densities and predict changes in potential cereal yield losses related to Striga.

Research objectives

The overall aim of this study is to quantify *Striga hermonthica* seed bank dynamics under field conditions and to evaluate the factors that can potentially influence transition rates from one life cycle stage to the next. The first objective is the development of methods through which the processes of seed bank replenishment (recruitment, survival to maturity, fecundity and total seed production) and seed bank depletion (seed mortality through ageing or pathogenic attack and germination) can be confidently quantified. The second objective is to quantify the rates and processes of seed bank replenishment and depletion under different environmental conditions and control options. The third, and final objective, is to use the obtained information to develop and parameterize a Striga seed bank model that would enable forward projections of long-term seed bank dynamics and host yields under different control options and management scenarios.

Outline of the thesis

Chapter 2 presents a quantification of *S. hermonthica* seed bank replenishment. Seed bank replenishment is determined for separate stage transitions in the life cycle; namely recruitment, survival to maturity, fecundity, and resulting seed production. Replenishment is determined under different environments, with different host duration, and in relation to different management strategies. A control treatment (a monoculture of a local long duration host) is compared to different control options such as improved short duration host, intercropping with a trap crop and weeding. The comparison is made in terms of demographic parameters of *S. hermonthica*.

Chapter 3 is an appraisal of the seed bag, or Eplee bag method, for determining seed bank depletion of seeds of plant species, in general, and *Striga* spp., in particular. Seed death was related to fungal activity and seed densities within seed bags. The seed bag method is critically evaluated and advantages and drawbacks are presented.

Chapter 4 deals with the measurement of different causes of seed bank depletion using an adapted seed bag method and the soil sampling method. Seed bank depletion and causes of seed death are quantified and related to different vegetation (crop) covers and the two methods are compared.

In Chapter 5, data obtained in one of the experiments are used to parameterize a *S. hermonthica* seed bank dynamics model. The model was adapted from previously proposed models and several components were added to describe seed bank dynamics in space and include demographic variability. The model was used to forecast the *S.*

hermonthica seed bank dynamics and potential host crop yields in relation to different crop systems and scenarios.

Chapter 6 is a synthesis and discussion of findings and implications of this study. The possible contributions of integrated Striga management (ISM) and participatory and action research are discussed.

CHAPTER 2

Demographic processes behind *Striga hermonthica* seed production in relation to control options

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Abstract

Understanding *Striga hermonthica* (hereafter Striga) seed production is one of the key elements to management of this severe parasitic and difficult to control weed in African agricultural systems. A multitude of control options have been proposed, but the effects of management and environmental factors on Striga seed production are poorly documented. This study thus focused on Striga reproduction as a key process in the life cycle. In five field experiments in three years in Mali and Niger, seasonal demography (recruitment, survival, fecundity) and resulting seed production were measured for a set of treatments and control options. These treatments included sowing date of the host, Striga seed density, host duration (e.g., cultivar), inter-cropping, weeding at flowering and organic amendments.

Maximum Striga seed production per cereal host plant was highly variable over years. Reducing host crop duration from around 120 to around 90 days reduced Striga seed production by 30 to 60%, whether through cultivar choice, sowing delay or premature harvesting of the host. Shorter host duration mainly reduced Striga survival to maturity and fecundity. A fivefold increase in initial seed bank density lowered recruitment proportions from the seed bank significantly but had no effect on fecundity, suggesting that density dependence operates primarily in pre-emergence and pre-flowering stages. A cohort study indicated that later emerging cohorts of the parasite contained more individuals, but contributed less to total reproductive output, especially when the season length was short. Seed production was reduced by weeding at Striga flowering through reduced survival and fecundity, while intercropping affected mainly recruitment and survival.

Introduction

Striga hermonthica (Del.) Benth. is a noxious, hemi-parasitic weed in semi-arid, sub-Saharan Africa and causes substantial yield loss in main cereal crops such as sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* (L.) R. Br.), maize (*Zea mays* (L.)) and sometimes in upland rice (*Oryza sativa* (L.)) (Parker & Riches, 1993). The most severe problems with Striga occur where soils are degraded, fields are continuously cropped with a cereal host, and organic and inorganic nutrient inputs are low (Sauerborn *et al*., 2003).

Despite extensive research efforts over the past decades, no simple solutions to Striga have been found (Oswald, 2005). Seed production is an important step in the life cycle of Striga as in most plants (Silvertown & Charlesworth, 2001), and information on seed production is crucial in developing integrated weed management systems and predicting the long-term effectiveness of management strategies (Norris, 2003).

Striga seeds are produced in large numbers (>200.000 seeds per plant), are very small (0.2 × 0.3 mm, 0.4 $\times 10^{-2}$ mg) and large proportions (>20%) of seeds remain viable in the soil for periods of two or more years, even when non-host trap crops are cultivated (Oswald & Ransom, 2001; Abunyewa & Padi, 2003). Because of these characteristics and a prolonged period of seed shed, direct measurement of the number of produced seeds in the field is difficult. As a result, most studies have limited their observations on Striga to counts of number of shoots or weight (Kanampiu *et al*., 2003; Ahonsi *et al*., 2004; Kroschel & Elzein, 2004; Lendzemo *et al*., 2005; Reda *et al*., 2005). Seed production is not always linearly related to the number of plants because pre-mature plant mortality of Striga as well as seed production per mature plant are density dependent and can vary enormously (Weber *et al*., 1995; Webb & Smith, 1996). So far, Striga seed production has been quantified in a few descriptive studies (Weber *et al*., 1995; Webb & Smith, 1996; Van Delft *et al*., 1997), but not in relation to control options. Consequently, the ecology of seed production and the effect of control options remain poorly understood. This chapter, therefore, focuses on the quantification of seed production in an effort to provide a sound basis for the development of integrated Striga management strategies.

Seed production can be divided into three subsequent life cycle processes or phases: recruitment (the fraction of the seed population that emerges as plants), survival of emerged plants to maturity and fecundity (seed production per mature plant). Recruitment combines a number of underground phases including germination, attachment and successful parasitism of the host. The effects of management strategies on seed production can be expected to differ depending on the potential processes it influences. Planting a short duration cereal host prevents many emerged Striga plants

from reaching maturity or full reproductive potential because of a reduced period between emergence and host maturity or end of the rainy season, leading to reduced seed production (Carsky *et al*., 1996). Shortening the duration of seed production by removing plants shortly after flowering can be expected to affect survival and fecundity and, therefore, to have a direct effect on seed production. Striga recruitment, survival to maturity and fecundity may further be affected by seed bank density (Rodenburg *et al*., 2006b), intercropping of a cereal with a non-host (Carsky *et al*., 1994) or additions of organic amendments to the soil (Sauerborn *et al*., 2003).

The goals of this study were (1) to analyse Striga demography of seed production in relation to host duration, season duration and seed bank density, (2) to evaluate the relative contribution of consecutive emerging Striga plant cohorts to seed production, and (3) to determine at which stages in the life cycle seed production can be suppressed by control options proposed in the literature.

Materials and methods

Experiments and aims

In total, five field trials were conducted in Mali and Niger in 2002-2004 (Tables 1 and 2). These experiments often serve more than one aim at the same time. Before details for individual experiments are discussed, their design to serve the formulated aims is summarized. The effect of the duration of the host on the Striga life cycle and seed production was studied through:

- The 2002 experiments in two locations in Mali, where at both locations Striga was grown on the same two sorghum varieties that among others differed in cycle length. The two sites considerably differ in rainfall and constitute a dry site and a relatively wet site for sorghum cultivation.
- The 2003 experiment, when the effects of host duration (a single variety but two harvest times) and length of the growing season (three sowing dates) on the parasites' life cycle duration and the ensuing seed production were studied at one of the 2002 locations.
- The 2004 experiments in Mali on sorghum and in Niger on millet when again Striga was grown on cultivars that differed in cycle length (for sorghum TIEM L and CMS63E, for millet SAD and 3/4HK), while in Mali again the cycle of the long duration cultivar was also artificially shortened by premature harvesting (TIEM S).

The effect of Striga seed density in the 2003 experiment was superimposed on the treatments to study effects of host and season duration on Striga seed production mentioned above.

Table 1. Overview of host species, *Striga hermonthica* infestation method and seed densities, treatments, and number of replicates for the different experiments.

Year	Site (experiment no.)	Host crop	Infestation method	Pre-conditioning	Treatments applied	*n*	Viable seed density applied (seed population, seeds m^{-2})
2002	Mali, Samanko (1)	Sorghum	Natural infestation	Natural in soil	Host duration (Tiemarifing, CSM63E [a])	8	3,730[b]
2002	Mali, Cinzana (2)	Sorghum	Natural infestation	Natural in soil	Host duration (Tiemarifing, CSM63E)	8	16,550[b]
2003	Mali, Samanko (3)	Sorghum	Artificial infestation Per plant hole at sowing	12-14 days imbibed in laboratory	Rainy season length (3 levels) Host duration (Tiemarifing, Tiemarifing short) Seed density (2 levels)	8	12,000 and 60,000 (source Samanko 2000)
2004	Mali, Samanko (4)	Sorghum	Artificial infestation Soil surface	7 days in soil	Control strategies[c] (6 levels)	6	20,100 (source Samanko 2003)
2004	Niger, Sadore (5)	Millet	Artificial infestation Soil surface at sowing	no pre-conditioning	Control strategies[c] (6 levels)	6	28,800 (source Bengou 1996)

[a] Tiemarifing, Long duration sorghum (control); CSM63E, Short duration sorghum; Tiemarifing short, Harvested at maturity short duration sorghum.

[b] In naturally infested soils, seeds were checked for intactness using the seed press test (Van Mourik *et al.*, 2003).

[c] Host cycle length was considered a control strategy in 2004 (treatments explained in Table 3).

Table 2. *Striga hermonthica* control options applied in experiments 4 and 5 in Samanko and Sadore, respectively.

Year	Site	Control options applied	Varieties (cereal-intercrop)	Code
2004	Mali, Samanko			
		Long duration sorghum (control)	Tiemarifing	TIEM L
		Long duration sorghum harvested at maturity of short cycle sorghum [a]	Tiemarifing	TIEM S
		Short duration sorghum	CSM63E	CSM63E
		Intercrop sorghum-*Desmodium uncinatum* [b]	Tiemarifing-*Desmodium uncinatum*	IC DES
		Intercrop sorghum-cowpea	Tiemarifing-Sangaranga	IC COW
		Weeding at *Striga* flowering	Tiemarifing	TIEM WEED
2004	Niger, Sadore			
		Long duration millet (control)	Sadore local	SAD
		Short duration millet	3/4 HK	3/4 HK
		Intercrop (millet-sesame)	Sadore local-Maradi local	IC SES
		Intercrop (millet-cowpea)	Sadore local-TN5-78	IC COW
		Weeding at *Striga* flowering	Sadore local	SAD WEED
		Organic amendment (0.2 kg m^{-2})	Sadore local	SAD ORG

[a] Because different varieties react different to *Striga* infestation the effect of variety, but also the period of presence of the host was evaluated. This was done by removing the aboveground parts of a long duration host at the moment of maturity of the short duration host.

[b] All intercrops were performed with the long duration host (Tiemarifing and Sadore local).

In 2003 (experiment 3), observations included the analysis of seed production of different cohorts of emerging Striga plants in order to quantify the seed production components separately for emergence cohorts on two of the three sowings.

In 2004, the effect of potential control options on recruitment, survival and fecundity were finally observed on sorghum in Mali (experiment 4) and millet in Niger (experiment 5) (Table 2). The control options included: weeding of Striga at flowering, intercropping with non-host crops and on millet, application of organic soil amendments.

General treatment details

In all years and at all sites, sorghum or millet sowing distances were 0.8 m between rows and 0.6 m within rows. Weeds were controlled by hoeing between 18 and 30 days after sowing (DAS). After this initial weeding, all weeds other than Striga were removed at least once every two weeks until harvest of sorghum and millet to facilitate Striga counts. Crops were harvested at maturity, except when crop duration was artificially shortened (TIEM S) in 2003 and 2004. Artificial shortening of sorghum duration was done through harvesting at flowering (2003) or at the time of maturity of the short duration host crop cultivar (2004). At the first weeding (18–25 DAS), crops were thinned to one sorghum plant per hill, unless otherwise mentioned below. Site and year specific details and events are given below. Rainfall data are shown in Fig. 1.

Treatment details by experiment

2002: Samanko, Mali (experiment 1) and Cinzana, Mali (experiment 2)

A short (cv. CSM63E) and a long duration sorghum cultivar (cv. Tiemarifing) were sown in fields naturally infested with Striga in Samanko and Cinzana according to a completely randomized design with eight replicates. Plot size was 3.2 m × 7.8 m, four rows with 13 sorghum plants each were sown per plot. Fertilizer (NPK, 17:17:17) was applied at a rate of 100 kg ha^{-1} as top dressing one week prior to sowing in Samanko and four days prior to sowing in Cinzana. Naturally occurring Striga seed densities (Table 1) were assessed at sowing by sampling the soil of eight equal sized squares in the experimental plot (bulked samples of four sub-samples to a depth of 10 cm) and extraction of seeds by use of a table top elutriator.

2003: Samanko, Mali (experiment 3)

A full factorial experiment was sown in 2003 (Table 1), in a randomized block design with three sowings [12-06-2003 (0 days sowing delay (DSD)), 30-06-2003 (18 DSD) and 18-07-2003 (39 DSD)], two Striga inoculation densities (12,000 and 60,000 Striga seeds $host^{-1}$) and two crop durations (long and artificially-shortened duration).

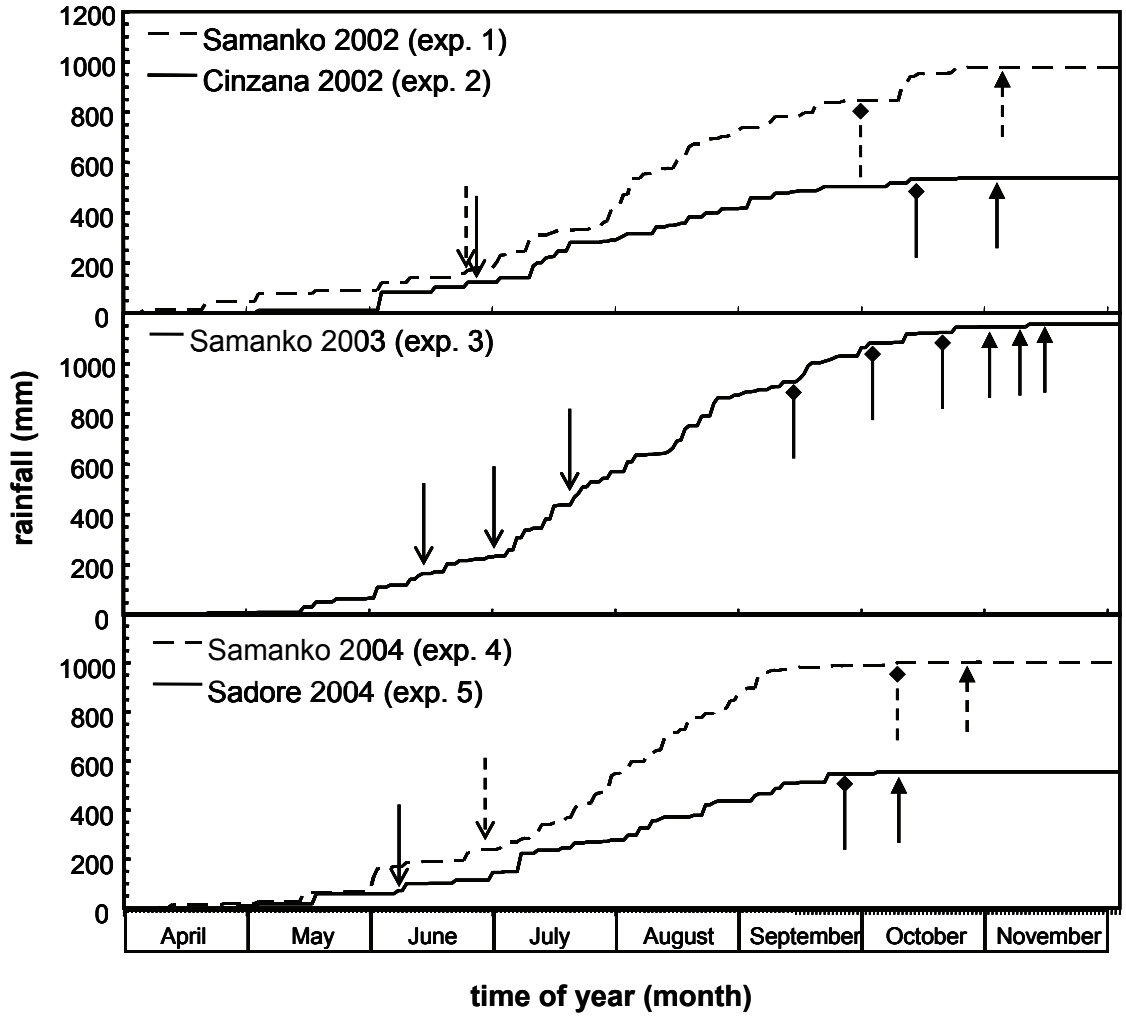

Fig. 1. Cumulative rainfall at Cinzana (Mali), Samanko (Mali) and Sadore (Niger) during experiments 1 and 2 (top graph), 3 (middle graph) and 4 and 5 (bottom graph). Arrows in June and July indicate dates of sowing of the host cereal (sorghum and millet). Diamonds and triangles in September, October and November indicate harvests of short duration (or artificially shortened duration) and long duration cereal hosts, respectively.

Plot size was 3.2 × 4.8 m, four rows with eight sorghum plants each were sown per plot. A single long duration host cultivar (cv. Tiemarifing) was used and the crop was harvested at crop maturity between 115 and 135 DAS (TIEM L) or around 90 DAS (TIEM S), mimicking the effect of a long and a short duration sorghum cultivar, without the interaction of cultivar differences in susceptibility or sensitivity to Striga. The field did not receive any fertilizer.

2004: Samanko, Mali (experiment 4) and Sadore, Niger (experiment 5)

An experiment was conducted on sorghum in Mali and one on millet in Niger, both

laid out as a randomized block design with six treatments and six replicates. Plots were inoculated through manual broadcasting of Striga seeds at a density of 20,100 seeds per host in Mali, and 28,800 seeds per host in Niger. The soil was then worked to a depth of 15 cm using a hoe. In Mali, the time between Striga inoculation and sowing of crops was one week, while in Niger, Striga inoculation and sowing were performed on the same day. In Mali, fertilizer (NPK, 17:17:17) was applied prior to sowing at a rate of 100 kg ha^{-1}. The experiment in Niger did not receive any fertilizer, as the field had been left fallow for more than five years. Treatments designed to suppress Striga included sowing a short duration host sorghum (CSM63E) or millet cultivar (3/4HK), intercropping the host with the non-hosts cowpea (*Vigna unguiculata* (L.) Walp, IC COW, cv. Sangaranga in Mali and cv. TN5-78 in Niger), sesame (*Sesamum indicum* (L.), IC SES, cv. Maradi local) or silverleaf desmodium (*Desmodium uncinatum* (Jacq.) DC., IC DES), weeding Striga at flowering (sorghum: TIEM WEED, millet: SAD WEED) and addition of 2000 kg farm yard manure ha^{-1} to a pure millet stand (SAD ORG) (summary see Table 2).

Intercrops were sown at the same time as the cereal crops. The sorghum cultivar CSM63E is moderately susceptible to Striga and the sorghum cultivar Tiemarifing is moderately susceptible and moderately tolerant to Striga (Rodenburg *et al*., 2006a). The millet cultivar 3/4HK and Sadore local are moderately susceptible to Striga, but nothing is known about their tolerance. Hosts in the intercrop were sown at the same density as sole stands and the intercrop was sown in the crop rows at 0.3 m distance from the host and between rows at 0.4 m from the host plant at the same position as within the host plant row, to maximize the root interaction of host and intercrop. All plots measured 3.2 m × 3.6 m.

Millet hills (Niger) were thinned to three plants per hill at 14 DAS and further thinned to one plant per hill at weeding, 28 DAS. The intercrops were thinned to two plants per hill at 16 and 31 DAS, respectively, for cowpea and sesame. Considerable numbers of hills in many plots had limited cowpea and desmodium establishment throughout the experiment in Mali. These hills were regularly resown. Weeding at Striga flowering (Striga plants were removed once from the field) occurred in Mali at 70 DAS and in Niger at 85 DAS.

Observations

Striga counts and harvests of immature dead plants (no seed capsules produced) and mature dead plants (at least one seed capsule produced per plant) were performed every 14 days. Near the end of the season, mortality of plants was high and observations were made weekly until all Striga plants had died. Dry weights of Striga plants were determined for each observation time by drying in a forced draught oven at

80 °C for 48 hours in paper bags. On the reproductive branches of mature plants, the number of well-formed capsules (opened and closed) was counted. In all years and at all harvests, at least 16 mature but unopened, green capsules were randomly selected from the main capsule bearing branch of Striga plants growing on a short and a long duration host crop. Capsules were packed separately in paper envelopes. These capsules were air dried for at least 1 week before they were opened and the number of seeds per capsule was counted under a microscope. The number of seeds per capsule was multiplied by the total number of capsules harvested for an estimate of seed production. The total number of seeds harvested was divided by the number of mature plants to obtain an estimate for fecundity. The experiments were terminated after all Striga plants had died.

For a cohort study, one host sorghum plant was selected at random from each replicate treatment plot from the first and the last of three sowing dates in experiment 3 (2003). All Striga plants that emerged on this host were labelled every three to four days according to time of emergence and subsequently divided into six "emergence" cohorts (21–40, 41–50, 51–60, 61–75, 76–90 and 91–120 DAS). These cohorts were monitored every two to three weeks by recording the number of immature dead plants and mature dead plants, as well as the number of capsules on the mature dead plants. Fecundity for any cohort was calculated by multiplying the number of capsules per cohort and the number of seeds per capsule, divided by the number of mature plants. If a cohort did not contain mature plants, mean fecundity over replications was calculated disregarding the replication with a missing cohort. Host and Striga material were dried in an oven at 80 °C for 48 hours.

Data processing and statistical analyses

Recruitment was calculated as number of emerged plants divided by the number of inoculated germinable seeds ($host^{-1}$) and survival until maturity was calculated as the number of mature plants divided by the total number of emerged plants. Fecundity was calculated as the number of seeds produced per mature plant. In 2002, six host plants per plot were observed, whereas in 2003 and 2004, four host plants per plot were observed. A sole stand of a long duration sorghum or millet host (cv. Tiemarifing (TIEM L), and cv. Sadore local (SAD), respectively, Table 2) was considered a reference treatment for comparison of any treatment aiming at reducing Striga seed production.

Prior to all analyses of variances and t-tests in GenStat v. 7.2, counts and weights were log-transformed ($\log_{10}$ (x+1)) and proportions were angle-transformed (arcsine $\sqrt{}$ (proportion)) to improve the distribution of residuals. Data from 2002 were subjected to a one-sided t-test for unpaired samples to determine whether estimates of

Table 3. Results of ANOVA analyses indicating significance of treatment effects on *Striga hermonthica* demography, dry weight and host dry weight in experiment 3 (Samanko, 2003). The experimental design was full factorial with days sowing delay (DSD), harvest time of host and *Striga hermonthica* seed density as treatments.

Treatment	Recruitment [a]	Survival	Fecundity [b]	Seeds produced	Striga DW (g)	Host DW (g)
Sowing delay (S) 0, 18, 39 days sowing delay	***	***	***	***	***	***
Host duration, artificial (H) TIEM L, TIEM S	ns	***	**	***	***	**
S. hermonthica seed density (D) 12,000 and 60,000 seeds host^{-1}	***	***	ns	ns	ns	**
Significant interactions (P<0.05)	no	H × D	no	no	S × H	S × H

[a] ANOVA, was performed on "Recruitment" and "Survival" after angular-transformation.

[b] ANOVA was performed on "Fecundity", "Seeds produced", "Striga DW" and "Host DW" after a log-transformation.

, * significant at P<0.01 and P<0.001, respectively.

Table 4. Demographic parameters and dry weight of *Striga hermonthica* as well as crop dry weight for long and short host crop duration and control options in Samanko and Cinzana (Mali) and Sadore (Niger) in experiments 1 and 2 (2002) and experiments 4 and 5 (2004). All values other than proportions (recruitment, survival to maturity) are on a per cereal host basis (1 host = 0.48 m^2).

Experiment	Cultivar / control option	Striga demography and biomass						Host and intercrop dry weight	
		Seed density	Recruitment [a]	Survival [a]	Fecundity [b]	Seeds produced [b]	Striga DW [b] (g)	Host DW (g)	Intercrop DW (g)
1. Mali, Samanko, 2002									
	CSM63E (short)	16,550	0.00135	0.395	15,000	121,000	15.6	105	-
	Tiemarifing (long)		0.00091	0.503	14,100	194,000	10	168	-
	Significance T-test		NS	NS	NS	NS	NS	0.015	
2. Mali, Cinzana, 2002									
	CSM63E (short)	3,730	0.0040	0.008	540	500	3.94	251	-
	Tiemarifing (long)		0.0051	0.023	200	3300	8.94	305	-
	Significance T-test		NS	0.042	0.016	0.038	NS	NS	
4. Mali, Samanko, 2004									
	TIEM WEED[c]	20,100	0.00020 [d]	0.00 -	- -	0 -	0.07 -	215 c [e]	-
	IC COW		0.00004 -	0.07 -	25,300 -	1,900 -	0.35 -	126 ab	329.7
	TIEM S		0.00012 -	0.03 -	23,800 -	6,400 -	2.18 -	182 bc	-
	CSM63E (short)		0.00023 -	0.12 -	10,200 -	6,700 -	2.50 -	85 a	-
	TIEM L		0.00007 -	0.11 -	52,700 -	17,800 -	2.54 -	231 c	-
	IC DES		0.00010 -	0.24 -	30,000 -	18,100 -	3.10 -	190 c	0.6
	SED		NS	NS	NS	NS	NS	28.9	84.71
5. Niger, Sadore, 2004									
	IC SES	28,800	0.00004 a[e]	0.08 b	7,200 ab	700 a	1.3 a	44 a	153
	SAD WEED		0.00102 b	0.02 a	4,600 a	2,000 ab	11.1 a	128 bc	-
	IC COW		0.00014 a	0.14 b	20,600 c	17,000 b	6.5 a	21 a	170
	3/4 HK		0.00077 b	0.40 c	15,600 bc	61,000 c	41.7 b	112 b	-
	SAD ORG		0.00103 b	0.42 cd	15,100 bc	197,000 c	50.1 b	174 c	-
	SAD		0.00111 b	0.53 d	18,800 c	282,000 c	51.3 b	137 bc	-
	SED		0.000241	0.057	3,890	35,000	16.72	23.4	NS

[a] ANOVA, LSD-tests and T-test were performed on "Recruitment" and "Survival" after angular-transformation.

[b] ANOVA, LSD-tests and T-tests were performed on "Fecundity", "Seeds produced" and "Striga DW" after a log-transformation.

[c] TIEM-SAD WEED (weeding at Striga flowering), IC COW-DES-SES (intercrop with cowpea-desmodium-sesame), TIEM L (Tiemarifing), TIEM S (Tiemarifing artificially shortened), CSM63E-3/4HK (short duration sorghum-millet), SAD ORG (long duration millet with organic amendments).

[d] No estimates of SED and significances of differences were possible due to too many plots without *Striga*.

[e] Means in the same column followed by the same letter are not significantly different according to the LSD-test ($P<0.05$).

demographic parameters were significantly different between cultivars with different crop host duration. In 2003 and 2004, general and one-way ANOVA were performed to test for the effect of treatments. These ANOVA's were followed by post-hoc LSD tests, to test for differences between treatments. The back transformed means and LSD's are shown in figures and tables.

Results

Annual variability of Striga demography and seed production

In Tables 3 and 4 and Figs 2 and 3, the results of all experiments are presented. Large differences in seed production were observed between years on the same long duration cultivar (Tiemarifing) in experiments 1, 3 and 4 in Samanko, Mali. These were mainly due to large differences in recruitment. Recruitment values ranged between 0.6×10^{-2} in experiment 1 in 2003 (Fig. 2) to 0.7×10^{-5} in experiment 4 in 2004 (Table 4). These large differences in recruitment rates occurred on cv. Tiemarifing, with only small differences in initial Striga seed densities of 12,000 and 20,100 seeds host^{-1} in experiment 3 (2003) and experiment 4 (2004), respectively.

The proportion of Striga plants that survived to maturity was much less variable and ranged between 0.53 in 2003 (Fig. 2) and 0.11 in 2004 (Table 4) under cv. Tiemarifing. The average number of seeds produced per mature Striga plant ranged between 50,000 in 2004 (Table 4) and 14,100 in 2002.

Subsequent Striga seed production per host was highly variable over years, ranging from 757,000 seeds in 2003 (Fig. 2) to 17,800 seeds in 2004 (2% of 2003) (Table 4). Details on the effects of cereal host crop duration, season length and seed density are given below.

Effects of host crop duration (cultivar or harvest time)

Host duration did not influence any of the Striga parameters (recruitment, survival, fecundity, seed production and dry weight) in experiment 1 (Table 4). The dry weight of the long duration host (TIEM L) was higher ($P=0.015$) than the short duration host (CSM63E). In experiment 2, survival to maturity and seed production were both higher ($P<0.05$) on the long duration host but fecundity was higher on the short duration host (Table 4). Host dry weight did not differ significantly.

Artificially shortening cereal host duration (TIEM S) in experiment 3 resulted in lower survival to maturity, lower fecundity and lower seed production ($P<0.05$) when compared to a long duration host (TIEM L) (Table 3 and Fig. 2). Dry weight of the host was also significantly lower when artificially shortened. A shorter host duration (TIEM S or CSM63E) did not affect any of the Striga parameters (Table 4), but a short

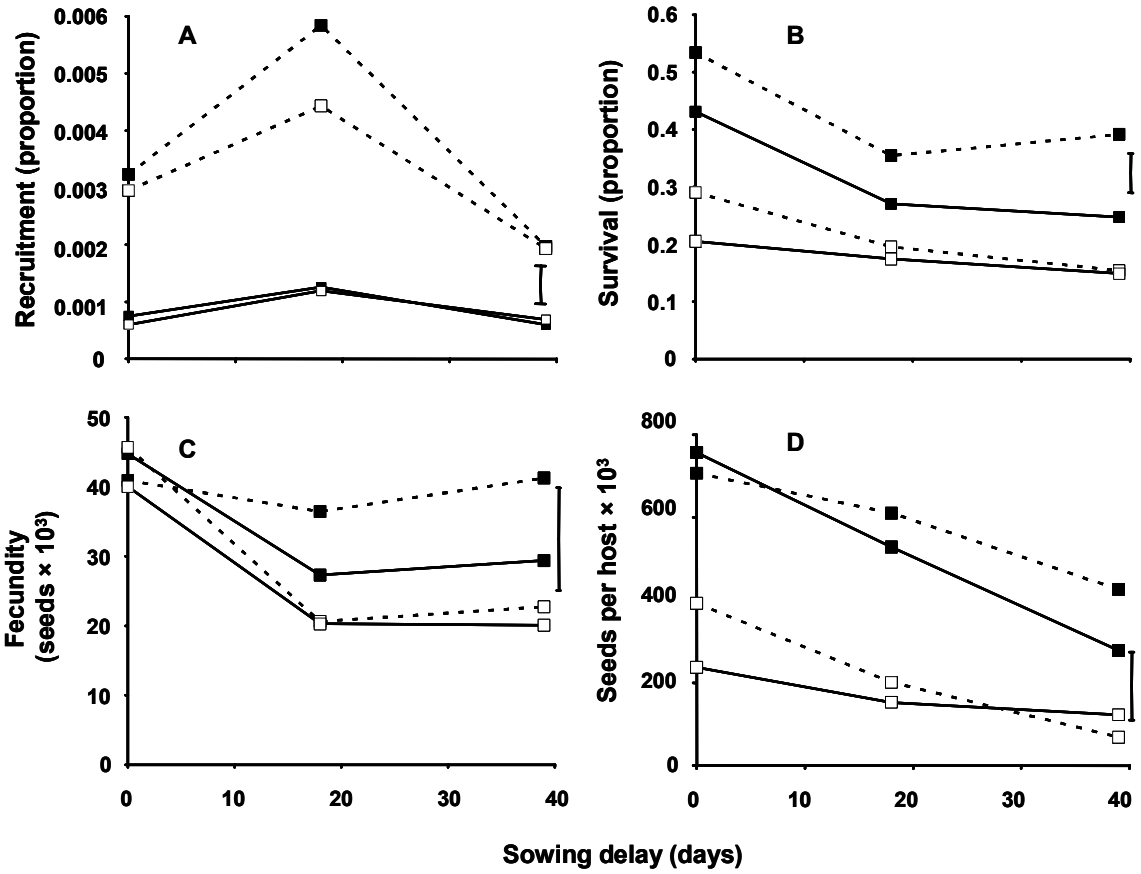

Fig. 2. *Striga hermonthica* recruitment, survival, fecundity and seed production (A-D) related to days sowing delay (DSD) in experiment 3 in 2003. Data are presented separately for the normal cycle long duration sorghum host (■) and the same host harvested at flowering (□), the high inoculation density of 60,000 *Striga hermonthica* seeds host^{-1} (solid lines) and the lower inoculation density of 12,000 seeds host^{-1} (dotted lines). Bars show the least significant difference (LSD) for comparison of any two treatment means, for significance of effects and interactions see Table 3.

duration host yielded less dry weight than a long duration host. Host duration in experiment 5 reduced survival to maturity of emerged Striga plants ($P<0.05$), but did not change any other parameter (recruitment, fecundity, seed production or Striga or host dry weight). In conclusion, host duration did not affect Striga recruitment or dry weight in any of the experiments (Tables 3 and 4). In two out of five experiments, a shorter host duration significantly reduced Striga seed production. Furthermore, in three out of five experiments, shorter host duration resulted in significantly lower survival to maturity.

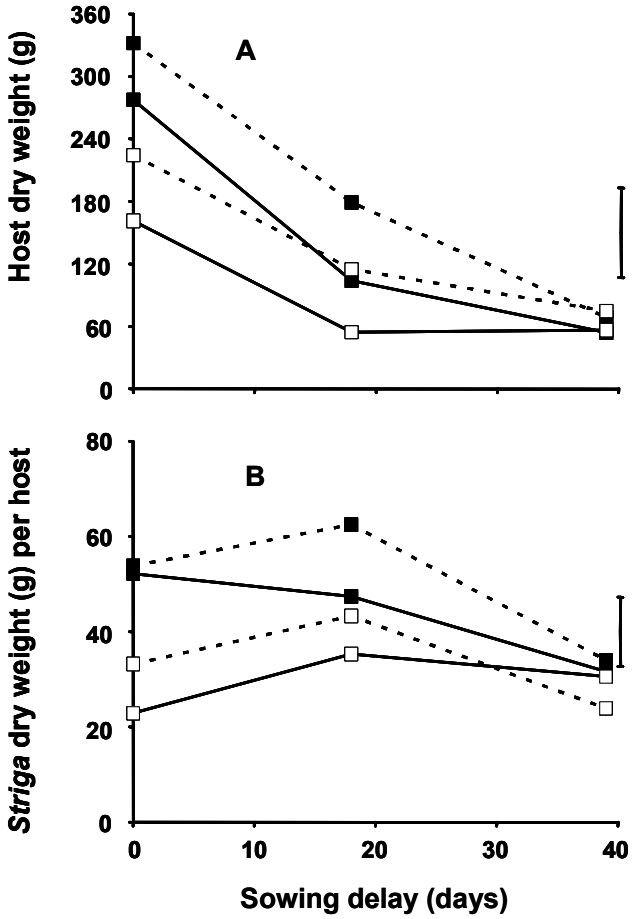

Fig. 3. Sorghum host (A) biomass and *Striga hermonthica* (B) biomass (per host) related to days sowing delay (DSD) in experiment 3. A long duration sorghum host (■) and an artificially shortened duration sorghum host (□) were evaluated. Solid lines represent a high inoculation density of 60,000 *Striga hermonthica* seeds host^{-1} and dotted lines represent a lower inoculation density of 12,000 seeds host^{-1}. Bars show the least significant difference (LSD) for comparison of any two treatment means (Table 3).

Effects of season length

Shortening the growing season by days sowing delay (DSD) significantly ($P<0.001$) affected Striga recruitment, survival to maturity, fecundity, seed production dry weight and host dry weight in experiment 3 (Table 3). Increase in DSD negatively affected survival to maturity, fecundity and total seed production (Fig. 2, Table 3). Striga recruitment at 18 DSD was higher ($P<0.05$) than the first and the last sowing for both the artificially shortened host and short duration host (Fig. 2A). The interaction between sowing delay and host duration affected survival to maturity, because no effect of sowing delay was observed on survival for the short duration host (TIEM S), while the first sowing showed a higher survival in the long duration host (TIEM L)

than the later sowings (Fig. 2B). Sowing delay and interaction between sowing delay and host duration affected Striga dry weight ($P<0.001$ and $P<0.01$, respectively). There was a peak of Striga dry weight in the second sowing (Fig. 3B and Table 3). Later sowing reduced ($P<0.001$) host dry weight. There was a significant interaction between effects of host crop duration and sowing delay on Striga dry weight ($P<0.05$), as there were no significant differences between sowing dates for an artificially shortened host but a significant difference for a long duration host (Fig. 3B).

Effects of Striga inoculation density

Higher seed density reduced Striga recruitment and survival to maturity ($P<0.001$) but did not affect fecundity or the total amount of seeds produced in experiment 3 (Fig. 2, Table 3). Although higher Striga seed density reduced host biomass in experiment 3 ($P<0.01$) Striga dry weight did not change subsequently (Fig. 3, Table 3).

Effect of emergence time of* Striga hermonthica *on seed production

The results of the cohort study in experiment 3 (Figs 4 and 5) yielded more detailed information in addition to the results shown in Fig. 2. First, it becomes clear from Figs 4A and 5A that emergence peaks were found from 76–90 DAS and from 51–60 DAS for the first and the last sowing, respectively. This accounts for both a long duration host (TIEM L) as for an artificially shortened duration host (TIEM S). Interestingly, these emergence peaks are around the same time in terms of day of the year, suggesting that somehow this emergence is synchronized, independent of host crop duration or sowing delay. Furthermore, no plants emerged after 90 DAS for the latest sowing. Smaller proportions of later emerging cohorts reach maturity for the earliest as well as the latest sowing. When looking at fecundity (Figs 4C and 5C), a long duration host allowed higher seed production than when its' duration was artificially shortened. The first cohort produced almost two times as many seeds on the long duration host than on the artificially shortened host.

There was a steep decline in fecundity for later emerging cohorts. Fecundity of plants from the same cohort was similar when comparing the first and the last sowing, however. Under ideal conditions (long duration host and early sowing), the average and maximum individual mature Striga plant fecundity within the first cohort was 107,000 and 313,000 seeds per mature Striga plant, respectively (Fig. 4C, individual plant fecundity not shown).

Total seed production per cohort was lower on the artificially shortened host than on a long duration host and lower with later sowing (Figs 4D and 5D). When looking at the first cohort however, seed production is the same for both host crop durations which is true for both the first and the last sowing. In other words, the difference,

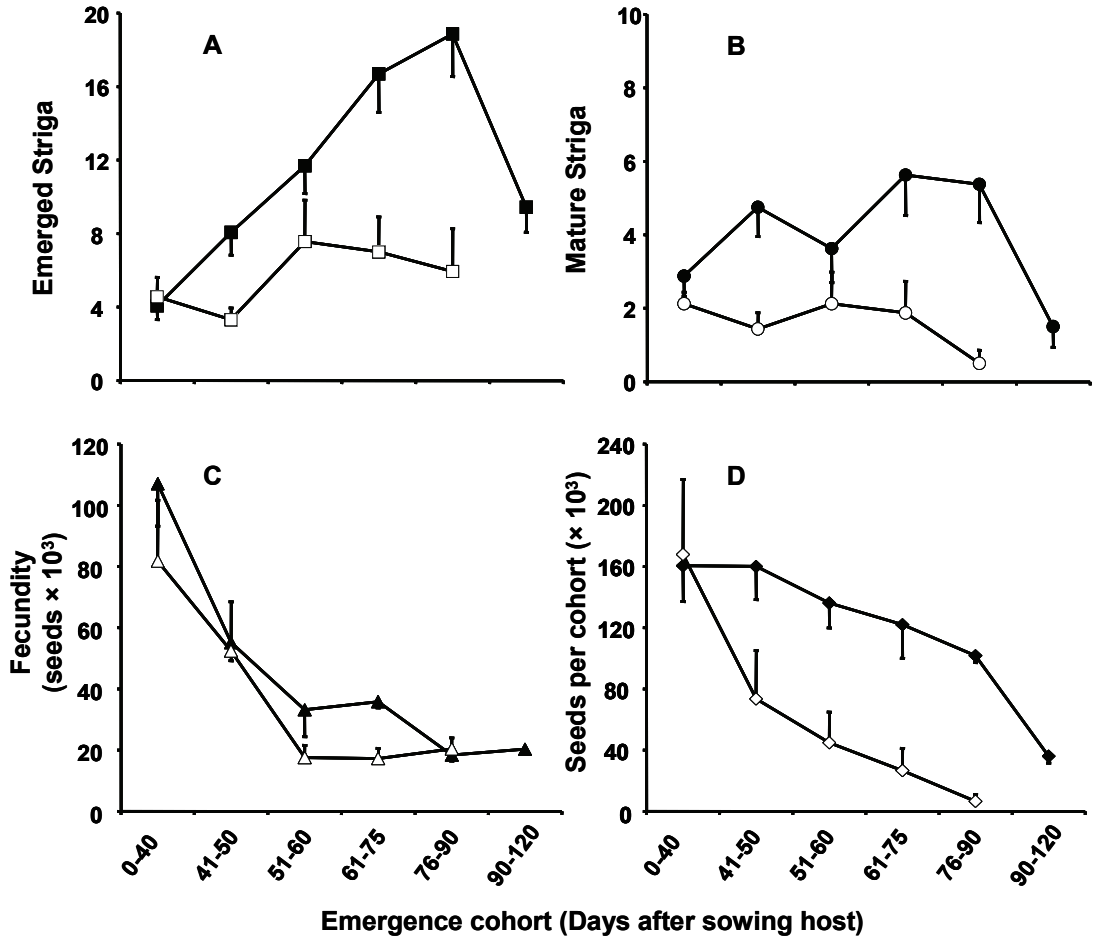

Fig. 4. Demography of separate emergence cohorts of *Striga hermonthica* from emergence to seed production (experiment 3, 2003) for a long duration sorghum host when sown on 0 (closed symbols) and 39 (open symbols) days in the experiment (delayed sowing is shorter season treatment). Graphs A and B represent the number of emerged and mature plants in each cohort per sorghum host, respectively. Graphs C and D represent fecundity per cohort (number of seeds produced per mature plant) and total number of seeds produced per cohort per sorghum host, respectively. Error bars in each graph represent standard errors of the mean (SEM). n=16.

between earlier and later sowings in terms of Striga seed production for both the long and artificially shortened sorghum host is due to lower overall seed production of later emerging cohorts.

The effect of control options

In experiment 4 (Samanko 2004), recruitment was very low on all treatments when compared to other years and sites (Table 4 and Fig. 2). In fact, recruitment was so low that none of the demographic parameters of Striga were significantly influenced by the

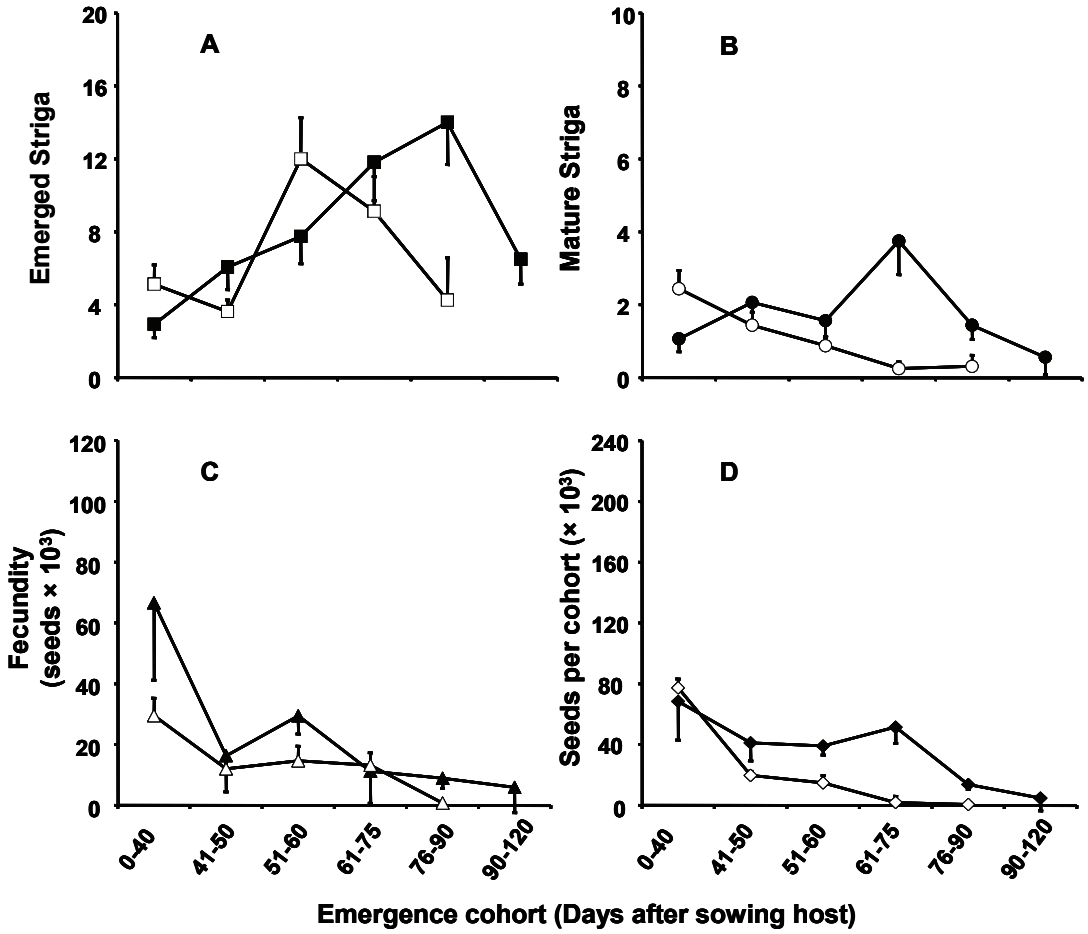

Fig. 5. Demography of separate emergence cohorts of *Striga hermonthica* from emergence to seed production (experiment 3, 2003) for an artificially shortened host (same cultivar as in Fig. 4) when sown on 0 (closed symbols) and 39 (open symbols) days in the experiment (delayed sowing is shorter season treatment). Graphs A and B represent the number of emerged and mature plants in each cohort per sorghum host, respectively. Graphs C and D represent fecundity per cohort (number of seeds produced per mature plant) and total number of seeds produced per cohort per sorghum host, respectively. Error bars in each graph represent standard errors of the mean (SEM). n=16.

control options (Table 4). With this very low recruitment, weeding at flowering prevented all Striga plants from reaching maturity and consequently no seeds were produced. Sorghum dry weight was affected ($P<0.05$) by different control options with CSM63E having particularly low dry weight and IC COW having lower dry weight ($P<0.05$) than the control (TIEM L). Cowpea had significantly more biomass production than silverleaf desmodium, which had very poor establishment and subsequently produced little dry weight. Furthermore, IC DES was not different from the control (TIEM L) considering host dry weight ($P>0.05$), because of the very low

biomass production of the intercrop. In Mali, the intercrop with cowpea reduced sorghum biomass by 50%, reduced Striga dry weight by 86% and Striga seed production by 89% as compared to the control treatment (TIEM L).

In experiment 5 (Niger, 2004) with pearl millet, recruitment was reduced ($P<0.05$) in both the intercrop treatments with sesame and cowpea (IC SES and IC COW, respectively) when compared to the control treatment (SAD). Recruitment on the control treatment was not significantly different from addition of organic amendments (SAD ORG), a short duration host (3/4HK) or weeding at Striga flowering (SAD WEED) (Table 4). Survival was significantly reduced ($P<0.05$) by the intercrops and weeding at Striga flowering (SAD WEED), compared to the control treatment (SAD). Fecundity of mature plants was reduced ($P<0.05$) by weeding at Striga flowering (SAD WEED) and by the intercrop of millet with sesame (IC SES), when compared to the long duration host cultivar (SAD). An intercrop of millet with cowpea (IC COW) did not affect fecundity as compared to the long duration host cultivar (SAD). Striga seed production was reduced ($P<0.05$) by intercropping sesame (IC SES), weeding at Striga flowering (SAD WEED) and intercropping cowpea (IC COW) when compared to seed production on a long duration host (SAD). However, adding organic amendments (SAD ORG) or planting a short duration millet cultivar (3/4HK) did not influence seed production significantly compared to the control. Striga dry weight was lower as a result of intercropping and weeding Striga at flowering compared to addition of organic amendments ($P<0.05$). Millet dry weight was strongly reduced ($P<0.05$) when intercropped with either sesame or cowpea, but not affected by weeding (SAD WEED) or addition of organic amendment (SAD ORG) in comparison to the control (SAD). The dry weights of the cowpea and sesame intercrops were not different from each other in experiment 5 (Niger, 2004). Intercropping cowpea reduced millet dry weight drastically by 85% and decreased Striga dry weight and seed production by 87% and 94%, respectively. More interestingly, the intercrop with sesame reduced host dry weight by 68% and reduced Striga dry weight and seed production by 97.5% and 99.8%, respectively.

Discussion

Factors determining the level of Striga hermonthica seed production

In this study, Striga seed production was affected significantly by different treatments, such as manipulated season length (2003), host crop duration (2002, 2003 and 2004), intercropping (2004) and weeding (2004), but not by differences in inoculation densities (2003).

Host crop duration

Shorter host crop duration significantly reduced Striga seed production in two out of five cases. However, these levels of seed production do not necessarily lead to reductions in seed bank density, as shown by the considerable amounts of seeds still produced by Striga on a short cycle host in some years and sites (Fig. 3 and Table 4). Also, short duration millet or sorghum hosts often produced less dry weight but did not necessarily support consistently less Striga dry weight (Fig. 4, Table 4). It is probable that there have been cultivar differences in terms of Striga resistance levels between short and long duration host cultivars in 2002 and 2004. Artificially reducing the duration of host presence by premature harvesting in 2003, led to a highly significant decrease in Striga survival to maturity, fecundity, seed production and dry weight indicating that the shorter duration at least explains part of the effect of shorter cycle hosts. The best comparison should have been in experiment 4 when both truly shorter cycle sorghum and an artificial shortened cycle were compared, but overall Striga performance was so low that these data cannot provide a proper answer.

Our observations support the observations of Carsky *et al*. (1996), who found significantly less increase in Striga seed bank density after two years of growing improved short duration sorghum cultivars compared to indigenous long duration sorghum cultivars. Van Ast *et al*. (2005) found that a delayed emergence date of Striga strongly reduced the number of flowers produced which indicates a reduction in potential seed production. Similarly, our results from the cohort study show that later emerging cohorts of Striga plants have lower survival to maturity, fecundity and subsequent seed production. We conclude that any intervention aiming at decreasing the time between first Striga emergence and crop maturity and harvest or Striga plant death will reduce the seed production.

Season length

Season length (i.e., days sowing delayed) significantly affected seed production through survival of plants to maturity and fecundity with a shorter season leading to less survival to maturity, lower fecundity and thereby to lower seed production. This decrease in seed production coincided with a decrease in host dry weight, but not in Striga dry weight. From this observation it can be concluded that with a shorter season more dry weight of the hemi-parasite was lost in the form of pre-mature dead plants and that mature plants did not reach their full reproductive potential, thereby reducing fecundity and total reproductive output. Seed production may depend on season length (manipulated within one year), although very low recruitment or low survival to maturity might override season length as determining factor. As far as we know, there is no literature available that could support or contradict our findings regarding season

length and Striga seed production.

Seed density

The differences in inoculation density of Striga seeds in the soil in 2003 did not significantly affect seed production, which suggested density dependence prior to seed production. This supports the suggestions and results of other studies (Doggett, 1965; Webb & Smith, 1996; Van Delft *et al*., 1997) as well as recent findings of Rodenburg *et al*. (2006b) and Van Ast *et al*. (2006). At the densities used in this study, density-dependence was most pronounced in recruitment, the step from seed density in the soil to emergence and was to a lesser extent observed between survival and maturity (Figs 3A and B). This density dependence clearly indicates the concept of maximum carrying capacity of a host is relevant in the sorghum - Striga relationship. However, from this study it is not clear if and at what stage of the life cycle density-dependent processes act at much lower densities of seeds in the soil. It is possible that at lower densities (a number of attachments far below the carrying capacity of a host), this density dependence is not expressed or expressed in other stages of the life cycle. In the experiment in Mali in 2004, Striga recruitment was extremely low considering inoculation densities in the soil, which indicates that other factors may have acted here.

Intercropping

Intercropping cereal hosts with sesame and cowpea significantly reduced the recruitment of Striga plants and subsequent seed production. The *Desmodium uncinatum* intercrop established poorly and growth was very slow which could explain that this intercrop had no effect on Striga (Table 4). Although Silverleaf desmodium has been found to be an interesting trap crop with allelopathic properties in East Africa (Khan *et al*., 2002), it may have difficulty establishing in the West African Sahel. Our data indicate this specific species of cover/fodder crop may not be a very promising one for this region, although there may be potential for other species from the same family if they are better adapted (Khan *et al*., 2006). The big drawback of the intercrops sown at the density and timing used in these experiments is that they reduced dry weight of the host considerably, which is an unwanted side effect sometimes found in intercrops (Fukai & Trenbath, 1993).

However, when intercrop densities are slightly lower or when sowing of the intercrop is delayed for one to two weeks, often no negative effects of competition are found, while in some cases, even positive effects of a legume intercrop on the cereal are found (Khan *et al*., 2006; Samaké *et al*., 2006). In addition to rotation with sesame (Hess & Dodo, 2004), there may be potential for sesame as intercrop to reduce Striga

seed production, albeit at lower densities or with different sowing regimes at which higher (acceptable) dry weight and yield of the cereal host may be expected, but Striga is still suppressed. To this aim additional research is warranted.

Many authors have studied the effect of intercrops on the number of emerged Striga plants (recruitment) (Carsky *et al*., 1994; Reddy *et al*., 1994; Oswald *et al*., 2002; Tenebe & Kamara, 2002; Kuchinda *et al*., 2003; Reda *et al*., 2005), but to our knowledge, only Carsky *et al*. (1994) monitored how many plants actually produced capsules. They found that the number of capsule-bearing Striga plants was negatively correlated with cowpea cover, although no effect of the intercrop on Striga emergence was found when compared to cereal monoculture. Carsky *et al*. (1994) concluded, that the reduced number of capsule forming plants was related to aboveground (i.e. shading) rather than belowground suppression (i.e., acting on germination and attachment). Our data from Niger in 2004 suggest that the higher density intercrop used in the experiment, acted not only on the survival to maturity step but also on the recruitment step (Table 4). Whether this is purely the effect of density, possibly even through suppression of the host itself, or whether also at lower densities intercrops may influence recruitment will need further study.

Weeding at Striga flowering

Weeding at Striga flowering was effective in reducing Striga seed production, but did not fully prevent seed production in Niger, 2004. It was observed that resprouting enabled plants to quickly form new flowers and produce seeds even after the millet host shoots had been harvested. Also, without weeding at Striga flowering, in 2002 and 2003 Striga plants continued to form new flowers and capsules until about three weeks after the host sorghum shoots had been harvested, confirming observations by Webb & Smith (1996). The difference in suppression of seed production between Mali and Niger suggests that prevention of seed shed by late weeding depends on emergence time and densities of Striga plants. Weeding will not completely suppress seed production if emergence levels are high and conditions for resprouting are favourable (i.e., humid conditions after cereal crop harvest).

Organic amendments

Organic amendments did not have any significant effect on Striga demographic parameters or dry weight. Although not significant ($P>0.05$), millet dry weight tended to be 25% higher after addition of organic amendments. Sauerborn *et al*. (2003) found lower Striga seed densities and emergence in fields with a higher organic matter content. However, adding organic amendments in a single year does not immediately change the organic matter content perceptibly. It is possible that in the long-term,

continuous addition of organic material can have suppressing effects on the Striga seed bank (Ahonsi *et al*., 2002). This suppressing effect may be related to increased microbial activity and attack of underground stages of Striga (seeds, germinated seeds, attached seedlings) by fungal pathogens (Van Mourik *et al*., 2005) or seed predators. However, we did not find a direct effect of organic amendments on aboveground demographic parameters of Striga in this study, with the quantity used (2 t ha^{-1}).

Striga seed production and population dynamics

Most studies that report seed production estimates, give no information on growing conditions of the (host) plants or the number of Striga plants per host (Andrews, 1945; Parker & Riches, 1993; Van Delft *et al*., 1997) with some (recent) exceptions (Webb & Smith, 1996; Van Ast *et al*., 2005; Rodenburg *et al*., 2006b). In this study, we have shown the value of analysing different stages in the Striga life cycle in order to assess at what step control options reduce seed production. This should help to combine different control options to optimize efficacy. For example, an intercrop can be combined with a short cycle host and weeding of the few plants that still emerge. In this way the population could be controlled throughout different stages of the life cycle. Because of the effects of the shorter host crop duration and the intercrop, the number of emerged plants will already be reduced and, therefore, the weeding would then take care of those escapees from the intercrop and short duration host. These escapees are expected especially in Striga favourable years, when emergence levels are high.

Concluding remarks

In this study, we quantified Striga seed production when growing on a typical long duration and relatively tolerant sorghum host in three seasons, setting a standard (control) seed production under normal conditions. In 2004 also seed production on a millet host was quantified in this way. In addition, a number of potentially Striga-suppressing treatments were evaluated and could be compared to this standard providing much more quantitative information supplementing previously reported Striga plant counts with actual produced seed numbers in evaluating control options. The presented seed production data could hereafter be linked to seed losses to make a quantitative estimate of seed bank dynamics over years. Eventually, this information will help to construct a quantitative model that can forecast seed bank dynamics under different combinations and sequences of control options and management strategies. By understanding the different aspects of seed bank ecology of Striga in addition to agronomical and economical evaluations of Striga control options of other studies, this study intends to aid in the development of integrated Striga management strategies.

CHAPTER 3

Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks*

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Abstract

Estimates of seed bank depletion rates are essential for modelling and management of plant populations. The seed bag burial method is often used to measure seed mortality in the soil. However, the density of seeds within seed bags is higher than densities in natural seed banks, which may influence mortality. As ample information was available for *Striga hermonthica* and as different methods for measuring seed mortality in the soil yielded contradicting estimates, this species was chosen. The aim of this study was to quantify the effect of fungi and seed density within buried mesh bags on mortality of seeds of *S. hermonthica*.

Seed bags were buried in soil and exhumed at time intervals to monitor mortality of the seeds in three field experiments during two rainy seasons. In 2002, the effect of fungal activity on seed mortality was evaluated in a fungi exclusion experiment. Differences in seed-to-seed interaction were obtained by using two and four densities within the seed bags in consecutive years. Densities were created by mixing 1000 seeds with 0, 10, 100, 1000 g of coarse sand.

Mortality rate was significantly lower when fungi were excluded, indicating the possible role of pathogenic fungi.

Decreasing the density of seeds in bags significantly reduced seed mortality which is suggested to be the result of decreased seed-to-seed contamination by pathogenic fungi.

Models of plant populations in general and annual weeds in particular often use values from the literature for seed bank depletion rates. These depletion rates have often been estimated by the seed bag burial method. Unrealistically high seed mortality rates may, therefore, be presumed because of an unnaturally high density of seeds within the bags which lead to an overestimation of the effects of soil or seed borne pathogens. Species that have been classified from such studies as exhibiting short-lived seed banks may need to be re-assessed using realistic densities either within seed bags or otherwise. Similarly, models of seed bank dynamics based on such overestimated depletion rates may lead to incorrect conclusions regarding their seed banks and perhaps, the management of weeds and rare species.

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Introduction

Soil seed banks play an important role in many plant populations and their dynamics have, therefore, been studied and modelled extensively to predict emergence and population development, especially for weeds (Grundy *et al*., 1999, 2003; Buckley *et al*., 2004). An important element in seed bank dynamics is seed bank depletion, which includes seed predation (Westerman *et al*., 2003), unsuccessful germination (Grundy *et al*., 2003), seed movement and seed mortality due to ageing and attack by pathogens (Londsdale, 1993). The seed bag burial method is used for monitoring the longevity and dormancy of plant seeds in soil seed banks (Rampton & Ching, 1966; Lewis, 1973; Egley & Chandler, 1978). This method is frequently used when very small seeds are being studied, such as those of parasitic weeds (Lopez Granados & Garcia Torres, 1999; Gbèhounou *et al*., 2000, 2003; Van Mourik *et al*., 2003). Seed bags have also been used to study the effect of fungi on soil seed mortality (Crist & Friese, 1993; Dalling *et al*., 1998).

A more realistic way to mimic a natural seed bank would be to create soil without seeds and then add fresh seeds at a density similar to that encountered in natural seed banks (Scopel *et al*., 1988; see Baskin & Baskin (1998) for a review of densities recorded for different species). Although soil or sand has been mixed with the seeds in bags in some studies (Teketay & Granstrom, 1997; Lopez Granados & Garcia Torres, 1999; Blaney & Kotanen, 2001), the amount of sand or soil has not been related to densities or seed-to-seed distances found in naturally-occurring soil seed banks. Studies rarely quantify the seed density by a number to weight or volume ratio of seeds to substrate (Lopez Granados & Garcia Torres, 1999; Blaney & Kotanen, 2001). This is surprising as seed-to-seed distance may play an important role in density regulated seed loss through predation or seed pathogens (Dalling *et al*., 1998). One exception is a study by Dalling *et al*. (1998) who simultaneously studied seed survival with the seed bag burial method and through soil sampling. Their data indicate a seed density dependence of seed survival.

For detailed assessments of mortality the seed bag burial method seems advantageous compared to soil sampling as known amounts of seeds can be monitored over time in the former while heterogeneity is likely to bias results from the latter method. In the present study the influence of seed density in seed bags was determined using *Striga hermonthica* (Del.) Benth., a typical r-strategist that can produce over 200,000 seeds per plant (Parker & Riches, 1993). Furthermore, an extensive but conflicting literature exists regarding seed mortality estimates of this species, ranging from 43% mortality after 2 years and up to 100% mortality in a single season.

With the seed bag burial method, mortality rates of *S. hermonthica* seeds have been estimated to range between 80 and 100% in the course of one rainy season in

field soils (Pieterse *et al*., 1996; Gbèhounou *et al*., 2003; Van Mourik *et al*., 2003). In these studies, samples of about 1000 seeds were buried in the field in nylon gauze bags with a 90–100 μm mesh and vegetation cover was prevented by frequent weeding. Pieterse *et al*. (1996) suggested that microbial activity caused most seed mortality. Van Mourik *et al*. (2003) estimated that with the method used about 86% of seed death during the rainy season (June–October) was caused by fungal activity. Using a soil sampling method, Van Delft *et al*. (1997) found depletion of about 70% and 50% after one year of fallow at 0–5 cm and 6–10 cm depths, respectively. Murdoch & Kunjo (2003) reported 43% depletion of the natural seed bank only over two rainy seasons on a field where the host crop sorghum (*Sorghum bicolor* (L.) Moench) was grown and seed bank replenishment was prevented. Similar results were found by Oswald & Ransom (2001), who used crop rotations with non-host trap crops. The authors also noted that depletion of the seed bank seemed to be highest where initial seed density was highest, indicating a possible density dependency in the process. It seems possible that burial of seeds in mesh bags may lead to an overestimate of natural rates of depletion of soil seed banks, in particular for *S. hermonthica*.

We address three questions: (1) To what extent does fungal activity determine the rate of *Striga* seed mortality when the seed bag burial method is used? (2) What is the effect of seed density within a seed bag on the rate of *Striga* seed mortality? (3) Does the seed bag burial method, as commonly used, provide realistic estimates of seed mortality in naturally occurring soil seed banks?

Materials and methods

Striga hermonthica is a hemi-parasitic weed growing on cereal crops and wild grasses in the Savanna and Sahel zones of sub-Saharan Africa. It poses an increasing threat to cereal production in these regions (Parker & Riches, 1993). Commonly, the number of seeds produced is higher than the seed mortality rate in the soil, leading to very high seed bank densities. Estimates of average seed bank densities of *Striga* species range from 1,800 to 414,600 seeds m^{-2}, taken from a field in Kenya (Oswald & Ransom, 2001) and Ghana (Sauerborn *et al*., 2003), respectively. The upper value is the highest ever recorded for any one species in a field (McIntyre, 1985; Baskin & Baskin, 1998).

S. hermonthica seeds are very small (0.2 m × 0.3 mm, 0.4×10^{-2} mg) and a single mature plant may produce more than 200,000 seeds (Parker & Riches, 1993). Seeds were collected from about 300–500 plants of a *S. hermonthica* population growing on sorghum at an experimental field station of the International Crops Research Institute for the Semi Arid Tropics (ICRISAT), Samanko, Mali, in November 2001.

Two sites were established at (1) the experimental field station of ICRISAT in Samanko, Mali and (2) the field station of the Institute d'Economie Rurale (IER) in

Cinzana, Mali. Samanko is located about ten km south of Bamako (8°54'W; 12°54'N) and has an average annual precipitation of about 950 mm year^{-1}. The length of the growing season is 150 days and the experimental field site has a sandy loam soil. Cinzana is located east of Segou (5°7'W; 13°15'N) and has an average annual precipitation of about 650 mm year^{-1}. Length of the growing season is approximately 120 days and the experimental field has a clay soil. Both sites have a monomodal rainfall pattern.

In 2002, 120 nylon gauze seed bags (5 cm × 5 cm, mesh size 90 μm, Stokvis & Smits B.V.) were either filled with 4 mg of *S. hermonthica* seeds alone or with the same amount of seed mixed with 10 g of coarse sand (0.3–0.8 mm). Organic debris was first removed from the sand by washing in a table-top elutriator. The sand was air dried and mixed with seeds before filling the seed bags. The seed-sand mixture gave a seed density of 100 seeds g^{-1} soil. Sixty bags were buried at each site, allowing 10 exhumation dates and 3 replicates for each of the two densities. Samples were buried in a randomized design, at 5 cm depth in Samanko and Cinzana on 17 and 21 June 2002, respectively. Over the course of the experiment, rainfall was 436 mm in Cinzana and 849 mm in Samanko. The experimental area measured 3 m × 5 m and was kept free of plants by weekly hand weeding. The samples were buried in groups of two treatments, 5 cm apart, in the centre of individual plots of 0.5 m × 0.5 m.

The fungi exclusion experiment in 2002 consisted of a fungicide and a control treatment, eight sampling dates and three replicates in a randomized design. Soil was exhumed as 48 separate cores, in a rectangle of 6 × 8 cores. Each core was dug in a square of 50 cm × 50 cm. Cores (10 cm diameter) were exhumed in three layers corresponding to depths of 0–5, 5–10 and 10–25 cm. After removing the cores, a PVC-tube (length 30 cm, diameter 10 cm) was inserted in each hole, leaving 5 cm of the tube above the soil surface. Exhumed soil was air dried at ambient temperatures (18.5–42 °C) and air humidity (58.6–80.9% RH) for 48 hours. On 26 June, the 10–25cm and 5–10 cm layers of soil were returned to the PVC tubes according to their original depth and position in the plot in order to conserve vertical and horizontal soil structure. The seed bags were placed on the soil and 4 mg of the fungicide APRON+® (Metalaxyl, Syngenta (US)) was sprinkled on top of the bags in the fungicide treatment. The remaining 5 cm of soil was added and incubation time began.

Before burial, seeds were surface-sterilized in the fungicide treatment by submerging the seed bags in 100 ml 1% NaClO, including 1 ml of the surfactant Tween 20® (polyoxyethylene sorbitan monolaurate, Merck Schuchardt) for five minutes and then rinsing with 200 ml distilled water. The seed bags were air-dried under laboratory conditions. In the fungicide treatments, 4 mg of fungicide was added on top of the soil every month; the experiment received 805 mm of rain within the

period of monitoring.

In 2003, four seed densities were tested, namely 1000 seeds mixed with 0, 10, 100, 1000 g of coarse sand seed bag^{-1}. The higher quantities of sand were additional, lower seed density treatments. As sand volume increased, bags had to be enlarged to 5 cm × 10 cm, and 10 cm × 20 cm, respectively. In total, 84 bags were buried on 17 June 2003, allowing seven exhumation dates and three replicates per density. Samples were buried at 5 cm depth in a randomized design in 1 m × 1 m subplots, divided into four 0.5 m × 0.5 m sections for each density treatment. During the monitoring period, the area received 952 mm of rain. Soil temperatures at 5 cm depth ranged between 20.5 °C and 47.7 °C in 2003 and plots were kept weed free by weekly hand weeding.

On exhumation of bags in 2002, soil was washed off and the content was immersed in 500 ml of saturated magnesium sulphate ($MgSO_4$) solution. While gently stirring the suspension for two minutes, inorganic soil particles sank to the bottom, whereas organic material (seeds) stayed in suspension. The upper 400 ml of suspension was then passed through a sieve filter with a mesh size of 100 µm. In 2003, seed bags were handled in the same manner except that 1000 ml of the magnesium sulphate solution was used and the upper 800 ml of suspension was filtered. The content of the lowest density treatment was first washed using a tabletop elutriator, to decrease sand volume. The sieve filter with seeds was thoroughly rinsed with tap water and seeds were air-dried for 30 minutes.

A 100–200 seed sample was selected from each bag for detailed analysis. In 2002, seeds were first imbibed in distilled water for at least 30 minutes before imbibing in 1% NaClO for five minutes to bleach the testa. In 2003, seeds were first bleached in a vial with 4 ml 1% sodium hypochlorite solution and 50 µl Tween 20® for 2 minutes, rinsed with distilled water and thereafter imbibed in distilled water for at least 20 minutes. After imbibition and bleaching, seeds were scored visually under a stereomicroscope for infected seeds, empty or intact seeds. First, infected seeds were scored and then the remaining seeds were pressed with a needle. If a white endosperm could be pressed from the seed testa, the seed was scored as intact and presumed healthy and if not, it was scored as being empty. Black (i.e., infected) and empty seeds were considered dead.

Statistical analysis

Mortality rates were quantified using probit analysis with the statistical software package GenStat v. 6.1. For the 2002 data, a probit model (GLM) was fitted with a treatment × slope interaction term to compare the curves fitted for the treatments (density and fungicide addition). The data from 2003 were similarly analysed using a probit model testing the hypothesis of separate slopes and intercepts for the different

density treatments. The fitted values of the probit models were transformed back into proportions to show the fitted curves in their sigmoidal form.

Results

In 2002, seeds lost viability rapidly at both sites, especially when the pure seed sample was used (Figs 1A, B). There were significant differences in the mortality rate between a pure seed sample and a sample mixed with 10 g of sand ($P<0.001$, df=33, n=36 for Cinzana and $P=0.029$, df=33, n=36 for Samanko). The fungicide treatment reduced the mortality rate (Fig. 1C) as shown by the significant difference in the slopes of the mortality curves for the two treatments ($P=0.012$, df=51, n=54). The proportion of dead seeds at the end of the rainy season was only 0.1 (SE, 0.024) where fungi were controlled with fungicide and 0.87 (SE, 0.018) in the absence of fungicide (Fig. 1C). The majority of dead seeds was classified as dead because of the presence of a black (infected) endosperm.

The differences in slopes between treatments were significant in an analysis of the 2003 data with the generalized linear model with probit link. The increase in residual sum of squares when fitting a common intercept was not significant. Thus, the model with common intercept and separate slopes was used (Fig. 2). Similar results were obtained when comparing the two density treatments also used in 2002 (Fig. 3), although overall mortality rate appeared to be greater. When comparing mortality of the pure seed sample with those for the three lower densities (10000, 1000 and 100 seeds 100 g sand^{-1}), all slopes were found to differ significantly ($P<0.05$ df=33, n=36). While no significant differences were found between the two intermediate densities, there were significant differences between the two intermediate densities and the lowest density (Fig. 2B).

The probit model gives a relatively good fit for the mortality of seeds in Cinzana ($R^2=0.76$), but less so for the mortality of seeds in Samanko ($R^2=0.64$) (Figs 1A, B). Around 60 days after burial (DAB) the fit is particularly poor to the 2002 data (Fig. 1B) and a similar pattern occurred in 2003 between 50 and 65 DAB (Fig. 2A). For the 2003 data, the model including all treatments explained the variation relatively well ($R^2=0.73$). It is also noteworthy that, as mean proportions of dead seeds move towards 0.5, the variance increases. This indicates that most of the individual values at a snapshot point in time are either high, or low. For instance, taking all 72 data points from the experiment in 2003, only 6 fell within the 0.4–0.6 range. The process of mortality within an individual seed bag therefore seems to be relatively quick.

Considering the density of seeds within a bag as a dose treatment, the relationship between average mortality at the end of the rainy season and density is density dependent (Fig. 3). In 2002, the proportion of dead seeds at the end of the rainy season

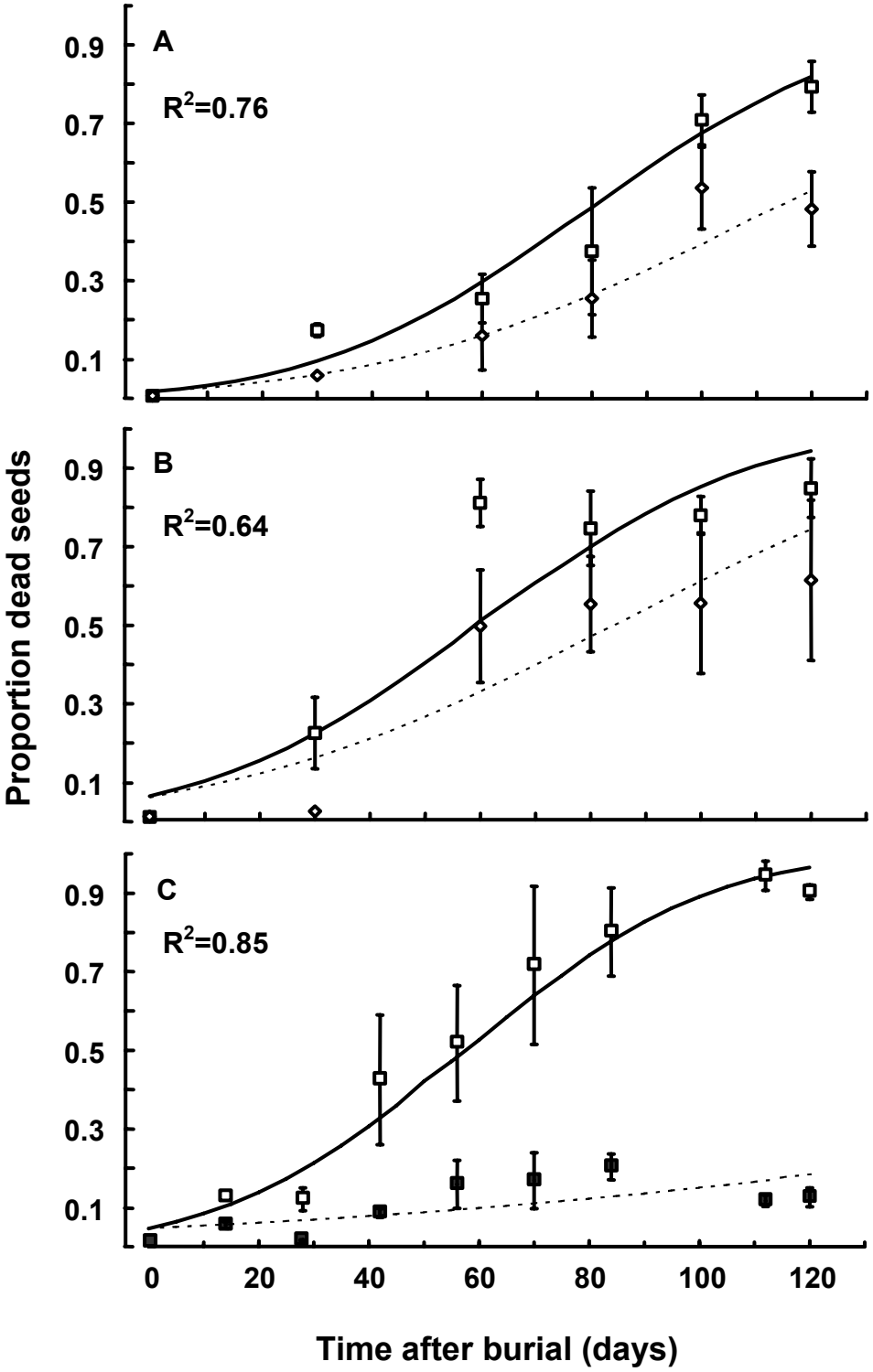

Fig. 1. Mortality of *Striga hermonthica* seeds during the rainy season (June-October) in Cinzana (A) and Samanko (B, C), Mali, 2002. Averages of a pure sample (squares) and a density of 1000 seeds 10 g^{-1} coarse sand (diamonds) in seed bags are given in (A) and (B). The black and open squares in (C) represent the curves fitted to the pure seed sample (solid line, highest seed density) and decreased density in (A) and (B) or fungicide treatment in (C) (dotted lines). Error bars represent SEM.

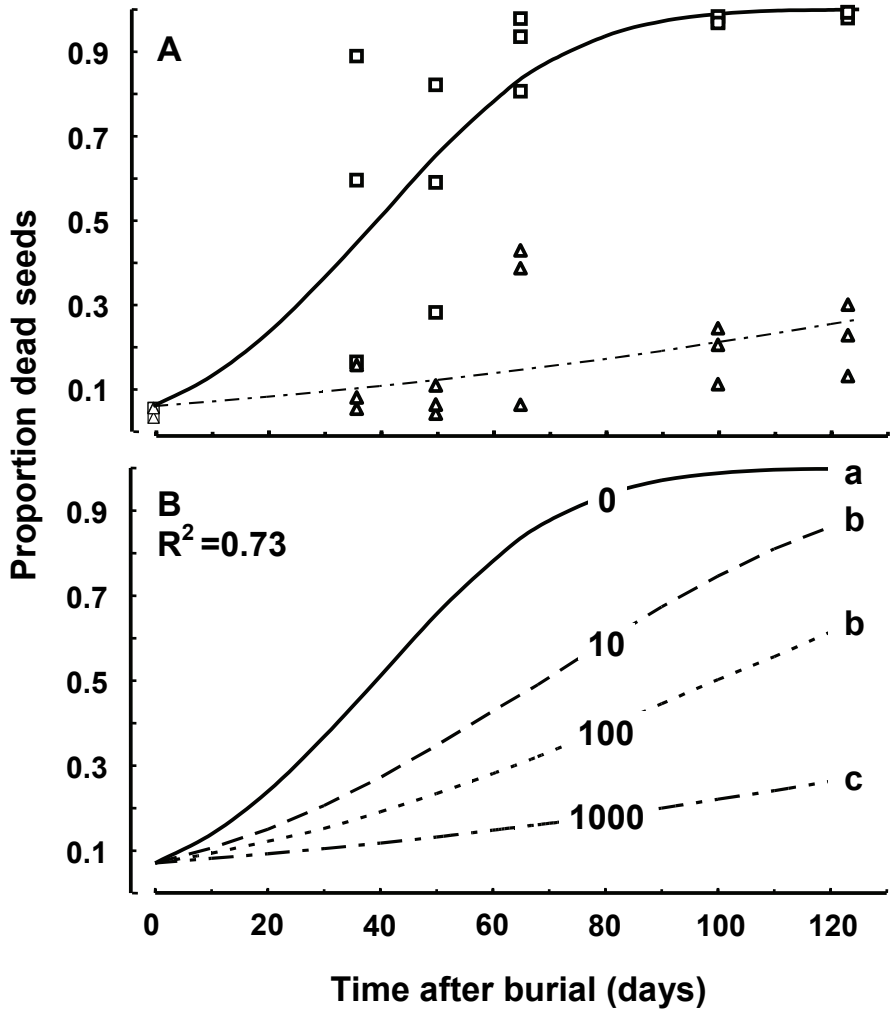

Fig. 2. Mortality of *Striga hermonthica* seeds during the rainy season (June-October) related to different seed densities in seed bags in Samanko, Mali, 2003. Individual data points of a pure sample (squares) and the lowest density of 1000 seeds 10 g sand^{-1} (diamonds) are given in (A). A probit model was fitted to the data of all densities, allowing multiple slopes and one intercept. In (B), the solid, striped, dotted and striped-dotted lines represent different slopes within the model fitted to the pure seed samples (highest density) and 1000 seeds mixed with 10, 100 and 1000 g sand, respectively. Different letters in (B) indicate significant differences between slopes, when comparing slopes of lines with an LSD test ($P < 0.05$).

was lower at the driest site (Cinzana). Furthermore the proportion of dead seeds in Samanko in 2002 was considerably lower than in 2003, for both density treatments. In 2003, a further decrease in densities yielded a concomitant wider spectrum of proportions of dead seeds.

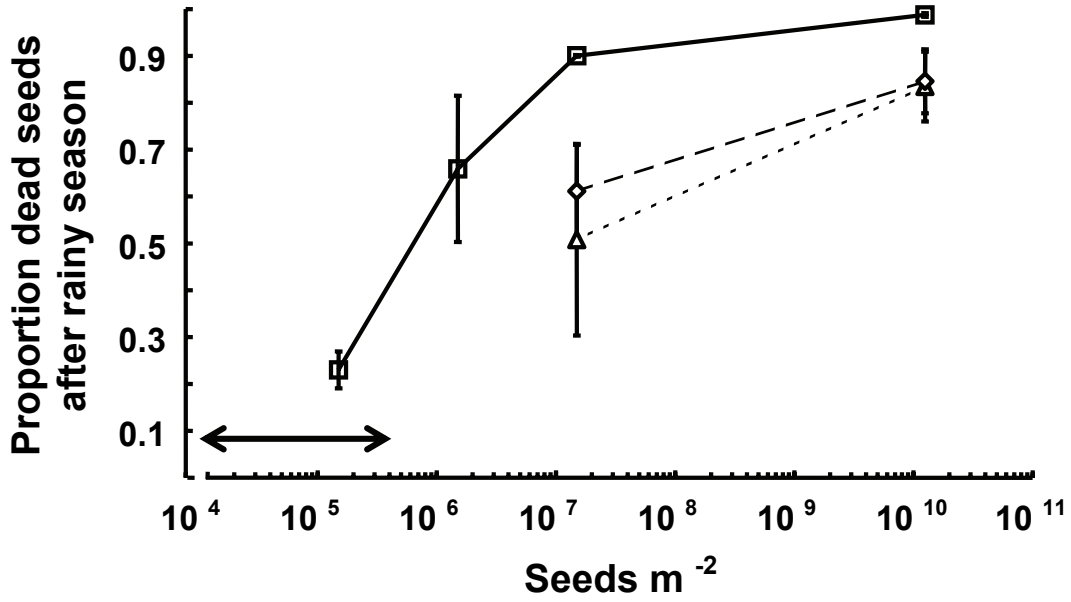

Fig. 3. Relation between seed density (seeds m^{-2}, calculated from the densities of seeds in the seed bags) and the proportion of dead seeds at the end of the rainy season. The averages and SEM of the last three replicates for the different density treatments are shown for Samanko 2003 (□), Samanko 2002 (◊) and Cinzana 2002 (Δ). In 2003, this was 123 days after burial (DAB), and for 2002, 120 DAB. The arrow in the graph indicates the range of densities that have been observed in field soils.

Discussion

Density and Striga hermonthica *seed mortality*

Increasing density and proximity of *Striga* seeds within a seed bag clearly increased the rate of mortality during the rainy season. We suggest that pathogenic fungi were attacking viable seeds, rather than that seeds, which had already lost viability, were being decomposed by saprophytic fungi. Sauerborn *et al*. (1996) reported this phenomenon in the laboratory with the soil-borne pathogenic fungus *Fusarium nyagamai* and showed with electron microscopic analysis that the mycelium of this fungus penetrated the seed coat of ungerminated, intact seeds and destroyed the endosperm. The proportion of dead seeds at the end of the rainy season in 2003 was much higher than in 2002 for both density treatments, at the same site and with the same seed lot. This may be due in part to the age of the seeds at the beginning of the experiment (in 2003, the seeds were 1 year older and the proportion of dead seeds was higher). There may also have been differences in fungal growth in response to soil humidity (Olaya *et al*., 1996) as rainfall and temporal soil humidity patterns vary between years.

The probit model is conventionally used for normally distributed population responses. These are most likely to occur under constant environmental conditions. Obviously, temperature and humidity varied in the field and it is not surprising that the model did not fit certain periods within the rainy season. Furthermore, as one seed in a bag becomes infected, the chance of infection increases for the other seeds in the same bag and the progress of the mortality curve would therefore be expected to be steeper. As timing of infection will differ between bags, a large bag-to-bag variation might also be expected.

If seeds are separated by an inorganic medium such as sand, the chance of one seed infecting others decreases. In this way, infection becomes a process that acts independently on individual seeds, rather than on the seed batch as a whole. Being inert, the sand is not a suitable substrate for fungal growth. It is possible that when the soil has more organic matter, the growth of fungal hyphae over a given distance becomes faster, thus reducing the effect of dilution.

The negative exponential model has often been used to model seed survival in field soils as an alternative to the probit model (Murdoch & Ellis, 2000). There are no theoretical considerations to reject the use of such a negative exponential model for depletion when scored on the basis of the number of seeds per unit volume of soil. It seems, however, only to be appropriate for seed depletion on a year-to-year basis and probably only where germination is the primary means of depletion. In this study, seed death is scored as a fraction of total seed number and the data follow a binomial distribution. For such data the negative exponential model is inappropriate and a probit model is preferred. The probit model appeared to provide a reasonable fit to the data over the relatively short wet season of around four months (Figs 1 and 2).

High mortality rates found in previous studies (Pieterse *et al*., 1996; Gbèhounou *et al*., 2003), correspond to the mortality rates of the higher density treatments in this study. The lower densities created in this study decreased mortality to a level similar to results from studies that used soil sampling methods (Van Delft *et al*., 1997; Oswald & Ransom, 2001; Murdoch & Kunjo, 2003), although the density was still relatively high (about 150,000 seeds m^{-2}). Interestingly, only one of the decreased density treatments falls within the range of naturally-occurring seed densities in the soil seed bank (Fig. 3). The seed bag method using pure or almost pure seed samples appears to yield an estimate of *S. hermonthica* seed mortality much greater than for natural seed banks.

Fungal pathogens and density in seed survival studies

This study shows that using the seed bag burial method, without mixing seeds with sand or soil, may yield very high mortality rates of seeds, as the chances of seed-to-seed infection are high. In many studies on seed mortality in the soil where the seed

bag burial method has been used, the possible effects of pathogenic fungi have not been considered or have been overlooked (Lewis, 1973; Egley & Chandler, 1978; Teketay & Granstrom, 1997). Where high mortality rates were found they were most often ascribed to viability losses due to physiological ageing and germination (i.e. absence of dormancy causes most seeds to germinate when conditions stimulate germination) although fungal attack may have played a role.

In contrast, some studies have explicitly looked at fungi as a possible cause of soil seed mortality. For instance, Blaney & Kotanen (2001) investigated the effect of fungicide addition on the recovery of seeds from native versus invasive plants. They did not find a difference between groups suggesting that the addition of fungicide improved seed recovery equally for both groups in a wetland site, indicating a general role of fungal pathogens on seed mortality. Lonsdale (1993) studied the seed bank of Mimosa pigra in the field using mesh bags to study seed losses and reported a small reduction (10-16%) in loss of seeds when a fungicide was added. In a semi-arid, shrub-steppe in Wyoming, USA, Crist & Friese (1993) found that three species with relatively small seeds (0.20–2.04 mg) lost substantial proportions of seeds within 3 months because of decomposition and pathogens (0.14–0.94). They also noted that two species with bigger seeds (3.80 and 27.03 mg) suffered almost no loss to these factors. Consequently, they classified the small seeded species as having transient seed banks, and suggested that this may explain the low density of their seed banks. Although they reduced chances of seed-to-seed contact as they positioned individual seeds 2 cm apart within the bags, no reference was given to the seed density in a natural seed bank.

If pathogenic fungi are found to be an important factor in determining seed mortality rate, there may be an important effect of seed density in the soil, as well as in seed bags. In a moist tropical forest in Panama, Dalling *et al*. (1998) found a reduction in the proportions of dead seeds of 0.47 and 0.39 after application of a fungicide in a seed bag burial experiment using seeds of pioneer trees. These authors were the first to report density dependent seed losses within the seed bank in addition to density dependent seedling mortality. Their conclusions were drawn based on results from a soil sampling method but were not related to their seed bag burial data. Interestingly, they found smaller differences in the proportions of dead seeds from the fungicide and control treatments when using the seed bag method further away from the tree crown (dispersal centre), where soil seed densities were considerably lower. This suggests that seed mortality because of pathogenic fungi was higher where the seed density in the soil surrounding the seed bags was considerably higher.

Previous studies have shown the relative importance of fungal activity in promoting seed mortality (Crist & Friese, 1993; Dalling *et al*., 1998; Blaney & Kotanen, 2001). However, very high seed densities were used and the relative

importance of fungi as a mortality factor may have been overestimated as compared to its role at naturally occurring densities.

Estimating seed bank depletion of soil seed banks

The role of microbial activity and pathogenic fungi in particular may be important for all seed burial studies in which high mortality rates are found, that cannot be attributed to other causes such as germination. It is possible, that these studies would have shown higher seed persistence had lower seed densities been employed. For species that show high mortality rates when the seed bag burial method is used, it is important to try to clarify whether the mortality was caused by fungal pathogens. If fungal promoted mortality does play a significant role, it is especially important to use realistic seed densities when using the seed bag burial method, or to explore alternative methods. In these cases, estimates obtained from seed bag burial studies with high seed density should not be used for parameterization of population models, where the aim is to describe seed bank dynamics.

However, seed bag burial could still be used as a method for testing the relative effects of different soil treatments on seed mortality (e.g., sterile versus non-sterile conditions or moisture treatments), or to study dormancy patterns of seeds buried in the soil (provided mortality is suppressed). In all cases the possible overestimation of seed mortality due to fungi should be considered. Reducing the density of seeds in the bags to naturally occurring levels alleviates the problem of overestimating mortality but it does make retrieval of seeds more laborious; alternatives such as seeding the soil at a certain density and sampling after time intervals may become more attractive. Moreover, where the current classification of a given species as having a transient soil seed bank depends on high density seed bag studies, further research may be needed to confirm or revise this classification.

CHAPTER 4

Striga hermonthica seed bank depletion under bare soil, fallow and different crops

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Abstract

Seed bank density is an important determinant of the pressure of the parasitic weed, *Striga hermonthica*, on its hosts. As part of an effort to quantify life cycle processes of this hemi-parasite, this chapter aims to quantify the rates of seed loss in the soil during the rainy season under different vegetation covers. Seed bank germination and depletion of Striga was measured in Mali and Niger during the 2004 rainy season under bare soil, fallow and different crops. The seed burial and retrieval methods used were (1) mesh seed bags filled with sand and Striga seeds and (2) soil inoculation and sampling after which seeds were extracted by means of wet sieving and flotation. Fates of exhumed seeds were assessed by a seed press test.

Seed germination contributed most to seed bank depletion under a variety of crop covers and fallow. Most germination was found in soil under the host crops, sorghum and millet, followed by the intercrops of a host and a non-host trap crop, non-host crops and fallow. The two methods yielded similar percentages of seed bank depletion. Combining data from parallel studies on seed production with presented data indicated that year-to-year seed bank reduction by germination would only be achieved if seed production was completely prevented. The results raise questions on the specificity of trap crops and whether differences reported previously in seed bank depletion between trap and host crops are simply caused by the prevention of seed production, rather than increased (suicidal) seed germination in the soil.

Introduction

The hemi-parasitic weed *Striga hermonthica* (Del.) Benth. infects staple food cereals in sub-Saharan Africa, and causes considerable yield losses in sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* (L.) R. Br.) and maize (*Zea mays* (L.)) (Gressel *et al*., 2004). For annual noxious weeds such as *Striga* spp., the persistence of the soil seed bank proves to be the main problem for control and management. The soil seed bank plays a very important role in population dynamics and when seed production is unreliable, the seed bank is essential for the survival of annual plant populations (Silvertown & Charlesworth, 2001). Good estimates of seed bank depletion rates are therefore essential to understand weed population ecology and design effective long-term management strategies.

Seed ageing, attack by pathogenic fungi, germination and seed predation are processes that deplete the soil seed bank. It is assumed that Striga seeds can stay viable for long periods in the soil. In the United States, 15% and 1% of seeds of the species *S. asiatica* were still viable after 12 years of burial in soil at depths of 60 cm and 15 cm, respectively (Bebawi *et al*., 1984). High depletion rates of over 50% over one or two rainy seasons reported in several studies in Africa can, therefore, not merely be attributed to seed ageing (Oswald & Ransom, 2001; Gbèhounou *et al*., 2003; Murdoch & Kunjo, 2003). Oswald & Ransom (2001) and Murdoch & Kunjo (2003) suggested that germination in response to root exudates was the main cause of seed bank depletion whereas Gbèhounou *et al*. (2003) suggested that microbial activity leading to germination or infection of seeds caused seed bank depletion. In these studies, the cause of seed death or the relative importance of different processes leading to seed bank depletion could not be clarified because of the method used.

Striga seeds need a chemical stimulant to trigger germination after a period of preconditioning (Vallance, 1950). Roots of hosts (Parker & Riches, 1993) and non-hosts (Egley, 1972) exude these chemicals. When a non-host plant triggers the germination of Striga seeds, the seedling will be unable to attach to the roots and dies (a process also known as suicidal germination).

The potential of crop rotation with non-host plants to deplete the Striga soil seed bank by suicidal germination has been assessed in the laboratory (Khan *et al*., 2002; Emechebe & Ahonsi, 2003; Gbèhounou & Adango, 2003; Olupot *et al*., 2003) and in the field (Oswald & Ransom, 2001; Khan *et al*., 2002; Gbèhounou & Adango, 2003; Murdoch & Kunjo, 2003). Great variability in seed germination was found during *in vitro* experiments in the laboratory (Emechebe & Ahonsi, 2003) and consistent comparisons between trap and host crops were often lacking (Gbèhounou & Adango, 2003). When trap and host crops were compared, seed germination was higher in response to host roots (i.e., maize and sorghum) than trap crop roots (i.e., cowpea,

soybean and *Celosia argentia* L.), except for cotton and *Desmodium* spp. (*Desmodium uncinatum* and *D. intortum*) that evoked germination responses comparable to sorghum and maize (Khan *et al*., 2002; Emechebe & Ahonsi, 2003; Olupot *et al*., 2003). It has been suggested that the variation in depletion of the Striga soil seed bank is accounted for by these differences in the stimulation of (suicidal) germination (Oswald & Ransom, 2001; Khan *et al*., 2002; Abunyewa & Padi, 2003; Murdoch & Kunjo, 2003). However, a clear comparison could often not be made between a host crop, trap crop and a mix of host crop and trap crop, because Striga was allowed to flower and shed seed on the host crop. In all cases, except for the intercrop with silverleaf desmodium this seed shed led to increase in the seed bank density. Only Murdoch & Kunjo (2003) compared Striga seed bank depletion under a cereal and a trap crop while preventing seed production completely under the cereal crop by weeding. In this manner, a true comparison between Striga seed bank depletion as caused by germination in response to a trap crop and a host crop could be determined.

Hypotheses on the basis of the literature would comprise (i) host crops like sorghum and millet would be more effective in stimulating germination than (non-host) trap crops or fallow, (ii) trap crops or false hosts like cowpea would induce higher germination than fallow weed species, (iii) a combination of a host and trap crop would generate a comparable germination to the host or slightly higher germination as total root length density would be higher, (iv) under bare soil, germination would be minimal while seed death through biological attacks would be the only or at least major seed loss factor.

Obtaining accurate estimates of the means of seed bank depletion is difficult and methods of measuring seed bank depletion directly or indirectly are still in development (Ishikawa-Goto & Tsuyuzaki, 2004; Fenner & Thompson, 2005; Van Mourik *et al*., 2005). Two methods have been used to measure Striga seed germination or mortality in the soil, namely the seed bag burial method (Eplee, 1975) and the soil sampling technique (Hartman & Tanimonure, 1991). To our knowledge, the two methods have never been compared in a single experiment. The advantage of the seed bag burial method is the placement of a known number of seeds at a known depth and location in a field, easy retrieval of seeds and an assessment of possible causes of seed death (Van Mourik *et al*., 2003). Disadvantages are the unnatural exposure environment (a nylon mesh bag in the soil) and the close proximity of seeds, which increases seed mortality due to infection by pathogenic fungi (Van Mourik *et al*., 2005). Decreasing seed density within a bag by mixing sand with seeds has, however, been shown to decrease the mortality due to pathogens, and allows other means of depletion to be quantified. Three classes of seeds are observed upon retrieval of seed bags: seeds with firm and white endosperm, empty seed coats and seeds with an

Table 1. Site and experiment details.

Site (coordinates)	Blocks observed	Sowing date	Cereal (trap) crop distances (m)		Annual rainfall (long-term av.) (mm)	Soil type
			Between row	Within row		
Samanko, Mali (12°54'N, 8°54'W)	4	26-06-2004	0.8 (0.6)	0.6 (0.4)	950	Sandy loam
Sadore, Niger (13°15'N, 2°17'E)	6	06-06-2004	0.8 (0.6)	0.6 (0.4)	560	Sand

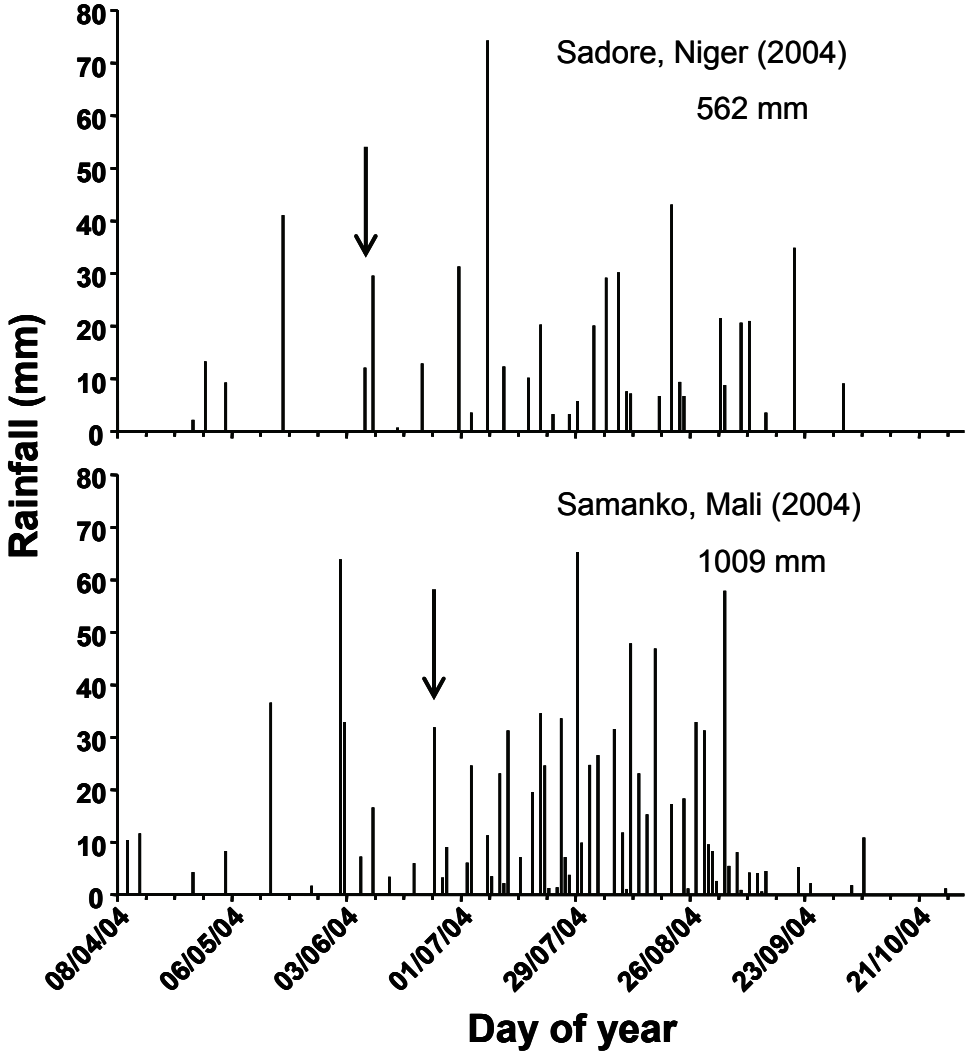

Fig. 1. Individual rainfall events in Sadore, Niger and Samanko, Mali during the rainy season of 2004. Arrows indicate dates of sowing.

unstructured black content. The latter were considered to have died through pathogenic attacks based on Van Mourik *et al*. (2003) who detected only 2.6% black seeds in seed bags retrieved from fungicide treated soil compared to 79.5% black seeds in the untreated control. Sauerborn *et al*. (1996) showed *Fusarium nyagamai* could penetrate viable, intact Striga seeds and infect the endosperm, which gives support to the assumption that seeds with black endosperm have been killed by fungal attack. Inoculating the soil and sampling after time intervals is an alternative way of assessing seed bank depletion, which is closer to natural conditions. Drawbacks are the heterogeneity of seed densities (depth and location) and laborious retrieval of seeds. The two methods, therefore, have advantages and drawbacks, but using both simultaneously will give insight into their accuracy and limitations.

The aims of this study were (1) to quantify the relative contribution of seed germination or seed death to seed bank depletion under different types of vegetative cover (Striga control options) with the improved seed bag burial method; (2) to compare estimates of seed bank depletion measured under different control options by soil sampling and seed extraction as well as the seed bag burial method; (3) to link germination of buried seeds to recruitment percentages found in a parallel study; and (4) to calculate yearly net seed bank increase or decrease under different Striga control options by the combination of seed bank depletion rates reported in this chapter with observations on seed production and seed bank replenishment (Chapter 2).

Materials and methods

Sites, husbandry and treatments

Two field experiments were carried out in 2004 on the ICRISAT experimental facilities in Mali and Niger (Table 1). The Samanko site is in the Sudanian zone and the field in Sadore lies in the Sahel zone and both have a monomodal rainfall pattern. Rainfall data for both sites in 2004 are shown in Fig. 1.

All crops were sown at the same time and at both sites, weeding and tillage was done before sowing. Plots without host crops measured 1.6 m by 3.6 m, containing three rows of the non-host crop if present. All plots with a host crop measured 3.2 m × 3.6 m, with the intercrop sown between and within rows around the two central rows of the host crop of the four-row plot. Fertilizer (NPK, 17:17:17) was applied at a rate of 100 kg ha^{-1} as a top dressing at the site in Mali only at 10 days prior to sowing, the crops in Niger received no fertilizer, unless otherwise specified. Cereal and trap crop hills were thinned to one plant per hill after three weeks.

In Mali, cowpea mortality was high during the first six weeks after sowing and hills were resown and treated with insecticides (FURADAN® Carbofuran, STEPC

(Côte d'Ivoire)) and fungicides (APRON+® (Metalaxyl, Syngenta (US)) twice. Plots were weeded by hoe three weeks after sowing and subsequently plots were hand-weeded (except for Striga plants) every two weeks. Two exceptions were the bare soil fallow which was hand weeded weekly from the first day and the weedy fallow, which was never weeded. Several Striga control options and crop covers such as a host crop, an addition of organic amendments to a host crop, an intercrop of a host and a trap crop, a trap crop, a fallow, or a bare soil were evaluated for their potential to deplete the soil seed bank by (suicidal) germination or seed death (Table 2). In the fallow treatment at both sites, broadleaf plant species dominated in number of species as well as percentage cover of the plots. Fallow vegetation cover in Samanko was 69.5% broadleaf species (of which only 1.3% leguminous species), 18.9% grass species, 2.6% cyperus species and 9% bare soil.

The Striga seeds used in Mali were collected in 2003 at the same site from a sorghum field (cv. Tiemarifing). In Niger, the seeds had been collected from a millet field in Bengou (Niger) in 1996. Both seed lots had been stored in closed glass jars under laboratory conditions (20–30 °C) prior to use. Striga seeds were broadcast one week before sowing the crops in Mali and on the same day as sowing in Niger.

Seed bag method

Striga seeds were buried in bags as described by Van Mourik *et al*. (2005) with approximately 1000 seeds in 25 g of coarse sand. Nylon gauze seed bags (10 cm × 10 cm, mesh size 90 µm, Stokvis & Smits B.V.) were buried at 7 cm depth on a line in the centre of each plot. Seed bags were buried 3 days prior to sowing crops in Mali and at sowing time in Niger. Treatment and sampling details are given in Table 2. Distances to the nearest host plant were 40 cm and to the nearest intercrop / trap crop plant were 30 cm. Bags were buried between rows of the host and where present, between plants within the row of the intercrop or non-host crop.

Seed bags were dug up from the field, air dried for 1 day and the contents were emptied into 500 ml of sucrose solution (855 g l^{-1} distilled water, specific gravity of 1.2). While gently stirring the suspension for two minutes, inorganic soil particles sank to the bottom, whereas organic material (i.e., seeds) started to float. The suspension was allowed to settle for at least 15 minutes. The upper 400 ml of suspension was then filtered (mesh size 100 µm) and rinsed with at least 500 ml tap water. Regular checking showed that in all cases, this method resulted in more than 90% retrieval of of seeds. Seeds that were retained on the filter were bleached in a vial with 4 ml 1% sodium hypochlorite solution and 50 µl Tween 20® (polyoxyethylene sorbitan monolaurate; Merck Schuchardt) for 2 minutes, rinsed with tap water and imbibed in tap water for at least 20 minutes. After imbibition and bleaching, a sub sample of

between 100–150 seeds was counted visually under a stereomicroscope at 20× magnification and separated into black seeds, empty seed coats and intact light brown seeds. Earlier testing (Van Mourik *et al*., 2003, 2005) revealed that by lightly pressing the seeds (hence: seed press test) the black seeds disintegrated indicating the microbial attack leading to seed death. Seeds that were empty when pressed were considered to have germinated (in some rare cases we did observe degenerated parts of radicles extruding from such seed coats). Firm seeds that had a transparent or slightly whitish intact endosperm were considered viable.

Soil sampling method

Plots were inoculated with 41,900 and 60,000 germinable Striga seeds per square meter Mali and Niger, respectively. For each treatment plot, the Striga seeds were mixed with 100 g coarse sand and broadcast by hand, after which the soil was cultivated to a depth of 15 cm. Soil samples were taken along a line in the centre of each plot next to the seed bags 10 days after sowing (DAS). At 150 DAS, a bulked sample from three sub-samples taken in the centre of each plot was analysed, because of high variation in the number of seeds per sample in earlier sampling, possibly due to heterogeneity of Striga seed infestation. Soil samples were air-dried and a 100 g sub-sample was taken for analysis. Seeds were separated from the soil as described by Hartman & Tanimonure (1991). Soil was wet-sieved through 850, 212 and 90 micron sieves. The material retained on the 90 micron sieve was then mixed with 600 ml of sucrose solution (specific gravity of 1.2) stirred for 2 minutes and allowed to settle for at least 15 minutes. The floating material and material in suspension (a mix of organic debris and Striga seeds) was decanted, filtered (mesh size 100 μm) and air dried. This sample was spread out over wet filter paper in lines and imbibed for 20 minutes before analysis with a microscope (20× magnification).

The number of intact and dead Striga seeds per sample was counted by the "seed press" test described above except that large amounts of organic debris meant black (infected) and empty (germinated) seeds could not be well distinguished and seeds were only distinguished into viable seeds and dead seeds. The efficiency of seed extraction from soil samples was estimated at 90%, based on three sample analyses in which either 0 or 100 seeds were added to a 100 g air dry soil sample.

Calculations on data and statistical analysis

For the seed bag method, percentages of empty and black seeds were calculated from evaluation of sub-samples of 100–150 seeds per seed bag per replicate. For the soil sampling method, the increase in the percentage of dead seeds was calculated as follows. First, the mean percentage of dead seeds was calculated for all samples at

Table 2. Treatments and codes of treatments evaluated for the causes and quantities of seed losses in 2004. A + indicates that a treatment has been sampled using the seed bag method or the soil sampling method.

Site	Treatments applied	Host - trap crop variety	Host presence	Code	Seed bag	Soil sampling	
						10 DAS	150 DAS
Mali, Samanko (n=4) [a]							
	Bare soil (weeding every week, control)	-	Without host	BARE SOIL	+	+	+
	Fallow with weed growth	-		FALLOW	+	+	+
	Cowpea trap crop	Sangaranga		COWPEA	+	+	+
	Long duration sorghum cultivar (~120 days)	Tiemarifing	With host	TIEM L	+	+	+
	Short duration sorghum cultivar (~90 days)	CSM63E		CSM63E	+	+	+
	Intercrop sorghum - cowpea	Tiemarifing - Sangaranga		IC COW	+	+	+
Niger, Sadore (n=6) [b]							
	Bare soil (weeding every week, control)	-	Without host	BARE SOIL	+	+	+
	Fallow with weed growth	-		FALLOW	+	+	+
	Sesame trap crop	Maradi local		SESAME	+	+	+
	Cowpea trap crop	TN5-78		COWPEA	+	+	+
	Long duration millet cultivar (~110 days)	Sadore local	With host	SAD	+	+	+
	Intercrop millet - sesame	Sadore local - Maradi local		IC SES	-	+	+
	Intercrop millet - cowpea	Sadore local - TN5-78		IC COW	+	+	+
	Millet with organic amendment of 0.2 kg m-2	Sadore local		SAD ORG	-	-	+

[a] 72 seed bags were buried in Mali consisting of four replicates, three sampling times (40, 100 and 140 DAS) and six treatments;

[b] 72 seed bags were buried in Niger consisting of six replicates, two sampling times (40 and 100 DAS) and six treatments.

10 DAS (n=24 in Mali and n=42 in Niger). Then, the individual percentages of dead seeds per sample of each replicate of a treatment taken 150 DAS were subtracted from the overall mean at 10 DAS to obtain the increase in percentage of dead seeds for this 140-day period. With these values, statistical analyses were carried out using GenStat v. 8. Angular transformations were performed on all percentages of empty and black seeds (seed bag method) or on dead seeds (soil sampling method) before analysis of variance with a test for orthogonal contrasts of different combinations of treatments. These contrasts (Figs 3 and 4) are essentially identical between sites and based on the hypotheses mentioned in the introduction.

The data on germination and seed bank depletion were combined with data on recruitment and seed production from Van Mourik *et al*. (in prep.). Dividing the recruitment data by germination data and multiplying by 100, the emergence as a percentage of germinated seeds was calculated for different sites, treatments and years. Depletion rates estimated from the seed bag method were subtracted from seed production data to calculate net seed bank change for different sites, treatments and years.

Results

Rainfall patterns for the two sites varied as expected (Fig. 1). The total in Mali (1009 mm) was slightly superior to the long-term average (950 mm), while the total in Niger (562 mm) was nearly the same as the long-term average (560 mm). Sowing was relatively late considering significant rains preceding sowing in Samanko, because of unfinished preparatory activities right after these rains. Sowing in Niger was relatively early but received enough rain for establishment and subsequent growth of all crops sown.

Using the seed bag method, the majority of dead seeds 140 DAS in Mali and 100 DAS in Niger were empty rather than infected (black) (Fig. 2). The large increase in number of empty seeds in a soil where active sorghum (70.2%) or millet (63.6%) roots were present compared to bare soil where active roots were virtually absent (20.8%–19.7%), implied that depletion was mainly caused by seed germination (Fig. 2).

Cover types: causes and extent of seed loss

Only the seed bag method allows for distinction between germination and biological attack as cause of seed loss. The percentage of seeds lost through biological attack (black seeds) was not significantly different between cover treatments (Tables 3 and 4). The percentage of empty (seed bag method, Figs 3 and 4) and intact (soil sampling method, Tables 2 and 3) seeds were both significantly ($P<0.005$) affected by cover treatments at both sites. Average percentages of empty seeds ranged from 20.8% (Mali, 140 DAS) or 19.7% (Niger, 100 DAS) under bare soil (no cover) to 71.4% in

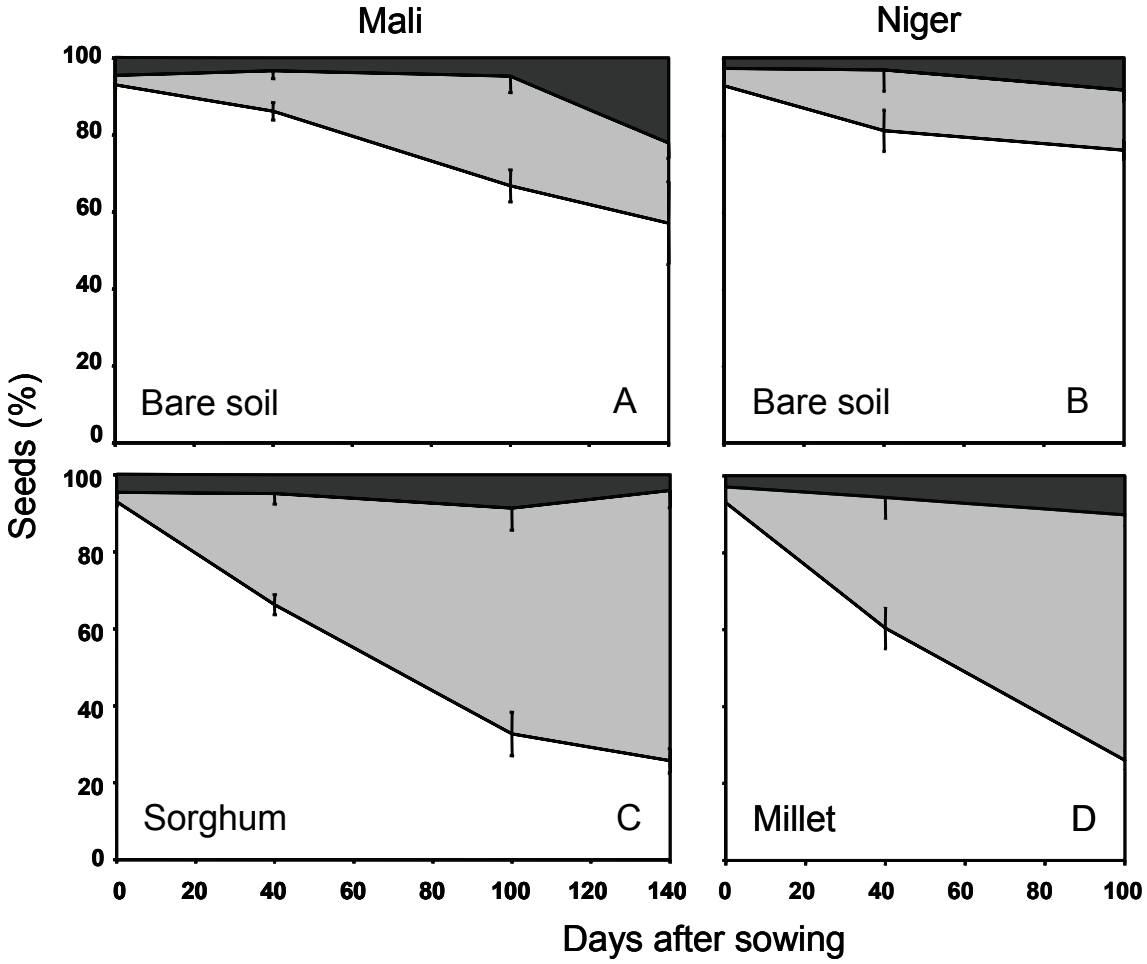

Fig. 2. Change in the percentages of black (black surface), empty (grey surface) and intact (white surface) *Striga hermonthica* seeds over a rainy season at two sites under bare soil or a host crop with the seed bag method. Error bars represent SEM, n=4 for Mali (A and C) and n=6 for Niger (B and D).

Mali under short duration sorghum cover (Fig. 3) and 63.6% under millet (Fig. 4).

Orthogonal contrast testing revealed comparable differences at the two sites despite the different host and trap crops, Striga populations and soil and rainfall conditions. Lower percentages of empty seeds were found under bare soil than any system with vegetative cover ($P<0.001$). Presence of a host cereal (short or long duration sorghum or millet stand or sorghum-cowpea or millet-cowpea) resulted in higher percentages of empty seeds than a cover where the host cereal was absent (cowpea, sesame or fallow) ($P<0.001$). Percentage of empty seeds was higher under a pure sorghum or millet host stand than under sorghum or millet - cowpea intercrop ($P=0.035$ and $P<0.001$, respectively). Sorghum duration had no effect on the percentage of empty seeds ($P=0.821$). The percentage of empty seeds in seed bags

Table 3. Percentages black (infected) and intact (viable) *Striga hermonthica* seeds 140 days after sowing (DAS) with the seed bag burial method and number of dead and intact seeds 10 and 150 DAS with the soil sampling method as a result of vegetative cover in Mali. Treatment codes in bold are systems that include the sorghum host. TIEM L; long duration sorghum, CSM63E; short duration sorghum, IC COW; intercrop sorghum-cowpea, FALLOW; weedy fallow.

	Seed bag		Soil sampling			
	140 DAS		10 DAS		150 DAS	
Treatment	%Black	%Intact	Dead	Total	Dead	Total
BARE SOIL	22.1	57.1	5.4	19.2	4.0	13.2
COWPEA	9.8	57.2	5.4	21.2	4.8	9.5
FALLOW	10.7	43.2	3.3	16.8	5.8	10.5
IC COW	7.1	33.5	7.0	30.5	15.6	21.8
TIEM L	4.0	25.7	5.7	23.2	10.3	13.5
CSM63E	10.3	18.4	6.2	22.0	8.5	10.2
P	NS	0.003	NS	NS	0.006	NS
SED		8.38			1.62	

Table 4. Percentages black (infected) and intact (viable) *Striga hermonthica* seeds 100 days after sowing (DAS) with the seed bag burial method and number of dead and intact seeds 10 and 150 DAS with the soil sampling method as a result of vegetative cover in Niger. Treatment codes in bold are systems that include the sorghum host. SAD; long duration millet), IC COW/SES; intercrop millet-cowpea/sesame, SAD ORG; millet with organic amendments, FALLOW; weedy fallow.

	Seed bag		Soil sampling			
	100 DAS		10 DAS		150 DAS	
Treatment	%Black	%Intact	Dead	Total	Dead	Total
BARE SOIL	8.0	72.3	1.0	9.2	3.2	12.0
SESAME	5.2	50.7	1.2	13.2	5.5	11.2
COWPEA	5.1	64.3	2.0	11.7	3.7	8.3
FALLOW	3.4	53.3	0.8	9.3	5.0	8.7
IC COW	6.3	50.9	1.3	8.0	4.7	7.7
IC SES	-	-	1.7	11.0	4.3	6.2
SAD ORG	-	-	-	-	3.7	6.3
SAD	10.1	26.0	2.0	11.3	3.8	5.5
P	NS	<0.001	NS	NS	<0.001	NS
SED		5.78			1.47	

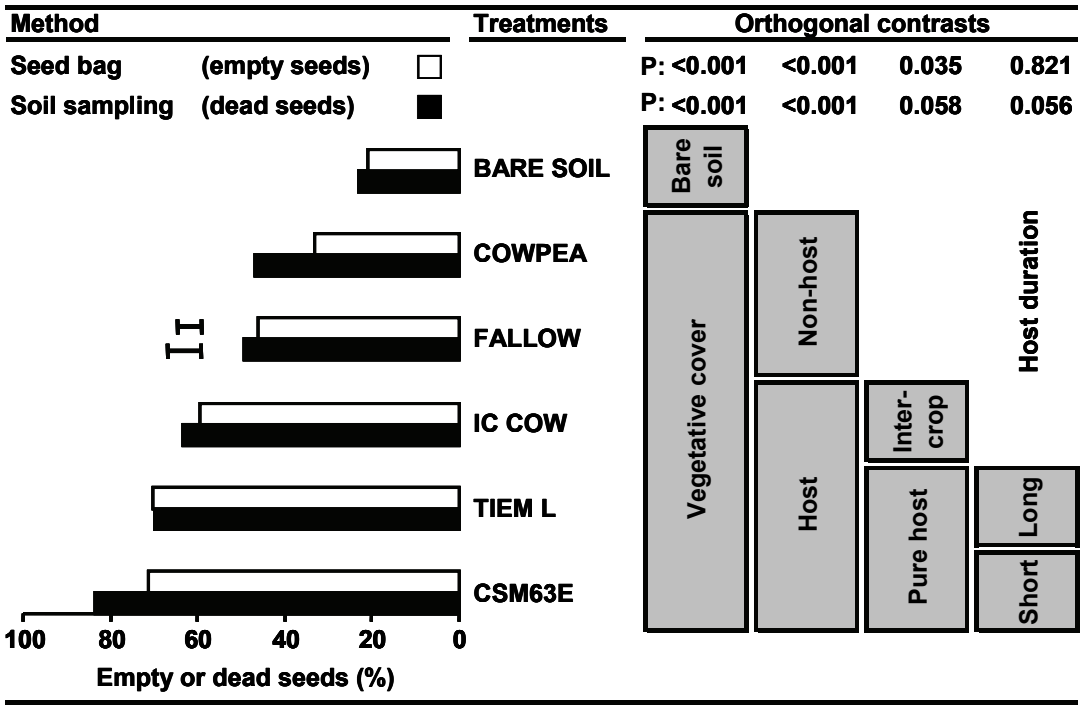

Fig. 3. Percentage of empty (germinated) seeds (white bars) from the seed bag method 140 DAS and the increase in percentages of dead seeds (black bars) from the soil sampling method 150 DAS in Mali. Error bars represent SED (df=15). To the right hand side are the results of orthogonal contrast testing for the two methods. Grey bars indicate which treatments are included in comparison of different groups. IC COW; intercrop sorghum-cowpea, TIEM L; long duration sorghum, CSM63E; short duration sorghum.

from vegetative cover treatments that did not include a cereal host, (i.e., sesame, cowpea and fallow) ranged from 33.1% (cowpea) to 46.1% (fallow) in Mali and from 30.6% (cowpea) to 44% (sesame) in Niger (Tables 3 and 4).

Using the soil sampling method, there were no differences between treatments in the number of dead, or in the total (dead and intact) number of seeds per soil sample taken 10 DAS in either site (Tables 3 and 4). In contrast, the number of dead seeds (but not the total number of seeds) differed significantly between cover treatments ($P<0.01$). The increase in percentage of dead seeds ranged from 22.9% (Mali) or 13.1% (Niger) under bare soil to 83.4% under short duration sorghum (Mali) or 60% under millet-sesame intercrop (Niger) and was significantly affected by cover treatments ($P<0.001$) (Figs 3 and 4).

A higher increase in percentage of dead seeds was found under vegetative cover than under a bare soil ($P<0.001$). Also, higher increases in the percentage of dead seeds were found under treatments with a host (short and long duration sorghum,

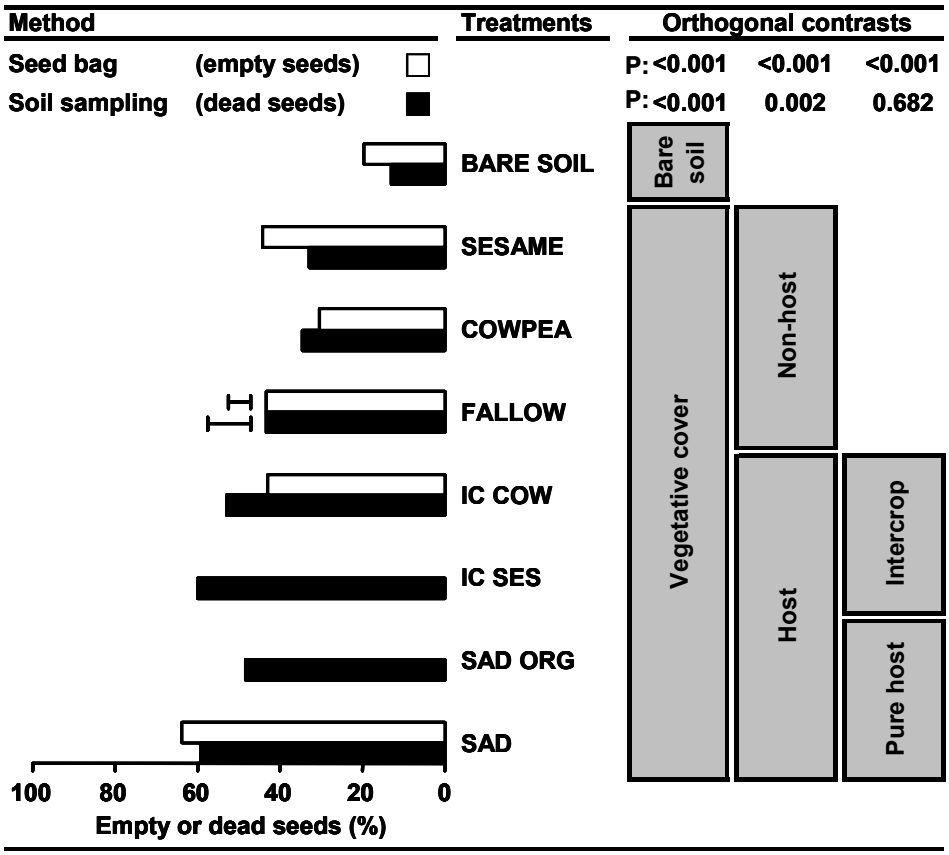

Fig. 4. Percentage of empty (germinated) seeds (white bars) from the seed bag method 100 DAS and the increase in percentages of dead seeds seeds (black bars) from the soil sampling method 150 DAS in Niger. Error bars represent SED (df=35). To the right hand side are the results of orthogonal contrast testing for the methods. Grey bars indicate which treatments are included in comparison of different groups. See Table 4 for explanation of treatment codes.

millet, sorghum or millet-cowpea or millet-sesame intercrop) than under those without (cowpea, sesame and fallow) ($P<0.05$). No significant difference was found when comparing increases in percentages of dead seeds under pure host to intercrops ($P>0.05$) or when comparing long and short duration sorghum treatments ($P>0.05$). Furthermore, no significant differences in the increase in percentage of dead seeds were found when comparing millet to millet with organic amendments ($P=0.309$) or when comparing intercrops of millet-cowpea with millet-sesame ($P=0.511$) (comparisons not shown in Fig. 4). Vegetative cover treatments without a cereal host caused increases in the percentage of empty seeds ranging from 46.6% (cowpea) to 49.4% (fallow) in Mali and from 32.9% (sesame), and 43.5% (fallow) in Niger.

Comparison of seed bag method and soil sampling method

Although the number of seeds available for analysis is rather different between the

seed bag and soil sampling method, percentages of empty (seed bag) and dead (soil sampling) seeds were similar between treatments (Figs 3, 4 and 5). Furthermore, Fig. 5 shows that the soil sampling method yielded slightly higher percentages increase in empty seeds in Mali relative to Niger, which was not always reflected to the same extent when the seed bag method was used. The data points from averages of treatments from the soil sampling method and the seed bag method are close to a hypothetical 1:1 relationship.

Linking seed germination to emergence

Emergence as percentage of germination in Mali (2004) was low for all treatments (<0.04%) and was lowest where sorghum was intercropped with cowpea (Table 5). A short duration sorghum (cv. CSM63E) had about three times higher emergence as percentage of germination than the long duration sorghum (cv. Tiemarifing), while germination percentages between the two cultivars were similar. A sorghum-cowpea intercrop gave lower emergence than the sole sorghum. In Niger (2004), emergence as percentage of germinated seeds under millet-sesame and millet-cowpea intercrops were only 4% and 20% of those under pure millet stands of the same cultivar, respectively.

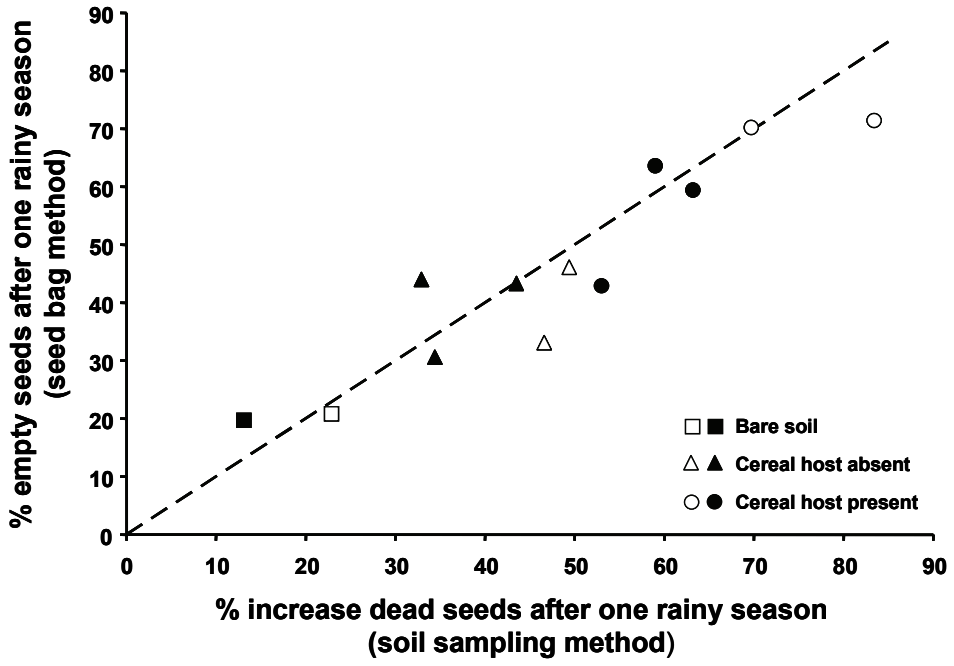

Fig. 5. Relationship between the percentage increase in dead seeds from the soil sampling method and the percentage of empty seeds from the seed bag method after a rainy season under different vegetative covers. Open and closed symbols are data from Mali and Niger, respectively. The dashed line represents a hypothetical 1 : 1 relationship between the results from analyses of the two methods.

Table 5. Percentage emergence of germination calculated with data from the seed bag method and recruitment data from Chapter 2.

Site	Treatment	Seed density [a]	%Germination [b]	%Recruitment [c]	%Emergence of germination
Mali, Samanko (2004)	IC COW (intercrop sorghum-cowpea)	20,100	59.4	0.004	0.007
	TIEM L (long duration sorghum)		70.2	0.007	0.010
	CSM63E (short duration sorghum)		71.4	0.023	0.032
Niger, Sadore (2004)	IC SES (intercrop millet-sesame)	28,800	53.4*	0.004	0.007
	IC COW (intercrop millet-cowpea)		53.4	0.014	0.026
	3/4HK (short duration millet)		63.6**	0.077	0.121
	SAD ORG (SAD with organic amendments)		63.6**	0.103	0.162
	SAD (long duration millet)		63.6	0.111	0.175
Mali, Samanko (2002)	CSM63E (short duration sorghum)	16,650	*71.4* [d]	0.135	0.189
	TIEM L (long duration sorghum)		*70.2*	0.091	0.130
Mali, Cinzana (2002)	CSM63E (short duration sorghum)	3,730	*70.2*	0.399	0.569
	TIEM L (long duration sorghum)		*71.4*	0.512	0.717
Mali, Samanko (2003)	TIEM L (long duration sorghum)	60,000	*71.4*	0.075	0.107
	TIEM L (long duration sorghum)	12,000	*71.4*	0.323	0.460

[a] Seed density is given in seeds per host; [b] Data from seed bag burial method; [c] Data from Chapter 2;

[d] Germination estimates from the seed bag method in 2004 were combined with recruitment estimates from indicated years;

* Germination of intercrop millet-cowpea (IC COW) is assumed for the intercrop millet-sesame (IC SES);

** Germination of long duration millet is assumed for a short duration millet (3/4HK) and millet with organic amendments (SAD ORG).

Emergence as percentage of germination were similar under a short duration millet (0.121%), a long duration millet (0.175%) and a long duration millet with organic amendments (0.162%).

Although the germination percentages were similar in Mali and Niger (70% and 64%, respectively; Table 5), the sites differed strongly in emergence. For long duration sorghum and millet stands, emergence as percentage of germination was 0.010% and 0.175% in Mali and Niger, respectively (Table 5). At the seed densities used and with a pure host stand, the percentage of germinated seeds that attached and emerged ranged from 0.01% to 0.72% over all years, with Mali having exceptionally low values in 2004 and high values in Cinzana in 2002. It is noticed that highest emergence of germinated seeds was found at the lowest seed bank densities (Mali, Cinzana, 2002).

Net seed bank changes

In 2004 in both Mali and Niger, the soil seed bank was most effectively reduced by a system with the host cereal but where seed production was almost completely prevented, for example, by weeding at Striga flowering. Because of the low recruitment rates in Mali in 2004, there was very low seed bank replenishment. This led to a decrease in the seed bank in all treatments, except for the pure stand of the long duration host cultivar (Tables 5 and 6). In the same year in Niger, three of the six treatments including a host cereal led to a net increase in the seed bank, namely short and long duration millet and millet with organic amendments (Table 6). The net seed bank decreased when millet was intercropped with sesame or cowpea, and decreased when weeded at Striga flowering. Inevitably, systems with a host-free vegetative cover such as sesame or cowpea always led to a seed bank decrease. A weedy fallow in the current study also led to seed bank reduction because no Striga seed production was observed in either site. In Mali, five Striga plants had emerged on wild grass hosts in one plot, but these never reached maturity.

Seed bank depletion rates found in 2004 were used to calculate net seed bank increase for different treatments in 2002 and 2003. If seed production occurred, this often led to large increases in the seed bank of up to nearly 60 fold in a single season (Table 6). In 2002 and 2003, treatments only included pure sorghum stands and in only one treatment with a short cycle sorghum host cultivar in Mali in Cinzana in 2002, a net decrease in the seed bank was calculated (Table 6). When looking at all years and only pure host stands (not including weeding at Striga flowering) there were only five and three cases out of 18 where the seed bank increased by less than 100% or even decreased. The net change and the initial seed density can be used to estimate seed bank densities at the end of the season. Estimates of seed bank density varied from 1,100 to 774,800 seeds per host plant (2,300 to 1,614,200 seeds m^{-2}).

Table 6. Net seed bank change calculated from results of soil sampling and data from Chapter 2.

Site	Treatment	Seed density [a]	%Depletion [b]	%Replenishment [c]	%Net change [d]
Mali, Samanko (2004)	TIEM WEED *	20,100	69.7	0	–69.7
	CSM63E (short duration sorghum)		83.4	18.9	–64.5
	IC COW (intercrop sorghum-cowpea)		63.2	5.4	–57.8
	TIEM S *		69.7	17.8	–51.9
	FALLOW		49.4	0	–49.4
	COWPEA		46.6	0	–46.6
	BARE SOIL		22.1	0	–22.1
	TIEM L (long duration sorghum)		69.7	89.0	19.3
Niger, Sadore (2004)	IC SES (intercrop millet-sesame)	28,800	60.0	1.8	–58.2
	SAD WEED *		59.0	5.2	–53.8
	FALLOW		43.5	0	–43.5
	SESAME		32.9	0	–32.9
	COWPEA		34.4	0	–34.4
	BARE SOIL		13.1	0	–13.1
	IC COW (intercrop millet-cowpea)		53.0	43.2	–9.8
	3/4HK (short duration millet) *		59.0	157.9	98.9
	SAD ORG (SAD with org. amendment)		48.4	513.3	464.9
	SAD (long duration millet)		59.0	733.6	674.6
Mali, Samanko (2002)	CSM63E (short duration sorghum)	16,650	*83.4* [d]	728	644.7
	TIEM L (long duration sorghum)		*69.7*	1171	1101.3
Mali, Cinzana (2002)	CSM63E (short duration sorghum)	3,730	*83.4*	13	–70.3
	TIEM L (long duration sorghum)		*69.7*	88	18.7
Mali, Samanko (2003)	TIEM S (artificially shortened sorghum)	60,000	*69.7*	395	325.4
	TIEM L (long duration sorghum)			1261	1191.3
	TIEM S (artificially shortened sorghum)	12,000	*69.7*	3266	3196.0
	TIEM L (long duration sorghum)			5888	5818.3

[a] Seed density is given in seeds host^{-1}; [b] Data from soil sampling method; [c] Data from Chapter 2; [d] Depletion estimates from soil sampling in 2004 were combined seed production estimates from indicated years;

* Depletion of long duration millet is assumed for a short duration millet (3/4HK).

Discussion

Crop cover, Striga (suicidal) seed germination and seed death

At both sites, host vegetation cover led to the highest percentage of empty seeds, with little difference between sites. It is argued that most empty seeds arise from germination because so many more empty seeds were found in soil where vegetation and thus more active roots were present than in bare soil. The percentage of empty seeds was therefore used to estimate germination. The percentage of black seeds, which was shown to indicate seed death through biological agents by Van Mourik *et*

al. (2005), remained low throughout the season, irrespective of treatment. In these fields and with the seed bag densities used, seed death through biological attack therefore did not contribute greatly to seed bank depletion.

The tested vegetation cover treatments differed in their effectiveness to stimulate Striga seed germination, and in order of decreasing effectiveness were host cereal crop > intercrop of host cereal with cowpea or sesame > non-host vegetation (sesame, cowpea or weeds) > bare soil. The depletion rates calculated as a result of host cereal crops are somewhat higher than depletion rates found in other studies (Murdoch & Kunjo, 2003) where the soil sampling method was used. The depletion rates found under trap crops were slightly lower than depletion rates found in other studies (Oswald & Ransom, 2001; Abunyewa & Padi, 2003; Murdoch & Kunjo, 2003). It has to be noticed that most other studies calculated depletion over two rainy seasons and so it is difficult to compare these depletion rates. The trap crops cowpea and sesame were no more effective in causing suicidal germination than the weedy fallow (a mixture of mono- and dicotyledonous wild plants). A recent study by Akiyama *et al*. (2005) indicates that strigolactones (a family of identified germination stimulants for Striga seeds) stimulate branching of arbuscular mycorrhiza. As symbiosis with arbuscular mycorrhizaea is a widespread phenomenon in the plant kingdom the chemical resemblance seems to imply that Striga stimulating root exudates may be produced by a much wider spectrum of plant species than a limited number of trap crops and host plants identified thus far. Furthermore, *S. asiatica* seeds have previously been shown to germinate in response to stimuli not related to root exudates such as mechanical (seed cuts and punctures) and chemical (treatments with sulphuric acid) scarification (Egley, 1972). It is, therefore, possible that many other soil processes, such as activity of soil micro-organisms and soil perturbation, can evoke Striga seed germination to some extent.

Seed bag method versus soil sampling method

The soil sampling method and seed bag method gave similar results but the soil sampling gave more variable results and was more labour intensive (Fig. 5). Also, the limited number of Striga seeds per soil sample makes calculations of percentages of dead and viable seeds less accurate. In addition, seed samples from the seed bags had much less debris and ensured a sufficient number of seeds for detailed analysis of the potential causes of seed bank depletion. Seed bags can also be produced and buried easily in on-farm trials where inoculation of soil is not allowed and where the natural infestation is extremely heterogeneous. Furthermore, trap and host crops can be tested in their ability to stimulate germination *in situ* as an alternative to *in vitro* techniques such as agar gel essays (Hess *et al*., 1992) and experiments with root exudates or

extracts of root cuttings (Emechebe & Ahonsi, 2003; Gbèhounou & Adango, 2003).

Striga seed germination and emergence

Germination was more stable than recruitment at the two sites in 2004. Data from this study indicate that poor emergence was not limited by germination but by intermediate stages between germination and emergence (Table 5). This suggests that seed bank replenishment of Striga is most influenced by processes in the stages after germination. This is further supported by the data for 2002 in Cinzana, Mali and for 2003 in Samanko, Mali at low density (Table 5). Even if we would assume germination had been 100% in those cases, the percentage emergence of germination would have been larger by a factor 2 to 3 than in all other cases. These differences are greater than any differences we observed between germination under different vegetation types.

Emergence levels can differ greatly between years at the same site (Hess & Williams, 1994; Bielders & Michels, 2002; Samaké *et al*., 2005) such that there are years when almost no Striga emergence occurs and where in the following year at the same site high infestations recur. It is not clear what causes this variability in recruitment levels between years, although rainfall patterns (particularly early season rainfall) in combination with sowing date (late sowing or resowing) appear to be important (Hess & Williams, 1994; Weber *et al*., 1995; Gbèhounou *et al*., 2004). In our experiment, large differences in recruitment between years were also observed (cf. Table 5, percentage recruitment TIEM L Samanko, Mali 2002 and 2004). Low recruitment could have resulted from an unfavourable environment (humidity or nutrients) during preconditioning, attachment or underground development (Boukar *et al*., 1996). As percentage germination in the year with the lowest recruitment was still 70%, it seems these differences may not relate to low germination percentages, but may have to do with differences in effective attachment to the host root (undirected radicle growth) or interrupted underground development of the attached parasites. Further study to elucidate the exact processes acting between germination and emergence would enhance our ability to predict Striga population behaviour.

Intercropping a cereal host with cowpea or sesame yielded germination percentages and seed bank depletion rates similar to pure stands of cereals, but caused considerable reductions in the percentages of germinated seeds that actually attach to the host and emerge. This reduction in emergence could occur in the stage of radicle elongation towards the host root, attachment to the host or establishment of the underground Striga seedling. We speculate that the lower emergence with intercropping arises during the phase of radicle elongation when the chemical gradient of the root exudates (germination stimulants) towards the host's root is distorted by

exudates from the intercrop. Further research into this process is needed to understand this step of the life cycle and the intervention options it provides.

Net Striga seed bank changes

The calculations of the net change in the Striga seed bank (Table 6) showed that depletion of the seed bank was highest when a host crop was grown and reproduction was avoided. Depending on the efficiency of preventing seed production, several treatments including a cereal host scored high in net seed bank depletion, such as a weeding at first Striga flowering and intercropping cowpea in Mali and sesame in Niger. On the contrary, if the same germination rates or even 100% germination had occurred during the 2002 and 2003 seasons, the seed production would still have overruled depletion, except at Cinzana (Mali) in 2002. The highest seed bank density that was predicted by combining these data with seed production data (1,614,200 seeds m^{-2}) is about twice the maximum density of Striga seeds ever reported (882,000 seeds m^{-2}, calculated from 294 seeds 100 g $soil^{-1}$; Oswald & Ransom, 2001). These predictions should, therefore, be treated as indicative of relative differences rather than as accurate indicators of attainable densities.

By estimating two stages of seed bank depletion (germination and seed death) and three stages relevant for seed bank replenishment (germination, emergence and seed production) separately, we were able to determine at what step in the Striga life cycle a treatment potentially decreases or increases the seed bank. In former studies, soil samples were taken in such a way, that only the net seed bank increase or decrease could be determined (Carsky *et al*., 1996; Oswald & Ransom, 2001; Abunyewa & Padi, 2003) or concentrated mainly on depletion by all processes in the absence of seed influx (Murdoch & Kunjo, 2003). The drawback of measuring the net change in the seed bank is that one cannot distinguish between different stages of the life cycle such as germination, emergence and seed production even though one treatment may involve a cereal host (and potential seed bank replenishment) and another may not. The advantage of the more detailed information on seed bank dynamics presented here is that alternative control options combining strong points of more than one system may be assessed more easily. For example, the higher efficacy of weeding at flowering at the lower Striga densities in Mali compared to Niger and the effect of intercrops on Striga densities implies that a good method of reducing Striga seed production would be to intercrop to lower emerged Striga plant density and then weed at Striga flowering. In this way farmers may be able to maintain their generally preferred option of cereal cropping even on fields infested with Striga field and they should also achieve a useful depletion of the soil seed bank.

Conclusion

The tested treatments showed little scope for effective elimination of the Striga seed bank with the use of only rotations with trap crops. Therefore the main focus of Striga control and management needs to be prevention of seed production because extremely high quantities of seeds are shed to the soil and are incorporated into the seed bank even if only a few Striga plants reach maturity and shed seed. In other words, there needs to be a zero tolerance strategy in seed production. Such a strategy will not, however, avoid Striga damage to cereal crops after a single year because considerable amounts of seeds will persist in the soil.

Farmers are often reluctant to leave fields fallow or use rotations with non-host crops such as legumes, due to limited land area and the need to produce sufficient staple cereal crops, such as sorghum, maize or millet (Sauerborn *et al*., 2000) and to reduce risk of complete crop failure (Peter & Runge-Metzger, 1994). Cropping systems that include a host cereal crop but effectively reduce Striga seed production should not, therefore, be dismissed as Striga control options. Of these systems, the intercrops as such are probably less effective than weeding at flowering in completely preventing seed production, but may be more acceptable to farmers because investment of money and labour directly yields fodder and seeds/beans of the intercrop. Weeding on the other hand, does not directly lead to increased revenues. The suppression efficacy of intercrops in farmers' fields, where intercrop densities will be lower than maintained in these trials, may be less and the density of intercrops and their Striga suppressive potential deserves attention in future research as well as agronomic and socio-economical aspects relative to the use of enhanced densities. It is suggested that integrating different control options (such as intercropping with weeding of any Striga plants that reach flowering) may achieve nearly complete prevention of seed bank input through shedding.

CHAPTER 5

Long-term management of *Striga hermonthica* – strategy evaluation with a spatio-temporal population model*

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Abstract

The parasitic weed *Striga hermonthica* poses a serious threat to cereal production in sub-Saharan Africa. Striga seed banks are long-lived, therefore, long-term effects of control strategies on the Striga seed bank only emerge after several years.

We developed a spatially explicit model to study the long-term effectiveness of control options and scenarios in preventing invasion of Striga into previously uninfested fields and in reducing established infestations.

Spatial expansion of Striga and decrease in millet yield in a field slowed down – on average – as a result of stochasticity of attachment of seedlings to the host. The spatial patterns of emerged Striga plants 4–7 years after point inoculation (e.g., of seeds in a dung patch) in the model resembled spatial distribution of Striga that is typically observed in farmers' fields.

Sensitivity analysis showed that all life cycle parameters greatly influenced seed bank dynamics and millet yield except for two slope parameters for the dispersal curve and the parameter for seed death other than germination in response to millet roots.

Simulations indicated that weeding and intercropping millet with sesame or cowpea decrease the Striga seed bank in the long-term, whereas rotations of millet with sesame or cowpea increase the seed bank. Millet allows for high seed bank replenishment that is not sufficiently offset by seed bank depletion in years of cowpea or sesame cropping.

Insight from simulations can be employed in a participatory learning context with farmers to have an impact on Striga control in practice.

* Weed Research (accepted)

Introduction

Striga hermonthica is a widespread hemi-parasitic weed on cereals in cropping systems of sub-Saharan Africa. It causes large reductions in cereal yield and can cause complete crop failure where infestations are severe (Parker & Riches, 1993). An estimated 26 million hectares of cereal fields are infested with *S. hermonthica* and *S. asiatica*, leading to an estimated loss in production of about 10.7 million tons (Gressel *et al*., 2004). According to farmers in Nigeria, the area and severity of infestation is increasing (Emechebe *et al*., 2004). New areas and fields are being colonized by Striga by means of cattle dung, infested crop seed and wind (Berner *et al*., 1996). Many control options have been developed and speculations have been made about their long-term effects on the Striga seed bank and cereal yields (Oswald, 2005). There is, however, very little data available on the long-term (>3 years) effects of control options and strategies on seed bank dynamics of Striga.

According to the concept of integrated weed management, there are economical advantages in taking a long term approach to weed management, and not focus entirely on prevention of short term crop losses (Jones & Medd, 2000). The evaluation of effects of control options on long-term Striga population dynamics involves long and costly research programs, and only a limited set of treatments can be tested. Modelling weed population dynamics is an attractive approach to assess potential long-term effects of control strategies and indicate their effectiveness.

Thus far, five Striga seed bank models have been published (Kunisch *et al*., 1991; Smith *et al*., 1993; Smith & Webb, 1996; Mullen *et al*., 2003; Westerman *et al*., 2007), all with specific questions and goals. However, these models suffer from three limitations. First, their parameterization is largely based on fragmented data from limited field observations, but mostly from pot and laboratory experiments. Second, the models do not incorporate spatial dynamics or stochasticity, which are probably essential components determining the colonization of previously uninfested fields by Striga from point inoculations (e.g., dung patches). Colonization of previously uninfested fields is a process that has not been studied or modelled yet. Third, except for Mullen *et al*. (2003), earlier models do not link Striga density to potential cereal yield. The relationship between emerged Striga shoots and millet yield proposed by Mullen *et al*. (2003) and taken from Webb & Smith (1996), was developed for modelling the competition between normal weeds and a crop (Cousens, 1985) and may not be applicable to a hemi-parasitic weed like Striga. Infection with Striga causes growth reductions in a host even before the weed has emerged, i.e., the mechanism is pathogenic rather than competitive and should be modelled accordingly.

In this chapter, we use a process-based, spatially explicit and stochastic model to evaluate options for long-term control of Striga infestations in cereal crops. The model

considers all relevant life cycle stages of Striga and is parameterized using empirical data on Striga seed germination and survival, recruitment, survival to maturity, fecundity, seed dispersal and cereal host yield (Chapters 2 and 4; Berner *et al*., 1996). Six cropping systems (within a single year) and seven rotations of these cropping systems are evaluated to generate plausible projections of long-term Striga seed bank dynamics and millet yield.

The aim of this study is (1) to describe a spatial-stochastic seed bank model for *S. hermonthica*, (2) to study the effects of stochasticity in attachment to the host and seed dispersal on the process of colonization of previously uninfested fields, (3) to study the influence of changes in the life cycle parameters on seed bank dynamics and millet yield, and (4) to identify effective control strategies of infested fields in terms of long term Striga seed bank reduction and millet yield.

Description of the spatial-stochastic model

The model simulates spread and population dynamics in a stage-structured population of Striga in a cropped field over a sequence of years, with a time step of one year (Fig. 1). The field (76.8 m × 76.8 m) is represented as a grid of cells, each measuring 0.8 m × 0.8 m. Each cell contains a single host plant, thus in total 96 × 96 hosts are considered. Striga seeds are dispersed from mature Striga plants growing on an infected host plant. The dispersed seeds are added to the soil seed bank of the cell to which they are dispersed at the end of each time step.

We distinguish seven life stages in Striga population development (Fig. 1): viable seeds in the seed bank at the start of the season (S_t), seeds germinated after stimulation by host roots (G), attached seedlings (A), emerged plants (E), mature reproductive plants (R), new seeds produced (P), newly shed viable seeds (V) and viable seeds in the seed bank after the season (S_{t+1}). The population size in each non-seed stage is modelled as a fraction of the population size of the previous life stage (Westerman *et al*., 2007). Seed bank dynamics from year t to year t+1 was modelled as:

$$S_{t+1} = S_t + V_t - M_t \qquad \text{(Eqn. 1)}$$

where S_t and S_{t+1} are the density of viable Striga seeds in the seed bank (seeds/cell) in year t and t+1 respectively, while V_t denotes the density of newly produced, viable seeds (seeds/cell) entering the seed bank in year t, and M_t denotes seed removal from the seed bank (seeds/cell) in year t.

Following the chain of events in the life cycle (Fig. 1), the density of new produced seeds (V_t) can be expressed as a fraction of the density of viable Striga seeds in the seed bank (S_t):

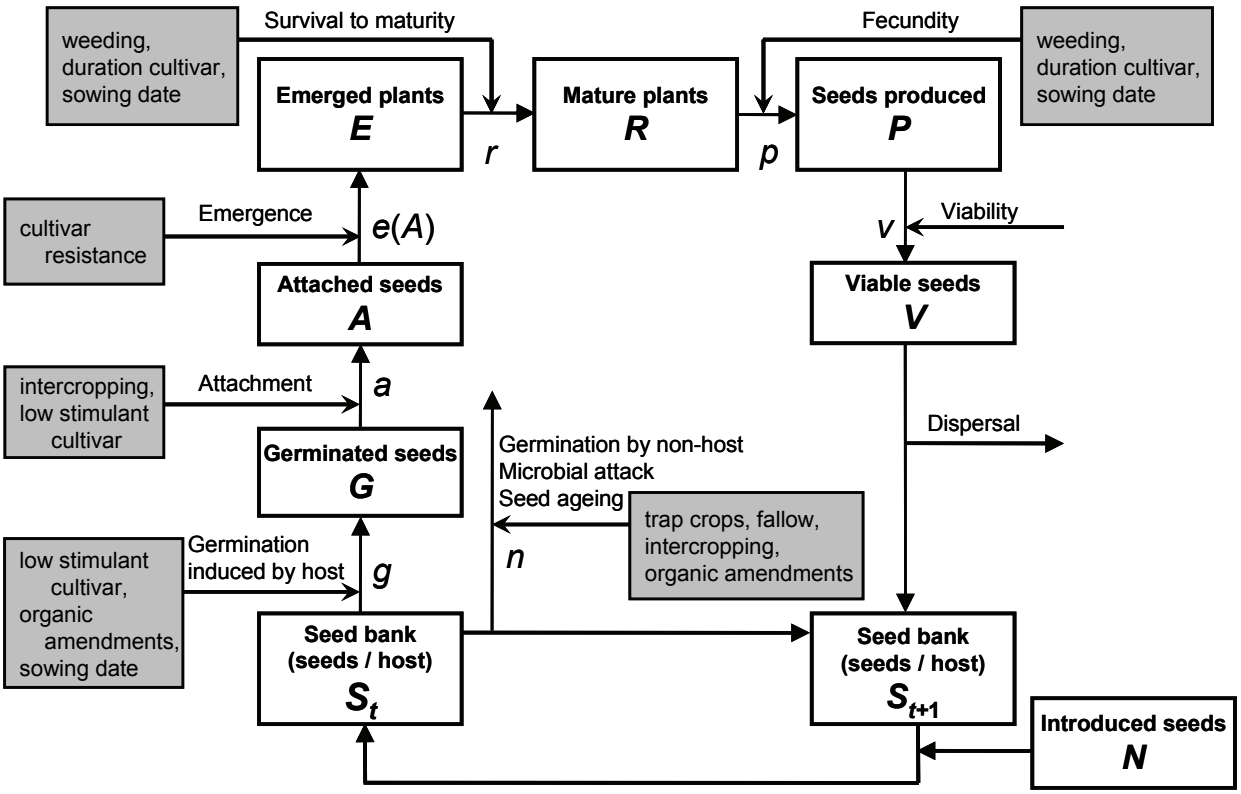

Fig. 1. Diagram of life cycle of *Striga hermonthica*. Model parameters are indicated in italics, white text boxes show state variables, and grey text boxes indicate at what processes different control options may act.

$$V_t = S_t \cdot g \cdot a \cdot e(A) \cdot r \cdot p \cdot v \qquad \text{(Eqn. 2)}$$

where g is the proportion of Striga seeds that germinate in response to crop host roots, a is the proportion of germinated seeds that attach to the host root, $e(A)$ is the proportion of attached seedlings that emerges, r is the proportion of emerged plants that reaches maturity, p is the seed production per mature Striga plant and v is the proportion of viable seeds (Fig. 1).

The attachment of Striga seeds to roots of host plants is modelled as a stochastic process. The density of seedlings that successfully attach to host plants (A, seeds/cell) is drawn randomly from a Poisson distribution with a mean of μ_A, with μ_A being the product of the density of germinated seeds and the average proportion of germinated seeds that attach to the host root (a).

The emergence of Striga seedlings on host plants is a density-dependent process. A function was deduced from a model of Yoda *et al*. (1963) for self-thinning of populations of juvenile plants. We describe the proportion of attached Striga seedlings that emerges, $e(A)$, as a function of the density of seedlings that successfully attach to host plants (A):

$$e(A) = \frac{K}{K + A} \qquad \text{(Eqn. 3)}$$

where K is the maximum density of emerged Striga per host plant (Table 1).

The number of viable Striga seeds that are lost from a cell (M_t) can be expressed in terms of number of viable Striga seeds in the seed bank (S_t):

$$M_t = S_t \cdot (g + n) \qquad \text{(Eqn. 4)}$$

where g is the proportion of Striga seeds that germinates in response to crop host roots and n is the proportion of seeds that are lost because of other causes than stimulation by host roots. This may be through spontaneous germination, germination in response to non-host roots, attack by pathogenic fungi or ageing (Table 1).

Seed dispersal of Striga

Mature Striga plants shed seeds that are dispersed and initiate new infections. We distinguish two dispersal modes for Striga seeds: short and long distance dispersal. Both dispersal modes are described using a Laplace dispersal kernel, essentially a rotated, radially symmetric negative exponential function (Skelsey *et al*., 2005). The spatial profile of dispersal of redistributed seeds is described as:

$$V = me^{-q_1 \cdot x} + (1 - m)e^{-q_2 \cdot x} \qquad \text{(Eqn. 5)}$$

where V is the density of viable shed seeds being dispersed at x meters, m is the proportion of seeds that is dispersed according to the short distance dispersal mode, q_1 and q_2 are the slope parameters for short and long distance dispersal (Table 1, Fig. 3). Seeds that are redistributed outside the field are lost from the system.

Yield of host plants

We adjusted a model by Elston *et al*. (1991) that relates yield of potato to the density of root parasitic potato cyst nematodes to model the relationship between the number of Striga seeds (*St*, seeds/cell) and yield of host plants (*Y*, g/plant):

$$Y = Y_{\max} \cdot \left[1 - \frac{(1 - w) \cdot S_t}{z + S_t} \right] \qquad \text{(Eqn. 6)}$$

where $Y_{\max}$ is the expected yield without Striga, w is the minimum yield expressed as fraction of $Y_{\max}$ and z is the density of viable Striga seeds at which half the maximum yield reduction is attained (Table 1).

Parameterization of life cycle processes

Parameter values for Striga emergence, seed dispersal and host plant yield were assessed using nonlinear regression in GenStat v. 8. Goodness of fit for the parameterization of the different curves was determined by the root mean square error (RMSE).

The model for self-thinning of populations of juvenile plants (Yoda *et al*., 1963) was parameterized using the relationship between the density of germinated seeds per host and the recruitment of emerged Striga (Eqn. 7) (Van Mourik, unpublished data):

$$E = \frac{a * G}{(1 + c * G)} \qquad \text{(Eqn. 7)}$$

where G is the number of germinated seeds and E the number of emerged plants, a is the proportion successful attachment, and a/c is the maximum number of emerged Striga per host (i.e., K in Eqn. 3) when G reaches infinity (Fig. 2).

Parameters for the seed dispersal curve were determined by fitting Equation 5 to data on the relationship between dispersal distance and Striga seed density in three cereal fields in Nigeria and Benin, West Africa (Berner *et al*., 1994). The model of Elston *et al*. (1991; Eqn. 6) was fitted to experimental field data of 2004 in Sadore, Niger from Van Mourik (unpublished; Fig. 4). Because our data set did not include a control yield in the absence of Striga, the maximum yield was set at an estimated 210 g per host for a long duration millet cultivar and 110 g per host for a short duration millet cultivar. Values of parameter w and z are given in Table 1. The millet yield at the end of a rainy season was related to the seed bank density at the start of that season (S_t).

The stochastic and spatial component

To study the effect of stochasticity, a spatial-stochastic and a spatial-deterministic model were developed. Furthermore, two inoculation methods were used to study the effect of colonization of previously uninfested fields. The first inoculation method was a point inoculation of Striga seeds at one host in the centre of the field and the second was a blanket inoculation of all hosts in a field. As a result, there were four ways of Striga introduction and simulation, namely (1) point inoculation with the stochastic model (point-stochastic), (2) point inoculation with the deterministic model (point-deterministic), (3) blanket inoculation with the stochastic model (blanket-stochastic) and (4) blanket inoculation with the deterministic model (blanket-deterministic). Spatial expansion and population growth of Striga was studied for each of these combinations. Simulations with the stochastic model were repeated 200 times, presented as averages and sometimes as individual realizations (Figs 6, 7 and 8).

Table 1. Overview of parameter values used in the *Striga hermonthica* seed bank model for six cropping systems. (1) a monoculture of a long duration millet (cv. Sadore local); (2) a monoculture of a short duration millet (cv. 3/4HK); (3) a monoculture of a long duration millet (cv. Sadore local) with additional weeding at Striga flowering (~75 DAS); (4) intercrop of a long duration millet with cowpea; (5) intercrop of a long duration millet with sesame, and (6) fallow or monoculture of cowpea or sesame.

Striga life cycle parameters			Crop systems					
			Monoculture millet host			Intercrop host-nonhost		Host absent
Parameter	Description	Dimensions	long duration (1)	short duration (2)	weeding at flowering (3)	millet cowpea (4)	millet sesame (5)	cowpea, sesame or fallow (6)
g	germination in response to host roots	seed∗seed^{-1}	0.6	0.6	0.6	0.3	0.3	0
n	germination through non-hosts + seed death	seed∗seed^{-1}	0.1	0.1	0.1	0.2	0.2	0.4
r	emerged plants that reach maturity	plant∗plant^{-1}	0.53	0.4	0.02	0.14	0.08	-
p	fecundity (seeds per mature plant)	seed∗plant^{-1}	18,800	15,600	4,600	20,600	7,200	-
v	viability of produced seeds	seed∗seed^{-1}	0.8	0.8	0.8	0.8	0.8	-
Density dependent emergence								
a	attachment to host roots	seedling∗seed^{-1}	0.0039	0.0101	0.0039	0.00048	0.00012	-
K	maximum number of Striga plants per host	Plant	82.3	16.6	82.3	82.3	82.3	-
c	$c = a/K$	-	0.000047	0.000661	0.000047	0.00000580	0.000002	-
Striga seed dispersal								
m	fraction seed dispersal over short distance	seed∗seed^{-1}	0.88	0.88	0.88	0.88	0.88	-
q_1	slope for short distance dispersal	1/m	5.63	5.63	5.63	5.63	5.63	-
q_2	slope for long distance dispersal	1/m	0.19	0.19	0.19	0.19	0.19	-
Millet yield parameters								
Y_{max}	maximum millet yield (0 Striga seeds)	gram	210	110	210	70	70	0
w	minimum millet yield (fraction) when Striga seed density reaches infinity	gram	0.0578	0.0712	0.0578	0.0578	0.0578	-
z	Striga seed density with 50% damage	gram∗seed^{-1}	810	340	810	810	810	-

Parameterization for different crop systems or control options

The life cycle processes of Striga in six different cropping systems were parameterized using data from field studies (Chapters 2 and 4) and are given in Table 1. These crop systems or control options were (1) monoculture of a long duration millet, (2) monoculture of a short duration millet, (3) monoculture of a long duration millet with weeding at Striga flowering, (4) intercrop of a long duration millet with cowpea, (5) intercrop of a long duration millet with sesame, and (6) fallow or a trap crop monoculture of cowpea or sesame (Table 1). Parameter values were estimated for each cropping system, e.g., for germination in response to hosts (g) or non-hosts (n), attachment (a), survival to maturity (r), fecundity (s), maximum millet head yield (Y_{max}), minimum yield (w) and the Striga seed damage coefficient (z) (Table 1). Parameters kept constant in all cropping systems were viability of produced seeds (v), the fraction of seeds that was dispersed over short distance (m) and slopes for short distance and long distance dispersal (q_1 and q_2, respectively).

Elasticity analysis

Elasticity of parameters (i.e., the relative change in model output per unit of relative change in the value of a parameter) was calculated with:

$$e_\theta = \frac{(Y_{\theta+} - Y_{\theta-})/Y_\theta}{(\theta_+ - \theta_-)/\theta} \qquad \text{(Eqn. 8)}$$

Where e is elasticity of a parameter, $Y_{\theta+}$ and $Y_{\theta-}$ is the model output after proportionally changing a parameter with value θ (+10% or –10%) and Y_θ is the value of the output after running the point stochastic model with an inoculation of 1,000 seeds on a central host millet plant in the field.

Results

Fitting of model equations

The relationship between the number of germinated seeds and the number of emerged plants (Eqn. 3) is presented in Fig. 2. Fits were adequate for the short duration millet host (R^2 = 0.45 and RMSE = 6.52) and for the local, long duration millet host (R^2 = 0.75 and RMSE = 15.53). The parameters a, c and K are given for a long and a short duration millet in Table 1.

The formula for dispersal distance to mature Striga plants (Eqn. 5) is presented in Fig. 3 and gave an excellent fit to the data (R^2 = 0.99 and RMSE = 5.52). The values of the parameters in the model were 0.88 (m), 5.63 (q_1) and 0.19 (q_2), as presented in Table 1.

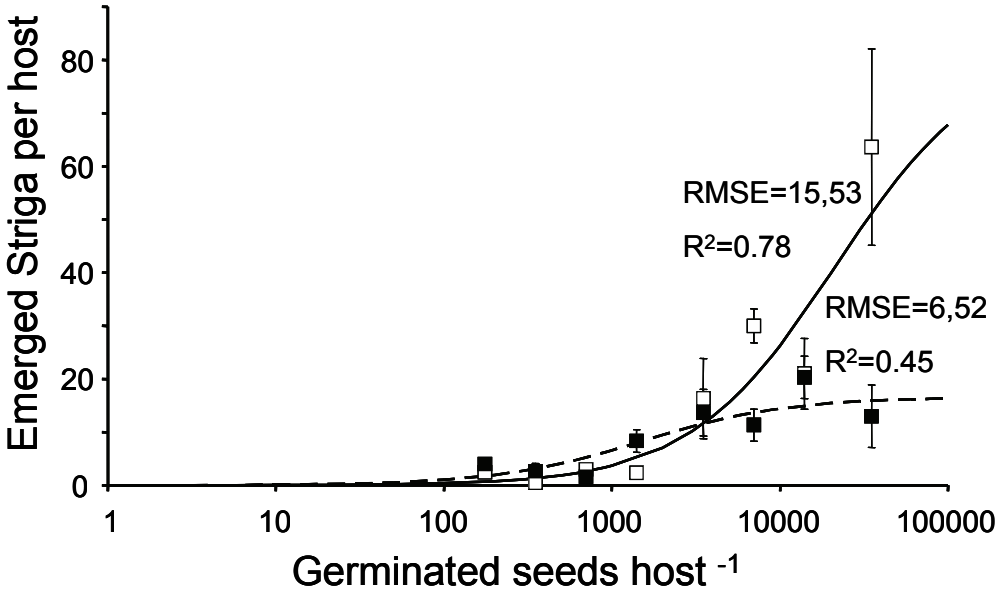

Fig. 2. Measured and fitted relationship between the number of emerged *Striga hermonthica* plants and the number of germinated seeds for a long (□, solid line) and a short (■, dashed line) duration millet cultivar. Error bars represent SEM.

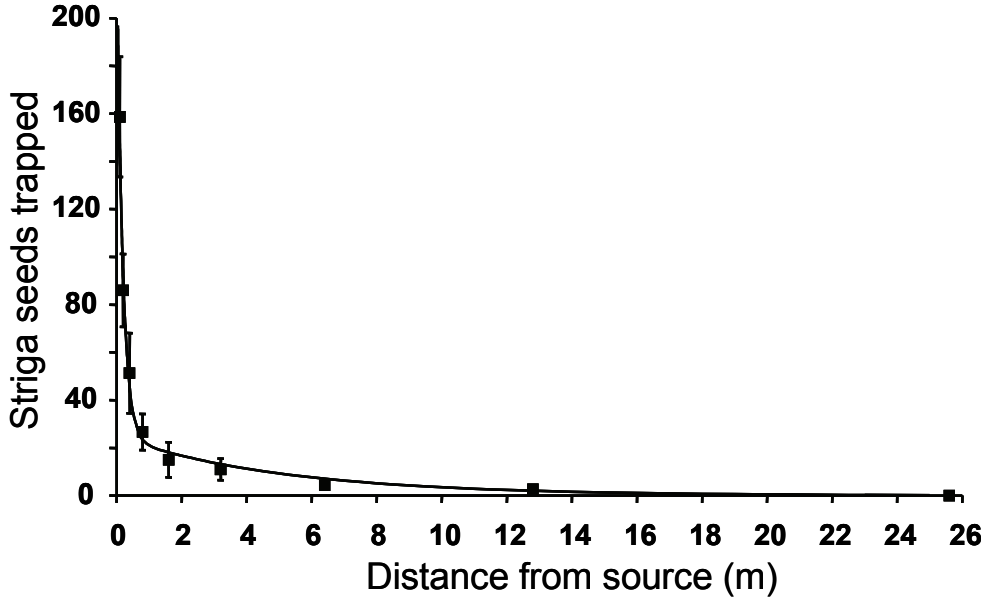

Fig. 3. Measured and fitted relationship between Striga seed density and distance from (mature) seed producing plants. Error bars represent SEM. Empirical data originate from Berner *et al*. (1994).

Finally, the formula for the relation between millet head yield and Striga seed density (Eqn. 6) gave an acceptable description of the data for the improved, short duration (R^2 = 0.56 and RMSE = 17.10) and the local, long duration millet cultivar (R^2 = 0.54 and RMSE = 45.03; Fig. 4).

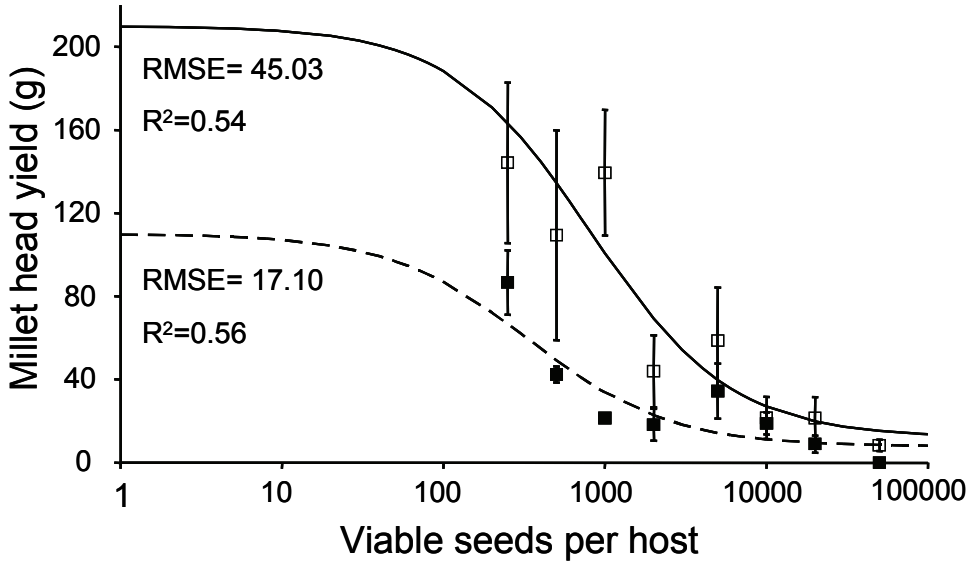

Fig. 4. Measured and fitted relationship between millet head yield and the number of viable *Striga hermonthica* seeds at the start of the rainy season for a long (□, solid line) and a short (■, dashed line) duration millet cultivar.

Stochasticity and the spatial component

In model runs with the stochastic model, establishment of Striga is either a failure or a success. Introduction of low densities of Striga seeds to a single host plant in a previously uninfested field may result in mostly failures, even under a permissive cropping system, but the success rate increases with higher amounts of inoculum (Fig. 5). A point inoculation with a Striga seed density of 1000 per hill resulted in nearly 100% establishment with the short duration millet but less permissive cropping systems had considerably lower establishment probabilities.

Differences in Striga seed bank dynamics and millet yield were observed between the stochastic and the deterministic model after point inoculations (Fig. 6). In simulations with the stochastic model, only 2.5% of point inoculations with 10 seeds per hill resulted in Striga establishment (Fig. 6A). In the few cases that Striga did establish, the initial rise in population level was higher than in the deterministic model. However, on average the stochastic model leads to lower seed bank increase and slower reduction in millet yield than the deterministic model (Fig. 6). After a point inoculation with 1000 seeds, 97.5% of the simulations resulted in successful Striga establishment in the stochastic model (Fig. 6C). At this density, the average outcome of the stochastic model approached that of the deterministic model. Production of the first Striga infected millet plant from the initial inoculum was observed until five year after introduction, i.e., some infestations, due to chance, did not give recruitment of adult plants until year 5.

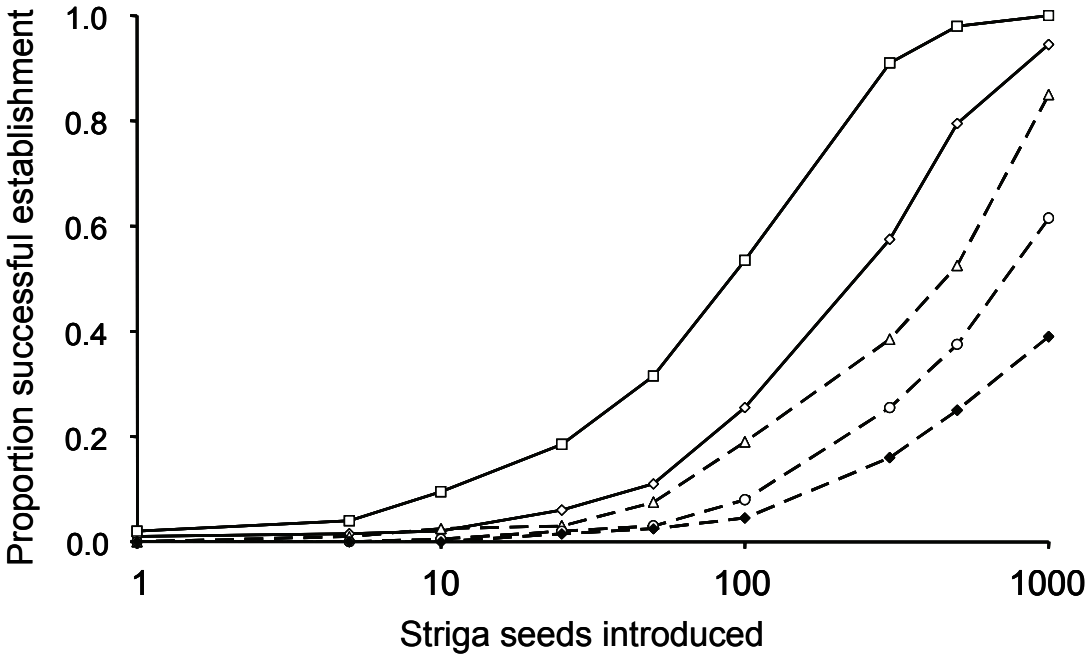

Fig. 5. Simulation of the proportion of successful establishments of *Striga hermonthica* (n=200) after 12 years of cultivation as function of the number of seeds introduced on a central host plant in a millet field. Evaluated scenarios are: a long duration millet (◊), a short duration millet (□), one year of non-hosts followed by three years of a long duration millet (Δ), two years of non-hosts followed by two years of a long duration millet (○) and three years of non-hosts followed by one year of a long duration millet (♦).

When using a blanket inoculation, the stochastic and deterministic models yielded nearly similar results (Fig. 7), i.e., the effect of stochasticity was largely nullified by the effect of averaging over a population of 96 × 96 millet plants. Only at the lower inoculum density of 10 seeds per millet host there was a slight reduction in the rate of seed bank increase and millet yield decrease (Figs 7A and 7B). At blanket inoculation densities of 1000 seeds per millet host, there was no appreciable difference in outcome between the two models.

A highly heterogeneous pattern of emergence was observed around the edges of the dispersal kernel (Fig. 8). At very low densities, Striga plants emerged on just a few hosts and produced a large amount of seeds, most of which stayed close to the centre of dispersal. The following year, this leads to spatially heterogeneous emergence patterns. In contrast, colonization occurs evenly when permissive cropping systems are used with the deterministic model. Fig. 8 exemplifies a single stochastic model simulation and in this particular realization, the rate of spatial expansion from the inoculated spot is larger than in the deterministic model.

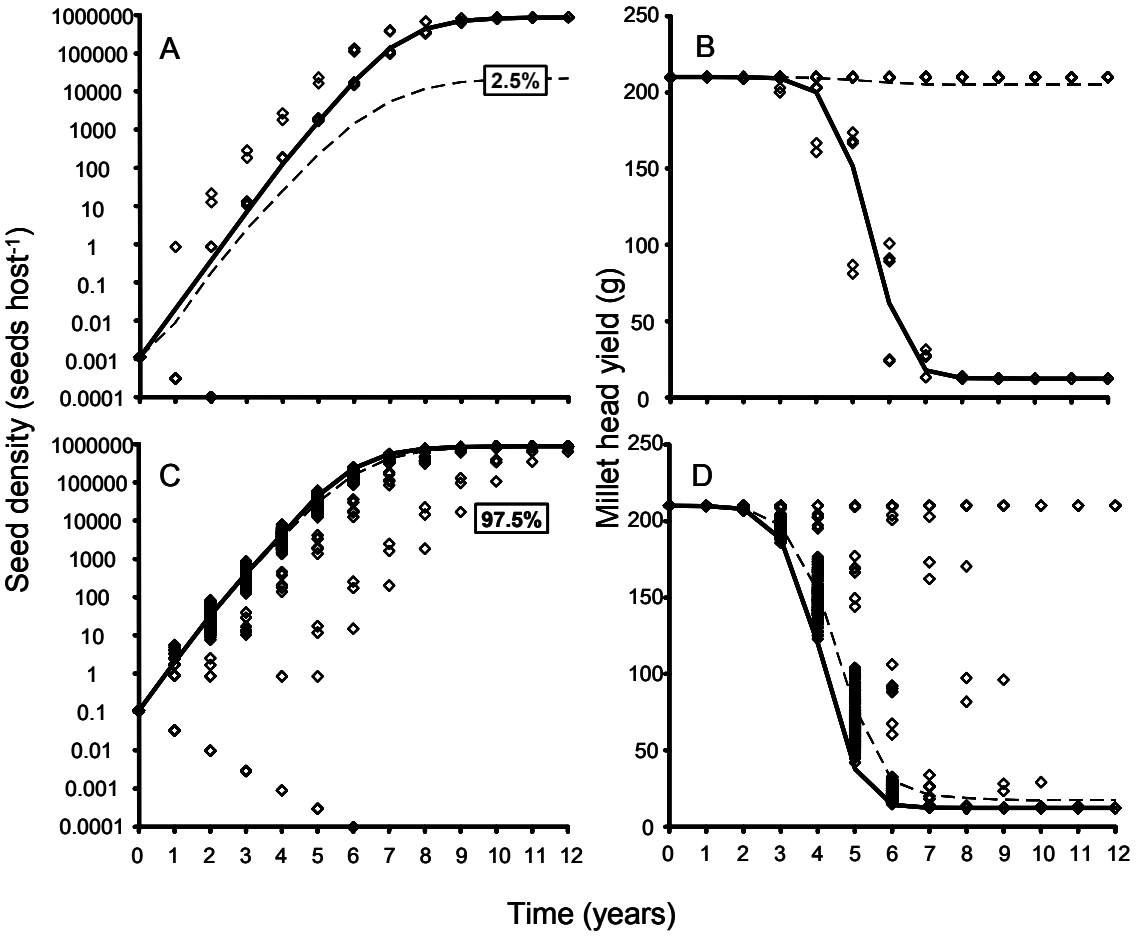

Fig. 6. Simulated seed density of *Striga hermonthica* (A, C) and potential millet head yield (B, D) during 12 years for a monoculture of millet after point inoculation of 10 (A, B) and 1000 (C, D) seeds on a millet host in the centre of the field. The deterministic model was run once and is represented by the continuous line. The stochastic model was run 200 times and diamonds indicate individual runs and the mean of all runs is presented as a dashed line. The percentages of successful establishments of the Striga population are indicated in A and C.

Elasticity analysis

The elasticity analysis of point inoculations shows that after three years of continuous millet cropping (during population increase and expansion phase), five of the eight parameters were influential in determining seed bank density, millet head yield and the number of infected hosts (Table 2). These were the fraction of seeds that germinate in response to host roots (g), the fraction of germinated seeds that attach to the host root (a), the fraction of emerged plants that reach maturity (r), fecundity (p) and the fraction of seeds that is dispersed over short distance (m). Output variables were less sensitive to changes in the fraction of seeds that germinate in response to non-host

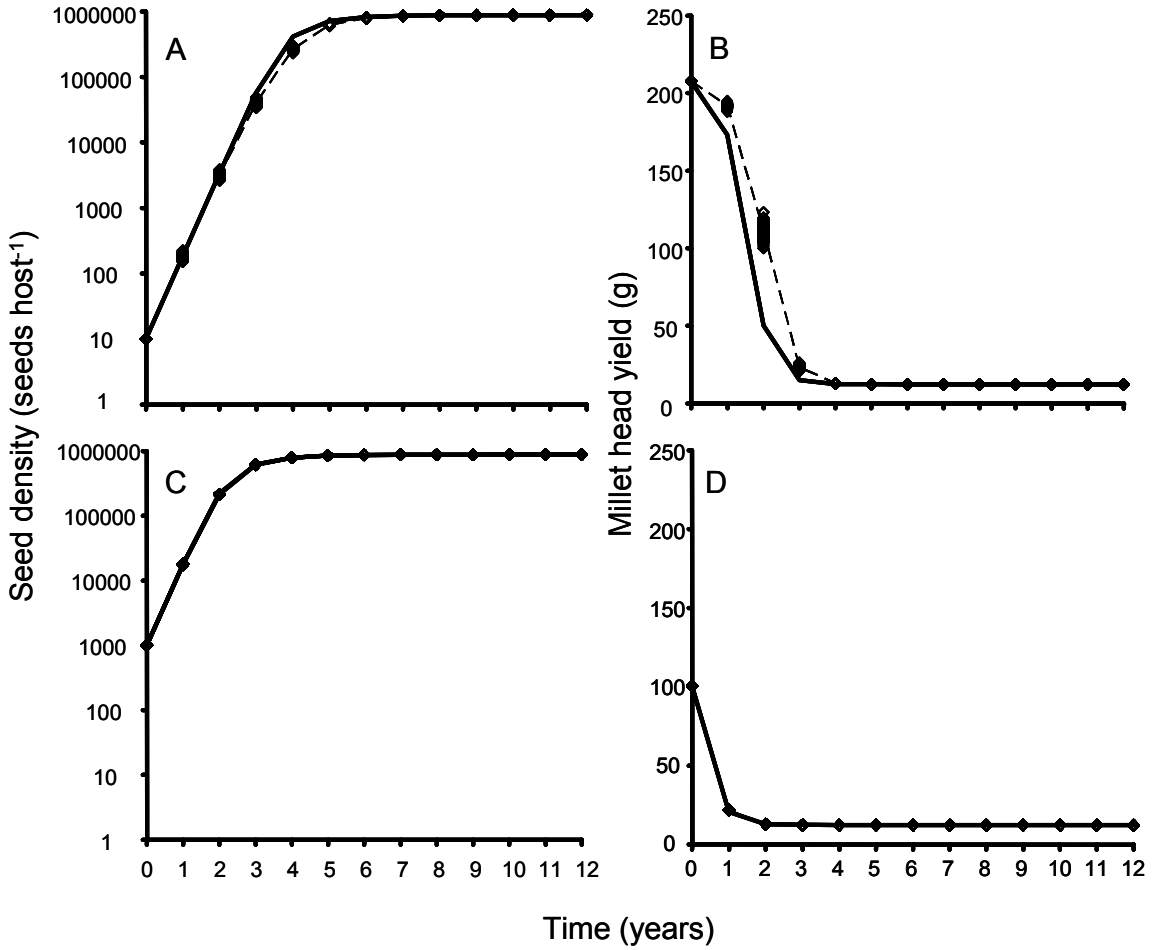

Fig. 7. Simulated seed density of *Striga hermonthica* (A, C) and millet head yield (B, D) during 12 years for a monoculture of millet after blanket inoculation of 10 (A, B) and 1000 (C, D) seeds on all millet hosts in a field. The continuous line represents the deterministic model, whereas the average curve of the stochastic model is presented as a dashed line. Stochastic model averages are based on 200 repetitions (diamonds indicate individual runs).

roots or die due to other causes (n) and the slope parameters for dispersal over short (q_1) and long distance (q_2).

Scenarios

The parameters for cropping systems 1 to 6 were used to simulate seed bank dynamics of Striga, the number of hosts infected and host yield over a period of 16 years. The annual population multiplication factor lambda (λ) was calculated for crop systems using the deterministic model and assuming parameter $e(A) = 1$ (Table 3). Cropping systems with $\lambda > 1$ will be considered "permissive" (crop systems 1 and 2) and those with $\lambda < 1$ "suppressive" (crop systems 3–6).

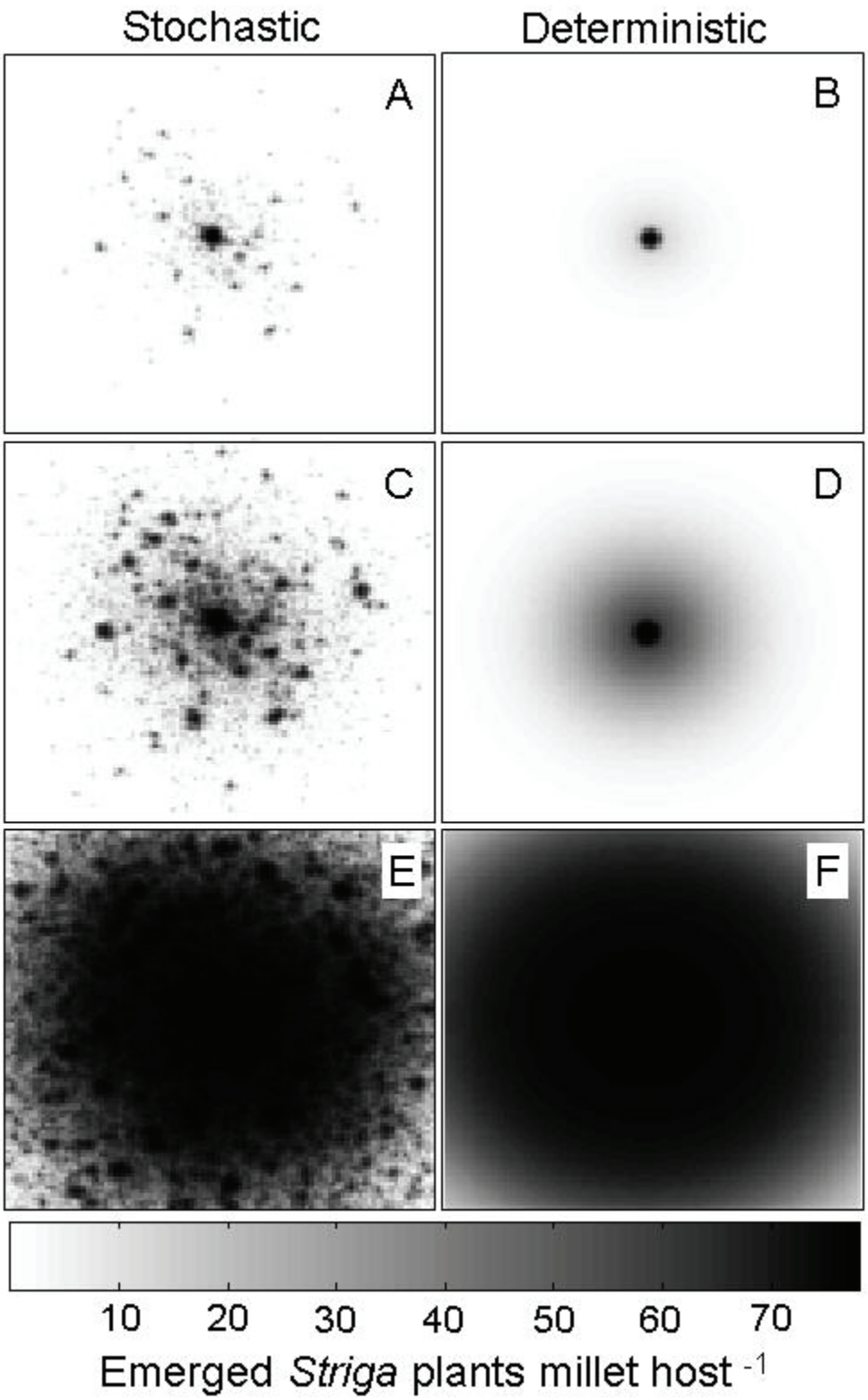

Fig. 8. Simulation of the expansion of a *Striga hermonthica* infestation in a millet field (long duration millet variety) from a single infected host inoculated with 2,000 seeds with a model that contains stochasticity (A, C, E) and a deterministic model (B, D, F). Frames A and B, C and D, and E and F depict the number of emerged Striga plants after 4, 5 and 7 years, respectively.

Table 2. Results of elasticity analysis for a selection of parameters when using the stochastic model after introduction of 2,000 seeds in the centre of a field (mean of 200 replications). Elasticities have been derived for modifications in parameter values (+10% and –10%) for three output variables (seed bank density, millet head yield and number of infected hosts) for 3-year simulations. *Striga hermonthica* population dynamics in year 3 characterize the increment phase. The elasticities indicated in bold highlight the most influential parameters. For explanation of parameter symbols, see Table 1.

Parameter	Seed bank density	Millet yield	Number hosts infected
g	**2.059**	**–0.151**	**1.964**
n	–0.126	0.010	–0.112
a	**1.769**	**–0.130**	**1.767**
r	**2.627**	**–0.172**	**1.682**
p	**2.785**	**–0.175**	**1.708**
m	**–2.437**	**0.602**	**–6.240**
q_1	–0.330	0.029	–0.268
q_2	0.077	0.050	–0.630

Monocultures of a long or a short duration millet (crop system 1 and 2) always lead to seed bank increase and millet head yield decrease, except when weeding at Striga flowering was performed (crop system 6) (Table 3). Rotations of non-hosts (fallow, cowpea or sesame) with millet monoculture one (scenario 7), two (scenario 8) or three (scenario 9) years in every four years still lead to a seed bank increase (Table 3, Fig. 9). The low millet head yield on the long term was the result of a high number of infected millet hosts in these systems. Moreover, averaging only one year millet harvest over four years reduced the average millet yield considerably. An intercrop of millet with cowpea (scenario 3) slowly reduced the Striga seed bank and the potential cumulative millet head yield was superior to any of the permissive crop systems from year four onwards (Fig. 9, Table 3). Among the suppressive scenarios (scenarios 3–6, 10–13), a monoculture of millet with weeding Striga at flowering (scenario 6) was the most effective in reducing the Striga seed bank and increasing millet head yield after 4, 8 and 12 years (Table 3). An intercrop of millet with sesame (scenario 5) was equally effective as millet with weeding Striga at flowering in reducing the Striga seed bank. However, potential millet head yield in scenario 5 was considerably lower than in scenario 6 due to competition with the sesame intercrop (see Chapter 2). Permanent year after year cropping of cowpea and sesame or a fallow (scenario 4) inevitably leads to seed bank decrease, but these strategies are less effective than intercropping millet with sesame (scenario 5) or a monoculture of millet with weeding at Striga

Table 3. Evaluated scenarios and their effects on (1) *Striga hermonthica* seed bank density, (2) the number of years until a 70%, 90% or 98% reduction of the seed bank density, (3) the number of infected hosts in year 4, 8 and 12, and (4) cumulative yearly millet head yield in year 4, 8 and 12 (average per host). The stochastic model was used with an initial uniform seed bank density of 1000 seeds per host (1562 seeds m^{-2}). Simulations are repeated 200 times. Lambda (λ) is the population multiplication factor without density dependent emergence or stochasticity.

Scenario	Crop system	Seedbank[a]	Years until seed bank reduction			% Infected hosts (at year)			Average millet yield (g) (at year)		
		(λ)	>70%	>90%	>98%	(4)	(8)	(12)	(4)	(8)	(12)
1	Long duration millet	+ (19.0)	-	-	-	100	100	100	37	25	21
2	Short duration millet	+ (30.6)	-	-	-	100	100	100	15	12	10
3	Millet-cowpea intercrop[b]	– (0.63)	9	12	>15	7.34	3.40	1.56	41	48	52
4	Monoculture nonhost	– (0.60)	3	4	7	0	0	0	0	0	0
5	Millet-sesame intercrop	– (0.30)	3	4	6	0.45	0.04	0	48	58	62
6	Millet with late weeding	– (0.47)	2	3	6	20.6	1.07	0.05	149	177	188
Rotation of crop systems[c]											
7	(4 - 1 - 1 - 1)	+	-	-	-	100	100	100	42	26	20
8	(4 - 4 - 1 - 1)	+	-	-	-	99.7	100	100	48	28	6
9	(4 - 4 - 4 - 1)	+	-	-	-	39.7	73.3	97.6	42	36	29
10	(4 - 3 - 3 - 3)	-	5	9	14	5.50	1.85	0.62	35	46	50
11	(5 - 4 - 3 - 6)	-	3	5	8	38.6	5.36	0.62	64	74	78
12	(4 - 5 - 4 - 3)	-	2	5	8	2.35	0.32	0.05	26	29	31
13	(4 - 5 - 5 - 5)	-	3	4	7	0.51	0.05	0	38	51	52

[a] + / – ; seed bank increase (permissive cropping system) / decrease (suppressive cropping system);

[b] Intercrops of millet with cowpea or sesame and weeding at Striga flowering ~ 75 DAS were performed with the long duration millet cultivar;

[c] Scenarios in cycles of 4 years where 4-1-1-1 means one year of a non-host system (crop system 4) followed by 3 years of a long duration millet monoculture (crop system 1).

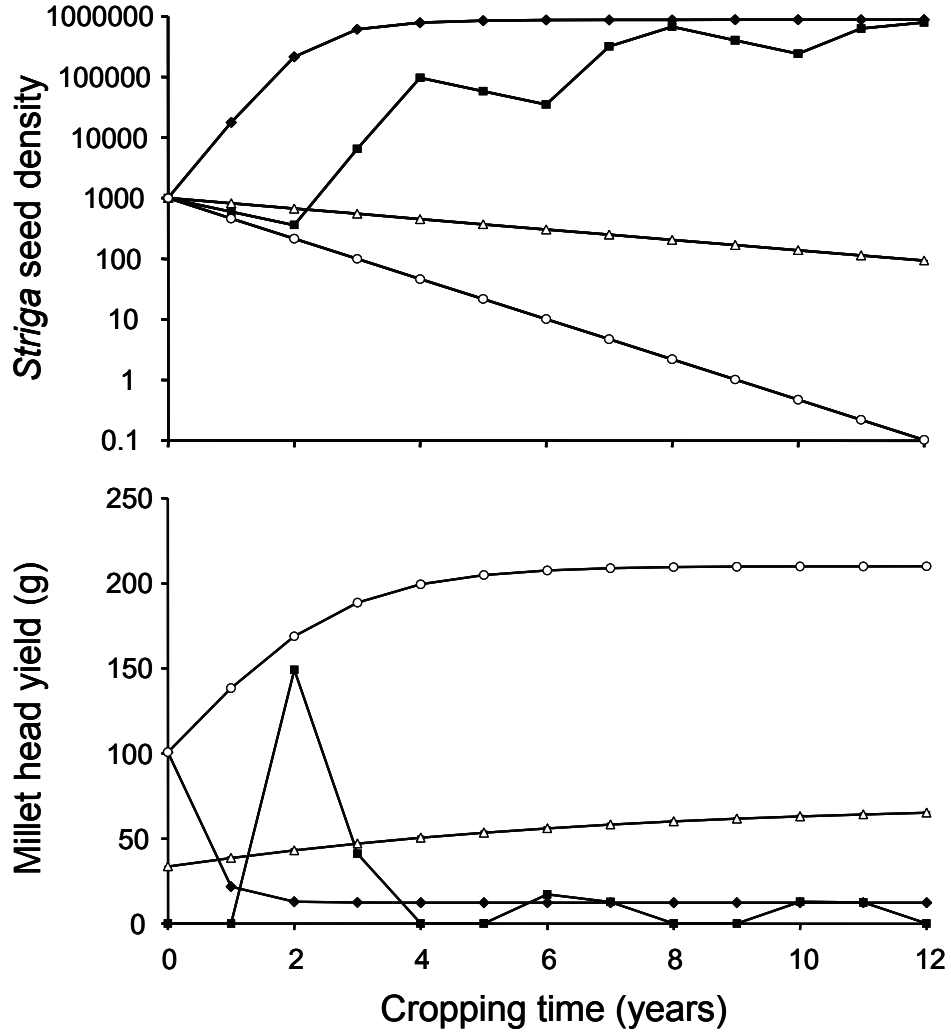

Figure 9. Simulated seed density of *Striga hermonthica* and millet head yield during 12 years for a monoculture of a long duration millet (♦), a rotation scheme of two years of cowpea, sesame or fallow followed by two years of a monoculture of a long duration millet (■), a millet-cowpea intercrop (Δ), and millet monoculture with weeding at Striga flowering (○).

flowering (scenario 6) due to the low germination rates of non-hosts rotations as compared to intercropping of millet with cowpea or sesame (Tables 1 and 3). Scenario 11 is also interesting as Striga seed bank density decreases relatively quick, the system is very diverse (millet-sesame, millet-cowpea, a non-host or fallow and millet monoculture with late weeding), while the cumulative millet yield is higher than that of continuous millet-sesame intercropping. Furthermore, it is expected that at year 4 of the scenario, the density of emerged and flowering Striga plants has already decreased considerably, making the "weeding at Striga flowering" less labour intensive than every year weeding in scenario 6.

Discussion

In this paper, a stochastic and spatially explicit model was developed to simulate the population dynamics of *S. hermonthica* and its effects on cereal production. The model describes situations that are typical for semi-arid crop production systems with millet, cowpea and sesame in sub-Saharan Africa. It is the first Striga population model that includes spatial and stochastic components, enabling an evaluation of effective control strategies to limit the process of establishment of Striga in previously uninfested fields. The parameterization is mostly based on new data on life cycle components of Striga on pearl millet under a variety of cropping practices in Niger (Chapters 2 and 4). The main findings are identification of a series of suppressive cropping systems and rotations and an assessment of vulnerability of permissive cropping systems and rotations to invasion by Striga. For instance, simulations indicated that crop rotations with a high proportion of intercrops and cropping systems that combine cereal monocultures with weeding of Striga prevented the build up of a Striga seed bank. Cropping sequences that are permissive to Striga, e.g., rotations with a high proportion of cereals and no weeding, will inevitably lead to failure of cereal production. This result was found both with the stochastic and with the deterministic model.

The stochastic model allows for the assessment of the probability of successful establishment in a previously uninfested field for different scenarios. The introduction of stochasticity thus creates an opportunity to explore the extent to which cropping systems are vulnerable to invasion. Projected seed bank dynamics were different when models with and without stochastic components were used. Stochasticity appeared very important for single host point inoculations at low densities and became less important for blanket inoculations and point inoculations at higher densities of seeds per host.

A calculation can illustrate that the chances of establishment of new infestations may not be very high. Berner *et al*. (1994) found densities of on average between 15 and 23 intact *Striga* spp. seeds per 10 cattle droppings outside and inside of infested fields in *Striga* spp. infested areas, respectively. This would mean that on average, 1.5 *Striga* spp. seeds are present in each cow dropping in uninfested fields within an infested region. Furthermore, they found 33% of millet seed lot samples infested with *Striga* spp. seeds (seed lots ranged between 1 and 3 kg). However, they reported a maximum of 80 *Striga* spp. seeds per lot. With a millet seed weight of 0.001 gram, this would mean a density of 80 *Striga* spp. seeds per 100,000 millet seeds, or one *Striga* spp. seed per 1250 millet seeds. The *Striga* spp. seed densities reported here are very low and consequently, only a very small part of introductions is likely to establish successfully.

In some situations (e.g., blanket inoculation with high seed densities) the results of

stochastic and deterministic models are similar. The real variability of processes such as attachment may, however, be greater than variability created by Poisson distribution, and a negative binomial distribution may in this case be more appropriate (Binns *et al*., 2000). In reality, we may expect that more life cycle processes have a stochastic nature and so a more elaborate model could be developed that includes stochasticity at multiple life cycle stages. Further research would be needed to assess the stochastic nature of the different phases in Striga development.

The stochastic model produced very heterogeneous patterns of emerged plants, especially at the fringes of the dispersal kernel where seed densities are very low. These emergence patterns on infected cereal crops are often observed in Striga infested fields (Van Delft *et al*., 1997) and are generally ascribed to soil heterogeneity (Hess *et al*., 2001). However, these patterns may thus also emerge from the intrinsic behaviour of the Striga seed bank at low densities. It is likely that both processes (i.e., stochasticity and soil heterogeneity) affect Striga distribution.

The elasticity analysis indicated that seed bank dynamics were affected by changes in nearly all parameter values of life cycle processes, except for germination in response to non-hosts (n) and the two slope parameters for the dispersal curve (q_1 and q_2). In addition, it appears that the most sensitive parameters (survival to maturity and fecundity) can be manipulated by control measures or crop systems. Control should focus on these steps if reduction of the Striga seed bank is the goal (Fig. 1). The fraction of seeds being dispersed over short distance (m) is probably more difficult to manipulate by control options and so less interesting from a management point of view. The proportion of seeds that germinate in response to host roots (g) appears another important parameter for equilibrium phase seed bank density. Germination and attachment are especially important for the increase in the number of infected millet plants in a field at the increment phase of the seed bank dynamics (i.e., at three years after introduction). This has important practical implications, as the Striga seed bank is expected to rarely reach maximum density because fields will be abandoned or other crops will be grown once millet yields start to decrease dramatically. In such a scenario (i.e., cereal cultivation for several years followed by fallow or non-host crops) the Striga seed bank will stay well below maximum equilibrium density and will often be found in the rapid increase phase of the growth curve (i.e., before 50% of the maximum equilibrium density is reached).

Comparison of model predictions lends credibility to the model results, and inspires trust that the long term predictions are relevant. For instance, simulations indicate that the most effective control method was a monoculture of millet with weeding at Striga flowering. The effectiveness of hand weeding to restore yields and reduce the Striga seed bank has been demonstrated in pearl millet and maize

(Ramaiah, 1987; Ransom & Odhiambo, 1994). The model further suggests that no cropping system or strategy can give satisfactory reduction of seed bank densities (more than 90% reduction) in less than 3 years. Indeed, when considering experiments in farmer fields, no experiment has ever shown reductions of more than 90% in seed bank density within two to three years (Oswald & Ransom, 2001; Abunyewa & Padi, 2003; Murdoch & Kunjo, 2003; Schulz *et al*., 2003; Franke *et al*., 2006). This should be taken into account when designing management strategies and discussing options with farmers. The slow reduction of seed bank densities due to germination and seed death further underscores the need for rigorous prevention of seed production for successful Striga control. This implies that infested plants escaping control should be killed or removed from a field before they shed seeds. Even if Striga was allowed to produce seeds once every four years, a seed bank increase may still be inevitable (Table 3, scenario 9).

Fitted equations reflected trends in the data quite well (Figs 2, 3 and 4), although some values of R^2 and RMSE gave moderate satisfaction. To our knowledge, the presented data are the only available, collected under field conditions. Further experimentation is needed to understand these relationships better and provide further data for parameterization. Despite these limitations, a clear advance has been made as the parameterization of earlier models was often based on theory and fragmented data from pot experiments or observations on farmers' fields (Kunisch *et al*., 1991; Smith *et al*., 1993; Smith & Webb, 1996; Mullen *et al*., 2003; Westerman *et al*., 2007).

Striga germination and attachment may be affected by the rainfall distribution in the beginning of each season and yield effects may differ between years (Hess & Williams, 1994; Weber *et al*., 1995). Also, the rainfall distribution and quantity determine yield differences per year that are not related to Striga disease pressure.

Despite the fact that many traditional cropping systems are intercropping systems with millet and cowpea, they often still suffer from high Striga infestations. Model simulations, however, indicate that intercropping millet with cowpea should suppress Striga. We suggest there are two main reasons for this contradiction. First, cowpea is often sown two to four weeks later in the season than millet in farmer practice whereas in the field experiment used for the parameterization, cowpea was planted at the same time as millet (Chapters 2 and 4). Second, cowpea sowing density under farmer practice is often much lower than the densities used in the field experiment. It would be very interesting to study the effects of cowpea intercropping on relative cereal and cowpea yields as well as the Striga seed bank dynamics at a range of intercrop sowing densities, arrangements and relative sowing dates of the intercrop and the cereal crop.

The efficacy of any control method in suppressing a pest is generally lower in a farmer field situation than in a researcher-managed trial. It is to be expected that

farmers will have less interest in re-sowing missing hills of an intercrop or rigorously uprooting or weeding Striga plants because labour and money are more limiting to a farmer. It is thus likely that the efficacy of control methods as indicated by the model is rather an overestimate than an underestimate for what can be expected in practice. To be effective, different control strategies should be combined in an integrated strategy to try to achieve maximum efficacy for Striga control and cereal yield increase (Debrah, 1994; Oswald, 2005). We do not know how different control strategies interact and whether combinations have additional positive effects in reducing Striga control and increasing crop yields. This is a very important question and should be a priority for future modelling studies and experimental field studies.

CHAPTER 6

General discussion

Objective and findings of this thesis

The aim of the work described in this thesis was to quantify the *Striga hermonthica* life cycle and use this knowledge to develop a Striga population model and study the long-term effectiveness of control strategies. Methods were developed to quantify Striga seed bank dynamics. Experimental quantification of seed bank dynamics addressed both replenishment (seed production) and depletion (seed losses). With the model, projections were made of seed bank dynamics and host yield under different control strategies.

Seed bank replenishment

In the analyses in Chapter 2, seed production was divided into recruitment, survival and fecundity. Recruitment was highly variable between years and in situations with very low recruitment, this process overruled processes later in the life cycle (i.e., low recruitment in itself was sufficient to suppress Striga and later stages were not able to compensate). Within years, reduction of cereal host duration reduced Striga survival to maturity and fecundity, but this was often not significant. Furthermore, the resulting number of seeds produced was often still high enough to increase the soil seed bank. Cohorts of early emerging Striga plants contributed most to total seed production, even though the number of plants was lower than that in later emerging cohorts. This was mainly due to a high fecundity of mature Striga plants that emerged early compared to those that emerged late.

Results from experiments 4 and 5 in Chapter 2, show that intercropping a cereal host with a non-host crop has the potential to reduce recruitment (by 12–96%), survival to maturity (by 73–85%), fecundity (by 0–61%) and total seed production (by 99.3–99.7%). At the crop densities studied, competition between intercrops and cereals significantly reduced cereal dry weight, which is unwanted. Late weeding at Striga flowering did not affect recruitment, but reduced survival (by 96–100%), fecundity (by 76–100%) and total seed production (by 99.3–100%). The maximum seed production estimate obtained (7.57×10^5 seeds per host or 1.58×10^6 seed m^{-2}) exceeded the highest densities in soils reported in the literature (Chapters 1 and 2), suggesting that there may be considerable but unidentified losses of (viable) seeds somewhere at or after seed shedding.

Seed bank depletion

The seed bag burial method is widely used to determine the rate of seed mortality in the soil (Rampton & Ching, 1966; Lewis, 1973; Egley & Chandler, 1978), especially for species with very small seeds (Eplee, 1975). However, as shown in Chapter 3, this method led to an overestimation of seed mortality due to a positive density dependence of mortality. Because of the close proximity of seeds within the seed bag, an infection of one seed by pathogenic fungi can spread through the seed lot within the seed bag and lead to a high rate of seed mortality. The infection rate was much lower when seeds were mixed with sand. Therefore, reducing the proximity of seeds in the seed bags, for instance through mixing with sieved soil, is desirable to measure the process of mortality of Striga seeds in the soil.

Results of the use of the adapted seed bag method in Chapter 4 under bare soil and different crop covers suggested that germination of seeds is the main cause of seed bank depletion during a growing season. All types of vegetative cover evoked a considerable proportion of germination, but germination was higher under a host crop than under non-host crops or wild plants. The adapted seed bag method and the soil sampling method yielded similar results in terms of estimated seed bank depletion within a season. The adapted seed bag method however, requires much less work than soil sampling and it enables separation of causes of seed mortality into infection with pathogenic fungi and germination (Chapter 4).

With seed bank densities, germination rates and recruitment rates determined in Chapters 2 and 4, it was possible to estimate what proportion of germinated seeds would emerge under different control measures. The proportions of germinated Striga seeds that emerged was much lower in intercrops than in pure host crops, suggesting an interference of the intercrop with the process of chemotropism, attachment, haustorium formation or underground development of Striga. The data suggest that recruitment was mainly related to bottlenecks in the Striga life cycle that occur *after* germination. Very low recruitment in a “bad or low Striga year” was caused at stages after germination and not by a low germination percentage. A combination of seed bank replenishment rates from Chapter 2 with seed bank depletion rates from Chapter 4, shows that crop systems including a cereal host caused seed bank changes with a factor between 0.46 and 60. Crop systems that did not include a cereal host caused seed bank changes with a factor between 0.50 to a factor of 0.67. The comparatively large reduction of the seed bank under crop systems including a cereal host was due to a high seed bank depletion.

Simulation of* Striga hermonthica *seed bank dynamics

Long-term projections of Striga seed bank dynamics were made with a simulation

model (Chapter 5). The produced model builds on an existing model by Westerman *et al*. (2007) and adds to this the elements of spatial dispersal and random variation in attachment. The model was parameterized with data from field experiments designed for this purpose. The inclusion of a spatial and stochastic component in combination with point inoculation in a field resulted in highly heterogeneous patterns of emerged Striga plants during the colonization period, a pattern often observed in farmer fields. Simulated seed bank dynamics from a deterministic and a stochastic model differed considerably with point inoculations (infestation of one host in a field), but was similar with blanket inoculations (infestation of all hosts in a field; Chapter 5).

A crop system without a host cereal was described as suppressive because it will cause a decrease in the Striga seed bank in one year. A crop system with a host that results in a net increase in the seed bank is called permissive. Crop systems with a host cereal can still be suppressive, if Striga seed production on the host cereal is offset by seed bank depletion. Crop systems that included a host cereal such as intercrops and a long duration cereal with late weeding, were more effective in reducing the Striga seed bank and increasing host cereal yield on the long-term than crop systems without host crops. Simulations showed that rotations with an alternation of suppressive crop systems and permissive crop systems often were not effective in reducing the Striga seed bank on the long-term, even if a permissive cropping system was used only once every four years. Of the evaluated control options in Chapter 5, only a pure millet stand with late weeding was able to reduce the Striga seed bank to less than 10% in 3 years. Moreover, only a pure millet stand with late weeding and millet intercropped with sesame could reduce the Striga seed bank to less than 2% in 6 years.

Implications of findings

Results on seed bank replenishment (Chapter 2) show that control measures can reduce seed production at different stages in the life cycle. Some techniques may primarily reduce recruitment levels (intercropping), whereas other techniques may act on survival to maturity (late weeding). As control techniques can be combined, there is space for optimization of Striga control in terms of seed bank replenishment.

An analysis of seed bank replenishment that distinguishes between recruitment, survival to maturity and fecundity allows for assessment of control options with respect to their potential to reduce Striga seed production. Moreover, it clarifies at what stages in the life cycle seed production is reduced. Observation of the number of emerged plants is often performed in experiments that evaluate Striga control options (Kanampiu *et al*., 2003; Ahonsi *et al*., 2004; Kroschel & Elzein, 2004; Lendzemo *et al*., 2005; Reda *et al*., 2005). This gives an indication of the Striga pressure but does not give information on seed production and long-term effects on the Striga seed bank.

If one wants to know the effect of control options on Striga seed production, regular counts of mature senescent plants, counts of seed capsules on mature plants and determination of the number of seeds per capsule observation are essential. However, for a full understanding of Striga seed bank replenishment and stages at which it can be disrupted, one needs to (1) determine seed bank density, (2) perform regular counts of immature dead plants, (3) perform regular counts of mature Striga plants, (4) determine the number of capsules on the mature plants and (5) determine the number of viable seeds per capsule. Regular counts are necessary because synchronization in emergence, survival or flowering does not occur and the Striga plants disintegrate quickly after premature death or senescence.

The results from the seed bag method with Striga seeds in Chapter 3 may have important implications for seed bank research in general, because similar seed bag methods have been used to evaluate seed survival of many other plant species such as other herbaceous plants, shrubs and trees (Crist & Friese, 1993; Dalling *et al*., 1998; Blaney & Kotanen, 2001). It is possible that some species may have wrongly been classified as having a transient seed bank through an artefact of the method and they may have to be re-assessed. The adapted seed bag method, described in Chapter 3, can be used as a tool for estimation of Striga seed germination rates under different crops, at different depths and at different distances from plant hills *in situ* in addition to the agar gel essay (Hess *et al*., 1992) and root exudate essays (Emechebe & Ahonsi, 2003; Gbèhounou & Adango, 2003).

Furthermore, the adapted seed bag method could be used in on-station and on-farm trials where adding seeds to the soil is not acceptable and where soil sampling would become unpractical because the seed bank is too heterogeneous (Hess *et al*., 2001). It remains to be studied which transitions in the life cycle limit recruitment most. Potential moments at which this limitation occurs, are (1) during the period the Striga radicle tip should make contact with the host root, (2) during attachment, (3) during penetration of the host root, (4) during haustorium formation, or (5) during underground seedling development.

Results from the modelling study indicated that at least 6 years of sustained effort would be needed to reduce the Striga seed bank to less than 2% of its original density, no matter how efficient the control technique. Therefore, control options should not aim at short-term complete eradication of Striga but rather aim at simultaneously suppressing Striga seed bank replenishment to an absolute minimum and limiting the negative effect of Striga on yields. Little is known about seed predation which could have important consequences for the effectiveness of control options.

A life cycle based approach to Striga control

Rodenburg *et al*. (2006a, b) and Van Ast (2006) found density dependence during emergence, survival and seed production of Striga plants. In the present study, density dependence was most pronounced at recruitment and survival to maturity. Therefore, a reduction in the number of germinated seeds, attached parasites, established parasites or emerged plants may be compensated by increased survival and fecundity, and does not necessarily lead to a reduction in seed bank replenishment. Using a Striga population model with density dependent elements, Westerman *et al*. (2007) showed that the long-term effectiveness of interventions early in the Striga life cycle may be reduced as a result of density dependence at later stages in the life cycle. Van Ast & Bastiaans (2006) showed that, if Striga attaches at a later stage of host development, the negative effect of Striga on the host is reduced, and that this process was mediated by seed density (i.e., high seed density resulted in early attachment).

A qualitative analysis of the life cycle may elucidate the advantages and disadvantages of different control strategies in terms of Striga seed bank reduction and negative effects of Striga on host crop yield (Fig. 1). If the Striga life cycle has density dependent steps, which appears plausible, then the effectiveness of control options to reduce seed production may *increase* as control options act at later stages closer to the seed production stage.

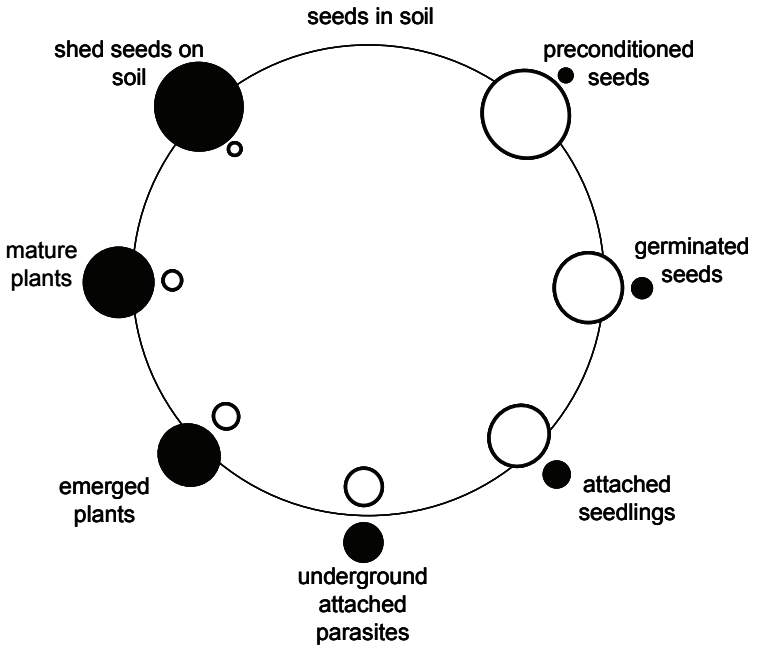

Figure 1. Life cycle and relative efficacy of a given reduction of numbers of each Striga development stage in reducing the seed bank (closed circles) and the negative effects of Striga on host yield (open circles).

However, if the objective of control is to prevent yield loss in the current year, it is important to target early phases of the Striga life cycle, because injury to the hosts accumulates from the earliest stages onwards. Early intervention is needed to protect the current year's yield, but for future yields this may not be enough. Whenever possible, interventions that act at later stages should be included to reduce seed bank replenishment and yields in subsequent years. Furthermore, any control option that reduces the time from attachment to the host and host maturity is suggested to reduce Striga survival to maturity, fecundity and seed production. An integrated Striga management (ISM) strategy should, therefore, aim at combining control options that intervene in early as well as late stages in the Striga life cycle and delay infection time of the host to a maximum.

Soil fertility, mycorrhiza and Striga

Although the present study did not address the issue of soil fertility, integrated Striga management should include soil fertility management. An interesting and largely unexplored area of Striga research is the interaction between soil nutrients, Striga seed densities and host yield under field conditions. There are indications that Striga seed bank densities, host infection and emergence levels are negatively related to the levels of soil organic carbon content and nutrients (Sauerborn *et al*., 2003). However, there is a lot of controversy on the effects of mineral and organic fertilizers on Striga emergence while the effects of fertilizers on seed production and long-term seed bank dynamics are unknown. Mineral and organic fertilizers can both diminish and increase the number of emerged Striga. An increase in Striga emergence was suggested to be associated with increased host yield (Pieterse & Verkleij, 1991). Nutrient addition increases the vigour of the cereal host which may increase its carrying capacity as is the case with insect parasites on insect hosts (Taylor, 1988).

Ayongwa *et al*. (2006) showed that with increasing nitrogen concentration of the host root, Striga seed germination in response to exudates from these roots was reduced. Striga germination was lowest at concentrations of 19.5 mg N per gram host root and no further reduction occurred at higher N-content. It may be speculated that with an increase in nitrogen fertilization, the levels of host root exudates is reduced resulting in a reduction in Striga seed germination. However, increased nitrogen fertilization may also increase the root length density of the host as well as the ability of a host to support a higher number of Striga parasites (i.e., a higher carrying capacity). Boukar *et al*. (1996) found a higher millet root dry weight, higher root length density in the first 10 cm and higher numbers of Striga haustoria attached to the root system after addition of nitrogen to pots.

Toxicity of high nitrogen levels to Striga could also play a role. Simier *et al*. (2006)

showed that nitrate had different toxicity levels for sorghum than for Striga. Up to a certain level of added nitrate (500 mg N per gram host) the leaf expansion and PSII photochemical efficiency of Striga were increased. However, beyond this level (1500 mg N per gram host), addition of more nitrate led to decreased Striga growth and premature death of Striga shoots, whereas no negative effects on the host were observed. From this information and a review of Pieterse & Verkleij (1991), one can expect that there is a threshold level of nitrogen fertilization, under which increased nitrogen leads to increased Striga emergence and above which increased nitrogen fertilization reduces Striga emergence.

The effects of fertilizers on seed production and long-term seed bank development are unknown. Although an initial increase in Striga recruitment and seed bank might be expected due to an increase of carrying capacity of host plants with increased nutrient availability, empirical evidence shows that Striga problems are most severe in situations with very low nutrient inputs. Also, fields that have been fertilized consistently have the lowest Striga seed densities in infested areas (Sauerborn *et al*., 2003). Therefore, an ISM strategy should always include measures that maintain if not improve soil fertility with appropriate use of mineral and organic fertilizer (Vanlauwe & Giller, 2006). Further investigations are needed to clarify the effect of organic and inorganic fertilizers on the interaction between cereal host and Striga and on Striga seed bank dynamics.

The relation between host plants, Striga and arbuscular mycorrhiza (AM) seems to be another potential reason for the apparent ambiguous relation between soil fertility, plant nutrition, hosts and Striga. Nutrient-deficient plants tend to produce exudates that attract mycorrhiza, e.g., through the effect on mycorrhizal branching (Akiyama *et al.,* 2005). These exudates also trigger Striga germination. Improving, e.g., phosphorus status of plants may in this case reduce Striga infection chances, though at the expense of a decreased mycorrhizal contribution to nutrition (Akiyama & Hayashi, 2006). Lendzemo *et al*. (2006) showed that AM fungi negatively impacted on Striga seed germination and that infection of sorghum with AM fungi reduced attachment and emergence of Striga. Also, AM fungi delayed the emergence time and enhanced the performance of the cereal host. Further investigations into the interactions between macro- and micronutrient levels, host cereal growth, Striga and mycorrhiza are necessary.

Control options and Integrated Striga Management (ISM)

From the very first studies on Striga onwards, many authors have suggested that the only true solution to the Striga problem should be an integration and combination of multiple control options. Saunders (1933) already noted “No single agronomic practice

will achieve the desired aim once the soil is heavily infested and it is only by a combination of practices that success can be achieved" (as cited in Fischer, 1999). After Debrah (1994) had stressed the importance of an integrated approach, more studies emerged that related to ISM directly or indirectly (Berner *et al*., 1996; Debrah *et al*., 1998; Schulz *et al*., 2003; Mullen *et al*., 2003; Ellis-Jones *et al*., 2004; Gbèhounou *et al*., 2004; Hess & Dodo, 2004; Lendzemo *et al*., 2005; Samaké *et al*., 2006). ISM through a combination of control options has proven to be effective in reducing Striga and has been adopted successfully by farmers in maize based systems in Nigeria (Schulz *et al*., 2003; Ellis-Jones *et al*., 2004; Franke *et al*., 2006).

There are many simple, but not always 100% effective control options available to farmers at present, new potential control options are emerging and some major breakthroughs and promising advances have been made (Table 1). Examples are (1) herbicide coated maize seeds (Kanampiu *et al*., 2001, 2003; Ahonsi *et al*., 2004), (2) intercropping maize and sorghum with *Desmodium* species (Khan *et al*., 2002, 2006, 2007), (3) biological control by *Fusarium oxysporum* (Yonli *et al*., 2004, 2006; Marley & Shebayan, 2005; Nekouam *et al*., 2006), (4) inoculation of soil and host plants with mycorrhiza (Lendzemo *et al*., 2005), and (5) marker assisted selection to breed high levels of resistance into farmer-preferred sorghum varieties (D. Kiambi, pers comm.).

Many of the control options mentioned above focus on sub-humid, maize based cropping systems. Unfortunately, there are fewer options available for the dryer, more marginal sorghum and millet based cropping systems that this thesis focussed on. The millet based cropping systems in the Sahel regions of West and Central Africa deserve greater research attention because the world's poorest of the poor live here. It is therefore important to assess how the successes and results can be implemented in other regions with maize based systems and how these can be adapted to sorghum and millet based systems.

Table 1 gives and overview of control options and their effects on different stages in the Striga life cycle, host crop yield, input and labour requirements, availability in maize, sorghum and millet and the potential for adoption by farmers. For instance, host resistance may act at the stages of haustorium formation, emergence and survival and it reduces the direct negative effect of Striga on the host. However, without Striga, cereal host yield does not increase and one can question whether the resistant host is adapted to prevailing soil and climatic conditions. Late weeding and removal of flowering plants are very effective in reducing survival to maturity of emerged Striga plants, seed production and seed shedding. Unfortunately, the labour demand is very high and it does not have a direct effect on host yield.

Although we do not exactly know how fertilizer application affects the Striga populations, we do know that the host yield generally increases. Intercropping the host

with a non-host may reduce attachment or recruitment and development of emerged plants (e.g., survival or fecundity of Striga plants). Intercropping is suggested to reduce the direct negative effect on the host and often does not require high investment but may require more labour. A combination of these control options is likely to reduce the Striga population at multiple stages in the life cycle and mitigate the negative effects of Striga on host yield. Furthermore, a reduction in the number of emerged and mature Striga plants is expected to reduce the labour requirement of late weeding and removal of Striga plants.

Furthermore, Table 1 can aid in modelling efforts towards the combination of control techniques in a similar way to a study by Grenz *et al*. (2005) with the parasitic weed *Orobanche crenata* Forsk. and broad bean (*Vicia faba* L.). The seed bank model presented in Chapter 5 could and should be linked (1) to a more sophisticated crop growth model and (2) to a soil model that simulates effects of long-term soil fertility management on plant nutrient levels.

ISM and the role of participatory action research

There is a great challenge and opportunity for action research and participatory experimentation to evaluate integrated Striga management strategies and ensure large-scale dissemination of these in areas with high Striga infestation levels. First of all, the importance of Striga in relation to other constraints to agricultural production should be determined by participatory village level interviews (Emechebe *et al*., 2004). If Striga does not rank high in the list of constraints it should not be a topic for participatory intervention. However, it may still be interesting to find out why it is not a main constraint if it is present. If Striga ranks as a main constraint, farmers' control measures should be determined before proposing any new strategies.

Recommended potential control measures from research have not yet found large scale application on farmers' fields, especially in the sorghum and millet based cropping systems. This may be due to (1) poor understanding of the biology of Striga and long-term effects of control options by farmers, (2) low efficacy of individual control options in reducing Striga to tolerable levels under farmers conditions, (3) lack of adaptability of control options to the local farming system, (4) high cost-benefit ratio of control options compared to existing farmer practice and resources, and (5) other socio-economical factors such as risk avoiding livelihood strategies, traditional land tenure systems and poor infrastructure like seed systems and markets (Debrah, 1994; Emechebe *et al*., 2004; Oswald, 2005).

Many farmers do not know the biology of Striga or how control options may affect Striga seed bank dynamics (pers. obs.). Farmers need to know the biology of Striga and how Striga affects the host before they can conceptualize integrated control and

Control option	Host (short duration)	Host resistance	Host tolerance	Host low stimulant	Late weeding (>60 DAS)	Removal of flowering plants	Herbicide applied on Striga plants	Early sowing	Delayed sowing	Transplanting	Organic fertilizer	Mineral fertilizer	Intercrop host / non-host	Intercrop host / *Desmodium* spp.	Rotation non-host (trap crop)	Herbicide coated crop seeds	Biological control (*Fusarium* spp.)	Soil inoculation with mycorrhiza	Soil solarization	Ethylene injection into soil	Hygiene (preventive measures)
May reduce Striga population during this process?																					
Seed shedding						‡											+				
Seed production	+		-		‡	+	‡	-	+	+	-/+	-/+	+	+		+	+					
Survival	+	+	-		‡		‡	-	+	+	-/+	-/+	+	+		+	+					
Emergence		+	-								-/+	-/+				+	+					
Haustorium formation		+	-								-/+	-/+				+	+	+				
Attachment										+	-/+	-/+	+	+	‡		+	+				
Germination				+				+	+	+	-/+	-/+	+	+			+	+		‡		
Preconditioning																	+		+			
New field infestation																	+				+	
Reduces direct negative effect of Striga on host		+	+	+				+	+	+	+	+	+	+	na	+	+	+	na	na	na	
Increases host yield without Striga	-			-/+				+	-	-	+	+	-/+	+				+				
High input cost	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	?	?	+	++	-	
High labour demand	-	-	-	-	+	+	+	-	-	+	+	-/+	-/+	-/+	-/+	-	?	?	+	++	-	
Availability maize	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	-	+	
Availability sorghum	+	+	+	+	+	+	+	+	-/+	+	+	+	+	-/+	+	-	-	-	+	-	+	
Availability millet	+	-	-	-	+	+	+	+	-/+	-/+	+	-/+	+	-	+	-	-	-	+	-	+	
Potential for adoption by farmers	+	+	+	+	-/+	-/+	-/+	+	-/+	-/+	+	+	+	+	+	+	?	?	-	-	-/+	

Table 1. Overview of Striga control options, potential effect on the Striga seed bank dynamics and host cereal yield as well as their input requirements and availability. Adapted from Debrah (1994), Emechebe *et al*. (2004) and Oswald (2005) with additions from the references and information in this thesis. The left column indicates what control options are considered while column headings indicate what stages or factors are affected by a control option. Explication of symbols: ++, yes very much so; +, yes; -, no; -/+, variable results; ?, unknown; na, not applicable.

make an informed decision on control options. For instance, the concept of prevention becomes a lot more tangible to farmers once they know the potential mechanisms for Striga seed dispersal and long-term effects of Striga infestation. By experimentation and observation, farmers will realize that one single control option may not be able to reduce the Striga population to acceptable levels but that combinations have a great potential. Through participatory interventions by scientists and extension agents, farmers will appreciate more the effects of control options on short-term and especially the effects on the long-term.

Therefore, it is essential to create a platform for farmers, extension workers and researchers to plan, experiment and discuss integrated Striga management strategies. In this way, farmers' knowledge can be complemented with researcher knowledge in the search for an integrated Striga management strategy. Table 1 can be adapted and used in participatory discussions between researchers, extension workers and farmers to develop optimal ISM strategies, in which case one can start with an empty table and jointly fill it in. Advantages and disadvantages of control options for Striga can be discussed from both perspectives. Newly developed control options may be combined with local control options and form a true integrated approach, both from the farmer and the researcher perspective.

Farmers are not in the first place Striga managers, but people who try to attain a certain number of goals and Striga can be more or less relevant an issue to deal with. Therefore it is very important to analyse the costs and benefits of an ISM strategy relative to current farmer practice and to farmer goals. If current research efforts focus more on testing control options and ISM in a participatory manner, both farmers and researchers can make more informed and intelligent decisions on how to increase yields, improve soil fertility, diversify (and commercialize) crops, spread risk and control Striga at the same time. As a successful parasite and weed, Striga (like other pests) is likely to adapt and evolve resistance to control options. The combination of control options should make a crop situation as difficult as possible for Striga to adapt to (Harker, 2004). Thus, it is essential to combine different control options in ISM and

at the same time look for new control options. All areas of research on Striga are valuable as long as we remember; *there is no one-and-only solution to the Striga problem*. The more diverse our control options are, the more chance we make at tackling Striga in diverse agro-ecologies, socio-economical conditions and over a long period.

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Summary

Striga hermonthica (Del.) Benth. is a parasitic weed and a major biotic constraint to cereal production in sub-Saharan Africa. A quantitative appraisal of the life cycle is the key to understanding how the Striga seed bank can be controlled or managed. This thesis presents experimental and modelling work that aims at a comprehensive quantification of the Striga life cycle. Experimental studies of the processes that determine population dynamics have focussed on seed bank replenishment (Chapter 2) and seed losses (Chapters 3 and 4). Subsequently, a model is constructed to explore options for long-term management of the seed bank by means of combinations of cultural and other control options (Chapter 5).

Striga seed production estimates were obtained from 5 field experiments in 3 years in Mali and Niger. Seasonal demography (recruitment, survival, fecundity) and resulting seed production were measured for a set of treatments and control options. These treatments included sowing date of the host, Striga seed density, host duration (e.g., cultivar), intercropping, late weeding at Striga flowering and organic amendments. Striga seed production per cereal host plant was highly variable over years. Reducing host crop duration from around 120 to around 90 days reduced Striga seed production by 30 to 60%, whether through cultivar choice, sowing delay or premature harvesting of the host. Shorter host duration reduced Striga survival to maturity and fecundity. A fivefold increase in initial seed bank density lowered recruitment proportions from the seed bank and survival significantly but had no effect on fecundity, suggesting that density dependence operates primarily in pre-emergence and pre-flowering stages. A cohort study indicated that later emerging cohorts of the parasite contained more individuals, but contributed less to total reproductive output, especially when the period between Striga emergence and maturity of sorghum was short. Seed production was reduced by weeding at Striga flowering through reduced survival and fecundity, while intercropping affected mainly recruitment and survival.

In order to quantify causes of Striga seed losses a critical reassessment and redesign of the seed bag burial method was needed. Seed bags were buried in soil and exhumed at time intervals to monitor mortality of the seeds in three field experiments during two rainy seasons. In 2002, the effect of fungal activity on seed mortality was evaluated in a fungi exclusion experiment. Differences in seed-to-seed interaction were obtained by using two and four densities within the seed bags in consecutive years. Densities were created by mixing 1000 seeds with 0, 10, 100, 1000 g of coarse sand. Mortality rate was significantly lower when fungi were excluded, indicating a role for pathogenic fungi. Decreasing the density of seeds in bags significantly reduced

seed mortality, which is suggested to be the result of decreased seed-to-seed spread of pathogenic fungi.

The adapted seed bag burial method and soil inoculation and sampling were used to quantify the processes behind seed bank depletion. Exhumed seeds from bags or soil sampling were extracted by means of wet sieving and flotation and fate of seeds was assessed by a seed press test. Seed germination and seed bank depletion of Striga were measured in Mali and Niger during the 2004 rainy season under bare soil, fallow and different crop covers (Chapter 4). Seed germination contributed most to seed bank depletion under a variety of crop covers and fallow. Most germination was found in soil under pure stands of the host crops sorghum and millet, followed by intercrops of these hosts and a non-host trap crops, pure stands of non-host crops and fallow. The two methods for measuring seed bank depletion yielded similar results. Combination of seed bank depletion with seed bank replenishment data from Chapter 2 indicated that year-to-year seed bank reduction by germination would only be achieved if seed production was completely prevented.

A spatially explicit model was developed to study the effectiveness of crop systems in preventing invasion of Striga into previously uninfested fields and in reducing established infestations. Spatial expansion of Striga and decrease in millet yield in a field slowed down – on average – as a result of stochasticity of attachment of seedlings to the host. The spatial patterns of emerged Striga plants 4–7 years after point inoculation (e.g., of seeds in a dung patch) in the model resembled spatial distribution of Striga that is typically observed in farmers' fields. Sensitivity analysis showed that all life cycle parameters greatly influenced seed bank dynamics and millet yield except for two slope parameters for the dispersal curve and the parameter for seed losses other than germination in response to millet. Simulations indicate that weeding and inter-cropping millet with sesame or cowpea decrease the Striga seed bank in the long-term, whereas rotations of millet with sesame or cowpea increase the seed bank.

Findings from the thesis and other related studies were used for the proposal of a life cycle based approach to Striga, that may aid in the development of integrated Striga management strategies. Such strategies, it is suggested, should also integrate soil fertility management, and possible interactions between soil fertility, mycorrhiza and Striga are discussed. The possible contributions of participatory and action research to integrated Striga management are finally discussed and it is concluded that control options currently available should be adapted to farmers' conditions, and combined, to achieve reduction of the Striga seed bank and mitigate the negative effects of Striga on the cereal host. At the same time, it is important to look for new control options, because it is likely that Striga will adapt.

Résumé

Le *Striga hermonthica* (Del.) Benth. est une plante parasitaire et une contrainte majeure à la production des céréales en Afrique sub-saharienne. Une évaluation quantitative du cycle de vie du Striga est la clé pour comprendre comment le stock de semences de Striga peut-être contrôlé ou géré. Cette thèse présente des travaux d'expérimentation et de modélisation qui visait à quantifier l'ensemble du cycle de vie du Striga.

Les expérimentations sur les processus qui déterminent la dynamique des populations de Striga ont été centrées sur le renouvellement du stock semencier (Chapitre 2) et la disparition des semences (Chapitres 3 et 4). Sur cette base, un modèle a été construit pour explorer les options de gestion à long-terme du stock semencier au moyen des combinaisons de cultures ou d'autres méthodes de lutte (Chapitre 5).

La production de graines de Striga a été mesurée dans cinq essais réalisées sur trois années au Mali et au Niger. La démographie saisonnière du Striga (recrutement -le taux de plante levées à partir du stock semencier total-, survie et fécondité) et la production de graines résultante ont été déterminées pour un jeu de traitements et d'options pratiques de contrôle. Ces traitements incluaient la date de semis de l'hôte, la densité des graines de Striga, la durée du cycle de l'hôte (entre autre fonction de la variété), la culture associée, le désherbage tardif au moment de la floraison du Striga et l'application de fumure organique. La production de graines de Striga par hôte a été très variable d'une année à l'autre. La réduction du cycle de l'hôte de 120 jours à 90 jours grâce au choix de la variété, au semis tardif ou à récolte précoce a engendré une diminution de 30 à 60 % de la production. Un cycle plus précoce a réduit la survie jusqu'à maturité du Striga et sa fécondité. Une augmentation d'un facteur 5 de la densité initiale des graines de Striga a significativement diminué les proportions de recrutement et de survie mais pas la fécondité, ce qui suggère que la réaction à la densité s'exprime principalement pendant les phases de pré-émergence et de pré-floraison. Une étude sur les cohortes de plantes a montré que celles qui émergent tardivement comportent plus d'individus, mais contribuent moins à la production totale de graines de Striga, en particulier quand le délai entre l'émergence du Striga et la maturité du sorgho était court. La production de graines a été réduite par le désherbage à la floraison du Striga en raison d'une réduction de la survie et de la fécondité, tandis que l'association de cultures a surtout affecté le recrutement et la survie.

Pour déterminer les causes de mortalité des graines de Striga dans le sol, il a été

nécessaire de réévaluer et de modifier la méthode des sachets établie par Eplee. Les sachets de semences étaient enfouis dans le sol et exhumés après différents intervalles de temps afin d'établir la mortalité des graines au cours de 4 essais au champ, pendant deux saisons des pluies. En 2002, les effets de l'activité fongique sur la mortalité des semences ont été mesurés dans un essai d'exclusion par fongicide. Les différences d'interactions graine à graine ont été obtenues en utilisant deux et quatre densités dans les sachets de semences pendant deux années consécutives. Les densités variables ont été créées en mélangeant 1000 graines avec 0, 10, 100 et 1000 g de sable grossier. Le taux de mortalité des graines a été significativement réduit lorsque les champignons avaient été éliminés, indiquant donc un rôle des champignons pathogènes. Une densité de graines plus faible a significativement réduit la mortalité, ce qui suggère une diminution de la transmission graine à graine des champignons.

Les méthodes de sachets de semences enterrés et de l'inoculation du sol ont été utilisées pour déterminer la diminution du stock de semences. Les graines exhumées provenant des sachets ou d'échantillons de sol étaient séparées par tamisage humide et flottaison et l'état des semences était évalué par un test de pression sur la cuticule. La germination des graines et la diminution du stock ont été mesurées au Mali et au Niger, pendant la saison des pluies de 2004, en sol nu, dans une jachère et dans des sols couverts par des cultures diverses (Chapitre 4). La germination des graines de Striga a été le principal facteur de diminution du stock de graines dans une gamme de culture et dans la jachère. Dans les sols sous culture pure de plante-hôte, mil ou sorgho, la germination a été la plus élevée, suivi par les associations de plantes hôtes et non-hôtes, les cultures pures de plantes non-hôtes et enfin les jachères. Les deux méthodes utilisées pour mesurer la diminution du stock de graines dans le sol ont abouti à des résultats similaires. La combinaison des données sur la diminution du stock avec celles du chapitre 2 sur remplissage du stock de graines a montré que la réduction de densité des graines d'une année à l'autre ne pouvait se produire que si la production était totalement inhibée.

Un modèle spatialisé a été développé pour étudier quels systèmes de cultures évitent l'établissement de Striga dans les champs non-infestés, mais aussi lesquels reduisent les infestations dans les champs déjà infestés. L'expansion spatiale du Striga et la décroissance des rendements du mil dans un champ est ralenti (en moyenne) au cours du temps en raison de l'attachement aléatoire des jeunes pousses sur leur hôte. La distribution spatiale des pieds de Striga 4 à 7 ans après une infestation ponctuelle (par exemple dans une bouse de vache) ressemblait à la distribution du Striga observée typiquement dans les champs des paysans. L'analyse de sensibilité des paramètres a montré que tous les paramètres du cycle du Striga avaient une grande influence sur la dynamique du stock de semences de Striga et sur le rendement du mil à l'exception

des deux paramètres de pente de la courbe de dispersion des graines et du paramètre de disparition des graines autre que par la germination induite par le mil. Les simulations ont montré que le désherbage tardif et les associations du mil avec le sésame ou le niébé diminuaient le stock de graines de Striga à long-terme tandis que les rotations mil/niébé ou mil/sésame augmentaient ce stock.

Les résultats de cette thèse et des études similaires ont été utilisés pour proposer une approche reposant sur le cycle de vie du Striga qui pourrait aider au développement de stratégies de gestion intégrée du Striga. Il est suggéré que de telles stratégies devront aussi incorporer des stratégies de gestion de la fertilité du sol et des interactions possibles entre la fertilité du sol, les mycorhizes et le Striga sont discutées. La possible contribution de la recherche participative et de la recherche-action à la gestion intégrée du Striga sont finalement discutées et il est conclu que les options de lutte actuellement disponibles devraient être adaptées aux conditions paysannes et combinées entre elles pour parvenir à réduire le stock semencier du Striga et atténuer ses effets négatifs sur la culture hôte. Dans le même temps, il est important de rechercher de nouvelles technologies de lutte contre ce parasite parce que le Striga s'adaptera probablement aux méthodes de lutte actuelles.

Samenvatting

Striga hermonthica is een parasitair onkruid en een belangrijke biotische groeireducerende factor van de graanproductie in Afrika bezuiden de Sahara. Kwantitatief inzicht in de levenscyclus is de sleutel tot kennis over hoe de Striga zaadbank kan worden bestreden of op niet-schadelijke niveaus kan worden gehouden. Dit proefschrift beschrijft experimenteel onderzoek en een kwantitatieve modelstudie met als doel de zaadbankdynamica van Striga te analyseren en te modeleren. Experimenteel veldonderzoek naar de processen die de populatiedynamica bepalen richtte zich op de productie van nieuwe zaden voor de zaadbank (Hoofdstuk 2) en zaadbankuitputting (Hoofdstukken 3 en 4). Vervolgens werd een populatiedynamisch model ontwikkeld om mogelijkheden voor beheer van de Striga zaadbank op lange termijn te voorspellen (Hoofdstuk 5).

Schattingen van de Striga zaadproductie werden gemaakt met data van vijf veldproeven die over een periode van drie jaar in Mali en Niger werden uitgevoerd. Demografie gedurende het seizoen (rekrutering, overleving tot reproductieve planten, zaadproductie per reproductieve plant) en de resulterende zaadproductie werden gemeten in verschillende, op bestrijding gerichte behandelingen. Deze behandelingen omvatten, zaaidatum van de gastheer, Striga zaaddichtheid, cyclus lengte van de gastheer (o.a. variëteit), mengteelt van de gastheer met een niet-gastheer, laat wieden op het moment van bloei van Striga en toevoeging van organisch materiaal. De zaadproductie van Striga varieerde tussen jaren. Verkorten van de cycluslengte van de gastheer van 120 dagen naar 90 dagen reduceerde de Striga zaadproductie met 30 tot 60%, onafhankelijk van het feit of dit werd veroorzaakt door variëteit, zaaidatum of vervroegd oogsten van de bovengrondse delen van de gastheer. Een vijfvoudige toename van de zaadbank verminderde de proportie rekrutering en overleving, maar had geen significant effect op de zaadproductie per reproductieve plant, wat suggereerde dat dichtheidsafhankelijke regulatie voornamelijk vóór de bloei optrad. Bestudering van opeenvolgende cohorten van opkomende Striga planten die bovengronds verschenen, wees erop dat latere cohorten meer planten bevatten, maar dat deze cohorten minder bijdroegen aan de totale zaadproductie. Wieden van Striga planten aan het begin van de bloei reduceerde de zaadproductie door het terugbrengen van overleving en zaadproductie per plant, terwijl mengteelt voornamelijk de rekrutering en de overleving reduceerde.

Om de oorzaken van de Striga zaadbank-uitputting te kunnen meten, moest eerst een kritische evaluatie van de standaard analyse methode gemaakt worden, die bestaat uit begraven en opgraven van Striga zaden in gazen zakjes (zogenaamde Eplee-

zakjes). Verschillende zaaddichtheden werden gecreëerd door de zaden te mengen met verschillende hoeveelheden zaad in de zakjes en deze werden begraven en met regelmatige tussenpozen in drie experimenten gedurende twee regenseizoenen in 2002 en 2003. In 2002 werd tevens het effect van de activiteit van schimmels op zaadmortaliteit geëvalueerd door schimmels in sommige behandelingen uit te sluiten. Verschillen in zaad-tot-zaad interactie werden verkregen door twee en vier dichtheden te creëren in de zakjes in respectievelijk 2002 en 2003. Dichtheden werden gecreëerd door 1000 Striga zaden te mengen met 0, 10, 100 of 1000 gram zand. De sterfte van zaden was aanzienlijk lager wanneer schimmels werden bestreden met fungiciden, wat aangaf dat pathogene schimmels een belangrijke rol speelden bij de mortaliteit. Een lagere dichtheid van zaden in de zakjes resulteerde in een kleinere toename van het percentage dode zaden. Dit zou het gevolg kunnen zijn van een vertraagde zaad-tot-zaad infectie door pathogene schimmels.

De aangepaste zakjesmethode en een methode gebaseerd op inoculatie en bemonstering van de zaadbank werden gebruikt om de processen die de zaadbank-uitputting bepalen, te kwantificeren. Zaden uit de zakjes en uit de volle grond werden geëxtraheerd en microscopisch geanalyseerd. Kieming van Striga zaden en zaadbank uitputting werden gemeten onder kale grond, braak met wilde planten, en onder een aantal gewassen (Hoofdstuk 4). Kieming was de voornaamste oorzaak van zaadbank uitputting onder braak en verschillende gewassen. De meeste kieming werd gevonden in bodems onder een monocultuur van de gastheer (gierst of sorghum), gevolgd door een mengteelt van gastheer en niet-gastheer gewassen (cowpea of sesam met gierst of sorghum), pure teelt van niet-gastheer gewassen (cowpea of sesam) en braak. De twee methoden gaven vergelijkbare schattingen van de zaadbankuitputting. Een combinatie van gegevens over zaadbankuitputting en zaadproductie uit Hoofdstuk 2, liet zien dat een jaarlijkse zaadbank afname door middel van kieming alleen mogelijk is als de zaadproductie volledig werd onderdrukt.

Een ruimtelijk model werd ontwikkeld om de effectiviteit van teeltsystemen ter voorkoming van vestiging van Striga in voorheen onbesmette velden of reductie van de Striga zaadbank op de lange termijn te voorspellen. Ruimtelijke verspreiding van Striga en afname van de opbrengst van gierst in een veld nam (gemiddeld) langzamer toe als gevolg van stochasticiteit in de hechting van de Striga zaailingen aan de gastheer. Ruimtelijke patronen van opgekomen Striga planten ca. 4 tot 7 jaar na de eerste besmetting op een enkele gastheer in het centrum van het veld leken op de patronen die in boerenvelden worden waargenomen. Een elasticiteitsanalyse liet zien dat alle parameters in de levenscyclus belangrijk zijn afgezien van Striga kieming in reactie op wortels van niet-gastheer gewassen en twee parameters voor de dispersiecurve van geproduceerde zaden. Simulaties suggereerden dat wieden op het

moment van Striga bloei en mengteelt van gastheer gewassen en niet-gastheer gewassen het meest effectief zijn in het terugbrengen van de zaadbank op de lange termijn. Rotaties van gierst met cowpea of sesam resulteerden niet in een afname van de Striga zaadbank op de lange termijn.

De bevindingen en conclusies van dit proefschrift en andere studies zijn gebruikt voor de ontwikkeling van een methodiek voor Striga beheer die gebaseerd is op de levenscyclus van Striga. Deze benadering kan helpen in ontwikkeling van strategieën voor geïntegreerd beheer van Striga. Dit soort strategieën moeten samengaan met maatregelen ter bevordering van de bodemvruchtbaarheid, en mogelijke interacties tussen bodemvruchtbaarheid, mycorrhiza en Striga worden besproken. De mogelijkheden voor participatief onderzoek als belangrijke aanvulling op het onderzoek naar geïntegreerd beheer van Striga worden tevens besproken. Er wordt geconcludeerd dat bestaande bestrijdingstechnieken moeten worden aangepast aan de omgeving en de gewassystemen van boeren, en dat meerdere technieken tegelijkertijd moeten worden gecombineerd om zowel een afname in de Striga zaadbank als een afname van de negatieve effecten van Striga infectie op graangewassen te realiseren. Tegelijkertijd is het belangrijk om nieuwe bestrijdingstechnieken te ontwikkelen omdat het aannemelijk is dat Striga zich op de lange termijn aanpast aan bestaande bestrijdingstechnieken.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities).

Review of literature (5 credits)
- Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks

Laboratory training and working visits (4.2 credits)
- *Striga hermonthica* seed collection ICRISAT-Bamako, B.P. 320, Bamako, Mali (2001)
- *Striga hermonthica* seed analysis ICRISAT-Bamako, B.P. 320, Bamako, Mali (2002, 2003)

Post-Graduate courses (3.8 credits)
- Basic statistics (2002)
- Advanced statistics (2003)
- Survival analysis (2004)

Deficiency, refresh, brush-up and general courses (2.8 credits)
- Population ecology; CWE (2002)

Competence strengthening / skills courses (3.4 credits)
- Research planning and management (2003)
- Career perspectives (2005)
- Endnote (2003)

Discussion groups / local seminars and other scientific meetings (6.8 credits)
- Plant and Crop Ecology (PhD discussion group) (2001-2005)
- ICRISAT, WARDA and ICRAF bi-weekly seminars (2004)

International symposia, workshops and conferences (7 credits)
- 22rd Annual seed biology & ecology meeting. Reading, UK (poster presentation) (2002)
- 23th Annual seed biology & ecology meeting. Cambridge, UK (presentation) (2003)
- Seed banks: Determination, dynamics and management. Reading, UK (presentation) (2004)
- 1st International symposium on the biology of non-weedy hemiparasitic (ex-) Scrophulariaceae. Wageningen, The Netherlands (poster presentation) (2004)
- Broomrape biology, control and management. COST-meeting, Action 849, Reading, UK (presentation) (2005)

Courses in which the PhD candidate has worked as a teacher
- Population ecology. CWE, Wageningen University, 20 days

Curriculum vitae

Thomas Alexander Van Mourik was born on November 27, 1976 in Heemstede, The Netherlands. He followed primary education at the Marijkeschool in Hillegom, from 1981 to 1989 and Secondary School at the Fioretticollege in Lisse, from 1989 to 1995. After this he pursued a study Biology at the Free University (VU) in Amsterdam and the University of Amsterdam (UvA), where he obtained BSc and MSc level in Biology with a specialization in Plant Ecology and Conservation Biology. During this study, he performed two thesis studies at the Institute for Biodiversity and Ecosystems Dynamics (IBED) of the UvA. The first study focused on self-incompatibility and the reproduction system of a rare and endangered plant in The Netherlands called *Arnica montana*. The other study focused on the effect of afforestation with an exotic pine tree (*Pinus patula*) on a native subpáramo ecosystem in the Andes of Colombia. After graduation at the VU, he took several temporary jobs until admission into a PhD programme of Wageningen University, funded by NWO-WOTRO[*]. During his PhD work, he collaborated with ICRISAT and IER in Mali and ICRISAT in Niger. Since October 2005, he is working as an Associate Professional Officer (APO) at ICRISAT in Mali. The subject of study is the same as for his PhD, *Striga hermonthica*, the difference being that in his current work, participatory tests on the integrated control of the Striga pest has become the more important part of his research activities.

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