Understanding the diverse roles of soil organic matter in the cereal – *Striga hermontica* interaction

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ABSTRACT

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The problem of the parasitic weed striga (*Striga hermonthica* (Del.) Benth.) has worsened for African farmers, in conjunction with degrading soil fertility. An analysis of the striga problem showed that scientists, policy makers and farmers conceptualise striga differently. Whether striga is viewed as a weed or a symptom of degraded soils raises two questions: Should farmers control striga, even when the impact on yields would be negligible? Or should fertility enhancement, leading to higher yields, be their focus, even when not accompanied by an immediate reduction in striga? This study seeks to understand how organic matter inputs affect nutrient dynamics, sorghum (*Sorghum bicolor* [L.] Moench) production and striga abundance.

Surveys in northern Cameroon showed that striga infestation increased over the past two decades. Increased land pressure led to reduced fallow periods and enhanced cereal (mono-) cropping. Reduced access to fertiliser and manure hampered options to improve soil fertility. Yields from farmers' fields did not correlate with striga incidence, confirming farmers' prioritisation of soil fertility, weeds, and labour as production constraints, rather than striga. The entry point to tackle low yields and the worsening of the striga situation should follow farmers' priority of alleviating low soil fertility.

Whether and how soil fertility improvement, through organic matter, enhances agricultural productivity and reduces striga, was investigated in field experiments. Organic matter amendments significantly depressed striga seed survival, with the strongest effect achieved at higher quality; presumably due to higher microbial activity. Organic matter enhanced soil water retention and soil temperature but without effects on striga seed survival. Organic matter did not affect soil ethylene concentrations. The effect of organic matter amendments was directly related to N mineralisation, both for better cereal growth and reduced striga survival. The organic matter amendments and use of fallow, as applied here, however, may not be practicable for the resource-poor farmer.

Increasing N-fertilisation increased sorghum root N mass concentration, which resulted in a lower striga seed germination. That relationship was linear up to a root N mass concentration of 19.5 mg g^{-1} where seed germination was close to but always still above 0%.

In a broader framework of the research findings, the ultimate solution for farm productivity for Africa is in sustainable farm intensification by investing in soil fertility. However, the prevailing land tenure system and limited access to fertiliser and organic matter need to be overcome. A new conceptual model is proposed, indicating how changes in both cereal yield and striga infestation over time co-vary with changes in soil fertility. The implication of this model is that recovery of soil fertility should be the priority. The challenge to agronomists remains to consider how to make farm intensification rewarding and attainable for resource-poor farmers. In areas where striga is an obstacle, an integrated scheme for the intensification of cereal cropping should start with integrated soil fertility management. Crop rotation and intercropping with selected non-host leguminous crops are essential ingredients.

Keywords: *Striga hermonthica*, *Sorghum bicolor*, soil fertility, organic matter, N-mineralisation, farmers' priority, production constraints, intensification.

PREFACE

When I look at the thesis work in retrospect, I am overwhelmed by the time, twist and turns the work has taken up to this final finish. However, I am comforted not only because it is completed, but most especially because I have now seen Striga in its broadest possible perspective. Since I started Striga work in 1987 fresh from college, I had always thought that there was disagreement on the Striga problem: e.g. plant pathologist versus weed scientist or science versus policy, to the detriment of the needy farmers.

The completion of this thesis was made possible thanks to many who intervened. I open up by thanking God Almighty, for giving me this opportunity to contribute to mankind's mission on earth.

Amongst the human beings that intervened, (indeed) I am unsure from where to begin expressing my sincere thankfulness since this thesis experienced a total change in the supervisory team along-the-way.

I therefore prefer to start from those with whom this thesis was initiated. I wish to express my profound thankfulness to: Professor Martin Kropff for accepting to be the initial promoter of this thesis; Professor Jan Goudriaan who strongly supported my PhD project as another promoter; and finally, Dr. Wouter Joenje my initial co-promoter, for his profound contributions in collaboration with my promoters in bringing the original PhD project acceptable for a doctorate degree work at Wageningen University. The contribution of Dr. Aad van Ast must be acknowledged through the Striga working group created at the then Department of Theoretical Production Ecology. Through this working group the various key-components of Striga research were clearly defined, making my research area distinct, without which encroachments might have made this work outdated over the long-lifespan of the thesis work. Aad assisted me even when I needed support on catering, to settle-in on arrival at Wageningen.

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I wish to thank the entire CWE staff who hosted me and gave me warmth during my stay at Wageningen. I can not recall all those who were involved by name, but for Henriette Drenth; and Wampie van Schouwenburg for her special and very valuable contribution in editing the booklet version of this thesis. I want here to express my gratitude to the staff of the Central Administration of Wageningen University, for all the arrangements with regards to travel to and from Wageningen and my stay in The Netherlands. Support from Dr. A. Otten (Biometrics) and of W. Roelofsen (Microbiology lab) of Wageningen University respectively in statistics and ethylene measurements is gratefully acknowledged.

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A huge chunk of thanks go to my family: my wife Vivian Ako who made enormous sacrifices on my behalf; my children, Shu Mattheus, Sirri-B. Pastors, Ngum Chappell and Akwen-Neg Gene, they share in the accomplishment of this thesis work through immeasurable sacrifices and sincere prayers to God. Among my family someone stands out special; ‘Ni’ Elvis. He put in an inestimable amount of material and moral support to see that I start and finish this work. He came in when I was in a mess and I can not recount how many times he rescued me when we had to communicate through the erratic fax and telephone networks, at the time internet and email was unknown at my research station and even in Cameroon at large. His intervention was so strategic and indispensable for this thesis work. Many thanks go to my mom, Anna Sirri; brothers, ‘Ta-a’ Ayongwa, Rev. Martin Ayongwa; sisters, Mary Bi-fuh, Joseper Lum, Elsie Manka, Evodia Asoh and Mercy Ngum, for I know they always put me in their prayers to God. I am not forgetting Evelyne Tifuh, ‘paa’ Fon

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M+yah, Thank you, Bedankt, Merci
Gideon Che AYONGWA Dschang, November 2010

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CHAPTER 1

General Introduction

The striga problem

The hemi-parasites of the genus *Striga* (Orobanchaceae) are widely distributed in Africa, in the drier grasslands and savannahs within the arid and semi-arid zone where annual rainfall lies between 500 and 1000 mm. The genus contains 40 species (Wolfe *et al*., 2005), of which 28 species occur in Africa (Mohamed *et al*., 2001).

Several species are parasitic on crops. Cowpea (*Vigna unguiculata* (L.) Wallp.) is parasitised by *S. gesnerioides* (Willd.) Vatke. On cereals three species of *Striga* are major pathogens: *S. asiatica* (L.) Kuntze, *S. aspera* (Willd.) Benth., and *S. hermonthica* (Del.) Benth. This thesis deals with *S. hermonthica* (purple or giant witchweed or striga[1]). Striga is limited to agro-ecosystems and endemic both in West and East Africa (Fig.1). It is a major pest on millet (*Pennisetum glaucum* (L.) R. Br.), sorghum (*Sorghum bicolor* (L.) Moench), maize (*Zea mays* L.), rice (*Oryza sativa* L.) and other cereals. Maize is most susceptible to striga (probably due to the fact that it did not co-evolve with the parasite), followed by sorghum and millet (Gurney *et al*., 1995; Kim *et al*., 1997). On these cereals, host-specific races of striga occur. Therefore, if a sorghum field infested by striga is replaced by pearl millet, the millet is initially almost free of striga – suggesting some form of resistance. However, because striga is an obligate out-breeder and these races still retain some inter-fertility, host switches regularly occur. Consequently, after a few years pearl millet can be equally infested by striga as the previous sorghum field (Olivier *et al*., 1998). The species is also inter-fertile with *S. aspera* (Mohamed *et al*., 2001).

Striga may not have been a problem in the traditional agricultural system but has become a problem possibly as the result of changes to the agricultural system. These changes were due to processes of agricultural intensification (shortening of fallow periods, continuous cropping, change from intercropping or crop rotations with legumes to cereal mono-cropping) that exceeded the carrying capacity of the environment (Kroschel, 1998).

The life cycle of striga

The life history strategy of striga makes it a very effective and ultimately harmful pest under the present agricultural systems. Its life cycle is depicted in Fig. 2.

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[1] In this thesis *Striga* refers to the genus; striga to the species *Striga hermonthica* specifically

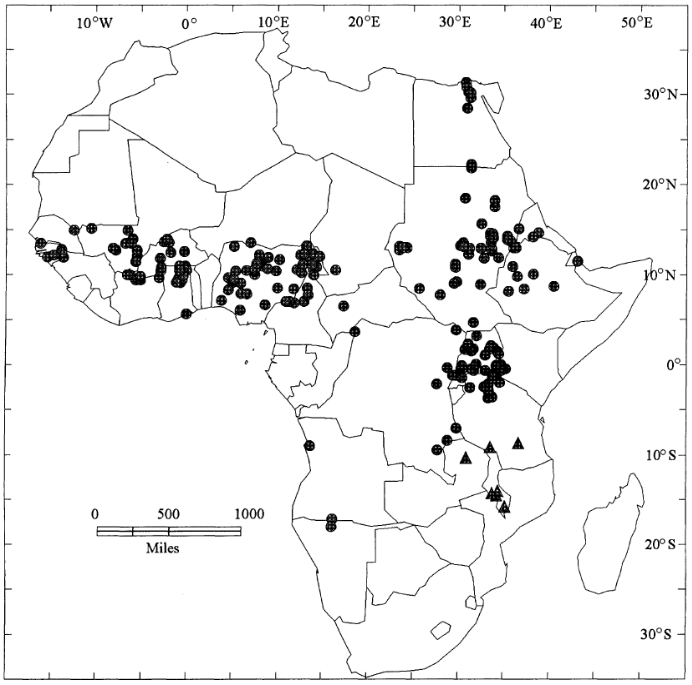

Fig. 1. Distribution of *Striga hermonthica* (filled circles) and *S. gracillima* (filled triangles) in Africa (Mohamed *et al*., 2001).

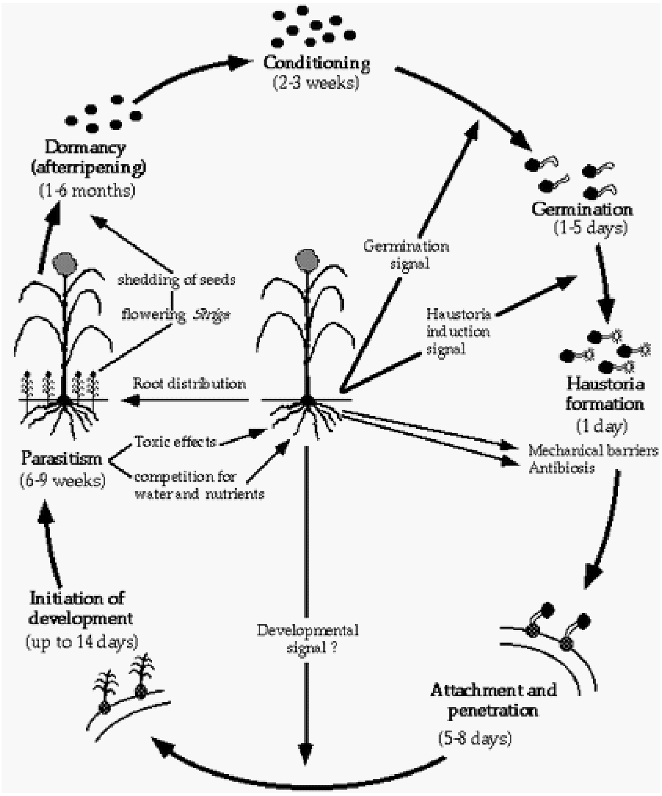

Fig. 2. Life cycle of *S. hermonthica,* showing approximate duration of each of the various stages (Kuiper, 1997).

Five major stages (germination, attachment, below-ground growth, growth after emergence, seed set) that confer special survival strategies to *Striga* species can be recognised.

- For dormant seeds to germinate they need to be conditioned (Olivier, 1996; Kim & Adetimirin, 2001) and subsequently exposed to host root exudates. *Striga* germination is primarily triggered by a class of specific chemicals (strigolactones) exuded by host roots (López-Ráez *et al*., 2008). Proximity to roots is therefore crucial. Different plant species (and varieties within plant species) exude different strigolactones. Synthetic strigolactones like GR 24 have the same effect (Johnson *et al*., 1976). *Striga* germination can also be induced by the application of ethylene (Egley & Dale, 1970). Most (if not all) plant species exude strigolactones, because these compounds form an essential element in the molecular dialogue between plant roots and arbuscular mycorrhizal fungi (Akiyama *et al*., 2005). It is likely that *Striga* species have hijacked this molecular dialogue.
- The next step involves the establishment of a parasitic relation with a host. This happens by means of a haustorium. It is through the haustorium that the host-parasite relationship is established. The haustorium sometimes fails to complete its penetration of the cortex (Ramaiah *et al*., 1991) and may also fail on reaching the endodermis, which provides a barrier for penetration (Saunders, 1933). The haustorium connection represents a crucial point of weakness in the host-parasite relationship. One could speculate that it is most likely that host specificity (low or high striga attachment and emergence) takes place at this stage rather than the previous.
- Upon establishment of the haustorium (and before striga emerges above-ground) the growth of the host plant is already depressed. A large part of the negative effect of host performance due to striga occurs almost immediately after infection and attachment (Van Ast *et al*., 2000), when the parasite interferes with host metabolism (Gurney *et al*., 1999). Graves *et al*. (1989) found that parasite-induced reduction in host photosynthesis occurred before emergence of the parasite above ground and accounted for 80% of the predicted loss. The reduction in the mass of infected sorghum plants can exceed the mass of the parasite they support by more than an order of magnitude. Yield losses by striga are larger than those induced by species of the holoparasitic genus *Orobanche*. In that latter case differences in biomass between infected and uninfected hosts can be largely accounted for by the biomass of the parasite (Hibberd *et al*., 1998). Press *et al*. (1990) concluded that competition for water and solutes by striga are unlikely to play a major role in determining reduction in host productivity. Apart from the direct withdrawal of host nutrients and water, the parasite disturbs the hormonal balance in its host in order to deflect resources from host growth into its own growth (Graves *et al*., 1989; Cechin & Press, 1993a; Gurney *et al*., 1999). Metabolic incompatibility was suggested as a major cause (Press *et al*., 1990). Rank *et al*. (2004) described the involvement of toxic compounds produced by

the parasite.

- After 4-6 weeks of its life underground striga emerges, and it can flower 2-3 weeks after above-ground emergence. This (brief) period provides the time window for direct striga management through hand-pulling which should be completed before seed set. Weeding while striga is still below-ground has adverse effects because it reduces competition below-ground between striga and weeds and also may serve as means for shoot propagation. Severity of infestation cannot be determined accurately from counts of striga numbers emerged, because under high striga pressure only 10 to 30% of striga attached on the roots emerge above the soil surface (Thalouarn & Fer, 1993). In its above-ground stage, striga has green leaves and is partly autotrophic for carbon, although data suggest that more than 50% of the carbon above-ground is still from its hosts (Press *et al*., 1991). Carbon fixed by striga is predominantly allocated to making new leaves, while support tissue still depends on photosynthates provided by the host (Santos-Izquierdo *et al*., 2008).
- As a r-strategist striga produces many minute seeds. The number of mature seeds per reproductive striga plant can range up to 200,000 (Parker & Riches, 1993). The minute seeds do not have any seed reserves, and therefore seed germination is linked to the proximity of suitable hosts. Striga seeds can persist in the soil until appropriate hosts are available. Seeds of striga can remain viable in the soil for a long time. However, data on seed viability that were determined in the lab (7 years for *S. asiatica* - Saunders (1933); at most 6 years for the same species according to Bebawi *et al.* (1984)) may not pertain to field conditions (Chapter 3). Because of high rates of natural seed decay, average life span is usually less than one year. A population dynamic model (Van Mourik *et al*., 2008) indicated that it is the high seed bank generated by a single mature striga plant that poses the real problem rather than actual seed longevity. Depleting seed banks (*e.g.* through hand-pulling and removing striga plants before seed set and dispersal) in infested fields remains a major challenge in striga control.

Striga damage in Africa

The area in Africa infested by *Striga* species is estimated at 50 million hectares, with 300 million farmers being affected. This results in estimated losses of $US 7 billion (Parker, 2009). Yield losses due to striga infestation vary from a few percent up to complete crop failure depending on crop species, crop variety and severity of infestation. Hearne (2009) mentions yield losses ranging from 35-72%. These parasitic plants thus represent one of the largest biological constraints for food production in Africa. It is likely that striga is the largest constraint for maize production, whereas for sorghum and millet striga comes second after granivorous birds.

For northern Cameroon, Ayongwa & Ngoumou (2001) stated that striga is the most persistent biological constraint to cereal production compared to insect pests, granivorous birds or elephant herds on the rampage. A broad assessment of striga-related crop damage in 1984 in northern Cameroon showed that 300 000 hectares of maize were seriously damaged by striga, resulting in a near-nil production of the crop (Parkinson *et al.*, 1991). All areas planted with sorghum and millet were also infested to varying degrees with striga. The area afflicted amounts to about a third of the country's total area. These large infestation levels were of national concern and motivated the government to request international assistance from FAO (UNDP-CMR/86/005/A/01/12. 1986). However, information and reports on striga before the actual FAO assistance was launched did not clearly show the importance and priority of striga relative to other crop production constraints. This formed a reason for such an analysis reported in chapter 2.

Grain yield losses are determined by the levels of resistance and tolerance (Rodenburg *et al.*, 2005) of the host genotype, by severity of infestation and by the levels of soil fertility. Highly susceptible crops (e.g. maize) or cultivars can be so severely damaged that ultimately striga growth and seed production itself is negatively affected (Kim *et al.*, 1997). Tolerant varieties suffer lower yield reduction and often produce 2 to 2.5 times the yield of susceptible varieties, especially under high infestation (Kim *et al.*, 2002). However, tolerant varieties contribute as much as (or even more than) susceptible varieties in the build-up of a striga seed bank. Egley (1971) found that striga reduced host-shoot yields by about 70% at low nutrient level and by about 45% at the highest nutrient level. Gworgwor & Weber (1991) showed that severity of striga attack on sorghum was highest at zero N application where striga emergence was very early on sorghum followed by the low N rate and the lowest attack at the higher and moderate rates of N. In the most infertile soils striga numbers may again go down (cf. Chapter 4), most probably due to fewer attachment sites on a malnourished host to sustain as much parasites (Ikie *et al.*, 2007; Ransom, 1999). These data suggest a strong interaction between striga damage and soil fertility.

Striga – weed or symptom of poor soil fertility?

The actual position of striga as a problem relative to other farmers' crop production constraints is unclear, but more importantly a fundamental question is raised; whether the conceptualisation of the 'striga problem' by scientists, policy makers and farmers is comparable.

From the point of view of a weed scientist striga is a weed, that is a plant that grows in an (agro-)ecosystem where it is unwanted. However, several arguments (summarised by Vissoh *et al.*, 2007) speak against this conceptualisation as a weed. Rural appraisals (Vissoh *et al.*, 2005) indicated that farmers listed weeds and striga as separate constraints (cf. Chapter 2). Because weeding is ineffective in controlling striga (in fact early weeding with its concomitant soil disturbance even promotes the subterranean phase of striga), it is better not to conceptualise striga as a weed. Apparently, from the perspective of a farmer striga is not a weed; but is rather regarded as a symptom of poor soil fertility (Chapter 2). Only few researchers (Orr & Ritchie, 2004) emphasised that striga is best regarded as a symptom of low soil fertility. Many researchers would probably rather subscribe to the viewpoint that low soil fertility masks the effectiveness of striga control strategies – without asking the question whether that viewpoint, from the perspective of the farmer, would demand a different approach to striga control.

The issue whether striga is a weed or a symptom has two dimensions – one from the perspective of causal mechanisms and the other from the perspective of practices that can improve the livelihoods of resource-poor farmers. Demonstrating that striga is a (parasitic) weed can easily be done by experiments under controlled conditions whereby cereals are grown in the absence and presence of striga, and where yield reduction of biomass or grain yield is calculated. Such experiments prove the nature of striga as a parasite. Farmer Field Schools have used this simple set-up to help discovery learning in cases where farmers apparently did not make the connection between striga and low yields. However, from the practical perspective, things look a bit different. If in cereal fields with abundant striga measures are taken to reduce striga numbers, often no increases in cereal yield are reported, unless measures are taken to improve the fertility of the soil (Oswald, 2005). Without soil fertility improvement striga management is apparently unsuccessful in terms of improved productivity. From a fundamental perspective this issue raises the question whether the trajectory that leads to increased striga numbers and reduced yields over time (for instance, Fig. 6 of Chapter 2 could also be read as indicating a sequence where increasing striga abundance causes lower yields) can just be reversed under successful management; or whether a different trajectory for recovery is asked for. And similarly, the question should be asked whether striga control options at low and high striga pressure can be the same or that rather different approaches are asked for. These points will be touched upon again in Chapter 6.

Striga, soil fertility and organic matter

Soil nutrient depletion in African cropping systems has expanded rapidly since the middle of the twentieth century (Stoorvogel & Smaling, 1998; Hartemink, 2006) due to land-use intensification necessitated by increasing population pressure and the lack of mineral fertiliser inputs and organic amendments. Soil fertility is not only generating the striga problem, but is an immense constraint to cereal production in the African savannahs, including northern Cameroon (Ayongwa & Ngoumou, 2001). Soils of the striga-prone area in northern Cameroon are often light-textured and thereby intrinsically poor in organic matter.

Their gradually intensified use has further decreased organic matter levels, often falling below 1% (Breband & Gavaud, 1985; Obale-Ebanga, 2001). Striga is most problematic on infertile and nutrient-impoverished soils with low organic matter.

Fertiliser trials had shown negative effects on striga incidence (Pesch & Pieterse, 1982; Farina *et al*., 1985; Mumera & Below, 1993; Gacheru & Rao, 2001) and reduce crop damage particularly when high rates are used. However, there is a need to understand the exact mechanisms by which the root stimulant production reacts to host root nutrient status (N, P or K) and how this relates to both striga and mycorrhizal stimulation. A well-nourished sorghum plant induces fewer striga seeds to germinate than a nitrogen-starved plant treated with water only (Kroschel, 1998). Fewer stimulated striga seeds may also mean delayed attack of the host, which may drastically reduce yield losses (Gurney *et al*., 1999; Van Ast, 2006). Replenishment of those nutrients through fertiliser application (for both P and N) and organic amendments (for N) is therefore imperative – both for improving soil fertility and crop yields, and for striga control.

Ransom (1999) stated that “perhaps the area most neglected in soil fertility related research is the role of soil organic matter (OM) on the establishment of striga”. The positive effect of N in high quality OM (low C:N ratio) in striga control (Farina *et al*., 1985; Gacheru & Rao, 2001; Sherif & Parker, 1988) may not exclude beneficial effects of low quality OM. Attributes of soil OM with a high C:N ratio, such as increase in soil water-holding capacity and reduction in maximum soil temperatures that may negatively affect striga, should be established by separation from effects of the N released upon decomposition of applied OM (cf. Chapters 3 and 4). Decline in striga pressure after OM amendments could also be due to decay of striga seeds by soil micro-organisms. The quantities and quality of organic matter needed to impact both yield and striga infestation might, however, be prohibitive to the adoption of management strategies by resource-poor farmers, a point further discussed in Chapter 6.

Control options for the resource-poor farmer

Ransom (2000) has suggested that soil fertility improvement should be addressed concurrently with striga control extension programmes. Addressing the soil fertility problem may be a good entry point for an integrated striga management. As stated by Ransom (2000) “striga is just one of the problems affecting cereal production in Africa and the constraints affecting the entire production system need to be considered when designing a research and extension program”.

Progress in striga control has been recently discussed by Oswald (2005) and Hearne (2009). The latter listed both available and potential control options and described their perceived limitations as well as potential for adoption and impact. Oswald (2005) classified control methods as direct or indirect methods. According to him, the direct striga control methods attack the parasite directly and have an effect on striga in the field but not always on the crop yield. Indirect methods rather aim at the cropping systems and soil fertility management, and try to control striga by making its growth conditions unfavourable. These indirect methods control striga in a more sustainable way and increase crop yields over time. A useful way of classifying striga control options thus, is whether they emphasise measures against striga abundance (push-pull technologies, mycoherbicides, IR-resistant maize, seed treatments) similar to direct control method; or whether they emphasise increases in crop productivity and profitability (application of mineral fertiliser or organic amendments, intercropping, crop rotation) comparable to the indirect control method above. Hearne (2009) confirmed that there still is not (and unlikely ever will come) a magic bullet for striga control. And even integrated striga control (ISC) practices would only be successful if they fit with the constraints and opportunities that resource-poor farmers face. Practices that are not effective under farmers' conditions (usually because of labour and/or cash constraints) are unlikely to be taken up by farmers. As stated by Orr & Ritchie (2004), strategies that are not linked to cash income will likely fail. Hearne (2009) explicitly noted the problem that several control methods have not been effective under farmers' conditions and have therefore not been taken up by farmers. While hand-pulling of striga before flowering (to prevent seed production and replenishment of seed banks) remains crucial in the long-term (Oswald, 2005), its effectiveness in the short-term to boost crop production, especially under conditions of poor soil fertility, may well make this a recommendation that is unlikely taken up by resource-poor farmers (Chapter 2). Almost all researchers agree that striga is prevalent and thrives best under degraded and unfertile soils. Normally one should then expect that enhancing soil fertility irrespective of levels achieved or time-frame necessary, striga pressure should respond by falling while grain yield also increases. However, there is sufficient evidence that striga pressure may only fall following application of relatively high doses of fertilisers (Mumera & Below, 1993; Kim & Adetimirin, 1997; Gacheru & Rao, 2001), while yield increases even under small fertiliser use. It seems necessary therefore to understand the role of organic matter of different quality for a better crop management in the field, accessible to the resource-poor farmer. As cereal yield is more responsive to minimal soil nutrient applied even under high striga infestations and its effect more tangible to farmers than the depressing effect of these same nutrients on striga, farmers tend to lean more on actions that boost yield than controlling striga (whose effects are less distinguishable in the short term and under field conditions). Farmers often need immediate and tangible returns on investments (ex. grain yield); addition of manure or fertiliser may thus serve as an incentive for further measures to better manage the crop.

The question that was posed earlier (striga as parasitic weed or as symptom of poor soil fertility) is relevant in this context, because it explicitly raises the question whether striga control options (when successful in reducing striga but without an impact on yields) or soil fertility enhancement (with higher yields, but sometimes without effect on striga numbers) have a larger chance of being adopted by farmers or not. Measures such as addition of organic amendments, inorganic fertilisers, intercropping and crop rotations (especially if N_2-fixing legumes are included) may primarily boost the productivity of the land – as a prerequisite of making striga control relevant for farmers in the first place. I will return to that issue (and hence the question along which trajectory the striga situation in conjunction with poor soil fertility should be tackled) in Chapters 4 and 6.

Aims and outline of the thesis

The objectives of this research project were to disentangle the various effects that organic matter inputs could have on striga-affected sorghum cropping systems in northern Cameroon. More specifically, it sought to understand how both quality and quantity of organic matter inputs would affect soil fertility and through that sorghum yield and striga dynamics. The research combined field (in researcher-managed field trials on farmers' fields in northern Cameroon) and laboratory experiments (executed at the International Institute of Tropical Agriculture (IITA) Ibadan - Nigeria).

Chapter 2 presents the magnitude and dynamics of striga infestation in northern Cameroon, on the basis of field survey data obtained in the period 1987-2005. It puts striga dynamics in the framework of production constraints. Chapters 3 and 4 look at the potential of organic matter management to control striga and to alleviate poor soil fertility in a field study. Whereas Chapter 3 tests mechanisms how organic matter can suppress striga (through impact on soil temperature, soil moisture retention, ethylene production, seed decay), Chapter 4 specifically addresses nitrogen release through decomposition of organic matter, and the impact of N release on sorghum production and striga dynamics. Chapter 5 reports how N application (levels, timing) affect the N status of sorghum and consequently the level of stimulation of striga seed germination. The overall discussion and conclusions of the studies and implications for field management of striga are discussed in Chapter 6.

CHAPTER 2

Striga hermonthica infestation in northern Cameroon: Magnitude, dynamics and implications for management*

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Abstract:

Surveys of *Striga hermonthica* (Del.) Benth.) (striga) infestation in northern Cameroon over the period 1987-2005 assessed striga dynamics and evaluated its control strategies. In that period the percentage of striga-infested fields increased in both the North and the Far-North Provinces. Striga incidence increased more in maize fields than in the already heavily infested sorghum fields, which remained almost constant. During the study period increased land pressure led to a reduction in the use of fallow and a higher frequency of cereal (mono-) cropping. Yields from farmers' fields did not correlate with striga incidence, confirming farmers' prioritisation of soil fertility, weeds, and labour for weeding as production constraints, rather than striga. We discuss how conceptualisation of striga as a weed in the research arena may have lead to a misunderstanding of farmers' constraints. The decline of the cotton industry reduced farmers' access to fertilisers, while access to organic manure remained limited, increasing the soil fertility constraint. We conclude that two decades of emphasis on striga were unsuccessful. Enhanced crop yield through soil fertility management should be the entry point to tackle low yields and further worsening of the striga situation.

Key words: Crop production constraint, Farmers' priority, Field survey, Soil fertility, Weeding

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Introduction

Northern Cameroon, situated in the Sudano-Sahelian Zone, consists of the North Province and Far-North Province and covers an area of 100,353 km^2 of which 85,000 km^2 represent almost the entire cotton belt of Cameroon (IRAD – PRASAC 1, 1999). About 82% of the area consists of arable land that could be cropped. Agriculture is the main source of subsistence for the local population and cereals are their source for staple foods.

Cotton (*Gossypium hirsutum* L.) is an important export crop of Cameroon and is the single most important cash crop in the two northern provinces. In the late 1980's the cotton production system enjoyed adequate technical and material support from the cotton development corporation (SODECOTON). Support to cotton production had its positive effect also on food crop production. Pesticides and fertilisers for the production of cotton were provided to farmers who subscribed to the prescriptions by SODECOTON at subsidised prices.

Traditionally, cotton in northern Cameroon was rotated with cereals to avoid a build-up of cotton pests and diseases. Farmers also used this rotation as an opportunity to exploit the residual fertility after a cotton crop for their cereal production. Otherwise, farmers hardly applied fertilisers to their principal cereal crop mainly because purchase costs were too high. Linkage between cotton production and food production weakened in the last decade due to the decline of the cotton sector, driven by lower cotton prices on the world market and increasing fertiliser prices (and decreasing fertiliser availability) as a consequence of structural adjustment programmes (Kossoumna Liba'a & Havard, 2006; Mbétid-Bessane *et al.*, 2006).

Soil fertility is an immense constraint to cereal production in the African savannah zone (Smaling & Braun, 1996; Ransom, 2000; De Ridder *et al.*, 2004; Schlecht *et al.*, 2006). Apart from the direct negative effects of low soil fertility on agricultural production and food security, low soil fertility increases susceptibility to biotic pests. A major biotic pest in the savannah region is formed by parasitic plants of the genus *Striga* (Orobanchaceae). Most important are *Striga hermonthica* (Del.) Benth., which is mainly found on cereals such as maize (*Zea mays* L.), sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* (L.) R. Br.), and rice (*Oryza sativa* L.), and *Striga gesnerioides* (Willd.) Vatke found on the legume cowpea (*Vigna unguiculata* (L.) Walp.). Increased *S. hermonthica* infestations are associated with soil fertility decline (Samaké *et al.*, 2005), which in turn is often a consequence of increasing pressure on land resources. Increased land pressure, due to increasing population densities, forced farmers to shorten the fallow period necessary for soil fertility regeneration and to change cereal–legume rotations into systems of continuous cereal mono-cropping (Abunyewa & Padi, 2003). Both processes potentially increase infestation with *S. hermonthica* (hereafter referred to as striga), setting into motion a downward spiral of agricultural productivity (Abunyewa & Padi, 2003; Ejeta, 2007).

In 1984, an assessment of crop damage in northern Cameroon revealed that 300,000 ha of maize were severely damaged by striga, often with a near-nil crop yield (Parkinson *et al.*, 1991). Sorghum, which constitutes the major staple food for the population, was infested over an even larger area, although exact data are lacking, but reduction in grain yield was often less dramatic (Parkinson *et al.*, 1991; Singh *et al.*, 1991). Based on these assessments, a technological package was proposed and implemented on farmers' fields by FAO under an assistance programme to the Cameroonian government from 1987 under a pioneer Pan-African striga control project. Components of the package included hand-pulling of mature striga plants, killing adult plants before flowering by application of herbicides, application of nitrogen fertiliser, using trap crops as intercrop or in rotation with crops that are hosts to striga, sowing striga-resistant or -tolerant crop varieties, and using early-maturing crop varieties.

Besides the introduction of the striga control package to farmers, a formal survey was carried out in farmers' fields to measure the intensity and magnitude of the striga problem. A decade after the FAO project on striga control started, the situation did not seem to have really changed and there was still no simple and efficient striga control method. An evaluation, which took place in 1999, put the striga problem in the more specific context of crop production constraints. After this 1999 survey, a third, less extensive survey was done in 2005. This survey was a rapid appraisal of the striga situation that looked only at numbers of infested fields and the level of infestation of host crops.

This paper reports the findings of these three surveys to analyse striga dynamics between 1987 and 2005. It reflects on the very limited success of an approach that prioritised the scientific analysis of the striga problem rather than the farmers' analysis of production constraints. We conclude with an attempt to reconcile farmers' perception of striga in relation to other crop production constraints and approaches to striga control.

Methodology

Three surveys were carried out in northern Cameroon, one in 1987 by a FAO striga project (CMR/86/005), and two in 1999 and 2005 by a PRASAC (Pôle Régional de Recherches Appliqués au Développement des Savanes d'Afrique Central) and an ARDESAC (Appui à la Recherche Régionale pour le Développement Durable des Savanes d'Afrique Centrale) project, respectively. The 1987 survey consisted of a detailed questionnaire. Interviews and field evaluation were done by two FAO experts. Villages were selected at random from a map of the region before each trip was undertaken. A total of 216 fields were visited, equally divided over the North and the Far-North Province, and distributed over 49 villages.

The surveys of 1999 and 2005 were carried out in two PRASAC benchmark territories: Mowo (Far-North Province) and Mafa-Kilda (North Province). These two territories are representative for the two provinces surveyed in 1987. Mafa-Kilda, which is situated mid-way in the North Province, is very accessible and lies in the River Benoué basin, at the frontier of farmland opened-up (between 1976 and 1982) by pioneer immigrant farmers from the densely populated Far-North Province (IRAD – PRASAC 1, 1999; IRAD – PRASAC 2, 1999). Mowo is located in the Far-North Province in a more densely populated and since long occupied area, where almost all soils are degraded and poor (IRAD – PRASAC 3, 1999). The climate in the Far-North Province is cooler and drier than that in the North Province (cf Fig. 1 for rainfall data).

In each bench-mark territory, 60 fields with sorghum or maize were selected during the 1999 survey. The two territories were sub-divided on a map into equally sized areas in order to ensure an even distribution of the 60 sample fields over the entire territory. The choice of fields to be surveyed was made as follows. Trained field staff was guided by the actual area of the territory and by certain reference points such as footpaths, hills and valleys. The surveyor then walked, while sampling, through the territory in a regular pattern, to cover the entire sub-divided area. At an average walking speed of 1 m/s second, the field staff stopped after 5 minutes walking since the last sampled field and then surveyed the nearest cereal field. After sampling the original position and walking direction was resumed and from there the operation was repeated until the desired number of fields had been surveyed.

Prior to the survey, a team of five persons was trained in the way in which the survey was to be carried out. The field owners were interviewed with the help of a structured questionnaire. The questionnaire opened with introductory questions to describe field size, time since the field was first cropped, sowing dates, crop management, and yield estimates. The second part of the questionnaire focused on identifying crop production constraints and a detailed study of the striga problem, in addition to observations at individual field level. A pre-test questionnaire on farmers' production constraints showed a large array of difficulties, of which the lack of financial means to procure farm inputs was the most prominent one. Given the project objectives, we focused on constraints that directly hampered crop production.

A targeted field observation throughout the entire cropping season with data collection on infestation levels and crop yield was carried out in 39 fields in the Far-North Province and 27 in the North Province. These fields, which were different from the ones surveyed earlier, were identified and selected at the start of the cropping season, based on the criterion of a long history of striga infestation as known by local agricultural extension staff. At crop establishment, a sampling area was pegged out for monitoring of striga dynamics. In each field the first corner of the sampling area was taken as the fourth row from the border of the

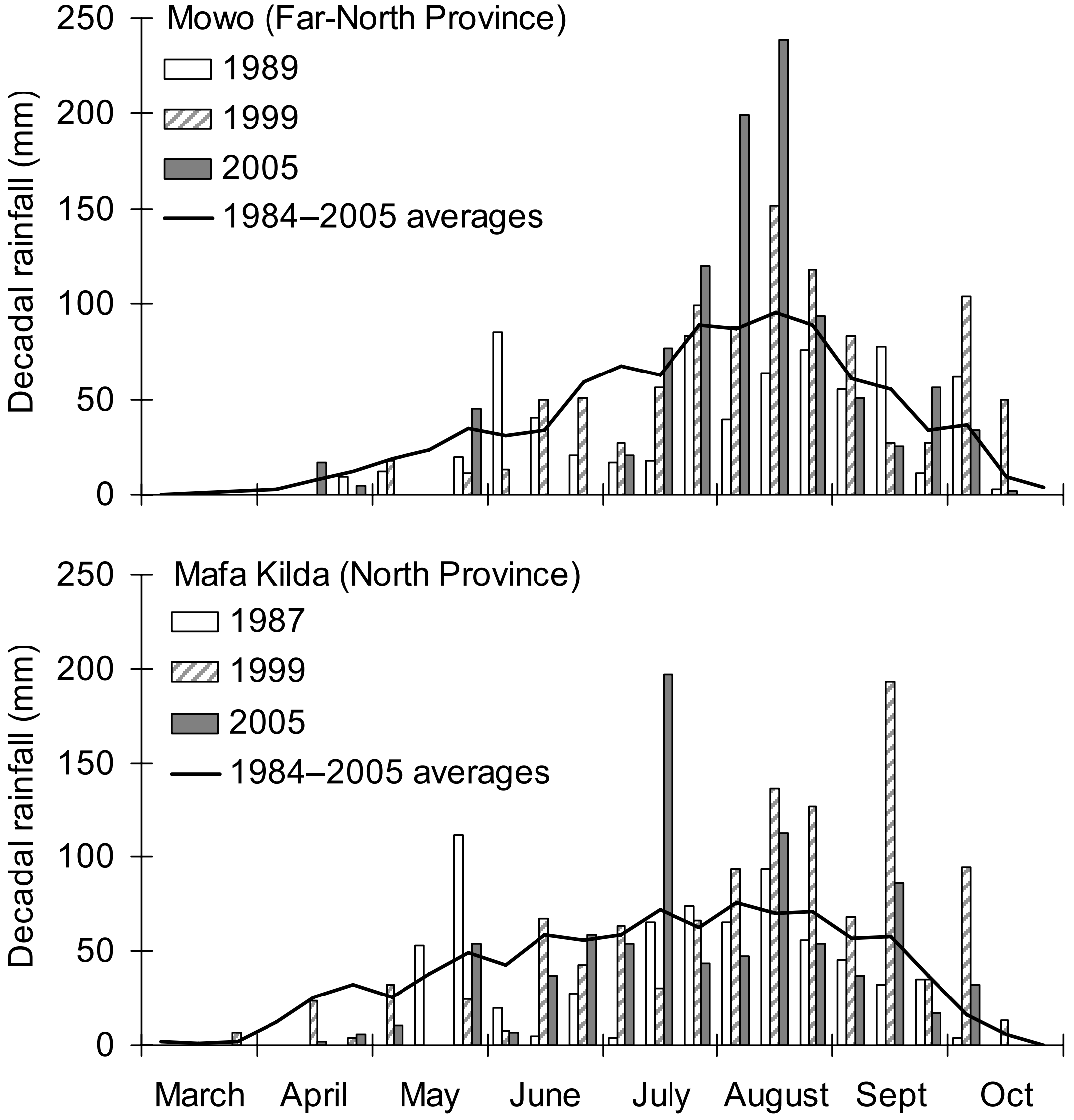

Fig. 1. Rainfall data as mm recorded per ten day period (days 1-10, 11-20 and 21-30/31 of each month) for the two benchmark sites Mowo and Mafa Kilda in the Far North and the North provinces in Cameroon, respectively. Data represent long-term averages between 1984 and 2005 (drawn lines) and rainfall recorded during the three survey years 1987, 1999 and 2005 (bars).

field at two meters in the row from the edge of the field. From this point a length of ten meters in the row was pegged out in rows 4, 6, 8, 10 and 12 and these plants were used to determine striga population density (severity, surface area 40 m^2). In rows 5, 7, 9, 11 and 13 six meters were pegged out and these plans were used to determine the number of cereal plants infested with at least one striga plant (incidence, surface area 24 m^2) and the total number of cereal plants. Planting distances for the cereal crop were 80 cm between and 50 cm within rows. Incidence and severity of striga infestation were recorded every 2 weeks in each of the 5 rows. These plants were harvested at maturity. After air-drying for 2 weeks the maize ears and sorghum panicles were threshed and weighed and grain moisture content was determined. Grain yields were expressed on the basis of 12% moisture content.

In 2005, a rapid appraisal of striga infestation was carried out by sampling 190 fields in the Far-North Province (Mowo) and 60 fields in the North Province (Mafa-Kilda).

The questionnaires for the field surveys and the observation sheets were manually coded and analysed statistically using the Statistical Analysis System (SAS) package. The General Linear Model was used to calculate correlations between grain yield and striga infestation. Average percentages of crops infested by striga and striga density were used for analysis. Frequency tables were used to identify the changes over time in striga infestation levels, striga control options, and cropping systems.

Results

The dominant cereal crops cultivated in the study area, in order of decreasing importance, were sorghum, maize and pearl millet (Fig. 2). Maize and sorghum were of comparable importance in the North Province, whereas sorghum was dominant in the drier Far-North Province. Pearl millet was sown in some years in some of the fields in the Far-North Province.

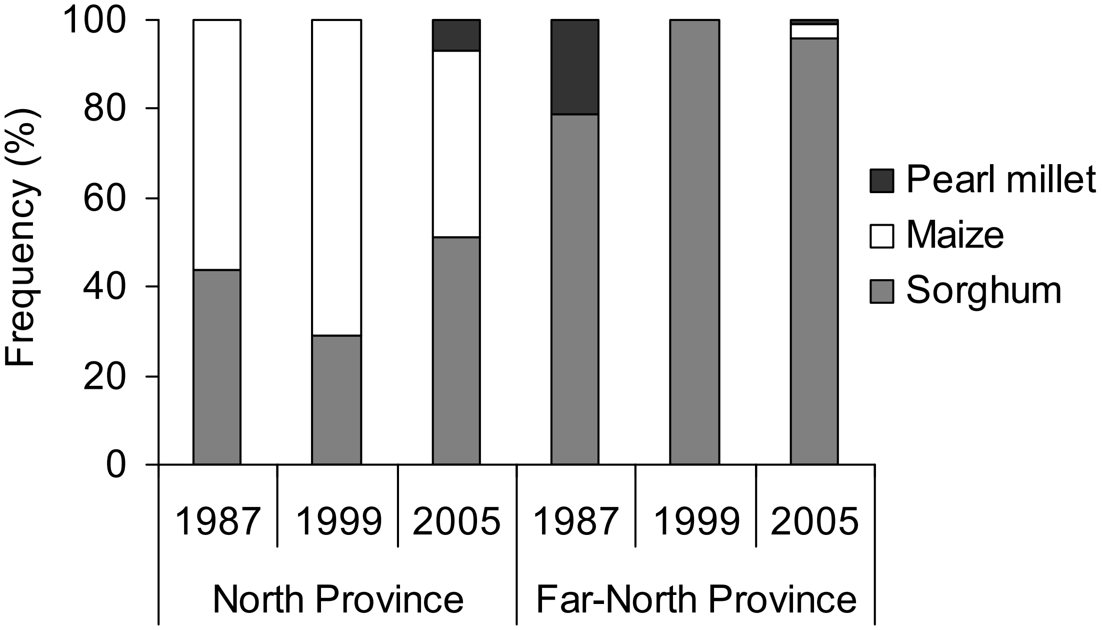

Fig. 2. Importance of the three cereals grown in the two territories in each of the three survey years. Frequencies as percentage of all cereal fields surveyed.

During the 1999 survey, 120 farmers each named at least three of the most important constraints to crop production. From their answers, 6 main constraints emerged (Fig. 3). Weed infestation of crops (and the need for weeding) was the major constraint at both locations, with low soil fertility coming second. In North Province, ravaging animals appeared an important constraint too, whereas labour scarcity was often mentioned in the Far-North Province. Striga, which was a separate category from weeds, was frequently mentioned in the Far-North Province, but hardly so in the North Province.

When specifically asked, most farmers indicated that striga was important. Between 1987 and 1999 the percentage of farmers who stated that striga was important, rose from 86 to 94 in the North Province and from 82 to 94 in the Far-North Province. In order to appreciate farmers' knowledge about striga, their ability to diagnose striga infestation before emergence of the parasite was investigated in 1999. Whereas the majority of farmers in Mowo claimed to be able to distinguish a striga-infested crop from a healthy one before emergence of the parasite, the farmers in Mafa-Kilda were not (Table 1). Farmers mentioned the following symptoms of striga infestation: (1) leaf discolouration or yellowing (30 respondents), (2) reduced growth (21 respondents), (3) stunting (7 respondents), (4) wilting (3 respondents), and (5) root deformation (3 respondents). Out of the 45 respondents who said to

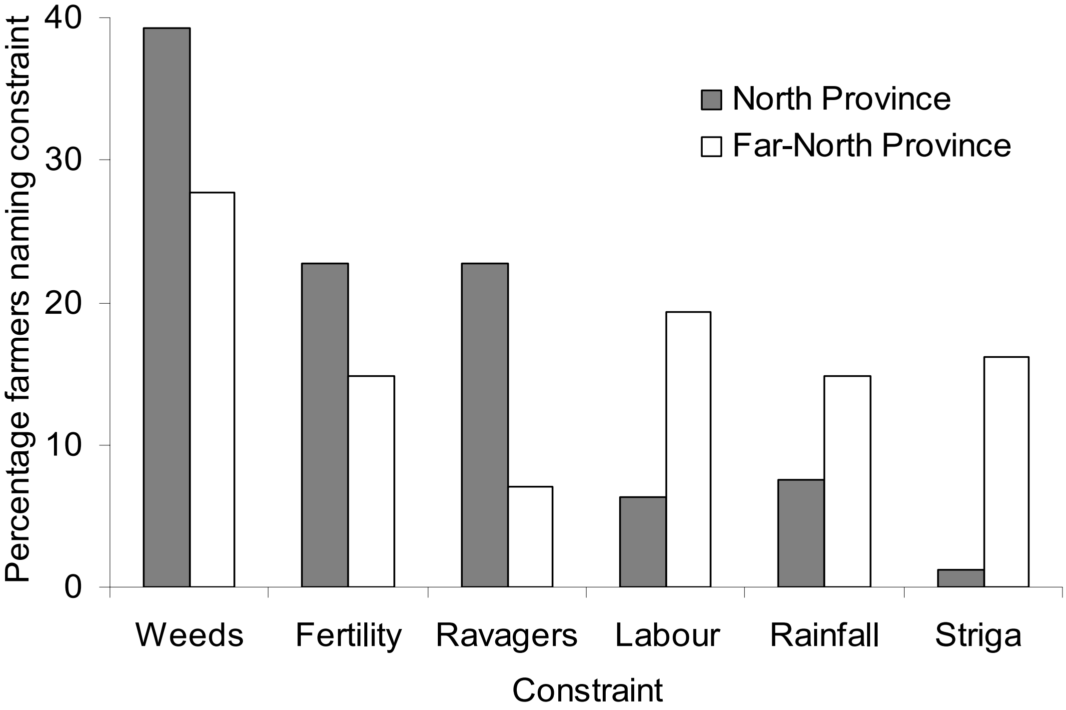

Fig. 3. Importance of production constraints as percentage of all constraints mentioned by the farmers in each of the two territories. Farmers were allowed to mention up to 3 major constraints.

Table 1. Farmers' response in the two territories to the question whether or not they were able to diagnose striga infestation in their crops. Results of the 1999 survey. Four farmers did not respond. The difference between the two territories was highly significant ($\chi^2 = 11.1$; $P<0.001$).

Territory	No. of respondents	Ability to diagnose	
		Not able	Able
Mafa-Kilda	31	25	6
Mowo	55	16	39
Total	86	41	45

be able to diagnose striga infestation before emergence, one could not describe a single symptom, 27 described one and 17 two or more symptoms.

Farmers were asked whether they perceived striga infestation to be increasing or decreasing and what they considered the major cause for such a change. The majority of farmers (72%) indicated that striga increased, and only 5 farmers (6%) thought it decreased. The majority of farmers (59%) who perceived an increase had no idea about underlying causes, while 31% held a decline in soil fertility responsible for the worsening striga situation. Three respondents thought that hand-pulling the infested plants affected striga infestation: one stated that it caused a decrease whereas two said it did not affect striga (Table 2).

Farmers were asked if they were able to control striga in their fields. In the Far-North Province more farmers said they were able to control striga in their fields than in the North Province. Whereas in the Far-North Province the percentage of farmers who claimed to be able to control striga remained constant (around 80%) over the period 1987–1999, the percentage of farmers in the North Province who made the same claim decreased over that period (from 70 to 35). Amongst striga control options (Table 3), hand-pulling was mentioned frequently during both surveys, but was not practised anymore in the North Province in 1999.

Table 2. Farmers' perception of changes in the striga situation over time and their causal explanation for observed dynamics. One farmer did not respond.

Status of striga infestation	Farmers' reasons for perceived changes					
	None	Hand-pulling	Fallow	Soil fertility	Flooding	Total
Increasing	38	0	4	20	2	64
No change	10	2	0	7	1	20
Decreasing	0	1	0	2	2	5
Total	48	3	4	29	5	89

Several farmers mentioned weeding separate from hand-pulling. Abandoning infested fields, which was practised in 1987, was not an option anymore in 1999. Some farmers in the North Province mentioned the sowing of a cereal they called *fonio* as an option for the control of striga. However, the corresponding crop was pearl millet (*P. glaucum*) and not fonio or hungry rice (*Digitaria exilis* (Kippist) Stapf). In 1999 a few farmers mentioned the use of inorganic fertilizers or organic manure as striga control method. Availability of organic (mainly animal) manure was higher in the Far-North Province than in the North Province. None of the farmers mentioned the use of herbicides, trap crops or specific cultivars as management options.

Striga incidence was higher in sorghum fields than in maize fields. The percentage of striga-infested maize fields increased between 1987 and 2005, while the percentage infested sorghum fields remained invariably high (Fig. 4).

There was no correlation between cereal grain yield and striga population density (Fig. 5). The vertical and horizontal lines in Fig. 5 indicate the averages of striga counts and grain yields for sorghum and maize, respectively. High striga counts always implied low yields, but low striga counts and low yields often occurred simultaneously. In other words: low yields were not necessarily caused by high striga incidence.

In several fields, striga occurred in patches. The patchy distribution could be explained by the relative position of trees in the fields and by the presence of termite mounts. Close to trees and termite mounts striga infestation was very low or absent. Tree species were not always identified, but many trees belonged to the species *Faidherbia albida* (Delile) A. Chev. Termite mounds were usually located under or close to trees. Soil characteristics also affected striga infestation: the number of infested stands was low on clay soils and very high on infertile sandy soils (Table 4).

Table 3. Numbers of farmers in the two provinces who mentioned different striga management practices, in 1987 and 1999.

Striga management practice	Far-North Province		North Province	
	1987	1999	1987	1999
Hand-pulling	47	38	47	0
Weeding	29	2	2	0
Crop rotation	0	18	0	0
Field abandonment	26	0	9	0
Fertilisation (organic and inorganic)	0	9	0	7
Millet cropping	0	0	0	6

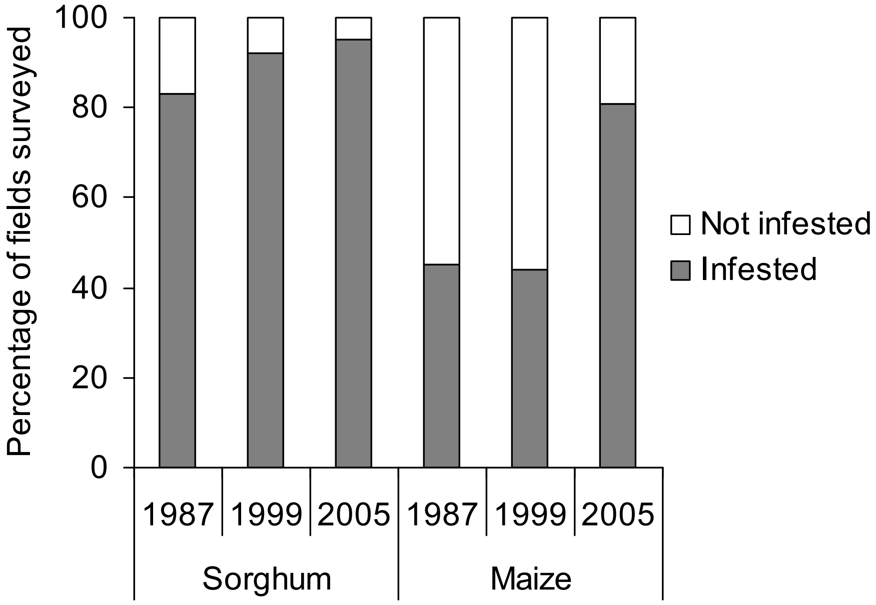

Fig. 4. Frequency with which surveyed maize and sorghum fields were infested with striga, as recorded in each of the three survey years.

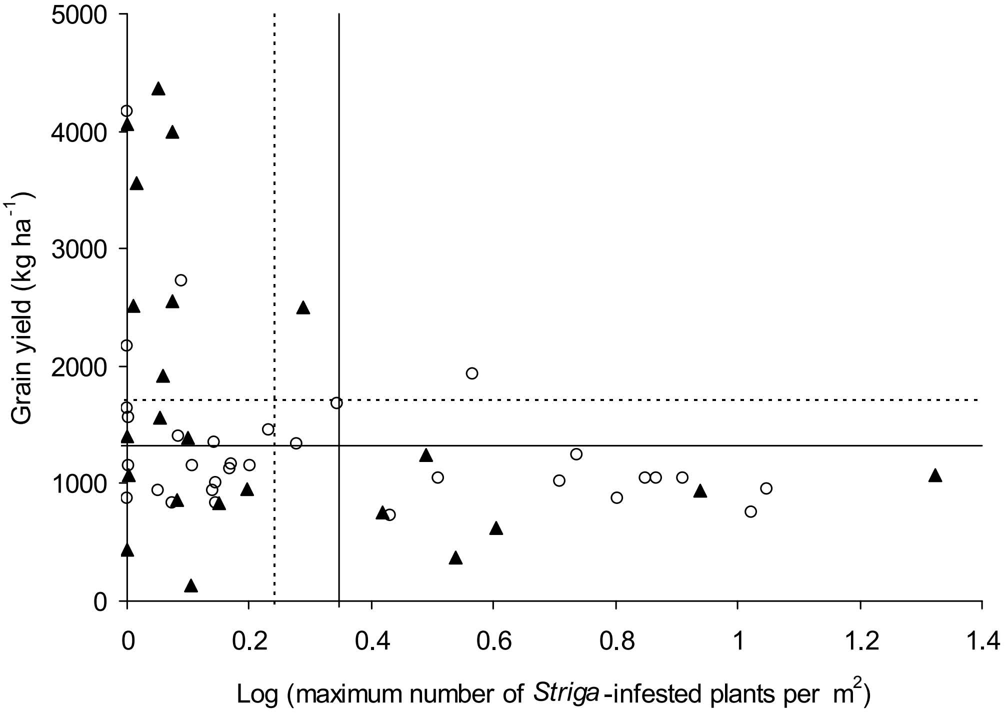

Fig. 5. Scatter plot of maize (triangles) and sorghum (circles) yields plotted against maximum striga incidence, combining the two territories surveyed in 1999. The drawn vertical and horizontal lines represent respectively average maximum striga count and average yield on sorghum fields (solid lines) and maize fields (dotted lines).

Table 4. Effect of soil type on proportion of crop stands infested with striga (± standard deviations).

Soil type	Sample size (n)	% crop stand infested
Clay	5	17.7 ± 10
Fertile degraded land	5	40.8 ± 24
Infertile degraded land	3	48.7 ± 33
Fertile sand	5	54.0 ± 41
Infertile sand	10	85.7 ± 22

Table 5. Crops and frequency (%) of being planted in the 4 years preceding cereal cropping in 1987 (1983-1986) and 1999 (1995-1998) in the North and Far-North Provinces of Cameroon as recalled by farmers in the 1987 and 1999 interviews.

	1987 interviews				1999 interviews			
	1983	1984	1985	1986	1995	1996	1997	1998
	North Province							
Sorghum	43	16	51	17	5	7	5	2
Maize	24	4	31	6	23	47	35	30
Millet	–	–	–	–	2	–	–	–
Cotton	11	46	7	60	27	20	20	48
Groundnut	4	24	7	12	13	10	35	15
Cowpea	–	–	–	–	–	–	–	2
Tuber crops	1	1	1	1	–	–	–	–
Fallow	9	7	3	5	–	3	2	3
No data[a]	8	2	–	–	30	13	3	–
Total	100	100	100	100	100	100	100	100
	Far North Province							
Sorghum	67	52	66	52	72	25	70	28
Millet	22	18	20	16	12	3	12	3
Cotton	4	22	6	25	17	72	18	67
Groundnut	1	4	2	1	–	–	–	–
Cowpea	1	–	–	–	–	–	–	–
Fallow	5	4	6	6	–	–	–	2
Total	100	100	100	100	100	100	100	100

[a] Farmers did not remember.

An analysis of the yearly cropping sequence as recalled by farmers over the 4 years preceding the 1987 and 1999 surveys in the Far-North Province revealed a consistent alternation (rotation) on part of the fields between cotton and cereals (Table 5). In the North Province a comparable pattern was observed for the 4 years preceding 1987, but not for the 4 years preceding 1999. This cotton–cereal rotation is practised by a majority of the farmers in the cotton belt of northern Cameroon. Both cowpea and groundnut are less prominent in the cropping system than cotton, especially in the Far-North Province, but for groundnut a comparable rotation was observed as for cotton in the North Province in the years preceding 1987. Legumes are usually intercropped as insurance against cereal crop failure. Fallow was practised fairly often in 1987 but was much less common in the later 1990s more specifically in Far-North province.

Discussion

The striga situation in northern Cameroon

Striga infestation in the Far-North Province over the period 1987–1999 remained invariably very high (from 84 to 91%), but that in the North Province worsened (from 67 to 88%). Similarly, infestation of sorghum (the main crop in the Far-North Province) and maize (together with sorghum the main crops in the North Province) with striga increased from 90 to 95% and from 46 to 81% between 1987 and 2005, respectively (Fig. 4). These trends confirm the farmers' perception of increased striga infestation: 72% of the interviewed farmers claimed that striga infestation levels had increased over that period (Table 2). Apparently, two decades of emphasis on striga in research and extension have not resulted in an improvement of the striga situation. The question can thus be posed whether the proposed techniques were technically inadequate or whether adoption of in principal effective techniques is the major constraint. We conclude that striga research and the techniques it has provided largely fail to address the heart of the problem, the declining soil fertility. Science generally communicates with farmers about the striga as a weed, but this does not correspond with farmers' perceptions and management. This mismatch is not specific for the study area, because similarly high and persistent infestation levels (80–90% of farmers' fields) have been reported for sorghum and maize in northern Nigeria (Dugje *et al*., 2006) and are probably characteristic for cereal cropping systems of resource-poor farmers in the Sahel.

At the same time, our surveys and field observations provided a paradoxical picture. We documented very high (Far-North Province) or increasing (North Province) percentages of infestation with striga. On the other hand, a large majority of farmers in the Far-North Province and as many as ca. 35% of the farmers in the North Province claimed to be able to control striga. Many farmers stated to apply hand-pulling, but evidence indicates (Table 2) that very few farmers considered hand-pulling effective. And finally, among the prioritisation of constraints mentioned, striga was not very high on the list (compared with weeds or soil fertility), but when asked further, almost all farmers suggested that striga was an important problem. Comparable contradictions have also been encountered in Ghana and Nigeria. In a survey in Ghana it was found that 80% of the farmers with striga in their fields adopted mechanical weeding or hand-pulling. However, at the same time the people that carried out the survey mentioned apparent ignorance of farmers concerning the effects of striga on crops (Aflakpui *et al*., 2008). Although 70% of the farmers in a different study in northern Nigeria mentioned weeding as a local striga control method, the study also reported that an integrated striga project increased striga weeding from 4 to 82% (Douthwaite *et al*., 2007). However the study did not specify the form(s) of weed management, but an earlier study in the same area and from the same research group reported that hand-pulling striga is decreasing (and ranked by farmers as very costly), while hoe-weeding is increasing and universally applied (Emechebe *et al*., 2004).

We propose two explanations for this paradox. Inconsistencies between surveys and field observations may be partly the result of the questionnaires (and interviewing staff) being too much geared towards striga. With the benefit of hindsight it is also evident that projects that tackle single aspects of farming systems are bound to have little effect. This is also true for S*triga* where it has become almost a *mantra* to state that only integrated striga control measures will be effective (Douthwaite *et al*., 2007; Kamara *et al*., 2008; Hearne, 2009). We think that very few farmers apply striga control measures; they rather manage their cropping systems in ways that also affect striga (Vissoh *et al*., 2008). Nevertheless the need for agro-ecosystem management leaves open the question whether the entry points for such integrated packages are to be found in striga, in any other constraint prioritised during surveys, or in the farming system at large.

Second, farmers' priorities were taken insufficiently into account due to the fact that researchers conceptualised striga differently from farmers, thereby misinterpreting their constraints. In retrospect, the importance of the relation between yield and striga population (Fig. 5) has been initially overlooked by us. Whereas a first inspection (and conventional interpretation) of the graph suggests a negative correlation between striga incidence and crop yield for both sorghum and maize (and hence can be read as implying that increasing striga numbers *cause* lower crop yields), dissection of that graph (especially the left part of it) suggests room for an alternative interpretation. That interpretation states that in the absence of striga crop yields vary substantially, suggesting that other constraints are more important than striga. The questionnaire (Fig. 3) did reveal such constraints. Weeds and soil fertility rather than striga were farmers' main constraints. Mentioning weeds implies labour as constraint (Fig. 3), because in the area weeding consumes 30-60% of farmer's time spent on their agricultural operations (M'Biandoun & Olina Bassala, 2007). Fig. 5 also indicates that striga incidence may vary widely without much relation to yield. This leaves open the question whether reducing striga by management would lead to returns on investment through improved yield. Fig. 5 therefore also supports farmers' claims that there is little effect of proposed striga management.

One reason why we misinterpreted the significance of weeds (and labour for weeding) stems from our conceptualisation of striga as weed (Vissoh *et al.*, 2007). From a scientific perspective a weed is a plant that grows at a place where humans do not want it to grow (mainly because its presence negatively affects the yield of the desired crop). From that perspective, striga is clearly a weed, albeit a special one. Farmers conceptualised weeds differently from scientists, as is clear from their mentioning both weeds and striga (in the Far-North Province) or only weeds (in the North Province) as constraints (Fig. 3). Although the scientists considered striga in their questionnaire as a weed category different from other weeds this does not necessarily imply conceptualising this difference in the same way as farmers. From a farmers' perspective, weeds are plants that emerge together with crops and that require labour to suppress them during early stages to allow the crops to perform, as the weeds cause low yield and grow better on more fertile soils. In their view, striga is a *symptom* of poor soil fertility rather than a *cause* of low yields (M'Biandoun & Olina Bassala, 2007; Stringer *et al.*, 2007). A major consequence of this differential conceptualisation is that weeding, when mentioned by farmers, is likely interpreted by scientists as striga management. This interpretation is in accordance with the observation that weeding was mentioned by many farmers in the study area (Table 3) and also in several countries of West Africa (Emechebe *et al.*, 2004; Douthwaite *et al.*, 2007;Aflakpui *et al.*, 2008). Hand-pulling striga, which is recommended to prevent seed set and seed dispersal, does not directly affect crop yield and is therefore not effective in the short term (Ransom, 2000). It is therefore not part of farmers' conceptualisation of weeding. While conventional hoe-weeding is even counter-productive as it improves conditions for striga during its below-ground stage (Woomer *et al.*, 2008). Lack of effectiveness of weeding (and more generally lack of effectiveness of human labour to control striga in the short term) makes striga essentially different from weeds and thus confirms that striga is not a weed.

Some farmers in the North Province mentioned rotation with pearl millet as a striga control strategy. Resistance of this crop to striga was observed repeatedly in the 2005 survey. We observed no pearl millet crop stand that was infested with striga, and even where this crop was intercropped with sorghum, only the sorghum plants were infested. In areas of Benin, where pearl millet is not commonly grown, farmers reported that this crop was not attacked by striga and sometimes the rotation with pearl millet was used as a striga control method (Gbèhounou *et al.*, 1991).

Because striga forms separate host races on sorghum and millet, initial striga resistance after cereal switches are not infrequent. However, because these host races retain interfertility and because striga is an obligate out-breeder, such resistance is rapidly broken (Olivier *et al.*, 1998). In the drier Far-North Province, where pearl millet occurs more frequently than in the North Province, no such effect of this crop on striga control was mentioned, which is in line with the fact that striga is a major problem in pearl millet in for instance Mali and Niger (Samaké *et al.*, 2005; Van Mourick *et al.*, 2008).

Why has the striga situation worsened?

Soil fertility constraints were prioritised by farmers, and farmers were aware of the link between soil fertility decline (and hence cereal yield decline) and an increase in striga infestation (Fig. 5). However, along the pathway of soil fertility decline, striga does not always increase and soils can become too impoverished to maintain high striga population levels. Such soils would be in the lower left part of the graph, with low striga numbers and low yields. Under such soil fertility conditions striga management would initially always seem to be a failure because reducing striga density will not increase yields and will therefore not be attractive to labour – and cash-constrained farmers. Soil fertility improvement, however, would initially result in somewhat higher striga numbers (Smaling *et al.*, 1991). Yet, we suggest that improving soil fertility as primary constraint constitutes the better way (Ransom, 2000). A study in Benin also demonstrated that effective striga management will only be of interest to farmers if soil fertility exceeds a threshold value. If not, striga management will absorb farmers' precious resources without any yield increase (Vissoh *et al.*, 2008).

Soil fertility improvement in the area had not occurred over the last two decades. The decline of the cotton industry (Kossoumna Liba'a & Havard, 2006; Mbétid-Bessane *et al.*, 2006), driven by low world market prices for cotton and increasing fertiliser costs due to structural adjustment programmes, has reduced the availability of fertiliser for cereals. The collapse of the cotton sector rather than striga seems ultimately responsible for the agricultural stagnation and lack of success of a striga programme that lasted for two decades.

Agricultural stagnation resulted in the lack of appropriate measures to maintain or improve soil fertility and hence resulted in soil fertility decline. In most of the territory of the Far-North Province, there has been increased pressure on available arable land due the rapid growing human population. The Far-North Province (Mowo territory) saw a 67% population increase between 1992 and 1996 (IRAD – PRASAC 3, 1999; Seignobos *et al.*, 1995). Increased pressure on the land reduced the fallow period in crop rotations, and increased cereal monocropping over cereal–legume rotations (Table 5).

Field abandonment or fallowing, which used to be an option for striga management mentioned by farmers in 1987, was not mentioned in 1999 (Table 3). The demographic pressure forced many farmers to migrate (organised migration) between 1974 and 1986 from the Far-North Province to the North Province (Koulandi, 2006; M'Biandoun & Olina Bassala, 2007) where land was still available, demographic pressure lower, soils more fertile or less degraded, and rainfall a bit more favourable. On this (virgin) land striga was still largely absent. Under these new agro-ecological conditions, a cereal-rich cropping pattern was again favoured, with maize partly replacing sorghum (Table 5). However, although striga started off as less of a problem, the introduced cropping pattern and gradual increase in land pressure led to a mounting striga incidence. The rise in striga infestation in maize between the 1999 and 2005 survey (Fig. 1) may also be further explained by the reduced access to inorganic fertiliser by farmers.

A cropping system based on a high frequency of cereals as striga-host with limited legumes in the rotation and in combination with little or no fallow and very limited use of inorganic fertiliser and organic manure for fertility restoration over the years worsened the striga situation. Cereal–legume intercropping and to a lesser extent rotating cereals with legumes, are important in reducing the seed bank of striga and its effect on the host (Oswald & Ransom, 2001; Schulz *et al*., 2003; Samaké *et al*., 2006;Van Mourik *et al*., 2008).

The way forward

With current soil fertility and crop management, densities of striga will remain (very) high. Fig. 5 shows that good yields were not obtained when striga density was high. Thus it is likely that average yields will decline as the best yields will be obtained from fewer and fewer fields if striga continues to increase. Improved management of cropping systems that would simultaneously lead to a reduction in striga would have to start from those constraints that farmers see as their priorities (Fig. 3). The role of scientists in this would be to investigate what interactions could make different possible approaches more or less likely to lead to effective improvement in farming systems income. Where labour (for weeding) is scarce, increases in yield (Kossoumna Liba'a & Havard, 2006; M'Biandoun & Olina Bassala, 2007) would improve productivity, but only if such changes do not demand large additional labour inputs. Since soil fertility decline is linked with the build-up of striga, an approach that looks only at controlling striga while neglecting the need for improving soil fertility would do little to restore on-farm productivity and make farming sustainable. Fig. 5 predicts that without soil fertility management farmers would attain low yields even at low striga levels.

Joint experimentation in farmers' fields is therefore needed to see how the negative spiral of low yields leading to low labour and land productivity – leading to low investing capacity – leading to soil degradation and high striga infestation – leading to low yields etc. can be broken. Where striga scientists have often advocated actions based on their understanding that attacking the striga problem would be the best entry point, actions based on farmer's priorities seem a better approach. The motor for improvement of soil fertility leading both to higher yields and reduced losses from striga could be provided by a cash crop for which the market is well organised. In the area of research, cotton has played this role with varying success (Kossoumna Liba'a & Havard, 2006).

However, cotton production in the region has a complex history. Kossoumna Liba'a & Havard (2006) recognized three stages in the period 1951–2002: (1) 1951–1974, when cotton was an obligatory crop imposed on farmers by the colonial government, (2) 1975–1994, when farmers could not do without cotton, because it was a source of obtaining credit facilities, farm-input subsidies and community infrastructure development. During this period, the area under cotton increased substantially compared with the first period. (3) 1994–2002, when the uncertainty with respect to the future of the cotton industry was high, and the area under cotton decreased and production stagnated. Nevertheless, inorganic fertiliser use in the period when the cotton area increased did not lead to an overall decrease in the presence of striga. In other words, the affordability of inorganic fertilisers is not enough for cotton growers to tackle the fertility and striga problem, and more integrated soil fertility management options that include a combination of organic and inorganic fertilisers will be needed (Vanlauwe & Giller, 2006).

Conclusions

Between 1987 and 2005, striga infestation in northern Cameroon increased despite 20 years of project support, of which the FAO (1987-1990, 1994 and 1995) provided the more striga focussed support. Increased pressure on the land, leading to a reduction in the use of fallow and to a cereal monocropping system, is responsible for the striga situation worsening. For farmers, striga was not a priority-one problem because their cereal yields could not be directly related to striga incidence. Soil fertility management is a crucial entry point. The low use of organic manure and decreased use of inorganic fertilisers after the collapse of the cotton sector indicate that this option may be difficult to attain. Yet, improved management of cropping systems that would lead to a reduction in striga has to start from those constraints (soil fertility, labour) that farmers identify as priorities.

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CHAPTER 3

Organic matter and seed survival of *Striga hermonthica* – Separating the roles of carbon and nitrogen

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Abstract

A study is presented of the different ways by which *Striga hermonthica* seed survival could be influenced by amendments of organic matter of different quality. In a field experiment, plots received a single dose of 6 ton organic matter per hectare but with large differences in quality in terms of C:N ratio and nitrogen release rates. Soil moisture, soil temperature and soil ethylene concentrations were measured, while buried nylon seed bags were periodically withdrawn from the soil and assayed for seed viability and germination. Maximal seed germination *in vitro* was obtained with 1 ppm ethylene at 48 hours of exposure time to stimulant, which was higher than with the artificial germination stimulant GR-24. Organic matter amendments significantly depressed *Striga hermonthica* seed survival. The effect was strongest with organic matter of high quality. Organic matter of low quality (high C:N ratio) enhanced soil water content during the first five days after a rainfall event and resulted in a 0.5 °C lower soil temperature. Observed peak ethylene concentrations in the soil were between 2 and 3 ppm, high enough to stimulate *Striga hermonthica* seed germination. However, observed seed survival did not correlate with soil ethylene concentrations. The latter in turn did not differ between qualities of the applied organic matter. Seed survival decreased with increasing time of burial, implying that the effect of seed decay may hardly be beneficial for the ongoing cropping season. Microbiological degradation of organic matter, including that of *Striga hermonthica* seeds, is proposed as the most probable cause of seed depletion in the soil as influenced by organic matter amendments.

Key words: Ethylene, seed bag, seed decay, C:N ratio, organic matter quality

Introduction

A major biotic pest in the savannah regions of Cameroon and Africa at large is formed by parasitic plants of the genus *Striga* (Orobanchaceae). Most important is *Striga hermonthica* (Del.) Benth., which is mainly found on cereals such as sorghum (*Sorghum bicolor* (L.) Moench), maize (*Zea mays* L.), pearl millet (*Pennisetum glaucum* (L.) R.Br.), and rice (*Oryza sativa* L.). Increased *Striga hermonthica* (Del.) Benth. (henceforward striga) infestations are associated with soil fertility decline, most especially in soils with low organic matter levels (Sauerborn *et al.* 2003; Samaké *et al*., 2005). Two strategies for the management of striga can be distinguished. One which aims at preventing striga development and seed production (through weeding, sowing of early maturing host-plant, integrating trap crops into the crop rotation and breeding of resistant host varieties) and the other based on soil fertility improvement (improved crop rotation and fallow, use of mineral and organic fertilisation). These measures for striga management are hampered by the unique survival strategy of the parasite, whereby it produces large amounts of seeds. One mature striga plant is capable of producing an enormous amount of tiny seeds, ranging from 5,000 up to 200,000, which may be dispersed by wind, water, animal or human activity (Parker & Riches, 1993). Striga seeds do not contain reserves and must therefore possess special survival strategies that include the ability to remain viable for a long time and germinate only in response to chemical cues exuded by host plants (Bouwmeester *et al*., 2003; Humphrey *et al*., 2006). These characteristics have rendered striga a severe problem for smallholder farmers in sub-Saharan Africa (Woomer *et al*., 2008; Hearne, 2009). Prevention of further build up of the seed bank through hand-pulling striga plants prior to seed shedding, and ultimately depletion of the seed bank of striga remain essential components in striga control (Oswald, 2005). However, such long-term strategies do not result in immediate benefits in terms of increased cereal yield and may therefore not be very attractive to resource-poor farmers (Ransom, 2000; Hearne, 2009).

Bebawi *et al*. (1984) reported that seeds of *S. asiatica* found below a depth of 30 cm remained viable in the soil for fourteen years. However, seeds buried in the uppermost 30 cm in the soil had a viability of less than 5 years. Work by Gbèhounou *et al*. (1996, 2003) suggested a much shorter life span of seeds in the soil, due to high mortality caused by soil moisture. Considering potential long-term seed viability, it is important to explore possibilities to accelerate striga seed decay. Various mechanisms have been proposed that lead to high seed mortality. Mechanisms include pathogens that act specifically against striga and then can live saprotrophically in the rhizosphere of cereals, such as *Fusarium oxysporum* Schlecht. f. sp. *strigae* (Venne *et al*., 2009). However, while such strains are effective against striga, they may not automatically result in higher cereal productivity. For that reason such biological agents for striga control need to be integrated with crop and soil management technologies that do have a positive yield effect. Increased striga mortality could also be caused by aspecific biological activity. Ransom and Odhiambo (1994) hypothesised that striga seeds decay following organic matter treatments and their subsequent decomposition. Vogt *et al.* (1991) found that striga infestation decreased with increasing soil organic matter levels. They stated that organic matter level is also the most important factor that preserves soil fertility; it could thus be hypothesised that enhancing soil organic matter levels would both positively affect yields and reduce the striga burden under farmers' conditions. Next to enhanced seed decay, Combari *et al.* (1990) observed in a germination assay that leachates from organic matter reduced the germination of striga. However, Sherif (1983) stated that organic matter had little influence on the development of striga and Smaling *et al.* (1991) observed that farmyard manure did not significantly reduce striga infestation. While in compound fields organic matter levels tend to be higher and striga levels lower than in bush-fields (Samake *et al.*, 2005).

Part of these contradictory results may relate to the different parameters measured, *viz.* striga seed germination, the dynamics of the striga seed-bank, or the number of emerged striga seedlings or the biomass of striga at the end of the cropping season. If the seed bank is of a very high density, the density related regulation of germination and emergence (Rodenburg *et al.*, 2006; Westerman *et al.*, 2007; Van Mourik *et al.* 2008) makes that striga emergence will unlikely reveal whether organic matter affects seed longevity. Also, organic matter quality could have differential effects on striga dynamics (Pieterse & Verkleij, 1991). High-quality organic matter with a low C:N ratio is easily decomposed, thereby releasing mineral nitrogen, whereas low-quality materials with high C:N ratios could, during the initial stages of decomposition, immobilise soil nitrogen. Low-quality materials could, however, also increase water-holding capacity of the soil (and hence rainfall use efficiency of crops) and decrease soil temperatures. Both soil moisture (Gbèhounou *et al.*, 1998) and soil temperature (Aflakpui *et al.*, 1998) have been put forward as potential mechanisms for the control of striga germination levels.

During decomposition of organic matter various organic compounds, including ethylene, are released. At high production and low enough consumption levels in the soil, ethylene could reduce striga seed numbers as striga seeds can germinate ('suicidal germination') in the absence of host roots if they are subjected to ethylene (Bebawi and Eplee, 1986; Babiker *et al.*, 2000). Ethylene has been successfully applied to control *S. asiatica* in the United States (Berner *et al.*, 1999) however these authors noted that this method is unaffordable and inappropriate in the ecological and socio-economic context of African farming. The question arises to what extent natural ethylene emission from decomposing organic matter can be used in striga seed bank depletion. Krantz (1997) and Kroschel (1998) reported that in northern Ghana soils of compound fields had higher organic matter levels and emitted higher amounts of ethylene than bush fields, and that ethylene concentrations in soils of compound fields were sufficient to induce suicidal striga germination. On the other hand studies by Elsgaard (2001) and Jäckel *et al*. (2004) indicate that when oxygen is present ethylene consumption may well be larger than ethylene production in organic matter rich soils.

The objective of this study was to test the contribution of various soil processes to striga seed survival as mentioned in the literature and attributed to enhanced soil organic matter levels. We explicitly looked at the role of organic matter quality. More specifically we tested the following hypotheses: (1) organic matter addition increases soil moisture and thereby reduces seed survival; (2) organic matter addition reduces soil temperature and thereby reduces seed survival; (3) organic matter addition increases ethylene concentrations in the soil to levels that are sufficient to induce suicidal germination of seeds and (4) seed decay is a function of decomposition rate of added material which enhances the direct biological attack on the seeds. The first two hypotheses concern effects depending on slow decay and effects would therefore primarily occur with organic matter of low quality, while the latter two refer to effects that would rather occur at higher decay rates so primarily with organic matter of high quality. We created organic matter of different qualities by using a single total amount of organic matter; made up from varying amounts of cotton seed cake (CSC: high-quality, low C:N) and cotton milling waste (CMW: low-quality, high C:N). The effects of organic matter decomposition and nitrogen mineralisation on the interactions between sorghum (grain yield, biomass accumulation) and striga (abundance, biomass) will be reported in an accompanying paper (Ayongwa *et al*., submitted chapter 4).

Material and Methods

Research site and treatments

The experiment was carried out 25 km south of Garoua, North Province, Cameroon, at an altitude of 350 m a.s.l. Soils are predominantly sandy (82% sand, 9% clay and 9% silt) and poor in organic matter (around 1%). Mean annual rainfall ranges between 900 and 1000 mm. The experiment was a single-factor trial in a randomised block design, comprising six treatments in five blocks. The treatments consisted of two sources of organic matter, cotton seed cake (CSC; 7.37% N) and cotton milling waste (CMW; 0.96% N) in different proportions, and a control (Table 1). Both products are by-products of the local cotton factory SODECOTON. Each individual plot measured 6m long and 4m wide with an inter-plot spacing of 1m. Plots were cleared and cleaned of debris and the soil ploughed manually. Then the cotton by-products were manually broadcasted as uniformly as possible and ploughed-in to about 15 cm using a shovel.

Table 1. A description of combinations of organic matter treatment and codes.

Treatment code	OM combination	N-content (kg ha^{-1})	Composite C:N ratio
Zero (control)	0 CSC + 0 CMW		-
6C	(6 tons CSC + 0 ton CMW) ha^{-1}	442	6.8
4.5C	(4.5 tons CSC + 1.5 ton CMW) ha^{-1}	346	8.7
3C	(3 tons CSC + 3 ton CMW) ha^{-1}	250	12.0
1.5C	(1.5 tons CSC + 4.5 ton CMW) ha^{-1}	154	19.5
6W	(0 tons CSC + 6ton CMW) ha^{-1}	57	51.7

Determination of soil moisture content

Soil moisture content was measured using the gravimetric method. Three sub-samples per plot (repetition) were taken from the upper 5 cm of the soil using metal cores. This sampling depth differs from the depth of seed burial (15 cm) as drying after a rainfall event takes place quickest and thus treatment effects are expected to be largest. Each core was covered tight with a lid to avoid loss of moisture through evaporation. The initial weights of the samples were determined within 30 minutes after taking the last soil sample. The samples were subsequently dried to a constant weight in an oven at 105 °C for 24 hours and weighed again to obtain the final mass. Sampling for soil moisture was done after every rainfall event. Moisture was determined at up to five consecutive days before the next rain. Daily rainfall in the experimental site was recorded using a rain gauge.

Determination of soil temperature

Temperature measurements were taken with the help of an electronic digital thermometer having a probe (TRACEABLE ®, Thomas scientific). Temperature readings were taken at the same moment when samples for moisture content were taken. The thermometer probe was inserted to a depth of 15 cm, a similar depth as that of the Eplee bags. Three readings were taken per plot. All soil moisture and temperature data were based on samples collected between 12h00 and 13h30 daily.

Determination of ethylene concentrations in the field

Gas collection chambers were buried in the centre of each plot, at a depth of 15 cm. A complete gas collection chamber was made from a hypodermic syringe without piston and with the proximal end of the syringe covered with a plastic gauze, preventing soil particles from entering the chamber while allowing air to diffuse freely between the syringe chamber and the surroundings. At the distal end of the syringe the metal needle was cut half-way and then connected to the soil surface by a rubber tube of about 40 cm long, whose internal diameter was approximately 1 mm, thus enabling to take gaseous samples without disturbing the soil. The syringe was positioned at a 45° angle relative to and inside a cylindrical PVC tube (height 7-10 cm; diameter 10 cm) such that the distal end of the gas collection chamber with the broken needle was held through the wall of the cylinder from where the rubber tubing extended out to the soil surface. This diagonal position of the chamber relative to the soil surface, prevented soil water from entering the gas collection chamber after rainfall. A metal clip was used as a tap to open and close the tube to the gas collection chamber at the level of the soil surface. At this extreme outlet of the rubber tube above the soil surface, a complete hypodermic syringe was then used to periodically withdraw gas samples from the underground gas collection chambers at known time intervals. The gas collection chambers were replicated 4 times per treatment. Gas samples were taken after every other day for one month following the burial of the organic matter in the soil. During each sampling, 4 ml of gas was siphoned from the installed gas collection chamber. The contents of the syringe were emptied into a sterile air-tight/water-tight glass vial, prior filled with bubble-less tap water. The gas injected displaced an equal volume of water, which was simultaneously withdrawn into another empty hypodermic syringe. The gas obtained was then stored in the glass vials in an inverted position, such that the water permanently sealed it against the glass wall until ready for analysis. Simultaneously, samples of pure grade ethylene (99.9%) from laboratory stock were injected into glass vials and stored using the same method to serve as a check on gas losses during the storage period. Gas samples in vials were analysed for ethylene concentrations some 12 months after collection using a gas chromatograph at the Laboratory of Microbiology, Wageningen University. Analyses of ten repeats each of the control samples of pure ethylene stored in vials against freshly obtained pure grade ethylene from the laboratory established an average 13.7% ethylene was lost in storage before analysis (dissolved in the water seal). The observations on the remaining gas samples were adjusted accordingly.

Striga seed survival

Striga seeds were collected from infested sorghum plants on farmers' fields around the experimental site in 2000 and 2001. Seeds were harvested from mature capsules of striga plants. Prior to fieldwork, the seeds were packaged in 5 cm by 5 cm nylon mesh Eplee bags, possessing a mesh opening of 90 μm in which a known number of striga seeds have been packaged (Berner *et al.*, 1997). Then 200 (in 2001), respectively 300 (in 2002) striga seeds were placed in the centre of each bag.

The Eplee bags were buried a week after ploughing and organic matter application at a depth of 15 cm in the centre of each experimental plot, a string attached to each bag extended from the soil surface to allow easy retrieval. One random bag was pulled up on a biweekly basis. During the 2002 season, when all the plots were under sorghum, PVC tubes were used to isolate the Eplee bags from a possible direct contact with host roots, which could stimulate the striga seeds in the bags to germinate. The PVC tubes of 20 cm diameter and 17 cm long were buried in the centre of each plot to 16 cm depth, leaving an outcrop of one centimetre above the soil.

Eplee bags were taken to the laboratory and processed for striga seed viability and germinability. Laboratory procedures for seed treatments, seed conditioning and application of germination stimulant were adopted from the techniques described by Berner *et al.* (1997). Seed losses from nylon mesh bags were also assessed in 2002 by counting total number of seeds recovered from the bags. The retrieved bags were transferred to the laboratory and washed under tap water to clean seed bags from soil particles and debris. The bags with their contents were sterilised by placement for 5 minutes in a 1% NaOCl solution, after which the bags were washed profusely under running tap water. The retrieved seed batch was split in two parts.

One batch of these striga seeds were assessed for viability using the Tetrazolium Red test (Gbèhounou, 1998). 1 ml of a 1% TTC solution was added to the seeds in small sealed test tubes, which were subsequently stored in the dark for 8 days at room temperature. At the end of the incubation, seeds were observed against a white background under a dissecting microscope.

The second batch was subjected to a germination test (see below). For comparison seeds from the same source as that buried in the field, but which had been stored under laboratory conditions, were also tested after conditioning. In order to condition these stored seeds were first surface-sterilised for 5 minutes using 1% NaOCl solution and later rinsed with tap water. After surface-sterilisation, the seeds were dried in open air. Glass fibre disks (5 mm diameter) were cut out from Whatman glass micro-fibre filter paper using a paper punch. Using forceps, 25 to 50 seeds were placed in each disc moistened with deionised water. A total of 100 seeds (4 to 5 disks of 20-25 seeds each) per treatment were then placed in a 9.5 cm diameter Petri dish lined with two layers of ordinary filter papers also moistened with deionised water. A circular hollow ring of aluminum foil (diameter approximately 2 cm, height 1.5 cm) was later placed in the centre of each Petri dish. The Petri dishes were closed and sealed with parafilm, wrapped in aluminum foil and placed in the dark at ambient temperatures (30°C ± 5 °C) for 14 days. Striga seeds exhumed from the field were presumed already conditioned. To test germination percentage of both field retrieved and laboratory stored seed batches, 300 µl of the synthetic germination stimulant GR-24 (10 mg L^{-1}) were added to the centre of the aluminium foil ring in each Petri dish. This level should avoid low germination due to prolonged conditioning in the field as observed by Matusova *et al.* (2004) Subsequently, the Petri dishes were re-sealed with parafilm, wrapped in aluminium foil and incubated in the dark for 48 hrs at room temperature (30 °C ± 5 °C). At the end of the incubation, germinated seeds were counted under a dissecting microscope (14X). Striga seeds were considered germinated when the germ tube protruded the seed coat.

Laboratory test to assess the efficacy of ethylene in inducing striga seed germination

To determine the effect of various ethylene concentrations on chance and rate of striga seed germination, the seeds were exposed to various concentrations of ethylene. Striga seeds were collected from Samayana Mali in 1996 for this experiment done in 1999 in Wageningen, The Netherlands. The seeds were first sterilised during 5 minutes using 1% NaOCl. The seeds were then thoroughly rinsed with de-ionised water, after which they were conditioned for 14 days on moist filter paper at a temperature of 30 ^{o}C. After the conditioning period the seeds were briefly dried to ease manipulation and then exposed to different treatments: GR-24 (positive control) and 0.01, 0.1, 1, 10 and 100 ppm of ethylene. These concentrations were based on research by Egley and Dale (1970). GR-24, the artificial germination stimulant was introduced as control in order to compare ethylene effects to standard striga seed germination assays.

Seeds were placed on moist glass fibre filter paper punches that were placed in airtight Petri dishes. These Petri dishes were made airtight by using grease and a viton rubber ring. Ethylene concentrations were established by replacing a volume of air in the Petri dish by an equal volume of ethylene of a known concentration by injection through a septum. The dishes were then incubated at 30 ^{o}C in the dark. At the time of scoring for germination the dishes were opened. Each time after closing the dishes the concentration of ethylene was re-established. Germination was scored at 0, 1, 2, 3, and 4 days after exposure to the germination stimulant, using a binocular microscope (14X). A seed was scored as germinated if the germination tube had protruded through the seed coat. Germination data were always obtained using four replicates i.e. four petri dishes per treatment.

Statistical analysis

The fraction of viable and germinated striga seeds from the retrieved seed bags was expressed relative to the control stored and pre-conditioned under lab conditions and treated with GR-24. Fractional data were arcsine-square root transformed. An analysis of variance was carried out on treatment means. Treatment means were separated using the LSD test. Correlations were calculated using Pearson's correlation coefficient (r). All analyses were done using the General Linear Model and ANOVA of the SAS package version 9.1 and GENSTAT 12th edition.

Results

Effect of organic matter amendments on striga seed germination (Fig. 1)

Striga seed germination was positively correlated with viability as established from the tetrazolium testing ($r=0.856$; $n=60$; $P<0.0001$). Germination of striga seeds retrieved after 10 weeks from the control fields (no organic matter added) was lower, resp. 25% (2001) and 55% (2002) than that of seeds stored in the laboratory, indicating natural seed demise under field conditions. There was a significant interaction between time of retrieval and the soil amendment treatment in both years ($P<0.005$), due to a much smaller effect of the amendments at the start of the rainy season. Striga seed germination significantly declined over time in all treatments and both years ($P<0.001$). At the end of the cropping season (ten or more weeks after burial) germination was lowest. All organic matter amendments reduced striga seed germination compared to the control in 2001, while only higher quality organic matter amendments reduced seed germination in 2002 ($P<0.001$). In both years addition of high-quality organic matter (6C, 4.5C) resulted in a stronger decline than addition of low-quality organic matter.

Ethylene and striga seed germination

Ethylene levels of 1 ppm and higher stimulated striga seed germination to the same extent as the artificial germination stimulant GR-24. Ethylene levels of 0.1 ppm and 0.01 ppm resulted in much lower germination. Seeds needed to be exposed for two days to achieve maximum germination (Table 2).

Table 2. Striga seed germination (%) for seeds subjected to different concentrations of ethylene (C2H4) or the standard artificial germination stimulant GR-24. Observations were made during four consecutive days. Means ($n=3$) in a column followed by different letters are not significantly different ($P<0.05$).

Exposure time (days)	1	2	3	4
Germination stimulant				
C_2H_4 0.01 ppm	14 a	29 a	28 a	26 a
C_2H_4 0.1 ppm	12 a	35 a	37 a	37 a
C_2H_4 1 ppm	35 ab	71 c	72 b	72 b
C_2H_4 10 ppm	22 ab	73 c	73 b	72 b
C_2H_4 100 ppm	38 b	76 c	76 b	75 b
GR – 24	30 ab	63 b	67 b	66 b

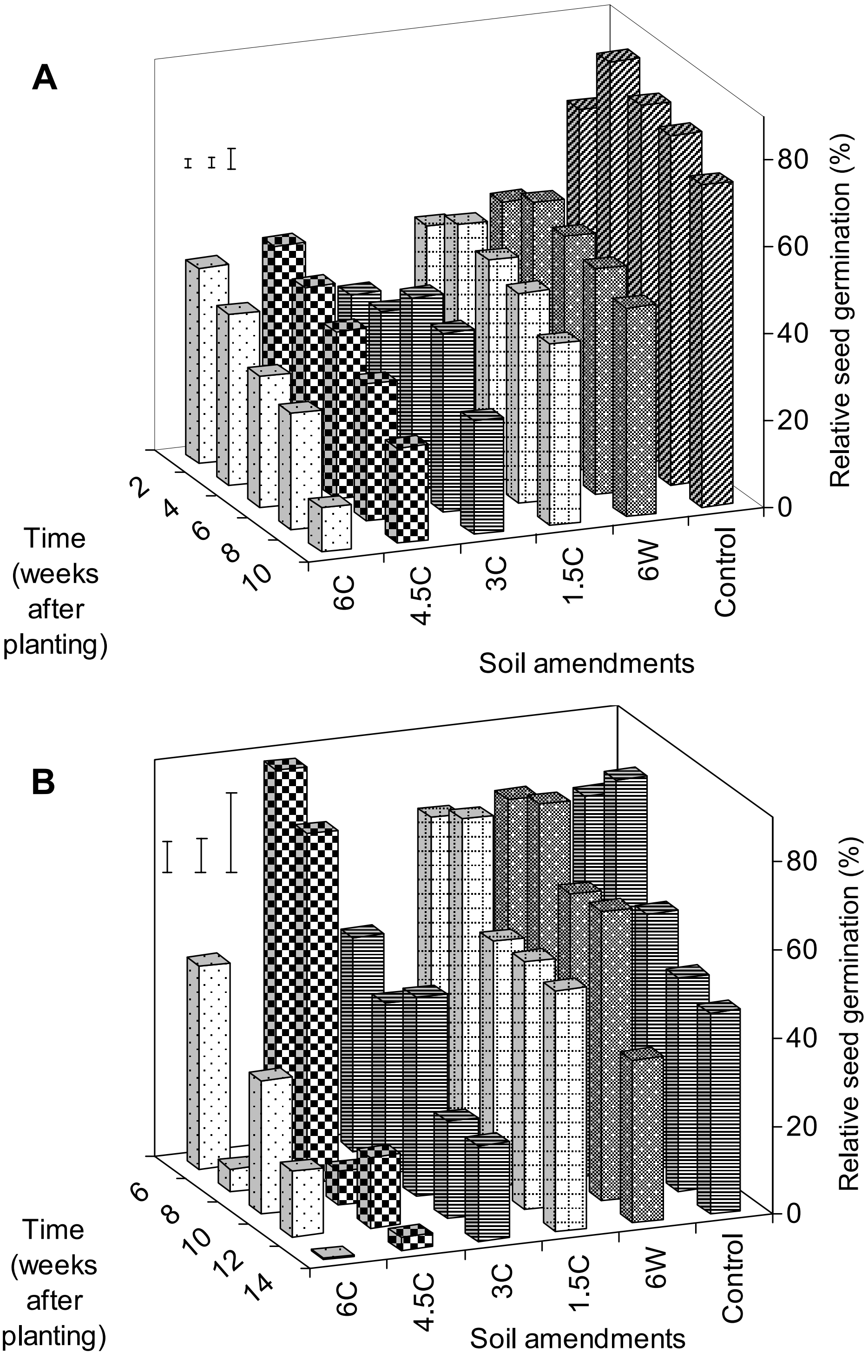

Fig.1. Germination of striga seeds in 2001 (A) and 2002 (B) stored in the soil for different periods of time (weeks) and in plots amended with different types of organic matter (for explanation of codes see Table 1). Germination is expressed as % of germination observed for dry stored seeds. Bars indicate standard errors of difference between means (n=4) from left to right respectively for comparison of means of a same treatment, means of a same time of retrieval and any two means.

Effect of organic matter amendments on soil moisture content

Soil moisture content rapidly declined after rainfall events. The addition of low-quality organic matter 1.5C and 6W resulted in higher soil moisture content compared to the control and addition of high-quality organic matter (4.5C and 6C) (Fig. 2). The rate of soil drying after addition of low-quality organic matter was less than for the high-quality organic matter. At the end of sampling time (110 hours) both 1.5C and 6W treatments retained significantly more water compared to the control and the high-quality treatments.

Effect of organic matter amendments on soil temperature

Organic matter application and sampling time significantly modified soil temperature, but the change was very small and in fact biologically not significant (Table 3). The lowest soil temperatures at 15 cm depth were recorded 72 hours after rainfall. Soil temperature was negatively correlated with soil humidity (r= -0.804; n=30; P<0.0001).

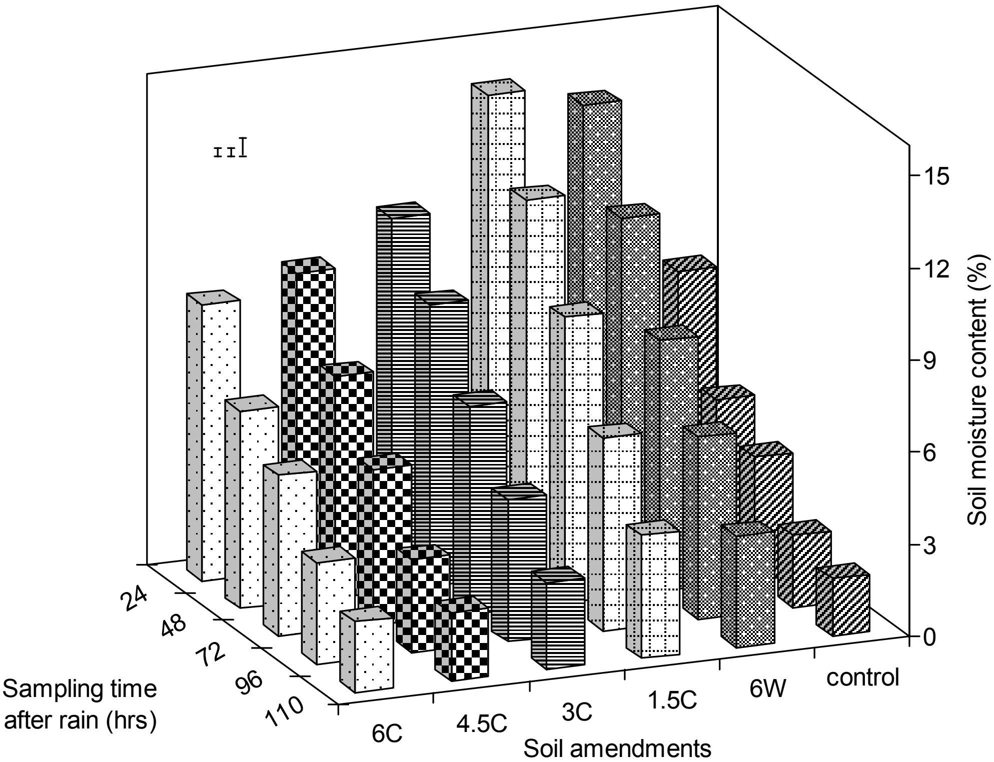

Fig. 2. Soil moisture content (% w/w) in 2001 during the first 5 days after a rainfall event in plots amended with different types of organic matter (for explanation of codes see Table 1). Bars indicate standard errors of difference between means (n=4) from left to right respectively for comparison of means of a same treatment, means of a same time after a rainfall event and any two means.

Table 3. Effect of organic matter amendments on soil temperature and over sampling time. Means (n=4) followed by different letters are significantly (P<0.05) different.

Treatment	Soil Temperature (^{o}C)
Organic matter	
Zero (0)	32.9a
6C	32.7ab
4.5C	32.4b
3C	32.4b
1.5C	32.3b
6W	32.4b
LSD	0.381
SED*	0.17
P **	0.012
Sampling time (hours)	
48	32.0b
72	29.9c
96	36.2a
120	32.1b
144	32.3b
LSD	0.348
SED*	0.16
P **	<0.0001
Interaction (OM x Time)	
P **	(0.13) NS

*Standard error of difference
**Probability of treatments effects (level of significance)

Ethylene production in the soil

Almost all measurements indicated ethylene levels above 1 ppm, the level that induces significant suicidal germination as presented above. Ethylene levels ranged from 0.5 to 3 ppm. There was a significant effect of time on ethylene levels, with ethylene levels being higher immediately after rainfall events. There was no significant effect of organic matter addition on ethylene levels (Table 4).

Table 4. Ethylene concentrations in air retrieved from the soil at 12 cm depth in plots amended with different amounts of organic matter (OM) at different numbers of days after burial in the soil (± standard error of the mean), n=4. For explanation of OM codes see Table 1.

OM	Days after burial of organic matter (DAB)					
	14	15	19	22	23	24
0	1.84 ±0.5	2.28 ±0.4	1.23 ±0.4	1.51 ±0.4	1.13 ±0.4	1.58 ±0.5
1.5C	1.57 ±0.5	1.88 ±0.4	0.72 ±0.4	1.88 ±0.4	1.34 ±0.4	1.58 ±0.5
3C	2.01 ±0.4	2.15 ±0.4	1.22 ±0.4	1.29 ±0.5	1.24 ±0.4	2.14 ±0.4
4.5C	2.98 ±0.4	1.52 ±0.4	0.94 ±0.4	2.40 ±0.4	1.37 ±0.4	2.17 ±0.4
6C	1.79 ±0.4	1.68 ±0.4	0.54 ±0.4	1.11 ±0.4	1.22 ±0.4	1.83 ±0.4
6W	missing	2.12 ±0.4	0.99 ±0.4	1.74 ±0.4	1.88 ±0.4	1.88 ±0.4

OM	Days after burial of organic matter (DAB)					
	28	30	31	33	36	40
0	1.62 ±0.4	1.50 ±0.4	1.82 ±0.4	1.31 ±0.5	2.84 ±0.4	1.83 ±0.4
1.5C	2.08 ±0.4	1.28 ±0.4	2.12 ±0.4	1.67 ±0.4	2.67 ±0.4	1.57 ±0.4
3C	2.11 ±0.4	1.25 ±0.4	1.50 ±0.4	2.33 ±0.4	1.68 ±0.4	2.05 ±0.4
4.5C	1.55 ±0.4	1.61 ±0.4	1.72 ±0.4	2.14 ±0.4	1.80 ±0.4	2.27 ±0.4
6C	1.52 ±0.4	1.17 ±0.4	2.34 ±0.4	1.34 ±0.4	1.84 ±0.4	1.64 ±0.4
6W	1.68 ±0.4	1.89 ±0.4	1.83 ±0.5	2.38 ±0.6	1.85 ±0.4	1.80 ±0.4
ANOVA [a]						
DAB	***					
OM	n.s.					
DAB X OM	n.s.					

[a] *** P<0.001; n.s. not significant

Discussion

Soil organic matter and the striga – cereal interaction

Research on organic matter in the framework of the striga problem has not systematically addressed the question how organic matter of different qualities impacts on the various stages in the life cycle of striga. In this study we investigated the impact of organic matter quality on viability and germination of striga seeds and tested three different mechanisms (moisture, temperature, and ethylene) for their potential role. Other studies looked at the impact of nitrogen nutrition (which accompanies decomposition of organic matter and subsequent N mineralisation) on the production of germination stimulants by sorghum roots (Ayongwa *et al.*, 2006) and the direct impact of nitrogen release (after decomposition of organic matter of different quality) on sorghum grain yield and biomass and its interaction with striga emergence and biomass production (Ayongwa *et al.*, submitted chapter 4).

To our knowledge, this is the first study that shows that different qualities of organic matter have differential effects directly on striga seed survival. The significant positive correlation between seed viability and germination indicates that germination tests provide a realistic assessment of the number of striga seeds that did not die-off. This despite the fact that seed retrieved from the field could potentially have been conditioned for such a long period (10 to 14 weeks after burial) that so-called secondary dormancy could have occurred (Dzomeku and Murdoch, 2007). The buried mesh bag method has been criticised by Van Mourik *et al.* (2005) because of density-dependent mortality within seed bags caused by seed-to-seed contamination. While estimates obtained with this method may therefore not be used for quantification of absolute loss rates caused by imposed treatments for instance needed as input to models of seed bank dynamics (Westermann *et al.*, 2007, Van Mourik *et al.*, 2008), the method retains its validity for a comparison between treatments within an experiment like soils amended with different levels and qualities of organic matter as reported here.

Without organic matter addition there was already a significant reduction of 46% in striga seed germination compared to laboratory storage. Our results showed that organic matter addition further reduced striga seed germination. Gbèhounou *et al.* (2003) obtained, in soils with 1% OM, a drastic reduction in seed germination from a maximum of 74% to 17% in a single rainy season. Van Mourik *et al.* (2003) attributed up to 80% seed loss under bare soil in a single cropping season in Mali to seed deterioration and showed that sterilisation reduced this seed loss to less than five percent. Ahonsi *et al.* (2002) attributed differences in striga infection in pasteurised soils and natural soil to soil biotic factors, while Pieterse *et al.* (1996) and Odhiambo (1998) had shown that soil fumigation with methyl-bromide significantly reduced the rate of seed demise in the soil. Natural striga-suppressive soils have been reported (Ahonsi *et al.*, 2004). The causal organisms (whether generalist saprotrophic fungi or specific seed-destroying fungi such as *Fusarium oxysporum* f. sp. *strigae*) have in most cases not been identified. The increase in seed losses after addition of organic matter of higher quality (resulting in higher decomposition and mineralisation) rather suggests that generalist saprotrophic fungi were most important in our study.

Low striga seed germination was most pronounced late in the season (10 to 14 weeks after burial). The implication is that the effect of seed decay most probably is inconsequential for the host crop grown in the same season. Considering also the potential bias in (and overestimate of) seed decay in mesh bags and potential slight underestimation of seed germination due to secondary dormancy (Dzomeku & Murdoch, 2007), it is impossible to judge from the current data whether the levels of seed decay observed would result in a gradual depletion of the seed bank over years; because depletion rate is generally slower than the rate of production of new seeds under continuous cropping (Van Mourik *et al.*, 2008). In fact much larger losses under field conditions were observed from seed stimulation by root exudates (Van Mourik, 2007), a process excluded in the current study.

Mechanisms of suppression of striga seed germination after organic matter amendments

Soil amendments significantly increased soil moisture by 2-3% point immediately after a rainfall event and 1% point five days later, with cotton milling waste (low-quality organic matter) performing best. Increased soil moisture retention is especially important for the sandy soils that are prevalent in northern Cameroon. Under the present farming systems in the savannah belt, where farm input is meagre and little vegetation is recycled, it may be difficult to increase soil organic matter levels to amounts sufficient to obtain soil moisture levels that will be unfavourable to striga seed survival (Sauerborn *et al.*, 2003). Further, our organic matter amendments (6 t ha^{-1}) are very high and it is unlikely that resource-poor farmers would have access to the quantities needed for application to all for their fields.

Since soils with a higher moisture content (i.e., soils to which organic matter of lower quality was added) resulted in higher seed survival, we conclude that soil moisture retention in these very sandy soils due to organic matter application is not an important mechanism in contributing to striga seed demise. The significant negative correlation between soil moisture and soil temperature suggests that addition of low-quality organic matter could result in lower soil temperatures. However, temperature effects were very small (0.5 °C) and confounded with soil moisture. As was concluded for soil moisture it is unlikely that these small differences affected striga seed survival. Oswald *et al.* (1999) suggested that the success of certain cereal-legume intercrops in reducing striga incidence in the field may be due to their ability to significantly lower soil temperature (through shading) to levels unfavourable for striga seed germination and development. However, it is highly likely that the impact of legumes on soil N dynamics (and the effects of increased N availability on the cereal – striga interaction) is much more important.

The importance of ethylene in striga seed dynamics raises questions on processes of ethylene production and consumption. Ethylene concentrations in waterlogged anaerobic soils are often orders of magnitude higher than in well-drained aerated soils as consumption is much lower in the absence of oxygen (Zechmeister-Boltenstern & Smith, 1998; Elsgaard, 2001). The question is pertinent whether differences between aerobic and anaerobic soils are mainly due to enhanced production or reduced breakdown of the compound in the absence of oxygen. Work by Zechmeister-Boltenstern & Smith (1998) indicates very high aerobic ethylene decomposition, resulting in very low steady states. They reported potential aerobic ethylene decomposition rates that were one or two orders of magnitude larger than production rates. Our data fit with these observations, as our soils exhibited low amounts of ethylene (but still above the concentration of 1 ppm, necessary to induce maximum striga germination *in vitro*) with no differences between the various forms of organic matter amendments and only small differences in time due to rainfall patterns. Our results contradict those obtained by Kranz (1997) who observed higher ethylene levels in compound-fields (OM levels 2.5%) compared to bush-fields (OM levels 1.4%). Our soil had only 1% soil organic matter. However, her studies included only a few measurements and sampling times, which may have resulted in chance differences. We argue that increasing soil organic matter levels from the current extremely low levels will not significantly affect ethylene levels, unless the indirect effects of organic matter addition cause a substantial decrease of ethylene consumption levels through reduction of oxygen availability, a possibility that is not supported by the presented data in this study.

Consequently, it is unlikely that in these coarse-textured soils differences in ethylene levels will exert a major impact in controlling striga dynamics. On vertisols, where in Cameroon muskwari sorghum cultivation is practiced (Obale-Ebanga, 2001), anaerobic conditions occur much more often. Such practices, which also rely on sorghum transplanting, reduce striga infestation, but we have not measured ethylene production in these soils. In these systems, the transplanting may in fact be of more impact in the striga dynamics (Van Ast *et al.*, 2005)

A role for nitrogen in striga seed demise?

Our results demonstrate that three mechanisms of the four studied mechanisms (effect of organic matter amendment on soil moisture, soil temperature, ethylene levels) were ineffective in reducing striga seed germination. Still germination levels were affected by organic amendments, with the largest effect occurring after addition of organic material of high quality. Combining this observation with the observation that biological activity in the soil leads to seed loss through direct decomposition of seeds and the increased decomposition rate of the higher quality material (Ayongwa *et al.,* submitted Chapter 4); we conclude that decomposition rate of striga seeds was the main mechanism. The higher N release could in principle have also lead to effects on sorghum N status and thus germination stimulant release (Ayongwa *et al.*, 2006) and enhance sorghum growth (Ayongwa *et al.*, submitted chapter 4) and through these affect striga germination and root colonisation but these effects were excluded with the use of the PVC tubes to avoid contact between sorghum roots and the seed bags.

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CHAPTER 4

Dynamics of host-parasite relations between *Sorghum bicolor* and *Striga hermonthica* – the influence of soil organic matter amendments of different quality

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Abstract

The dynamics of the interactions between *Striga hermonthica* (striga) and a sorghum host when subjected to a range of organic matter amendments was studied in a field experiment during three cropping seasons, following a three-factorial design with (i) bare-fallow versus continuous cropping, (ii) two striga infection levels and (iii) five organic matter levels, a single inorganic fertiliser treatment of 120 kg N ha^{-1} and a control. The effects of two different cotton by-products and their mixtures on sorghum yield were well described by their N mineralisation pattern. The impact of organic amendments in the sorghum production system was directly related to N-mineralisation in at least the first three cropping years. There was an increasing negative effect of organic matter on striga as the quality of the applied material increased. The emerged numbers of striga were well described by N-release after one month, while striga biomass and sorghum biomass were well described by N-release after three months. As a stand-alone measure, addition of low-quality organic matter is even disadvantageous in cropping systems, as it leads to equal sorghum performance with rather an increase in striga numbers. Implications for integrated soil fertility and striga management under different infestation levels of striga are discussed.

Key words: cotton by-products, N-mineralisation, grain yield, striga infestation

Introduction

Plant production systems in the African savannah are predominantly based on cereals such as sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* (L.) R.Br.), maize (*Zea mays* L.) and rice (*Oryza sp.)*. Sorghum, millet and rice (*Oryza glaberrima* Steud.) are traditional staples, whereas maize and asian rice (*O. sativa* L.) have been recently introduced in the savannah and sahelian zones as new cereals and are gradually replacing the traditional sorghum, millet and rice crops. In the savannah region, the productivity of these cereals is hampered by various abiotic and biotic constraints. Species of the plant-parasitic genus *Striga* (Orobanchaceae) represent the largest single biological barrier to food production in Africa (Hearne, 2009; Parker, 2009). In northern Cameroon, *S. hermonthica* (Del.) Benth. (purple witch-weed, henceforth striga) is the most important species parasitising cereals. In that region striga is considered the most destructive and persistent crop pest (Parkinson *et al.,* 1991; Ayongwa & Ngawa, 1999), though farmers consider it a lesser constraint compared to soil fertility (Ayongwa *et al*., 2010). Striga is endemic in the savannah region and has very strongly increased due to increased pressure on the land (Abunyewa & Padi, 2003; Ejeta, 2007; Ayongwa *et al*., 2010). In former times, striga was controlled by shifting agriculture, where short periods of cropping (a few years) were followed by prolonged bush fallows (10-20 years) (Weber *et al*., 1995; Kranz *et al*., 1998). Long fallows restored soil fertility and acted as a break in the weed cycle (De Rouw, 1995). Shorter fallows (or even continuous cropping) without adequate nutrient replenishment led to a decline in soil fertility. This process was exacerbated by a shift from crop rotations, where cereals and legumes were alternated or were grown intercropped, to cereal mono-cropping systems. Both the decline in soil fertility and the cereal mono-cropping resulted in the build-up of striga (Abunyewa & Padi, 2003). Because of the linkage between poor soil fertility and striga, approaches that look only at controlling striga while neglecting the need for improving soil fertility would do little to restore on-farm productivity to the level that would make farming sustainable (Ransom, 2000; Sauerborn *et al*., 2003; Ayongwa *et al*., 2010).

Soil fertility restoration depends on the inputs of mineral nutrients such as nitrogen and phosphorus. Because mineral fertilisers are usually unavailable to or too expensive for resource-poor farmers, and because the sandy soils of the savannah region in northern Cameroon are prone to leaching of these nutrients, organic resources are a necessary addition to inorganic fertilisers (Bationo *et al*., 2007). However, despite the large importance of organic residues, very little of it is returned to the soil. Almost all crop residues are used as fodder, cooking fuel or building material and therefore removed from the fields (Abunyewa & Padi, 2003; Sauerborn *et al*., 2003). Next to their important contribution to a healthy soil, organic amendments can also play a direct role as effective control measure against striga. Several studies observed that striga infestation decreased with increasing soil organic matter levels (Vogt *et al*., 1991; Sauerborn *et al*., 2003, Samake *et al.,* 2005). However, these studies did not provide any insight in the underlying mechanisms. Sherif & Parker (1986) found that chicken manure at high application rates (15 t ha^{-1}) delayed striga emergence on sorghum, but that other organic manure sources with lower nitrogen concentration had no effect in reducing striga. Leaf litter of nitrogen-fixing legumes (with low C:N ratio) as organic resource was also effective in suppressing striga and in increasing yields (Gacheru & Rao, 2001; Weisskopf *et al*., 2009). However, some reports disagree with this contribution of organic matter to striga control. Ikie *et al*. (2007) showed that chicken manure (applied at 100 kg N ha^{-1}) enhanced striga emergence compared to the control (zero manure) and an equivalent amount of N applied as inorganic fertiliser. Smaling *et al*. (1991) reported that neither farmyard manure nor mineral fertiliser significantly reduced striga infestation.

Kranz (1999) noted beneficial effects of organic amendments and suggested that both high-quality litter (release of substantial amounts of nitrogen) and low-quality litter could be beneficial. However, the way organic matter of different quality could affect the interactions between cereals and striga is unknown. Only very few studies compared the effects of organic matter quality (here defined by the C:N ratio) on striga infestation (Gacheru & Rao, 2001). In our study of the effects of organic matter quality on striga control (Ayongwa *et al.,* submitted Chapter 3) several potential beneficial effects of low-quality organic matter on soil properties (effects on water-holding capacity, effects on temperature, release of ethylene that induces suicidal germination of striga seeds) could not be confirmed as a potential contributor to striga control. We concluded that the major effect of organic matter on the performance of striga seed viability was likely due to its nitrogen release pattern which affected the activity of saprotrophic organisms that decayed striga seeds.

In this paper we expand on the role of organic amendments on sorghum productivity and striga dynamics, and compare amendments of various qualities with nitrogen fertiliser. We tested the impact of organic matter of different qualities (by mixing in various ratios of organic material of different quality) under conditions of low and high striga pressure. We also tested for these effects under continuous cropping and after two years of bare fallow. More specifically we tested the following hypotheses: (1) The beneficial effect of organic by-products of cotton can be completely described by reference to nitrogen release during decomposition; (2) Organic amendments of low quality will increase striga numbers (due to a positive effect on sorghum performance), but amendments of high quality will have a direct negative impact on striga severity and incidence; (3) The effect of organic amendments on sorghum yield increase is dependent on the degree of striga infestation; (4) The above-mentioned effects of organic amendments are larger under continuous sorghum cropping than in systems that include fallowing.

Material and Methods

Experimental design and layout

The experiments were carried out from 2000-2002 in Djallingo village, northern Cameroon (North Province, 15 kilometres south of Garoua, longitude 13°30' E, latitude 9°20' N). The field experiment was a three-factorial experiment with 28 treatments (2x2x7) in a Randomised Complete Block Design with five replications:

Factor 1 (striga, 2 levels), high-level infected[*] soil (high striga) or low-level infected soil (low striga);

Factor 2 (Cropping practice, 2 levels), three years sorghum cropping (continuous-cropping) or two years bare fallow followed by a single year of sorghum (fallow).

Factor 3 (Soil amendment, 7 levels), 6 ton ha^{-1} of organic amendment consisting of Cotton Seed Cake (CSC – high quality material) and/or Cotton Milling Waste (CMW – low quality material) in 5 different combinations, (i) 6 ton ha^{-1} CSC; (ii) 4.5 ton ha^{-1} CSC plus 1.5 ton ha^{-1} CMW; (iii) 3 ton ha^{-1} CSC plus 3 ton ha^{-1} CMW; (iv) 1.5 ton ha^{-1} CSC plus 4.5 ton ha^{-1} CMW; (v) 6 ton ha^{-1} CMW; (vi) control (no application of organic amendment); (vii) 120 kg ha^{-1} nitrogen (as urea). Each experimental unit was 6 m by 4 m (24 m²), crop spacing was 75 cm between rows and 20 cm within rows and an inter-plot spacing of 1 m. This gave 8 crop rows of 4 meters long with 160 sorghum plants. Data were collected from 96 sorghum plants in the middle-most rows, *i.e.* from an area of 3.2 m by 4.5 m (14.4 m²).

Table 1. Description of organic matter treatment combinations. N mass fraction of cotton seed cake was 73.7 mg g^{-1}, that of cotton milling waste (CMW) 9.6 mg g^{-1}. N release after one and three months calculated on the basis of MiNiP (Janssen, 1984 and 1996), N release for mixtures calculated on the assumption of a simple additive effect of both amendments. See text for details.

CSC (t ha^{-1})	CMW (t ha^{-1})	C:N ratio	N released in 1 month (kg ha^{-1})	N released in 3 months (kg ha^{-1})
6	0	6.8	183	342
4.5	1.5	8.7	135	259
3	3	12	86	177
1.5	4.5	19.7	38	93
0	6	52.1	-11	11

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[*] In this paper the terms infection or infection level refer only and specifically to the density of striga seed in the soil. The terms infestation or infestation level refer to the number of striga plants observed in a plot or on a sorghum plant.

Management practices

The experiment was run for three successive cropping seasons (June to November of 2000, 2001, and 2002) and the various treatments were repeated on the same plot each year, with changes made only in the fallow treatments. Fallowed plots were not planted and kept bare by weeding during the first two seasons (2000 & 2001) and cropped under sorghum in the last year (2002) to assess cumulative after-effects of the various treatments on non-cropped soil. All plots were naturally infected with striga seeds, to varying and undetermined levels.

The low-striga plots were obtained by treating the plots twice with 99.9% grade ethylene at an interval of 14 days at the start of the rainy season in May of 2000 and 2001. This ethylene treatment was adapted from Eplee & Norris (1987). Pure ethylene gas in cylinders connected by a 20 meters long heavy-duty rubber hose to a soil injector was used. Ethylene was injected in moist soil at a constant pressure of 3.5 bars, which roughly covers a circle with a radius of 0.5 m. A grid of ropes delineating 1 m^2 squares was laid out per plot in order to enable precise and easy gas injection at the interjections of the ropes. Sorghum was sown 14 days after the second gas injection, to avoid attachment of striga seeds that had germinated in reaction to the ethylene. The buds of flowering striga plants were nipped systematically at the onset of flowering to avoid seed setting.

The high-striga plots were obtained in the first year by additionally infecting plots with seeds harvested during the 1999 cropping season. At the start of the 2000 rainy season, these plots were infected at a rate of 3000 germinable striga seeds per sowing hole (20,000 striga seeds per square metre) applied in a furrow trenched to coincide with the sowing rows following the method described by Berner *et al*. (1997). Striga plants were allowed to flower and produce and shed seeds on the plots.

Four to five sorghum seeds of the striga-sensitive variety CK 60B (Van Ast *et al*., 2005; Rodenburg *et al*., 2006a) were sown and thinned to 1 plant per sowing-hole 14 days later.

All plots received a basal dose of superphosphate (P_2O_5) and potassium oxide (K_2O) of 40 kg ha^{-1}. The urea treatment with 120 kg N ha^{-1} was split into two doses: 90 kg N, applied and incorporated at thinning and the last 30 kg applied and incorporated just after weeding, at 4 weeks after sowing. The organic matter treatments were applied on the surface and subsequently manually ploughed into the soil using shovels ten days before sowing of the crop. Experimental fields were kept free of all other weeds by hand-pulling weekly.

The perennial grass *Vetiveria nigrita* Benth. of low stature and thick undergrowth and of rapid establishment, was planted in between individual experimental units as a border plant. This served to limit striga seed contamination between neighbouring plots through either wind or water transport of seeds. The entire experimental field was fenced year around to prevent grazing animals from getting in.

Observations

The number of emerged striga was counted on all plots on a weekly basis till harvest. At sorghum maturity panicles were harvested and air-dried for 2 weeks, then threshed and grains were further dried at 70 °C for 48 hours to determine dry weight. Above-ground sorghum stover and all striga shoots were harvested at ground level, air-dried for two weeks and weighed on-the-spot. This biomass did not leave their respective plots to avoid loss of produced striga seeds.

Data analysis

Nitrogen release by the organic amendments was calculated with the model MiNiP (Janssen, 1984, 1996). We calculated the total amount of N released after 1 month and 3 months (Table 1). Model settings were: soil protection factor 1.0 (soils consist of 82% sand, 9% silt and 9% clay); dissimilation: assimilation ratio of the microbial biomass 2.0; C:N ratio of microbial biomass 10; constant temperature of 28°C; and no water limitation for decomposition. Apparent initial age for both amendments was set at 1.57 years.

The General Linear Model (GLM) analysis was used to regress field data of striga numbers and biomass, and sorghum grain and biomass yield on calculated N supplied from organic matter. A stepwise regression procedure was followed to obtain the best model fit. Values of infestation levels (maximum emerged striga plants per square metre) were log transformed to normalise data. Analyses were done using both GENSTAT 12th edition and SAS version 9.1 packages.

Results

Rainfall in the three years showed the normal within-season pattern, while totals were within the range that is observed in the area. However, the last cropping year was relatively dry (Fig. 1).

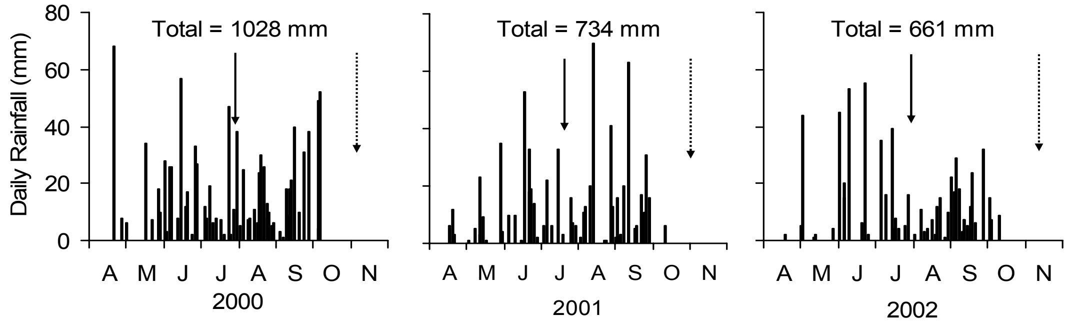

Fig. 1. Daily rainfall record (April to November) in Djallingo village (Garoua) during the three cropping seasons. Continuous arrows point to sowing dates, while discontinuous arrows point at harvest dates for sorghum grain.

N dose and sorghum performance

The GLM analysis showed that N dose, striga infection level, and the interaction N dose * striga infection level contributed significantly ($P<0.05$) to the explanation of variation in sorghum grain yield and biomass in all three cropping years (Table 2). In the first year (2000) N doses had a small effect on sorghum biomass and yield under low striga infection level, while at the higher striga infection level the linear effect of N dose on sorghum grain yield was larger (Fig. 2A). Sorghum biomass showed a non-linear response to N dose, both when striga infection level was low and when it was high (Fig. 2B). In the second (2001) and third (2002) cropping season the effect of N dose on yield was much larger and the relationship between grain yield and N dose was best described by a quadratic function (Table 2, Fig. 2C, 2E). In 2002, fallow and the N dose * fallow interaction were also significant ($P<0.05$) sources of variation in observed yields (Table 2). Sorghum biomass showed the same pattern in those years (Fig. 2D, 2F).

The picture for sorghum biomass in all three years is complicated as striga infestation severity (maximum striga count m^{-2}, strigaMax in Table 2) had an independent effect (Table 2, Fig. 3) from N dose, while it was itself also affected by N dose (Fig. 4). The level and to some extent the tilt of the reaction planes for sorghum biomass on the combination of N dose and striga infestation level were different when a field had a low infection level (Fig. 3A,C and E) or a high infection level (Fig. 3B, D and F). Treatment effects on grain yield in 2002 followed the same pattern as shown here for biomass (not shown). This effect of striga infestation level (strigaMax in Table 2) was in most cases accompanied by an independent effect of the striga infection level (striga in Table 2). Striga infection level significantly contributed to changes in grain yield and sorghum biomass (especially in 2000 and 2001) with lower yield at the high striga infection level (Table 2, Fig. 2). However, no differences in grain yield and sorghum biomass were found in the control (zero N applied) in 2002 between both infection levels while the effect of N dose on yield and biomass was much higher when striga infection level was low (Fig. 2E, 2F). In 2002, grain weight and sorghum biomass were dependent on the soil cover (crop or bare fallow) in the preceding two years. Plots that had been kept under bare fallow in 2000 and 2001 yielded more grain and biomass than plots under continuous cropping (Fig. 2E, 2F) at the lower N doses, while the effect of bare-fallow was reduced at the higher N doses, especially for grain yield. The harvest index for 2000 was lower (average of 0.08 ±0.01) compared to those for 2001 and 2002 (0.17 ±0.02 and 0.17 ±0.01 respectively). In the three cropping seasons, mean yields after addition of 120 kg inorganic N were not different under both striga infection levels. Addition of inorganic N in general had the same impact on sorghum as addition of the equivalent (calculated) amount of N through organic amendments with the exception of 2002 in the continuous-cropping plots (Table 2, significant contribution of N-source) when the production was lower with inorganic fertilisers (Fig. 2E, 2F).

The variances accounted for by the explanatory terms for grain yield and sorghum biomass were always above 75% and consistently lower for the harvest index (Table 2).

Table 2. Summary of the ANOVA table for the regressions of yield parameters (grain yield, sorghum above-ground biomass and harvest index) on applied nitrogen and the observed maximum striga count (strigaMAX). For each year and yield parameter all significant (P<0.05) terms are given with their corresponding F-value and the degrees of freedom (DF), while the percentage variance explained by the combined terms is also indicated. Blocks are only included when contributing to the explanation of variance. In 2002, fallowing is included as an explanatory term. N-linear and N-quadratic refer respectively to a linear and a quadratic relation to the N-dose applied, striga to the infection level treatment, and fallow to the management practice difference in 2000 and 2001, while N-source refers to the distinction between inorganic and organic N.

Year	Grain Yield			Above-ground biomass			Harvest Index		
	Source	DF	Variance ratio	Source	DF	Variance ratio	Source	DF	Variance ratio
2000	N-linear	1	27.0***	N-linear	1	26.5***			
	Block	4	26.6***	Block	4	16.2***	Block	4	22.1***
	striga	1	40.7***	striga	1	55.3***	striga	1	17.0***
	N-lin.* striga	1	5.4*	N-qaudratic	1	7.0*	N-lin.* striga	2	7.3***
				strigaMAX	1	7.0*			
	Variance explained: 76%			*Variance explained: 83%*			*Variance explained: 63%*		
2001	N-linear	1	87.6***	N-linear	1	199.7***	N-linear	1	29.2***
	N-qaudratic	1	31.8***	N-qaudratic	1	75.1***	N-qaud.*striga	2	8.8***
	Block	4	3.0*				Block	4	8.9***
	striga	1	66.8***	striga	1	53.8***	striga	1	6.1*
				strigaMAX	1	18.0***			
	Variance explained: 82%			*Variance explained: 91%*			*Variance explained: 59%*		
2002	N-lin	1	100***	N-linear	1	163***	N-linear	1	27.2***
	N-qaudratic	1	44.7***	N-qaudratic	1	84.2***	N-qaudratic	1	10.6**
	N-lin.* striga	1	17.0***	N-lin. * Striga	1	31.3***			
	Block	4	11.6***	Block	4	8.5***	Block	4	6.4***
	strigaMAX	1	20.1***	strigaMAX	1	95.1***	strigaMAX	1	21.8***
	N-lin.* Fallow	1	9.2**	N-lin.* Fallow	1	7.5**	N-lin.* Fallow	1	8.3**
	Fallow	1	29.6***	Fallow	1	63.5***	Fallow	1	5.1*
				N-source	1	7.0**			
	Variance explained: 76%			*Variance explained: 86%*			*Variance explained: 45%*		

Significance of F-value: *P<0.05; **P<0.01; ***P<0.001

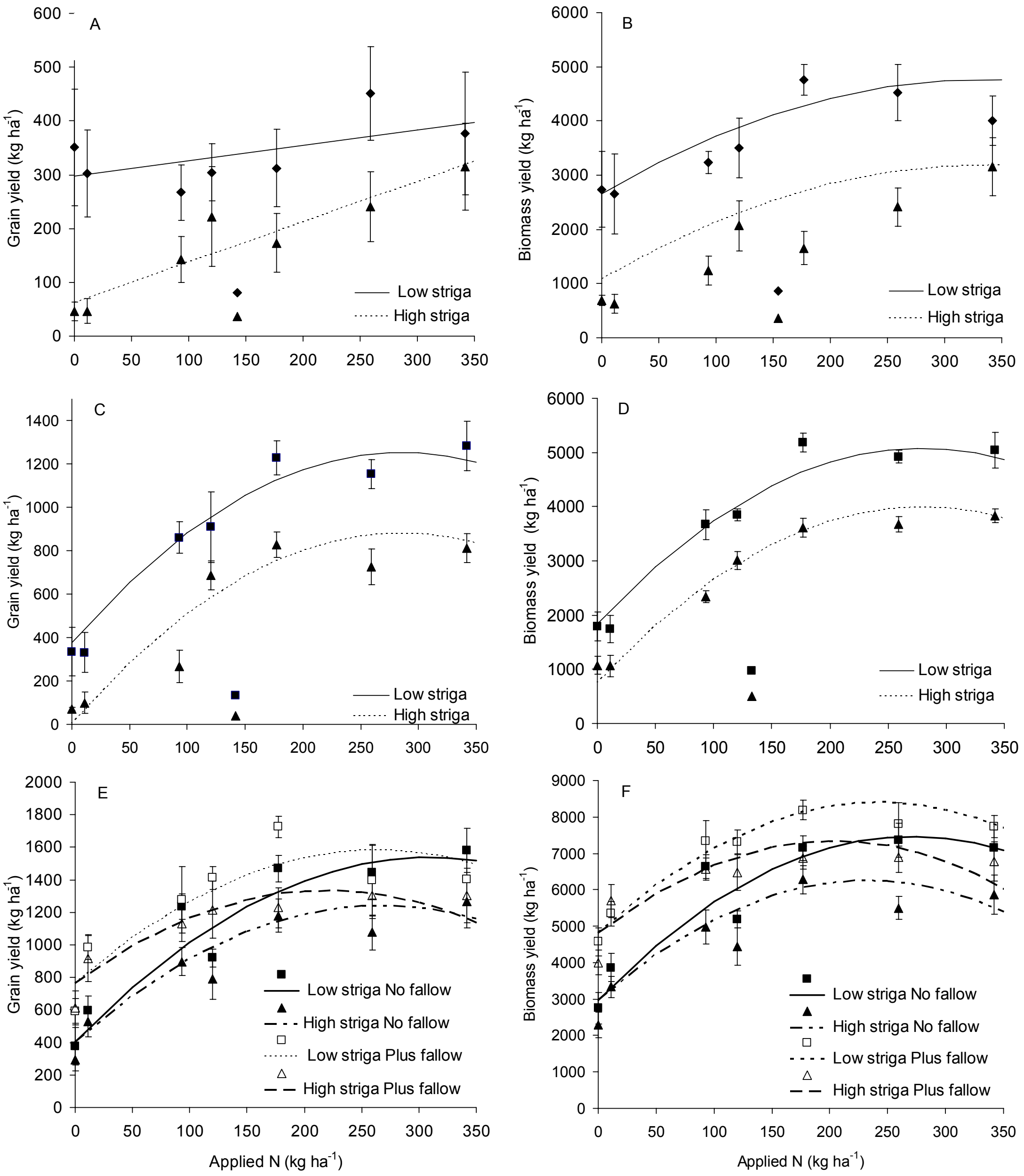

Fig. 2. Regression of sorghum yield response to N supply: in year 2000 for grain yield (A) and harvest biomass yield (B), year 2001 for grain yield (C) and biomass yield (D), year 2002 after continuous cropping (-Fallow) and bare fallow (+Fallow) for grain yield (E) and biomass yield (F). -striga and +striga refer respectively to inherent and artificially enhanced striga infection levels. The lines are model outcome estimates of yield or harvest index response to N supply (cf. Table 1), while data points are averages adjusted to theoretical maximum striga counts. Error bars are standard errors of means data points.

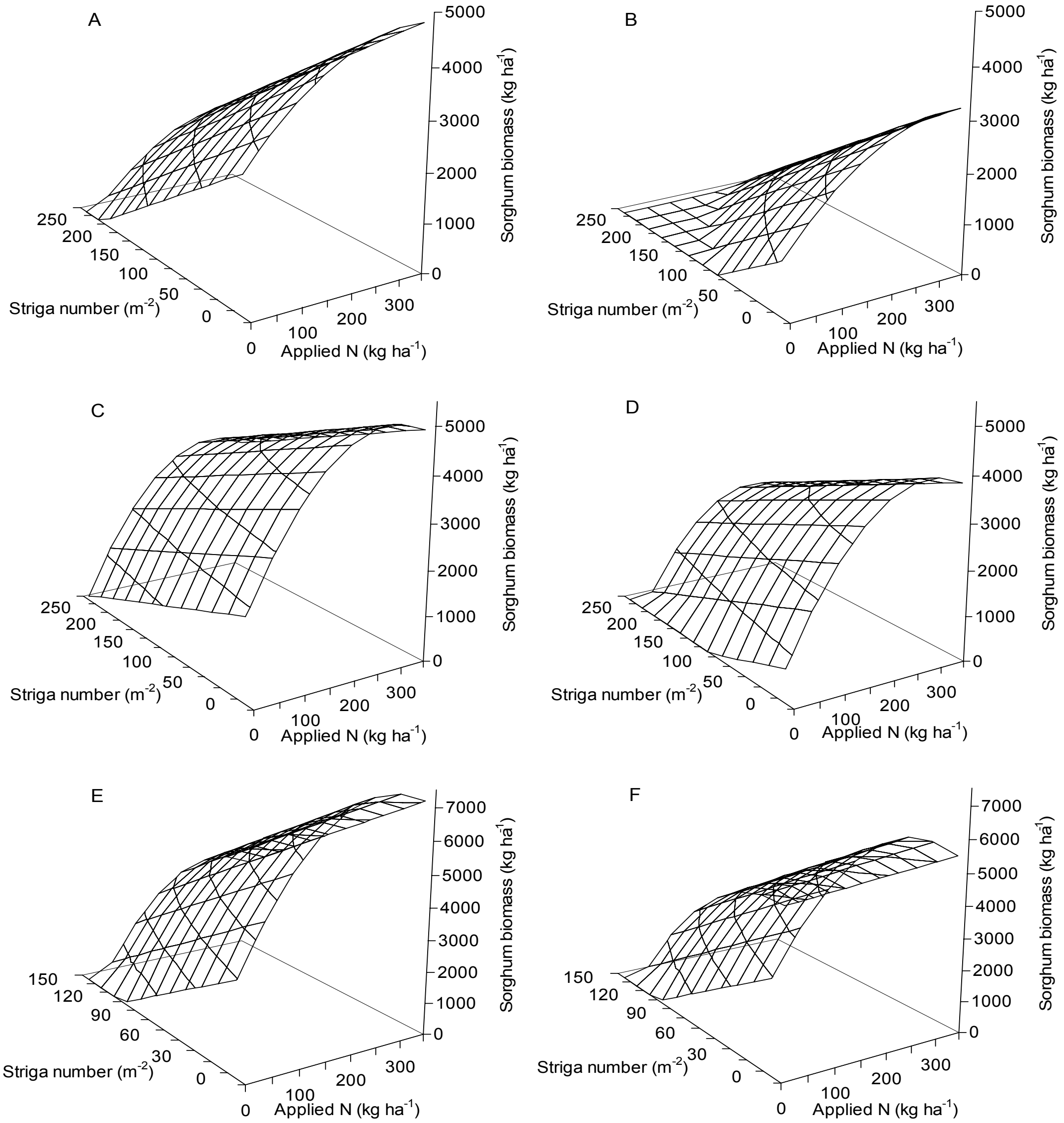

Fig. 3. Reaction surfaces of sorghum biomass (kg ha^{-1}) on applied nitrogen (kg ha^{-1}) and striga infestation levels (maximum number of plants.m^{-2}) for 2000 (A,B), 2001 (C,D) and 2002 (E,F) and for the low striga (A, C, E) and high striga (B, D, F) infection levels. The reaction plane may reach negative yields at very high striga levels, but the combination of very low N and very high striga does not co-occur in the field, hence planes have been truncated. There were no interactions between the effects of N dose and maximum striga counts on yield. For statistics of the regressions see Table 2.

N dose and striga performance

The striga infection treatment led to significantly higher numbers of striga emerged in the high-striga plots in all three years (Fig. 4). To assess the effect of the N released by the organic amendments, the released N after one month was used (Table 1). In 2000, N-dose did not affect the maximum number of emerged striga plants (Table 3). In 2001 and 2002, striga infection level alone accounted for respectively around 80% and 50 % of the overall percentage explained variance in maximum striga counts. In those two years the maximum number of emerged striga plants increased compared to the control level at low organic N doses (up to 38 kg N ha^{-1} released within one month after sowing), especially at the higher striga infection level and decreased thereafter (Fig. 4B and C). This effect was most pronounced under continuous cropping in 2002 (Fig. 4C). Without organic amendments (control treatment) maximum striga counts were lower than for the first two N doses. Under bare fallow, the change in slope for effect of N dose on maximum striga count was steeper for the high-striga plots compared to the low-striga plots. The striga numbers also differed according to N source in 2002 (Table 3).

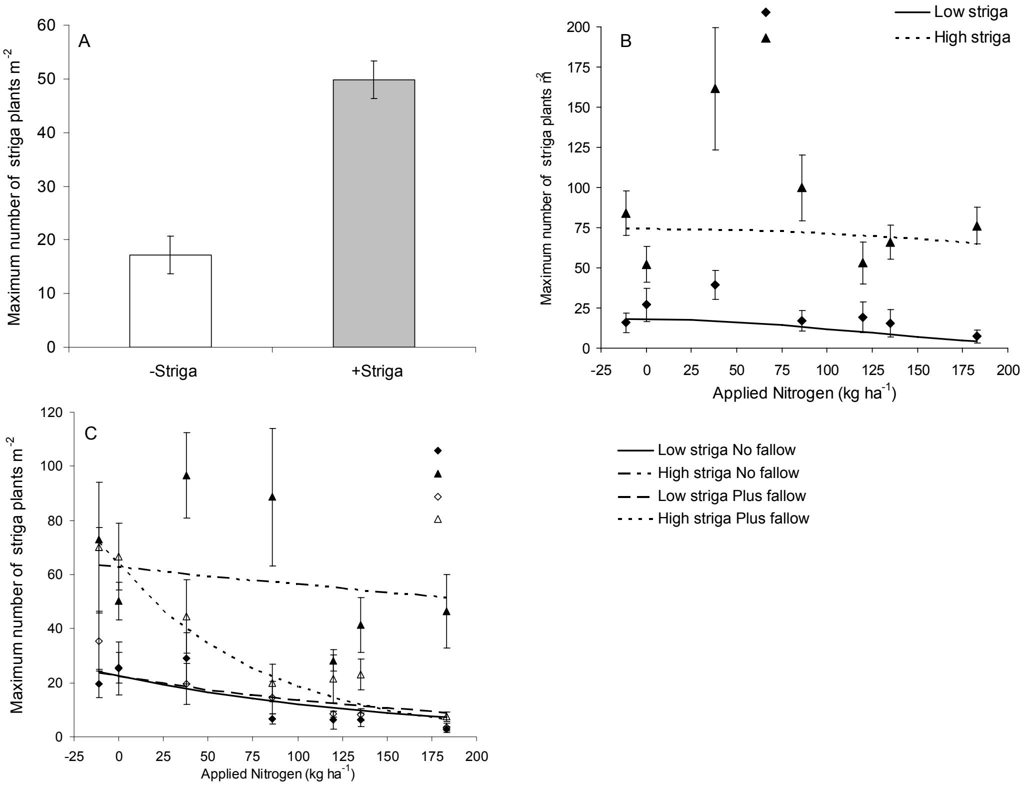

Fig. 4. The maximum number of striga plants m^{-2}. For 2000 (A) the only significant treatment effect was observed for the striga infection treatment (enhanced (high striga) and inherent (low striga) infection levels). In 2001 (B), maximum striga numbers were correlated with applied N and lines differed between high striga and low striga infections. In 2002 (C) The correlation between maximum striga numbers and applied N showed an interaction with striga infection levels and fallow practice (sorghum following either two years bare-natural fallow (plus fallow) or two years continuous sorghum cropping (no fallow)). Lines are based on back-transformed data from calculated regression coefficients of log-transformed actual striga counts on applied nitrogen, while data points presented are averages of actual striga counts. Error bars are standard errors of mean values.

Table 3. ANOVA table for significant explanatory terms (P<0.05) when maximum striga counts (A) or when striga biomass for 2001 and 2002 combined (B) were regressed on applied nitrogen. In 2000 only striga infection as an explanatory variable is significant, so only this ANOVA is presented. For an explanation of the terms see the caption of Table 2.

A

Cropping year	Explanatory term	Degrees of Freedom	Variance ratio	% variance explained
2000	Striga	1	43.6***	33.0
2001	Block	4	3.3*	58.5
	Striga	1	81.2***	
	N-quadratic	1	5.2*	
	N-quadratic* striga	1	4.8*	
2002	Block	4	4.4**	62.9
	Striga	1	111.***	
	N-linear	1	69.2***	
	N-source	1	14.0***	
	N-linear *Fallow	1	8.9**	
	N-linear*Fallow*striga	2	12.4***	

B

Cropping year	Explanatory term	Degrees of Freedom	F Value	% variance explained
2001 & 2002 combined	N-linear	1	39.4***	61.5
	Striga	1	90.8***	
	N-linear*Fallow	1	18.1***	
	Cropping year	1	22.3***	
	N-linear*Cropping year	1	10.2**	
	N-source	1	25.5***	
	Block	4	5.1**	
	N-source*Cropping year	1	6.2*	

Significance of ANOVA: *P<0.05; **P<0.01; ***P<0.001

The released N from organic matter after three months was the major source of variation for striga biomass, observed only in 2001 and 2002 (Table 3B, Fig. 5). Striga infection level, N source, cropping year and the interaction between N dose and fallowing were also significant sources of variation (Table 3B). Total variance explained in the regression was 60%. Striga biomass linearly decreased with increasing N dose. Addition of inorganic N fertiliser reduced striga biomass more than an equivalent amount of N that was released during decomposition of organic resources (Fig. 5). Striga biomass was higher in 2002 than in 2001 (Fig. 5B). Striga biomass was also higher in fields that were artificially infected (Fig. 5C, Table 3B) and in 2002 in fields under continuous cropping (Fig. 5A). The slope of the relation between striga biomass and N dose under bare fallow was steeper than that for continuous cropping in 2002 (Fig. 5A). There is a trend that striga biomass, like striga numbers, initially increases with N dose up till 100 kg N before falling (Fig. 5). This trend is more pronounced at higher striga infection level and under continuous cropping.

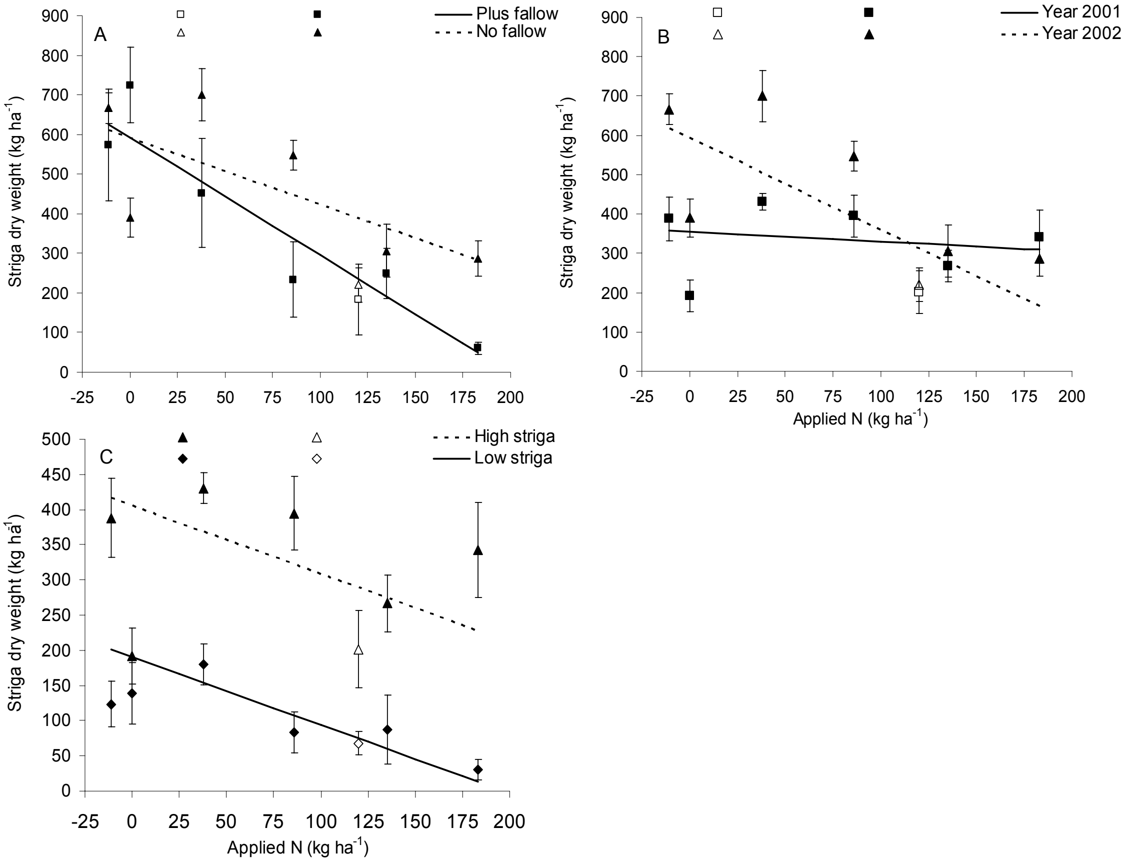

Fig. 5. Regression of striga biomass on amount of N applied: with (+fallow) or without bare-fallowing (-fallow) (Fig. A), compared between cropping seasons 2001 and 2002 (Fig. B) and under artificially enhanced striga (+striga) and inherent striga (-striga) infection (Fig. C). Lines are based on regression model coefficient estimates, while data points presented are averages of actual striga biomass for Fig. A,B & C. Open markers are for inorganic N as against closed ones for organic N. Error bars are standard errors of mean values.

Discussion

Modelling nitrogen release through MiNiP

In our parameter settings we used the same apparent initial age (1.57 years) for both organic amendments. We have been unable to find literature data for cotton seed cake (CSC) or cotton milling waste (CMW). Janssen (1996) listed organic amendments in three classes, and mentioned among examples of his class 1 amendment (with an apparent initial age less than 1.6) digestive leaves, young roots and rice straw, so material with a substantial variation in C:N ratio. While in general litter quality and apparent initial age are correlated, we think that our approach of assuming the same apparent initial age for CSC and CMW has two advantages. First, by assuming the same age, the substrates (and their mixtures in different ratios) all decay at the same rate, which results in N-mineralisation rates that are additive. While there has been debate about litter interactions, the current consensus, based on meta-analysis, is that positive and negative litter interaction effects on decomposition cancel each other out (Srivastava *et al.*, 2009). Second, by choosing this conservative approach, we could already demonstrate the robustness of this simple model in predicting aspects of sorghum and striga performance. More complex models (by co-varying initial apparent age with litter C:N ratios) in the absence of hard data would introduce the risk of curve fitting.

For correlations with N mineralisation we used cumulative N-mineralisation after one month for striga numbers, and cumulative N-mineralisation after three months for striga biomass and sorghum biomass. Striga numbers are primarily determined by germination and attachment that occur the first 4-6 weeks after sowing of the sorghum host, while striga biomass is determined by the crop – parasite interaction over the full sorghum cycle of three months.

Impact of organic amendments on sorghum yield

The effect of application of cotton by-products on yield was well described by the amount of N mineralised during the first three months after application. Although the standard error of the yields observed at any of the doses of applied N is large (Fig. 2), we suggest that this variation is likely due to inherent differences in soil fertility and striga seed densities at the start of the experiment, not all of which was captured by the use of the randomized blocks. Possibly (but to a lesser extent) inaccuracies in the spatial application of organic resources in the different plots may also have resulted in variability.

The additive effect of substrates of high and low quality in different ratios supports that the effects of organic matter amendments, in at least the first three years of their use, can be largely understood through their effects on N dynamics. Support for this conclusion is gained by the observation that the effect of 120 kg N as inorganic fertiliser on sorghum grain and biomass yield was not different from what would be predicted from an equivalent amount of organic N (except for sorghum yield and biomass in 2002 on the continuous-cropping plots) (Fig. 2). Also the fact that the control (zero organic matter application, versus six ton in all organic amendment treatments) fits well in the regression models for sorghum performance (Fig. 2) indicates that the carbon contribution to the soil through organic matter application did not have additional effects on the sorghum production system over the study period. The observed lower effect of the equivalent amount of inorganic N in the continuous-cropping plots in 2002 could be interpreted as an indication that in these highly degraded, continuously-cropped plots, fertiliser response is limited by organic matter levels (Vanlauwe *et al.,* 2010). However, for a full analysis of the cause of any such longer-term effects the current study does not provide the proper database.

The increase in sorghum grain and biomass yield obtained after a two-year bare fallow compared with continuous cropping confirmed the role of fallowing in natural soil fertility recovery (Tian *et al.*, 2005; Ouattara *et al.*, 2006). The observation that the difference between fallow and continuous cropping depended on the amount of applied N during the three years (Fig. 2 E&F), as the response curves of yield on N-dose approach each other towards the higher N-doses, is an indication that also the effect of bare fallow was mainly through its effect on fertility. It has to be noted here that during the fallow period the same organic amendments were applied on the different plots as in their corresponding planted equivalents.

The harvest index in 2000 was lower than that in 2001 and 2002. Although at first sight this increase in harvest index could be interpreted as a first sign of agro-ecosystem recovery due to organic matter addition, especially with CK-60B, a cultivar that is highly sensitive to striga, this does not seem probable upon further analyses. Alternatively, external factors, unrelated to soil fertility and striga management could have been responsible for this effect. In 2000 granivorous birds (*Quelea quelea*) attacked the field during the milking stage. Bird scaring was applied during grain filling in 2001 and 2002. In other words the increase in harvest index is spurious and serves as a caution against optimism that short-term additions of organic matter could result in visible yield effects. Also because the increase in harvest index was equally true for all treatments, including the control where no organic amendments were applied, the ecosystem recovery hypothesis does not seem appropriate.

Impact of organic amendments on striga

The effect of organic matter amendments on striga numbers and biomass increased over the study period with no effects in 2000 against an overall increasing positive effect in 2001 and 2002 as quality of the applied organic matter improved (Fig. 4). However, contrary to sorghum yield, when inorganic fertiliser was applied at the same dose of N as that of organic amendments it had a more negative impact on striga biomass (Fig. 5). Given the pronounced effect of the treatments on striga numbers it seems this larger effect is partly related to the lower striga density. Ikie *et al*. (2007) found that urea significantly lowered striga emergence in the field, compared to an equivalent N dose of poultry manure. However, because in our study the inorganic N was only applied at a single rate (120 kg N ha^{-1}) no full comparison can be made between organic and inorganic N applications and the slope of the regression on inorganic N application cannot be established.

Mineral N could affect the interaction between sorghum and striga both through a reduced striga germination (Ayongwa *et al*., 2006) and a strengthening of the sorghum plants leading to reduced yield losses due to striga. If low-quality organic matter was added (resulting in net immobilisation of N during the first month), striga abundance and biomass were enhanced, suggesting that natural seed decay was unimportant. This conclusion is supported by the accompanying study that established the enhanced seed decay only occurred later in the season after the sorghum crop had been infested (Ayongwa *et al*., submitted Chapter 3).

This does not imply that there could be no role of organic matter of low quality in enhancing natural seed demise. However, even when the low-quality material was added during a bare fallow for two years, the striga numbers did not decrease compared to the control at either of the two infection levels (Fig. 4C), so any enhanced seed demise leading to also reduced striga infestation would require much longer study periods and possibly also longer application periods. This phenomenon could be partly due to density dependence in the emergence as observed for striga (Rodenburg *et al*., 2006a; Van Ast, 2006; Van Mourik *et al.*, 2008). In order to investigate long-term prospects of natural seed demise through addition of low-quality organic matter, it is imperative to prevent striga from seed setting in the next generation. This was done in the low striga treatment, yet in the control without organic amendments striga numbers were not reduced in the three years of this study (data not shown). From this we conclude that reducing the seedbank through weeding prior to seed set alone is not a short-term solution. Our conclusion confirms earlier published studies reporting that weeding striga before seed set reduced seed banks in the soil by 48 %, only after four seasons of implementation (Ransom, 2000; Oswald, 2005). Combining this reduction with the mentioned density dependence implies even longer periods before reductions in striga infestation can be expected.

The organic matter amendments that released moderate quantities of N do seem to have increased the carrying capacity of the sorghum (cf. Rodenburg *et al*., 2006a) to the extent that more striga biomass was produced (Fig. 5B and 5C) which may then also lead to higher seed-bank replenishments (Van Mourik, 2007). Rodenburg *et al.* (2006b) and Van Mourik (2007) reported that seed capsule numbers and striga seed production were linearly correlated with above-ground striga biomass which allows for an easy assessment of the effect of treatments on striga seed-bank replenishment. At the high striga infection level, where seed setting was not avoided, this could have been an additional cause for the initial enhanced striga infestation levels. The significantly lower striga counts observed under the zero fertiliser treatment compared to organic amendments that released a calculated amount of N below 38 kg ha^{-1} during the first month may also suggest that suboptimal N rates through organic forms are counterproductive in striga management.

It may be, though, that not the quantity but the rate of release of the nitrogen is essential for a positive effect on the sorghum-striga system. Work by Verkleij *et al.* (1994) and Kim & Adetimirin (1997) also indicated that the timing of inorganic N application is more important than total amount applied. Early release, even of small quantities of N could potentially avoid high loads of attached striga parasites through their effect on the sorghum root N status observed as under laboratory conditions (Ayongwa *et al.*, 2006). Before any recommendations along these lines are made further field validation of this potential effect would need to be made.

Finally the study shows that, under continuous cropping and with moderate striga infections, reduction in *Striga* infestation and biomass can be achieved with high nitrogen rates of 120 kg N ha^{-1} or above but this will take several years (Fig. 4B & 4C). At high striga infection rates more time or nitrogen is probably needed. Whether a complementary striga control method such as hand-pulling or intercropping must be envisaged to reduce the striga infection and ensuing infestation levels quicker remains to be established and will also depend on the consequences for the accompanying yields and thus economics. For such highly infected plots it can be expected that a non-host crop to which organic amendments are applied would combine suicidal germination with enhanced seed decay and thus be more effective (Ikie *et al.*, 2007; Van Mourik, 2007).

Impact of striga on yield

In 2000 and 2001 grain yield was not directly related to observed striga numbers, however for sorghum biomass during all years (and for grain yield in the third year), the yield was lower when there was a higher striga infestation (Table 2, Fig. 3). Van Ast (2006) observed a proportional 4.3% increase in yield reduction per emerged striga plant in a pot experiment. However, estimating quantities in this relationship under field conditions is very far from resolved. The striga density-dependence (Thalouarn & Fer, 1993; Rodenburg *et al.*, 2006a; Van Ast, 2006; Van Mourik *et al.*, 2008) makes it difficult to quantify the relationship between yield and striga infestation. Finally, because even a tiny number of striga plants may cause a disproportionate fall in host yield, striga counts are unreliable as indicator for yield reduction in the field (Graves *et al.*, 1989; Gurney *et al.*, 1999). Also our results show that under field conditions not all yield reduction in plots that differ in striga infestation levels can be attributed to striga numbers alone (Table 2, Fig. 3), and that the relation depends also partly on striga infection level of the plot, itself another indication of strong density dependence of emergence success of striga (cf. Van Mourik , 2007).

The triangular relation between Sorghum, Striga and applied N

The reaction planes for yield (kg ha^{-1}) to the combination of N-dose (kg ha^{-1}) and striga infestation levels (maximum number of plants m^{-2}) at the two levels of striga infection indicate that at the same N-dose the yield is lower when there are more striga plants emerging (Fig. 3). The regression of maximum striga numbers on N-dose (Fig. 4A and 4B) furthermore indicates that the yield effect of organic amendments is greater when initial infection levels are lower, because at higher N-doses the maximum striga counts are lower. The inverse is true, though, at higher initial infection levels. In other words at lower striga infection levels, yield not only moves up the nutrition slope but also up the lower striga counts slope (Fig. 3), and these effects occur simultaneously. At high initial infection levels, though, as the yield would move up the N nutrition slope it moves down the striga density slope due to the initially increasing striga numbers as N nutrition improves.

We propose this interaction has been the cause for the contradictory statements in the literature on effects of improving soil fertility in striga-infected fields. Thus, Smaling *et al.* (1991), Kamara *et al.* (2007) and Vanlauwe *et al.* (2008) found that fertiliser application did not significantly affect striga infestations, while Ikie *et al.* (2007) stated that poultry manure rather gave a higher striga emergence compared to zero fertiliser applied, although also a higher sorghum yield. Sauerborn *et al.* (2003) reported that striga infestation was negatively related to total nitrogen content of the soil, while Ahonsi *et al.* (2002) reported that N application could increase or decrease striga severity depending on whether the soil was pasteurised or not. Our data and analyses suggest the initial striga infection level in the soil and the initial fertility level determine where fields could be located on the reaction planes in Fig. 3, and so which effects may be expected.

Because timing of N supply from the organic amendments is central in boosting sorghum yield (throughout sorghum growth) and in depressing striga (at the start of sorghum growth), timing of N release during decomposition is very important. With amendments of low quality, N mineralisation will be delayed to the final period of the three months. This delay (and initial N immobilisation) means N deficiency during early host growth and consequent higher striga germination stimulant production (Ayongwa *et al.*, 2006). The later N release may then in turn enhance sorghum growth of already striga infested plants leading to higher striga biomass.

Implications for management

From the perspective of yield increases on striga-infected fields, organic matter amendments alone may not be very practicable under the conditions that resource-poor farmers face, because of the high quantities of high-quality organic matter that is required (cf. Sauerborn *et al.*, 2003). Organic manure from animals is also very scarce, because of the other uses for it, and because of the amount of land needed to produce reasonable amounts for a hectare of cropped land (De Ridder *et al.*, 2004). Natural fallows have become less available, due to the pressure on land (Stringer *et al.*, 2007; Dugje *et al.*, 2008; Ayongwa *et al.*, 2010) and the prevailing tenure rules that force farmers to still pay for the rented land even when it is fallowed (Teyssier, 2004; Koulandi, 2006). Both factors rather stimulate cereal mono-cropping without soil fertility replenishment, thereby exacerbating the striga problem.

Inorganic fertilisers also result in sorghum yield increases and may be more effective in reducing striga numbers than organic manure (Ikie *et al.*, 2007). However, accessibility of nitrogen-containing mineral fertilisers is limited, and the situation in the study area has worsened after the collapse of the cotton sector (Kossoumna Liba'a & Havard, 2006; Mbétid-Bessane *et al.,* 2006; Ayongwa *et al.*, 2010). Recent work with micro-doses of fertiliser in comparable deprived farming systems elsewhere on the Sahel (Tabo *et al.*, 2006) may indicate, though, there is a potential for introduction of small applications of fertiliser directly in the planting hole. This would indeed affect early-season plant nutrient status and thus the sorghum-striga relation.

Where only small quantities of organic matter are available of relatively poor quality it must be clear that applying these on heavily infected fields without the addition of inorganic N sources should not be recommended. In addition alternative low-input systems may be needed. Work in northern Cameroon (Naudin *et al.*, 2005) with life mulch of the grass *Brachiaria ruziziensis* Germain & Everard, whose root system makes up to a third of its total biomass and which has shown to be suppressive to striga, has high potentials for field management of this parasite. *B. ruziziensis* is presently extended to farmers as forage for animals.

Conclusion

In reference to the hypotheses put forward in the introduction the following can be concluded for the current study:

- The effect of organic amendments from different quality on both sorghum grain yield and biomass production and on striga infestation differences can be well predicted from estimates of N mineralisation after respectively three and one month.
- The consequence is that organic amendments may both have a positive effect on striga emergence or a depressing effect on striga emergence dependent of the N release profile of the organic amendment and on the striga infection level of the soil.
- Fallowing for two years does have a minor positive effect on both yields and striga

infestation levels when not accompanied by soil fertility enhancing methods.

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CHAPTER 5

Root nitrogen concentration of sorghum above 2% produces least *Striga hermonthica* seed stimulation*

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Abstract

A series of pot and laboratory experiments was carried out to assess the effects of N status of sorghum roots and timing of N application (as NH_4NO_3) on the germination of *Striga hermonthica (*striga) seeds. Root N concentrations varied from 10 mg N/gram to 26 mg N/gram.

The cut root and the root exudates technique used in assaying striga seed germination gave similar results. However, the cut root technique was easier to handle and more discriminating at low germination levels.

Striga seed germination per unit sorghum root mass followed a broken stick model. It decreased with increasing root N concentrations, reaching lowest levels at a root N concentration of 19.5 mg N/gram, after which no further reduction occurred. It was not possible to reduce striga seed germination to a zero level.

Timing of N application influenced the time a higher N concentration is reached, not the striga seed germination. Both timing and rate of N application are important in maintaining root N concentrations above 19.5 mg N/gram, thereby potentially reducing striga germination in the field. Translation of results to reductions in infection levels and yield losses is hampered by density dependent relations after the striga germination stage.

Key words: Bio-assay, cut root technique, germination stimulants, root exudates.

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Introduction

Species of the genus *Striga* (Orobanchaceae), also known as witch weed, are obligate root hemi-parasites of flowering plants. They pose a serious constraint to cereal and legume crop production in the drier savannas of Africa (Sauerborn, 1991a). *Striga hermonthica* (Del.) Benth. (hereafter striga) is the most important species of the genus that parasitises cereals and some natural grasses in most of Africa (Parkinson *et al*., 1991; Kim & Adetimirin, 1997; Ayongwa & Ngawa, 1999). The obligate nature of striga means that it can only complete its life cycle in the presence of its host plant, although it is partly independent of its host's carbon for survival. Before a striga seed germinates it must pass through a period of preconditioning and then has to be stimulated by specific chemicals. These specific chemicals have been identified as sesquiterpene strigolactones and the biosynthetic pathway has been elucidated by Matusova *et al.* (2005) as carotenoid-derived. Strigolactones are also signal molecules that induce the formation of a branched hyphal network in germinating mycorrhizal fungal spores (Akiyama *et al.,* 2005). This double role of strigolactones suggests that the plant's nutritional status is involved in both plant – fungus signalling and in affecting the amounts or activity of striga germination stimulants.

The germination stage in the development of striga therefore represents a distinct and critical point at which control methods may be targeted. Reduction in amounts or activity of germination stimulants produced by cereals host plants could provide means to reduce numbers of seeds germinating at a particular point in time and space. Low stimulant production by cereal roots has been shown to be a mechanism of host plant resistance/tolerance to striga infections (Weerasuriya *et al*., 1993; Heller & Wegmann, 2000). The link between the plant's nutritional status and striga tolerance / resistance suggests that fertiliser applications could reduce striga. Various forms of nitrogen fertiliser can suppress striga either by direct contact with the parasite's seeds inhibiting its germination or indirectly by inducing host plants to exude lower amounts of germination stimulants (Sauerborn, 1991b; Igbinnosa *et al*., 1996; Kroschel, 1998). Cechin & Press (1993b) found that a concentration of ammonium nitrate of 3 mM in the growth medium significantly reduced striga germination rates and attachment to its sorghum host, compared to 1 and 0 mM. They concluded that ammonium nitrate reduced the production of stimulatory compounds or their specific leakage from host roots. Similarly, Adetimirin & Kim (1999) and Mumera & Below (1993) found that both nitrogen rate and timing of nitrogen fertiliser application were critical in suppressing striga in the field. The timing of N application was found to be more important in suppressing striga emergence and host plant damage than N application rate (Verkleij *et al*., 1994) and total amount of N applied (Kim & Adetimirin, 1997). In a bioassay Sherif & Parker (1988) observed that inorganic nitrogen fertilisation reduced striga germination stimulation through sorghum root exudates by about half compared to stimulation by sorghum roots of unfertilised plants, while chicken manure, another nitrogen source, did not. Kroschel (1998) reported that a well-nourished sorghum plant using various nitrogen sources induced fewer striga seeds to germinate than nitrogen starved plant treated with water only.

These findings of the indirect suppressive effect of nitrogen fertiliser treatment via host root exudates suggest that host plant tissue nitrogen concentration or some plant physiological mechanism linked with different levels of nitrogen nutrition are at the origin of the reduced striga seed germination. This does indeed link well with the role the involved chemicals seem to play in enhancing mycorrhizal symbiosis (Matusova *et al*., 2005; Akiyama *et al*., 2005). However, a quantification of the N concentration effect has not yet been provided. A slightly different hypothesis was postulated by Ahonsi *et al.* (2002) following their finding that N application suppressed striga under normal soil conditions, but that N application enhanced striga infestation levels in maize when the soil was pasteurised, a result they also found in a second study (Ahonsi *et al*., 2004). They postulated that the effect of the N application may therefore also have been through an enhanced activity of soil biota that enhances soil suppressiveness to striga. It would therefore seem relevant to study the relation between striga germination and plant nutrition by analysing the actual nutritional status, so N in the root tissue, rather than the N application.

If a well-nourished plant produces fewer stimulants as suggested by Kroschel (1998), it implies that there must be some time lapse or adaptation period between the poorly nourished state and the well-nourished state, before onset of reduced stimulant production. Assessing the significance of this time delay should provide more insight in the interaction between time of N fertiliser application and N application rates or total amounts of N applied in suppressing striga emergence.

The hypotheses under investigation were:

(1) The number of striga seeds germinating per unit root mass decrease from N-starved sorghum plants (i.e. with minimum N concentration) reaching lowest levels in plants with a certain maximum nitrogen concentration.

(2) The time of N application leads to differences in N-concentration and through that to differences in numbers of striga seeds germinating.

Material and Methods

Experimental conditions

Three experiments were carried out under screen-house and laboratory conditions at the International Institute of Tropical Agriculture (IITA) Ibadan – Nigeria, between January and May in 2000, 2001 and 2002. The IITA campus Ibadan (7°30'N, 3°54'E) has a monthly temperature range of 21.3 °C to 31.2 °C and a mean annual rainfall of 1282 mm distributed in a bimodal regime, with a dry season from November to March (Moormann *et al*., 1985).

Experiment 1 was used to test the two bioassay methods for striga seed stimulation and was carried out in 2000. Hypothesis one was tested with the same experiment 1 and with experiment 2 carried out in 2001. The second hypothesis was tested through experiments 2 and 3 (the latter carried out in 2002). Essentially, the experiments were carried out using the same methods. The only difference was in the timing and amount of applied fertiliser, and in experiment 1 in the way the bioassay was carried out.

Striga seeds used for these experiments were obtained from Bida in the Niger State (northern Nigeria) and were harvested at the end of the cropping season of 1999, 2000 and 2001 for use respectively in the experiments in 2000, 2001 and 2002. Striga seeds used for the germination assays were first of all preconditioned following the procedure described by Berner *et al*. (1997).

Sorghum (*Sorghum bicolor*) variety CK-60B, which is highly striga susceptible, was used. Sorghum seeds were sown in pots of 17 cm diameter filled with fine sand. The nutrient status of the sand used in the experiments is shown in Table 1. The plants were later thinned to 7 plants per pot. At least 5 replicates of pots of 7 plants each per N fertiliser treatment were made and these pots were then displayed in a completely randomised design in the screen-house. A basal rate of P & K was supplied using 820mg KH_2PO_4 per kg sand to ensure adequate plant nutrition except for N.

Table 2 and 3 indicate the treatments of the various experiments. All N was added as ammonium nitrate (NH_4NO_3).

The N treatments of experiment 1 and 2 were split into three applications, one before sowing, one at 6 and one at 12 days after sowing. This was done to ensure the maximum possible N uptake whilst reducing incidence of possible N toxicity by higher doses. In experiment 2 the sand was washed as a deliberate act to further impoverish the soil, in order to widen the range for the expected root N concentrations for the different N fertiliser treatments. All pots were maintained at field capacity by daily watering.

Table 1. Nutrient status of sand used for all experiments.

Experiment number	pH	% Org C	% N	P (mg/kg)*
1 & 2	4.3	0.14	0.03	4.5
2 Washed Sand	6.0	0.08	0.007	1.9
3	6.0	0.33	0.026	2.6

* P-Bray I

Table 2. Nitrogen fertiliser treatments in experiments 1 and 2.

Levels of N fertiliser	Experiment 1 N rates (mg/kg)	Experiment 2 N rates (mg/kg)
1	0	Washed sand
2	60	0
3	120	15
4	240	30
5	360	60
6	-	120
7	-	240

Table 3. Nitrogen fertiliser treatments in experiment 3. DAS: days after sowing of sorghum.

Number of Treatment	Treatment regime
1	No N at sowing (Control)
2	15 mg N at sowing
3	15 mg N at sowing + 100 mg N at 7 DAS
4	15 mg N at sowing + 100 mg N at 10 DAS
5	15 mg N at sowing + 100 mg N at 13 DAS
6	15 mg N at sowing + 100 mg N at 16 DAS
7	15 mg N at sowing + 100 mg N at 19 DAS
8	100 mg N at sowing
9	0 mg N at sowing +100 mg N at 7 DAS
10	0 mg N at sowing +100 mg N at 10 DAS
11	0 mg N at sowing +100 mg N at 13 DAS
12	0 mg N at sowing +100 mg N at 16 DAS
13	0 mg N r at sowing +100 mg N at 19 DAS

Germination test

Experiment one was also aimed at testing two bioassay methods for striga seed germination. Plants were subjected to the cut root and root exudates techniques 21 days after sowing. The cut root and root exudates techniques were adopted respectively from Berner *et al*. (1997) and Kroschel (2001). All pots were assembled and ten plants were randomly selected from the pots from which roots were carefully washed free of the soil/sand particles for use in the root exudates technique. The remaining plant roots were similarly washed free of soil/sand particles and used for the cut root method.

Clean striga seeds of tested viability/germinability were used for the cut root and root exudates assays. Assessment of germination intensity in the laboratory was done under a dissecting microscope by counting the number of preconditioned striga seeds germinating 2 days after receiving stimuli from either equal mass of fresh cut roots (cut-root technique) or 3000 µL of root exudates (root-exudates technique). A seed was scored as germinated if the root tip (radicle) protruded through the seed coat. The number of germinating seeds was then expressed as a percentage of the total number that received the germination stimulant per disc, per radial position and per Petri dish. The percentage striga seed germination was then compared and expressed relative to the positive and the negative controls, respectively 300 µL of GR-24 (10 mg L^{-1} solution), a synthetic germination stimulant; and 300 µL of de-ionised water as a blank.

Each treatment was made up of five Petri dishes (each a replicate) each made up of 4 radial positions of 4 to 5 punched glass-fibre discs (internal replicates) (Fig. 1).

Statistical analysis

A simple linear correlation analysis was used to study the correlation between the assay techniques. Percentage of germinated striga seeds was averaged per Petri dish, making 5 replicates per treatment. The original data without any transformation were used for

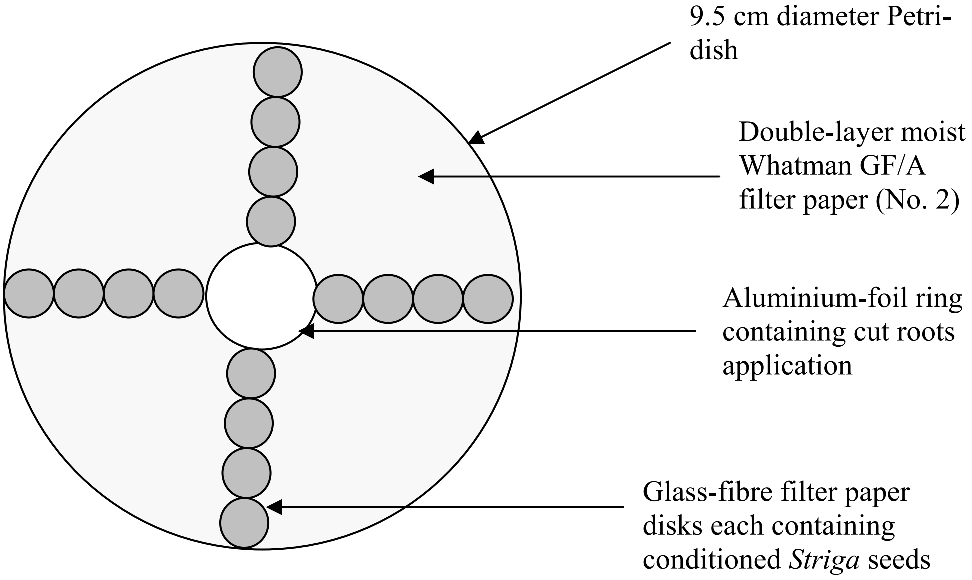

Fig.1. Schematic view of Petri dish set-up for assessment of striga seed response to applied germination stimuli.

analysis. The germination data were fitted to a nonlinear model with a cut-off point at the X-axis (a so-called broken-stick model). The SAS package (Release 8, Cary NC, USA) was used to fit the model and test model parameters.

Results

Comparison of germination techniques

A comparison of striga seed germination obtained from the root exudates technique and from the cut root technique showed a strong positive correlation between both methods ($r=0.778$; $n=50$; $P<0.001$; Fig. 2). Considering the good fit between both methods, we will report only the results of the cut root technique. A slight deviation from linearity could be observed at low seed germination. The cut root technique was more sensitive in conditions of low seed germination. At levels where the root exudates method yielded germination percentages close to zero, the cut root technique still showed substantial variation in germination (Fig. 2).

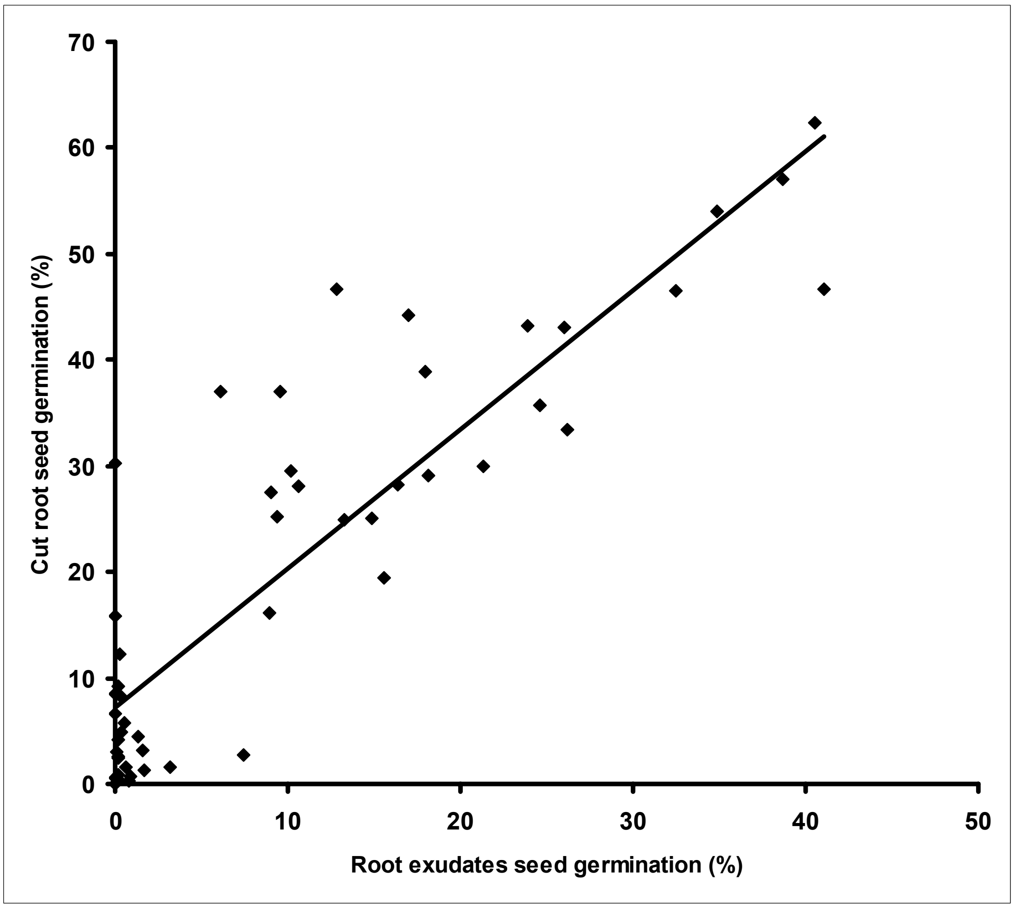

Fig. 2. Correlation between striga seed germination counts obtained with the cut root technique and root exudates technique. The correlation coefficient for the indicated regression line is 0.778.

Root N concentration and striga germination

The three experiments provided highly consistent results (Fig. 3). A nonlinear model (broken stick model) gave the best fit and accounted for 94% of the variation. No root N concentrations lower than 10 mg N/gram were noted. Increasing root N concentrations decreased striga seed germination, till levels of 19.5 mg N/gram, after which no further reduction was observed. At the critical level there was still some striga seed germination, although it was less than 5%. The level at which striga germination flattened off was significantly lower in experiment 3 than in experiments 1 and 2. Parameter estimates (means, standard error, and confidence limits) for critical root N concentration, slope, and germination above the critical root N concentration are given in Table 4. The reduction in striga seed stimulation achieved for experiment 1, 2 and 3 was respectively, 96, 93 and 99%.

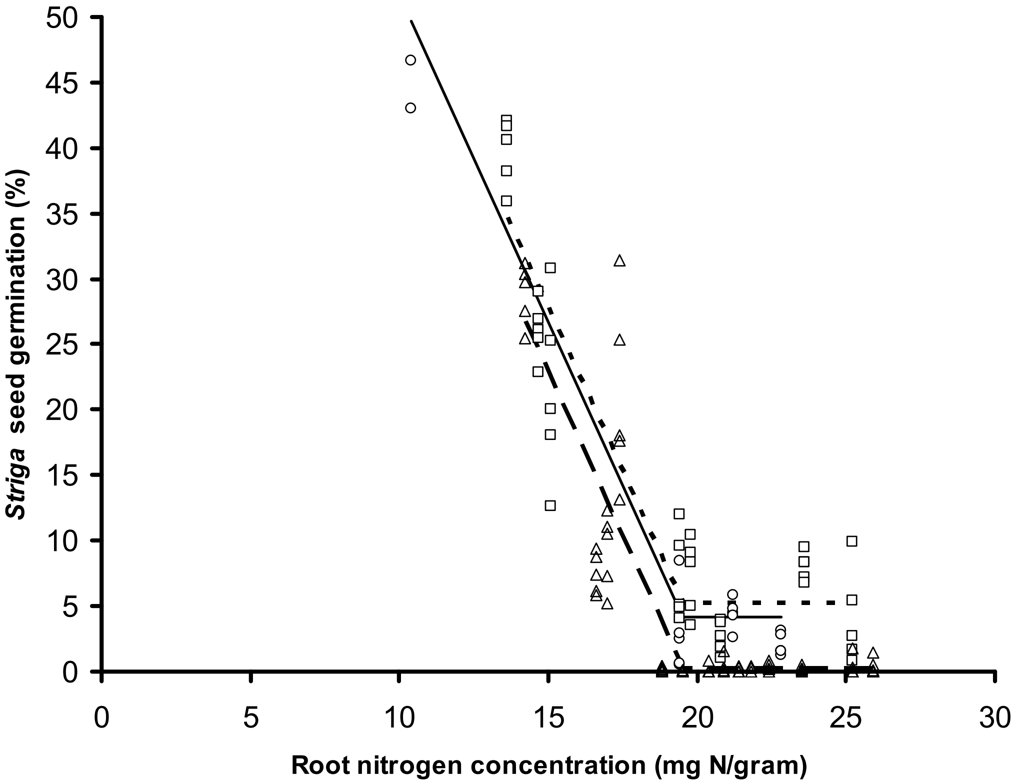

Fig. 3. Correlation between sorghum root N concentration and striga seed germination in experiments 1 (circles and drawn line), 2 (squares and dotted line) and 3 (triangles and broken line).

Table 4. Parameter estimates for the broken-stick model for root nitrogen concentration effects on striga seed stimulation.

Parameter	Estimate	Std Error	95% Confidence Limits	
Critical Root N (mg /g)	19.5	0.42	19.0	20.0
Slope [% germination / (mg N/g)]	-50.03	4.2	-58.68	-41.39
Minimum germination exp. 1	4.15	2.18	-0.339	8.63
Minimum germination exp. 2	5.18	1.63	1.81	8.55
Minimum germination exp. 3	0.224	1.22	-2.29	2.74

Effects of timing of N application

There was a general trend of increasing root nitrogen concentration with increasing time delay for assaying for striga germination (Fig. 4). From the graph it was estimated that, when enough nitrogen was provided, a time lapse of five days was sufficient to reach the critical root N concentration of 19.5 mg N/gram (the cut-off point in the broken stick model).

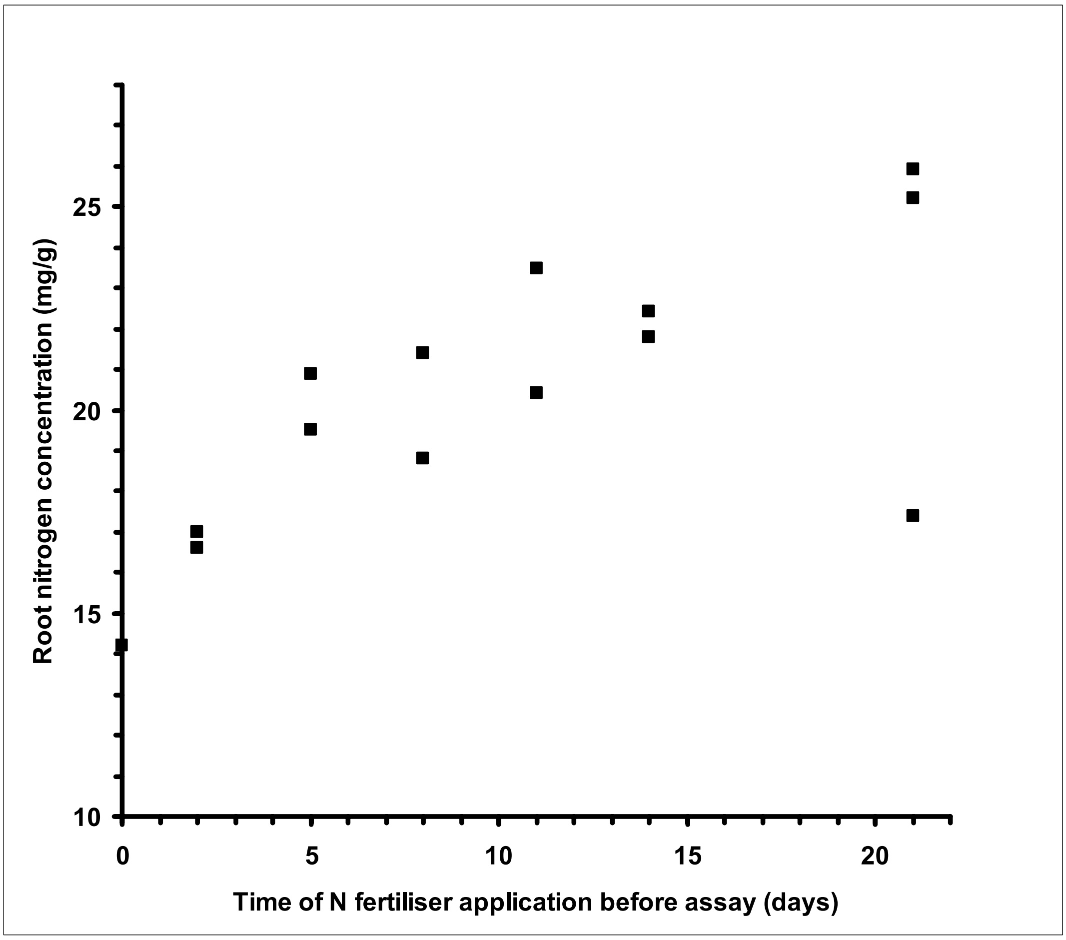

Fig. 4. Effect of N application time on sorghum root N concentration. The applications time is given in days before the moment roots were used in the assay for striga germination.

Discussion

Germination assays

The significant positive correlation between the cut root and the root exudates techniques shows that both techniques produced similar results. This conclusion suggests that techniques are substitutable. However, there are two reasons to prefer the cut root technique over the root exudates technique. First, the cut root technique is more cost efficient and simpler to execute. Second, and more importantly so, the discriminative power of the techniques at root N concentrations close to minimum striga seed germination are quite different. At root N concentrations around 20 mg N/gram, the root exudates technique indicated zero germination, while the cut root technique was much more sensitive to relatively small variations around this critical N level. Because of that greater discriminatory power (especially relevant in the case of the relationship between critical root N concentration and striga seed germination), we note that the cut root technique clearly outperforms the root exudates technique. This may be due to the inherent difference between the techniques as it has to be noted that the exudates from the root exudates technique will gradually degrade without replenishment during the assay, while the roots in the cut root method will continue to produce all kinds of both germination stimulating (strigolactones, ethylene) and germination inhibiting (e.g. ABA) chemicals. Especially when the roots provide a low level of net stimulation this could result in no germination in the root exudates technique. Our results support the claim by Berner e*t al*. (1997) who found that the root exudates technique did not provide a reliable quantitative measure of the ability of plants to stimulate striga germination. The only uncertainty remains whether the higher germination at low striga germination stimulation could be due to the ethylene production by the cut roots reported by Emechebe *et al*. (2003). As we did not include an ethylene trap our results do not allow clarifying this further.

Root N concentration and striga germination

All three experiments consistently showed that striga germination decreased with increasing N concentration of root tissue up to a critical level, after which no further reduction was noted. A negative effect of root N concentration (or more general of tissue N concentration) on striga seed germination had been observed previously by Sherif and Parker (1988), Raju *et al.* (1990), Bebawi *et al.* (1991), Cechin and Press (1993b) and Kroschel (1998). However, none of these authors quantified the relationship between root N concentration and striga germination.

To the best of our knowledge, our study is the first one that quantifies that relationship. It shows a very robust pattern that can best be described by a broken stick, i.e. decreasing germination with increasing root N concentrations till a critical level, after which no further reduction occurred. Remarkably, the critical N concentration was also very robust, showing no differences between the different experiments. However, there was some variation in the minimum germination percentage of striga, which varied between less than 1% and 5%, above this critical value.

Previous work by Raju *et al.* (1990), Bebawi *et al.* (1991) and Cechin and Press (1993b) was all based on a root exudates extraction method that extracts root exudates through the root-sand nutrient medium with the risk of simultaneously extracting root exudates alongside residual inorganic N. This procedure thus may confound both the direct effect of inorganic N on striga seed germination as seen by Pesch & Pieterse (1982), with the indirect effects of N on striga seed germination through changes in cereal root exudates. In our studies we excluded the possibility that the N fertiliser treatment directly caused a reduction in seed germination, and therefore demonstrated that variation in host tissue N concentration triggers the mechanism.

The mechanism by which tissue N triggers reduction in striga stimulation intensity is yet unclear. It seems that somehow the host's root stimulants are modified: either quantities are considerably reduced or amounts of different components make exudates less active in striga seed stimulation. Recent work by Akiyama *et al.* (2005) has shown a link between striga stimulants and the stimulants of mycorrhizal colonisation. Mycorrhizal colonisation of sorghum has been shown to lead to increased inflow of N, P, K, Ca, Mg, Fe, Zn and Cu (Ibijbijen *et al.,* 1996; Bagayoko *et al.,* 2000). Fertiliser trials have shown negative effects of N, but not of P or K on striga incidence (Farina *et al.,* 1985; Gacheru & Rao, 2001), but these studies did not look at seed germination. Evidently, there is a need for further work in which the exact mechanisms are unravelled by which the root stimulant production reacts to root nutrient status (N, P or K) and how this relates to both striga and mycorrhizal stimulation.

However, even at or above the critical root N concentration there still was some striga seed germination (between 0 and 5%). These results contradict earlier observations by Bebawi *et al.* (1991), who obtained zero striga seed germination at the highest N levels. This residual level of seed germination suggests that under farmers' field conditions, irrespective of the level of fertiliser application, it will never be possible to completely eliminate striga seed germination. The probability of striga making successful union with a susceptible cereal host in the field depends on many things including numbers of hosts' root and their spatial distribution and number of stimulated striga seeds and their spatial distribution (Van Delft, 1997). Van Mourik *et al.* (2005) reported average densities of striga seed bank to range from 1800 to 414600 seeds m^{-2}, based on a literature search. Considering these huge numbers of striga seeds a residual stimulation of 1 % may still produce (highly) infested cereal fields. This residual effect could explain why high N fertiliser applications sometimes still produce high infestation levels in farmers' fields. As there is a clear density dependency between numbers of striga seeds and number of emerging striga plants which may be partly due to a density dependent relation between the amount of germinated striga seeds and final recruitment (Westerman *et al.*, 2006) lowering striga stimulation by 95% will not translate automatically to a comparable reduction in striga numbers. As again the relation between yield reduction and number of emerged striga plants shows a clear density dependency (Rodenburg *et al.*, 2006), the effects on yield of such a reduction in germination cannot be easily predicted. It is also clear, then, that reducing seed germination of striga through enhancing sorghum root N concentrations must be applied in concert with other management practices that reduce or eliminate striga.

Effects of timing of N application

Because the attainment of the critical root N concentration necessary for lowest striga germination must be through uptake and assimilation of mineral nitrogen, timing of fertiliser application is crucial. Root nitrogen concentration increased with time of application following plant uptake in our experiment where soil N availability was not limiting (Fig. 4). The time lapse between the poorly nourished state and attainment of the critical root nitrogen concentration is about five days. There is apparently no time lapse between the attainment of this minimum critical root N concentration and onset of mechanisms of reduced striga seed germination. This conclusion implies that if soil nitrogen is not limiting, it will take a very short period between attainment of optimum root nitrogen concentration and induction of the reduction in host plant exudation. However, if soil N is limiting, plant growth could subsequently result in dilution of the root N concentration thereby increasing striga seed germination. From a practical point of view this could mean that N fertiliser treatments, at the start of the cereal planting and growing season with irregular rainfall with enhanced leaching risks, can have quite variable effects on striga germination and subsequent attachment and emergence.

Such unavoidable problems in N fertiliser application could explain inconsistencies reported in the use of optimum nitrogen fertiliser rates in controlling striga infestations. While various authors showed that N application significantly suppressed striga in cereal cultivation systems (Agabawi and Yournis, 1965; Farina *et al.*, 1985; Gworgwor and Weber, 1991), Bebawi (1981) noted that there was no consistent host plant response to N fertilisation with regard to reduced striga infestations.

Under field conditions in the Sahel, where erratic rainfall often renders N fertiliser management difficult, the notion of timing may turn out to be more important than the application rate. This will be more so for the major source of N fertilisation which is farm yard manure or some other form of organic N.

The presented study shows clear evidence of a strong correlation between root nitrogen status and striga germination stimulation by roots. However, improving root N status never led to a complete suppression of germination stimulation. The results indicate that experiments to test effects of nutrition on striga infection or suppression should include root nutritional status in the observations. The recent findings on the synthetic pathway of strigolactones (Matusova *et al.*, 2005) and the linkage there seems to exist between plant signalling for mycorrhizal branching and for striga germination (Akiyama *et al.*, 2005) in combination with the here presented results call for further research into the role plant nutrition could play in the reduction of the striga germination and the ways in which this can be translated into management practices.

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CHAPTER 6

General Discussion

Scope of the thesis

The starting point of my thesis was to enhance understanding of options to reduce the negative impact of striga in farmers' field through the use of organic amendments. I studied the effect of organic amendments on sorghum growth and striga dynamics. Mechanisms by which organic matter affects striga and striga seed bank dynamics were assessed (Chapters 3 and 4). In order to understand the role of mineral N, which is released during decomposition of organic amendments, I executed experiments on the role of mineral N. I also looked at the significance of mineral N in modifying cereal root stimulation of striga seed germination (Chapter 5). Through a number of surveys I studied the striga situation and the impact of long-term attempts to manage striga in northern Cameroon (Chapter 2) in order to come up with management proposals that fit with the socio-economic conditions that farmers face. The results of that study led to reconsideration of assumptions related to striga management and the management of soil fertility. The use of organic matter in these agro-ecosystems is supposed to have two outcomes, *viz.,* improvement of crop yield and a reduction of striga. However, the results made it imperative to reflect on this double role of organic matter and ways in which farmers, extension workers and scientists conceptualise striga in relation to poor agronomic performance.

This general discussion briefly highlights the major findings of the different ways organic amendments influence the cereal- striga system (Fig. 1). The main focus, however, is on the importance that farmers assign to soil fertility, labour, weeds and striga as their constraints (Chapter 2). The discussion will propose options how technical research can be used to improve soil and crop management and cereal production, in cases where striga is present.

Research findings

Surveys in northern Cameroon that spanned a period of twenty years showed that striga increased over time (Chapter 2). However, contrary to my initial ideas, striga was not listed among the top priority constraints that farmers face. Inspection of Fig. 5 of that Chapter suggests an explanation for that contradiction. The graph shows that cereal production and striga population density were often not significantly related because low yields occurred on fields that ranged widely in striga density. Only cases of high cereal production coincided with conditions where striga was absent or occurred in low densities. For farmers soil fertility and weeds and not striga (implying that for farmers striga is NOT a weed!) were their priority crop production constraints. That conclusion forced me to reconsider the striga problem as only one (and not even the most important one) of the constraints farmers face. Farmers' constraints were much more related to soil fertility, which a majority of striga scientists have often linked to worsening striga infestations.

In Chapters 3, 4 and 5, I described how organic matter amendments could affect the striga-sorghum system, with an emphasis on six processes (cf. Fig. 1):

1. N released from decomposing organic matter could increase N uptake and enhance crop performance (Chapter 4);
2. N released from decomposing organic matter could increase the N status of the cereal and thereby modify root exudation and reduce striga seed germination (Chapter 4&5);
3. Organic matter could enhance microbial decomposer activity which then reduces striga seed density (Chapter 3&4);
4. Organic matter could alter ethylene concentrations in the soil and thereby deplete striga seed density (Chapter 3);
5. Organic matter could enhance water retention of the soil, which is in turn supposedly detrimental to striga seed survival (Chapter 3);
6. Organic matter could lower soil temperatures with a negative impact on striga seed germination and subsequent emergence. (Chapter 3).

The results described in Chapter 3 indicated that the latter three processes were of no significance to striga dynamics. The effect of organic matter amendments was directly related to N mineralisation, both for better cereal growth (Chapter 4), and reduced striga survival (Chapter 3&4).

In Chapter 5, I describe experiments that showed that with increasing N-fertilisation the N mass fraction in the root increased, which resulted in a reduced stimulation of striga seed germination. I proposed this to be due to a reduction in root exudation, though the latter was not explicitly measured. That relationship was linear up to a root N mass fraction of 19.5 mg g^{-1} where seed germination was close to but always above 0%.

Striga as an indicator of soil fertility depletion

Interviews and experiences with farmers in the striga-prone areas show that in newly opened-up farmland during the first two to three years of farming, even without fertiliser, striga is not or hardly a problem. It becomes a problem from the fourth year onwards and farmers consider its presence an indicator of depleted and degraded soils. Where and when (fallow) land availability was not a problem farmers could abandon their fields to open new farmland when soil fertility declined (and striga incidence increased) (Chapter 2). Traditionally, in most of African savannah, land was cropped for 2-4 years and fallowed for the next 8-12 years (Weber *et al.*, 1995). In the traditional systems of northern Ghana a fallow

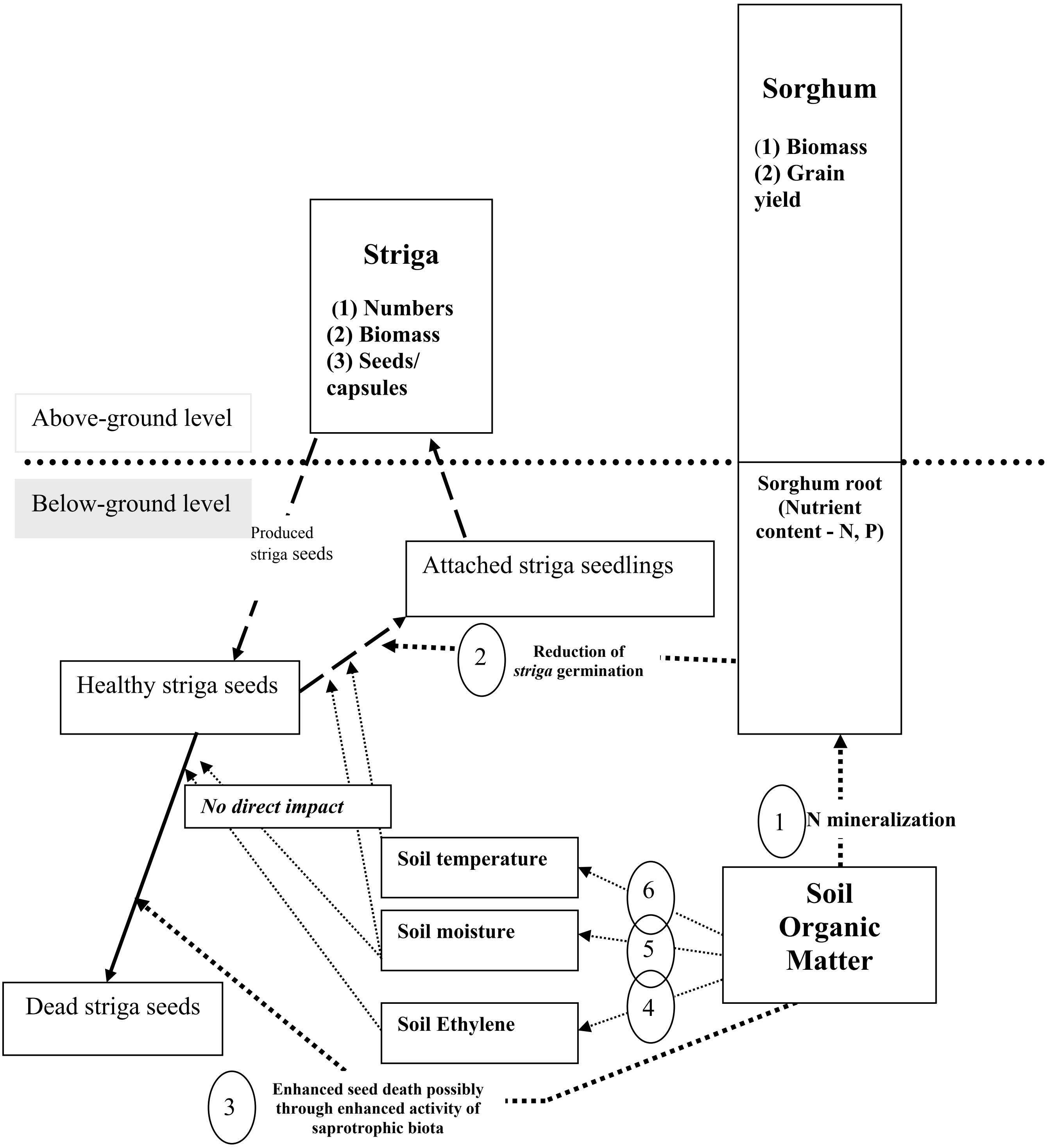

Fig.1. Conceptual diagram showing how organic matter management could affect the sorghum - striga system. The thick dotted arrows depict the principal processes through which organic matter impacts on the system, the thin dotted arrows indicate processes of negligible consequence to striga dynamics. The bold arrow indicates material flow, bold broken arrows are flows that have not been studied in the current work. The numbers along the arrows refer to the processes described in the text.

of 10-15 years alternated with a cultivation period of 4-6 years in the bush fields (Kranz *et al.*, 1998). In both situations, the practices were used mainly to regenerate soil fertility. Due to land scarcity farmers have been obliged to continue farming on the same piece of land for many years. There has also been a tendency to switch from mixed cropping and crop rotations to cereal monocropping. Several factors contributed to that switch. The decline of the cotton sector (and the decline of availability of mineral fertilisers) has reduced that crop. Furthermore, cereal cropping is more profitable than rotations with legumes and also demands less labour. Consequently striga incidence and infestation worsened. These processes account for the worsening striga situation in the North Province which was largely striga-free before the settlement of immigrants from the (densely populated) Far-North Province (Chapter 2).

Following this logic, Albert (1999) questioned whether there was a striga problem or whether the occurrence of striga had to be regarded simply as a symptom of deteriorating soil fertility (Porteres, 1948; Vogt *et al.*, 1991; Kranz *et al.*, 1998; Adamou *et al.*, 2007; M'Biandoun & Olina Bassala, 2007). In fertile soils with higher organic matter levels, striga is not a major problem and yields are much higher (Ransom, 1999; Sauerborn *et al.*, 2003, Samake *et al.*, 2005).

This question led to a new conceptualisation of the striga problem. A model that links cereal yield decline and striga infestation over time as driven by soil fertility decline (ultimately caused by increased land pressure and lack of nutrient inputs) is shown in Fig. 2.

The first part of this model (thick drawn arrow in Fig. 2) has been usually regarded as a scheme that relates decline in cereal yield as *caused* by striga. However, I now propose that both factors covary with an external driving variable, changes in soil fertility status. The model then shows how with declining soil fertility cereal yields go down and striga pressure increases. Under the classical interpretation, recovery of the system should follow the same trajectory but in the opposite direction – that is, successful interventions reduce striga numbers and result in increased yields (dotted arrow). The alternative interpretation leads to different proposals regarding management priorities. I hypothesise, based on field experiments with low-quality organic matter (Chapter 4 and Appendix 1, Fig. 1), that reducing striga infestation in depleted soils will have no impact on cereal yield; it is even conceivable that cereals yields will further decline in the absence of soil fertility management (thin drawn arrow in Fig. 2). Inspection of the literature also suggests that reducing striga often did not result in higher yields (Webb & Smith, 1996; Oswald, 2005; Van Ast *et al.*, 2005; Dugje *et al.*, 2008). On the other hand, improving soil fertility with the use of mineral fertilisers or organic amendments will increase cereal yield but will often initially increase striga infestation (Ransom, 1999; Ahonsi *et al.*, 2002; Ikie *et al.*, 2007) because of improvement of crop growth, which allows for more sites for striga attachment (broken lines in Fig. 2). A maintained management that enhances soil fertility, though, will eventually lead

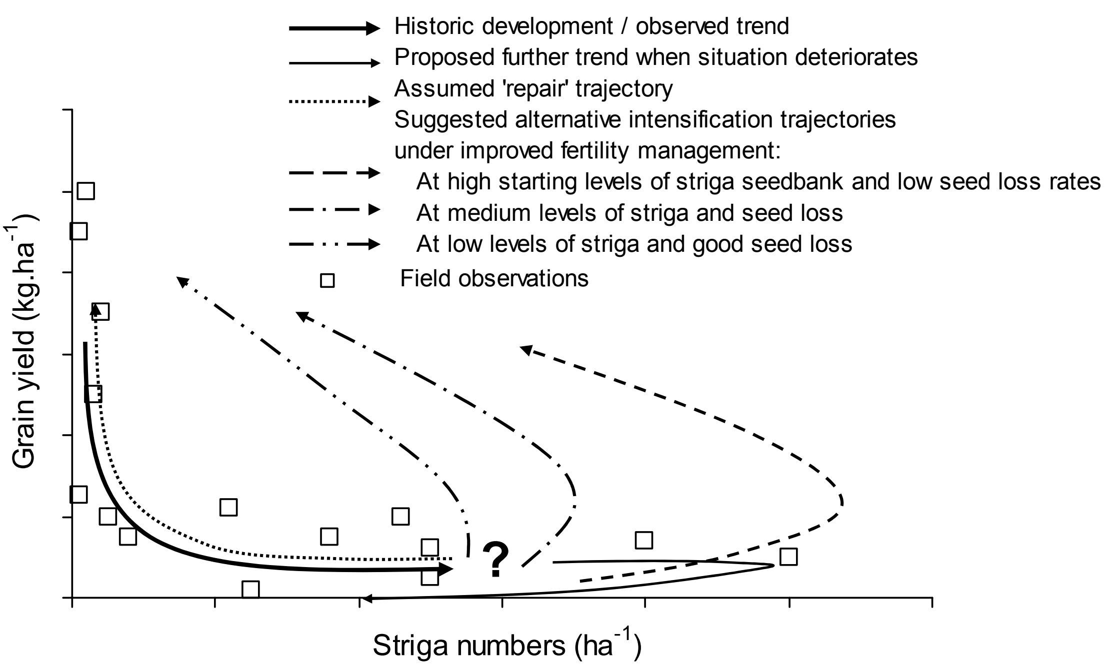

Fig. 2. A conceptual scheme that plots grain yield against numbers of emerged striga plants. The different arrows indicate dynamics over time, with the temporal scale undefined. The data points and thick drawn arrow are inferred from observations on data on farmers' fields (Chapter 2, Fig. 5) and indicate the dynamics under continuous low-input cereal monocropping. The thin drawn line extends dynamics over longer periods when even a decrease in striga numbers could occur as carrying capacity of the cereal collapses. The dotted line indicates the apparent implied trajectory of re-establishment of productivity through intensive striga control programs. The three broken arrows indicate hypothesised trajectories under soil fertility restoration based on the data presented in chapter 4 and further discussed in appendix 1, Fig. 1.

to reduction in numbers of attached striga and improved yields. Again, data with high-quality organic matter (Chapter 4) support that hypothesis.

This new conceptualisation leads to the more basic question: Should we then first remediate soil fertility decline (through enhanced organic matter inputs together with mineral fertilisers) or should we first alleviate the striga problem? While my thesis started under the assumption that striga management should be top priority, my results now lead me to prefer the first option. In this discussion I will analyse striga management in the West African savannah in order to bring science more in line with farmers' realities.

Striga relative to other constraints faced by farmers

The surveys described in Chapter 2 are unique, not only because it led me to reconceptualise striga-as-a-problem, but also because most surveys on striga incidence

(Albert, 1999; Traore & Yonli, 1999; Dugje *et al*., 2006; Aflakpui *et al*., 2008) did not span such a long period. Because I looked at all crop production constraints, it became clear that soil fertility and weeds (and the need for labour for weeding) and not striga were priority constraints. From the survey it became clear that for farmers striga is not a weed, and that hand-pulling striga was not considered a form of weeding. Hand-pulling to deplete the striga seed bank is labour-intensive and costly, and profits can only be reaped in the long term (Oswald, 2005). The pressure on land is such that households that want to feed their members need to produce more on the same or even less land. Farmers need money to buy fertilisers in order to raise soil fertility. This constraint poses a real problem to crop intensification.

The required intensification implies a need for investment in the soil, which is made more difficult by the prevailing land tenure system, especially for farmers on short-term land-lease. The present land tenure regime in most northern Cameroon is a heritage from colonial times modified by the Cameroonian state. It is therefore a mixture of a legal and customary system (Teyssier, 2004; Koulandi, 2006). Cameroonian law treats all untitled land as belonging to the state, but allows village chiefs as custodians of the land to lease land to individual farmers. Farmers can formally not have land registered as their property, but only acquire usufruct rights through leases. As rent seeking by these chiefs is not uncommon, leases are usually for unspecified periods (but in practice for short periods only), making investments in the land uninteresting (Debrah 1994; Ayongwa & Ngawa, 1999). There is need for a joint commitment by policy makers, researchers, extension and farmers to alleviate these limitations to change.

Improving soil fertility eventually overcomes striga

Kim *et al.* (1997) found a rapid decrease in striga infestation at experimental stations and on large commercial farms due to high use of N fertilisers. Sauerborn *et al*. (2003) showed that fields that have been fertilised consistently had the lowest striga seed densities. Such observations may give rise to the optimism that improving soil fertility would immediately result in reduced striga pressure. However, in Fig. 2 above I suggest that with lower availability and use of fertilisers initial soil fertility improvements will likely result in increased striga density. Chapter 4 provides data to evaluate both alternatives and to estimate the time needed for striga reduction as a function of N input. The data demonstrate organic amendments always lead to grain yield increases (Chapter 4, Fig. 3 & 4), and that these yield increases scale directly with the amounts of N released from the organic amendments. However, when the infection level of the soil is high, striga pressure increases especially when low amounts of N released through decomposition of organic matter are added. There is thus an initial rise in striga pressure, while in the third year pressure may or may not fall to an equal level to that obtained in the first year (Chapter 4 and discussed in Appendix 1). At lower initial infection levels of the soil or higher N input the reduction in striga numbers seems to occur earlier and faster.

Organic matter amendments seem to regulate striga density less than short fallow, where the combination of no new seed production and natural seed decay results in a depletion of the seed bank and hence in a reduced striga pressure. A two-year fallow with continuous organic matter addition, even under high striga pressure, increased grain yield and reduced striga infestation. However, fallowing in combination with organic matter amendments is an unrealistic option for farmers. The use of other crops that are striga non-hosts (formerly called trap crops) could achieve the same result (Kayeke *et al.*, 2007). Next to such rotations, intercropping cereals with legumes could be effective, in fact possibly more effective (Van Mourik, 2007).

However, in view of the constraints that farmers face, long-term soil fertility improvements that do not pay off in the first year(s) are not worth the investment in cash and labour. Control options that imply investments on the short term without simultaneous benefits are not acceptable for farmers. The question is getting over the high cost of fertiliser and also the organic matter supply, because it is already used for various other purposes. Outlets for farm produce at prices that are profitable to farmers remain a key driver for intensification. The challenge to agronomists is to consider how to make farm intensification rewarding. A major question to agronomists would be whether intensification leads to aggravation of the striga problem and whether high striga levels would annihilate any improvements to productivity through intensification. Striga should only be considered for intervention if it ranks high among the list of constraints to crop intensification by farmers.

Immediate reduction in striga numbers is possible only above a N threshold level. Simier *et al.* (2006) showed that the N level of toxicity for striga and sorghum were not the same. An addition of a 1.5 L nutrient solution of KNO_3 weekly for 2 weeks in pots, at a maximum nitrate load of 1500 mg Nitrate N added to the pots per gram host was toxic to striga and eventually caused its death; whereas there was no detrimental effects of that N-level on sorghum. The amounts of N fertiliser that effectively depress striga in the field ($\geq$120 kg N ha^{-1} as per Kim & Adetimirin, 1997 or Kim *et al.* 1997) are outside the reach of resource-poor farmers. There is need for field work to evaluate how smaller amounts of well placed fertiliser (micro-doses; Tabo *et al.*, 2009) can be managed to effectively increase yields and at the same time depress striga.

In Chapter 3, I described that the striga seed survival was more strongly reduced for organic matter amendments with a low C/N ratio. A negative effect of N fertiliser on striga seed germination had been observed previously by Pesch & Pieterse (1982), Sherif & Parker (1988), Raju *et al.* (1990), Bebawi *et al.* (1991) and Cechin & Press (1993b), although the controversy on the mechanisms by which N suppresses striga remains unresolved.

Relationships between tissue N and striga germination had not been quantified before. On the basis of experiments described in Chapter 5 a critical level at 19.5 mg N gram^{-1} root dry matter achieved maximum reduction of striga seed germination. In Chapter 4 and 5 I looked only at nitrogen, and did not study phosphorus. This decision may be justified by the fact that in the dry savannah of the Sahel, N rather than P is usually the limiting nutrient during the start of the rainy season. Nitrogen improved crop yield (Chapter 4) and also reduced stimulation of striga seed germination (Chapter 5).

Akiyama *et al.* (2005) showed that strigolactones, molecules responsible for striga seed germination, also induce mycorrhizal colonisation. Strigolactone production is upregulated when phosphate availability is low (Yoneyama *et al.*, 2007; Yoneyama *et al.*, 2008), and under these conditions the arbuscular mycorrhizal symbiosis is most relevant. Lendzemo *et al.* (2007) showed that germination of striga seeds after exposure to root exudates from sorghum colonised by AM fungi was significantly reduced. Reduced emergence (likely due to reduced germination) was also noted in a field experiment, but reduced striga numbers did not result in increased cereal yield (Lendzemo *et al.*, 2005). There is need for further work in understanding how organic matter addition could affect AM fungal performance, considering that AM fungi specifically proliferate in patches of organic matter. Next to P-starvation, N starvation was also mentioned to upregulate strigolactone exudation (Yoneyama *et al.*, 2008). The ways in which the relative supply of N and P regulate strigolactone exudation and hence germination of striga, in relation to the regulation of the mycorrhizal symbiosis, demands further study.

The importance of timely N management

The controversy on the role of N fertiliser in suppressing striga (Gworgwor & Weber, 1991; Smaling *et al.*, 1991; Reda *et al.*, 2005; Kabambe *et al.*, 2007; Kamara *et al.*, 2007) may be related to the timing of its application. Verkleij *et al.* (1994) and Kim & Adetimirin (1997) found that the timing of N application was more important in suppressing striga than N application rate. This corresponds well with the conclusions of the studies reported in Chapter 5. Because striga seed preconditioning period takes 14 days on average, it should in principle be possible for farmers to adequately manage N fertilisation with the onset of the rainy season (assuming predictable rainfall at the start of the rainy season), such that the cereal host acquires the maximum tissue N necessary to maximally reduce germination of striga seed. The placement of micro-doses of N fertiliser close to seed should be sufficient to boost tissue N concentration of the cereal seedling within the first 21-30 days after sowing. There is need for research to establish optimum amounts of micro-doses needed and ways of application from a farmer's perspective. With the use of participatory learning and action research, farmers should adopt this technique easily.

Additive effects of organic amendments and inorganic N fertiliser

Whereas there was a good fit between grain yield and N supply by either organic or inorganic sources, the same was not true for changes in striga pressure (biomass) (Chapter 4). There was a much larger decline in striga biomass after application of inorganic N compared to applications of organic matter that released the same amount of N I suggest two possible explanations. An early dose of inorganic N boosts root N levels, which reduces strigolactone exudation to the point that striga germination is reduced. It is also possible that there is a direct toxic effect of mineral N on striga seeds (Pesch and Pieterse, 1982). Given the importance of timely supply of N in relation to striga dynamics, organic matter may not be able to play the same role as inorganic N. The rate of decomposition of organic matter may not be fast enough for enhancing root N status of sorghum seedlings, implying that farmers need to resort to small doses of inorganic nitrogen. This does not preclude use of organic amendments, as inorganic fertiliser use efficiency is better in soils with higher organic matter levels (Wubeneh & Sanders, 2006; Vanlauwe *et al.,* 2010). Low effectiveness of high doses of inorganic N in the dry savannah is caused by leaching as a result of the low organic matter content of the sandy soils. Organic matter greatly improves water and nutrient retention of the soil, and thus increases use efficiency of inorganic fertilisers.

Natural seed decay is important in striga dynamics

Natural seed demise is an important phenomenon in striga population dynamics (Gbèhounou, 1998; Odhiambo & Ransom, 1995; Ransom, 2000; van Mourik, 2007). In an experiment under fallow, Gbèhounou (1998) showed that striga seed viability and germination reduced steadily over time and at the end of a two-year burial period in the soil there were hardly any viable seeds left. Van Mourik (2007) obtained a much lower reduction with 23% dead seeds under bare soil in a single cropping season in Mali. In this thesis I showed in Chapter 3 a fall in striga seed germination within a season in all treatments. In Chapter 4 I showed that during a 2-year bare-fallow period organic matter caused a substantial striga seed decay, which also resulted in lower striga infestation, even before the last organic matter application during the 3rd season. Although the seed burial study suffered from the same methodological bias (Van Mourik *et al.*, 2005) as the study of Gbèhounou (1998), the finding that infestations were significantly lower provides evidence of the importance of this natural dying-off process of striga seeds. Considering that most fields are now under continuous cereal cropping with an annual addition of new striga seeds, one may wonder how natural seed demise can be effectively managed by farmers. An appropriate combination of rotation and especially intercropping with non-host plants can be used to reduce striga seed-bank densities (cf. Gbèhounou, 1998).

The role of micro-organisms in this decomposition process, enhanced by the availability of organic matter, needs to be better understood. Two different mechanisms have been proposed. One mechanism is linked to the existence of striga-suppressive soils, where specific pathogens such as *Fusarium oxysporum* f.sp. s*trigae* suppress striga seeds (Nekouam *et al*., 2006; Yonli *et al*., 2006). The other mechanism links decomposer activity aspecifically to the total activity of the microbial community. The relation between organic matter quality (a proxy for general microbial activity) and seed decay lends support to the second mechanism (cf. Van Mourik *et al*., 2003). Under the first mechanism one would expect patchy striga levels; under the second mechanism one would rather find uniform reduction in striga densities. No clear patchiness (striga-suppressive hotspots) was observed.

The direct seeding and mulch based cropping systems (DMC) (a form of conservation agriculture) which is inciting a good number of farmers in Northern Cameroon to abandon ploughing and revert to direct seeding (Naudin *et al*., 2005) fits well with the no-tillage management that favours lower striga infestations (Hess & Ejeta, 1987; Van Delft, 1997). Lendzemo (2004) indicated that ploughing also disrupts mycorrhizal networks. Further, DMC using *Brachiaria* significantly increased soil organic matter and reduced striga infestation without a significant negative impact on the sorghum intercrop (Naudin *et al*., 2005; Kayeke *et al*., 2007; Husson *et al*., 2008). Management through conservation agriculture seems to be the most rewarding striga management option. The main constraint to this conservation agriculture remains the existing land tenure system and the nomadic herding that allows for random feeding of livestock on available vegetation. The administrative and the traditional authorities in this region need to show the good will of managing these obstacles (Naudin *et al*., 2005).

Farmers who are not using their striga-infested soils for cereals, have an option of planting legumes such as cowpea and soybean that can be cash earners and import N into the soil (Carsky *et al*., 1994; Samake, 2003). The motor for improvement of soil fertility leading both to higher yields and reduced losses to striga could be provided by a cash crop for which the market is well organised. In former times cotton did play that role (Chapter 2).

The future of cereal cropping in northern Cameroon/drier savannas in the presence of striga

There seems to emerge a general consensus that only integrated soil fertility management can result in yield improvements; and such management should also lead to reduction of striga (Carsky *et al*., 1996; Esilaba *et al*., 2000; Ransom, 2000; Oswald & Ransom, 2001). However, it should be taken into account that no single striga-control component can give a 100% control of the parasite; and even where this is possible, eliminating striga without addressing the other constraints, will have very little success at best. There is no outstanding successful programme that is apparent from literature (Schulz *et* *al*., 2003; Emechebe *et al*., 2004; Oswald, 2005). One may wonder again if overemphasis on striga as the cause rather than as symptom of low agricultural productivity explains this lack of success. Looking at the Cameroonian context, an integrated scheme (comprising several components) that also contributes to striga control is proposed:

- The central focus is on boosting yields through improving soil fertility which often also reduces striga. There is first and foremost the need to address the crucial and endemic problem of soil fertility in the dry savannah of western Africa (Chapter 2; Ransom, 2000; Schlecht *et al*., 2006; Vanlauwe & Giller, 2006; Vanlauwe *et al.,* 2010)
- Another focal point is crop rotation or (preferably) intercropping. Rotations and intercropping will reduce the seed bank. Substantial amounts of striga seeds will decay naturally in the soil or through suicidal germination and in the absence of seed replenishment, the seed bank reduces drastically in a two-year period (Gbèhounou, 1998; van Mourik, 2007; Chapter 3).
- Then the programme can address the problem of planting material by making available high-yielding and improved-quality seeds that fit farmers' socio-economic and agro-climatic conditions and aspirations. This should limit infection and re-infection of clean farmland. With the present functional national structure that insures production and control of quality-seed, farmers can acquire desired crop seeds at planting time. The national agricultural research system, in collaboration with farmer groups and NGOs, now develops planting material that suits the varying agro-ecological zones of the country (Highly Indebted Poor-Countries initiative of the Cameroon government in quality seed production).

The two focal points of improving soil fertility and crop rotation/intercropping integrate best if related to farm size. "Sahelian farmers tend to cultivate increasing amount of land with modest organic inputs" (Samake, 2003) to meet with the growing population. This reveals often counterproductive when striga comes into the picture. As farm intensification remains the ultimate option in farm productivity and as fertilisers are rather expensive for the resource-poor farmer; farmers in this region need to consider reducing farm sizes to meet with optimum fertiliser requirements. The use of fertilisers on smaller farms should then compensate for the large farm size option foregone; making fertiliser management and land productivity more rewarding. In addition or as an alternative, these farmers need to adopt a rotation/intercropping system with appropriate crops so as to suit with specific fertiliser and family-food needs, and also striga control options. Wubeneh & Sanders (2006) found that farm size is negatively related to fertiliser adoption, as small farms are more under pressure to adopt inorganic fertiliser and other intensive production techniques.

Other components in the scheme such as hand-pulling striga plants before flowering

(Ransom,1999), injection of ethylene gas to diminish the striga seed bank (Eplee, 1992), planting striga-tolerant or resistant cereal cultivars (Rodenburg, 2005), host-seed coating (Kanampiu *et al*., 2001), introduction of striga-antagonist Fusaria into the soil (Nekouam *et al*., 2006) and transplanting sorghum (Van Ast *et al*., 2005) will reduce and/or delay striga infestation but not necessarily increase cereal yield. Because they do not address farmers' primary constraints, these components may not fit with farmers priorities (Chapter 2), and should only be used where they strengthen effects of improving fertility.

Whereas most work has been done using maize, emphasis needs to be put on sorghum and millet that are more suitable crops in the dry savannah in the Sahel than maize.

Concluding remarks

Organic matter amendments improve soil fertility (hence cereal yield), and through it reduce striga although the latter process takes more time, and is also dependent on existing striga infection levels of the soil. Due to structural adjustment programmes and the decline of the cotton sector, mineral fertilisers are usually too expensive and their availability too low. Farmers therefore have to rely on the use of organic amendments as the only source of fertilisation, but available quantities are limited and quality is often rather low. Under such conditions, it is most rewarding to concentrate application on the richer and more productive portions of their fields or reduce farm sizes to meet minimum doses required. In so doing the surplus production obtained compensates for the poorest (unproductive) fields which are not under host-crop, while at the same time striga is better managed. These unproductive fields not under striga-host may then be cropped with crops less demanding in soil fertility in an appropriate rotation system. Striga should only be considered a problem if it is a priority constraint to crop intensification by farmers, otherwise degraded (exhausted) soils remains the obstacle for the smallholder farmer. So proper soil fertility improvement eventually should be sufficient to overcome the striga burden, allowing for grain yield production which is economically acceptable.

APPENDIX 1

Changes in sorghum yield and striga infestations over time

The data presented in chapter 4 can also be presented in a different way. In Chapter 2 and Chapter 6, sorghum yields have been plotted against striga numbers as an indication of the combinations of yield and infestation that do or do not co-occur. In these graphs, observations on the relationship between striga infestation (maximum number of emerged striga plants) and yield made in different years are included. However, it might be useful to explicitly indicate the observations on the same plots over different years to indicate trajectories of change. Such plots of sorghum stover yield against striga infestation per treatment, where the 3 cropping seasons are indicated separately revealed differences between the trajectories of change of the different treatments (Fig. 1). The figure is based on stover yields as in the first year of study, grain yield data are compromised by bird damage (Chapter 4). For a comparison over years, stover yield thus is used as indicator of the changes over the years. Considering the low coefficient of variation in harvest index, stover yield is a good predictor for grain yield.

Depending on the combination of quality of the applied organic matter and striga infection level, sorghum stover yield remained roughly the same or increased with successive cropping seasons, with higher increase when more N was released by the organic matter. This is evident from the yield arrow always moving upward. However, the infestation arrow moves both in left and right directions, depending on both N addition level and on striga infection level. At the high striga infection level, striga infestation *increased* from the first to the second cropping year in all treatments receiving organic amendments before falling in the third season in the higher N-supply treatments. At the low striga infection level the *decrease* was generally more pronounced, *i.e.* starting earlier and reaching low numbers at lower N application levels. Further, the two-year bare-fallow in which the organic amendments were also applied during the fallow years (likely resulting in decreased infection levels due to seed demise) both improved grain yield and *reduced* striga infestation; compared to fields under continuous sorghum cropping receiving the same organic amendments, with the exception of the control at high striga infection level.

The graphs in Fig. 1 in broad terms support the conceptual framework put forward in Chapter 6, Fig. 2.

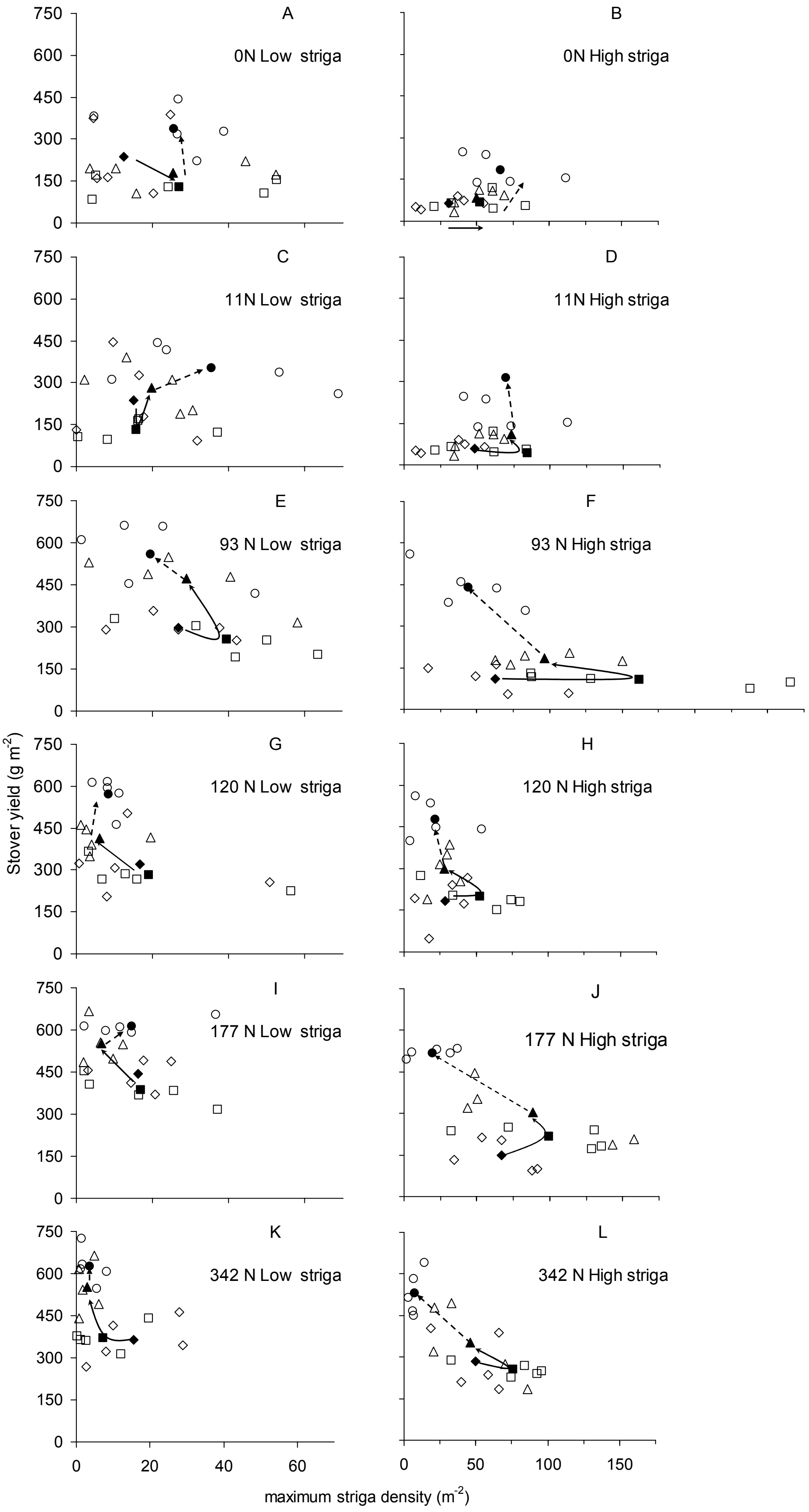
A
0N Low striga
B
0N High striga
C
11N Low striga
D
11N High striga
E
93 N Low striga
F
93 N High striga
G
120 N Low striga
H
120 N High striga
I
177 N Low striga
J
177 N High striga
K
342 N Low striga
L
342 N High striga
Stover yield (g m-2)
0
150
300
450
600
750
0
20
40
60
0
50
100
150
maximum striga density (m-2)

Fig. 1 (opposite page). Plots of sorghum stover yield and striga infestation density from a selection of organic matter treatments. Symbols represent data for different years as follows: diamonds are for year 2000, squares for year 2001, triangles for year 2002 continuous cropping and circles for year 2002 after 2-year bare-fallow, open symbols are individual replicates, closed data points averages. Figure titles are N doses applied, followed by the striga infection level. The drawn arrows indicate the combined directions of change in both variable between 2000 and 2002, the dotted arrow indicate how in 2002 cultivation after fallow compares to cultivation after two years of sorghum cultivation.

REFERENCES

Abunyewa, A.A., Padi, F.K., 2003. Changes in soil fertility and *Striga hermonthica* prevalence associated with legume and cereal cultivation in the sudan savannah zone of Ghana. Land Degradation & Development 14, 335-343.

Adamou, I., Pierre, N.J., Pogenet, P., Tchimbi, B., Gonlaina, G., 2007. Soil degradation in the Sudano-guinea savannas of Mbe, Cameroon: farmers' perception, indicators and soil fertility management strategies. Research Journal of Agriculture and Biological Sciences 3, 907-916.

Adetimitin, V.O., Kim, S.K., 1999. Farm level options for controlling *S. hermonthica* on maize in Africa. In: Advances in parasitic weed control at on-farm level, vol. 1. Eds J. Kroschel, H. Mercer-quarshie, J. Sauerborn. Margraf-Verlag, Weikersheim Germany, pp 89-101.

Aflakpui, G.K.S., Bolfrey-Arku, G. E.-K., Anchirinah, V.M., Manu-Aduening, J.A., Adu-Tutu, K.O., 2008. Incidence and severity of *Striga* spp. in the coastal zone of Ghana - Results and implications of a formal survey. Outlook on Agriculture 37, 219-224.

Aflakpui, G.K.S., Gregory, P.J., Froud-Williams, R.J., 1998. Effect of temperature on seed germination rate of *Striga hermonthica* (Del.) Benth. Crop Protection 17, 129-133.

Agabawi, K.A., Younis, A.E., 1965. Effect of nitrogen on growth and nitrogen content of *Striga hermonthica* Benth. and *Sorghum vulgare* Lur. grown for forage. Plant & soil 23, 295-304.

Ahonsi, M.O., Berner, D.K., Emechebe, A.M., Lagoke, S.T., 2002. Effect of soil pasteurisation and soil N status on severity of *Striga hermonthica* (Del.) Benth. in maize. Soil Biology & Biochemistry 34, 1675-1681.

Ahonsi, M.O., Berner, D.K., Emechebe, A.M., Lagoke, S.T., 2004. Effects of ALS-inhibitor herbicides, crop sequence, and fertilisation on natural soil suppressiveness to *Striga hermonthica*. Agriculture, Ecosystems & Environment 104, 453-463.

Akiyama, K., Matsuzaki, K., Hayashi, H., 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435(7043), 824-827.

Albert, H., 1999. Farmers in northern Ghana and the problem of *Striga* In: Advances in parasitic weed control at on-farm level, vol. 1. Eds J. Kroschel, H. Mercer-quarshie, J. Sauerborn. Margraf-Verlag, Weikersheim Germany, pp 27-43.

Ayongwa, G.C., Ngoumou, T.N., 2001. Evaluation de la situation du parasite *Striga* sur cereales dans deux terroirs du Nord- Cameroun: Mowo et Mafa-Kilda. AFPP-Dix Huitième Conference du COLUMA, Journées internationales sur la lutte contre les mauvaises herbes. Toulouse – 5, 6, 7 Décembre 2001, pp 1117-1124.

Ayongwa, G.C., Ngawa, L., 1999. Report of the Striga project during the 1994/95 cropping seasons. In: Advances in parasitic weed control at on-farm level, vol. 1. Eds J. Kroschel, H. Mercer-quarshie, J. Sauerborn. Margraf-Verlag, Weikersheim Germany, pp 297-305.

Ayongwa, G.C., Stomph, T.J., Belder, P.J., Leffelaar, P.A., Kuyper T.W., (submitted, chapter 3) Organic matter and seed survival of *Striga hermonthica* – Separating the roles of carbon and nitrogen.

Ayongwa, G.C., Stomph, T.J., Emechebe, A.M., Kuyper, T.W., 2006. Root nitrogen concentration of sorghum above 2% produces least *Striga* seed stimulation. Annals of Applied Biology 149, 255-262.

Ayongwa, G.C., Stomph, T.J., Hoevers, R., Ngoumou, T.N., Kuyper, T.W., 2010. *Striga hermonthica* infestation in northern Cameroon: Magnitude, dynamics and implications for management. NJAS - Wageningen Journal of Life Sciences 57, 159-165.

Ayongwa, G.C., Stomph, T.J., Kuyper, T.W., (submitted, chapter 4). Soil organic matter quality and the interaction between *Sorghum bicolor* and *Striga hermonthica*.

Babiker, A.G.T., Ma, Y.Q., Sugimoto, Y., Inanaga, S., 2000. Conditioning period, CO_2 and GR24 influence ethylene biosynthesis and germination of *Striga hermonthica*. Physiologia Plantarum 209, 75-80.

Bagayoko, M., George, E., Römheld, V., Buerkert, A., 2000. Effects of mycorrhizae and phosphorus on growth and nutrient uptake of millet, cowpea and sorghum on a West African soil. Journal of Agricultural Science 135, 399-407.

Bationo, A., Kihara, J., VanLauwe, B., Waswa, B., Kimetu, J., 2007. Soil organic carbon dynamics functions and management in West African agro-ecosystems. Agricultural System 94, 13-25.

Bebawi, F.F., Eplee, R.E., 1986. Efficacy of ethylene as a germination stimulant of *Striga hermonthica* seed. Weed Science 34, 694-698.

Bebawi, F.F., 1981. Response of sorghum cultivars and *Striga* population to nitrogen fertilisation. Plant & Soil 59, 261-267.

Bebawi, F.F., Eplee, R.E., Harris, C.E., Norris, R., 1984. Longevity of witchweed (*Striga asiatica*) seed. Weed Science 32, 494-497.

Bebawi, F.F., Khalid, S.A., Musselman, L.J., 1991. Effect of urea nitrogen on stimulant activity of sorghum and germination capacity of *Striga*. In: Proceedings of the 5th International Symposium of Parasitic Weeds. Eds L.J. Musselman, A.D. Worsham, C. Parker. Nairobi Kenya, pp 458-461.

Bebawi, F.F., Eplee, R.E., Harris, C.E., Norris, R., 1984. Longevity of witchweed (*Striga asiatica*) seed. Weed Science 32, 494-497.

Berner, D.K., Schaad, N.W., Volksch, B., 1999. Use of ethylene-producing bacteria for stimulation of *Striga* spp. seed germination. Biological Control 15, 274-282.

Berner, D.K., Winslow, M.D., Awad, A.E., Cardwell, K.F., Mohan Raj, D.R., Kim, S.K.,

1997. *Striga* Research Methods - A manual. IITA, Ibadan, Nigeria.

Bouwmeester, H.J., Matusova, R., Sun, Z.K., Beale, M.H., 2003. Secondary metabolite signalling in host-parasitic plant interactions. Current Opinion in Plant Biology 6, 358-364.

Breband, P., Gavaud, M., 1985. Les sols et les ressources en terres du Nord-Cameroun. Institut Français de Recherche Scientifique pour le développement en Cooperation. Edition de l'ORSTOM Paris. pp 120-130.

Carsky, R.J., Nokoe, S., Lagoke, S.T.O., Kim, S.K., 1996. Maize yields determinants in farmer-managed trials in the Nigerian northern guinea savanna. Experimental Agriculture 34, 407-422.

Carsky, R.J., Singh, L., Ndikawa, R., 1994. Suppression of *Striga hermonthica* on sorghum using cowpea intercrop. Experiemental Agriculture 30, 349-358.

Cechin, I., Press, M.C., 1993a. Nitrogen relations of the sorghum-*Striga hermonthica* host-parasite association: growth and photosynthesis. Plant, Cell & Environment 16, 237-247.

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

Combari, A., Pinneau, R., Schiavon, M., 1990. Influence du degré de decomposition de produits organiques sur la germination des graines de *Striga hermonthica*. Weed Research 30, 29-34.

De Ridder, N., Breman, H., Van Keulen, H., Stomph, T.J., 2004. Revisiting a 'cure against land hunger': soil fertility management and farming system dynamics in the West African Sahel. Agricultural Systems 80, 109-131.

De Rouw, A., 1995. The fallow period as a weed-break in shifting cultivation (tropical wet forests). Agriculture, Ecosystems & Environment 54, 31-43.

Debrah, S.K., 1994. Socio-economic constraints to the adoption of weed control techniques: The case of *Striga* control in the West African semi-arid tropics. International Journal of Pest Management 40, 153-158.

Douthwaite, B., Schulz, S., Olanrewaju, A.S., Ellis-Jones, J., 2007. Impact pathway evaluation of an integrated *Striga hermonthica* control project in Northern Nigeria. Agricultural Systems 92, 201-222.

Dugje, I.Y., Kamara, A.Y., Omoigui, L.O., 2008. Influence of farmers' crop management practices on *Striga hermonthica* infestation and grain yield of maize (Zea mays L.) in the savanna zones of northeast Nigeria. Journal of Agronomy 7, 33-40.

Dugje, I.Y., Kamara, A.Y., Omoigui, L.O., 2006. Infestation of crop fields by *Striga* species in the savanna zones of Northeast Nigeria. Agriculture, Ecosystems & Environment

116, 251-254.

Dzomeku, I.K., Murdoch, A.J., 2007. Modelling effects of prolonged conditioning on dormancy and germination of *Striga hermonthica*. Journal of Agronomy 6, 235-249.

Egley, G.H., 1971. Mineral nutrition and the parasite-host relationship of witchweed. Weed Science 19, 528-533.

Egley, G.H., Dale, J.E., 1970. Ethylene, 2-chloroethylphosphonic acid and witchweed germination. Weed Science 18, 586-589.

Ejeta, G., 2007. The *Striga* scourge in Africa: a growing pandemic. In: Integrating New Technologies for *Striga* Control: Towards Ending the Witch-hunt. Eds G. Ejeta, J. Gressel. World Scientific Publishing Co., Hackensack, pp 3-16.

Elsgaard, L., 2001. Ethylene turn-over in soil, litter and sediment. Soil Biology & Biochemistry 33, 249-252.

Emechebe, A.M., Ahonsi, M.O., Kureh, I., Alabi, S.O., Gbehounou, G., Adango, E., 2003. Ability of excised root and stem pieces of maize, cowpea and soybean to cause germination of *Striga hermonthica* seeds. Crop Protection 22, 347-353.

Emechebe, A.M., Ellis-Jones, J., Schulz, S., Chikoye, D., Douthwaite, B., Kureh, I., Tarawali, G., Hussaini, M.A., Kormawa, P., Sanni, A., 2004. Farmers' perception of the *Striga* problem and its control in northern Nigeria. Experimental Agriculture 40, 215-232.

Eplee, R.E., 1992. Witchweed (*Striga asiatica*): An overview of management strategies in the USA. Crop Protection 11, 3-7.

Eplee, R.E., Norris, R.S., 1987. Field research techniques. In: Parasitic Weeds in Agriculture. Ed. L.J. Musselman, Volume 1, *Striga*. Boca Raton, CRC Press Inc., pp 271-280. Esilaba, A.O., Reda, F., Ransom, J.K., Wondimu Bayo, Gebremehdin Woldewahid, Beyenesh Zemichael, 2000. Integrated nutrient management strategies for soil fertility improvement and *Striga* control in Northern Ethiopia. African Crop Science Journal 8, 403-410.

Farina, M.P.W., Thomas, P.E.L., Channon, P., 1985. Nitrogen, phosphorus and potassium effects on the incidence of *Striga asiatica* (L.) Kuntze in maize. Weed Research 25, 443-447.

Gacheru, E., Rao, M.R., 2001. Managing *Striga* infestation on maize using organic and inorganic nutrient sources in western Kenya. International Journal of Pest Management 47, 233-239.

Gbèhounou, G., 1998. Seed ecology of *Striga hermonthica* in the Republic of Benin: host specificity and control potentials. Ph.D. thesis, Free University Amsterdam.

Gbèhounou, G., Egbers, W.S., Verkleij, J.A.C., Pieterse, A.H., 1991. A survey of *Striga* infestation in Borgou and Atacora Provinces. In: Proceedings 5th International Symposium on Parasitic Weeds, CIMMYT. Eds J.K. Ransom, L.J. Musselman, A.D.

Wosham, C. Parker. Nairobi Kenya, pp 137-142.

Gbèhounou, G., Pieterse, A.H., Verkleij, J.A.C., 1996. The decrease in seed germination of *Striga hermonthica* in the course of the rainy season is due to a dying-off process. Experientia 52, 264-267.

Gbèhounou, G., Pieterse, A.H., Verkleij, J.A.C., 2003. Longevity of *Striga* seeds reconsidered: results of a field study on purple witch-weed (*Striga hermonthica*) in Bénin. Weed Science 51, 940-946.

Graves, J.D., Press, M.C., Stewart, G.R., 1989. A carbon balance model of the sorghum-Striga hermonthica host-parasite association. Plant Cell & Environment 12, 101-107.

Gurney, A.L., Ransom, J.K., Press, M.C., 1995. The parasitic angiosperm *Striga hermonthica* can reduce photosynthesis of its sorghum and maize hosts in the field. Journal of experimental Botany 46, 1817-1823.

Gurney, A.L., Press, M.C., Scholes, J.D., 1999. Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*. New Phytologist 143, 573-580.

Gworgwor, N.A., Weber, H.C., 1991. Effect of N-application on sorghum growth, *Striga* infestation and the osmotic pressure of the parasite in relation to the host. Journal of Plant Physiology 139, 194-198.

Hartemink, A.E., 2006. Assessing soil fertility decline in the tropics using soil chemical data. Advances in Agronomy 89, 179-225.

Hearne, S.J., 2009. Control – the *Striga* conundrum. Pest Management Science 65, 603-614.

Heller, R., Wegmann, K., 2000. Mechanisms of resistance to *Striga hermonthica* (Del.) Benth. in *Sorghum bicolor* (L.) Moench. In: Breeding for *Striga* Resistance in Cereals. Eds B.I.G. Haussmann, D.E. Hess, M.L. Koyama, L. Grivet, H.F.W. Rattunde, H.H. Geiger. Margraf-Verlag, Weikersheim, Germany. pp 19-28.

Hess, D.E., Ejeta, G., 1987. Effect of cultural treatments on infestations of *Striga hermonthica* (Del.) Benth. (Schrophulariaceae) on sorhum in Niger. In: Proceedings of the 4th International Symposium on Parasitic Flowering Plants. Eds H.C. Weber, W. Forstreuter. Philipps-Universität, Marburg, Germany, pp 367-375.

Hibberd, J.M., Quick, W.P., Press, M.C., Scholes, J.D., 1998. Can source-sink relations explain response of tobacco to infection by the root holoparasite angiosperm *Orobanche cernua*? Plant, Cell & Environment 21, 333-340.

Humphrey, A.J., Galster, A.M., Beale, M.H., 2006. Strigolactones in chemical ecology: waste products or vital allelochemicals? Natural Product Reports 23, 592-614.

Husson, O., Michellon, R., Charpentier, H., Razanamparany, C., Moussa, N., Naudin, K., Razafintsalama, H., Rakotoarinivo, C., Andrianaivo, A.P., Rakotondramanana, Seguy, L., 2008. Le contrôle du *Striga* par les systèmes semis direct sur couverture végétale permanente (SCV). Manuel pratique du semis direct à Madagascar Vol. 1 Chapitre 3.

Ibijbijen, J., Urquiaga, S., Ismaili, M., Alves, B.J.R., Boddey, R.M., 1996. Effect of arbuscular mycorrhizas on uptake of nitrogen by *Brachiaria arrecta* and *Sorghum vulgare* from soils labelled for several years with 15N. New Phytologist 133, 487-494.

Igbinnosa, I., Cardwell, K.F., Okonkwo, S.N.C., 1996. The effect of nitrogen on the growth and development of giant witchweed, *Striga hermonthica* Benth.: effect on cultured germinated seedlings in host absence. European Journal of Plant Pathology 102, 77-86.

Ikie, F.O., Schulz, S., Ogunyemi, S., Emechebe, A.M., Togun, A.O., 2007. Influence of legume cropping patterns and organic/inorganic soil amendments on *Striga* seedbank and subsequent sorghum performance. Advances in Environmental Biology 1, 11-19.

IRAD – PRASAC1, 1999. Synthèse du diagnostic global PRASAC au Nord-Cameroun. IRAD/PRASAC, Garoua, Cameroon.

IRAD – PRASAC2, 1999. Terroirs villageois de Mafa Kilda. Résultats du diagnostic global IRAD/PRASAC, Garoua, Cameroon.

IRAD – PRASAC3, 1999. Terroirs villageois de Mowo. IRAD/PRASAC, Garoua, Cameroon.

Jäckel, U., Schnell, S., Conrad, R., 2004. Microbial ethylene production and inhibition of methanotrophic activity in a deciduous forest soil. Soil Biology & Biochemistry 36, 835–840.

Janssen, B.H., 1984. A simple method for calculating decomposition and accumulation of young soil organic-matter. Plant & Soil 76, 297-304.

Janssen, B.H., 1996. Nitrogen mineralization in relation to C:N ratio and decomposability of organic materials. Plant & Soil 181, 39-45.

Johnson, A.W., Roseberry, G., Parker, C., 1976. A novel approach to *Striga* and *Orobanche* control using synthetic germination stimulants. Weed Research 16, 223-227.

Kabambe,V.H., Kanampiu, F., Nambuzi, S.C., Kauwa, A.E., 2007. Evaluation of the use of herbicide (Imazapyr) and fertilizer application in integrated management of *Striga asiatica* in maize in Malawi. African Journal of Agricultural Research 2, 687-691.

Kamara, A.Y., Ellis-Jones, J., Amaza, P., Omoigui, L.O., Helsen, J., Dugje, I.Y., Kamai, N., Menkir, A., White, R.W., 2008. A participatory approach to increasing productivity of maize through *Striga hermonthica* control in northeast Nigeria. Experimental Agriculture 44, 349-36.

Kamara, A.Y., Menkir, A., Chikoye, D., Omoigui, L.O., Ekeleme, F., 2007. Cultivar and nitrogen fertilization effects on *Striga* infestation and grain yield of early maturing tropical maize. Maydica 52, 415-423.

Kanampiu, F.K., Ransom, J.K., Gressel, J., 2001. Imazapyr seed dressings for *Striga* control on acetolactate synthase target-site resistant maize. Crop Protection 20, 885-895.

Kayeke, J., Sibuga, P.k., Msaky, J.J., Mbwaga, A., 2007. Green manure and inorganic fertiliser as management strategies for witchweed and upland rice. African Crop Science Journal 15, 161-171.

Kim, S.K., Adetimirin, V.O., 2001. Conditioning effects of *Striga hermonthica* seed on field performance of maize. Crop Protection 20, 159-161.

Kim, S.K., Lagoke, S.T.O., Thé, C., 1997. Observations on field infection by witchweed (*Striga* species on maize in west and Central Africa. International Journal of pest Management 43, 113 - 121.

Kim, S.K., Adetimirin, V.O., 1997. Response of tolerant and susceptible maize varieties to timing and rate of nitrogen under *Striga hermonthica* infestation. Agronomy Journal 89, 38 – 44.

Kim, S.K., Lagoke, S.T.O., Thé, C., 1997. Observations on field infection by witchweed (*Striga* species) on maize in West and Central Africa. International Journal of Pest Management 43, 113-121.

Kim, S.K., Adetimirin, V.O., Thé, C., Dossou, R., 2002. Yield losses in maize due to *Striga hermonthica* in West and Central Africa. International Journal of Pest Management 48, 211-217.

Kossoumna Liba'a, N., Havard, M., 2006. Mutations de la filière cotonnière dans les provinces septentrionales du Cameroun – Perception et stratégies paysannes. Cahiers de Géographie du Québec 50, 65-82.

Koulandi, J., 2006. Rural resettlement, cotton cultivation and coping strategies in the Benue river basin, northern Cameroon. PhD Thesis, University of Tromsø, Norway.

Kranz, B., Fugger, W.D., Kroschel, J., Sauerborn, J., 1998. The influence of organic manure on *Striga hermonthica* (Del.) Benth. Infestation in Northern Ghana. In: H.P. Blume, H. Egger, E. Fleischhauer, A. Hebel, C. Reij, K.G. Steiner. Eds. Towards sustainable land use: furthering cooperation between people and institutions. Advances in GeoEcology 31 (1), 615 -619.

Kranz, B., 1997. Die Entwicklung der parasitischen Blutenpflanze *Striga hermonthica* (Del.) Benth. (Scrophulariaceae). PLITS 7 (3) Verlag Josef Margraf, Weikersheim, Germany, pp.154.

Kranz, B., 1999. Bedeutung von organischer Düngung für die Keimung und das Auftreten der parasitischen Blütenpflanze *Striga hermontica* (Del.) Benth.. PhD Thesis University of Hohenheim, Agroecology 2, APIA-Verlag, Laubach , Germany.

Kroschel, J., 1998. *Striga*- How will it affect African agriculture in the future ? - An ecological perspective. PLITS 16, 137-158.

Kroschel, J., 2001. A Technical manual for parasitic weed research and extension, Dordrecht, The Netherlands: GTZ – University of Hohenheim, Kluwer Academic Publishers. pp 35 –41.

Kuiper, E., 1997. Comparative studies on the parasitism of *Striga aspera* and *Striga hermonthica* on tropical grasses. PhD thesis Vrije Universiteit, Amsterdam The Netherlands.

Lendzemo, V. W., 2004. The tripartite interaction between sorghum, *Striga hermonthica* and arbuscular mycorrhizal fungi. PhD Thesis, Wageningen University, The Netherlands.

Lendzemo, V.W., Kuyper, T.W., Kropff, M.J., Van Ast, A., 2005. Field inoculation with arbuscular mycorrhizal fungi reduces *Striga hermonthica* performance on cereal crops and has the potential to contribute to integrated *Striga* management. Field Crops Research 91, 51-61

Lendzemo, V.W., Kuyper, T.W., Matusova, R., Bouwmeester, H.J., Van Ast, A., 2007. Colonization by arbuscular mycorrhizal fungi of sorghum leads to reduced germination and subsequent attachment and emergence of *Striga hermonthica*. Plant Signalling & Behavior 2, 58-62.

López-Ráez, J.A., Matusova, R., Cardoso, C., Jamil, M., Charnikova, T., Kohlen, W., Ruyter-Spira, C., Verstappen F., Bouwmeester, H., 2008. Strigolactones: ecological significance and use as a target for parasitic plant control. Pest Management Science 64, 471-477.

M'Biandoun, M., Olinda Bassala, J.-P., 2007. Savoir paysan et fertilité des terres au Nord-Cameroun. Cahiers Agricultures 16, 185-196.

Matusova, R., Rani K., Verstappen, F.W.A., Franssen, M.C.R., Beale, M.H., Bouwmeester, H.J., 2005. The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanche* are derived from the carotenoid pathway. Plant Physiology 139, 920-934.

Matusova, R., Van Mourik, T.A., Bouwmeester, H.J., 2004. Changes in the sensitivity of parasitic weed seeds to germination stimulants. Seed Science Research 14, 335–344.

Mbétid-Bessane, E., Havard, M., Djondang, K., 2006. Évolution des pratiques de gestion dans les exploitations agricoles familiales des savanes cotonnières d'Afrique centrale. Cahiers Agricultures 15, 555-561.

Mohamed, K.I., Musselman, L.J. Riches, C.R., 2001. The genus *Striga* (Scrophulariaceae) in Africa. Annals of the Missouri Botanical Garden 88, 60-103.

Moormann, F.R., Lal, R., Juo, A.S.R., 1985. The soils of IITA. A detailed study of eight soils near Ibadan, Nigeria, with special reference to their agricultural use. IITA Technical Bulletin No. 3. 3rd Edn., Ibadan, Nigeria: IITA.

Mumera, L.M., Below, F.E., 1993. Role of nitrogen in resistance to *Striga* parasitism of maize. Crop Science 33, 758 – 763.

Naudin, K., Balarabe, O., Séguy, L., Guibert, H., Charpentier, H., Boulakia, S., Abou Abba, A., Thézé, M., 2005. A four-year timeframe to develop and begin extension of direct seeding mulch-based cropping systems, in the cotton belt of North Cameroon.

agroecologie.cirad.fr/content/download/7095/.../1130450435.pdf. Accessed 31/8/2009.

Nekouam, N., Marley, P.S., Emechebe, A.M., Akpa, A.D., 2006. Development and assessment of *Fusarium Oxysporum*-based mycoherbicide for control of *Striga hermonthica* in sorghum. Archives of Phytopathology and Plant Protection 39, 197-203.

Obale-Ebanga, F., 2001. Impacts of agricultural land use histories on soil organic matter dynamics and related properties of Savannah soils in North Cameroon. PhD thesis, University of Amsterdam, the Netherlands.

Odhiambo, G. D., Ransom, J. K., 1995. Long term strategies for *Striga* control. In: Proceedings of the Fourth East and South African Maize Conference, CIMMYT. Eds. D. Jewell, S. Waddington, J.K. Ransom, K. Pixley. Harare, pp. 263 - 266.

Odhiambo, G.D., 1998. Studies on witchweed [*Striga hermonthica* (Del.) Benth.] seed longevity and maize (*Zea mays* L.) productivity under different management systems in Kenya. Ph.D. Thesis, University of Reading, Reading, UK p. 198.

Olivier, A., 1996. La relation entre le *Striga hermonthic*a et ses hôtes : une synthèse. Canadian Journal of Botany 74, 1119-1137.

Olivier, A., Glaszmann, J.C., Lanaud, C., Leroux, G.D., 1998. Population structure, genetic diversity and host specificity of the parasitic weed *Striga hermonthica* (Scrophulariaceae) in Sahel. Plant Systematics & Evolution 209, 33-45.

Orr, A., Ritchie, J.M., 2004. Learning from failure: smallholder farming systems and IPM in Malawi. Agricultural Systems 79, 31-54.

Oswald, A., 2005. *Striga* control-technologies and their dissemination. Crop Protection 24, 333-342.

Oswald, A., Ransom, J.K., 2001. *Striga* control and improved farm productivity using crop rotation. Crop Protection 20, 113-120.

Oswald, A., Ransom, J.K., Abayo, G., Kroschel, J., Sauerborn, J., 1999. Intercropping – An option for *Striga* control. In: Advances in parasitic weed control at on-farm level, vol. 1. Eds J. Kroschel, H. Mercer-quarshie, J. Sauerborn. Margraf- verlag, Weikersheim Germany, pp. 171-179.

Ouattara, B., Ouattara, K., Serpantie, G., Mando, A., Sedogo, M.P., Bationo, A., 2006. Intensity cultivation induced effects on soil organic carbon dynamics in the western cotton area of Burkina Faso. Nutrient cycling in agroecosystems 76, 331-339.

Parker, C., 2009. Observations on the current status of *Orobanche* and *Striga* problems worldwide. Pest Management Science 65, 543-459.

Parker, C., Riches, C.R., 1993. Parasitic Weeds of the World: Biology and Control. CAB International, Wallingford UK.

Parkinson, V., Njinyam, S., Ayongwa, G.C., Ngawa, L., 1991. The F.A.O. *Striga* project in Cameroon. In: Combating *Striga* in Africa. Ed. S.K. Kim. IITA, Ibadan Nigeria, pp.

126-133.

Pesch, C., Pieterse, A.H., 1982. Inhibition of germination in *Striga* by means of urea. Experientia 38, 559-560.

Pieterse, A.H., Verkleij, J.A.C., 1991. Effect of soil conditions on *Striga* development - a review. In: Proceedings Fifth International Symposium on Parasitic Weeds, Nairobi Kenya, pp. 329-339.

Pieterse, A.H., Verkleij, J.A.C., Den Hollander, N.G., Odhiambo, G.D., Ransom, J.K., 1996. Germination and viability of *Striga hermonthica* seeds in Western Kenya in the course of the long rainy season. In: Proceedings of the 6th International Symposium on Parasitic Weeds, Cordoba, Spain, pp. 457-464.

Porteres, R., 1948. Les Plantes indicatrices de niveau de fertilite du complexe culturale edapho-climatique en Afrique Tropicales. Agronomie Tropicale 3, 246-257.

Press, M.C., Graves, J.D. Stewart, G.R., 1990. Physiology of the interaction of angiosperm parasites and their higher plant hosts. Plant Cell & Environment 13, 91-104.

Press, M.C., Smith, S., Stewart, G.R., 1991. Carbon acquisition and assimilation in parasitic plants. Functional Ecology 5, 278-283.

Raju, P.S., Osman, M.A., Soman, P., Peacock, J.M., 1990. Effects of N, P and K on *Striga asiatica* (L.) Kuntze seed germination and infestation of sorghum. Weed Research 30, 139-144.

Ramaiah, K.V., Cildley, V.L., House, L.R., 1991. A time course study of early establishment stages of the parasitic angiosperm *Striga asiatica* on susceptible sorghum roots. Annals of Applied Biology 118, 403-410.

Rank, C., Rasmussen, L.S., Jensen, S.R., Pierce, S., Press, M.C., Scholes, J.D., 2004. Cytotoxic constituents of *Alectra* and *Striga* species. Weed Research 44, 265-270.

Ransom, J.K., 1999. The Status quo of *Striga* control: cultural, chemical and integrated aspects. In: Advances in parasitic weed control at on-farm level, vol. 1. Eds J. Kroschel, H. Mercer-quarshie, J. Sauerborn. Margraf- verlag, Weikersheim Germany, pp. 133 - 143.

Ransom, J.K., 2000. Long-term approaches for the control of *Striga* in cereals: field management options. Crop Protection 19, 759-763.

Ransom, J.K., Odhiambo, G.D., 1994. Long term effect of fertility and hand-weeding on *Striga* in maize. In: Biology and management of *Orobanche*. Eds A.H. Pieterse, J.A.C. Verkleij, S.J. ter Borg. Proceedings of the 3rd International Workshop on *Orobanche* and related *Striga* research. Royal Tropical Institute, The Netherlands, pp. 513-519.

Reda, F., Verkleij, J. A. C., Ernst, W. H. O., 2005. Intercropping for the Improvement of Sorghum Yield, Soil Fertility and *Striga* Control in the Subsistence Agriculture Region of Tigray (Northern Ethiopia). Journal of Agronomy & Crop Science 191, 10-19.

Rodenburg, J., 2005. The role of sorghum genotype in the interaction with the parasitic weed *Striga hermonthica*. PhD thesis, Wageningen University, Wageningen, The Netherlands.

Rodenburg, J., Bastiaans, L., Kropff, M.J., 2006a. Characterization of host tolerance to *Striga hermonthica*. Euphytica 147, 353-365.

Rodenburg, J., Bastiaans, L., Kropff, M.J., van Ast, A., 2006b. Effects of host plant genotype and seed bank density on *Striga* reproduction. Weed Research 46, 251-263.

Rodenburg, J., Bastiaans, L., Weltzien, E., Hess, D.E., 2005. How can field selection for *Striga* resistance and tolerance in sorghum be improved? Field Crops Research 93, 34-50.

Samaké, O., 2003. Integrated crop management strategies in sahelien land use systems to improve agricultural productivity: A case study in Mali. PhD Thesis, Wageningen University, The Netherlands.

Samake, O., Smaling, E.M.A., Kropff, M.J., Stomph, T.J., Kodio, A., 2005. Effects of cultivation practices on spatial variation of soil fertility and millet yields in the Sahel of Mali. Agriculture, Ecosystems and Environment. 109, 335–345.

Samaké, O., Stomph, T.J., Kropff, M.J., Smaling, E.M.A., 2006. Integrated pearl millet management in the Sahel: effects of legume rotation and fallow management on productivity and *Striga hermonthica* infestation. Plant & Soil 286, 248-257.

Santos-Izquierdo, B., Pageae, V., Fer, A., Simier, P., Robins, R.J., 2008. Targeted distribution of photo-assimilate in *Striga hermonthica* (Del.) Benth. parasitic on *Sorghum bicolor* L. Phytochemistry Letters 1, 76-80.

Sauerborn, J., 1991a. The economic importance of the phytoparasites *Orobanche* and *Striga*. In: Proceedings of the 5th International Symposium of Parasitic Weeds, pp. 137-143. Nairobi, Kenya : CIMMYT.

Sauerborn, J., 1991b. Parasitic flowering plants – Ecology and Management. Weikersheim, Germany: Margraf Verlag. Pp. 35–41.

Sauerborn, J., Kranz, B., Mercer-Quarshie, H., 2003. Organic amendments mitigate heterotrophic weed infestation in savannah agriculture. Applied Soil Ecology 23, 181-186.

Saunders, A.R., 1933. Studies in phanerogamic parasitism with special reference to *Striga lutea* Lour. South Africa Department of Agriculture Science Bulletin 128, 1-56.

Schlecht, E., Buerkert, A., Tielkes, E., Bationo, A., 2006. A critical analysis of challenges and opportunities for soil fertility restoration in Sudano-Sahelian West Africa. Nutrient Cycling in Agroecosystems 76, 109-136.

Schulz, S., Hussaini, M.A., Kling, J.G., Berner, D.K., Ikie, F.O., 2003. Evaluation of integrated *Striga hermonthica* control technologies under farmer management. Experimental Agriculture 39, 99-108.

Seignobos, C., Iyebi-Mandjeck, O., Nassourou, A., 1995. Terroir de Balaza-Domayo: Saturation foncière et muskuwaari. ORSTOM, Paris.

Sherif, A.M., 1983. Effect of nitrogen and organic matter on *Sorghum bicolor* (Moench) and *Striga hermonthica* (Benth.). M.Sc. thesis, University of Reading, UK.

Sherif, A.M., Parker, C., 1988. Effect of nitrogen sources and organic matter on *Sorhum bicolor* L. Moench and *Striga hermonthica* Benth. Ethiopian Journal of Agricultural Science 8, 19 – 35.

Simier, P., Constant, S., Degrande, D., Moreau, C., Robins, R.J., Fer, A., Thalouarn, P., 2006. Impact of nitrate supply in C and N assimilation in the parasitic plant *Striga hermonthica* (Del.) Benth (Scrophulariaceae) and its host *Sorghum bicolor* L. Plant, Cell & Environment 29, 673-681.

Singh, L., Ndikawa, R., Rao, R., 1991. Integrated approach to *Striga* management on sorghum in North Cameroon. In: Proceedings of the 5th International Symposium of Parasitic Weeds. Eds J.K. Ransom, L.J. Musselman, A.D.Worsham, C. Parker. CIMMYT, Nairobi Kenya, pp. 223-226.

Smaling, E.M.A., Braun, A.R., 1996. Soil fertility research in sub-Saharan Africa: new dimensions, new challenges. Communications in Soil Science and Plant Analysis 27, 365-386.

Smaling, E.M.A., Stein, A., Sloot, P.H.M., 1991. A statistical analysis of the influence of *Striga hermonthica* on maize yields in fertilizer trials in Southwestern Kenya. Plant & Soil 138, 1-8.

Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., Wright, J.P., 2009. Diversity has stronger top-down than bottom-up effects on decomposition- meta-analysis decomposition rates. Ecology 90, 1073-1083.

Stoorvogel, J.J., Smaling, E.M.A., 1998. Research on soil fertility decline in tropical environments: integration of spatial scales. Nutrient Cycling in Agro-ecosystems 50, 151-158.

Stringer, L.C., Twyman, C., Thomas, D.S.G., 2007. Learning to reduce degradation on Swaziland's arable land: enhancing understanding of *Striga asiatica*. Land Degradation & Development 18, 163-177.

Tabo, R., Bationo, A., Diallo-Maimouna, K., Hassane, O., Koala, S., 2006. Fertilizer micro-dosing for the prosperity of small-scale farmers in the Sahel: Final Report. Global theme on agroecosystems, report 23. ICRISAT, Niamey, Niger 28pp. http://ejournal.icrisat.org/mpii/v3i1/pdfs/24-2006.pdf.

Teyssier, A., 2004. La régulation fonciere au Cameroun: entre regimes communautaires et aspirations citoyennes. Cahiers Agricultures, 13, 522 – 527.

Thalouarn, P., Fer, A., 1993. Le *Striga*, un ravageur de cultures vivrières: le point sur les connaissances recentes et sur les methodes de lutte. Cahiers Agricultures 5, 167-182.

Tian, G., Kang, B.T., Kolawole, G.O., Idinabo, P., Salako, F.K., 2005. Long-term effects of fallow systems and lengths on crop production and soil fertility maintenance in West Africa. Nutrient cycling in Agroecosystems 71, 139-150.

Traore, H., Yonli, D., 1999. Study of farmers' perception of the *Striga* problem and inventory inventory of indigenous *Striga* control methods in Burkina Faso. In: Advances in parasitic weed control at on-farm level, vol. 1. Eds J. Kroschel, H. Mercer-quarshie, J. Sauerborn. Margraf- verlag, Weikersheim Germany, pp.197-205.

Van Ast, A., 2006. The influence of time and severity of time and severity of Striga infection on the *Sorghum bicolor-Striga hermonthica* association. PhD Thesis, Wageningen University, Wageningen, The Netherlands.

Van Ast, A., Bastiaans, L., Katile, S., 2005. Cultural control measures to diminish sorghum yield loss and parasite success under *Striga hermonthica* infestation. Crop Protection 24, 1023-1034.

Van Ast, A., Bastiaans, L., Kropff, M.J., 2000. A comparative study on *Striga hermonthica* interaction with a sensitive and a tolerant sorghum cultivar. Weed Research 40, 479-493.

Van Delft, G.J., 1997. Root Architecture in relation to avoidance of *Striga hermonthica* infection. PhD thesis, University of York, York, England.

Van Mourik, T.A., 2007. *Striga hermonthica* seed bank dynamics: process quantification and modelling. PhD Thesis, Wageningen University, Wageningen, The Netherlands.

Van Mourik, T.A., Stomph, T.J., Murdoch, A.J., 2005. Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. Journal of applied Ecology 42, 299-305.

Van Mourik, T.A., Stomph, T.J., Westerman, P.R., 2003 Estimating *Striga hermonthica* seed mortality under field conditions. Aspects of applied biology 69, 187-194.

Van Mourik, T.A., Bianchi, F.J.J.A., Van der Werf, W., Stomph, T.J., 2008. Long-term management of *Striga hermonthica*: strategy evaluation with a spatio-temporal population model. Weed Research 48, 329-339.

Vanlauwe, B., Bationo, A., Chianu, J., Giller, K.E., Merckx, R., Mokwunye, U., Ohoikpehai, P., Pypers, P., Tabo, R., Shepherd, K.D., Smaling, E.M.A., Woomer, P.L., Sanginga, N., 2010. Integrated soil fertility management; operational definition and consequences for implementation and dissemination. Outlook on Agriculture 39, 17-24.

Vanlauwe, B., Giller, K.E., 2006. Popular myths around soil fertility management in sub-Saharan Africa. Agriculture, Ecosystems & Environment 116, 34-46.

Vanlauwe, B. Kanampiu, F. Odhiambo, G.D. De Groote, H. Wadhams, L.J., Khan, Z.R. 2008. Integrated management of *Striga hermonthica*, stemborers and declining soil fertility in western Kenya. Field Crop Research 107, 102-115.

Venne, J., Beed, F., Avocanh, A., Watson, A., 2009. Integrating *Fusarium oxysporum* f. sp. strigae into cereal cropping systems in Africa. Pest Management Science 65, 572-580.

Verkleij, J.A.K., Luttikholt, L., Yehouenou, A., Egbers, W.S., Pieterse, A.H., 1994. Interaction between N-fertiliser and the parasitic weed, *Striga hermonthica* (Del.) Benth. In: Biology and management of *Orobanche*. Eds A.H. Pieterse, J.A.C. Verkleij, S.J. ter Borg. Proceedings of the 3rd International Workshop on *Orobanche* and related *Striga* research. Royal Tropical Institute, The Netherlands, pp. 520-527.

Vissoh, P.V., Gbèhounou, G., Ahanchédé, A., Kuyper, T.W., Röling, N.R., 2005. Weeds as agricultural constraints to farmers in Benin: results of a diagnostic study. NJAS - Wageningen Journal of Life Sciences 52, 305-329.

Vissoh, P.V., Gbèhounou, G., Ahanchédé, A., Röling, N.G., Kuyper, T.W., 2008. Evaluation of integrated crop management strategies employed to cope with *Striga* infestations in permanent land use systems in southern Benin. International Journal of Pest Management 54, 197-206.

Vissoh, P.V., Mongbo, R., Gbèhounou, G., Hounkonnou, D., Ahanchédé, A., Röling, N.G., Kuyper, T.W., 2007. The social construction of weeds: different reactions to an emergent problem by farmers, officials and researchers. International Journal of Agricultural Sustainability 5, 161-175.

Vogt, W., Sauerborn, J., Honisch, M., 1991. Striga hermonthica, distribution and infestation in Ghana and Togo on grain crops. In: Proceedings of the 5th International Symposium of Parasitic Weeds. Eds J.K. Ransom, L.J. Musselman, A.D.Worsham, C. Parker. CIMMYT, Nairobi Kenya, pp. 372-377.

Webb, M., Smith, M.C., 1996. Biology of *Striga hermonthica* (Schrophulariaceae) in Sahelian Mali: effects on pearl millet yield and prospects of control. Weed Research 36, 203-211.

Weber, G., Elemo, K., Lagoke, S., Oikeh, S., 1995. *Striga hermonthica* in farming systems of the northern guinea Savannah. Research Monograph, No. 19, Resource and Crop Management Division, IITA Ibadan 69pp

Weerasuriya, Y., Siame, B.A., Hess, D., Ejeta, G., Butler, L.G., 1993. Influence of conditions and genotype on the amount of *Striga* germination stimulants exuded by roots of several host crops. Journal of Agricultural & Food Chemistry 41, 1492-1496.

Weisskopf, L., Akello, P., Milleret, R., Khan, Z.R., Schulthess, F., Gobat, J.M., Le Bayon, R.C., 2009. White lupin leads to increased maize yield through a soil fertility-independent mechanism: a new candidate for fighting *Striga hermonthica* infestation? Plant Soil 319, 101-114.

Westerman, P.R., Van Ast, A., Stomph, T.J., Van der Werf, W., 2007. Long-term management of the parasitic weed *Striga hermonthica*: Strategy evaluation with a population model. Crop Protection 26, 219-227.

Wolfe, A.D., Randle, C.P. Liu, L., Steiner, K.E. 2005. Phylogeny and biogeography of Orobanchaceae. Folia Geobotanica 40, 115-134.

Woomer, P.L., Bokanga, M., Odhiambo, G.D., 2008. *Striga* management and the African farmer. Outlook on Agriculture 37, 277-282.

Wubeneh, N.G., Sanders, J.H., 2006. farm-level adoption of sorghum technologies in Tigray, Ethiopia. Agricultural Systems 91, 122-134.

Yoneyama, K., Xie-XiaoNan, Kusumoto, D., Sekimoto, H., Sugimoto, Y., Takeuchi, Y., 2008. Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. Planta 227, 125-132.

Yoneyama, K., Yoneyama, K., Takeuchi, Y., Sekimoto, H., 2007. Phosphurus deficiency in red clover promotes exudation of orobanchol the signal for mycorrhizal symbionts and germination stimulants for root parasites. Planta 225, 1031-1038.

Yonli, D., Traoré, H., Hess, D.E., Sankara, P., Séréme, P., 2006. Effects of growth medium, *Striga* seed burial distance and depth on efficacy of Fusarium isolates to control *Striga hermonthica* in Burkina Faso. Weed research 46, 73-83.

Zechmeister-Boltenstern, S., Smith, K.A., 1998. Ethylene production and decomposition in soils. Biology & Fertility of Soils 26, 354-361.

SUMMARY

The parasitic plant -or weed- *Striga hermonthica* (striga), can be found on a range of cereals where it often causes severe yield reductions. It is very common in the drier areas of Africa, especially on infertile soils. Striga is among the major constraints to cereal production, thus threatening sustainable food production. The striga problem has worsened for African farmers, in conjunction with degrading soil fertility. The life history of striga confers it with special survival strategies, making it a very effective and ultimately harmful pest under the present agricultural systems. Poor soil fertility is not only generating the striga problem, but in itself is already an immense constraint to cereal production in the African savannahs. Without soil fertility improvement striga management is apparently unsuccessful in terms of a lack of improvement in cereal productivity.

When analysing the approach to the striga problem till present, we are left with the impression that scientists, policy makers and farmers consider and conceptualise striga very differently: a weed, a parasitic plant or a symptom of poor soil fertility. The issue whether striga is a weed or a symptom of adverse conditions has two aspects – one is related to questions on causal mechanisms and the other to questions which agronomic practices to reduce or control striga would have the larger chance of being adopted by farmers. Should farmers control striga, even when the impact on yields would be negligible? Or should fertility enhancement, leading to higher yields, be their focus, also when not accompanied by a reduction in striga numbers? Another related question may also be asked: Can striga control options at low and high striga pressure be the same or are rather different approaches required? This thesis seeks to examine how improving soil fertility through the use of organic amendments (here specifically by-products from cotton) can improve sorghum production systems suffering from striga infections. More specifically, this research work seeks to understand how quality (nitrogen content) and quantity of organic matter inputs affect soil properties and through that, sorghum production and striga dynamics.

In Chapter 2 surveys are presented of striga infestation in northern Cameroon, over a period of almost 20 years (1987–2005); to assess striga dynamics and evaluate the success –or rather lack of success– of proposed control strategies. In that period it was found that the percentage of striga-infested maize fields increased, while in the already heavily infested sorghum fields it essentially remained constant. During the study period the increased land pressure led to a reduction in the use of fallow to restore the soil and cereal-legume intercropping or rotational cropping and a higher frequency of cereal (mono-) cropping. Yields from farmers' fields did not correlate with striga incidence as low yields were recorded on fields with largely varying striga density. These observations confirmed farmers' prioritisation of soil fertility, weeds, and labour for weeding as production constraints, rather

than striga –which was not considered a weed–. During the same period farmers experienced reduced access to fertiliser input due to the decline in the cotton industry, while access to organic manure remained limited, further hampering their options to improve soil fertility. The results from this study –two decades of emphasis on striga were unsuccessful– led to a reconsideration of assumptions related to striga management and the management of soil fertility. Rather than primarily focusing on striga as constraint, the entry point to tackle low yields and the further worsening of the striga situation should follow the constraints as prioritised by farmers. In order to investigate whether and how soil fertility improvement through use of organic matter could enhance agricultural productivity and in this way reduce striga in farmers' fields, a large field experiment was carried out as reported in chapters 3 and 4.

In Chapter 3, I studied the different ways organic matter amendments of different quality affect striga seed survival. In three consecutive years plots received a single dose of 6 ton organic matter per hectare per cropping season but with large differences in quality in terms of nitrogen mass concentration and therefore nitrogen release rates. Soil moisture, soil temperature and soil ethylene concentrations were measured, while buried nylon seed bags were periodically withdrawn from the soil and assayed for seed viability and germination. Laboratory tests showed that maximal seed germination was obtained in Petri dishes with 1 ppm ethylene at 48 hours of exposure time to this stimulant. Organic matter amendments in the field significantly depressed striga seed survival. The effect was strongest with organic matter of high quality so the most easily degradable material. Organic matter of low quality (with a low nitrogen mass concentration) enhanced soil water content during the first five days after a rainfall event and reduced soil temperature by 0.5 °C. These changes, though, could not explain the lower seed survival of striga. Observed peak ethylene concentrations in soil were between 2 and 3 ppm, in principle high enough to stimulate striga seed germination. However, observed seed survival did not correlate with soil ethylene concentrations. The latter in turn did not differ between qualities of the applied organic matter. Seed survival decreased with increasing time of burial, implying that the effect of seed decay is long-term and may hardly be beneficial during the ongoing cropping season. Microbiological degradation of organic matter, including that of striga seeds, is proposed as the most probable cause of seed depletion in the soil as influenced by organic matter.

In the second part of the experiment (Chapter 4), striga and sorghum performance as affected by organic matter amendments was studied during three cropping seasons, following a three-factorial experiment. Next to the quality of organic amendments I studied the role of the striga infection level –by manipulating the density of striga seeds in the soil– and compared three consecutive years of sorghum cropping with two years of fallow followed by one year of sorghum. The effect of the different mixtures of cotton by-products on sorghum yield were well described by the N mineralisation, as obtained through calculations with a simple model. A good correlation was observed in all three years between sorghum productivity and N released through mineralisation. There was an increasing negative effect of organic matter on striga as the quality of the applied material increased. I found that addition of low-quality organic matter is disadvantageous in striga-infected cereal fields as it leads to equal sorghum performance with rather an increase in striga numbers and biomass, which in turn will lead to further enhancing the striga seed bank. The question remains as to the implication of these findings for the local farmers. From the perspective of yield increase and striga management, these studied organic matter amendments may not be practicable for the resource-poor farmer, because of the high quantities of high-quality organic matter required. The same is true for the studied fallow period. While it improved sorghum yield and reduced striga infestation, such fallows are impracticable at the current land pressure.

In Chapter 5 I studied the role of nitrogen nutrition of young sorghum plants on the stimulating effect of their roots on striga seed germination, in a series of pot and laboratory experiments. Both amount and timing of N application affected sorghum root nitrogen mass concentrations and through this the stimulating effect of roots on the germination of striga seeds. Roots with a higher nitrogen mass concentration stimulated striga germination less, which seems a clear indication that less of the germination stimulants were exuded by the roots. Striga seed germination decreased linearly with increasing root N mass concentrations until a root N mass concentration of 19.5 mg N g^{-1}, after which no further reduction occurred. At all higher mass concentrations still some striga germination was observed. It was not possible to reduce striga seed germination to a zero level.

In the final discussion (Chapter 6) I place the findings in a broader framework. After a brief summary of the major findings I present a new perspective on the research and control of striga. The constraints to cereal production as farmers perceive will have to be taken as starting point: so soil fertility management. As sustainable farm intensification remains the ultimate solution in Africa, there is a need for farmers to invest in the soil and to increase soil fertility. However, there are several constraints to such investments. The prevailing land tenure system provides farmers only short-term secured access to the same fields, making more long-term investments in the land that do not also pay-off on the short term uninteresting and difficult for the small-scale farmer. In addition the options for farmers to buy fertilisers are restricted. Finally also, the availability of organic matter is very limited; both because of limited availability *per se* and because of competing uses like animal feed for roaming herds and fuel for cooking, etc. There is need for a joint commitment and effort from policy makers, researchers, extension workers and farmers to alleviate these limitations to change. In this chapter I introduce a new conceptual model that links changes in cereal yield and striga infestation over time as driven by changes in soil fertility. The underlying data for this model have usually been interpreted as an indication how decline in cereal yield was *caused* by striga. However, it is now proposed that both factors co-vary with an external driving variable, which is soil fertility. The model shows the logics behind the observed low sorghum yields at a broad range of striga densities. The new model proposes that recovery of the agricultural system will follow a different trajectory than degradation. Under the classical interpretation successful interventions to reduce striga numbers would automatically result in increasing yields. The options for recovery of the system essentially rely on soil fertility, while only after soil fertility improvement has set in striga pressure may modify the trajectory to some extent. The implication of the model is therefore that recovery of soil fertility should be the priority. The fundamental question remains how to reach this aim while availability in terms of both quantities and quality of the necessary fertilisers and organic matter is limited for the resource-poor farmer. In view of the constraints that farmers face, long-term soil fertility improvements that do not pay off in the first year(s) are not worth the investment in cash and labour. Outlets for farm produce at prices that are profitable to farmers therefore remain a key driver for sustainable intensification. The challenge to agronomists is to consider how to make farm intensification rewarding and attainable for resource-poor farmers.

Finally I propose an integrated scheme for the intensification of cereal cropping in areas where striga is an obstacle, with a focus on northern Cameroon but with potential applicability in the Sahel and possibly even sub-Saharan Africa at large. The starting point is integrated soil fertility management, focusing on yield improvements but with an eye for reduction of striga pressure. Crop rotation and intercropping with selected non-host leguminous crops are essential ingredients. There is yet no single striga-control component that can give a 100% control of the parasite, especially when infection levels are high. There are techniques available if and when additional striga control is essential, although it has to be acknowledged that some of these may not be currently affordable for the majority of smallholder farmers. And as long as these farmers do consider soil fertility their main priority and not striga, it is ineffective to consider striga as entry point for the improvement to agricultural production in striga-infected areas.

RÉSUMÉ

La plante parasite ou la mauvaise herbe *Striga hermonthica* (striga), très fréquente sur les sols pauvres des régions sèches de l'Afrique, provoque souvent des baisses de rendement sévères sur une gamme variée de céréales. Considérée comme l'une des contraintes majeures à la production de céréales, elle menace la production alimentaire durable. L'infestation du striga s'est aggravée pour les agriculteurs africains, en rapport avec le déclin de la fertilité des sols. Le cycle de vie du striga lui confère des stratégies spéciales de survie, le rendant très nuisible dans les systèmes agricoles actuels. La pauvreté des sols n'accentue pas seulement l'infestation du striga, mais constitue en soi une contrainte forte pour la production céréalière dans les savanes d'Afrique. L'amélioration de la productivité céréalière passe nécessairement par l'amélioration de la fertilité des sols permettant aussi de lutter contre le striga. L'analyse des problèmes du striga semble montrer que les scientifiques, les décideurs et les agriculteurs le considèrent et le caractérisent différemment : une mauvaise herbe, une plante parasite ou un symptôme de la pauvre fertilité des sols. Cette distinction tient aux deux aspects suivants : l'un est lié à des questions sur les mécanismes de causalité de la baisse du rendement et l'autre à des questions parmi lesquelles les pratiques agronomiques visant à réduire ou lutter contre le striga auraient plus de chance d'être adoptées par les agriculteurs. Les agriculteurs doivent-ils lutter contre le striga quand bien même l'impact sur les rendements serait négligeable ? Ou bien doivent-ils mettre l'accent sur l'amélioration de la fertilité du sol conduisant à des rendements plus élevés en dépit de la présence du striga ? Une autre question associée peut également être posée : Peut-on avoir les mêmes options de contrôle de cette plante parasite quelle que soit son intensité dans la parcelle ou des approches différentes sont-elles nécessaires? Cette thèse vise à examiner comment l'amélioration de la fertilité des sols par l'utilisation d'amendements organiques (spécifiquement le tourteau et les coques de coton) peut améliorer les systèmes de production du sorgho infestés par le striga. Plus spécifiquement, ce travail de recherche vise à comprendre comment la qualité (teneur en azote) et la quantité des apports de matières organiques affectent les propriétés du sol et par là, la production du sorgho et la dynamique du striga.

Dans le chapitre 2, sont présentés les résultats des études sur l'infestation du striga au nord Cameroun sur une période de près de 20 ans (1987-2005). Ces études visaient à analyser la dynamique de cette plante et à évaluer le succès ou plutôt le manque de succès des stratégies de lutte proposées. Ces études ont montré que l'infestation par le striga a augmenté dans les champs de maïs et est restée constante dans ceux de sorgho. Au cours de cette période, la pression foncière accrue a conduit à une réduction d'utilisation de la jachère, ainsi que des cultures associées céréales légumineuses et des rotations des cultures, stratégies

proposées pour restaurer la fertilité des sols. Il a également été noté une fréquence plus élevée de la monoculture des céréales.

Les rendements des champs des agriculteurs n'étaient pas corrélés avec l'infestation du striga, car de faibles rendements ont été enregistrés sur des champs dont l'infestation par le striga était très variable. Ces observations ont confirmé que pour les agriculteurs, les contraintes de production sont en priorité dues à la fertilité des sols, aux mauvaises herbes et à la main d'œuvre pour le désherbage plutôt qu'au striga qui n'était pas considéré comme une mauvaise herbe. Au cours de la même période, l'accès des agriculteurs aux engrais minéraux a été réduit en raison de la chute de la production cotonnière, et l'accès à la fumure organique est resté limité, entravant davantage leurs options d'amélioration de la fertilité des sols. Les résultats de ces deux décennies d'études/recherches sur le striga n'ont pas été concluants, d'où un réexamination/ré-évaluation des hypothèses relatives à la gestion du striga et à la fertilité des sols. Plutôt que de se concentrer sur le striga comme contrainte, le point de départ pour les analyses de la faiblesse des rendements et de l'aggravation de l'infestation du striga doit s'appuyer sur les contraintes prioritaires des agriculteurs. Afin de voir comment l'amélioration de la fertilité des sols par l'utilisation de la matière organique pourrait accroître la productivité agricole et par conséquent réduire l'infestation du striga dans les champs des agriculteurs, une expérimentation de terrain a été effectuée (voir chapitres 3 et 4).

Dans le chapitre 3, j'ai étudié les effets de différentes qualités de matière organique sur la survie des graines du striga dans le sol. Pendant trois années de cultures consécutives (de 2000 à 2002), les parcelles ont reçu une dose unique de 6 tonnes de matières organiques par hectare et par campagne agricole, mais avec de grandes différences dans la qualité en termes de concentration en azote et donc de taux de libération de l'azote. La méthodologie du travail a consisté à la mesure de l'humidité du sol, de la température du sol et des concentrations d'éthylène du sol ; les sacs de semences du striga en nylon enterrés ont été régulièrement retirés du sol et analysés pour déterminer la viabilité des graines et leur taux de germination. Les tests de laboratoire ont montré que le taux de germination des graines le plus élevé a été obtenu dans des boîtes de Pétri avec 1 ppm d'éthylène à 48 heures de temps d'exposition à ce stimulant. Les amendements organiques dans le sol ont diminué de façon significative la survie des graines de striga. L'effet le plus fort a été obtenu avec la matière organique de haute qualité donc le matériau le plus facilement dégradable. La matière organique de faible qualité (avec une faible teneur en azote) a amélioré la teneur en eau du sol au cours des cinq premiers jours après une pluie et a réduit la température du sol de 0,5 °C. Ces changements, cependant, ne pouvaient pas expliquer la plus faible survie des semences du striga. Les concentrations de pointe d'éthylène observées dans le sol étaient comprises entre 2 et 3 ppm, valeurs assez élevées en principe pour stimuler la germination des graines de striga. Cependant, la survie des graines observées n'était pas corrélée avec les concentrations d'éthylène du sol. Ce dernier paramètre à son tour ne différait pas entre les qualités de la matière organique appliquée. La survie des graines a diminué avec l'augmentation du temps d'enterrement ; ce qui implique que l'effet de la décomposition de la semence est à long terme et peut difficilement être bénéfique pendant la saison de culture en cours. La dégradation microbiologique de la matière organique, y compris celle des graines de striga, est proposée comme la cause la plus probable de la diminution du nombre de graines dans le sol sous l'influence de la matière organique.

Dans la deuxième partie de l'expérimentation (chapitre 4), l'effet de la matière organique sur l'infestation du striga et le rendement du sorgho a été étudié pendant trois saisons de culture dans un dispositif d'essai factoriel à trois facteurs. En plus de l'effet de la qualité des amendements organiques sur l'infestation du striga, j'ai également étudié le rôle du niveau d'infestation du striga par la manipulation de la densité de graines dans le sol, comparant 3 années consécutives de culture du sorgho avec 2 ans de jachère suivie d'une année de sorgho. L'effet de différents mélanges de sous produits du coton sur le rendement du sorgho a été bien décrit par la minéralisation de l'azote d'après les calculs avec un modèle simple. Une bonne corrélation a été observée pendant les 3 années entre la productivité du sorgho et l'azote libéré par la minéralisation. Il y a eu un effet négatif accru de la matière organique sur le striga lorsque la qualité de la matière appliquée augmentait. Il a été observé que l'apport de matières organiques de faible qualité est défavorable dans les champs de céréales infectés par le striga car elle conduit au maintien du rendement du sorgho avec plutôt une augmentation de l'infestation par le striga et de la biomasse, ce qui augmente davantage le stock de graines de striga. La question demeure quant à l'implication de ces résultats pour les agriculteurs locaux. Dans la perspective d'accroissement/amélioration des rendements des céréales et de la gestion du striga, les amendements organiques étudiés risquent de ne pas être adoptés par les agriculteurs pauvres en raison des quantités élevées de matières organiques de haute qualité requises. Ceci est également vrai pour la jachère ; bien qu'elle améliore le rendement du sorgho et contribue à la réduction de l'infestation du striga, elle est difficilement praticable en raison de la pression foncière actuelle.

Dans le chapitre 5, j'ai réalisé une série d'essais en pots et en laboratoire, pour étudier le rôle de la nutrition azotée des jeunes plants de sorgho et l'effet stimulant de leurs racines sur la germination des graines de striga. Le taux d'azote et la période de son application ont affecté la concentration en azote des racines du sorgho stimulant ainsi la germination des graines du striga. Les racines avec une concentration d'azote plus élevée ont faiblement stimulé la germination du striga, ce qui apparaît comme une indication claire qu'une faible quantité de stimulant de germination a été exsudée par les racines. La germination des graines du striga diminuait de façon linéaire avec l'augmentation des concentrations d'azote dans les racines jusqu'à un seuil de 19,5 mg N g^{-1} au delà duquel aucune autre réduction ne s'est produite. Aux concentrations les plus élevées, le taux de germination du striga était très faible, mais il n'a pas été possible d'obtenir un taux nul.

Dans le chapitre 6, les résultats sont discutés dans un contexte plus large. Après un bref résumé des principales conclusions, une nouvelle perspective de recherche sur la lutte contre le striga est présentée. Les contraintes à la production de céréales telles que perçues par les agriculteurs, en l'occurrence la gestion de la fertilité des sols, devront être prises comme point de départ. Etant donné que la durabilité de l'intensification des exploitations agricoles reste la solution ultime en Afrique, il y a nécessité pour les agriculteurs à investir dans l'amélioration de la fertilité des sols. Toutefois, il existe plusieurs contraintes à ces investissements. Le système foncier en vigueur ne sécurise pas l'accès des agriculteurs aux mêmes terres cultivables sur une longue période. Il ne favorise donc pas l'investissement des petits agriculteurs pour améliorer la fertilité des terres. En outre, les agriculteurs ont peu de possibilités d'accès aux engrais minéraux. De même, la disponibilité de fumure organique est réduite, car la production est limitée par les déplacements des troupeaux à la recherche de nourriture, et une partie est utilisée à d'autres fins, comme combustible pour la cuisine. Il y a nécessité d'un engagement et effort commun de la part des décideurs, chercheurs, vulgarisateurs et agriculteurs pour atténuer ces restrictions au changement. Dans ce chapitre est présenté un nouveau modèle conceptuel reliant l'évolution du rendement des céréales aux infestations du striga au cours du temps en rapport avec les changements dans la fertilité des sols. Les données sous-jacentes de ce modèle ont généralement été interprétées comme une indication de la baisse du rendement des céréales due au striga. Toutefois, il est maintenant proposé que les deux facteurs co-varient avec une variable externe principale, qui est la fertilité du sol. Le modèle montre la logique qui explique les faibles rendements du sorgho observés sur une large gamme de densités d'infestation par le striga. Le nouveau modèle propose que la restauration du système agricole suivra une trajectoire différente de celle de la dégradation. Selon l'interprétation classique, des interventions efficaces pour réduire le taux d'infestation du striga entraîneraient automatiquement l'augmentation des rendements. Les options de restauration du système reposent essentiellement sur la fertilité des sols ; l'infestation par le striga ne pourra être modifiée qu'après l'amélioration de la fertilité des sols. Le modèle implique donc que la restauration de la fertilité des sols doit être la priorité. La question fondamentale reste à savoir comment atteindre cet objectif étant donné que la disponibilité en termes de quantités et de qualités nécessaires des engrais minéraux et de matière organique est limitée pour les petits agriculteurs pauvres. Compte tenu des contraintes auxquelles les agriculteurs sont confrontés, des investissements en argent et en travail dans l'amélioration de la fertilité des sols à long terme, qui ne rapportent pas, la(les) première(s) année(s) n'intéressent pas les agriculteurs. L'écoulement (la vente) des produits agricoles à des prix incitatifs pour les agriculteurs reste donc un facteur clé pour l'intensification durable. Le défi pour les agronomes est d'examiner les moyens d'intensification agricole accessibles et rentables pour les agriculteurs pauvres.

Enfin, un système intégré pour l'intensification des cultures céréalières est proposé pour le nord du Cameroun où le striga constitue une contrainte forte, mais avec possibilité d'application au Sahel voire en Afrique subsaharienne. Le point de départ est la gestion intégrée de la fertilité du sol en se concentrant sur l'amélioration des rendements, mais avec un regard sur la réduction de la pression du striga. La rotation des cultures et la culture en association avec certaines cultures non hôte du striga sont des ingrédients essentiels. En effet, aucune composante de lutte contre le striga ne peut donner un contrôle du parasite à 100%, en particulier lorsque les niveaux d'infestation sont élevés. Des techniques de lutte contre le striga sont disponibles, mais il faut reconnaître que certaines d'entre elles pourraient ne pas être actuellement applicables par la majorité des petits agriculteurs ; et tant que ces agriculteurs considèrent la fertilité du sol comme leur principale priorité, il est inefficace d'envisager le striga comme point de départ pour l'amélioration de la production agricole dans les zones infestées par cette plante parasite.

SAMENVATTING

De parasitaire plant (onkruid) *Striga hermonthica* (striga), die voorkomt op verschillende graangewassen en daar zeer grote opbrengstreducties teweegbrengt, is in de drogere streken van Afrika wijd verbreid. Met name op onvruchtbare bodems is striga een van de grootste problemen voor de teelt van graangewassen. Duurzame voedselproductie in Afrika loopt daardoor ernstig gevaar. Striga is een steeds groter probleem geworden voor de arme Afrikaanse boer, in samenhang met het verlies van bodemvruchtbaarheid. Striga is gekenmerkt door bijzondere overlevingsstrategieën, die de plant zo'n effectieve en schadelijke parasiet maken, met name onder de daar heersende landbouwpraktijken. Maar lage bodemvruchtbaarheid is niet alleen de oorzaak voor de verslechterende striga-situatie, ze is zelf ook een geweldige beperking voor de graanproductie in de Afrikaanse savanneregio. Zonder verbetering van de bodemvruchtbaarheid is beheer van striga een mislukking gebleken aangezien de oogsten niet zijn toegenomen.

Wanneer we kijken naar de manier waarop het striga-probleem tot nu toe benaderd is, kunnen we ons niet aan de indruk onttrekken dat onderzoekers, beleidsmakers en boeren elk met een andere bril naar striga kijken en daardoor een verschillend beeld van de situatie hebben. Voor sommigen is striga een onkruid, voor anderen een parasitaire plant, en voor weer anderen een symptoom van lage bodemvruchtbaarheid. De vraag of striga een onkruid is of een symptoom van andere ongunstige omstandigheden heeft twee kanten. Enerzijds is er de vraag naar de oorzakelijke mechanismen. Anderzijds is er de vraag welke maatregelen voor strigabestrijding of -beheersing de grootste kans op succes hebben ook gebruikt te worden door de boeren. Moeten ze striga bestrijden, ook als het effect daarvan op de graanopbrengst zeer beperkt is? Of moeten ze de bodemvruchtbaarheid verbeteren, zodat de opbrengst toeneemt, ook als dat geen directe beperking van de aantallen striga geeft? Een daarmee samenhangende vraag is die naar de mogelijkheden om striga te bestrijden bij verschillende plaagdruk: zijn de mogelijkheden is alle gevallen dezelfde of moet de bestrijding plaagdrukafhankelijk zijn? Dit proefschrift probeert een antwoord te geven op de vraag hoe verbetering van de bodemvruchtbaarheid door middel van organische stof (hier specifiek restproducten van de katoenteelt) de productie van sorghum kan verbeteren onder omstandigheden waar striga nu zeer grote schade aanricht. Meer in het bijzonder onderzoekt dit proefschrift het effect van hoeveelheid en kwaliteit (stikstofgehalte, bemestend effect) van organische stof op bodemeigenschappen en daarmee op sorghumopbrengst, en de dynamiek van striga.

Hoofdstuk 2 beschrijft waarnemingen over een periode van bijna twintig jaar (1987-2005) in Noord Kameroen aan de dynamiek van striga en blikt terug op het succes (of liever het ontbreken van succes) van maatregelen om striga te bestrijden. Het bleek dat in die periode het percentage door striga aangetaste maïsvelden toenam. In sorghumvelden, die al zeer zwaar aangetast waren, bleef de aantasting op hetzelfde niveau. Gedurende deze twintig jaar nam de druk op land toe, hetgeen leidde tot verkorting van de periode dat land braak ligt om te herstellen. Ook veranderde het teeltsysteem van wissel- en mengteelt van granen en o.a. vlinderbloemigen naar een systeem waar continu graan werd geteeld. Het bleek daarnaast dat er geen goed verband bestond tussen de mate van striga-aantasting en de opbrengst van sorghum of maïs. Deze waarneming (velden met lage opbrengst hadden zeer verschillende dichtheden van striga) bevestigt de prioritering door boeren, die bodemvruchtbaarheid, onkruid (waartoe ze striga niet rekenen!) en gebrek aan arbeidskrachten om onkruid te wieden als hun voornaamste belemmeringen beschouwen. In die twintig jaar nam daarnaast de beschikbaarheid van kunstmest af, als gevolg van de ineenstorting van de lokale katoenindustrie. Naast gebrek aan kunstmest hebben boeren ook maar zeer beperkt toegang tot organische stof, zodat de bodemvruchtbaarheid eigenlijk niet of nauwelijks verbeterd kan worden. De uitkomsten van deze studie (bijna twintig jaar nadruk op striga was eigenlijk een mislukking) leidden ertoe dat de veronderstelling die ten grondslag ligt aan de bestrijding van striga en het beheer van bodemvruchtbaarheid herzien moest worden. In plaats van de aandacht primair te richten op striga bleek het noodzakelijk te starten met de belangrijkste belemmeringen zoals boeren die ervaren. Dit betekent dat het uitgangspunt moest worden de lage graanopbrengst als gevolg van de lage bodemvruchtbaarheid; en de mogelijkheden om via organische stof de productiviteit van de landbouw te verhogen (en via die weg striga te bestrijden). Daartoe werd een groot veldexperiment uitgevoerd dat in hoofdstuk 3 en 4 is beschreven.

In Hoofdstuk 3 onderzocht ik de effecten van organische stof van verschillende kwaliteit op het overleven van strigazaden. Daartoe werd in drie opeenvolgende jaren aan velden 6 ton organische stof per hectare en per jaar toegevoegd, maar met gebruikmaking van organische stof met verschillende stikstofgehaltes en daardoor verschillende snelheden waarmee de stikstof vrijkomt. De effecten van organische stof op het bodemvochtgehalte, op de bodemtemperatuur en op de hoeveelheid ethyleengas die gevormd werd tijdens de afbraak van de organische stof werden gemeten. Voor een beeld van de dynamiek in overleving gedurende het seizoen werden op verschillende tijdstippen zaden (die in aparte zaadzakjes werden ingegraven) opgegraven om overleving en kiemkracht te bepalen. Uit laboratoriumtesten bleek dat strigazaden het beste kiemen als de ethyleenconcentratie in een petrischaal 1 ppm bedraagt, en nadat ze 48 uur aan die concentratie zijn blootgesteld. Toediening van organische stof in het veld leidde tot een lager percentage overlevende zaden en dit effect was het grootste bij de best afbreekbare organische stof (dus bij de hoogste kwaliteit organische stof). Organische stof van lage kwaliteit (en met een laag stikstofgehalte) leidde tot een hoger bodemvochtgehalte gedurende de eerste vijf dagen na een regenbui en verlaging van de bodemtemperaturen met 0.5 °C; maar beide veranderingen waren niet de oorzaak van de lagere overleving van strigazaden. De in de bodem waargenomen ethyleenconcentraties waren maximaal 2-3 ppm. Zulke concentraties zijn in principe genoeg om zaadkieming te stimuleren. Maar er bleek geen verband te bestaan tussen de ethyleenconcentratie en de waargenomen zaadkieming. Er bleek ook geen verband tussen de kwaliteit van de organische stof en de ethyleenconcentratie. Het percentage overlevende zaden was lager bij zaadzakjes die aan het einde van het seizoen werden uitgegraven, hetgeen er op wijst dat het effect van het afsterven van zaden eerder een lange-termijn effect is dat slechts een beperkte rol speelt tijdens het desbetreffende groeiseizoen. De afbraakactiviteit door micro-organismen, die tegelijk met de afbraak van organische stof ook zaden afbreken, is de meest waarschijnlijke wijze waarop organische stof bijdraagt aan het uitputten van de zaadbank in de bodem.

In het tweede deel van het veldexperiment (beschreven in Hoofdstuk 4) onderzocht ik de groei van zowel striga als sorghum na toediening van organische stof gedurende drie achtereenvolgende jaren in een factoriële proef met drie behandelingen. Naast organische-stofkwaliteit onderzocht ik in deze proef het belang van plaagdruk (door de zaaddichtheid van striga te manipuleren) en het effect van drie jaar continue sorghumteelt in vergelijking met een periode van twee jaar braak gevolgd door één jaar sorghum. Het effect van de verschillende mengsels van bijproducten van katoen op de sorghumopbrengst kon zeer goed worden beschreven op basis van de hoeveelheid stikstof zoals die volgens een simpel berekeningsmodel vrijkwam tijdens de afbraak. Dat verband was in elk van de drie onderzochte jaren duidelijk. Bij organische stof van hogere kwaliteit was er een sterker negatief effect op striga. Ik stelde vast dat de situatie verslechterde bij toedienen van organische stof doordat de sorghumopbrengst niet toenam terwijl het aantal strigaplanten daarentegen juist wel groter werd evenals de geproduceerde strigabiomassa, en dit laatste weer leidde tot een verdere toename van de zaadbank van striga. De vraag rest wat de betekenis van deze proeven is voor de lokale boeren. Immers, de bestudeerde hoeveelheden organische stof van deze hoge kwaliteit zijn voor boeren niet of nauwelijks beschikbaar. Ook het gebruik van braak dat leidde tot hogere sorghumopbrengst en lagere aantallen striga is bij de huidige druk op het land voor deze boeren eigenlijk geen optie.

In Hoofdstuk 5 onderzocht ik de rol van de stikstofvoeding van jonge sorghumplanten op de stimulerende werking van hun wortels op strigakieming in een aantal pot- en laboratoriumexperimenten. Zowel de hoeveelheden toegediend stikstof als het tijdstip van toediening hebben effect op de stikstofconcentraties in de sorghumwortel en daarmee op de stimulerende werking van wortels op strigakieming. Plantenwortels met een hogere stikstofconcentratie stimuleerden de kieming minder, een aanwijzing voor verminderde productie van kiemstimulerende stoffen. Er was een rechtlijnig negatief verband tussen stikstofconcentratie in de wortel en het percentage gekiemde strigazaden, tot aan een concentratie van 19.5 mg g^{-1}. Bij hogere concentraties was er geen verder effect. In alle gevallen bleek nog een klein percentage zaden te kiemen. Het bleek dus niet mogelijk de kieming van strigazaden tot nul terug te brengen.

In de slotdiscussie (Hoofdstuk 6) plaats ik mijn resultaten in perspectief. Na een korte samenvatting van de belangrijkste resultaten van mijn onderzoek, kom ik tot een nieuw perspectief op onderzoek naar en bestrijding van striga. Uitgangspunt moet zijn de beperkingen voor de graanproductie zoals boeren die ervaren. Dat betekent dat het beheer van bodemvruchtbaarheid uitgangspunt moet zijn. Omdat alleen een duurzame intensivering een oplossing biedt voor de landbouwproductie in Afrika zullen boeren in de bodem moeten investeren en de bodemvruchtbaarheid verhogen. Er zijn echter verschillende belemmeringen voor zulke investeringen. Het heersende systeem van landgebruiksrechten leidt ertoe dat boeren slechts zekerheid van landgebruik hebben voor enkele jaren. Daarom zijn boeren weinig geneigd te investeren in bodemvruchtbaarheid, als zulke langetermijninvesteringen op korte termijn niet ook rendabel zijn. De mogelijkheden voor boeren om kunstmest te kopen zijn daarnaast beperkt. Ook de beschikbaarheid van organische stof en de concurrentie om die organische stof tussen verschillende gebruiksvormen (verbetering van bodemvruchtbaarheid, voer voor langstrekkende kuddes vee, brandstof om te koken, etc.) vormen verdere beperkingen. Het is derhalve noodzakelijk dat onderzoekers, voorlichters, beleidsmakers en boeren zich gezamenlijk committeren en de inspanning leveren om deze beperkingen op te heffen. In dit hoofdstuk introduceer ik een nieuw conceptueel model dat de relatie aangeeft tussen veranderingen in de graanopbrengst en aantallen strigaplanten onder druk van veranderende bodemvruchtbaarheid. Tot nog toe werden de achterliggende gegevens voor dit model geïnterpreteerd als een indicatie hoe de toename in striga de *oorzaak* is van de afname van de graanoogst. In het hier voorgestelde model is het oorzakelijke verband verlegd; beide processen (afname graanproductie, toename striga) worden gelijkelijk *veroorzaakt* door de afnemende bodemvruchtbaarheid. Dit model maakt ook het samengaan van sterk verschillende aantallen striga bij lagere graanoogst aannemelijk. Het model geeft tevens aan dat *herstel* van deze landbouwsystemen langs een andere weg zal verlopen dan de degradatie. Onder het oude model was bestrijding van striga (en afnemende aantallen) automatisch voldoende voor herstel van de graanproductie. Onder het nieuwe model wordt dat automatisme doorbroken. De herstelmogelijkheden van het systeem worden allereerst bepaald door de bodemvruchtbaarheid en pas in tweede instantie door de plaagdruk door striga. Dat impliceert dan ook dat herstel van de bodemvruchtbaarheid de allerhoogste prioriteit moet hebben. De vraag blijft dan natuurlijk hoe dit herstel bewerkstelligd kan worden gegeven de schaarste of onbeschikbaarheid in termen van zowel kwaliteit en kwantiteit van kunstmest en organische meststoffen. In het licht van de omstandigheden van de arme boeren zijn maatregelen die op lange termijn pas effect sorteren volstrekt onaantrekkelijk. Boeren zullen geen geld en arbeid investeren, tenzij daar een verhoging van hun productie op korte termijn tegenover staat. Dit impliceert de noodzaak dat boeren een betere prijs krijgen voor hun landbouwproducten. Zolang dat niet het geval is, blijft een duurzame intensivering van de landbouw onhaalbaar. Landbouwkundige onderzoekers moeten dus met voorstellen komen hoe die duurzame intensivering bereikt kan worden en dus aantrekkelijk is voor arme boeren.

Voor noord Kameroen (en waarschijnlijk voor grotere delen van de Sahel, en wellicht zelfs voor heel Afrika ten zuiden van de Sahara) stel ik ten slotte een schema voor dat tot zulke intensivering van de graanteelt kan leiden. Uitgangspunt is daarbij duurzaam bodemvruchtbaarheidsbeheer, dat resulteert in hogere opbrengsten en een lagere plaagdruk van striga. Vruchtwisseling (wisselbouw) en mengteelten met vlinderbloemigen die geen gastheer van striga zijn vormen een zeer belangrijk element. Om striga te beheersen op sterk aangetaste velden kan men niet volstaan met één enkele maatregel, want geen enkele maatregel geeft vooralsnog 100% succes, zeker niet wanneer de strigadruk groot is. Mogelijkheden tot specifieke aanvullende bestrijding van striga zijn beschikbaar. Men moet echter accepteren dat vooralsnog verschillende van deze strategieën door veel kleine boeren niet gerealiseerd kunnen worden. En zolang boeren striga niet als hun grootste prioriteit beschouwen (en bodemvruchtbaarheid wel), is het weinig effectief om striga als aangrijpingspunt te beschouwen voor het verbeteren van de landbouwproductie in gebieden die met striga geïnfecteerd zijn.

CURRICULUM VITAE

Gideon Che Ayongwa was born on June 5th 1962, in Bafut Cameroon. On completion of primary school in 1972 with a pass in the FSLC exam, he gained admission into CPC Bali and then CCAST Bambili for secondary school education; from where he obtained with pass the General Certificate of Education, Ordinary and Advanced levels respectively. That same year in 1980 after the Advanced level, he took up a teaching-job appointment for two years at the Presbyterian Secondary School Batibo. Then in 1982, he passed an admission exam in to the National Advanced School of Agriculture – University Centre Dschang; for a 5 year course in agriculture, where he graduated with the degree of “Ingenieur Agronome” with honours, specialising in Crop Production. He was then absorbed in to the Cameroon public service, where he served as the national counterpart in the FAO/UNDP Pan-African project on Striga control. Later in 1989, he was appointed to the Central Administration of the Ministry of Agriculture as Deputy Chief of Service for Phytosanitary interventions. In 1991 he received a British Council Scholarship award for an MSc at Imperial College– University of London, to specialise in Weed Science. While in the UK he also did a course on Technical Training for Trainers at Wolverhampton University. On graduation in 1993, Gideon returned to Cameroon where he continued work on the control of Striga and Striga weed complexes. In 1998 he joined the Institute of Agricultural Research, shortly after gaining admission into a PhD programme of the then Wageningen Agricultural University. Alongside his thesis work Gideon Ayongwa researched in the use of multipurpose crops in conservation agriculture adapted to resource-poor farmers and alternative weed management for sustainable agriculture. He has also been involved in the co-supervision of several university students for their ‘Maîtrise’ and ‘Ingénieur Agronome’ degree programmes, both at the then Garoua and the present Dschang research station. Most of his work experience has been devoted to developmental agriculture with the small-scale, resource-poor farmers. He continues work with agricultural research and hopes to continue there alongside training at all levels, after graduation from the doctorate programme. Gideon is married to Vivian Ako and father of four, Shu Matthews, Sirri Pastors, Ngum Chappell and Akwen-Neg Gene.

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