# The role of sorghum genotype in the interaction with the parasitic weed *Striga hermonthica*

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# The role of sorghum genotype in the interaction with the parasitic weed *Striga hermonthica*

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# Abstract

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This thesis presents a study on the interaction between the parasitic weed *Striga* (*S. hermonthica* [Del.] Benth.) and the cereal crop sorghum (*S. bicolor* [L.] Moench). Its main objective was to find suitable measures for the selection of breeding material (crop genotypes) with superior levels of resistance or superior levels of tolerance to *Striga*. To meet this objective the physiological background of tolerance, the relation between *Striga* infestation, infection and yield loss and the effect of host genotype on *Striga* parasitism and reproduction were studied.

These host-parasite interactions were studied with 4-10 different sorghum genotypes differing in level and mechanism of defence against *Striga*. Field experiments carried out in Mali were used for yield assessments and development and validation of selection measures. Through pot and agar-gel experiments, aboveground resistance measures were validated with observations on belowground stages. Pot experimentation was also used to create infection response curves and to measure photosynthesis and chlorophyll fluorescence to develop tolerance measures.

*Striga* parasitism and reproduction, and the detrimental effect of *Striga* on crop yield can significantly be reduced through crop genotype choice. Maximum aboveground *Striga* number is a reliable selection measure for resistance. *Striga* flowerstalk dry weight can be used to identify genotypes that reduce *Striga* reproduction. The maximum relative yield loss is a suitable selection measure for tolerance in susceptible genotypes, while for more resistant genotypes the relative yield loss per *Striga* infection seems more appropriate. For these tolerance measures, yield assessment of nearby uninfected controls is indispensable. Chlorophyll fluorescence, more precisely photochemical quenching and electron transport rate, may enable screening for tolerance without this requirement.

Keywords: *Striga hermonthica*, *Sorghum bicolor*, selection measures, resistance, tolerance, genotypes.

# Preface

In November 2000, I started as a PhD student at the Crop and Weed Ecology Group (CWE) of Professor Martin Kropff at Wageningen University (WU). For this opportunity as well as for all the support, trust and friendship I received over the past five years, I need to acknowledge a great number of people.

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Jonne Rodenburg Cotonou, October 2005

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# Contents

# CHAPTER 1

# General introduction

## The parasitic weed *Striga hermonthica*

One of the major biotic constraints to cereal production in sub-Saharan Africa is *Striga hermonthica* (Del.) Benth. (Sauerborn, 1991). This parasitic weed species from the Orobanchaceae (formerly: Scrophulariaceae) family parasitizes on cereals like rice (*Oryza glaberrima* [Steudel] and *O. sativa* [L.]), pearl millet (*Pennisetum glaucum* [L.] R. Br. or *P. americanum* [L.] K. Schum), maize (*Zea mays* [L.]) and sorghum (*Sorghum bicolor* [L.] Moench) (Parker, 1991; Johnson et al., 1997). In sub-Saharan Africa, where problems with *Striga hermonthica* (*Striga*) are most severe, 94 % of all the area under cereal production is cultivated with one of its host crops. Sorghum is the most widely cultivated cereal crop in this region with 25.5 million ha under cultivation, which is 30.6% of the total area under cereal crops in 2004 (FAOSTAT, 2004). Infection by *Striga* can cause yield losses of a few percentages up to complete crop failure, depending on crop species, crop variety and severity of *Striga* infestation (Doggett, 1965; Riches and Parker, 1995; Adetimirin et al., 2000a). *Striga* problems are often associated with low soil fertility and marginal environments with high cropping intensities and therefore mostly affect resource-poor subsistence farmers (Kroschel, 1999; Ransom, 2000).

## The life cycle of *Striga*

*Striga* is an obligate hemi-parasitic plant implying that it needs a host plant to fulfil its life-cycle, but, having chlorophyllous leaves, is not entirely dependent on its host for its metabolite requirements (Kuijt, 1969). The life cycle of the parasite follows a series of developmental stages going from seed to seed producing plants. Like many other plant species, *Striga* seeds have a period of primary dormancy before the seeds are able to germinate. For *Striga* this period is 6 months (Vallance, 1950). A second prerequisite for germination is the preconditioning of the seed, which requires about two weeks of humid and warm (25-35° C) conditions (Vallance, 1950; Parker and Riches, 1993). Preconditioned *Striga* seeds will then need secondary metabolites (xenognosins), derived from the host root, for germination (Saunders, 1933; Vallance, 1950; Yoder, 2001). These xenognosins also serve to direct the radicle of the *Striga* seedling towards the host root (Williams, 1961a;b). Within four days after germination the radicle needs to find a host root to start formation of a haustorium and penetrate the host root (Riopel and Timko, 1995). The haustorium is a specialized organ that connects the parasite to the xylem of the host root enabling the transport of water and solubles from the parasite to the host (Kuijt, 1977). The xylem to xylem connection is established soon (48-60 hours) after attachment and penetration of the haustorium into the host root tissue (Ramaiah et al., 1991; Riopel and Timko, 1995). Once the xylem connection is established, the *Striga* can start to develop and grow to the soil surface.

First *Striga* emergence aboveground is reported to occur around 35 to 45 days after crop sowing (DAS) or three to six weeks after attachment (Doggett, 1988; Olivier et al., 1991; Webb and Smith, 1996; Adetimirin et al., 2000b; Haussmann et al., 2001a). Aerial parts of *Striga* turn green upon exposure to daylight. The aboveground vegetative stage is followed by flowering, which starts around 4 weeks after emergence, and seed production and dissemination, which start around 4 weeks after first flowering at 90 to 120 DAS (Doggett, 1988; Webb and Smith, 1996). Seed size of *Striga hermonthica* is between 0.2 and 0.3 mm (Parker and Riches, 1993). Estimates on seed production per plant vary from between 5,000 to 85,000 seeds per reproductive plant (Andrews, 1945; Stewart, 1990; Webb and Smith, 1996). Since large quantities of seed will survive the dry season following seed dispersion, a series of cropping seasons with the same host crop will lead to a quick build-up of the *Striga* seed bank (Weber et al., 1995) and consequently result in increasingly high infections and decreasing crop yields.

## *Striga* effects on its host

*Striga* has lower leaf chlorophyll contents and lower photosynthetic rates than related non-parasitic plant species (De La Harpe and Visser, 1979; Shah et al., 1987; Tuquet et al., 1990). Therefore, despite the green leaves, *Striga* continues to benefit from its host after emergence (Seel et al., 1992; Pageau et al., 1998). Transpiration rates of aboveground *Striga* exceed that of its host, show little to no response to darkness and only reduce when the host is subjected to water stress (Press et al., 1987a, 1988; Ackroyd and Graves, 1997). This principle ensures a constant flux of water from the host to the parasite (Raven, 1983; Schulze et al., 1984; Press et al., 1987b; Shah et al., 1987; Pageau et al., 2003). Through this transfer *Striga* subtracts carbon assimilates (Rogers and Nelson, 1962; Okonkwo, 1966; Press et al., 1987b), water, nutrients (nitrate) and amino-acids (Pageau et al., 2003) from its host.

However, it was found that the loss in biomass production of a host plant caused by *Striga* infection largely outweighs the *Striga* biomass attached to it. It was therefore concluded that *Striga* does not only act as a sink for its host plant but has additional negative effects on the host plant (Press and Stewart, 1987). Upon *Striga* infection abscisic acid levels increase while levels of cytokinins and giberellic acid decrease (Drennan and El Hiweris, 1979). By changing this balance of plant growth regulators in the host, *Striga* negatively affects host photosynthesis (Press and Stewart, 1987; Gurney et al., 1995) and alters the biomass allocation of its host. More biomass is allocated to the roots at the expense of the stem (Graves et al., 1989). Furthermore *Striga* reduces the water use efficiency (Gebremedhin et al., 2000) and strongly affects the water economy of the host plant through its high transpiration rates (Shah et al., 1987; Press et al., 1987a, 1988; Ackroyd and Graves, 1997). These *Striga*-induced modifications of the host plant are thought to be the main causes for host yield loss.

## Control options

Since *Striga* is primarily a problem in small-scale subsistence farming systems with few options for external inputs, control options must be low-cost and practical. A multitude of control options against *Striga* have been studied ranging from cultural measures like transplanting, delayed sowing or the use of trap crops (e.g. Doggett, 1988; Carsky et al., 1994b; Gbehounou and Adango, 2003; Gbehounou et al., 2004; Hess and Dodo, 2004), chemical control or soil fumigation (e.g. Bebawi and Eplee, 1986; Eplee and Norris, 1987; Carsky et al., 1994a), biological control (e.g. Kroschel and Muller Stover, 2004; Lendzemo et al., 2005) and host plant resistance (e.g. Williams, 1959; Kim et al., 1998). Despite the high potential of some of those solutions, no single option on its own has proven to be both sufficiently effective and durable as well as economically and practically applicable for low-input farming systems (Joel, 2000). Integration of various low-cost control options has proven to be a suitable approach (Berner et al., 1996; Schulz et al., 2003).

An important element of this integrated approach is host plant defence. Two main groups of defence mechanisms against *Striga* can be distinguished: resistance and tolerance. Resistance against *Striga* reduces the infection level of a host plant, while tolerance enables the host plant to perform well, despite the parasitic infection. Host resistance is thought to be the most economical and potentially the most effective control option against root diseases and soil borne pathogens (Shew and Shew, 1994) and therefore a potentially acceptable *Striga* control option to resource-poor farmers (Hess and Ejeta, 1992; Debrah, 1994). Yet, complete resistance, or immunity, against

*Striga* has not been found to date. Because few *Striga* infections can already seriously harm the host plant, resistance alone may not be enough to prevent crop losses. It is therefore recommended to direct breeding efforts towards finding varieties that combine resistance with high levels of tolerance (Haussmann et al., 2001a).

## Conceptions and knowledge gaps

Over the past 75 years many breeders and researchers worked on resistance and tolerance against various species of *Striga* in a range of host plant species (e.g. Saunders, 1933; Williams, 1959; Doggett, 1965; Obilana, 1984; Ramaiah et al., 1990; Olivier et al., 1991; Hess et al., 1992; Efron, 1993; Cubero et al., 1994; Johnson et al., 1997; Kim et al., 1998; Haussmann et al., 2000a; Wilson et al., 2000). These efforts resulted in useful varieties with high resistance or tolerance and important insights in mechanisms behind these forms of defence. Examples of these achievements are the work on sorghum varieties Framida and SRN39 by various research groups (El Hiweris, 1987; Olivier et al., 1991; Hess and Ejeta, 1992; Arnaud et al., 1999; Mohamed et al., 2003). Still, many questions related to mechanisms behind host resistance and tolerance remain to be resolved. Subsequently, measures and methods for selection of good parent material for breeding need to be improved.

Complete defence against *Striga* entails a combination of resistance and tolerance. While resistance lowers the number of *Striga* infections, tolerance reduces the negative effects of the infection. Breeding for resistant host plant varieties with superior levels of tolerance requires the separate selection of parental lines with either superior resistance or superior tolerance and hence appropriate selection measures for each trait. However, resistance and tolerance are often confounded, both in definitions and in selection measures. In *Striga* research resistance is often described as the mechanism that ensures lower infection and higher yields (Doggett, 1988; Hess and Haussmann, 1999). However, higher yields do not only depend on infection pressure (a result of resistance) but also on the consequence of infection on host performance (tolerance). Hence for identification of resistance one should focus on infection level alone. Resistance is often expressed in aboveground *Striga* numbers either at a fixed point in time or at its maximum (Olivier et al., 1991; Johnson et al., 1997; Adetimirin et al., 2000b; Wilson et al., 2000). It is, however, not clear whether this provides accurate information on what happens belowground and at what moment and what frequency the aboveground numbers should be counted.

Tolerance is the ability of a variety to support equally severe levels of infection as other varieties of the same species, without the associated yield loss (Caldwell et al., 1958; Doggett, 1988). The difficulty with the identification of tolerant lines is its entanglement with resistance. No one line will have exactly the same resistance level. Consequently, infection levels will also vary among tolerant lines. To assess the level of tolerance of a certain line, the *Striga* effects on yield need to be corrected for the infection load. But as long as the relation between *Striga* infection and yield loss is unknown, a fair correction cannot be carried out.

Also, the physiological background for tolerance has been poorly understood. It was shown that tolerant varieties are often able to maintain high rates of photosynthesis under *Striga* infection (Gurney et al., 1995, 2002a). Principals behind this mechanism are not completely resolved yet and options for the application of physiological measurements to identify tolerant genotypes are not fully explored yet. It is expected that the development of fair and practical selection measures for tolerance, either based on crop yield or host plant physiological parameters, will greatly enhance breeding efforts against *Striga*.

Host resistance is believed to reduce *Striga* seed production, through a reduction in *Striga* development rate or *Striga* numbers (Weber et al., 1995; Haussmann et al., 2000b). A reduction in aboveground *Striga* numbers, caused by resistance, does however not necessarily lead to a reduction in *Striga* seed production. The lower intra-specific competition with lower aboveground *Striga* numbers may enable higher seed production per individual *Striga* plant and hence compensate, at least partly, for the reduction in plant numbers. Whether or not selection for resistant host plant genotypes also implies selection for genotypes supporting lower *Striga* reproduction remains an important question to be solved.

## Objective and approach

The objective of this study was to find suitable field selection measures that facilitate breeders in finding breeding material (genotypes) with superior levels of resistance and tolerance, serving both the short term goal of ensuring crop yield and the long term goal of lowering *Striga* seed bank density.

The parasite - host plant interactions were studied with *Striga* (*Striga hermonthica* [Del.] Benth) and sorghum (*Sorghum bicolor* [L.] Moench). A selection of ten different sorghum genotypes with different levels and mechanisms of defence against *Striga* was used to study resistance and tolerance. This selection encompassed the sensitive and susceptible genotypes CK60-B and E36-1, the resistant genotypes N13 and Serena, the tolerant genotypes Seredo and Tiémarifing and the tolerant and resistant genotypes CMDT39, Framida, IS9830 and SRN39. The physiological work as well as the study on the relation between yield loss and infection was conducted with a selection of four of those ten genotypes: CK60-B, E36-1, Framida and Tiémarifing.

Three field experiments (in 2001, 2002 and 2003) and two pot experiments (in 2001 and 2003) were conducted at the research station of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in Mali. One agar-gel test and two pot experiments (in 2003 and 2004) were conducted in the laboratory and the greenhouse of Wageningen University (WU) in The Netherlands. Field plots were artificially infested with known quantities of viable *Striga* seeds, over the whole surface to a depth of 5-10 cm, to simulate farmer field conditions. Adjacent *Striga*-free control plots were treated with ethylene gas (in cases of prior infestation) or kept free from *Striga* infestation (in the newly cleared *Striga*-free field of 2002). Field experiments were rain fed and lightly fertilized. Pot experiments consisted of pots with known *Striga* infestation levels and *Striga*-free controls. Sorghum plants in pots received regular water gifts to ensure non-water-limited conditions, and moderate fertilizer gifts comparable to the field experiments.

## Outline of the thesis

In Chapter 2, selection measures for resistance are evaluated and selection measures and methods for tolerance are explored. This chapter particularly deals with the problems of quantifying host tolerance in the field. In the subsequent chapter (Chapter 3) the relations between *Striga* infestation, *Striga* infection and host plant yield loss are further studied and consequences and options for an adequate screening procedure for host plant tolerance are discussed. In Chapter 4, the host plant photosynthesis of tolerant versus sensitive genotypes is studied in order to enhance the understanding of some physiological principals that play a role in withstanding *Striga* effects. Additional objective of this study was to explore the options to use non-destructive and quick measurements as a selection tool for tolerance. The effects of host plant genotype and seed bank density on *Striga* reproduction are studied in Chapter 5. In the General discussion (Chapter 6) results of the present study are discussed and related to earlier work and outcomes of other studies.

# CHAPTER 2

# How can field selection for *Striga* resistance and tolerance in sorghum be improved?[1]

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## Abstract

Breeding for high yielding *Sorghum bicolor* varieties with effective resistance and tolerance against the hemi-parasitic weed *Striga hermonthica* requires suitable selection measures for both characteristics. The objective of this research was to constitute a set of practical selection measures that contain independent, reliable and discriminative criteria for resistance and tolerance. Ten sorghum genotypes were grown in the field with and without *Striga* infestation in a split-plot design in 3 successive years (2001-2003) using different *Striga* infestation levels (low, high and intermediate). Resistance against *Striga* in the belowground stages was determined separately in an agar-gel assay and a pot trial.

The addition of *Striga*-free control plots facilitated the calculation of the relative yield loss, which represents the result of resistance and tolerance combined. Correlation analysis indirectly demonstrated that both resistance and tolerance are important yield determining traits under *Striga* infestation. Tolerance was relatively more important under low *Striga* infestation levels, whereas resistance was relatively more important at high infestation levels. With respect to resistance, both the area under the *Striga* number progress curve (*ASNPC*) and maximum aboveground *Striga* number ($NS_{max}$) turned out to be discriminative and consistent selection measures. Both measures also corresponded well with the expression of resistance during belowground stages of the parasite. It proved more difficult to arrive at a satisfactory measure for tolerance. Inclusion of *Striga*-free plots is an essential step for the determination of tolerance, but in itself not sufficient. It provides a basis for the determination of the relative yield loss, which then needs to be corrected for differences in infection level resulting from genotypic differences in resistance. A linear correction for infection level disregards the density dependency of the relative yield loss function. It is expected that clarification of the relation between *Striga* infection level and yield loss, provides a solid basis for the development of unambiguous tolerance measures in the field. This will enable the breeder to select for resistance and tolerance separately, which is likely to result in the optimum combination of both defence mechanisms.

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## Introduction

*Striga hermonthica* (Del.) Benth. (Scrophulariaceae, popular name: witchweed) is an out-crossing, obligate hemi-parasitic weed species that attacks roots of tropical Gramineae, including sorghum (*Sorghum bicolor* [L.] Moench), pearl millet (*Pennisetum glaucum* [L.] R. Br.), maize (*Zea mays* [L.]) and upland rice (*Oryza sativa* [L.]). Besides withdrawal of water, nutrients and assimilates, *Striga* damages its host by inducing enzyme and plant hormone changes, disrupting host water relations and carbon fixation (Press et al., 1996). According to Mboob (1989), 40% of the arable land in sub-Saharan Africa is infested with *Striga*. For six West African countries the total *Striga*-infested area was estimated at 5 million ha which is around 52% of the total grain production area (Sauerborn, 1991). Yield losses due to *Striga* infection of cereals in West Africa average 24% (10-31%), but in areas of heavy infestation losses reach 90-100% in some years (Sauerborn, 1991).

Problems with *Striga* appear to be associated with degraded environments and are most severe in subsistence farming systems with little options for external inputs. Farmers are clearly in need of low-input solutions to *Striga* problems, for both the short and the long term. In the long term, the goal is to diminish *Striga* presence through depletion of *Striga* seed bank and limitation of *Striga* seed production (Obilana, 1988). In the short term, the goal is satisfactory grain yield under *Striga* infestation. Yield under *Striga* infestation is determined by the yield that would be achieved in the absence of *Striga* and the reduction caused by this biotic stress factor. This yield reduction is a function of the infection level and the response of the crop to this infection. Breeding for improved crop performance under *Striga*-infested conditions, which may benefit farmers without requiring high external inputs (Obilana, 1988), might consequently be focussed on resistance, to reduce the infection level, or on tolerance, to diminish the consequences of infection.

According to the definitions of Parker and Riches (1993), resistance, the opposite of susceptibility, applies to genotypes that show fewer infections. A suitable selection measure for resistance should thus include the number of attached or emerged parasites. For practical reasons, selection for resistance is often based on number of aboveground *Striga* plants alone. A relevant question is whether this number is indeed a good selection criterion. Does it give a good reflection of the number of attached parasites? Furthermore, this number is the result of various belowground stages (e.g. germination, attachment, belowground development), and screening based on the overall result might unintentionally lead to the exclusion of genotypes with a high level of partial resistance in one of these life-cycle stages. Such genotypes may in fact be good candidates for gene pyramiding.

Resistance against *Striga* is sometimes used in a broader sense and described as a mechanism that ensures lower infection and higher (or satisfactory) host yields (Doggett, 1988; Hess and Haussmann, 1999). This definition not only includes the level of infection, but also the consequences of infection on host performance. Hence tolerance is included in this definition of resistance and no clear distinction is made between the two defence mechanisms (e.g. Kim et al., 2002). It is evident, that in the absence of immunity, the combination of resistance and tolerance is the most promising and durable breeding objective (Haussmann et al., 2001b). For obtaining the best combination of both traits, selection for both components separately seems the best approach.

Tolerance, the opposite of sensitivity, is the ability to support equally severe levels of a pathogen, disease or parasitic weed as other varieties of the same species, without the associated impairment of growth or losses in grain yield or quality (Caldwell et al., 1958; Doggett, 1988; Ejeta et al., 1991). Tolerance on its own is difficult to quantify, as it is always confounded with a certain degree of resistance. Each genotype possesses its own level of resistance, making it difficult to directly assess the level of tolerance or compare the level of tolerance among genotypes. Furthermore, identification of tolerance requires *Striga*-free plots as a reference next to infested plots, as each genotype will have its own yield level, which will also be influenced by the specific environment where the screening takes place. The aforementioned constraints likely explain why research on defence against *Striga* in sorghum has been focussed more on resistance than on tolerance. A clear separation of tolerance and resistance as well as suitable characterisations for both traits seem beneficial to an efficient use of these defence mechanisms in crop improvement (Shew and Shew, 1994). Suitable measures should ideally meet various criteria like appropriateness (does the measure unambiguously represent the characteristic?), discriminativeness (is the measure making differences between genotypes sufficiently clear?), stability and objectivity (are selections based on the measure consistent over years and infestation levels?), repeatability (does the measure sufficiently express genetic variation?) and, last but not least, practicability (is the measure easy to determine?). The objective of this paper is to evaluate, improve and search for independent and practical field selection measures for resistance and tolerance against *Striga hermonthica* in sorghum, using *Striga*-free next to *Striga*-infested plots.

## Material and methods

*Genetic materials*

For all experiments, 10 sorghum genotypes were used: CK60-B, CMDT39, E36-1, Framida, IS9830, N13, Seredo, Serena, SRN39 and Tiémarifing. The objective was to use a range of genotypes that differed in degree and type of resistance and tolerance against *Striga hermonthica* (Table 1). *Striga* seed for field and pot infestation, was collected in Samanko (all experiments) and in Doumba, 80 km north-east of Samanko (agar-gel-assays only) and harvested from plants that parasitized sorghum.

*Field trials*

A series of field trials was conducted during three cropping seasons (2001-2003), at the ICRISAT-Mali field station in Samanko, 20 km south-west of Bamako, at the northern side of the river Niger (latitude 8°54"W and 12°54"N, altitude 329 m). Average mean temperature of the study site is 29.1°C during the cropping season (June-November). The climate type is Sudanese, characterised by one single rainy season between May and October. Mean annual rainfall at the field station is 950 mm, of which 96% falls between May and October. Experimental plots were laid on washed out, ferruginous tropical soils with wash-out spots and concretions and a sandy loam texture. Table 2 presents soil fertility parameters of the main plots of the three fields (2001, 2002 and 2003) after fertilization, as well as rainfall data of the three cropping seasons.

In all years a split-plot design was used with either five (2001), eight (2002) or six (2003) replicates (Table 3). In 2001 and 2002 there were two main plot levels: *Striga*–free (control) and *Striga*-infested. In 2003 there were three main plot levels: *Striga*-free (control), low *Striga* infestation (L) and high *Striga* infestation (H). In each case, sorghum genotype was used as sub-plot factor. In each year a different field was used. The 2001 and 2003 experiments were sown in previously infested fields. Control plots were created through ethylene gas ($C_2H_4$, purity 99.98%) injections with a backpack ethylene applicator as described by Bebawi et al. (1985). The gas was injected twice, at a 4-day interval following a 0.5 - 0.5-m grid. Upon injection of the probe in the soil, gas was released for 3 s at a pressure of 3.5 bar. Ethylene injections resulted in nearly complete absence of *Striga* infection. The 2002 experiment was laid on a *Striga*-free field. *Striga* plots were created through artificial *Striga* infestation of the whole soil surface till a depth of 5 (2001) and 10 cm (2002 and 2003) with 45,000 (2001), 200,000 (2002), 30,000 and 150,000 viable *Striga* seeds $m^{-2}$ (2003).

Table 1. Name, race, origin (NE = north-eastern, S = southern, E = eastern) and reported defence mechanism of the selected sorghum genotypes.

| Genotype | Race | Origin | Defence mechanism | Reference |
|---|---|---|---|---|
| CK60-B | Kafir | NE. Africa/ USA | Sensitive/ Susceptible | Olivier et al. (1991) |
| CMDT39 | Guinea | Mali | Tolerant/ Resistant | ICRISAT/ IER (pers. commun.) |
| E36-1 | Caudatum | Ethiopia | Susceptible | ICRISAT (pers. commun.) |
| Framida | Caudatum | S. Africa | Tolerant/ Resistant | El Hiweris (1987), Arnaud et al. (1996) |
| IS9830 | Caudatum | Sudan | Tolerant/ Resistant | El Hiweris (1987), Ramaiah (1988) |
| N13 | Durra | India | Resistant | Maiti et al. (1984) |
| Seredo | Caudatum | Uganda | Tolerant | Haussmann et al. (2001a) |
| Serena | Caudatum | E. Africa | Resistant | El Hiweris (1987) |
| SRN39 | Kafir | Unknown | Tolerant/ Resistant | El Hiweris (1987) |
| Tiémarifing | Guinea | Mali | Tolerant | ICRISAT (pers. commun.) |

Table 2. Soil fertility indicators: pH ($H_2O$; 1:2.5), C-organic (% C.O.), P-available (Bray-1; mg P $kg^{-1}$) and N-total (mg N $kg^{-1}$) of the main plots of the study fields in 2001-2003 as determined shortly after fertilization, and cumulative rainfall (mm) at Samanko (Mali) for the three rainy seasons at three different moments (before sowing (at start), at 56 days after sowing (DAS) and at harvest).

| | 2001 | | 2002 | | 2003 | | |
|---|---|---|---|---|---|---|---|
| | Control | *Striga* | Control | *Striga* | Control | *Striga* (L) | *Striga* (H) |
| pH | 4.9 | 4.9 | 5.6 | 5.6 | 5.0 | 4.9 | 5.1 |
| C-organic | 0.3 | 0.3 | 0.7 | 0.7 | 0.4 | 0.4 | 0.4 |
| P-available | 10.3 | 9.2 | 18.7 | 21.0 | 12.0 | 12.2 | 13.6 |
| N-Total | 238.2 | 227.5 | 471.1 | 486.4 | 251.4 | 248.4 | 256.3 |
| Cum. rainfall | | | | | | | |
| At start | 233.1 | | 243.7 | | 260.3 | | |
| At 56 DAS | 758.5 | | 738.6 | | 882.6 | | |
| At harvest | 922.1 | | 978.5 | | 1147.3 | | |

In 2001, artificial *Striga* infestation was accomplished with seeds from 1998 (viability: 82.5%). In 2002 a mixture of *Striga* seeds was used from 1995, 1996, 1997 and 2001 (mean viability: 73%). In 2003 the mixture consisted of *Striga* seeds from 1995 to 1998 and 2001, but because of its low viability (10.5%) *Striga* seeds from 2002 (viability: 78.7%) were added to arrive at the desired infestation levels.

Table 3. Information on field experiments in 2001- 2003

| | Year | | |
|---|---|---|---|
| Parameter | 2001 | 2002 | 2003 |
| Replications | 5 | 8 | 6 |
| Fertilization | 17-17-17 (N:P:K) kg ha$^{-1}$ | 34-34-34 (N:P:K); gypsum 100 kg ha$^{-1}$ | 34-34-34 (N:P:K) kg ha$^{-1}$ |
| Sub-plot size | 12.80 m$^2$ | 24.32 m$^2$ | 20.48 m$^2$ |
| Main-plot levels | 2 (*Striga*, *Striga*-free) | 2 (*Striga*, *Striga*-free) | 3 (*Striga* low, *Striga* high, *Striga*-free) |
| Spacing of plants | 0.20-0.80 m | 0.40-0.80 m | 0.40-0.80 m |
| Sowing date | July 13 | July 6 | July 5 |
| *Striga* infestation levels (seeds m$^{-2}$) | 0 and 45,000 | 0 and 200,000 | 0, 30,000 and 150,000 |
| *Striga* infestation depth | 0.05 m | 0.10 m | 0.10 m |
| Area/number of plants used to assess grain yield | 1.60 m$^2$/ 10 plants | 3.20 m$^2$/ 10 plants | 2.56 m$^2$/ 8 plants |
| Ethylene injections | Two times | None | Two times |

Each sub-plot, representing one sorghum genotype, comprised four crop rows of 4.0 (2001), 7.6 (2002) and 6.4 m (2003) length with a row spacing of 0.8 m and a plant distance in the row of 0.2 (2001) and 0.4 m (2002 and 2003). After soil tillage (till 0.3 m depth), and levelling, the field was fertilised with 100 (2001) and 200 kg N-P-K ha$^{-1}$ (2002 and 2003) (17%N, 17%P, 17%K). In 2002 an additional 100 kg gypsum ha$^{-1}$ was applied to raise soil pH. Sorghum was sown on 13 July 2001, 6 July 2002 and 5 July 2003 at six seeds per pocket and a depth of 2-4 cm. Plants were thinned to one plant per pocket at 21 days after sowing (DAS).

Aboveground *Striga* numbers were counted every two weeks from *Striga* emergence till harvest of the crop. Simultaneously, in 2001 and 2002 *Striga* vigour scores, on a scale from 1 to 9, were given, depending on height and number of branches of individual plants (Haussmann et al., 2000b). Sorghum grain yield (*Striga*-infested and *Striga*-free) was determined, based on 10 (2001 and 2002) and 8 (2003) plants per sub-plot, representing an area of 1.6 (2001), 3.2 (2002) and 2.6 m$^2$ (2003). Panicles were harvested at maturity and air dried before threshing and weighing. Maturity was determined for each genotype separately.

Resistance and tolerance of the various genotypes were estimated based on the field observations. Four *Striga* infection measures were used to indicate the level of resistance: (1) number of aboveground *Striga* plants at harvest ($NS_{harvest}$), (2) maximum number of aboveground *Striga* plants ($NS_{max}$), (3) area under the aboveground *Striga* number progress curve (*ASNPC*) and (4) area under the *Striga* severity progress curve (*ASVPC*). *Striga* severity is the product of *Striga* number and *Striga* vigour score. The maximum number of aboveground *Striga* plants ($NS_{max}$) was introduced as, due to mortality, the maximum number was not always obtained at final harvest, but more often at earlier counts. The *ASNPC*, as outlined by Haussmann et al. (2000b) was calculated as:

$$ASNPC = \sum_{i=0}^{n-1} \left[S_i + S_{(i+1)}/2\right]\left(t_{(i+1)} - t_i\right) \qquad (1)$$

where $n$ is the number of *Striga* assessment dates, $S_i$ is the *Striga* number at the $i^{th}$ assessment date, $t_i$ the number of days after sowing at the $i^{th}$ assessment date. The *ASNPC* is a measure of the total *Striga* emergence throughout the season. *ASVPC* was calculated likewise, with $S_i$ representing the *Striga* severity score.

Sorghum yield from *Striga*-free plots ($Y_C$; kg ha$^{-1}$) was used as a control and represented the attainable yield. The attainable yield is the yield that could be obtained under the specific environmental conditions, in the absence of biotic stresses (Rabbinge, 1993). Combining this yield with the sorghum yield from adjacent *Striga*-infested plots ($Y_S$) was the basis for the derivation of tolerance measures. The first measure of tolerance was the relative yield loss due to *Striga* (*RYL*):

$$RYL = \left(Y_C - Y_S\right)/Y_C \qquad (2)$$

In an additional measure the *RYL* was divided by the maximum number of aboveground *Striga* plants, to obtain the *RYL* caused by a single *Striga* plant. This yields the second tolerance measure $a_{linear}$. This measure implicitly assumes a linear relation between relative yield loss and *Striga* infection level.

### *Pot trial*

A pot trial was conducted in 2001, at the same site as the field trials, in Samanko, Mali. The pot trial comprised a randomised block design in six replicates, with ten sorghum genotypes grown under *Striga* infestation. Plant distances were 0.35 m in the row and 0.7 m between rows. Pots of 10 L content were filled with 10 kg of a sand-soil-compost mixture (3:3:2). *Striga* infestation level was 4 viable *Striga* seeds cm$^{-3}$ in the upper 5 cm (origin: Samanko, year: 1995, viability: 71.2%). After mixing through the soil, *Striga* seeds were preconditioned for 12 days in the pots.

Sorghum was sown on 16 July (4-5 seeds per pot at 2-3 cm depth) and thinned to one plant per pot at 14 DAS. Number of below- and aboveground *Striga* plants ($NS_{bg}$ and $NS_{ag}$ respectively) were counted at 77 DAS.

*Laboratory trial*

Two agar-gel assays were conducted, in 2002 in a laboratory of Wageningen University, in Wageningen, The Netherlands, with ten sorghum genotypes and *Striga* seeds from two different locations in Mali (Samanko and Doumba) in eight replicates. The agar-gel assay developed by Hess et al. (1992) is a quick tool to screen sorghum genotypes for their ability to stimulate *Striga* seed germination. Agar-gel (0.7 % agar-agar) was added to a Petri dish containing sterilised and preconditioned (12 days at 28°C in the dark) *Striga* seeds. The radicle of a 24 h old sorghum seedling was inserted in the solidified agar. After five days (at 28°C in the dark) the total number of *Striga* seeds as well as the number of germinated *Striga* seeds was counted and the fraction of germinated seeds (*GS*) calculated. Furthermore, the distance from the sorghum radicle to the furthermost germinated *Striga* seed (*GD*; mm) was determined.

*Statistical analyses*

An analysis of variance (ANOVA) was carried out to analyse the data, followed by a comparison of means with the least significant difference (L.S.D.) using the Genstat (release 6.1) statistical software package. To meet the assumptions of the analysis of variance some data were subjected to transformation prior to analysis, following procedures recommended by Sokal and Rohlf (1995, pp. 413-41). On field data involving *Striga* counts logarithmic transformations ($\log(X+c)$, where $X$ is the original, individual observation and $c$=1.0) were applied. On belowground data involving counts with zeroes present, square root transformations ($(X + c)^{1/2}$, where $X$ is the original observation and $c$=0.5) were applied.

Binomial distributed data, e.g. the fraction germinated *Striga* seeds, were subjected to a GLM regression analysis with binomial errors followed by a pair-wise comparison of means by a t-test, in Genstat, following McCullagh and Nelder (1989, pp. 98-107) and Payne et al. (1993, pp. 413-26).

Pearson's correlations are presented throughout, based on treatment means, carried out with the SPSS (version 10.0) statistical software package. Correlations in this study were phenotypic correlations ($r$). Due to relative high environmental variation (see Results) genetic correlations could not be calculated.

Repeatability ($R$) of resistance measures and yield were calculated following:

$$R = (V_G + V_{Eg})/V_P \quad = 1 - (V_{Es}/V_P) \tag{3}$$

where $V_P$ is the total phenotypic variance, which is composed of three components: (1) $V_G$ the genetic variance, (2) $V_{Eg}$ the environmental variance due to permanent environmental effects on the phenotype and (3) $V_{Es}$ the environmental variance due to temporary or localized environmental effects on the phenotype (Falconer and Mackay, 1996, pp.136-37). Repeatabilities set an upper-limit to the heritability of a selection measure.

## Results

*Resistance*

Table 4 shows the mean, repeatability and ranking of all genotypes for each year and infestation level according to four different measures for resistance: $NS_{harvest}$, $NS_{max}$, *ASNPC* and *ASVPC*. Only in 2003 the *ASVPC* was not determined. In 2002 and 2003H, the experiments with the highest infection levels, $NS_{max}$ and *ASNPC* appeared more discriminative than $NS_{harvest}$. Repeatabilities of $NS_{max}$ and *ASNPC* were also higher than for $NS_{harvest}$ in most of the cases, except for 2003H. Comparison between measures shows that all measures, except $NS_{harvest}$, appoint the same three most resistant genotypes within years.

Also for the least resistant genotypes, ranking based on $NS_{harvest}$ deviated from that based on the other measures. There was a highly significant correlation between the different measures in all years except for $NS_{harvest}$ in 2002. In this year $NS_{harvest}$ did not show a significant correlation with one of the other resistance measures, while correlation between the other measures was still highly significant (Table 5). Ranking of most resistant and least resistant genotypes corresponded reasonably well between years, except for some cases. In 2001, representing the lowest infestation level, CMDT39 belonged to the group of three most resistant genotypes at the expense of IS9830. In 2002 ($NS_{max}$, *ASNPC* and *ASVPC*), CMDT39 was ranked within the group of three lowest resistant genotypes at the expense of Seredo. The three most resistant genotypes, based on $NS_{max}$ and *ASNPC*, throughout the three years were N13, IS9830 and SRN39. CK60-B, E36-1 and Seredo showed to be poorly resistant, whereas CMDT39, Framida, Serena and Tiémarifing held an intermediate position.

Table 4. Means, rankings (1-10) and repeatabilities (*R*) of different measures used to express resistance in the field in 2001, 2002 and 2003 (low infestation: L and high infestation: H). Mean *Striga* number at harvest ($NS_{harvest}$), maximum aboveground *Striga* number ($NS_{max}$), area under the *Striga* number progress curve (*ASNPC*) and area under the *Striga* severity progress curve (*ASVPC*). All measures are expressed per host plant.

| Year (level) | Genotype | $NS_{harvest}$ | | | $NS_{max}$ | | | *ASNPC* | | | *ASVPC* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2001 | CK60-B | 0.70 | bc[a] | 8[b] | 2.14 | b | 9 | 73.3 | ab | 9 | 226.0 | ab | 9 |
| | CMDT39 | 0.22 | cd | 2 | 0.60 | de | 2 | 16.1 | c | 3 | 31.5 | d | 2 |
| | E36-1 | 2.73 | a | 10 | 7.30 | a | 10 | 187.4 | a | 10 | 473.2 | a | 10 |
| | Framida | 0.41 | bcd | 5 | 1.19 | bcd | 6 | 34.3 | bc | 7 | 62.4 | bcd | 6 |
| | IS9830 | 0.58 | bcd | 6 | 0.82 | cde | 4 | 16.0 | c | 2 | 32.7 | d | 3 |
| | N13 | 0.04 | d | 1 | 0.11 | e | 1 | 3.9 | d | 1 | 6.7 | e | 1 |
| | Seredo | 0.66 | bc | 7 | 1.92 | bc | 8 | 60.2 | ab | 8 | 145.6 | abc | 8 |
| | Serena | 0.98 | b | 9 | 1.44 | bcd | 7 | 33.3 | bc | 6 | 68.5 | bcd | 7 |
| | SRN39 | 0.31 | bcd | 3 | 0.66 | de | 3 | 23.8 | bc | 4 | 53.5 | cd | 4 |
| | Tiémarifing | 0.32 | bcd | 4 | 0.96 | bcd | 5 | 29.5 | bc | 5 | 61.8 | bcd | 5 |
| | S.E.D[c] | 0.091 | | | 0.109 | | | 0.255 | | | 0.302 | | |
| | R | 0.48 | | | 0.62 | | | 0.48 | | | 0.46 | | |
| 2002 | CK60-B | 53.7 | a | 10 | 92.1 | a | 10 | 3774.7 | a | 10 | 31044.6 | a | 10 |
| | CMDT39 | 8.8 | cd | 2 | 84.5 | a | 8 | 3356.4 | a | 8 | 19723.2 | ab | 9 |
| | E36-1 | 25.4 | b | 6 | 91.5 | a | 9 | 3588.2 | ab | 9 | 17578.2 | bc | 8 |
| | Framida | 19.5 | b | 4 | 48.8 | b | 4 | 1895.7 | ab | 4 | 8413.0 | de | 4 |
| | IS9830 | 22.8 | b | 5 | 26.5 | c | 2 | 925.8 | bc | 2 | 4919.4 | e | 2 |
| | N13 | 7.7 | d | 1 | 8.6 | d | 1 | 308.0 | bc | 1 | 2141.9 | f | 1 |
| | Seredo | 53.5 | a | 9 | 67.9 | a | 6 | 2540.0 | c | 6 | 10374.3 | cd | 5 |
| | Serena | 53.1 | a | 8 | 74.7 | ab | 7 | 2876.4 | d | 7 | 12501.6 | bcd | 7 |
| | SRN39 | 26.3 | ab | 7 | 32.7 | c | 3 | 1121.0 | d | 3 | 5901.0 | e | 3 |
| | Tiémarifing | 17.8 | bc | 3 | 63.9 | ab | 5 | 2448.1 | e | 5 | 11375.3 | cd | 6 |
| | S.E.D. | 0.152 | | | 0.081 | | | 0.074 | | | 0.117 | | |
| | R | 0.43 | | | 0.73 | | | 0.84 | | | 0.66 | | |
| 2003L | CK60-B | 8.20 | a | 10 | 13.32 | a | 10 | 473.2 | a | 10 | | | |
| | CMDT39 | 3.63 | bc | 8 | 5.85 | bc | 8 | 165.3 | ab | 8 | | | |
| | E36-1 | 5.19 | ab | 9 | 10.91 | ab | 9 | 307.3 | ab | 9 | | | |
| | Framida | 1.50 | d | 3 | 3.26 | cde | 4 | 97.6 | bc | 4 | | | |
| | IS9830 | 1.45 | d | 2 | 1.78 | e | 2 | 47.9 | c | 2 | | | |
| | N13 | 0.28 | e | 1 | 0.42 | f | 1 | 5.6 | d | 1 | | | |
| | Seredo | 2.48 | bcd | 6 | 4.75 | cd | 6 | 138.0 | bc | 5 | | | |
| | Serena | 2.51 | bcd | 7 | 5.07 | cd | 7 | 162.7 | ab | 7 | | | |
| | SRN39 | 1.74 | cd | 4 | 2.52 | de | 3 | 47.9 | c | 3 | | | |
| | Tiémarifing | 2.39 | cd | 5 | 4.40 | de | 5 | 146.2 | abc | 6 | | | |
| | S.E.D. | 0.126 | | | 0.139 | | | 0.256 | | | | | |
| | R | 0.50 | | | 0.49 | | | 0.55 | | | | | |
| 2003H | CK60-B | 20.23 | a | 10 | 50.2 | a | 10 | 1785.5 | a | 10 | | | |
| | CMDT39 | 7.79 | bcd | 5 | 18.3 | bcd | 5 | 634.3 | bcd | 5 | | | |
| | E36-1 | 9.69 | bc | 6 | 27.9 | ab | 7 | 892.3 | bc | 7 | | | |
| | Framida | 11.19 | b | 7 | 23.8 | bc | 6 | 844.3 | bc | 6 | | | |
| | IS9830 | 5.92 | cd | 4 | 11.9 | de | 3 | 404.5 | de | 3 | | | |
| | N13 | 1.34 | e | 1 | 2.6 | f | 1 | 81.2 | f | 1 | | | |
| | Seredo | 11.71 | ab | 8 | 31.6 | ab | 9 | 1139.2 | ab | 9 | | | |
| | Serena | 11.88 | ab | 9 | 28.6 | ab | 8 | 951.8 | abc | 8 | | | |
| | SRN39 | 4.38 | d | 2 | 7.7 | e | 2 | 290.1 | e | 2 | | | |
| | Tiémarifing | 4.90 | d | 3 | 14.2 | cde | 4 | 508.3 | cde | 4 | | | |
| | S.E.D. | 0.115 | | | 0.129 | | | 0.148 | | | | | |
| | R | 0.62 | | | 0.49 | | | 0.67 | | | | | |

[a] Means in the same column followed by the same letter are not significantly different according to L.S.D. test (*P*<0.01).

[b] Numbers 1-10 in the third column of each criterion, indicate ranking.

[c] Data were analysed after log(*X*+1)-transformation. S.E.D.-values of transformed data are given. Means in table are back-transformed. Degrees of freedom: 36 (2001), 63 (2002) and 45 (2003).

Table 5. Pearson's correlation coefficients (one-tailed) between four different *Striga* resistance measures: *Striga* numbers at harvest ($NS_{harvest}$), maximum number of aboveground *Striga* plants ($NS_{max}$), area under the *Striga* number progress curve (*ASNPC*) and area under the *Striga* severity progress curve (*ASVPC*), for three different years, 2001, 2002 and 2003 (low infestation: L and high infestation: H)

| | | Year (level) | | | |
|---|---|---|---|---|---|
| Correlated traits | | 2001 | 2002 | 2003L | 2003H |
| $NS_{harvest}$ | $NS_{max}$ | 0.975* | 0.462 ns[a] | 0.977*[b] | 0.983* |
| $NS_{harvest}$ | *ASNPC* | 0.947* | 0.448 ns | 0.984* | 0.985* |
| $NS_{harvest}$ | *ASVPC* | 0.923* | 0.419 ns | | |
| $NS_{max}$ | *ASNPC* | 0.991* | 0.998* | 0.986* | 0.997* |
| $NS_{max}$ | *ASVPC* | 0.974* | 0.867* | | |
| *ASNPC* | *ASVPC* | 0.993* | 0.891* | | |

a Not significant; * Significant at the *P*< 0.01 level

### *Belowground information*

A pot-trial was conducted to determine the extent to which the number of emerged *Striga* plants (aboveground: $NS_{ag}$) reflects the number of attached *Striga* plants (belowground: $NS_{bg}$). The results presented in Table 6 show that the number of attached *Striga* plants correlated significantly with the number of emerged *Striga* plants ($r$=0.871, $P$<0.01). Repeatabilities of $NS_{bg}$ and $NS_{ag}$ were however very low (0.25 and 0.31).

By combining the results of the pot trial with an agar-gel assay it was assessed whether resistance against individual life-cycle stages of the parasite (germination, attachment and emergence) should be separately considered in the selection process. Table 6 shows the fraction of germinated seeds (*GS*) and the maximum germination distance from the sorghum root (*GD*) for the various genotypes. Germination of the two *Striga* batches with different origins did not differ significantly and consequently their results were combined. The two measures for germination stimulation (*GS* and *GD*) yielded similar results and correlated significantly with one another ($r$= 0.865, $P$< 0.01). None of the germination measures correlated significantly with numbers of attached or emerged *Striga* plants as observed in the pot experiment ($r$ ($GS$-$NS_{bg}$)=0.304; $r$ ($GS$-$NS_{ag}$)=0.072).

Table 6. Means, standard error's (S.E.) or 95% confidence intervals (95% C.I.), repeatability (*R*) and rankings (1-10) of fraction of germinated *Striga* seeds (*GS*) and maximum germination distance (*GD*, mm) observed in the agar-gel tests and mean number of *Striga* attachments ($NS_{bg}$) and emergence ($NS_{ag}$) at 77 DAS from the pot trial. Data are expressed per sorghum plant or sorghum seedling.

| | Germination | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Genotype | *GS*[a] | S.E. | | | *GD* (mm) [b] | 95% C.I. | | |
| CK60B | 0.0258 | 0.0090 | b | 4 | 3.67 | [1.80, 6.11] | d | 4 |
| CMDT39 | 0.0974 | 0.0183 | cd | 9 | 13.06 | [8.85, 18.04] | ab | 7 |
| E36-1 | 0.1572 | 0.0196 | d | 10 | 17.72 | [11.06, 25.90] | ab | 9 |
| Framida | 0.0003 | 0.0008 | a | 2 | 0.15 | [0.0, 0.56] | e | 1 |
| IS9830 | 0.0016 | 0.0019 | a | 3 | 0.41 | [0.0, 1.01] | e | 3 |
| N13 | 0.0788 | 0.0129 | c | 7 | 18.15 | [11.51, 26.26] | a | 10 |
| Seredo | 0.0966 | 0.0146 | cd | 8 | 7.16 | [3.55, 11.89] | cd | 5 |
| Serena | 0.0613 | 0.0112 | bc | 5 | 11.49 | [6.11, 18.47] | bc | 6 |
| SRN39 | 0.0003 | 0.0008 | a | 1 | 0.33 | [0.0, 1.29] | e | 2 |
| Tiémarifing | 0.0738 | 0.0133 | c | 6 | 13.20 | [8.29, 19.21] | ab | 8 |
| *R* | | | | | 0.57 | | | |

| | Attachment and Emergence | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Genotype | $NS_{bg}$ [b] | 95% C.I. | | | $NS_{ag}$ [b] | 95% C.I. | | |
| CK60B | 5.65 | [3.97, 7.77] | a | 9 | 7.51 | [2.63, 9.96] | a | 10 |
| CMDT39 | 3.42 | [2.29, 4.41] | abc | 5 | 2.74 | [0.0, 6.50] | abcd | 7 |
| E36-1 | 5.75 | [1.85, 10.19] | a | 10 | 4.38 | [0.18, 8.38] | ab | 8 |
| Framida | 4.70 | [0.62, 9.95] | ab | 8 | 4.25 | [0.0, 9.67] | abc | 9 |
| IS9830 | 0.71 | [0.00, 2.10] | c | 1 | 0.62 | [0.0, 1.28] | cd | 2 |
| N13 | 1.43 | [-0.03, 4.30] | bc | 3 | 0.21 | [0.0, 0.85] | d | 1 |
| Seredo | 2.19 | [1.40, 3.65] | abc | 4 | 2.70 | [0.48, 3.65] | abcd | 6 |
| Serena | 3.30 | [0.93, 8.47] | abc | 7 | 1.78 | [0.12, 2.98] | bcd | 5 |
| SRN39 | 1.69 | [-0.19, 3.08] | abc | 2 | 0.80 | [0.0, 1.67] | bcd | 3 |
| Tiémarifing | 3.26 | [1.19, 5.65] | abc | 6 | 1.32 | [0.0, 2.28] | bcd | 4 |
| *R* | 0.25 | | | | 0.31 | | | |

[a] *GS* has a binomial distribution and is analysed with a GLM regression analysis, degrees of freedom: 158.

[b] Means of *GD*, $NS_{bg}$ and $NS_{ag}$ are back-transformed from ANOVA with $(X+0.5)^{-1/2}$ transformed data. Means followed by the same letter are not different at the $P=0.001$ level of significance for *GD* and at the $P=0.01$ level of significance for *GS*, $NS_{bg}$ and $NS_{ag}$. Numbers 1-10 in the fourth column of each criterion, indicate ranking. Degrees of freedom are 159 (*GD*) and 45 ($NS_{bg}$ and $NS_{ag}$).

Table 7. Means and rankings of 10 sorghum genotypes for grain yield (kg ha$^{-1}$) under *Striga* infestation ($Y_S$) and control conditions ($Y_C$), relative yield loss due to *Striga* (*RYL*) and relative yield loss per *Striga* plant ($a_{linear}$) per year (2001-2003) and level (L or H).

| Year (level) | Genotype | $Y_S$ | | | $Y_C$ | | | *RYL* | | $a_{linear}$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2001 | CK60-B | 352 | c[a] | 10[b] | 1093 | abc | 5 | 0.68 | 10 | 0.297 | 7 |
| | CMDT39 | 816 | abc | 6 | 1019 | abc | 6 | 0.20 | 5 | 0.321 | 9 |
| | E36-1 | 799 | abc | 7 | 798 | bc | 9 | 0.00 | 1 | 0.000 | 1 |
| | Framida | 1164 | ab | 3 | 1481 | a | 2 | 0.21 | 8 | 0.162 | 6 |
| | IS9830 | 1405 | a | 1 | 1438 | ab | 4 | 0.02 | 2 | 0.024 | 2 |
| | N13 | 501 | c | 9 | 761 | c | 10 | 0.34 | 7 | 2.849 | 10 |
| | Seredo | 1237 | ab | 2 | 1564 | a | 1 | 0.21 | 6 | 0.094 | 4 |
| | Serena | 631 | bc | 8 | 1480 | a | 3 | 0.57 | 9 | 0.326 | 8 |
| | SRN39 | 888 | abc | 4 | 988 | abc | 7 | 0.10 | 4 | 0.144 | 5 |
| | Tiémarifing | 886 | abc | 5 | 979 | abc | 8 | 0.09 | 3 | 0.083 | 3 |
| | S.E.D. | 307.0 | | | 315.8 | | | | | | |
| | *R*[c] | 0.21 | | | 0.14 | | | | | | |
| 2002 | CK60-B | 188 | e | 10 | 1072 | de | 9 | 0.82 | 9 | 0.0088 | 5 |
| | CMDT39 | 333 | de | 9 | 1589 | cd | 7 | 0.79 | 8 | 0.0089 | 7 |
| | E36-1 | 346 | de | 8 | 2203 | ab | 4 | 0.84 | 10 | 0.0089 | 6 |
| | Framida | 1543 | b | 2 | 2400 | ab | 3 | 0.36 | 4 | 0.0065 | 4 |
| | IS9830 | 2434 | a | 1 | 2178 | ab | 5 | -0.12 | 1 | -0.0041 | 1 |
| | N13 | 792 | cd | 5 | 900 | e | 10 | 0.12 | 2 | 0.0124 | 10 |
| | Seredo | 1185 | bc | 3 | 2522 | a | 1 | 0.53 | 5 | 0.0064 | 3 |
| | Serena | 698 | cd | 7 | 2477 | a | 2 | 0.72 | 7 | 0.0091 | 8 |
| | SRN39 | 990 | c | 4 | 1146 | de | 8 | 0.14 | 3 | 0.0040 | 2 |
| | Tiémarifing | 711 | cd | 6 | 1893 | bc | 6 | 0.62 | 6 | 0.0094 | 9 |
| | S.E.D. | 248.7 | | | 291.2 | | | | | | |
| | *R* | 0.63 | | | 0.50 | | | | | | |
| 2003L | CK60-B | 546 | e | 10 | 1174 | ef | 9 | 0.53 | 10 | 0.0236 | 3 |
| | CMDT39 | 1481 | bc | 5 | 1955 | bc | 6 | 0.24 | 7 | 0.0332 | 6 |
| | E36-1 | 1063 | cd | 8 | 1970 | bc | 4 | 0.46 | 9 | 0.0231 | 2 |
| | Framida | 1743 | ab | 3 | 1812 | cd | 7 | 0.04 | 1 | 0.0060 | 1 |
| | IS9830 | 1693 | ab | 4 | 2030 | bc | 3 | 0.17 | 2 | 0.0452 | 7 |
| | N13 | 702 | de | 9 | 931 | f | 10 | 0.25 | 6 | 0.2860 | 10 |
| | Seredo | 1747 | ab | 2 | 2289 | b | 2 | 0.24 | 4 | 0.0239 | 4 |
| | Serena | 1986 | a | 1 | 2658 | a | 1 | 0.25 | 5 | 0.0303 | 5 |
| | SRN39 | 1115 | cd | 7 | 1501 | de | 8 | 0.26 | 3 | 0.0568 | 9 |
| | Tiémarifing | 1445 | bc | 6 | 1967 | bc | 5 | 0.27 | 8 | 0.0533 | 8 |
| | S.E.D. | 217.1 | | | 182.9 | | | | | | |
| | *R* | 0.59 | | | 0.71 | | | | | | |
| 2003H | CK60-B | 288 | e | 10 | 1174 | ef | 9 | 0.75 | 9 | 0.0113 | 2 |
| | CMDT39 | 1206 | abc | 3 | 1955 | bc | 6 | 0.38 | 4 | 0.0115 | 3 |
| | E36-1 | 411 | de | 9 | 1970 | bc | 4 | 0.79 | 10 | 0.0150 | 7 |
| | Framida | 921 | bcd | 5 | 1812 | cd | 7 | 0.49 | 6 | 0.0121 | 4 |
| | IS9830 | 1576 | a | 1 | 2030 | bc | 3 | 0.22 | 1 | 0.0124 | 5 |
| | N13 | 708 | de | 8 | 931 | f | 10 | 0.24 | 2 | 0.0599 | 10 |
| | Seredo | 863 | bcd | 6 | 2289 | b | 2 | 0.62 | 8 | 0.0144 | 6 |
| | Serena | 1133 | abc | 4 | 2658 | a | 1 | 0.57 | 7 | 0.0152 | 8 |
| | SRN39 | 861 | bcd | 7 | 1501 | de | 8 | 0.43 | 5 | 0.0229 | 9 |
| | Tiémarifing | 1327 | ab | 2 | 1967 | bc | 5 | 0.33 | 3 | 0.0109 | 1 |
| | S.E.D. | 264.9 | | | 182.9 | | | | | | |
| | *R* | 0.37 | | | 0.71 | | | | | | |

[a] Means in the same column followed by the same letter are not significant different according to the L.S.D. test ($P$<0.001). Exceptions are: $Y_C$ 2001 ($P$=0.096) and $Y_S$ 2001 ($P$=0.037). Degrees of freedom: 36 (2001), 63 (2002) and 45 (2003L and H).

[b] Numbers 1-10 in every second or third column, indicate ranking. [c] *R* means Repeatability.

These data showed low stimulation of germination (*GS*) and low numbers of attachments and emergence ($NS_{bg}$ and $NS_{ag}$) at IS9830 and SRN39 and an absence of resistance in any of these stages for E36-1. At Framida and CK60-B, *GS* was low and medium-to-low but $NS_{bg}$ and $NS_{ag}$ were relatively high, whereas at N13, *GS* was high but $NS_{bg}$ and $NS_{ag}$ very low. Serena, Seredo, Tiémarifing and CMDT39 held an intermediate position in every stage.

*Tolerance*

Table 7 presents yield under *Striga* infestation ($Y_S$), yield under *Striga*-free conditions ($Y_C$), relative yield loss due to *Striga* (*RYL*) and relative yield loss per maximum aboveground *Striga* plant ($a_{linear}$). The *RYL* was calculated directly from the yields presented in Table 7. The $a_{linear}$ was calculated by dividing *RYL* by the maximum number of aboveground *Striga* plants ($NS_{max}$, Table 4). In 2002 and 2003, $Y_C$ was much higher (on average 1.6 times) than in 2001 for nearly all genotypes. Exceptions were CK60-B and N13 in 2002 and 2003 and Framida in 2003. For $Y_S$ large differences in ranking between years were observed. CK60-B and E36-1 were consistently ranked within the group of lowest yielding genotypes. IS9830 and Framida belonged consistently to the highest yielding genotypes under *Striga*-infested conditions, except for Framida in 2003H. Tiémarifing was a rather constant intermediate genotype, concerning $Y_S$. Only in 2003H it was ranked somewhat higher. The repeatability of $Y_S$ was low, especially in 2001 (0.21). This indicates a low upper-limit of heritability and a large contribution of environmental variation to the phenotypic variation of this trait.

Rankings based on *RYL* were not very consistent. Throughout the years, seven genotypes were ranked among the three genotypes with the highest *RYL*. Only CK60-B (four times) and E36-1 (three times) appeared more than once in this group. Six genotypes were ranked among the three genotypes with the lowest *RYL* and only IS9830 appeared more than twice in this group. Relative yield loss is the result of resistance and tolerance combined. For a fair assessment of tolerance, the *RYL* needs to be corrected for infection level. The $a_{linear}$ expresses the average relative yield loss per emerged *Striga* plant. Correction of *RYL* for the infection level had important consequences for the ranking of the different genotypes. In 2003, CK60-B was the genotype that suffered most from *Striga* infection but if relative yield loss was related to the number of infections it was found that the yield loss per *Striga* plant was modest. For N13 exactly the opposite was found. Compared to the other genotypes *RYL* was either moderate (2003L) or even low (2003H). Relating this *RYL* to the number of *Striga* plants revealed that with this genotype the damage per *Striga* plant was by far the largest. The three most tolerant genotypes based on $a_{linear}$ were difficult to identify due to inconsistency throughout the years and infestation levels. Table 7 shows that over the years and infestation levels, eight genotypes were ranked as most tolerant based on $a_{linear}$, of which four of them only once (Seredo, SRN39, Framida and CMDT39). The other four genotypes all belonged two times to the group of three most tolerant genotypes (E36-1, Tiémarifing, IS9830, and CK60-B). Among the group of eight genotypes Tiémarifing (two times), SRN39, and CMDT39 were also ranked among the three least tolerant genotypes in other years or infestation levels.

### *Phenotypic correlations*

In this study resistance, tolerance and yield under *Striga*-free conditions were used as a complementary set of traits that together determine yield under *Striga*. From a breeding perspective it is relevant to find out how well each of these traits correlates to the yield under *Striga* infestation, as an indication for their significance. Table 8 shows results of the phenotypic correlations between yield under *Striga* infestation ($Y_S$) and control yield ($Y_C$), relative yield loss (*RYL*), and maximum number of emerged *Striga* plants ($NS_{max}$). $NS_{max}$ represents resistance, whereas *RYL* represents the outcome of all defence mechanisms combined including resistance. Only in the two low infested fields (2001 and 2003L), $Y_C$ was found to correlate significantly with $Y_S$ ($r$= 0.584 and 0.886, $P$= 0.038 and < 0.01, respectively). The *RYL* was found to correlate significantly with $Y_S$ in all situations. Significance of this correlation increased with infestation level (going from the lowest to the highest infested fields: $P$= 0.013, 0.016, 0.008 and 0.002). The $NS_{max}$ correlated significantly with $Y_S$ only in the highest infested field (2002; $r$= -0.633, $P$=0.025). A significant correlation between *RYL* and $NS_{max}$ was found in all situations, except in 2001, the lowest infested field.

Table 8. Pearson's correlations coefficients between yield under *Striga* infestation ($Y_S$), yielding ability ($Y_C$), maximum *Striga* number ($NS_{max}$) and the relative yield loss (*RYL*) for 2001, 2002, 2003L (low *Striga* infestation level), and 2003H (high *Striga* infestation level).

| Correlated traits | | Year (level)<br>2001 | 2002 | 2003L | 2003H |
|---|---|---|---|---|---|
| $Y_S$[a] | $Y_C$ | 0.584* | 0.390 | 0.886** | 0.506 |
| $Y_S$ | *RYL* | -0.692* | -0.809** | -0.674* | -0.730** |
| $Y_S$ | $NS_{max}$ | -0.079 | -0.633* | -0.383 | -0.521 |
| *RYL* | $NS_{max}$ | -0.218 | 0.944** | 0.835** | 0.849** |

[a] Correlations are one-tailed.
* Correlation is significant at the 0.05 level of significance.
** Correlation is significant at the 0.01 level of significance.

## Discussion

*Factors determining yield under Striga infestation*

Abiotic growth factors, like temperature, radiation and availability of water and nutrients, combined with the physiological and morphological characteristics of a genotype determine the attainable yield of a crop (Rabbinge, 1993). The actual yield will in general be lower than the attainable yield, due to the presence of biotic stress factors, like *Striga*. Yield reduction due to *Striga* is determined by the infection level and the consequences of infection for crop production. Analogous to this, the defence mechanism of a crop can be separated into resistance, the ability to reduce the infection level, and tolerance, the ability to minimize the consequences of infection. Results of this study show that the correlation between *RYL*, representing the effect of resistance and tolerance combined, and the yield under *Striga* infestation becomes stronger with an increase in infestation level. Simultaneously, the correlation between attainable yield and yield under *Striga* infestation decreases at higher infestation levels. Moreover, the correlation study demonstrates that at high infestation levels resistance becomes an increasingly important component of the overall defence mechanism against *Striga*. Implicitly this suggests that tolerance is a relatively more important mechanism at low infestation levels. Combining host plant resistance with tolerance and high yielding ability has often been proposed as durable control measure against parasitic angiosperms (Kim, 1991; DeVries, 2000; Kling et al., 2000; Haussmann et al., 2001a,b; Pierce et al., 2003; Showemimo, 2003). Our findings support this approach.

For obtaining the best combination of traits, the potentially best sources of resistance, tolerance and yielding ability need to be identified. In breeding programs against *Striga*, the number of emerged *Striga* plants, and the yield under *Striga* infestation are often important selection criteria. Selection based on those two traits alone unintentionally ignores tolerance. This can be illustrated by the results of CMDT39 and E36-1 in 2001. These genotypes had equal yields under *Striga* (816 and 799 kg.ha$^{-1}$, respectively) but a significant difference in number of emerged *Striga* plants (0.6 and 7.3, respectively). In such a situation screening based on yield and *Striga* number alone would favour the genotype with the lowest *Striga* number (CMDT39) which implies a negative selection for tolerance. This could be avoided if a proper selection measure for tolerance would be available. For this reason this study explored the opportunities for defining a practical set of field selection measures that takes into account both resistance and tolerance.

To achieve this, a group of genotypes was selected with a wide range of modes and levels of defence mechanisms against *Striga*. As a result the selected group of genotypes consisted of different sorghum races (Guinea, Caudatum, Kafir and Durra) and origins with only two local sorghum genotypes (CMDT39 and Tiémarifing). The specific levels of control yield, tolerance and resistance of the various sorghum genotypes in this study may therefore be affected by genotype x environment interactions and *Striga* population (e.g. Botanga et al., 2002; Oswald and Ransom, 2004). For this reason it is often recommended to screen at multiple locations and with different *Striga* populations (Ramaiah, 1987a; Haussmann et al., 2000b; Omanya et al., 2004). However, the aim of this study was not to identify the best genotypes but to evaluate and improve the current screening procedures and measures.

### *Complexity of tolerance*

Screening for tolerance requires a field design with *Striga*-free control plots next to *Striga*-infested plots. As sorghum yield is determined by many environmental factors, this set-up offers the best possibility for estimating the gap between attainable and actual yield. The ratio between this gap and the attainable yield expresses the relative yield loss (*RYL*). So far, only few studies have used a factorial design with *Striga*-infested and *Striga*-free control plots in the same field (Efron, 1993; Kim and Adetimirin, 1997a; Gurney et al., 1999; Adetimirin et al., 2000a,b; Kim et al., 2002). It requires infesting *Striga* free fields (Efron, 1993; this study), which is not always possible, or the creation of *Striga*-free control plots within *Striga*-infested fields. Technically this can be achieved by using ethylene gas (this study) or methyl bromide (Gurney et al., 1999) but this is very expensive. Furthermore, ethylene injections do not guarantee total absence of *Striga* (personal observation).

In some situations it is already possible to separate tolerance from resistance based on *RYL* and infection level. In 2001 for instance, yield of E36-1 under *Striga*-infested conditions was identical to the yield under *Striga*-free conditions despite a relatively high infection level ($NS_{max}$: 7.3 plants per host plant). This indicates the presence of a tolerance mechanism. For N13, with a mean $NS_{max}$ of only 0.1, resistance seems the most important mechanism. However, not in all cases it is so easy to disentangle the contribution of tolerance and resistance to the overall defence mechanism. As mentioned earlier, tolerance is defined as the reaction of genotypes that germinate and support as many *Striga* plants as other genotypes without the same severity of yield reductions. In reality however, as shown in this study, clear differences in *Striga* infection level exist between genotypes. This implies that for obtaining an independent measure for tolerance, the yield reduction due to *Striga* should be corrected for *Striga* infection level. Consequently, *RYL* in itself is not an independent measure of tolerance, as it is always confounded with resistance. The high correspondence between the ranking based on $NS_{max}$ and the ranking based on *RYL* in 2002 for instance follows from the fact that resistance is included in *RYL*. As *RYL* depends on both resistance and tolerance, it is not surprising that rankings based on *RYL* are inconsistent over years. Infestation levels varied over years and, as earlier demonstrated, the importance of resistance and tolerance varies with infestation level. The importance of correction for *Striga* infection level is also demonstrated by data published by Efron (1993). Correction of the *RYL* of the low resistant maize hybrid 8338-1 for the simultaneously observed *Striga* counts, would appoint this genotype as the most tolerant instead of the most sensitive one. Contrary to earlier statements made by Kim (1991) and Efron (1993) *Striga* counts may be very important for the accurate assessment of tolerance.

However, simply expressing the relative yield loss per aboveground *Striga* plant proved to be insufficient. Such a linear correction for infection pressure assumes an identical negative effect of every additional *Striga* plant on yield. Data presented in Table 7 illustrate this assumption to be incorrect. With an increase in aboveground *Striga* numbers, the $a_{linear}$ decreases drastically (e.g. 2001 vs. 2002). Additional evidence that the relation between *RYL* and *Striga* infection level is not linear is provided by data on CK60-B in Table 7. At a very low infection level (2001) already a *RYL* of 60% was attained, while at a 40 times higher infection level (2002) the *RYL* was only 82%.

For a proper assessment of tolerance in the field, one needs to know how to correct for genotype-dependent differences in *Striga* infection level. This means that the relation between *Striga* infection and yield loss should be known. The correction factor for *Striga* infection should be obtainable from field observations, and preferably be based on an aboveground resistance measure such as $NS_{max}$. With non-parasitic weeds that mainly affect crop plants through resource competition, a progressively declining yield loss with increasing weed numbers is generally observed (e.g. Weaver et al., 1987; Spitters et al., 1989). This relation can be accurately described by a rectangular hyperbola, which is characterised by the initial slope, the yield loss caused by the first weed added to a weed free crop, and the maximum yield loss at high weed density (Cousens, 1985). Webb and Smith (1996) suggested that a similar relation would hold for parasitic weeds. For a single sorghum genotype, Gurney et al. (1999, 2000) observed a declining marginal yield loss with increasing *Striga* dry weight. Although *Striga* dry weight is not a straightforward resistance measure and not linearly related to *Striga* number, the observation confirms that the relation between yield loss and infection level is not proportional.

The initial slope ($a_{hyperbolic}$) of the assumed hyperbolic relation between relative yield loss and number of *Striga* plants ($NS_{max}$ or *ASNPC*), representing the yield reduction due to the very first *Striga* plant, could be a good measure to express tolerance. A preliminary calculation of the $a_{hyperbolic}$ was made, under the assumption that for each of the genotypes ultimately a maximum relative yield loss of 100% would be obtained. As expected, the rankings of $a_{linear}$ and $a_{hyperbolic}$ proved to be reasonably comparable at low infection levels (2001 and 2003L) but deviated significantly at higher infection levels (2002 and 2003H). However, the current data suggest that with genotypes such as IS9830 and Framida severe *Striga* infection will never result in complete failure of the host. This implies that tolerance might be characterised by two components: (1) the initial slope of the relation between relative yield loss and *Striga* infection level and (2) the attainable relative yield loss. It will then be valuable to assess tolerance at least at two infection levels: low (infection initiation), to get a good estimation of the initial slope, and high (infection saturation), to estimate the maximum relative yield loss. Furthermore, it is not evident that the relation between relative yield loss and *Striga* infection always obeys the same function. For instance, observations on E36-1 show that some genotypes may be very tolerant at low infection levels and very sensitive at high infection levels. This indicates the possible presence of an infection threshold beyond which the initial tolerance collapses. Further research is needed to resolve the relation between relative yield loss and *Striga* infection, and to investigate whether a similar relation holds for all *Striga* hosts (independent of genotype). This should lead to a practical field selection measure, which helps the cereal breeder to identify genotypes with superior tolerance.

### *Field selection measure for resistance*

A reliable resistance measure is a prerequisite for the identification of both resistance and tolerance. Of the resistance measures, the *Striga* number at harvest ($NS_{harvest}$) is an easy measure to obtain but not very discriminative. Moreover, selection based on $NS_{harvest}$ proved to be insufficiently consistent over years and infestation levels. This trait was characterised by low repeatabilities, especially in 2001 and 2002, implying large contributions of environmental and error variation to the phenotypic variation. Moreover, harvest time is genotype dependent and determines to a large extent the fraction of emerged *Striga* plants that still remain at the time of observation. The area under the *Striga* number progress curve, *ASNPC*, as introduced by Haussmann et al. (2000b) is an appropriate measure as it incorporates infection time. In order to avoid differences caused by the genotype-dependent length of the growing season (harvest moment), the *ASNPC* was calculated between two fixed points in time (39 and 102 DAS) for all genotypes and all years. The *ASNPC* demonstrated to be one of the most discriminative, objective and complete measures. Repeatabilities of *ASNPC* were reasonably high, which confirms results of Omanya et al. (2004). Only in 2001, with a low infection level, repeatability was rather low. The *ASVPC* is considered less suitable as resistance measure because vigour scores are due to subjectivity and might also be affected by host tolerance. This might explain the somewhat lower repeatabilities observed for *ASVPC* compared to the repeatabilities of $NS_{max}$ and *ASNPC*. Omanya et al. (2004) reported that expression of genetic variation (by sorghum genotypes) for vigour scores is rather inconsistent. Furthermore, assigning appropriate vigour scores to the counted *Striga* plants, requires additional time. Maximum aboveground number of *Striga* plants ($NS_{max}$), earlier used, with millet, by Wilson et al (2000, 2004), turned out to be a more objective measure than counts at harvest time. It proved to be very consistent over years and equally discriminative as the *ASNPC*. Correlation between $NS_{max}$ and *ASNPC* was found to be highly significant irrespective of year and infestation level. A slight advantage of $NS_{max}$ over *ASNPC* is that one could save time because regular counts can be started later, around the time when the maximum number of aboveground *Striga* plants is expected. Still more than one count is required for determining $NS_{max}$, as it is not known on beforehand when exactly the maximum can be found and this moment will also differ between genotypes. Adetimirin et al. (2000b) who worked with maize, and Omanya et al. (2004), working with sorghum, proposed a single count at around 56 DAS and 77 DAS respectively. Additional analyses in the current study revealed that *Striga* numbers around 77 DAS correlated better with *ASNPC* and $NS_{max}$, and had a higher mean repeatability (averaged over years, $R$=0.64) than *Striga* numbers at 56 DAS ($R$=0.39). Selection based on a single count around 77 DAS is therefore expected to correspond well with selection based on *ASNPC* or $NS_{max}$.

### *Usefulness of belowground observations*

Kim (1996) and Ejeta et al. (2000) stressed the importance of belowground *Striga* observations in the assessment of resistance. Because this kind of observations is difficult to make in the field, one has to find other media, such as Petri-dishes and pots to study belowground processes. Techniques, such as the agar-gel test or a pot trial, permit the researcher to get insight in resistance during the stages that are most harmful for the crop and to acquire this information within a relatively short period of time and at low costs (Omanya et al., 2004). Disadvantages of pot trials are its high labour requirements, artificial root conditions and, according to Haussmann et al. (2000b) and Omanya et al. (2000), inconsistent correlation with field experiments. Results from the pot trial presented in this study showed nevertheless a ranking that corresponded reasonably well with the ranking based on maximum number of emerged *Striga* plants in the field. However, the 95% confidence intervals for $NS_{bg}$ and $NS_{ag}$, were very large and the repeatabilities of these measures were very low (0.25 for $NS_{bg}$ and 0.31 for $NS_{ag}$) which confirms earlier results from Omanya et al.(2004). The absence of correlation between the germination measures from the agar-gel test and the numbers of attached and emerged *Striga* plants in the pot trial suggests that genotypes with an effective belowground resistance mechanism in a very specific stage (germination) are not necessarily identified by aboveground counts. Therefore screening with the help of assays that only address a very specific life-cycle stage is indeed useful for detecting specific resistance mechanisms. This observation confirms earlier statements from Kim (1996) and Ejeta et al. (2000).

Combination of aboveground measures and information on germination stimulation revealed a very effective resistance mechanism in N13. This genotype stimulates abundant *Striga* seed germination which nevertheless resulted in extreme low numbers of *Striga* infection. This suggests the presence of a resistance mechanism that operates after germination stimulation. For that reason, genotypes with high germination stimulation should not be discarded as they might have valuable other sources of resistance. Results from CK60-B show that low germination stimulation on its own is not a useful characteristic, as it can still result in abundant parasitism. These observations indicate that in a selection process genotypes should never be selected or rejected after evaluation of a single resistance mechanism alone. Following the ranking of resistance based on a single mechanism, SRN39, Framida and IS9830 (germination stage) and N13 (attachment stage) would be good sources for pyramiding resistance genes. This confirms results from Maiti et al. (1984), Ramaiah (1984, 1987a), Vasudeva Rao (1984), El Hiweris (1987), Olivier et al. (1991), Hess et al. (1992), Ejeta et al. (2000), Heller and Wegmann (2000), and Omanya et al. (2004).

In conclusion, the maximum number of aboveground *Striga* plants showed to be a reliable measure for resistance as a reasonable correspondence between number of belowground attachments and maximum number of emerged *Striga* plants was observed. This measure also proved to be discriminative and consistent over years. Screening based on number of aboveground *Striga* plants in combination with yield under *Striga* infestation is likely to result in a negative selection for tolerance. The addition of *Striga*-free control plots allows the determination of the relative yield loss, which represents the effect of resistance and tolerance combined. Relative yield loss itself was found to be an inconsistent screening measure. The reason for this inconsistency might be that the relative contribution of resistance and tolerance to the overall defence against *Striga* depends on *Striga* infestation level. Tolerance was found to be relatively more important at low infestation levels, whereas resistance was found to be more important at high infestation levels. A fair comparison of tolerance among genotypes is difficult to make, as genotypic differences in resistance cause major differences in infection level. Corrections for these differences in infection level are difficult to make as long as the relation between relative yield loss and *Striga* infection level is not resolved. After clarification of this relation an independent tolerance measure can be derived. This will facilitate the breeder to identify genotypes with superior tolerance against *Striga* in the field.

# CHAPTER 3

# Characterization of host tolerance to *Striga hermonthica*[1]

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## Abstract

One of the most promising control options against the parasitic weed *Striga hermonthica* is the use of crop varieties that combine resistance with high levels of tolerance. The aim of this study was to clarify the relation between *Striga* infestation level, *Striga* infection level and relative yield loss of sorghum (*Sorghum bicolor*) and to use this insight for exploring the options for a proper screening procedure for tolerance. Pot experiments in which four sorghum genotypes were exposed to a range of *Striga* infestation levels, ranging from 0.0625 to 16 seeds $cm^{-3}$, were conducted in Mali in 2003 and in a greenhouse in The Netherlands in 2003 and 2004. Observations included regular *Striga* emergence counts and sorghum grain yield at maturity.

There were significant genotype, infestation and genotype × infestation effects on sorghum yield. The relation between infestation level and infection level was density dependent. Furthermore, the relation between *Striga* infection level and relative yield loss was non-linear, though for the most resistant genotype Framida only the linear part of the relation was obtained, as even at high infestation levels only moderate infection levels were achieved. The results suggest that for resistant genotypes, tolerance can best be quantified as a reduced relative yield loss per aboveground *Striga* plant, whereas for less resistant genotypes the maximum relative yield loss can best be used. Whether both expressions of tolerance are interrelated could not be resolved. Complications of screening for tolerance under field conditions are discussed.

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[1] Euphytica (accepted)

## Introduction

The obligate hemi-parasitic weed *Striga hermonthica* (Del.) Benth is a major constraint to cereal production in the semi-arid to sub-humid tropics of Africa. Yields of host plants infected by *Striga* can be severely reduced (Obilana, 1983; Rodenburg et al., 2005). *Striga* attacks most of the tropical *Gramineae* species, including several important agricultural species like sorghum (*Sorghum bicolor* [L.] Moench), pearl millet (*Pennisetum glaucum* [L.] R. Br.), maize (*Zea mays* [L.]) and upland rice (both *Oryza glaberrima* [Steudel] and *O. sativa* [L.] [Johnson et al., 1997]).

One of the most promising control options against *Striga* is the use of crop varieties with improved levels of resistance and tolerance against this parasite. Resistant genotypes have fewer infections, while tolerant genotypes show less impairment of growth or losses in grain yield when exposed to similar levels of infection than other varieties of the same species (Parker and Riches, 1993). The converse of resistance is susceptibility, while the converse of tolerance is sensitivity. Every host genotype combines a specific level of resistance with a specific level of tolerance. Breeding for those characteristics requires suitable selection criteria. Many different selection measures have been developed for resistance. All of these measures are based on the number of aboveground *Striga* plants and vary from a single count at a specific moment in time (Adetimirin et al., 2000b; Omanya et al., 2004) or the maximum number of aboveground *Striga* plants (Wilson et al., 2000; 2004; Rodenburg et al., 2005) to the area under the *Striga* number progress curve (*ASNPC*) (Haussmann et al., 2000b; Omanya et al., 2004; Rodenburg et al., 2005). Complete resistance, also referred to as immunity against *Striga*, has not yet been found. Therefore, a host variety that combines superior levels of resistance and tolerance is an obvious breeding objective and has been proposed in many studies (e.g. Kim, 1991; DeVries, 2000; Kling et al., 2000; Haussmann et al., 2001a,b; Pierce et al., 2003; Showemimo, 2003; Rodenburg et al., 2005).

Different measures of tolerance have been proposed, ranging from host plant damage scores to yield, yield loss, or relative yield loss under *Striga* infestation (Efron, 1993; Kim, 1994; Adetimirin et al., 2000b; Gurney et al., 2002a; Kim et al., 2002). None of these measures account for the difference in resistance among genotypes and hence they ignore the fact that the observed damage is due both to *Striga* infection level (resistance) and the extent to which the specific genotype endures these infections (tolerance). Consequently, differences among genotypes in level of yield reduction cannot simply be attributed to tolerance only. It seems that the only way to obtain an unbiased comparison of the level of tolerance among genotypes would be to create identical infection levels for all genotypes. Theoretically this might be achieved by exposing all genotypes to a range of infestation levels. However, realization of such a range under field conditions is difficult, if not impossible, and definitely costly. Another alternative might be to correct the observed damage of each genotype for its *Striga* infection level. Such a correction requires that the relation between *Striga* infection level and yield loss is known. Studies in which the biomass of the parasite was used as infection measure suggest that the relation between *Striga* infection level and yield loss is non-linear and characterized by a diminishing slope with increasing infection level (Gurney et al., 1999; 2000; Rodenburg et al., 2005). Whether this type of relation also holds for the relation between *Striga* number and yield loss is not yet clear. Nor is it known whether such a relation has a general validity or is genotype specific. The aim of this study was to resolve the relationship between *Striga* infestation level, *Striga* infection level and yield loss for a number of sorghum genotypes, and to explore options for the development of a screening procedure for tolerance to *Striga* infection.

## Material and methods

*Experimental sites and plant material*

Four sorghum (*Sorghum bicolor* L. Moench) genotypes were grown at a range of *Striga* (*Striga hermonthica* (Del.) Benth.) infestation levels, including *Striga* free controls, in pot experiments in Mali (2003) and The Netherlands (2003 and 2004). The sorghum genotypes used in this study (CK60-B, E36-1, Framida and Tiémarifing) were selected for their supposed differences in resistance and tolerance (Table 1). The *Striga hermonthica* seeds, used for infestation were collected at Samanko, Mali in 1998 (for experiments conducted in 2003 and 2004 in The Netherlands) and 2001 (for experiment conducted in 2003 in Mali) from plants parasitizing sorghum. The seed viability was 70% (2003, The Netherlands), 88% (2003, Mali) and 60% (2004, The Netherlands). In all experiments, only the upper 10 cm of the soil in each pot was infested with *Striga* seeds. Table 2 presents an overview of the materials and methods of the different experiments.

Table 1. Overview of defence mechanisms (resistance and tolerance) against *Striga hermonthica* in the four selected sorghum genotypes: CK60-B, E36-1, Framida and Tiémarifing, based on literature sources and personal communication

| Defence mechanism/ Genotype | CK60-B | E36-1 | Framida | Tiémarifing |
|---|---|---|---|---|
| Resistance | - | - | + | - |
| Tolerance | - | - | - | + |

Sources: El-Hiweris, 1987; Gurney et al., 1995; Ast et al., 2000; D. E. Hess/ ICRISAT, pers. commun.

Table 2. Summary of materials, methods and environmental conditions of the three experiments: 2003S, 2003W and 2004W

| Parameter/ Pot experiment | 2003S | 2003W | 2004W |
|---|---|---|---|
| Year | 2003 | 2003 | 2004 |
| Location | Samanko (Mali) | Wageningen | Wageningen |
| Environment | Open-air | Greenhouse | Greenhouse |
| Mean day temperature (°C) | 29 | 28 | 28 |
| Pot volume (L) | 17 | 12 | 17 |
| Soil mixture (sand: soil: compost) | 3:1:2 | 3:1 | 3:1 |
| Fertilizer application (kg $ha^{-1}$ N:P:K) | 42.5:42.5:42.5 | 50:42:75 | 50:42:75 |
| Plant spacing (m) | 0.4 - 0.8 | 0.3 - 0.8 | 0.3 - 0.5 |
| *Striga* seed viability (%) | 80 | 70 | 60 |
| *Striga* infestation levels (viable seeds $cm^{-3}$) | 0, 0.125, 0.25, 0.5, 1.0 and 2.0 | 0, 0.5, 1.0 and 3.0 | 0, 0.0625 (CK60-B and E36-1), 0.125, 0.25, 0.5, 1.0, 2.0, 4.0, 8.0 and 16.0 (Framida and Tiémarifing) |
| Replicates | 8 | 7 | 8 |
| Sowing date | 11 July | 26 May | 28 April |
| Harvest time (DAS) | 120 | 92-106 | 106 - 112 |

### *Open-air experiment*

One pot experiment (2003S) was carried out in the open-air from 11 July to mid November 2003 (2003S) at the ICRISAT field station in Samanko, 20 km Southwest of Bamako, the capital of Mali (latitude: 8°54”W and 12°54”N, altitude: 329 m). The climate type in this area is Sudanese, characterized by a single rainy season between May and October. The mean temperature during the cropping season (June-November) was 29.1°C and the mean annual rainfall at the field station was 950 mm. In addition to natural rainfall, pots were watered by hand to create conditions without water limitation.

Pots used in this experiment had a volume of 17 litres and a diameter of 29 cm. Soil used for the experiment was a 3:1:2 quartz sand: arable soil: compost mixture. To improve the drainage capacity of the pots, a 3 cm layer of gravel was put on the bottom of each pot. After infesting the soil with *Striga* seeds, all pots were kept moist for 10 days to allow preconditioning of the *Striga* seeds. Pot spacing in the plot was 0.4 m (centre – centre) and plots were separated by an additional row of 0.4 m wide. An equivalent of 42.5 kg N, 42.5 kg P and 42.5 kg K per hectare was applied in a single fertilizer (N-P-K: 1-1-1) dressing just prior to sowing. The sorghum seeds were sown at a rate of five sorghum seeds per pot. Thinning to one plant per pot was done at 17 days after sowing (DAS). Harvests of all aboveground parts of sorghum and *Striga* plants were done at 120 DAS.

This experiment consisted of a split-plot design in eight replicates with sorghum genotype at the plot level, and six *Striga* infestation levels at the sub-plot level. *Striga* seeds were mixed through the upper 10 cm of the soil at infestation levels of 0 (control), 0.125, 0.25, 0.5, 1.0 and 2.0 viable *Striga* seeds $cm^{-3}$ of soil.

### *Greenhouse pot experiments*

Two pot experiments were conducted in a tropical greenhouse of Wageningen University in The Netherlands from 26 May to mid-September 2003 (2003W) and from 28 April to mid-August 2004 (2004W). Day length was held constant at 12 h (between 08.00 and 20.00 h). Supplemental light was provided by 400 W sodium vapour lamps that automatically switched on during daytime when global solar radiation dropped below 400W $m^{-2}$. Day temperatures did not fall below 28°C. Mean relative humidity was kept between 50 and 70% for the duration of the experiments. Pots received water every two days, to create conditions without water limitation. Soil used for the experiment was a 3:1 quartz sand: arable soil mixture. After infesting the pots with *Striga* seeds, all pots were kept moist for 10 days to allow preconditioning of the *Striga* seeds. The sorghum seeds were pre-germinated for 36 hours before they were sown at a rate of three seeds per pot. Thinning to one plant per pot was done at seven DAS.

The pot experiment of 2003 (2003W) consisted of a split-plot design in seven replicates with sorghum genotype at the plot level and four *Striga* infestation levels at the sub-plot level. *Striga* seeds were mixed through the upper 10 cm of the soil at infestation levels of 0 (control), 0.5, 1.0 and 3.0 viable *Striga* seeds $cm^{-3}$ of soil. Pots used for this experiment had a volume of 12 litres and a diameter of 28 cm. Pot spacing in each plot was 0.3 m and plots were separated by an additional row of 0.5 m wide. An equivalent of 50 kg N, 42 kg P and 75 kg K per hectare was applied in a single fertilizer (N-P-K: 12-10-18) dressing at 35 DAS. Plants were harvested at physiological maturity of the different sorghum genotypes at 92 (Framida), 99 (E36-1 and Tiémarifing) and 106 DAS (CK60-B).

The pot experiment conducted in 2004 (2004W), consisted of a split-plot design in eight replicates with sorghum genotype at the plot level, and nine *Striga* infestation levels at the sub-plot level. A wider range of *Striga* infestation densities was chosen to facilitate the analysis at extreme low and high densities of *Striga* infection. *Striga* seeds were mixed through the upper 10 cm of the soil. Framida and Tiémarifing received *Striga* infestation densities of 0.0, 0.125, 0.25, 0.5, 1.0, 2.0, 4.0, 8.0 and 16.0 seeds $cm^{-3}$ (0-10 cm). For the more susceptible genotypes, CK60-B and E36-1, the highest infestation level was replaced by an additional low infestation level of 0.0625 seeds $cm^{-3}$. Pots used in this experiment had a volume of 17 litres and a diameter of 30 cm. Pot spacing in each plot was 0.3 m and plots were separated by an additional row of 0.2 m wide. An equivalent of 50 kg N, 42 kg P and 75 kg K per hectare of fertilizer (N-P-K: 12-10-18) was applied in a single dose before sowing. Harvests of all genotypes were conducted at 105 and 106 DAS, except for plants that were not yet mature. This last category of plants was harvested at 112 DAS.

### *Observations*

*Striga* counts were performed every two to three days, up to 61 DAS (2003S), 56 DAS (2003W) and 49 DAS (2004W) and were conducted weekly after these dates. From these regular *Striga* counts the maximum aboveground *Striga* numbers ($NS_{max}$) were derived. At maturity of the cereal plants, sorghum panicles and aboveground *Striga* plants of every pot were harvested. Sorghum panicles were sun- (2003S) or oven- (2003W and 2004W) dried. Panicles were threshed and kernel yield ($DW_{kernel}$) was determined. The relative yield loss ($RYL$) was calculated as:

$$RYL = [(Y_c - Y_s)/Y_c] \times 100\ (\%)$$

where $Y_c$ is the average kernel yield of all control plants of a specific genotype and $Y_s$ is the observed yield ($DW_{kernel}$) of an individual plant grown under *Striga* infestation. Average control yields were used to reduce variability of *RYL*.

*Statistical analyses*

Data on $NS_{max}$, $DW_{kernel}$ and *RYL* were subjected to analyses of variance (ANOVA), followed by a comparison of means with the least significant difference (L.S.D.), using the Genstat (release 7.1) statistical software package. $NS_{max}$ and $DW_{kernel}$ were subjected to square root ($[X+c]^{1/2}$ transformations, where $X$ is the original, individual observation and $c$=0.5), prior to analysis, to meet the assumptions of the analysis of variance, following procedures recommended by Sokal and Rohlf (1995). The *RYL* percentages were arc-sinus (or angular) transformed prior to analysis of variances, following procedures recommended by Sokal and Rohlf (1995). Negative *RYL* values (six cases for 2003W with N =84, 11 cases for 2003S with N =160 and six cases for 2004W with N =256) were replaced by zeros before statistical analysis.

## Results

*Sorghum yields and infestation levels*

Table 3 shows the results of an analysis of variance on $DW_{kernel}$ for each experiment. In 2004, only eight infestation levels were used in the analysis of variance. To balance the experimental design, infestation levels of 0.0625 seeds $cm^{-3}$ (CK60-B and E36-1) and of 16.0 seeds $cm^{-3}$ (Framida and Tiémarifing) were left out of the analysis.

Table 3. Analysis of variance of sorghum kernel dry weight per host plant of the three experiments: 2003S, 2003W and 2004W, with genotype and infestation level as factors

| Experiment | Source of Variation | df | Mean Square [a] | F-value |
|---|---|---|---|---|
| 2003W | Genotype (G) | 3 | 44.03 | 156.0* |
| | Infestation level (I) | 3 | 29.22 | 136.7* |
| | G X I | 9 | 6.19 | 29.0* |
| 2003S | Genotype (G) | 3 | 337.98 | 38.9* |
| | Infestation level (I) | 5 | 152.53 | 24.1* |
| | G X I | 15 | 19.41 | 3.1* |
| 2004W | Genotype (G) | 3 | 98.24 | 71.7* |
| | Infestation level (I) | 7 | 39.05 | 51.2* |
| | G X I | 21 | 3.95 | 5.18* |

* Significant at the 0.01 probability level

[a] Data are square-root-transformed ($[X+0.5]^{1/2}$) to meet requirements for ANOVA

Table 4. Total sorghum kernel dry weight (g plant$^{-1}$) per genotype (CK60-B, E36-1, Framida and Tiémarifing), *Striga* infestation level (0, 0.125, 0,25, 0.5 1.0, 2.0, 3.0, 4.0 and 8.0 seeds cm$^{-3}$) and experiment (2003S, 2003W and 2004W)

| | | Infestation level (seeds cm$^{-3}$) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 0 | 0.125 | 0.25 | 0.5 | 1.0 | 2.0 | 3.0 | 4.0 | 8.0 |
| 2003W | CK60-B | 25.7a | | | 0.3g | 0.0g | | 0.0g | | |
| | E36-1 | 20.3b | | | 6.6e | 3.4f | | 1.9f | | |
| | Framida | 24.5ab | | | 21.1ab | 20.7ab | | 15.6cd | | |
| | Tiémarifing | 20.8ab | | | 14.8cd | 13.0d | | 18.1c | | |
| 2003S | CK60-B | 47.9cd | 11.8fgh | 15.1efg | 3.9gh | 3.9gh | 1.6gh | | | |
| | E36-1 | 110.8a | 5.2gh | 0.6h | 3.5gh | 1.0h | 4.7gh | | | |
| | Framida | 122.9a | 45.5cd | 102.5ab | 80.1abc | 36.8de | 57.7bcd | | | |
| | Tiémarifing | 99.5ab | 79.8abc | 59.3bcd | 47.1cd | 28.1def | 13.3efg | | | |
| 2004W | CK60-B | 40.6a | 2.6fg | 1.2fgh | 2.7fg | 0.5gh | 0.0h | | 0.0h | 0.0h |
| | E36-1 | 23.3bc | 2.8fg | 2.5fg | 2.5fg | 3.3f | 0.6fgh | | 1.2fgh | 0.5gh |
| | Framida | 30.1ab | 22.9bc | 23.9bc | 20.8c | 19.8cd | 13.0de | | 9.8e | 11.0e |
| | Tiémarifing | 26.0bc | 10.3e | 12.1e | 8.6e | 10.0e | 11.4e | | 11.2e | 8.5e |

Values in the same column or row, followed by a different letter are significantly different ($P$<0.01; S.E.D.'s: 1.30 [2003W], 0.26 [2003S] and 0.46 [2004W]). Means in the table are back-transformed from square-root transformation ($[X+0.5]^{1/2}$), S.E.D. values are not.

Yields of E36-1, Framida and Tiémarifing in the control treatment in 2003S were much higher than yields in the control treatments obtained in the greenhouse-experiments in The Netherlands (Table 4). In Mali, yield of CK60-B in the control was significantly lower than that of the other genotypes, whereas in Wageningen yield of CK60-B in the control was as good or significantly better than that of other genotypes (E36-1 [2003W and 2004W] and Tiémarifing [2004W]). Yields of CK60-B and E36-1 plants infected with *Striga* were always significantly lower at comparable levels of infestation, than the yields of Framida and Tiémarifing, except for Tiémarifing at the highest infestation level in 2003S. Complete crop failure was only found with CK60-B in Wageningen at infestation levels of 1.0 (2003W) and 2.0 seeds cm$^{-3}$ (2004W) and higher.

In all experiments, yields of CK60-B and E36-1 at the lowest infestation level were already significantly lower than in the control. Tiémarifing also showed a significant yield decrease at the lowest infestation level in the two greenhouse experiments (2003W and 2004W). In 2003S, a significant yield reduction for Tiémarifing was observed beginning with the third infestation level (0.5 seeds cm$^{-3}$). Significant yield reductions in Framida were only obtained at the higher infestation levels (3 seeds cm$^{-3}$ in 2003W; $\geq$1 seeds cm$^{-3}$ in 2003S and $\geq$0.5 seeds cm$^{-3}$ in 2004W). The yield reduction of Framida obtained at an infestation level of 0.125 seeds cm$^{-3}$ in 2003S was a clear exception.

### *Relative yield loss as a function of infestation level*

Figure 1 shows fairly consistent genotype specific yield loss responses in relation to varying *Striga* infestation levels. Initial yield loss responses of CK60-B and E36-1 were much more severe than those of Framida and Tiémarifing. The maximum relative yield losses of CK60-B and E36-1 approached 100% and were generally much higher than those of Framida and Tiémarifing (always below 80%). In the 2004W experiment (Figure 1C), relative yield losses at the high infestation level of 16.0 seeds cm$^{-3}$ were still only 75% (Framida) and 66% (Tiémarifing). While relative yield losses of Tiémarifing seemed to have reached a maximum at the applied *Striga* infestation levels, those of Framida seemed to continue to increase. Furthermore, at the given inoculum levels, the relation between *Striga* infestation level and relative yield loss seemed linear for Framida whereas a clear density dependency was observed for the other genotypes.

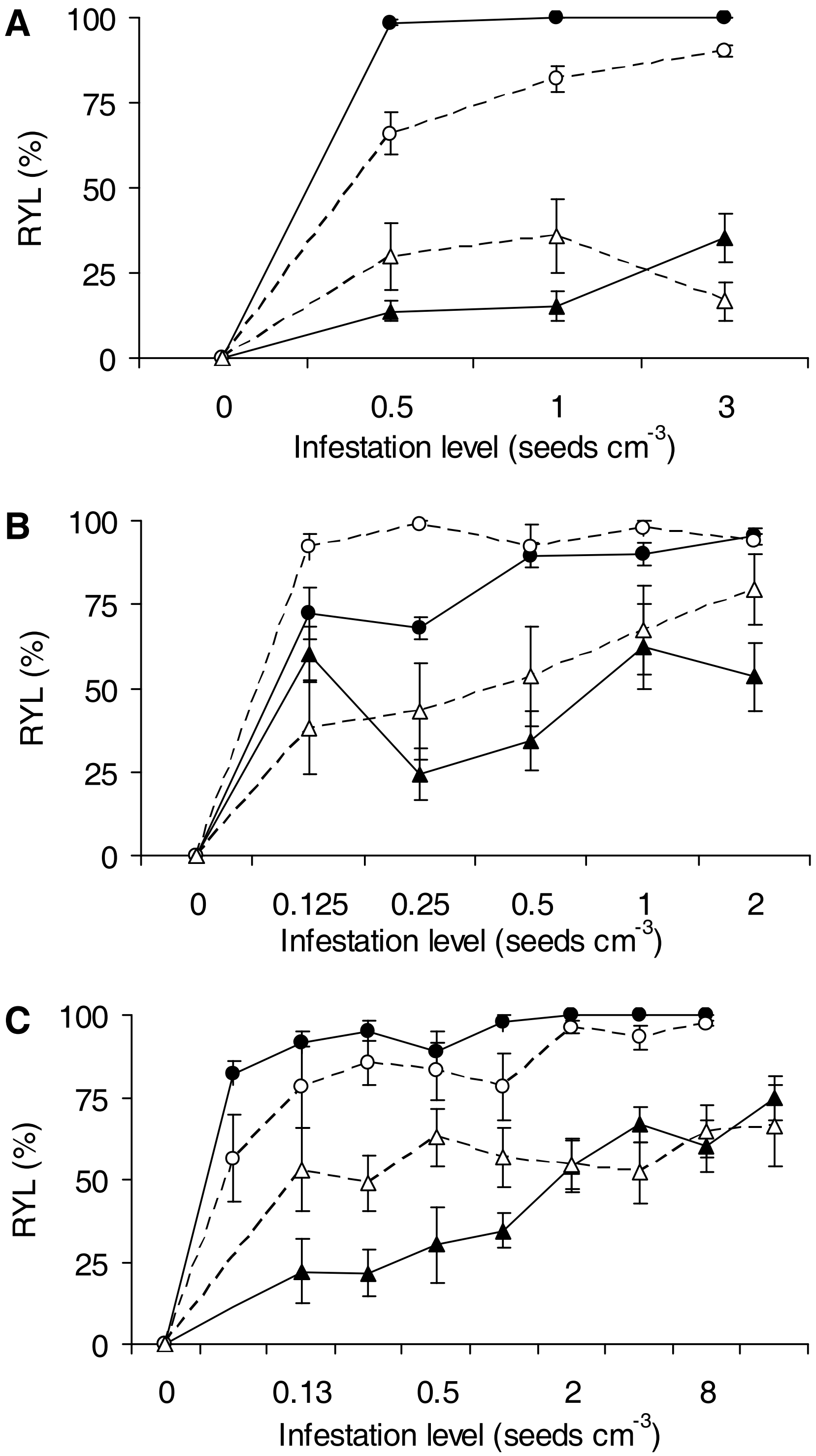

Figure 1. Relative yield loss (*RYL*: %) of four sorghum genotypes (CK60-B [closed circles], E36-1 [open circles], Framida [closed triangles] and Tiémarifing [open triangles]) as a function of *Striga* infestation level (seeds cm$^{-3}$) in 2003 in the greenhouse in Wageningen: 2003W (A), in the open-air in Samanko: 2003S (B) and in 2004 in the greenhouse in Wageningen: 2004W: (C)

### *Relation between infestation and infection level*

Figure 2 shows the maximum aboveground *Striga* plant numbers ($NS_{max}$) per infestation level and sorghum genotype in each experiment. The maximum number of aboveground *Striga* plants per host plant was much higher for all genotypes in the experiment conducted in Mali. At an infestation level of 1 seeds cm$^{-3}$, the average $NS_{max}$ values were 68.6 for 2003S, 32.3 for 2003W and 21.2 for 2004W. The minimum and maximum *Striga* infestation levels within an experiment differed a factor 6 (2003W) and a factor 16 (2003S) in 2003. Despite this wide range, the differences in maximum number of aboveground *Striga* plants within a genotype were relatively small.

In general, CK60-B and E36-1 always had large maximum aboveground *Striga* numbers, whereas *Striga* numbers on Framida were always relatively small. Tiémarifing had intermediate and erratic infection numbers, sometimes comparable to Framida and sometimes comparable to E36-1. In 2003W, maximum aboveground *Striga* numbers on CK60-B and E36-1 were always significantly higher than on Framida and Tiémarifing with the exception of infestation level 1.0 where $NS_{max}$ on E36-1 was not significantly different from that on Tiémarifing. No significant genotype × infestation level effect on $NS_{max}$ was observed in the 2003S experiment. Here Framida had a significantly lower $NS_{max}$ than the other three genotypes.

Based on these results, an even wider range of infestation levels was used in the 2004W experiment. For each genotype, the highest infestation level was 128 times higher than the lowest infestation level. This resulted in significant differences between the lowest and the highest maximum number of aboveground *Striga* plants for all genotypes. However, the wide infestation range still only resulted in a ratio of 2.4 (CK60-B), 4.4 (E36-1), 23.9 (Framida) and 4.4 (Tiémarifing) between the highest and the lowest infection level. Again, $NS_{max}$ on CK60-B and E36-1 were always significantly higher than on Framida, while $NS_{max}$ on Tiémarifing was intermediate. For CK60-B and Tiémarifing, it appeared that within this range of infestation levels, a maximum for $NS_{max}$ was reached, whereas for E36-1 and Framida $NS_{max}$ still gradually increased with an increase in infestation level.

### *Relative yield loss per genotype and aboveground infection level*

The average infection levels of CK60-B and E36-1 were not significantly different from one another in any experiment (Table 5). Average infection levels of CK60-B and E36-1 were higher than that of Framida and Tiémarifing, except for 2003S.

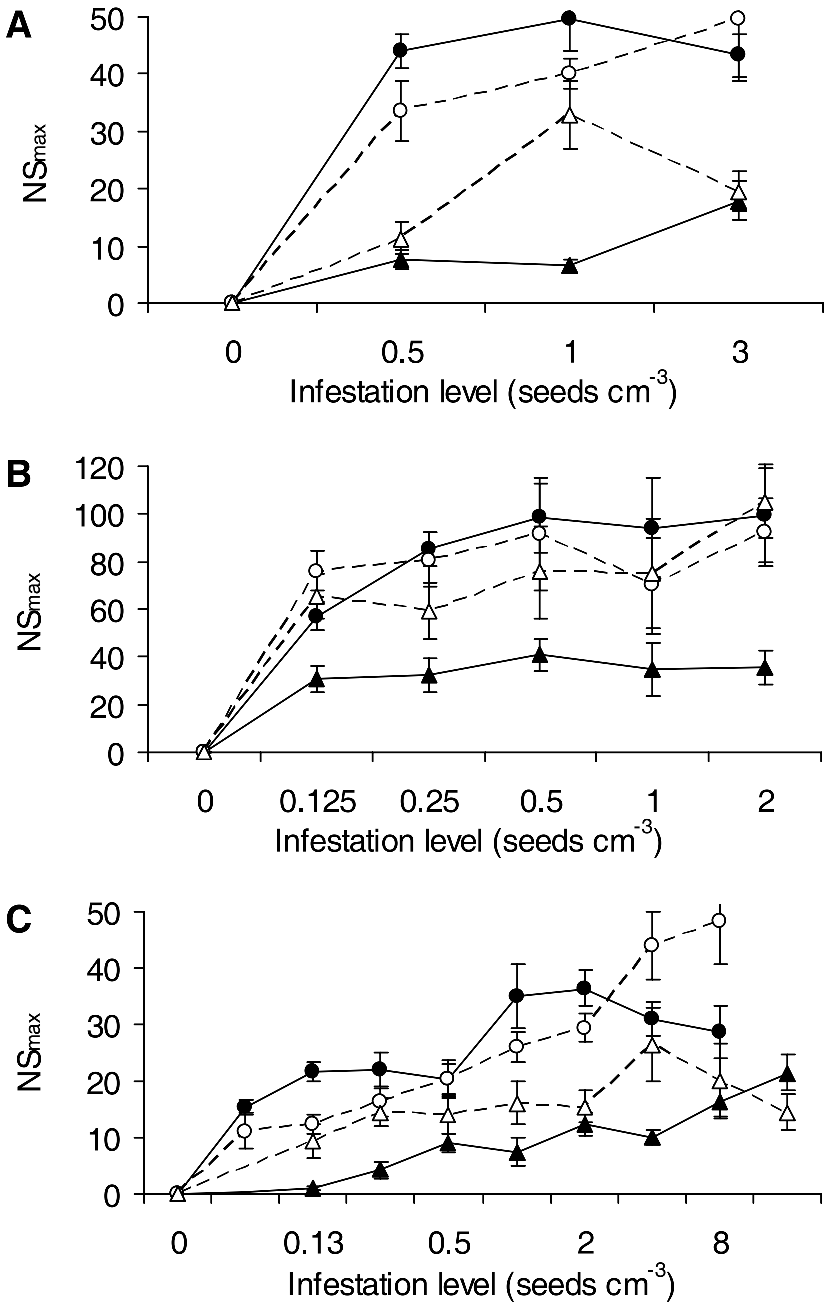

Figure 2. Maximum aboveground *Striga* numbers ($NS_{max}$) at four sorghum genotypes (CK60-B [closed circles], E36-1 [open circles], Framida [closed triangles] and Tiémarifing [open triangles]) as a function of *Striga* infestation level (seeds $cm^{-3}$) in 2003 in the greenhouse in Wageningen: 2003W (A), in the open-air in Samanko: 2003S (B) and in 2004 in the greenhouse in Wageningen: 2004W (C).

Table 5. Main genotype effects on maximum aboveground *Striga* numbers ($NS_{max}$) and relative yield loss ($RYL$: %) of the three experiments: 2003S, 2003W and 2004W

| | | $NS_{max}$ | | $RYL$ | |
|---|---|---|---|---|---|
| 2003W | CK60-B | 45.1 | a[a] | 99.4 | a |
| | E36-1 | 39.3 | a | 80.3 | b |
| | Framida | 9.0 | c | 19.1 | c |
| | Tiémarifing | 19.3 | b | 22.8 | c |
| | S.E.D[b] | 0.28 | | 4.16 | |
| 2003S | CK60-B | 81.4 | a | 85.0 | b |
| | E36-1 | 77.1 | a | 97.8 | a |
| | Framida | 32.2 | b | 45.4 | c |
| | Tiémarifing | 69.7 | a | 56.5 | c |
| | S.E.D | 0.56 | | 4.99 | |
| 2004W | CK60-B | 26.6 | a | 98.1 | a |
| | E36-1 | 25.9 | a | 93.1 | b |
| | Framida | 7.1 | c | 38.8 | d |
| | Tiémarifing | 14.1 | b | 58.7 | c |
| | S.E.D | 0.24 | | 3.82 | |

[a] Means in the same column, followed by a different letter are significantly different at the 0.01 ($RYL$) or 0.001 ($NS_{max}$) probability level. Data on $NS_{max}$ were square root-transformed ($[X+ 0.5]^{1/2}$) while data on $RYL$ were arc-sinus transformed for ANOVA.

[b] Test statistics (probabilities and S.E.D.'s) are based on transformed data, whereas values in table are back-transformed

In two of the three experiments (2003W and 2004W), average relative yield loss of E36-1 was significantly lower than that of CK60-B, indicating that E36-1 could be less sensitive than CK60-B. In 2003, exactly the opposite was observed. Although the average infection level of Framida was always significantly lower than that of Tiémarifing, the average *RYL* of Tiémarifing was only significantly higher than that of Framida in the 2004W experiment. Relative yield reductions of both genotypes were significantly lower than those of CK60-B and E36-1 in all experiments.

The relationship between infection level and relative yield loss is presented in Figure 3. It is obvious that both in 2003W and 2003S the range of infection levels for each of the genotypes was narrow ($NS_{max}$ in 2003W: 43-50 [CK60-B], 34-50 [E36-1], 7-18 [Framida] and 11-33 [Tiémarifing]; in 2003S: 57-100 [CK60-B], 70-93 [E36-1], 31-41 [Framida] and 59-105 [Tiémarifing]). This makes it difficult to resolve the relation between infection level and relative yield loss of the genotypes. Furthermore, there was no specific range of infection levels in which all four genotypes were represented.

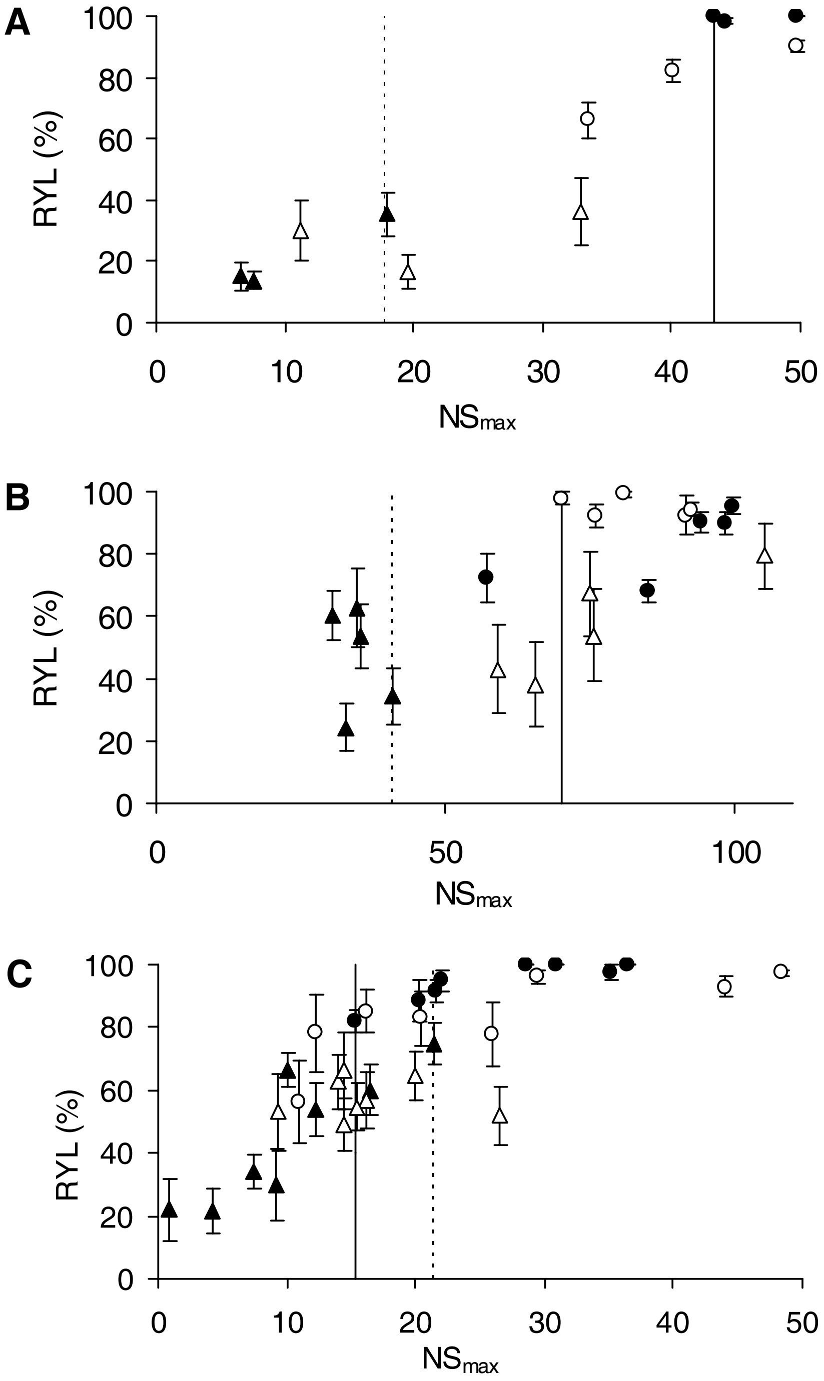

Figure 3. Relative yield loss (*RYL*: %) of four sorghum genotypes (CK60-B [closed circles], E36-1 [open circles], Framida [closed triangles] and Tiémarifing [open triangles]) as a function of *Striga* infection level ($NS_{max}$: maximum *Striga* numbers) in 2003 in the greenhouse: 2003W (A) and in the open-air: 2003S (B) and in 2004 in the greenhouse: 2004W (C). Vertical lines in the figure indicate the highest infection level of the most resistant genotype (dotted) and the lowest infection level of the most susceptible genotype (solid).

This is obvious from Figures 3A and 3B, where the dotted vertical line, representing the highest infection level of the most resistant genotype, is found at the left hand side of the solid vertical line, representing the lowest infection level of the most susceptible genotype. A broader range of infection levels was obtained for all four genotypes in 2004. CK60-B was characterized by infection levels ranging from 15-36 *Striga* plants. Even at the lowest infection level, *RYL* was already higher than 80%. At higher infection levels, 100% *RYL* was observed. E36-1 had an even broader range of infection levels, ranging from 11- 48 aboveground *Striga* plants. *RYL* was 55% at the lowest infection level and gradually increased until it reached nearly 100% at the highest infection level. The *RYL* of Framida was characterized by a nearly linear increase with *Striga* infection level. *RYL* at the lowest infection level was 22% and increased to 75% at the highest infection level ($NS_{max}$= 21.5). Infection levels for Tiémarifing varied from 9 to 27 *Striga* plants per pot, however, *RYL* did not show much variation and averaged 57%.

Overlapping infection levels were observed in all four sorghum genotypes in 2004W (Figure 3C). This range varied from 15.4 (lowest infection of CK60-B obtained at an infestation level of 0.0625 seeds $cm^{-3}$) to 21.5 (highest infection level of Framida obtained at an infestation level of 16 seeds $cm^{-3}$) aboveground *Striga* numbers. In this range of infection levels, Tiémarifing and Framida showed to be significantly ($P<0.001$) more tolerant than CK60-B and E36-1, with relative yield reductions of 85.3% for CK60-B, 84.1% for E36-1, 67.5% for Framida and 60.2% for Tiémarifing.

## Discussion

The results of the 2003 experiments showed that differences in *Striga* infestation level did not result in proportional differences in infection level. In 2003W, infestation levels that differed six-fold only resulted in infection levels that differed three-fold, whereas in 2003S infestation levels that differed sixteen-fold resulted in infection levels that differed less than two-fold. These results clearly indicate that the relation between *Striga* infestation and *Striga* infection is density dependent, confirming earlier observations by Smith and Webb (1996). The 2003 experiments confirmed the results of earlier studies (e.g. El Hiweris, 1987; Hess 1989; Arnaud et al., 1999; Ast et al., 2000) on the resistance of Framida and the susceptibility of CK60-B and E36-1.

Since substantial numbers of aboveground *Striga* plants (> 25) were obtained at the lowest infestation levels for most genotypes, it was not possible to explore the relation between infection level and relative yield loss at low levels of infection. The relatively narrow range of infection levels also made it hard to conclude whether the maximum relative yield loss was attained at the highest infection level. This was particularly true for Tiémarifing and Framida, which did not yet reach 100% yield loss. Consequently, the exact course of the relation between *Striga* infection level and relative yield loss could not be completely resolved with the 2003 experiments.

In two of the three experiments, the narrow range of infection levels for each genotype, combined with the distinct differences in resistance level among genotypes, resulted in the absence of a common infection range for all genotypes. Hence, a direct comparison of tolerance between the various genotypes was not possible. However, some indications for differences in tolerance between genotypes were obtained. In 2003S, Framida and Tiémarifing had comparable relative yield losses; however, the average *Striga* infection level of Tiémarifing was twice as high. This result suggests that Tiémarifing is the more tolerant genotype.

In an attempt to overcome the aforementioned problems, the *Striga* infestation range in the 2004 experiment was expanded. Each genotype was exposed to infestation levels that differed 128-fold and the infestation range was made genotype specific. For the more susceptible genotypes (CK60-B and E36-1), infestation levels varied from 0.0625 to 8.0 seeds cm$^{-3}$, whereas the more resistant genotypes (Framida and Tiémarifing) were exposed to infestation levels varying between 0.125 and 16.0 seeds cm$^{-3}$. The range of infection levels was much smaller than the range of infestation levels. The size of these infection ranges, expressed as the ratio between maximum and minimum infection level, varied between genotypes (CK60-B: 2.4; Tiémarifing: 2.8; E36-1: 4.4; Framida: 23.9). Again this demonstrates the density dependence of the relation between infestation and infection. Main reason for the narrow range of infection levels for three of the four genotypes was the absence of low infection levels (< 10 aboveground *Striga* plants). This indicates that, in order to obtain such low infection levels for susceptible genotypes, extremely low infestation levels are required, which comprises the risk of not obtaining any infection at all.

Despite the differences in *Striga* infection level among genotypes, a small overlapping range of infection levels was obtained. Within this range, each genotype was represented by data obtained from just two (CK60-B, E36-1 and Framida) or three (Tiémarifing) infestation levels. Under these conditions, Tiémarifing and Framida were significantly more tolerant than CK60-B and E36-1. Sensitivity of CK60-B was earlier reported by Gurney et al. (1995) while tolerance of Tiémarifing was observed by Ast et al (2000). However, to arrive at this conclusion, only 36% of the experimental units were used. This demonstrates that, regardless of practical difficulties, the strategy to create identical infection levels to facilitate a direct screening for tolerance is very inefficient.

Table 6. Overview of defence mechanisms (resistance and tolerance) against *Striga hermonthica* in the four selected sorghum genotypes: CK60-B, E36-1, Framida and Tiémarifing, based on observations from the three experiments: 2003S, 2003W and 2004W

| Defence mechanism/ Genotype | CK60-B | E36-1 | Framida | Tiémarifing |
|---|---|---|---|---|
| Resistance | - | - | + | +/- |
| Tolerance | - | - | +/- | + |

Based on the outcomes of this study two modifications concerning the information presented in Table 1 are made (Table 6). First, Tiémarifing appeared not as susceptible as CK60-B and E36-1, though clearly less resistant than Framida. Second, Framida proved more tolerant than CK60-B and E36-1 though still less tolerant than Tiémarifing.

Main objective of the current study was not to compare genotypes at identical infection levels, but rather to resolve the relation between *Striga* infection level and yield loss of the host. It was anticipated that clarification of this relation would enable the development of a suitable screening procedure for tolerance. In Figure 4, a three-quadrant representation of the relationship between *Striga* infestation level, infection level and relative yield loss is given for the results obtained in 2004W. This presentation form was adopted from the nutrient supply, nutrient uptake and crop yield response curves introduced by de Wit (1953). The figure is composed of three quadrants, where the upper-left quadrant (quadrant II) represents the relation between *Striga* infestation level and relative yield loss, the lower-right quadrant (quadrant IV) represents the relation between *Striga* infestation level and *Striga* infection level and the upper-right quadrant (quadrant I) represents the relation between *Striga* infection level and relative yield loss. Note that in this figure, in contrast to Figures 1 and 2, *Striga* infestation level is presented on a linear scale. Quadrant II shows two main response types to *Striga* infestation. CK60-B and E36-1 (Figure 4A and 4B, respectively) represent genotypes where complete or nearly complete yield losses were attained at low infestation levels. Framida and Tiémarifing (Figure 4C and 4D, respectively) represent genotypes where relative yield losses seem to stabilise around 60-70% at high infestation levels. The main difference between these two genotypes was that Tiémarifing obtained this level already at low infestation levels, whereas with Framida a more gradual increase in relative yield loss with infestation level was observed. For *Orobanche* (spp.) in carrot and pea, Bernhard et al. (1998) found a rectangular hyperbola describing the relation between seed infestation level and yield loss. At low infestation levels they observed a gradual increase in yield loss with increasing infestation level, comparable to what was observed with Framida, resulting in complete crop failure at high infestation levels, identical to the results obtained with CK60-B and E36-1.

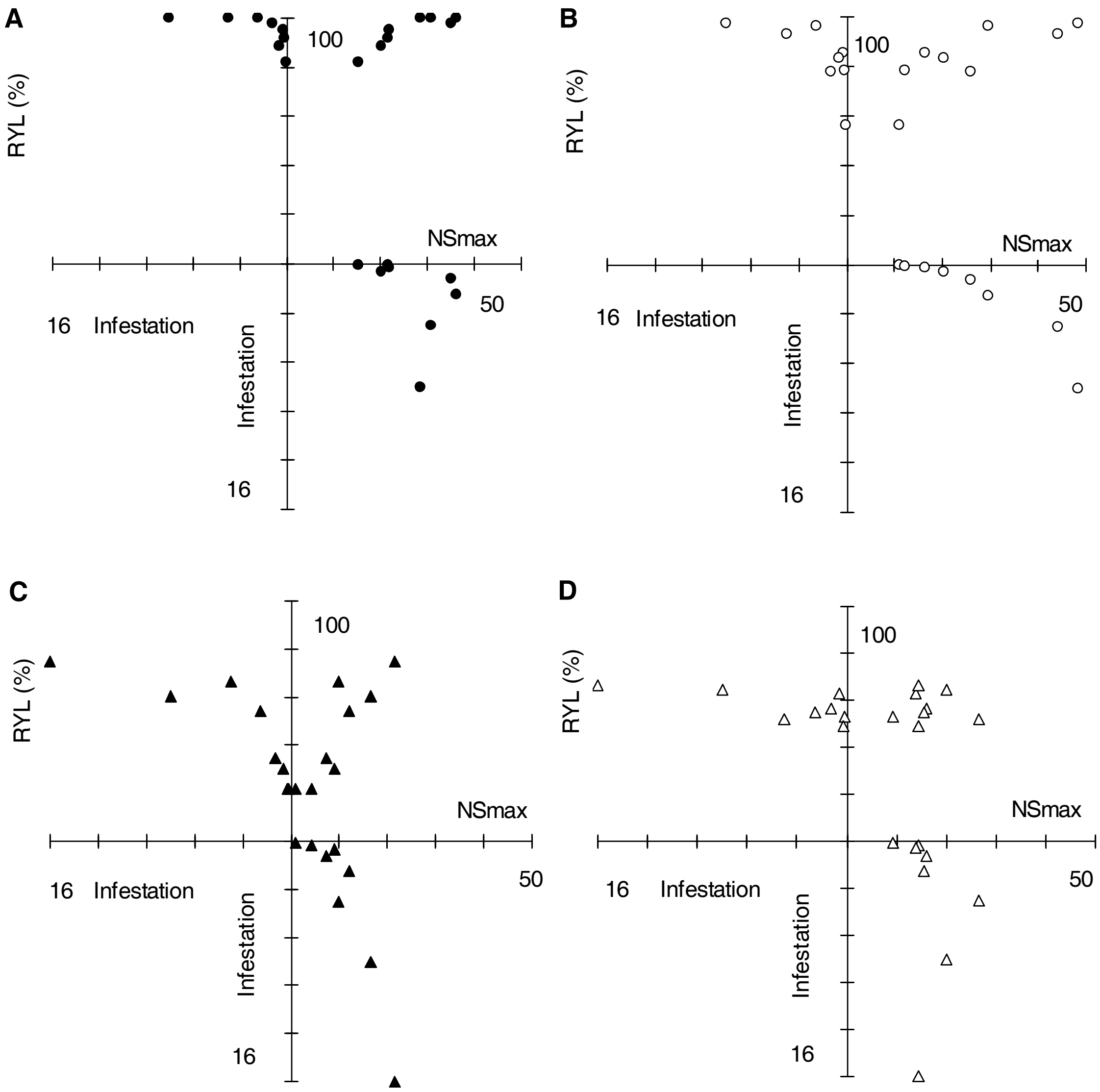

Figure 4. Three-quadrant representations of the relations between *Striga* infestation level, *Striga* infection level ($NS_{max}$) and relative yield loss (*RYL*: %) of four different sorghum genotypes: CK60-B (A), E36-1 (B), Framida (C) and Tiémarifing (D), as observed in 2004 in the greenhouse in Wageningen (2004W)

The two quadrants on the right hand side provide further information on how the relation between *Striga* infestation level and relative yield loss was achieved. Quadrant IV contains the relation between *Striga* infestation and *Striga* infection and as such shows the level of resistance of a certain genotype. For both E36-1 and Framida this relation developed according to a rectangular hyperbola. Such a relationship between *Striga* infestation and *Striga* infection level was previously reported by Smith and Webb (1996) and confirms the earlier observation on density dependence. With E36-1, low infestation levels resulted in relatively high infection levels and the number of infections further increased in response to higher *Striga* seed densities. Framida was more resistant, with few infections at low infestation levels and the number of infections increased slowly as infestation level increased. Another type of response was observed with CK60-B and Tiémarifing. For those two genotypes, relatively high infection rates were observed at low seed densities: however, the infection rate did not continue to rise as infestation levels increased. CK60-B differed from Tiémarifing as it had a steeper initial increase in number of infections, it attained its maximum infection level at a lower infestation level, and its maximum number of infections was higher. The relationships observed for CK60-B and Tiémarifing could result from a reduced carrying capacity of the host plant at higher infestation levels, following reduced host vigour. It could also result from increased intra-specific competition following a higher number of belowground *Striga* attachments or from a combination of both. Consequently, screening for host plant resistance under very high infestation levels, using number of aboveground *Striga* plants as screening measure, might result in an overestimation of the level of resistance of susceptible genotypes. Kim et al. (1998) and Haussmann et al. (2000b) also suggested that this might be possible.

Quadrant I represents the relationship between *Striga* infection and relative yield loss and conveys the level of tolerance of a certain genotype. Three genotypes (CK60-B, E36-1 and Tiémarifing) seemed to reach or approach their maximum relative yield losses in 2004. Complete crop failure was observed for CK60-B and E36-1, whereas the maximum relative yield loss for Tiémarifing was only around 57%. For these three genotypes, the relative yield loss at low infection levels was not observed and remained unresolved. For Framida, the relationship between infection and relative yield loss was observed over a wide range and in this trajectory a nearly linear increase in relative yield loss was observed with an average yield loss of 4% per *Striga* infection.

Koskela et al. (2002) reported a similar relationship between parasite infection level and host damage for the holoparasite *Cuscuta europaea* parasitizing on *Urtica dioica*. Gurney et al. (1999) found a negative and exponential relationship between yield and parasite load for *Striga hermonthica* parasitizing on sorghum, where parasite load was expressed as *Striga* dry weight. These findings do not necessarily contradict findings of the current study. Rather, given the difficulties of obtaining a complete infection range for a single genotype, the current observations only cover parts of the relation between infection level and relative yield loss. Also with Framida one might expect that the relation between infection level and relative yield loss will eventually reach a saturation level. Whether this saturation level corresponds to complete crop failure or is found at a lower level of yield reduction remains unresolved. It is evident that the saturation level of the relation between infection level and relative yield loss is one of the ways through which tolerance can come to expression. Tiémarifing is an example of this. At the same time, the three genotypes for which a maximum relative yield loss was observed will possess an initial trajectory in which the relative yield loss increases with infection level. E36-1 already shows part of this trajectory. The steepness of this initial increase, expressed as relative yield loss per *Striga* plant, represents another expression of tolerance. The current results however do not allow verifying whether for the other three genotypes this increase deviates from the 4% yield loss per *Striga* plant obtained with Framida. For the same reason it remains unclear whether a lower maximum relative yield loss, as observed for Tiémarifing, goes along with a reduced initial slope, or whether those two exist independently.

Conducting large scale screening for tolerance at multiple infestation levels is not realistic. Determination of the relative yield loss already requires the presence of *Striga*-free control plots adjacent to *Striga* infested plots (e.g. Gurney et al., 1999; Rodenburg et al., 2005). Control plots in the field can be created by use of methyl bromide (e.g. Gurney et al., 1999) or ethylene injections (e.g. Bebawi et al., 1985; Bebawi and Eplee, 1986) which are both rather expensive and laborious. An alternative is the infestation of *Striga* free fields, which is undesirable. Furthermore, measures should be taken to prevent contamination of control plots with *Striga* seeds from adjacent infested plots. Additionally, for a reliable selection, also sufficient replications (≥ 5) are needed as was already shown by Haussmann et al. (2000b). Due to variation in *Striga* virulence (e.g. Bebawi and Farah, 1981), and significant genotype × environment interactions (e.g. Haussmann et al., 2001a; Oswald and Ransom, 2004), stability of tolerance levels in a genotype should be tested at multiple locations. Compared to screening at one infestation level and a control plot, the installation of multiple infestation levels, to facilitate the estimation of tolerance, will only further increase these practical difficulties.

Kim (1991) suggested that screening for tolerance could best take place at high infestation levels. The current results indicate that differences in maximum relative yield loss, and thus tolerance, between susceptible and moderately resistant genotypes can well be detected in this way, as was shown by the comparison between Tiémarifing, CK60-B and E36-1. For more resistant genotypes this approach proved less suitable, due to the fact that it was not possible to obtain infection levels that are high enough to cause the maximum relative yield loss. For breeding programs that try to develop genotypes that combine superior resistance with high levels of tolerance, as suggested by Ramaiah and Parker (1982), Haussmann et al. (2000b) and Pierce et al. (2003), screening based on the maximum relative yield loss seems less appropriate, as particularly the expression of tolerance at lower infection levels is of interest. For those resistant genotypes, expressing tolerance as the ratio between relative yield loss and infection level seems more appropriate. Main bottleneck here is that if the relation between relative yield loss and infection level is described by a rectangular hyperbola, this ratio will decrease with increasing infection level. Such a linkage with resistance hampers an unbiased estimation of tolerance. Screening at more than one infestation level might improve the estimation of the proposed ratio, but, as was mentioned earlier, is not a realistic option.

In conclusion, two compatible tolerance measures are proposed based on yield response. For resistant genotypes a reduced relative yield loss per aboveground *Striga* plant indicates tolerance, whereas for less resistant genotypes the relative yield loss as such provides the best indication. Consequently, screening for tolerance based on the yield response of a genotype is difficult when the selection pool contains genotypes with largely different and unknown levels of resistance. As the need for unravelling resistance and tolerance is evident, the results of this study emphasize the need for a proper alternative method for screening for tolerance.

# CHAPTER 4

# Can host plant tolerance to *Striga hermonthica* be detected by photosynthesis measurements?[1]

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## Abstract

The photosynthetic response of four sorghum genotypes (CK60-B, E36-1, Framida and Tiémarifing) differing in level of tolerance to *Striga hermonthica* was measured at different moments in time in pot experiments conducted in 2003 and 2004. *Striga* infection significantly reduced $CO_2$ assimilation rate ($A$) of sorghum plants. This process was found indicative for tolerance, as sensitive genotypes were affected earlier, more severe and already at lower infestation levels than more tolerant genotypes. This observation was confirmed in 2004, when it was demonstrated that the $CO_2$ assimilation rate of infected and uninfected sorghum plants, measured during the early stages (26 and 48 DAS) correlated very significantly with their final kernel yield. However, $CO_2$ assimilation as screening measure was shown to have some serious constraints. The measure did not enable a clear distinction between superior and moderately tolerant genotypes, it still requires *Striga*-free controls due to genotype effects on assimilation rate and measurement systems based on gas exchange are costly.

In 2004, photochemical quenching ($Pq$), non-photochemical quenching ($NPq$), electron transport rate through PSII ($ETR$) and the ratio of $CO_2$ assimilation over electron flow ($A\ ETR^{-1}$) were determined along with $CO_2$ assimilation rates. All of these chlorophyll fluorescence parameters correlated highly significantly with $CO_2$ assimilation rate. Based on discriminative ability, practicability and cost effectiveness, $Pq$ and $ETR$ were found to carry the highest potential to serve as a screening measure for tolerance to *Striga*. Screening is recommended to be conducted between first *Striga* emergence and sorghum flowering and at infestation levels of at least 300,000 viable *Striga* seeds $m^{-2}$. In contrast to existing screening methods that need control plots that are expensive and difficult to obtain, both parameters facilitate screening at one infestation level and without the requirement of *Striga*-free control plots.

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## Introduction

*Striga hermonthica* (Del.) Benth. is an obligate hemi-parasitic $C_3$ plant of the *Orobanchaceae* (formerly: *Scrophulariaceae*) family that parasitizes monocotyledonous hosts of the *Gramineae* and *Poaceae* families. Among the $C_4$ hosts of *Striga* are some important cereal crops such as, pearl millet (*Pennisetum glaucum* [L.] R. Br. and *P. americanum* [L.] K. Schum), maize (*Zea mays* [L.]) and sorghum (*Sorghum bicolor* [L.] Moench) accounting for an estimated 25, 27 and 31% of the total area under cereal production in sub-Saharan Africa (FAOSTAT, 2004). More than half of the total cereal production area in this region is estimated to be infested with *Striga* (Sauerborn, 1991).

Infection by *Striga hermonthica* seriously reduces host plant yield (Bebawi and Farah, 1981; Doggett, 1982; Vasudeva Rao et al., 1989). Average yield losses due to *Striga* in West Africa are estimated to range between 10 to 31% and can reach 100% in severely infested fields (Sauerborn, 1991). *Striga* is one of the most serious causes of yield reduction of sorghum and a major constraint to food production in semi-arid Africa (Doggett, 1982; Parker and Riches, 1993). *Striga* parasitizes on the host root, subtracting host carbon assimilates (Rogers et al., 1962; Okonkwo, 1966; Press et al., 1987b), water, nutrients (nitrate) and amino-acids (Pageau et al., 2003). However, the drain of assimilates and nutrients only accounts for 16 to 20% of the total growth reduction of the host (Press and Stewart, 1987; Graves et al., 1989, 1990). The remaining 80 to 84% is caused by other effects of *Striga* infection on host performance, often referred to as phytopathological or toxic reactions. Known biochemical reactions upon *Striga* infection are decreased levels of host growth regulators such as cytokinins and giberellic acid (Drennan et al., 1979), and increased levels of abscisic acid (ABA) in the host plant (Drennan et al., 1979; Taylor et al., 1996; Ackroyd et al., 1997; Frost et al., 1997). The affected hormone balance may be responsible for the modified host plant allometry as observed in many studies (e.g. Egley, 1971; Graves et al., 1989; Cechin et al., 1993; Clark et al., 1994; Gurney et al., 1995, 1999; Boukar et al., 1996; Frost et al., 1997; Watling and Press, 1997; Gebremedhin et al., 2000; Sinebo and Drennan, 2001). The increased levels of ABA cause reduced stomatal conductance, a phenomenon often observed, particularly during the early stages of infection (Press and Stewart, 1987; Press et al., 1987a; Gurney et al., 1995, 1999; Taylor et al., 1996; Ackroyd et al., 1997; Frost et al., 1997). Reduced stomatal conductance was found to be one of the reasons for reduced photosynthesis of infected hosts (Prabhakara Setty and Hosmani, 1981; Press and Stewart, 1987; Press et al., 1987; Graves et al., 1989; Smith et al., 1995; Gurney et al., 1995, 1999). An increased level of photoinhibition was also found as a response to *Striga* infection (Gurney et al., 2002a).

In some host plant species, genotypes with tolerance against *Striga* have been identified (e.g. Efron, 1993; Kim, 1994; Gurney et al., 2002a). Tolerance is the ability of the host plant to endure the presence of a pathogen, disease or parasite with minimized symptoms or damage (Parlevliet, 1979). Varieties with improved tolerance can play a key-role to increase cereal production in *Striga* infested areas (Gurney et al., 1999). Hence tolerance is an important breeding objective. One of the constraints to breeding for tolerance against *Striga* is the absence of a suitable selection procedure. The presence of tolerance in a host plant genotype results in a lower relative yield loss at comparable *Striga* infection levels than sensitive genotypes of the same host species. However, as much as genotypes differ in tolerance, they can differ in resistance. Consequently, it is difficult to compare genotypes at identical infection levels. A direct quantification of tolerance based on relative yield loss is thus hampered by the entanglement of this measure with resistance (Rodenburg et al., 2005). To overcome this problem it was recommended to conduct screening for tolerance at more than one *Striga* infestation level (Rodenburg et al., Accepted), whereas the inclusion of *Striga*-free control plots is required for the calculation of relative yield loss. These prerequisites make screening for tolerance expensive and laborious and hence create the need for an alternative procedure. A suitable selection measure should facilitate an easy, quick and reliable quantitative assessment that enables the comparison of tolerance among a group of genotypes without the need for various infestation levels and control plots.

Some studies observed that tolerant host plant genotypes are able to maintain high levels of photosynthesis upon infection (Gurney et al., 1995, 2002a). The current study explored options for the use of photosynthesis and related chlorophyll fluorescence measurements in screening sorghum genotypes for tolerance to *Striga*. For that reason two pot experiments were conducted in which the leaf photosynthetic response of four sorghum genotypes with different levels of tolerance, to *Striga* infection, was measured at different moments in time.

Table 1. Characterization of the four sorghum genotypes used in the 2003 and 2004 experiment

| | CK60-B | E36-1 | Framida | Tiémarifing |
|---|---|---|---|---|
| origin | USA/ North-east Africa | Ethiopia | Southern Africa | Mali |
| type | | | | |
| morphology | short | medium | medium | long |
| race | kafir | caudatum | caudatum | guinea |
| photoperiodicity | insensitive | insensitive | insensitive | sensitive |
| cycle length (days) | 100-110 | 120-130 | 120-130 | 120-130 |
| grain colour | white | cream | red | white |
| resistance | very low | very low | high | medium |
| tolerance | very low | low | medium | high |

## Materials and methods

*Experimental sites*

Two pot experiments, one in 2003 and the other in 2004, were carried out in the tropical greenhouse of Wageningen University, The Netherlands. Day length was held constant at 12 hours (08.00 am to 20.00 pm). Additional light was provided by high-pressure sodium lamps (400W SON-T Agro-Philips lamps) when incoming radiation dropped below 910 µmol $m^{-2}$ $s^{-1}$ (PAR). Day temperatures did not fall below 28°C. Mean night temperature was 24°C. Mean relative humidity was kept between 50 and 70% for the whole duration of the experiments. Pots received water every two days, to create non-water-limited conditions.

*Plant material and genetics*

Host plant species used in this study was *Sorghum bicolor* (L.) Moench. The study comprised two sensitive and susceptible (CK60-B and E36-1), one resistant and moderately tolerant (Framida) and one tolerant and moderately resistant sorghum genotype (Tiémarifing). Furthermore, genotypes differed in origin, race, grain colour and morphology (Table 1). *Striga hermonthica* seeds were collected in 1998 in Samanko (Mali) from *Striga* plants parasitizing sorghum. Seed viability was 70% (2003) and 60% (2004).

*Experimental set-up*

Both pot experiments consisted of a split-plot design in seven (2003) and five (2004) replications, with four sorghum genotypes at the plot level, and four (2003) and two (2004) *Striga* infestation levels at the split-plot level. The *Striga* infestation levels, expressed in number of viable *Striga* seeds $cm^{-3}$ of soil, were: 0 (control), 0.5, 1.0 and

3.0 in 2003 and 0 (control) and 4.0 in 2004. A 3:1 quartz sand: arable soil mixture was used in both experiments. *Striga* seeds were mixed through the upper 10 to 12 cm soil layer. After infesting the soil with *Striga* seeds, all pots, including the uninfested ones, were kept moist for 10 days to allow preconditioning of the *Striga* seeds. The sorghum seeds were pre-germinated for 36 hours before they were sown at a rate of 3 seeds per pot, on 26 May (2003) and 28 April (2004). Thinning to one plant per pot was done at 7 days after sowing (DAS). Pot spacing in the plot was 0.3 m and between plots 0.8 m (2003) and 0.5 m (2004). Before sowing (2004) or 35 days after sowing (2003), fertilizer was applied in both experiments in a single dose, equivalent to 50 kg N, 42 kg P and 75 kg K per hectare (N-P-K; 12:10:18).

### *Measurements and observations*

Leaf $CO_2$ assimilation rates (*A*) of sorghum were measured at 19, 33, 47 and 61 DAS (2003) and at 26, 48, and 75 DAS (2004). In the 2003 experiment different plants were measured at each observation time, as after photosynthesis measurement these plants were used for destructive sampling (data not reported). In 2004 the same plants were used for repeated measurements. Measurements were always made halfway along the length of the youngest fully expanded leaf. This did not include the flag leaf. Stomatal conductance (*gs*) and intra-stomatal $CO_2$ concentration (*Ci*) were calculated based on transpiration rates (*Tr*) and vapour pressure deficits of the leaves that were measured along with $CO_2$ assimilation rates.

Photosynthesis was measured with two different open systems. In 2003, photosynthesis was measured with the LCA2 from the Analytical Development Company (ADC) Hoddesdon, UK. An external heat filtered light source was used to maintain irradiance at a constant value of 1800 µmol $m^{-2}$ $s^{-1}$ (PAR) ensuring light saturation. Environmental conditions at the time of measurement were comparable to the growing conditions. Leaf chamber temperature ranged between 28 and 35 °C (mean: 31°C), the inlet $CO_2$ concentration was around 360 ppm with generally less than 50 ppm depletion. Photosynthetic rate was recorded when the rate of $CO_2$ exchange had been steady for 5 minutes. One single measurement (including adaptation time) took about 15 minutes.

In 2004, photosynthesis and chlorophyll fluorescence were measured with the LICOR-6400-40. This system has an incorporated light source with a programmable light intensity and an integrated modulated chlorophyll fluorescence measurement system. After a dark adaptation period of 5 minutes, photosynthesis and fluorescence responses were measured at 0, 200, 400, 800 and 1600 (at 26 DAS) or 2000 (at 48 and 75 DAS) µmol $m^{-2}$ $s^{-1}$ (PAR). During the measurements, leaf temperature ranged between 28 and 33 °C (mean: 31°C), the inlet $CO_2$ concentration was 400 ppm and depletion never exceeded 24 ppm.

Chlorophyll fluorescence measurements were used to derive the electron transport rate through PSII (*ETR*), as well as the level of photochemical (*Pq*) and non-photochemical quenching (*NPq*). For the derivation of *ETR*, first the electron transport efficiency of PSII ($\Phi_2$) was calculated as:

$$\Phi_2 = (1 - Ft) / Fm' \qquad (1)$$

where *Ft* is the steady-state fluorescence emission, and *Fm'* is the maximum fluorescence emission induced by a saturating light pulse in the light (Genty et al., 1989). *ETR* was then calculated as:

$$ETR = \Phi_2 \rho f_{abs} I \qquad (2)$$

where $\rho$ is the factor to account for the partitioning of energy between the two photosystems (PSI and PSII), $f_{\mathrm{abs}}$ is the absorbtivity of the leaf and *I* is the light intensity (PAR) (Genty et al., 1989). Parameter $\rho$ was set to 0.5, which is a common value (Maxwell and Johnson, 2000; Rascher et al., 2000), and assumes that at any light level the excitation energy is equally distributed between PSI and PSII. The absorbtivity was set to 0.8, which indicates that of the incoming photosynthetically active radiation 80% is absorbed by the leaf (Goudriaan and Laar, 1994).

Photochemical quenching of fluorescence (*Pq*) was computed as:

$$Pq = (Fm' - Ft)/(Fm' - Fo') \qquad (3)$$

where *Fo'* is the basic fluorescence in the light when all PSII centres are oxidized by a period of far-red light (Schreiber, 1986). Finally, non-photochemical quenching (*NPq*) was computed as:

$$NPq = (Fm - Fm')/Fm' \qquad (4)$$

where *Fm* is the maximum fluorescence emission induced by a saturating light pulse in the dark (Genty et al., 1989).

In both experiments aboveground *Striga* counts were done at each photosynthesis measurement time. Sorghum kernel weight of each individual plant at harvest time was assessed after drying (48 h at 70° C) and threshing of the panicles.

### *Statistical analysis*

All data were subjected to analysis of variance followed by a comparison of means with the least significant difference (L.S.D.) using the Genstat (release 6.1) statistical software package. Linear regression analysis and Pearson correlation tests were done with the SPSS (version 10.0) statistical software package.

Table 2. Average first *Striga* emergence time (DAS), average aboveground *Striga* numbers at time of photosynthesis measurements and average kernel dry weight (DW: g) for control and *Striga* infected plants and relative yield loss (*RYL*: %) of the four sorghum genotypes in the 2003 and the 2004 experiment.

| | | *Striga* numbers | | | Kernel DW | | |
|---|---|---|---|---|---|---|---|
| 2003 | Emergence | 33 DAS | 47 DAS | 61 DAS | Control | *Striga*-infected | *RYL* (%) |
| CK60-B | 30.3a | 2.5 | 8.9 | 34.5a | 25.8a | 0.0d | 100 |
| E36-1 | 28.3a | 2.5 | 11.6 | 41.3a | 20.3b | 2.0d | 90 |
| Framida | 33.0a | 1.1 | 4.3 | 17.1b | 24.5ab | 15.8c | 36 |
| Tiémarifing | 42.3b | 2.5 | 7.9 | 10.7b | 21.2b | 18.2bc | 14 |
| S.E.D. | 2.26 | | | 9.94 | 1.82 | | |
| *P* | 0.011 | | | 0.03 | <0.001 | | |
| 2004 | Emergence | 26 DAS | 48 DAS | 75 DAS | Control | *Striga*-infected | *RYL* (%) |
| CK60-B | 33.8a | - | 4.2a | 22.8a | 40.6a | 0.0e | 100 |
| E36-1 | 40.0ab | - | 4.3a | 23.3a | 23.6c | 1.6e | 93 |
| Framida | 49.0bc | - | 1.3b | 7.5b | 30.5b | 10.2d | 67 |
| Tiémarifing | 56.2c | - | 0.2b | 7.5b | 26.4bc | 14.3d | 46 |
| S.E.D. | 5.19 | | 0.84 | 4.71 | 2.31 | | |
| *P* | 0.002 | | <0.001 | 0.005 | <0.001 | | |

[a] for 2003, only data of the highest *Striga* infestation level (3.0 seeds $cm^{-3}$) are presented

[b] values in the same column, within a year, followed by a different letter, differ significantly ($P<0.05$)

# Results

### *Striga infection and sorghum yield loss*

In Table 2, results on *Striga* infection and sorghum yield loss are presented for the highest *Striga* infestation levels (2003: 3.0 seeds $cm^{-3}$; 2004: 4.0 seeds $cm^{-3}$). In 2003, first *Striga* emergence on CK60-B, E36-1 and Framida was significantly ($P<0.05$) earlier than on Tiémarifing. In the 2004 experiment, *Striga* on CK60-B emerged significantly ($P<0.01$) earlier than on Framida and Tiémarifing. Furthermore *Striga* emergence on Tiémarifing was significantly later than on E36-1. In 2003, at 61 DAS, aboveground *Striga* numbers on CK60-B and E36-1 were significantly ($P<0.05$) higher than on Framida and Tiémarifing. No differences were observed before that time. In 2004, differences between these genotypes were already found at 48 DAS ($P<0.001$) and were still present at 75 DAS ($P<0.01$).

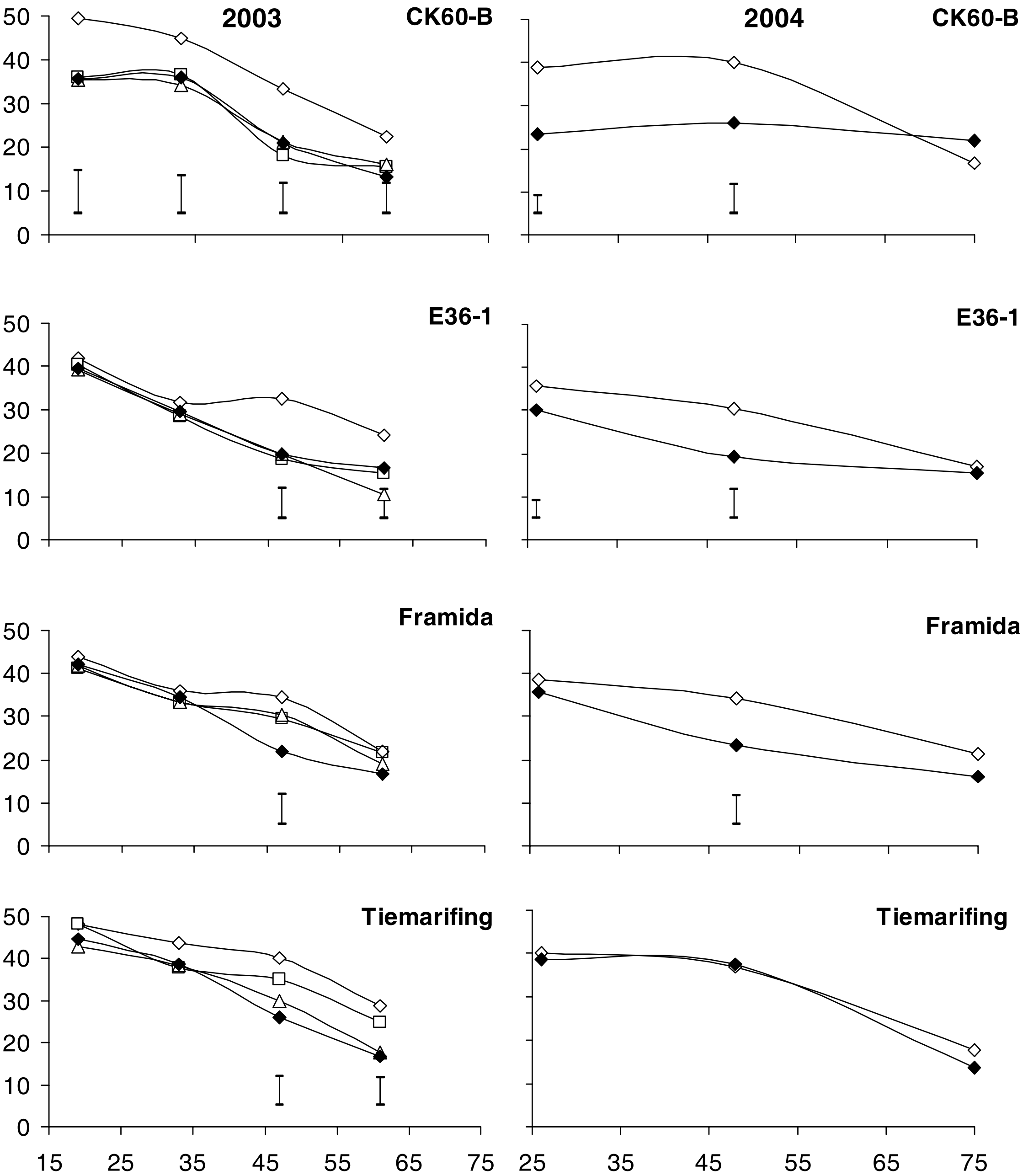

Figure 1. CO$_2$ assimilation rate (*A;* µmol CO$_2$ m$^{-2}$ s$^{-1}$; y-axis) over time (DAS; x-axis) for four sorghum genotypes (CK60-B, E36-1, Framida and Tiémarifing) at different *Striga* infestation levels (seeds cm$^{-3}$): 0.0 (open diamonds), 0.5 (squares), 1.0 (triangles) and 3.0 (closed diamonds) in 2003 (left) and 0.0 (open diamonds) and 4.0 (closed diamonds) in 2004 (right). Light intensity ([400-700 nm]; µmol photon m$^{-2}$ s$^{-1}$): 1800 (2003) and 1600-2000 (2004). Bars represent (genotype × *Striga*) L.S.D. ($P$<0.05) values from one-way ANOVA.

In 2003, *Striga* infection significantly ($P < 0.001$) reduced sorghum kernel dry weight of all genotypes except Tiémarifing (Table 2). *Striga* infection resulted in complete (CK60-B) to nearly complete (E36-1) yield loss for the sensitive genotypes, and yield losses of 36% for Framida and only 14% for Tiémarifing. In 2004, *Striga* infection significantly ($P<0.001$) reduced sorghum kernel dry weight of all genotypes. Again, yield loss of CK60-B was most severe (100%), followed by E36-1 (93%), Framida (67%) and Tiémarifing (46%).

### *$CO_2$ assimilation rate*

In both 2003 and 2004, $CO_2$ assimilation rates ($A$ in µmol $m^{-2}$ $s^{-1}$) of control plants gradually decreased over time (Figure 1). These observations had coefficients of variation (CV) between 8.5 and 17.2 %, but a much higher value at the last observation date in 2004 (75 DAS: CV = 32.4%). Significant differences between $A$ of control plants of the four genotypes were observed in 2003 at 33 DAS ($P<0.01$) and 47 DAS ($P<0.05$) and in 2004 at both 26 ($P<0.05$) and 48 DAS ($P<0.01$). In both experiments, E36-1 was significantly lower than either CK60-B (2004 at 48 DAS), Tiémarifing (2003 at 47 DAS and 2004 at 26 DAS), or both of them (2003 at 33 DAS).

The response of the various genotypes to *Striga* infection differed considerably. In 2003 (left side of Figure 1), $CO_2$ assimilation rates of infected plants of CK60-B were significantly reduced compared to the control plants ($P<0.01$) at 19 and 47 DAS, irrespective of infestation level, at 33 DAS at infestation levels of 1.0 and 3.0 seeds $cm^{-3}$ ($P<0.05$) and at 61 DAS at 0.5 ($P<0.05$) and 3.0 seeds $cm^{-3}$ ($P<0.01$). The same was found for E36-1 at 47 DAS at all infestation levels ($P<0.01$) and at 61 DAS at 0.5 and 3.0 ($P<0.05$) and 1.0 seeds $cm^{-3}$ ($P<0.01$). Significant reductions in $CO_2$ assimilation rate of infected plants of Framida were only found at 47 DAS at the highest infestation level ($P<0.01$), while Tiémarifing was significantly ($P<0.01$) affected at 47 and 61 DAS at the two highest infestation levels.

In 2004 (right side of Figure 1), *Striga* infection resulted in significant ($P<0.01$) reductions in $CO_2$ assimilation rates of CK60-B and E36-1 at 26 and 48 DAS. $CO_2$ assimilation rate of Framida was only significantly ($P<0.01$) reduced at 48 DAS. Tiémarifing was the only genotype without a significant reduction in $CO_2$ assimilation rate due to *Striga*-infection at any observation date. As photosynthesis and kernel dry weight in 2004 were measured on the same plants, a direct correlation between $CO_2$ assimilation rate and kernel dry weight could be made. A highly significant ($P<0.001$) correlation between kernel dry weight and $CO_2$ assimilation measured at 26 and 48 DAS was found (r = 0.61, N = 40; for both dates). No such correlation was found with the $CO_2$ assimilation rates measured at 75 DAS.

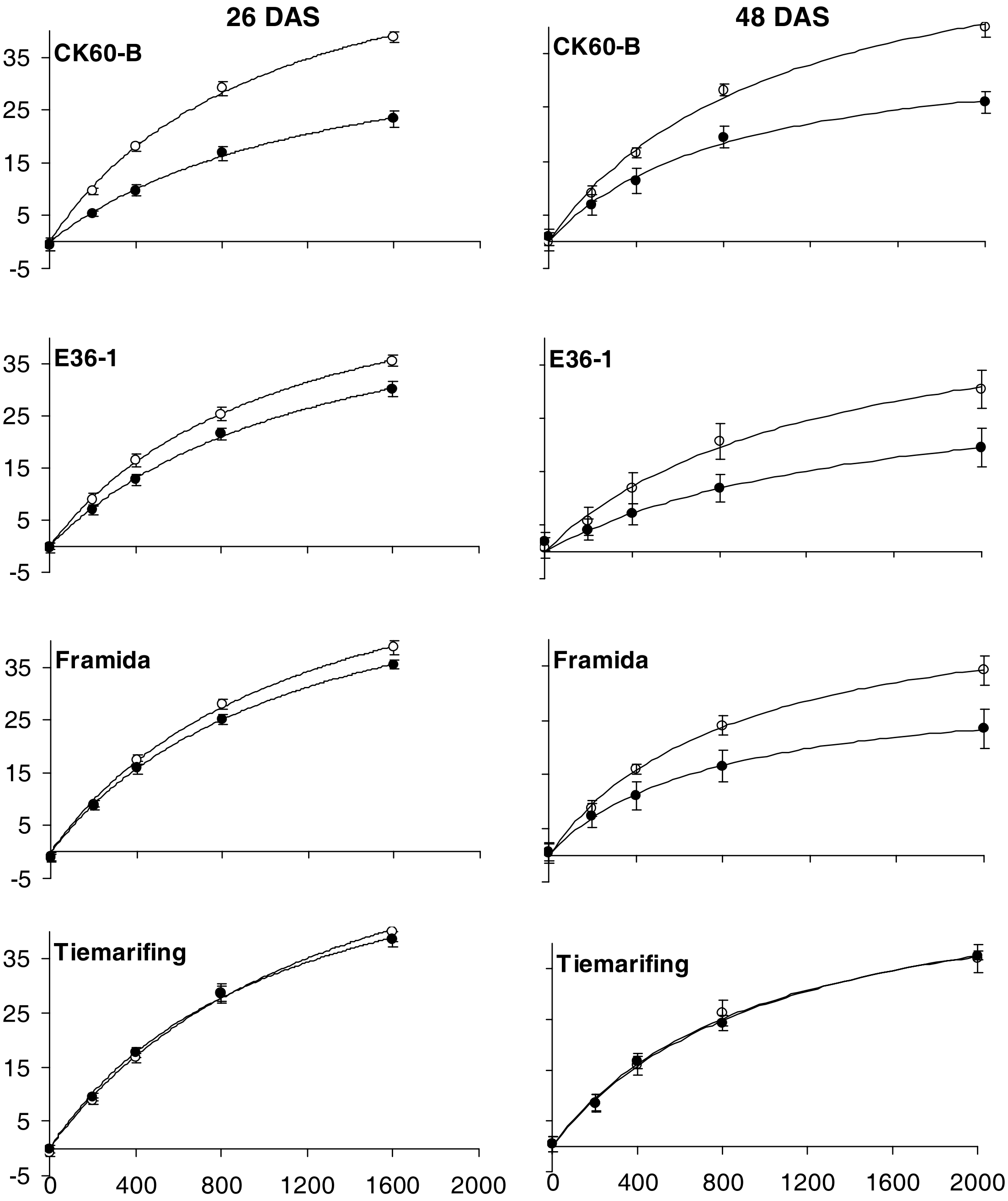

Figure 2. $CO_2$ assimilation rate (*A;* µmol $CO_2$ $m^{-2}$ $s^{-1}$; y-axis) measured at different light intensities (PAR [400-700 nm]; µmol photon $m^{-2}$ $s^{-1}$; x-axis) on four sorghum genotypes (CK60-B, E36-1, Framida and Tiémarifing) for control (open symbols) and *Striga*-infected plants (closed symbols) at 26 (left) and 48 DAS (right) in the 2004 experiment. Bars represent (+/-) standard errors of means.

In 2004, photosynthesis was measured at a range of light intensities and the corresponding photosynthesis-light response curves of control and infected plants are presented in Figure 2. At 26 DAS (left side of Figure 2), $CO_2$ assimilation of CK60-B was negatively ($P$<0.01) affected by *Striga* at all light intensities. For E36-1 *Striga* effects were significant ($P$<0.05) at 200 and 800 µmol PAR $m^{-2}$ $s^{-1}$ and highly significant ($P$<0.01) at 400 and 1600 µmol PAR $m^{-2}$ $s^{-1}$, at this stage. $CO_2$ assimilation of infected Framida and Tiémarifing plants were not significantly reduced at 26 DAS. At 48 DAS (right side of Figure 2), significant reductions ($P$<0.05) in $CO_2$ assimilation rate of infected CK60-B plants were observed at 200 µmol PAR $m^{-2}$ $s^{-1}$ and highly significant ($P$<0.01) reductions at all other light intensities. For E36-1 and Framida highly significant reductions ($P$<0.01) were observed at the three highest light intensities. *Striga* had no significant effect on $CO_2$ assimilation of Tiémarifing at any light intensity.

Table 3. Transpiration rate (*Tr;* mmol $H_2O$ $m^{-2}$ $s^{-1}$), stomatal conductance (*gs;* mol $m^{-2}$ $s^{-1}$) and intra-stomatal $CO_2$ concentrations (*Ci*; ppm) of *Striga*-infected (3.0 [2003] - 4.0 [2004] seeds $cm^{-3}$) and uninfected (0.0) plants at 47 DAS (2003) and 48 DAS (2004). The *r*-values represent the correlation coefficients between the parameters and the $CO_2$ assimilation rate.

| | Seeds $cm^{-3}$ | CK60-B | E36-1 | Framida | Tiémarifing | $r_{(1\text{-tailed})}$ |
|---|---|---|---|---|---|---|
| 2003 | | | | | | (N=80) |
| *Tr* | 0.0 | 4.6a[a] | 4.4a | 4.5a | 4.6 | 0.86**[b] |
| | 3.0 | 3.1b | 2.9b | 3.0b | 4.0 | |
| | S.E.D | 0.47 | 0.23 | 0.42 | | |
| *gs* | 0.0 | 0.31a | 0.29a | 0.31a | 0.36 | 0.90** |
| | 3.0 | 0.15b | 0.13b | 0.16b | 0.25 | |
| | S.E.D | 0.055 | 0.035 | 0.038 | | |
| *Ci* | 0.0 | 91.6 | 85.8 | 89.3 | 115.6 | -0.02 |
| | 3.0 | 64.3 | 64.3 | 64.2 | 99.5 | |
| | | | | | | |
| 2004 | | | | | | (N=40) |
| *Tr* | 0.0 | 5.0a | 3.5 | 4.4 | 4.7 | 0.85** |
| | 4.0 | 3.4b | 2.3 | 2.9 | 5.1 | |
| | S.E.D | 0.27 | | | | |
| *gs* | 0.0 | 0.19a | 0.13a | 0.16 | 0.18 | 0.92** |
| | 4.0 | 0.12b | 0.08b | 0.10 | 0.20 | |
| | S.E.D | 0.011 | 0.017 | | | |
| *Ci* | 0.0 | 42.1 | 24.5 | 35.1a | 39.0 | 0.08 |
| | 4.0 | 42.8 | 29.1 | 22.1b | 65.0 | |
| | S.E.D | | | 3.68 | | |

[a] values in the same column within the same year followed by a different letter are significantly ($P$<0.05) different

### *Transpiration and stomatal conductance*

Transpiration rate (*Tr* in mmol $H_2O$ $m^{-2}$ $s^{-1}$), stomatal conductance (*gs* in mol $m^{-2}$ $s^{-1}$) and intra-stomatal $CO_2$ concentration (*Ci* in ppm) measured at 47 (2003) and 48 DAS (2004) are presented in Table 3. Values represent those associated with the measurement of $CO_2$ assimilation rate (*A*) at the highest light intensity and conducted for control sorghum plants and sorghum plants exposed to the highest *Striga*-infestation level.

Significant reductions in *Tr* and *gs* of *Striga*-infected plants were commonly found with the more sensitive cultivars. In both years *Tr* and *gs* correlated highly significantly ($P<0.01$) with $CO_2$ assimilation rate (*A*). The significant negative *Striga* effects on $CO_2$ assimilation rate measured at 47 and 48 DAS were always associated with significant reductions in transpiration rate and stomatal conductance. Only for E36-1 in 2004 the reduction in *A* was not accompanied with a significant reduction in *Tr*. A significant reduction in *Ci* was only observed with Framida in 2004. This reduction was not associated with a significant reduction in $CO_2$ assimilation. In both 2003 and 2004 no correlation between intra-stomatal $CO_2$ concentration and $CO_2$ assimilation was observed.

### *Chlorophyll fluorescence*

In Figure 3, various parameters that were calculated based on the chlorophyll fluorescence measurements conducted in 2004 at 26 (left side) and 48 DAS (right side) are presented. Apart from photochemical quenching (*Pq*), non-photochemical quenching (*NPq*) and electron transport rate (*ETR* in µmol $m^{-2}$ $s^{-1}$) the ratio of $CO_2$ assimilation over electron flow through PSII ($A\ ETR^{-1}$) is presented. Presented data are based on the measurements conducted at the highest light intensity (1600 µmol PAR $m^{-2}$ $s^{-1}$at 26 DAS; 2000 µmol PAR $m^{-2}$ $s^{-1}$ at 48 DAS).

For control plants, the CV of all parameters at both observation dates was smaller than the CV of the $CO_2$ assimilation rate (26 DAS: 8.5% and 48 DAS: 16.4%) measured at the same time, on the same plants. Particularly for *NPq* (CV = 2.0% and 3.1%), $A\ ETR^{-1}$ (CV = 3.5% and 6.8%) and *Pq* (CV = 4.0% and 8.3%) the differences in CV, compared to those of the $CO_2$ assimilation rate, were considerable, whereas for *ETR* a relatively small difference was observed (CV = 7.0% and 12.9%). Significant genotype differences between control plants were only observed at 26 DAS for *Pq* ($P<0.05$) and at 48 DAS for *NPq* ($P<0.05$) and $A\ ETR^{-1}$ ($P<0.01$).

*Striga* effects on each parameter were analysed per measurement time (26 DAS and 48 DAS). Values of *Pq* and *ETR* were significantly (at 48 DAS: $P<0.05$) to highly significantly (at 26 DAS: $P<0.01$) affected by *Striga* infection for CK60-B.

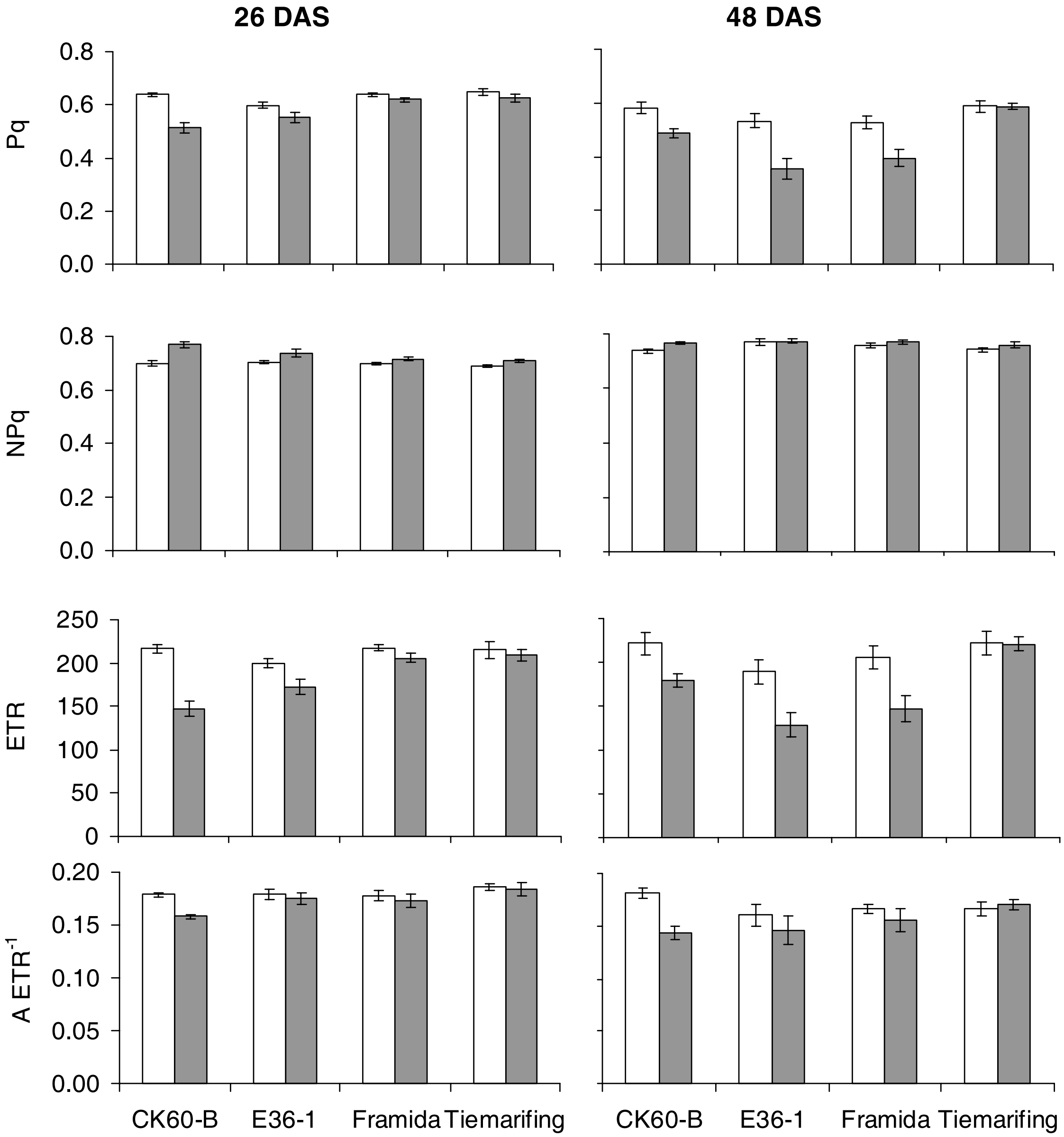

Figure 3. Photochemical quenching (*Pq*), non-photochemical quenching (*NPq*), electron transport rate (*ETR*: µmol $m^{-2}$ $s^{-1}$) and photosynthesis per electron transport (*A* $ETR^{-1}$) measured on four sorghum genotypes (CK60-B, E36-1, Framida and Tiémarifing) for control (open bars) and *Striga*-infected plants (shaded bars) at 26 (left) and 48 DAS (right) in 2004. Bars represent (+/-) standard error of means.

For E36-1 these parameters were also negatively affected at both dates ($P<0.05$ at 26 DAS; $P<0.01$ at 48 DAS), while for Framida highly significant ($P<0.01$) *Striga* effects on *Pq* and *ETR* were only found at 48 DAS. An increase in *NPq* was only observed for CK60-B and E36-1 at 26 DAS ($P< 0.01$) and for CK60-B at 48 DAS ($P< 0.05$), whereas the ratio $A\ ETR^{-1}$ was only significantly ($P<0.01$) reduced for CK60-B at both observation dates. For Tiémarifing, none of these chlorophyll fluorescence parameters were negatively affected by *Striga*. All four chlorophyll fluorescence parameters, measured at both *Striga* infected and uninfected sorghum plants, correlated highly significantly ($P< 0.01$) with $CO_2$ assimilation rate, at both measurements times (Table 4). Relative reductions in $CO_2$ assimilation rate correlated highly significantly ($P<0.01$) with *Pq*, *ETR* and $A\ ETR^{-1}$ values measured on *Striga*-infected plants at both observation dates ($P<0.01$). For *NPq* correlations were highly significant ($P<0.01$) at 26 DAS and significant ($P<0.05$) at 48 DAS.

Figure 4 shows the observed and fitted relation between $CO_2$ assimilation (*A*) and electron transport (*ETR*) measured at 200, 400, 800 and 1600 or 2000 μmol $m^{-2}$ $s^{-1}$ (PAR) for infected and uninfected plants of each genotype at both measurement times (26 DAS: left side of Figure 4, and 48 DAS: right side of Figure 4). For all genotypes a linear relation through the origin gave an adequate description of the relation between *A* and *ETR*, indicating that the number of molecules of $CO_2$ reduced per electron flowing through PSII was independent of light intensity. Analysis of variance per genotype and measurement time revealed that CK60-B was the only genotype showing a significant ($P<0.001$) decrease in slope for the infected compared to the control plants at both measurement times. This observation is identical to the conclusion drawn from the observations at the highest light intensity only (Figure 3).

Table 4. Correlations between $CO_2$ assimilation rate (*A*), relative reduction in $CO_2$ assimilation rate (*Δ A*) and electron transport (*ETR*) the ratio $CO_2$ assimilation per electron transport ($A\ ETR^{-1}$) and photochemical (*Pq*) and non-photochemical (*NPq*) quenching

| | | N[a] | 26 DAS | | 48 DAS | |
|---|---|---|---|---|---|---|
| A | *ETR* | 40 | 0.94 | **[b] | 0.95 | ** |
| | $A\ ETR^{-1}$ | | 0.70 | ** | 0.79 | ** |
| | *Pq* | | 0.91 | ** | 0.93 | ** |
| | *NPq* | | -0.86 | ** | 0.70 | ** |
| Δ A | *ETR* | 20 | -0.91 | ** | -0.86 | ** |
| | $A\ ETR^{-1}$ | | -0.70 | ** | -0.88 | ** |
| | *Pq* | | -0.85 | ** | -0.84 | ** |
| | *NPq* | | 0.89 | ** | 0.51 | * |

[a] Correlations with photosynthetic rate were analyzed with all data (control and *Striga*-infected plants), correlations with relative photosynthetic rate where analyzed based on *Striga*-infected plants only

* and ** indicate significant correlations at the 0.05 and 0.01 probability level, respectively.

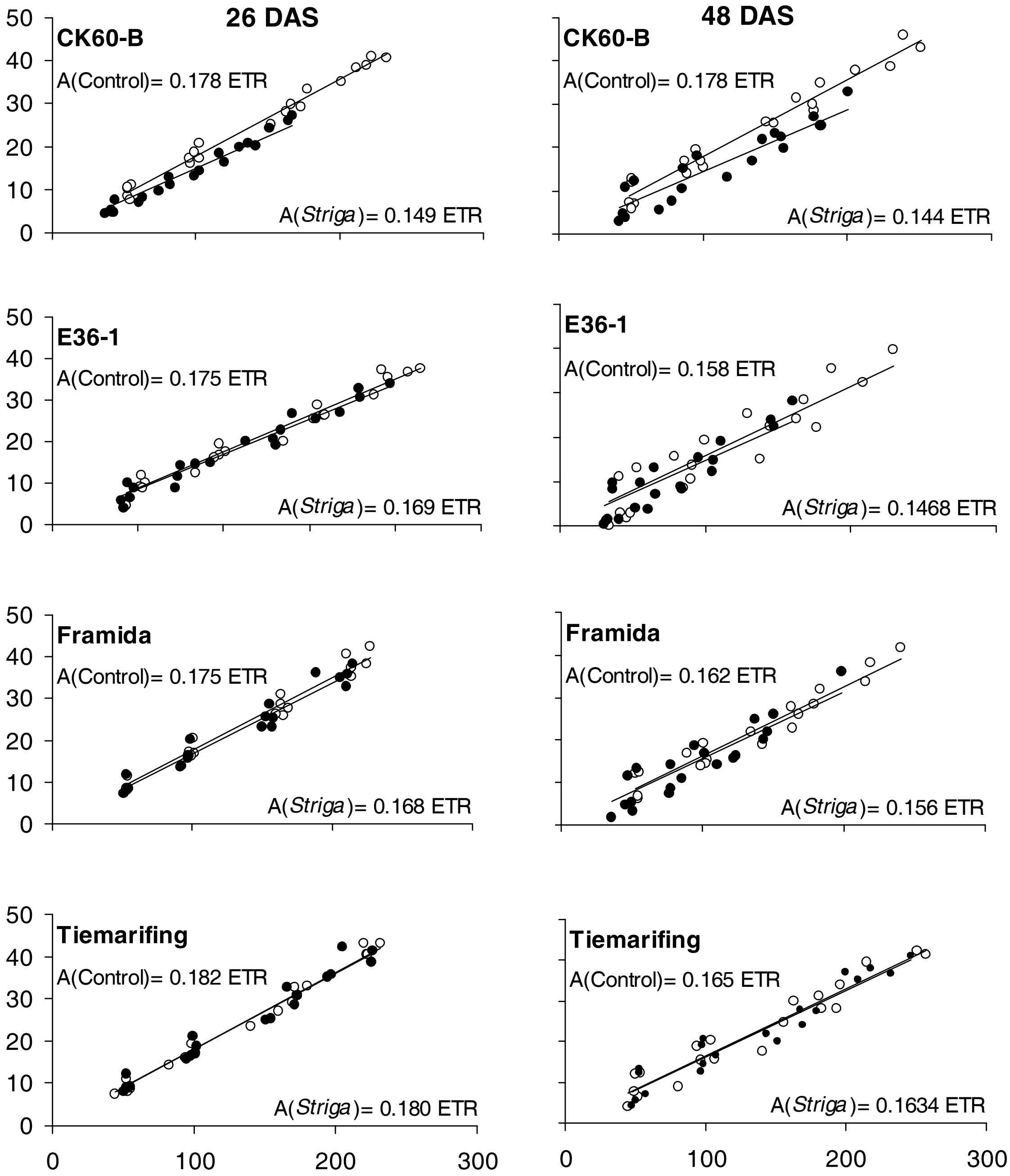

Figure 4. $CO_2$ assimilation rate (*A*; µmol $CO_2$ $m^{-2}$ $s^{-1}$; y-axis) as a function of electron transport rate (*ETR*; x-axis) measured on four sorghum genotypes (CK60-B, E36-1, Framida and Tiémarifing) for control (open symbols) and *Striga*-infected plants (closed symbols) at 26 (left) and 48 DAS (right) in 2004. Lines represent best fits obtained through linear regression.

## Discussion

*Genotype specific Striga effects on $CO_2$ assimilation rate*

The observations on $CO_2$ assimilation rate largely correspond to the earlier classification of sorghum genotypes with respect to tolerance and resistance to *Striga*, which was based on relative yield loss due to *Striga* and aboveground *Striga* numbers (Rodenburg et al., Accepted). CK60-B was earlier identified as a very susceptible and very sensitive genotype. This genotype showed immediate and highly significant reductions in $CO_2$ assimilation rate upon *Striga* infection during its vegetative stage. E36-1 was earlier identified as a very susceptible and sensitive genotype. This was reflected in the *Striga* effects on $CO_2$ assimilation of this genotype. E36-1 showed highly significant negative *Striga* effects on $CO_2$ assimilation but these effects were exposed in a later stage than those on CK60-B. Framida was earlier identified as a resistant and moderately tolerant genotype. The genotype showed highly significant negative photosynthesis responses upon *Striga* infection but not at all observation times and only at high infestation levels. Negative effects on $CO_2$ assimilation appeared later than on CK60-B. Tiémarifing was earlier identified as tolerant and moderately resistant. This genotype showed highly significant *Striga* effects on $CO_2$ assimilation in 2003 but only at the latest measurement dates and highest infestation level. In the 2004 experiments, despite the presence of *Striga*, effects on photosynthesis of Tiémarifing were even completely absent.

The significant correlation between $CO_2$ assimilation measured at 26 and 48 DAS and kernel dry weight is a further indication that photosynthesis is an important indicator of the performance of *Striga*-infected sorghum plants. The absence of a significant correlation between kernel dry weight and $CO_2$ assimilation measured at 75 DAS shows that during later growth stages photosynthesis is less indicative.

The ability to maintain high rates of $CO_2$ assimilation as mechanism to endure parasite infection was earlier reported by Gurney et al (2002a). They also suggested that this characteristic could be used as a screening measure for tolerance. Photosynthesis as screening measure for tolerance against biotic stresses has earlier been proven useful with *Septoria nodorum* in wheat (Scharen and Krupinsky, 1969). Selection measures should enable a quick and reliable assessment and preferably be low-cost. Obviously, the selection measure should discriminate clearly between tolerant and non-tolerant genotypes. Another requirement would be that in the absence of *Striga* the measure shows little variation, both within and among genotypes. Absolute measurements under *Striga* infestation, without *Striga* free controls, would than be sufficient to make a selection among genotypes.

Despite the relatively high coefficients of variation (CV: 8.5% to 32.4%), rates of $CO_2$ assimilation of control plants of different genotypes were significantly to highly significantly different in four of seven measurements. This indicates that measurements on control plants are required for a selection based on $CO_2$ assimilation rate. Following this procedure, only in 2004 at 48 DAS, Tiémarifing could be identified as the most tolerant genotype. If selection would have been based on measurements of 2003 only, Framida would probably been falsely identified as the most tolerant genotype. Hence, $CO_2$ assimilation rate might not always be a reliable selection measure. Other serious constraints to the use of $CO_2$ assimilation rate as screening measure are the relatively long time needed per measurement and the high costs of photosynthesis measurement systems.

In both experiments, $CO_2$ assimilation rate correlated very strongly with transpiration rate and stomatal conductance. Significant reductions in $CO_2$ assimilation were never associated with significant reductions in the intra-stomatal $CO_2$ concentration. It must be noted that internal $CO_2$ concentrations are not measured directly but result from calculations based on stomatal conductance. Stomatal conductance, in turn, is computed based on transpiration rate and the vapour pressure difference between inside and outside the leaf (Von Caemmerer and Farquhar, 1981). Due to that, the calculated internal $CO_2$ concentrations are sensitive to small perturbations or measurement errors. Still the observations suggest that *Striga* effects on stomatal conductance are not the main reason for photosynthetic reduction because such a response would lead to a transitional decrease of the internal $CO_2$ concentration due to the increased resistance for $CO_2$ diffusion (Kropff, 1987). This confirms results of an earlier study by Press et al. (1987a), but seems to contradict findings from Frost et al. (1997). A direct effect of *Striga* on the photosynthetic apparatus of its host plant offers good perspectives for using chlorophyll fluorescence to replace the $CO_2$ exchange measurements.

### *Chlorophyll fluorescence parameters as screening measure*

The regulation of photosynthesis in response to stress involves the protection of the photosynthetic apparatus. Photochemical and non-photochemical quenching are two essential elements of this photoprotection (Ort and Baker, 2002). Photochemical quenching is proportional to the energy transfer to the functional photosynthesis reaction centres. Non-photochemical quenching (*NPq*) refers to the process of dissipation of the excess excitation energy in the PSII antennae as heat, whereby down-regulation of PSII electron transport efficiency is triggered. As the capacity for photochemistry of leaves reduces under stress conditions, both photochemical and non-photochemical quenching are potentially suitable measures for stress severity

(Schreiber, 1986) or stress tolerance (Harbinson, 1995). This was demonstrated by studies on cold tolerance in maize (Schapendonk et al., 1989a; Fracheboud et al., 1999) and drought tolerance in wheat (Havaux and Lannoye, 1985), barley (Nogues et al., 1994; Olsovska et al., 2000) and potato (Schapendonk et al., 1989b, 1992). Some of the *Striga* effects show remarkable resemblance with drought stress effects (e.g.White and Wilson, 1965; Björkman and Powles, 1984) which opens the way for rapid selection of *Striga* tolerant genotypes, using fluorescence analyses. The observations in 2004, when chlorophyll fluorescence was measured in addition to $CO_2$ assimilation, confirm this. All four chlorophyll fluorescence parameters (*ETR*, $A\ ETR^{-1}$, *Pq*, *NPq*) of *Striga* infected plants showed a strong correlation with $CO_2$ assimilation rate or the relative reduction in $CO_2$ assimilation rate due to *Striga* infection. In addition, all parameters were characterized by a relatively small CV and in spite of this only in three occasions (*Pq* at 26 DAS and *Nq* and $A\ ETR^{-1}$ at 48 DAS) a significant genotype difference between control plants was observed. This indicates that for screening purposes measurements on control plants do not always seem to be a prerequisite. As also the equipment required for measurement of chlorophyll fluorescence costs only about 10% of that of the gas exchange equipment, screening based on chlorophyll fluorescence is a cost effective alternative to screening using photosynthesis measurements based on gas exchange.

Clear differences in suitability of the various fluorescence parameters for use as screening measure are present. The most straightforward approach to estimate photosynthetic capacity from fluorescence analysis is provided by *ETR*, which is based on the efficiency of electron transport through PSII ($\Phi_2$) and the absorbed light intensity. Parameter $\Phi_2$ is based on *Ft* and *Fm'*, which are both measured in the light. At 26 DAS, CK60-B and E36-1 could already be identified as sensitive genotypes and at 48 DAS Framida also showed a significant reduction in *ETR* and could be distinguished from Tiémarifing. Determination of *ETR* requires fairly stable or saturated light intensities throughout the selection procedure, as *ETR* is dependent on light intensity. The ratio $A\ ETR^{-1}$ showed to be independent of light intensity. However, the photosynthesis per electron transport only helped to identify CK60-B as a sensitive genotype. Possibly a reduction in photosynthesis per electron transport only appears in very sensitive genotypes, or at relatively high levels of infection. For this reason it is not believed to be a helpful parameter for the identification of superior tolerant genotypes. Furthermore, the calculation of this ratio would require the determination of both chlorophyll fluorescence and $CO_2$ assimilation rate.

For the sensitive genotypes, significant increases in non-photochemical quenching (*NPq*) following *Striga* infection were observed at 26 (CK60-B and E36-1) and 48 DAS (only CK60-B). Based on *NPq* values, no distinction could be made between Framida and Tiémarifing at any measurement time. Moreover, in absolute terms the increases observed with the sensitive genotypes were marginal. For instance the *NPq* values measured on infected plants of CK60-B and E36-1 at 26 DAS fall well in the range of *NPq* values obtained on non-infected plants at 48 DAS. For that reason, *NPq* is not considered a very suitable screening measure for tolerance, particularly not in the absence of control plants. Another disadvantage of *NPq* is that its calculation involves *Fm*, which means that chlorophyll fluorescence should also be measured in the dark, requiring a dark-adaptation period.

Photochemical quenching (*Pq*) showed to alter significantly upon *Striga* infection in sensitive genotypes. Tiémarifing was the only genotype with virtual unchanged *Pq* values due to *Striga* infection throughout the experiment. Hence, through measurement of *Pq* it is possible to identify genotypes with superior levels of tolerance. Possible drawback is the observed presence of a significant genotype effect on *Pq* values of *Striga*-free control plants at 26 DAS, which would require the inclusion of control plants in the screening trial, to calculate relative changes. However, at 48 DAS the genotype effect on control values of *Pq* was not longer present. It is therefore expected that *Pq* of uninfected control plants only shows a genotype effect at certain (early) phenological stages. Major constraint for *Pq* measurements as selection tool seems to be the requirement of far-red light to determine *Fo'*. Provision of far-red light is often not available on standard equipment for measuring chlorophyll fluorescence. However, such a technical constraint could be overcome. Alternatively, a method is available which estimates *Fo'* through a simple equation involving the minimum fluorescence yield in the dark-adapted state (*Fo*), the maximum fluorescence yield in the dark-adapted state (*Fm*), and the maximum fluorescence yield in the light-adapted state (*Fm*') (Oxborough and Baker, 1997). Disadvantage of this alternative is again the requirement to conduct fluorescence measurements in both light and dark-adapted conditions.

### *Development of a screening protocol*

Based on the current results it is concluded that chlorophyll fluorescence parameters, particularly *ETR* and *Pq*, carry good potential for the development of a discriminative and cost effective screening procedure for host plant tolerance to *Striga hermonthica*. This however requires the design of a measuring protocol that should be evaluated with a wider range of genotypes and preferably with combined measurements of gas exchange and fluorescence to test for what conditions the attempted screening protocol is actually valid. Earlier studies where chlorophyll fluorescence measurements were used as selection measure for tolerance (e.g. Havaux and Lannoye, 1985; Nogues et al., 1994; Fracheboud et al., 1999; Olsovska et al., 2000) dealt with abiotic stresses such as cold or drought. *Striga* is a biotic stress and this implies some additional difficulties for screening. As much as genotypes may differ in tolerance to an biotic stress factor, they may differ in resistance. Equivalence of parasite infection or removal of resistance effects as a confounding factor is one of the first requirements for measuring tolerance (Schafer, 1971), and typically this aspect was identified as the main constraint for developing a simple screening procedure based on actual yield data (Rodenburg et al., Accepted). Differences in *Striga* effects on photosynthesis and chlorophyll fluorescence between genotypes as found in this study may partly result from differences in resistance, since significant differences in aboveground *Striga* numbers were observed between Tiémarifing and Framida on the one hand and CK60-B and E36-1 on the other. Completely cancelling out all differences in resistance seems impossible. The most practical solution would be to use very high infestation levels (three to four viable *Striga* seeds cm$^{-3}$ equivalent to 300- 400,000 seeds m$^{-2}$ of the upper 10 cm in the field). This should prevent that more resistant genotypes, such as Framida in this study, will be falsely identified as tolerant, due to the fact that they simply do not have enough infections to damage the host plant sufficiently. Use of high levels of *Striga* infestation in screening trials for tolerance against *Striga* was earlier recommended by Kim (1991).

In agreement with other reports (e.g. Olivier et al., 1991a; Ast et al., 2000; Rodenburg et al., Submitted), resistance also resulted in significantly delayed parasitism and hence later effects. Because of differences in *Striga* emergence between genotypes the screening should not be carried out too early. For a reliable and fair screening based on photosynthesis or chlorophyll fluorescence measurements *Striga* should have had sufficient opportunity to establish on all genotypes. In addition, this study showed that screening also has an upper time limit. The 2004 experiment showed that after flowering (50% flowering stages were recorded between 52 and 61 DAS) of sorghum, photosynthesis did no longer correlate with yield and was no longer consistent with observed overall tolerance or sensitivity of the genotype to the parasite. The most significant differences in photosynthesis and chlorophyll fluorescence in this study were found in the early stages of the host-parasite relation. This is expected, based on the earlier observation by Parker and Riches (1993) that *Striga* exerts already severe effects on the host when host plants are young and *Striga* is still belowground. Early *Striga* effects on photosynthesis were observed in several other studies as well (e.g. Graves et al., 1989, 1990; Gurney et al., 1995). It is therefore recommended to do the screening shortly after first *Striga* emergence and well before sorghum flowering. A solution to correct for the delay in parasitism could be to make measurement time for each genotype dependent on first *Striga* emergence or to conduct measurements on two specific moments in time.

# CHAPTER 5

# Effects of host plant genotype and seed bank density on *Striga* reproduction[1]

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## Abstract

Prevention of seed input in the seed bank of *Striga hermonthica* infested fields is an important objective of *Striga* management. In three consecutive years of field experimentation in Mali, *Striga* reproduction was studied for ten sorghum genotypes at infestation levels ranging from 30,000 to 200,000 seeds m$^{-2}$. Resistance was identified as an important determinant of *Striga* reproduction, with the most resistant genotypes (N13, IS9830 and SRN39) reducing *Striga* reproduction with 70-93% compared to the most susceptible genotype (CK60-B). Seed bank density was another factor having a significant effect on *Striga* seed production. The relation between seed bank density and *Striga* reproduction was non-linear. Density-dependent reduction in seed production resulted mainly from intra-specific competition between aboveground *Striga* plants. For the most susceptible genotypes density dependence also occurred in the earlier belowground stages. *Striga* reproduction continued beyond crop harvest. At the high infestation level just 8% of the total reproduction was realized after harvest, whereas at the low infestation level 39% was attained after harvest. Even though host plant genotype plays a significant role in *Striga* reproduction, calculations indicated that only at very low infestation levels the use of the most resistant genotype was able to lower the *Striga* seed bank.

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[1] Submitted to Weed Research

## Introduction

Cereal production in the semi-arid to sub-humid tropics is often limited by the obligate, out-crossing, hemi-parasitic weed *Striga hermonthica* (Del.) Benth, a member of the Orobanchaceae (formerly: Scrophulariaceae) family. *Striga hermonthica* parasitizes on roots of cereals like sorghum (*Sorghum bicolor* [L.] Moench), pearl millet (Pennisetum glaucum [L.] R. Br.), maize (Zea mays [L.]) and upland rice (both Oryza glaberrima [Steudel] and O. sativa [L.]; [Johnson et al., 1997]). Infection by *Striga* can cause severe yield losses of up to 80-85%, depending on the level of resistance and tolerance of the specific host genotype (Obilana, 1983; Rodenburg et al., 2005). The *Striga* problem has become increasingly important in the sub-Saharan regions of Africa (Lagoke et al., 1991). This increase is caused by the good reproduction opportunities for *Striga* plants that are created by an intensification of land use, where suitable host plants are grown continuously on the same fields (Weber et al., 1995). *Striga* produces numerous, very small seeds per plant. *Striga* seed size is 0.2 to 0.3 mm (Parker and Riches, 1993). Estimates of seed production per plant vary from 5,000 up to 85,000 seeds per reproductive plant (Andrews, 1945; Stewart, 1990; Webb and Smith, 1996). One host plant can support several seed producing *Striga* plants simultaneously and a substantial part of the newly produced *Striga* seeds survive the subsequent dry season until the next cropping season. Therefore, the *Striga* seed bank in the soil easily increases with every new cropping season with the same host species. Delft et al. (1997) concluded that only two to three seed producing *Striga* plants per $m^2$ would be enough to balance the seed bank. Prevention of seed input in the seed bank and reduction of the soil seed bank of *Striga* infested fields are among the most important objectives for *Striga* management (Ramaiah, 1987b). Host plant defence mechanisms against *Striga* can contribute to this (Hess and Haussmann, 1999), particularly since host resistance against *Striga* is expected to reduce *Striga* seed production (Doggett, 1988; Ejeta et al., 2000).

Complete resistance, or immunity, against *Striga* in cereals has not yet been reported. Even varieties possessing the most effective resistance mechanisms against *Striga* can still not completely prevent some individual *Striga* plants to emerge and complete their life-cycle (e.g. Rodenburg et al., 2005). The assumed reduction in seed production rate of resistant genotypes has been attributed to a slower development of *Striga*, a reduced number of emerged *Striga* plants, or a reduced number of flowering and capsule bearing *Striga* plants ( Weber et al., 1995; Carsky et al., 1996; Kim and Adetimirin, 1997b). Objective of this study was to test whether there is a significant host plant genotype and seed bank density effect on *Striga* reproduction. It was hypothesized that resistant genotypes, that reduce the number of aboveground *Striga* plants, are able to create a proportional reduction in *Striga* seed production. In that case, screening for resistant genotypes will automatically yield genotypes that reduce *Striga* reproduction. An additional objective was to find a characteristic for *Striga* seed production that is simple and easy to measure. Furthermore, it was investigated whether *Striga* seed production continues after harvest of the host plant and how significant this additional post-harvest seed production is.

## Material and Methods

### *Genetic material*

The host species in this study is *Sorghum bicolor* (sorghum), because it is the most important host species for reproduction of *Striga hermonthica* (Weber et al., 1995). Ten different sorghum genotypes were selected: CK60-B, CMDT39, E36-1, Framida, IS9830, N13, Seredo, Serena, SRN39 and Tiémarifing. These genotypes originate from different parts of the world and were selected for their differences in level and mechanism of defence against *Striga*. The genotypes ranged from resistant (N13) to susceptible (E36-1) and from tolerant (Tiémarifing) to sensitive (CK60-B) and comprised various combinations of these reaction types (Ast et al., 2000; Hess, 1989; Olivier et al., 1991; Rodenburg et al., 2005). *Striga hermonthica* seeds, used to create *Striga* infested plots, originated from Samanko, Mali and were derived from plants parasitizing on sorghum. In 2001, *Striga* seed from 1998 was used (viability 82.5%) and in 2002 a mixture of seed from 1995-1997 and 2001 (viability 73%) was used. In 2003, a mixture of *Striga* seed from 1995-1998 and 2001 (viability 10.5%) was used, supplemented with seeds from 2002 (78.7%) to arrive at the desired infestation level.

### *Location*

The field trials were conducted in 2001, 2002 and 2003 at the ICRISAT field station in Samanko, 20 km Southwest of Bamako, the capital of Mali (latitude: 8°54”W and 12°54”N, altitude: 329 m). The climate type is Sudanese, characterized by a single rainy season between May and October. The average temperature during the cropping season (June-November) is 29.1°C. Mean annual rainfall at the field station is 950 mm, of which 96% falls between May and October.

Each year a different field was used, adjacent to that of the previous year. Experimental fields had sandy-loam, ferruginous tropical soils with wash out spots and concretions. Table 1 presents soil fertility parameters of the main plots of the three fields (2001-2003) after fertilization. Figure 1 presents cumulative rainfall, in the 3 cropping seasons, over time.

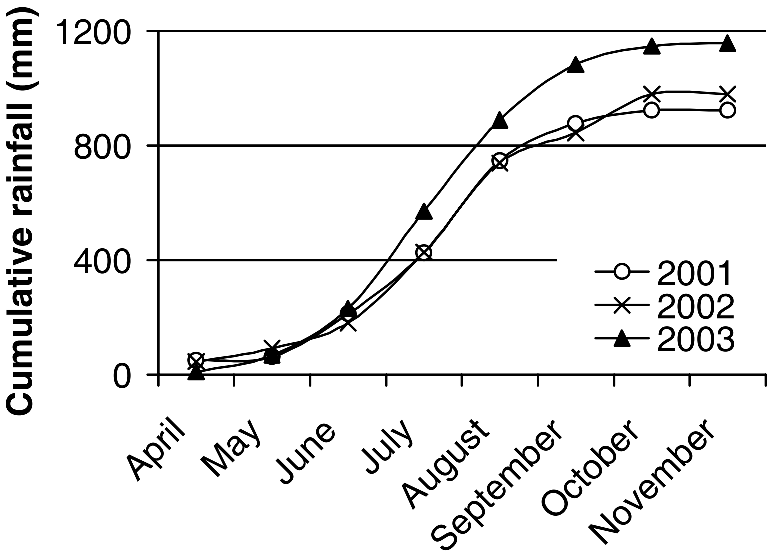

Figure 1. Cumulative rainfall (mm) during the cropping seasons of 2001-2003, in Samanko, Mali.

Table 1. Soil fertility parameters after fertilization: pH ($H_2O$; 1:2.5), C-organic (% C.O.), P-available (Bray-1; mg P $kg^{-1}$) and N-total (mg N $kg^{-1}$) of the main plots of the study fields from the three years (2001, 2002, 2003 low infestation [L] and 2003 high infestation [H])

| | 2001 | 2002 | 2003 (L) | 2003 (H) |
|---|---|---|---|---|
| pH | 4.91 | 5.59 | 4.93 | 5.07 |
| C-organic | 0.27 | 0.70 | 0.35 | 0.37 |
| P-available | 9.17 | 21.01 | 12.15 | 13.56 |
| N-Total | 227.5 | 486.4 | 248.4 | 256.3 |

*Experimental design*

In 2001 and 2002, a completely randomised block design with sorghum genotype (10) as treatment was used in either five (2001) or eight (2002) replicates. In 2003 a split-plot design in eight replications was used with two *Striga* infestation densities (high [H] and low [L]) at the main-plot level and ten sorghum genotypes at the sub-plot level. Each plot or sub-plot, representing one sorghum genotype, contained four crop rows, of 4 m (2001), 7.6 m (2002) and 6.4 m (2003) of which the middle two rows were used for observations. Row distance was 0.8 m and plant distance in the row was 0.2 (2001) and 0.4 m (2002 and 2003), corresponding to plant densities of 62,500 (2001) and 31,250 plants $ha^{-1}$ (2002 and 2003).

*Field preparation*

The soil of the experimental field was tilled, levelled and fertilized prior to *Striga* infestation and sorghum sowing. Fertilization was done at a rate of 100 (2001) and 200 kg $ha^{-1}$ (2002 and 2003) of N-P-K (17-17-17) and in 2002 gypsum (100 kg $ha^{-1}$) was added to increase soil pH. Artificial *Striga* infestation of the upper 5 (2001) and 10 cm (2002 and 2003) was created by dispersing *Striga* seeds mixed with sand. This was done 2 weeks before sowing of the host plant crop, to allow pre-conditioning of the *Striga* seeds. *Striga* infestation levels were 45,000 (2001), 200,000 (2002) and 30,000 (2003L) and 150,000 (2003H) viable *Striga* seeds $m^{-2}$. In all years, blocks or main-plots were surrounded by small dikes to prevent *Striga* inflow from adjacent blocks through soil run-off after rain showers. Sorghum was hand sown at 13 (2001), 6 (2002) and 5 July (2003), with six seeds per pocket at 3 cm depth. Sorghum plants were thinned to one plant per pocket at 21 days after sowing (DAS). Throughout the season, experimental plots were kept free of weeds other than *Striga hermonthica*. Harvest time depended on sorghum genotype and year (110-119 DAS in 2001, 102-132 DAS in 2002 and 118-132 DAS in 2003).

*Observations and sampling*

In each plot, *Striga* sampling areas, containing either ten (2001 and 2002) or four (2003L and 2003H) host plants, were selected for observations on the parasitic weed. First *Striga* emergence date ($E_{date}$) and dates of first flowering ($F_{date}$) were registered. Aboveground *Striga* plants (result of emergence and death) were counted weekly (2001) or bi-weekly (2002 and 2003). These counts were used to determine the maximum aboveground *Striga* number ($NS_{max}$).

In 2001 and 2002, the number of generative *Striga* plants was counted at crop harvest, resulting in $NS_{gen}$. In both years, all (living and dead; generative and vegetative) aboveground *Striga* plants of the sampling area were collected at harvest, dried and weighted for total aboveground *Striga* dry weight ($DW_{tot}$). Dry weight of the flowerstalks was separately determined ($DW_{stalks}$). Flowerstalks were defined as the generative part of the branches of a *Striga* plant, from the oldest flower or capsule to the top.

In 2003, starting from the first *Striga* flowering date, dead generative *Striga* plants were collected weekly from the observation plots and together with the living generative plants that were sampled at harvest used for assessment of $NS_{gen}$, $DW_{tot}$ and $DW_{stalks}$. Additionally, *Striga* seed production in 2003 was estimated based on the number of capsules produced throughout the growing season. For all generative plants (dead or living) at harvest, the number of capsules was counted, resulting in the total number of capsules ($NR_{caps}$). This method ensured inclusion of all generative plants in the assessment of reproductive effort. In the adjacent observation area of equal size (four host plants) collection of dead *Striga* plants, and the observation of *Striga* characteristics, continued after harvest until all plants were dead. Comparison of the results of both sampling areas gives an indication of the importance of *Striga* seed production after harvest of the crop. Just after sorghum harvest in 2003, ten ripe seed capsules from five randomly selected *Striga* plants (two capsules per plant) were sampled in each individual sub-plot. Those seed capsules were dried and its content was weighted to get an estimate of the seed production per capsule. Additionally individual *Striga* seed weight was assessed.

### *Statistical analyses*

Data on $E_{date}$, $F_{date}$, $NS_{max}$, $NS_{gen}$, $DW_{tot}$, $DW_{stalks}$ and $NR_{caps}$ were subjected to analyses of variance (ANOVA), followed by a comparison of means with the least significant difference (L.S.D.), using the Genstat (release 7.1) statistical software package. To meet the assumptions of the analysis of variance, prior to analysis all data, except *Striga* development dates, were subjected to square root ($[X+c]^{1/2}$) transformation, where $X$ was the original, individual observation and $c$ was set to 0.5 (Sokal and Rohlf, 1995).

In tables with comparisons between genotypes, rankings from 1 to 10 were used. Rank 1 was assigned to the best performing genotype, from the *Striga* control perspective, and rank 10 was assigned to the worst performing genotype (e.g. the genotype with the highest capsule number, *Striga* number or dry weight).

Correlations in this study were one-tailed Pearson's correlations, based on individual data points (original data or square-root transformed: $[X+c]^{1/2}$, with $c$=0.5). Correlations and linear regressions were carried out with the SPSS (version 10.0) statistical software package. Correlations in this study were phenotypic correlations ($r$). Due to relatively high environmental variation it was not possible to calculate genetic correlations.

Repeatabilities set an upper-limit to the heritability of a variable. Repeatability ($R$) of capsule numbers was calculated according to Falconer and Mackay (1996):

$$R = (V_G + V_{Eg})/V_P = 1 - (V_{Es}/V_p)$$

where $V_P$ is the total phenotypic variance, which is composed of three components: (1) $V_G$ the genetic variance, (2) $V_{Eg}$ the environmental variance due to permanent environmental effects on the phenotype and (3) $V_{Es}$ the environmental variance due to temporary or localized environmental effects on the phenotype.

Table 2. First *Striga* emergence ($E_{date}$) and first flowering dates ($F_{date}$), in days after sowing (DAS), and ranking (numbers 1-10) per sorghum genotype and infestation level, for three subsequent years (2001 - 2003) and infestation levels (2003L: low and 2003H: high).

| | 2001 | | | | 2002 | | | | | | 2003L | | | | | | 2003H | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $E_{date}$ | | $F_{date}$ | | $E_{date}$ | | | $F_{date}$ | | | $E_{date}$ | | | $F_{date}$ | | | $E_{date}$ | | $F_{date}$ | |
| CK60-B | 33.6 | 10 | 73.6 | 9 | 28.9 | de[a] | 9 | 66.9 | d | 10 | 37.3 | b | 10 | 77.5 | e | 10 | 28.8 | 10 | 75.1 | 10 |
| CMDT39 | 38.4 | 5 | 79.2 | 4 | 32.5 | abc | 4 | 74.8 | ab | 3 | 43.9 | ab | 3 | 88.3 | bcd | 7 | 32.3 | 4 | 83.1 | 2 |
| E36-1 | 37.6 | 6 | 73.4 | 10 | 28.6 | e | 10 | 70.1 | bcd | 8 | 37.9 | b | 8 | 85.4 | de | 9 | 30.6 | 8 | 79.3 | 7 |
| Framida | 37.2 | 7 | 81.0 | 2 | 32.0 | abc | 5 | 74.1 | abc | 5 | 47.5 | a | 2 | 93.9 | abc | 3 | 34.4 | 2 | 78.0 | 9 |
| IS9830 | 44.2 | 2 | 78.2 | 6 | 33.6 | ab | 3 | 75.5 | a | 1 | 37.4 | b | 9 | 91.3 | abcd | 5 | 29.4 | 9 | 79.0 | 8 |
| N13 | 40.8 | 3 | 78.9 | 5 | 31.6 | bcd | 6 | 69.4 | cd | 9 | 50.3 | a | 1 | 96.7 | a | 1 | 31.6 | 6 | 83.3 | 1 |
| Seredo | 37.0 | 8 | 80.6 | 3 | 33.6 | ab | 2 | 75.4 | a | 2 | 38.5 | b | 7 | 92.4 | abcd | 4 | 31.9 | 5 | 81.4 | 4 |
| Serena | 36.4 | 9 | 76.8 | 8 | 31.1 | bcd | 7 | 74.6 | ab | 4 | 43.8 | ab | 4 | 95.3 | ab | 2 | 37.3 | 1 | 81.3 | 5 |
| SRN39 | 44.2 | 1 | 81.0 | 1 | 34.8 | a | 1 | 70.5 | abcd | 7 | 38.6 | b | 6 | 87.0 | cd | 8 | 33.8 | 3 | 80.9 | 6 |
| Tiémarifing | 39.2 | 4 | 77.2 | 7 | 30.5 | cde | 8 | 72.4 | abc | 6 | 41.9 | ab | 5 | 90.3 | abcd | 6 | 31.5 | 7 | 82.0 | 3 |
| S.E.D. (df) | ns[b] | | ns | | 1.42 | (79) | | 2.56 | (79) | | 4.38 | (79) | | 4.05 | (79) | | ns | | ns | |
| mean | 38.9 | | 78.0 | | 31.7 | | | 72.4 | | | 41.7 | a[b] | | 89.8 | a | | 32.1 | b | 80.3 | b |

[a] means in the same column followed by a different letter are significantly different at the 0.05 level

[b] ns means not significant

[c] emergence and flowering are significantly affected by *Striga* infestation level ($P<0.001$)

## Results

### *Striga emergence and flowering*

Only in 2002 and in 2003L host plant genotype had a significant ($P<0.05$) effect on first *Striga* emergence and flowering dates (Table 2). In 2002, *Striga* plants on E36-1 and CK60-B emerged significantly earlier than on most other genotypes whereas on SRN39, Seredo and IS9830 emergence was significantly delayed compared to some other genotypes. In 2003L, emergence was significantly delayed on Framida and N13, compared to most other genotypes. In both years, genotype rankings based on flowering dates corresponded roughly with rankings based on emergence dates. However the data also show that early emergence did not automatically result in early flowering and vice versa (e.g. SRN39 and Serena in 2002 and CMDT39 in 2003L). *Striga* development response to host genotype is rather erratic. Throughout the years, early (rank 1 to 3) and late (8 to 10) emergence was observed at six different genotypes and early and late flowering was observed at seven and eight different genotypes, respectively. The only genotypes with a consistent fast development are CK60-B and E36-1. *Striga* on SRN39 emerged consistently late compared to the other genotypes. However, this was not followed by consistent later flowering.

Both emergence and flowering dates of *Striga* were significantly ($P<0.001$) affected by *Striga* seed bank density in 2003 (Table 2). In the low infested plots, *Striga* development (both emergence and flowering) was on average 9.5 days later than in the high infested plots. Furthermore in 2001 at 45,000 seeds $m^{-2}$, *Striga* emergence and flowering were on average 7 and 5.5 days (respectively) later than in 2002 at 200,000 seeds $m^{-2}$.

### *Striga numbers*

In all years, there was a significant genotype effect ($P<0.01$) on both maximum number of aboveground *Striga* plants per host plant ($NS_{max}$) and number of generative *Striga* plants per host plant ($NS_{gen}$) (Table 3). Within years and infestation levels, genotype rankings on $NS_{max}$ corresponded to rankings on $NS_{gen}$. Furthermore, rankings based on $NS_{max}$ and $NS_{gen}$ were relatively stable over years and infestation levels, except for CMDT39. Throughout the years, the highest maximum number of *Striga* plants, as well as the highest number of generative plants was recorded on genotypes CK60-B, E36-1, Seredo and Serena (mostly ranked as 10, 9, 8 and 7). Genotype N13, always ranked as 1 (often significantly) and SRN39 and IS9830 had very low numbers as well while Framida and Tiémarifing held intermediate positions. In 2003, no major differences in genotype rankings based on $NS_{max}$ were found between the low and high infestation level.

Table 3. Means and rankings (numbers 1-10) of maximum number of aboveground *Striga* plants ($NS_{max}$) and number of generative *Striga* plants ($NS_{gen}$) per genotype, year (2001 - 2003) and infestation level (2003L:low and 2003H:high); all parameters are expressed per host plant (equivalent to 0.32 $m^{-2}$).

| | 2001 | | | | | | 2002 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $NS_{max}$ | | | $NS_{gen}$ | | | $NS_{max}$ | | | $NS_{gen}$ | | |
| CK60B | 2.4 | ba | 9 | 0.4 | bc | 6 | 103.1 | a | 10 | 35.3 | ab | 9 |
| CMDT39 | 0.6 | cd | 2 | 0.2 | bc | 2 | 92.6 | a | 8 | 10.5 | de | 2 |
| E36-1 | 7.9 | a | 10 | 1.8 | a | 10 | 99.9 | a | 9 | 20.0 | cd | 7 |
| Framida | 1.3 | bc | 6 | 0.3 | bc | 5 | 54.0 | c | 4 | 16.4 | cd | 5 |
| IS9830 | 0.9 | bcd | 4 | 0.4 | bc | 7 | 29.3 | d | 2 | 11.3 | de | 3 |
| N13 | 0.1 | d | 1 | 0.0 | c[c] | 1 | 9.3 | e | 1 | 5.7 | e | 1 |
| Seredo | 2.2 | b | 8 | 0.5 | bc | 8 | 81.8 | ab | 7 | 22.5 | bc | 8 |
| Serena | 1.7 | bc | 7 | 0.6 | b | 9 | 80.9 | ab | 6 | 42.3 | a | 10 |
| SRN39 | 0.7 | cd | 3 | 0.3 | bc | 3 | 33.6 | d | 3 | 14.8 | cd | 4 |
| Tiémarifing | 1.2 | bc | 5 | 0.3 | bc | 4 | 67.9 | bc | 5 | 17.6 | cd | 6 |
| S.E.D.[b] (df) | 0.26 | (49) | | 0.15 | (49) | | 0.61 | (79) | | 0.65 | (79) | |

| | 2003L | | | | | | 2003H | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $NS_{max}$ | | | $NS_{gen}$ | | | $NS_{max}$ | | | $NS_{gen}$ | | |
| CK60B | 20.9 | a | 10 | 12.5 | a | 10 | 64.8 | a | 10 | 32.1 | a | 10 |
| CMDT39 | 7.1 | bc | 6 | 4.7 | b | 8 | 30.0 | cd | 5 | 14.9 | bcd | 5 |
| E36-1 | 17.1 | a | 9 | 9.6 | a | 9 | 48.9 | ab | 9 | 19.7 | b | 9 |
| Framida | 5.7 | bc | 5 | 2.3 | b | 4 | 37.3 | bcd | 6 | 18.4 | bc | 7 |
| IS9830 | 3.3 | cd | 2 | 2.0 | bc | 2 | 16.6 | e | 3 | 10.3 | de | 3 |
| N13 | 0.8 | d | 1 | 0.2 | c | 1 | 4.2 | f | 1 | 2.6 | f | 1 |
| Seredo | 8.1 | b | 8 | 4.5 | b | 7 | 43.1 | bc | 8 | 19.5 | b | 8 |
| Serena | 7.9 | bc | 7 | 3.6 | b | 6 | 38.7 | bcd | 7 | 15.1 | bcd | 6 |
| SRN39 | 3.4 | cd | 3 | 2.2 | b | 3 | 16.1 | e | 2 | 7.3 | e | 2 |
| Tiémarifing | 5.0 | bc | 4 | 3.2 | b | 5 | 25.6 | de | 4 | 11.9 | cde | 4 |
| S.E.D.[b] (df) | 0.48 | (79) | | 0.38 | (79) | | 0.64 | (79) | | 0.43 | (79) | |

[a] Values in the same column followed by a different letter are significantly different from one another at the 0.01 level

[b] ANOVA was based on square root $(X+0.5)^{1/2}$ transformations, S.E.D. -values of transformed data are given

[c] Value $NS_{gen}$ N13 in 2001 = 0.04

### *Striga biomass*

Sorghum genotype had a significant effect ($P<0.05$) on total aboveground *Striga* dry weight at harvest ($DW_{tot}$) in 2001, 2002, 2003L and 2003H as well as on flowerstalk dry weight ($DW_{stalks}$) in 2001, 2003L and 2003H (Table 4). In 2003, there were highly significant main effects of both genotype and infestation level (not shown) on $DW_{tot}$ and on $DW_{stalks}$ ($P<0.001$). There were significant (one-tailed) correlations between means of $DW_{tot}$ of different years ($P<0.05$; not shown), except between 2001 and 2002, the years with the lowest and highest infection level. The good correlations were also reflected in rather consistent genotype rankings for $DW_{tot}$ over years. Throughout the years and infestation levels, relative high values of $DW_{tot}$ were recorded on CK60-B (ranked 9-10), CMDT39 (except in 2001), E36-1 (except in 2002), Tiémarifing and Seredo whereas, relative low values of $DW_{tot}$ were recorded on N13 (ranked 1), SRN39 and IS9830.

Genotype rankings based on $DW_{tot}$ and $DW_{stalks}$ were largely similar. There were significant (one-tailed) correlations between means of $DW_{stalks}$ of different years ($P<0.05$; not shown), except between 2001 and 2002. Consequently, genotype ranking based on $DW_{stalks}$ of 2002, 2003L and 2003H corresponded largely with one another. Throughout the years, consistently high $DW_{stalks}$ were recorded on CMDT39 and CK60-B. *Striga* on N13 produced the lowest flowerstalk dry weight throughout the years. On other resistant genotypes, SRN39 and IS9830, *Striga* also produced relatively low flowerstalk biomass, except in 2001 (IS9830 and SRN39) and 2002 (SRN39).

Remarkable were the relatively low *Striga* dry weights in 2002. Both $DW_{tot}$ and $DW_{stalks}$ in 2002 were much lower than in plots of 2003H, whereas the maximum numbers of aboveground *Striga* plants ($NS_{max}$) in 2002 were higher than in 2003H. Again, this might be due to the difference in observation methods between both years.

### *Striga numbers and reproduction*

Correlations between *Striga* number ($NS_{max}$ and $NS_{gen}$) and *Striga* reproduction parameters ($DW_{stalks}$ and $NR_{caps}$) were highly significant ($P<0.01$) in all years and at all infestation levels (Table 5). Figures 2A-D show observed variation in $NS_{max}$ and $DW_{stalks}$ among genotypes for different years and infestation levels. Identical infection levels resulted often in strongly different $DW_{stalks}$, whereas there were also cases where different infection levels resulted in comparable $DW_{stalks}$. This shows that $DW_{stalks}$ is not only a result of $NS_{max}$ and, consequently, that there are genotype effects on reproduction other than resistance alone. Dotted lines in these figures indicate the minimum and maximum flowerstalk production per emerged *Striga* plant.

Table 4. Means and ranking (numbers 1-10) of total aboveground *Striga* dry weight at harvest ($DW_{tot}$: g) and dry weight of generative *Striga* parts at harvest ($DW_{stalks}$: g) per genotype, year (2001 - 2003) and infestation level (2003L:low and 2003H:high); all parameters are expressed per host plant (equivalent to 0.32 m$^{-2}$).

| | 2001 | | | | | | 2002 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $DW_{tot}$ | | | $DW_{stalks}$ | | | $DW_{tot}$ | | | $DW_{stalks}$ | | |
| CK60-B | 2.1 | a[a] | 9 | 0.7 | a | 10 | 40.3 | a | 10 | 10.7 | | 10 |
| CMDT39 | 0.2 | b | 2 | 0.1 | c | 2 | 38.7 | ab | 9 | 10.0 | | 9 |
| E36-1 | 2.9 | a | 10 | 0.5 | ab | 9 | 23.1 | cd | 5 | 5.3 | | 5 |
| Framida | 0.4 | b | 5 | 0.1 | c | 3 | 16.0 | cde | 3 | 4.2 | | 1 |
| IS9830 | 0.4 | b | 4 | 0.2 | bc | 6 | 14.6 | de | 2 | 4.2 | | 2 |
| N13 | 0.2 | b | 1 | 0.0 | c[c] | 1 | 11.8 | e | 1 | 4.9 | | 4 |
| Seredo | 0.7 | b | 7 | 0.1 | c | 4 | 23.5 | bcd | 6 | 4.9 | | 3 |
| Serena | 0.7 | b | 6 | 0.2 | bc | 8 | 26.2 | abcd | 7 | 6.7 | | 7 |
| SRN39 | 0.4 | b | 3 | 0.2 | bc | 5 | 17.0 | cde | 4 | 5.7 | | 6 |
| Tiémarifing | 0.7 | b | 8 | 0.2 | bc | 7 | 27.3 | abc | 8 | 7.3 | | 8 |
| S.E.D.[b] (df) | 0.176 | (49) | | 0.098 | (49) | | 0.642 | (79) | | ns[d] | | |

| | 2003L | | | | | | 2003H | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $DW_{tot}$ | | | $DW_{stalks}$ | | | $DW_{tot}$ | | | $DW_{stalks}$ | | |
| CK60-B | 57.7 | a | 10 | 20.8 | a | 10 | 98.9 | a | 10 | 30.9 | a | 10 |
| CMDT39 | 24.2 | bc | 8 | 9.4 | b | 9 | 61.1 | b | 8 | 18.9 | b | 8 |
| E36-1 | 28.7 | b | 9 | 8.7 | b | 8 | 58.9 | b | 7 | 16.3 | bc | 5 |
| Framida | 6.8 | de | 2 | 2.4 | cd | 2 | 51.9 | bc | 5 | 16.4 | bc | 6 |
| IS9830 | 7.7 | d | 3 | 3.3 | c | 4 | 42.5 | bc | 3 | 14.6 | bcd | 4 |
| N13 | 0.7 | e | 1 | 0.4 | d | 1 | 20.2 | d | 1 | 7.8 | d | 1 |
| Seredo | 15.1 | bcd | 7 | 5.3 | bc | 6 | 66.6 | b | 9 | 19.7 | b | 9 |
| Serena | 10.7 | cd | 5 | 3.7 | c | 5 | 49.6 | bc | 4 | 13.0 | bcd | 3 |
| SRN39 | 7.9 | d | 4 | 3.1 | cd | 3 | 30.6 | cd | 2 | 9.0 | cd | 2 |
| Tiémarifing | 14.0 | bcd | 6 | 5.6 | bc | 7 | 55.2 | bc | 6 | 17.4 | b | 7 |
| S.E.D.[b] (df) | 0.861 | (79) | | 0.485 | (79) | | 0.997 | (79) | | 0.552 | (79) | |

[a] Values in the same column followed by a different letter are significantly different from one another at the 0.05 level

[b] ANOVA was based on square root transformations ($X$+0.5)$^{1/2}$, S.E.D. values of transformed data are given

[c] Value of N13 2001 $DW_{stalks}$ = 0.004

[d] ns means not significant

Table 5. Pearson correlations between maximum aboveground *Striga* numbers ($NS_{max}$) and number of generative *Striga* plants and harvest ($NS_{gen}$), *Striga* flowerstalk dry weight at harvest ($DW_{stalks}$), and capsule number per host plant ($NR_{caps}$) at harvest, per year (2001 - 2003) and infestation level (2003L:low and 2003H:high); all parameters are expressed per host plant.

| | | 2001 | 2002 | 2003L | 2003H |
|---|---|---|---|---|---|
| $NS_{max}$ | $DW_{stalks}$ | 0.64 | 0.38 | 0.80 | 0.58 |
| | $NR_{caps}$ | | | 0.79 | 0.56 |
| $NS_{gen}$ | $DW_{stalks}$ | 0.69 | 0.49 | 0.90 | 0.78 |
| | $NR_{caps}$ | | | 0.89 | 0.74 |

[a] All data were square root-transformed $(X+0.5)^{1/2}$

[b] all (one-tailed) correlations are significant ($P<0.01$)

From these figures it appears that particularly on E36-1 and Seredo flowerstalk dry weight per emerged *Striga* plant was often low. For N13, the results depended a lot on infestation level. At low infestation levels (2001 and 2003L), flowerstalk production was negligible, whereas at high *Striga* infestation levels (2002 and 2003H) the relatively low total flowerstalk production resulted from few emerged *Striga* plants with a very high flowerstalk production per emerged *Striga* plant.

Figures 3A-D show the relations between maximum aboveground *Striga* numbers ($NS_{max}$) and reproductive potential of *Striga* plants for ten genotypes at two infestation levels, as observed in 2003. A five times higher infestation level of 2003H compared to 2003L resulted in a proportional increase in $NS_{max}$ for almost all genotypes, except the least resistant ones (E36-1 and CK60-B). This increase in number of emerged *Striga* plants was accompanied with a disproportional increase in $DW_{stalks}$ (Figure 3A), with the most resistant genotype (N13) as a clear exception.

Figure 3B shows the relation between flowerstalk dry weight per aboveground *Striga* plant ($DW_{stalks}$ per $NS_{max}$) and maximum aboveground numbers ($NS_{max}$). This figure shows negative slopes for most genotypes, confirming that at higher infection levels the reproductive effort per *Striga* plant is diminishing. For some of the least resistant genotypes (E36-1, Seredo and Serena) the differences in *Striga* flowerstalk dry weight per plant between the low and the high infestation levels were relatively small, whereas for some of the more resistant genotypes these differences were relatively large (SRN39, Tiémarifing and CMDT39). For the most resistant genotype (N13) flowerstalk production per *Striga* plant increased with infestation level. Furthermore, from these observations it appears that at a low infestation level genotypes primarily differed in flowerstalk dry weight (reproductive potential) of individual *Striga* plants rather than in the number of *Striga* plants they support.

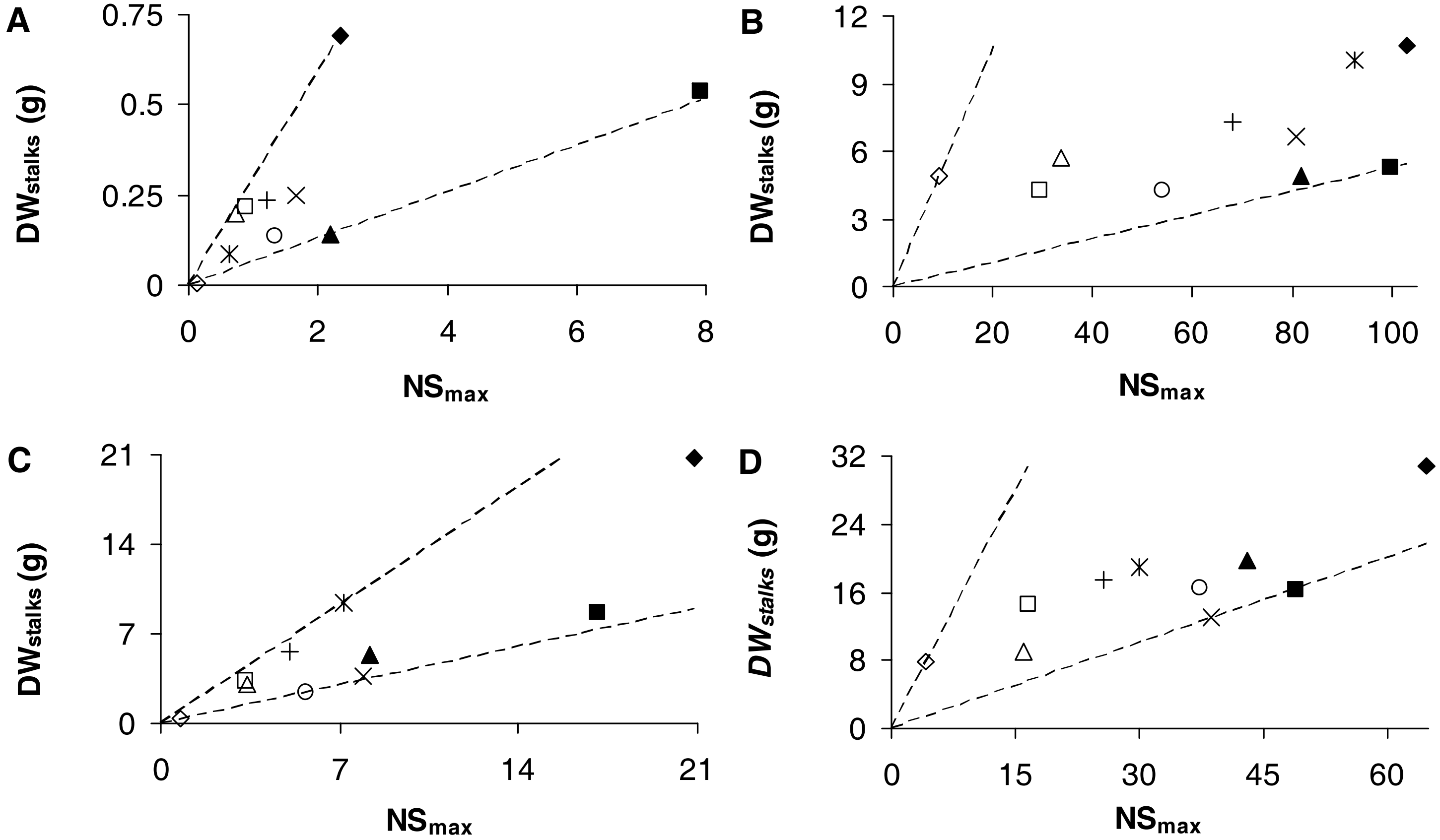

Figure 2. *Striga* flowerstalk dry weight ($DW_{stalks}$ g) as a function of maximum number of aboveground *Striga* plants ($NS_{max}$) for different years and infestation levels: 2001 (A), 2002 (B) 2003 low infestation (C) and 2003 high infestation (D); for 10 different sorghum genotypes: CK60-B (closed diamonds), CMDT39 (asterixes), E36-1 (closed squares), Framida (open circles), IS9830 (open squares), N-13 (open diamonds), Seredo (closed triangles), Serena (crosses), SRN39 (open triangles) and Tiémarifing (plus signs); dotted lines indicate the variation; all parameters are expressed per host plant (equivalent to 0.32 $m^{-2}$).

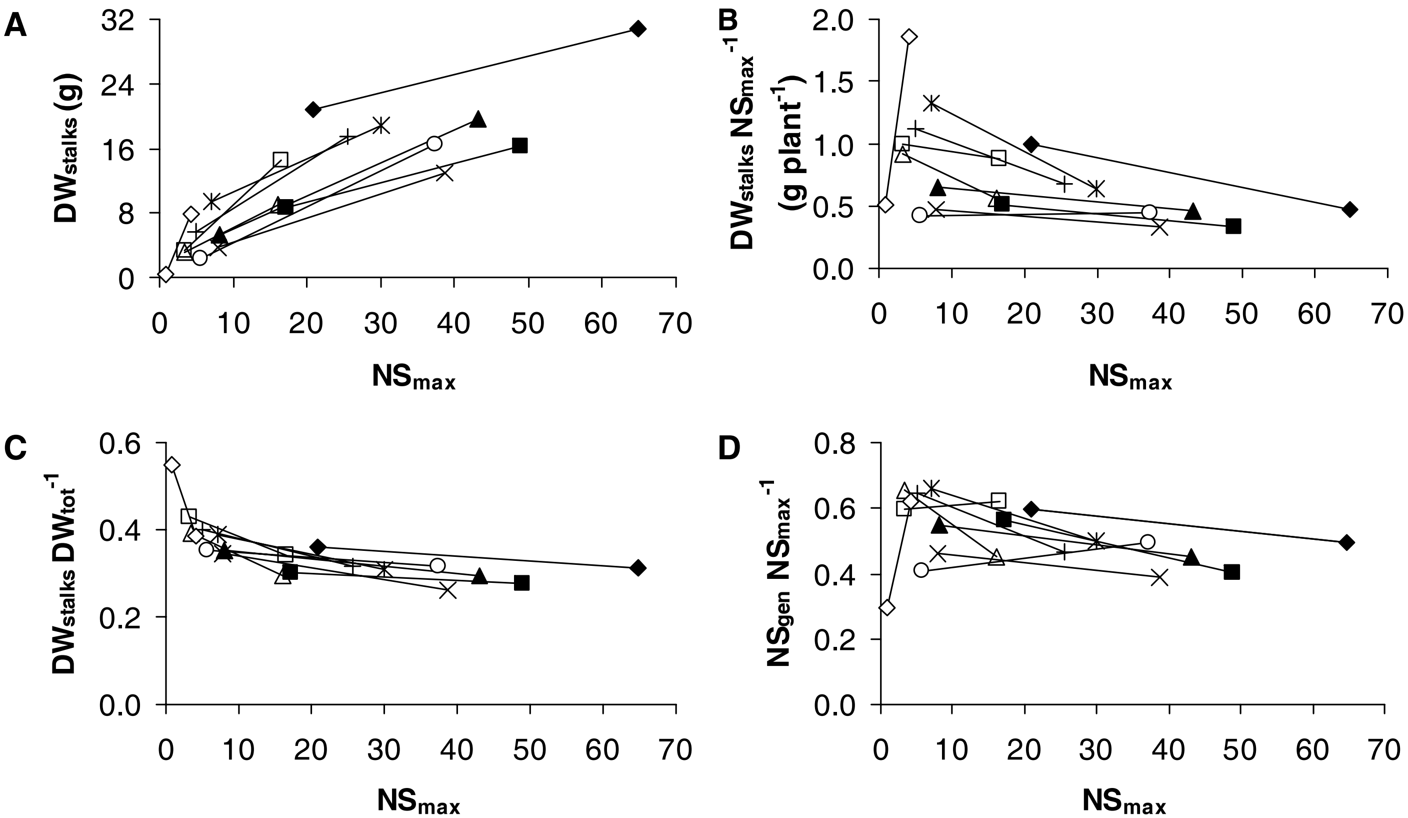

Figure 3. Flowerstalk dry weight ($DW_{stalks}$ g: A), flowerstalk dry weight per aboveground *Striga* plant ($DW_{stalks}$ $NS_{max}{}^{-1}$ g plant$^{-1}$: B), flowerstalk dry weight per total *Striga* dry weight ($DW_{stalks}$ $DW_{tot}{}^{-1}$ : C) and fractions of generative plants of total aboveground *Striga* number ($NS_{gen}$ $NS_{max}{}^{-1}$: D) as a function of number of aboveground *Striga* plants ($NS_{max}$) as observed in 2003 at two infestation levels and at 10 sorghum genotypes: CK60-B (closed diamonds), CMDT39 (asterixes), E36-1 (closed squares), Framida (open circles), IS9830 (open squares), N-13 (open diamonds), Seredo (closed triangles), Serena (crosses), SRN39 (open triangles) and Tiémarifing (plus signs); all parameters are expressed per host plant (equivalent to 0.32 m$^{-2}$).

The more resistant genotypes facilitated heavier flowerstalks per *Striga* plant than the more susceptible ones. At high infestation levels, differences in $NS_{max}$ between genotypes were more pronounced than differences in flowerstalk dry weight per *Striga* plant.

Figure 3C shows the relation between aboveground *Striga* numbers and biomass partitioning to the generative parts (fraction $DW_{stalks}$ over $DW_{tot}$). This relation shows a non-linear decrease of biomass allocated to the flowerstalks with increasing number of emerged *Striga* plants. The relation is rather consistent, independent of genotype, indicating that the variation in allocation pattern can merely be attributed to differences in number of emerged plants. The fraction of *Striga* shoot biomass allocated to the flowerstalks ranged from 0.55 to 0.25.

Figure 3D shows the relation between the fraction generative *Striga* plants ($NS_{gen}$ over $NS_{max}$) and the aboveground *Striga* numbers ($NS_{max}$), per genotype and infestation level. For most of the genotypes, the generative fraction decreased with increasing infection levels. Exceptions were N13 and IS9830, the most resistant genotypes and Framida, an intermediate genotype. Among the other seven genotypes, the more resistant ones (SRN39, CMDT39 and Tiémarifing) showed a steeper negative slope between the low and the high infestation level than the more susceptible ones (CK60-B, E36-1, Seredo and Serena). The relation between the fraction of generative plants and the maximum number of aboveground *Striga* plants is comparable with the relation between flowerstalk dry weight per *Striga* plant and aboveground *Striga* numbers as shown in Figure 3B. A wide variation in fraction generative plants was observed among genotypes, particularly at low infection levels.

### *Striga dry weights and reproduction*

Figure 4 shows the relation between total aboveground *Striga* dry weight and number of capsules (4A) and between *Striga* flowerstalk dry weight and number of capsules (4B) as observed in 2003. Both total aboveground *Striga* dry weight and *Striga* flowerstalk dry weight correlate significantly with capsule number ($P<0.01$; $r= 0.90$ and 0.94 respectively). Both relations appear to be linear in the range of observed dry weights in this trial. According to the linear regression, one gram of flowerstalks corresponds to 18.6 capsules.

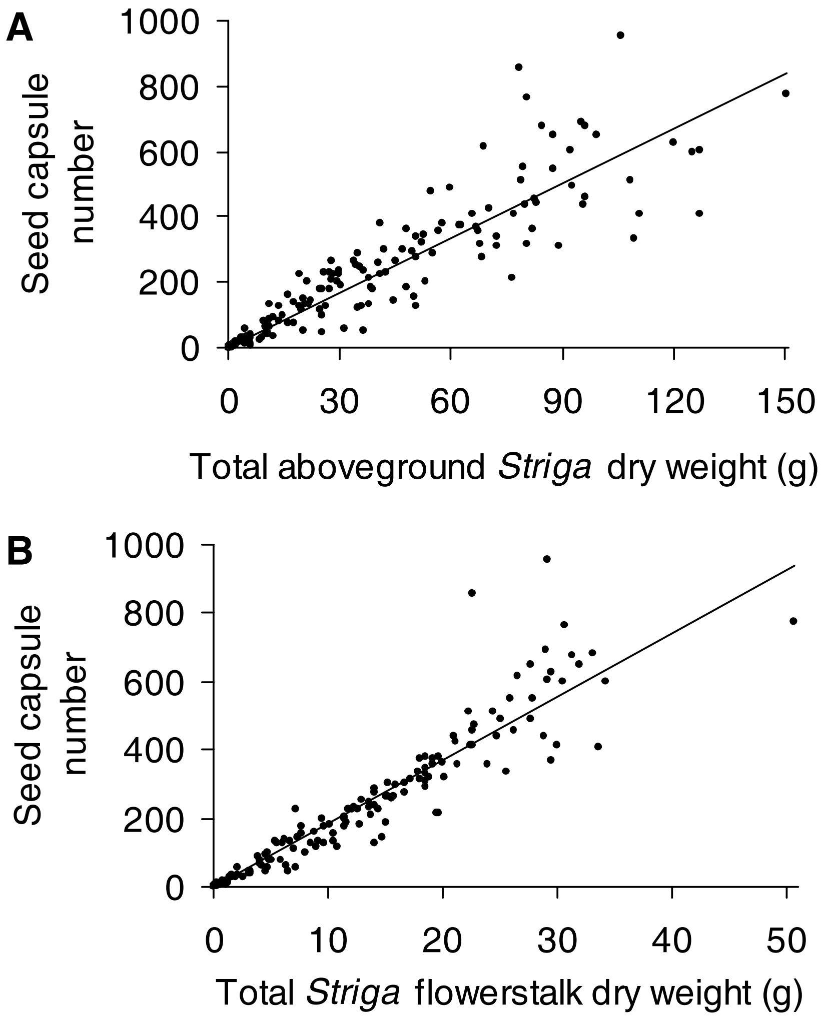

Figure 4. Relation between total aboveground *Striga* dry weight ($DW_{tot}$) and *Striga* seed capsule number (y=5.59 $DW_{tot}$; $R^2$=0.80; A) and flowerstalk dry weight ($DW_{stalks}$) and *Striga* seed capsule number (y=18.57 $DW_{stalks}$; $R^2$=0.88; B). Both observations were done in 2003 at crop harvest; all parameters are expressed per host plant (equivalent to 0.32 $m^{-2}$).

### *Capsule production*

Mean time span between crop harvest and the end of the *Striga* life-cycle was 28 days but depended on host genotype (range: 24 [E36-1] to 34 days [IS9830]; data not shown). Table 6 presents the results of the ANOVA of genotype, infestation level and sampling time effects on capsule production per host plant ($NR_{caps}$) in 2003. There were significant main effects of genotype, infestation level and sampling time on capsule production ($P$<0.01) and a significant infestation level × sampling time interaction ($P$=0.016).

Table 6. ANOVA of infestation level, sorghum genotype and sampling time effects on *Striga* seed capsule number per host plant in 2003

| | Source of variation | df | MSS | F | F-prob. (*P*) |
|---|---|---|---|---|---|
| Overall | | | | | |
| | Infestation level (*I*) | 1 | 3274.44 | 20.66 | 0.003 |
| | Genotype (*G*) | 9 | 610.80 | 15.09 | <0.001 |
| | *I* x *G* | 9 | 27.99 | 0.69 | 0.715 |
| | Time (*T*) | 1 | 208.25 | 16.62 | <0.001 |
| | *I* x *T* | 1 | 74.07 | 5.91 | 0.016 |
| | *G* x T | 9 | 11.73 | 0.94 | 0.496 |
| | *I* x *G* x *T* | 9 | 17.77 | 1.42 | 0.186 |
| Per infestation level | | | | | |
| High | Genotype | 9 | 257.12 | 6.39 | <0.001 |
| | Time | 1 | 16.96 | 1.76 | 0.189 |
| | *G* x *T* | 9 | 23.91 | 2.48 | 0.016 |
| Low | Genotype | 9 | 381.67 | 9.38 | <0.001 |
| | Time | 1 | 265.35 | 17.22 | <0.001 |
| | *G* x *T* | 9 | 5.59 | 0.36 | 0.949 |

At the high infestation level significantly more *Striga* seed capsules were produced than at the low level and at the end of the life-cycle significantly higher numbers of seed capsules were produced than at crop harvest. This last phenomenon was only significant at the low infestation level, as became evident from the ANOVA's that were separately conducted per infestation level. This last analysis also revealed a significant genotype × sampling time effect at the high infestation level.

Table 7 presents genotype effects on seed capsule number per infestation level and per sampling time separately. At all sampling times and infestation levels $NR_{caps}$ of *Striga* plants parasitizing N13 was significantly lower than on all other genotypes. Capsule production on CK60-B was significantly higher than on any other genotype, throughout sampling times and infestation levels. Apart from these differences there were significant differences between the high capsule production of *Striga* plants on CMDT39 and E36-1 and the low capsule production on Framida, IS9830 and SRN39 at the low infestation level.

Table 7. Means, ranks (1-10) and repeatabilities (*R*) of number of *Striga* seed capsules produced in 2003 ($NR_{caps}$) per host genotype and infestation level (Low, High) and time (crop harvest, end life-cycle); capsule number is expressed per host plant (equivalent to 0.32 $\mathrm{m}^{-2}$).

| | Low | | | | | | | High | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | harvest | | end | | mean | | | harvest | | | end | | | mean | | |
| CK60-B | 383.3 | 10 | 523.0 | 10 | 450.6 | a[a] | 10 | 624.0 | a[b] | 10 | 637.1 | a | 10 | 630.5 | a | 10 |
| CMDT39 | 151.3 | 8 | 235.4 | 9 | 191.0 | b | 9 | 332.2 | bc | 7 | 347.3 | bc | 8 | 339.5 | bc | 7 |
| E36-1 | 156.5 | 9 | 201.7 | 8 | 178.3 | bc | 8 | 329.3 | bc | 6 | 288.5 | bc | 4 | 308.6 | bc | 6 |
| Framida | 36.5 | 2 | 99.1 | 4 | 64.0 | d | 3 | 272.1 | bc | 5 | 297.8 | bc | 5 | 284.8 | bc | 5 |
| IS9830 | 39.6 | 3 | 105.4 | 5 | 68.6 | d | 4 | 256.5 | bc | 4 | 224.8 | bcd | 2 | 240.4 | bc | 4 |
| N13 | 2.8 | 1 | 16.1 | 1 | 8.2 | e | 1 | 111.4 | de | 2 | 77.8 | e | 1 | 93.8 | d | 1 |
| Seredo | 92.6 | 6 | 97.5 | 3 | 95.1 | bcd | 6 | 364.7 | b | 9 | 372.8 | b | 9 | 368.9 | b | 9 |
| Serena | 60.5 | 5 | 115.9 | 6 | 86.0 | cd | 5 | 194.7 | cd | 3 | 245.7 | bc | 3 | 219.4 | bc | 3 |
| SRN39 | 46.1 | 4 | 66.4 | 2 | 55.8 | d | 2 | 110.6 | de | 1 | 306.8 | bc | 6 | 196.3 | cd | 2 |
| Tiémarifing | 101.9 | 7 | 172.9 | 7 | 135.0 | bcd | 7 | 344.0 | bc | 8 | 345.8 | bc | 7 | 345.1 | b | 8 |
| S.E.D. (df) | ns[d] | | | | 2.26 | (159) | | 2.5 | (159) | | | | | 2.24 | (159) | |
| mean | 86.2a[c] | | 141.0b | | | | | 277.0 | | | 299.5 | | | | | |
| *R* | 0.48 | | 0.38 | | | | | 0.34 | | | 0.39 | | | | | |

[a] Values in the same column followed by a different letter are significantly different at the 0.01 probability level. Means in table are back-transformed from $(X+0.5)^{1/2}$ transformations, S.E.D. values of transformed data are given

[b] Values of the high infestation level (harvest and end) followed by a different letter are significantly different at the 0.05 probability level

[c] Values in the same row followed by a different letter are significantly different at the 0.001 level of probability

[d] ns means not significant (genotype × time effect)

At the high infestation level, there were significant differences between the high *Striga* reproduction on Seredo and Tiémarifing and the low reproduction at SRN39. Genotype ranking at the low infestation level differed from the ranking at the high infestation level, except for four genotypes. At the low infestation level the highest capsule production was reached on CK60-B, CMDT39 and E36-1, whereas at the high infestation level this group consisted of CK60-B, Seredo and Tiémarifing. At the other extreme, the lowest *Striga* capsule production was found on N13, SRN39 and Framida in the low infested plots and on N13, SRN39 and Serena in the high infested plots.

The differences in mean capsule numbers between the two infestation levels decreased between crop harvest and the end of the life-cycle. For the lower infestation level, $NR_{caps}$ at harvest time was around 61% of the final capsule production (the capsule production till the end of the life-cycle), whereas at the higher infestation level, already around 92% of the final capsule number was produced at crop harvest. Repeatabilities ($R$) of $NR_{caps}$ were lower than 0.5 in all cases, implying that more than half of the phenotypic variation observed should be attributed to environmental and error sources rather than genetic variation.

There was no significant effect of sorghum genotype ($P$=0.592), or infestation level ($P$=0.324) on seed weight per capsule (data not shown). The grand mean of seed weight per capsule was 2.41 $10^{-3}$ g (S.E. = 0.053 $10^{-3}$). As mean individual *Striga* seed weight was determined to be 4.5 $10^{-6}$ g, one capsule contained on average 536 seeds.

## Discussion

### *Methodology for estimating Striga reproduction*

In the field, *Striga* seeds are formed and disseminated over a period of several weeks. Quantification of the total seed production of a single *Striga* plant or a population of plants at a single point in time is therefore less accurate. In 2001 and 2002, reproductive success was estimated based on $DW_{stalks}$ measured at sorghum harvest. As a result, plants that had decomposed (due to early death) before that time were not included and for that reason this estimate most likely represents an underestimate of the actual reproductive success. This also explains the relatively low flowerstalk dry weight per emerged *Striga* plant in these years, ranging from 0.04 to 0.53 g. In 2003, when the procedure was extended and dead generative *Striga* plants were collected weekly, this ratio ranged from 0.33 to 1.85 g per emerged plant. Analysis on these ratios between flowerstalk dry weights derived exclusively from plants at harvest (in 2003) resulted in fractions ranging from 0.07 to 0.57 g per emerged plant. These ratios are very much in line with those found in 2001 and 2002. The same explanation could be given for the observed lower ratios of $NS_{gen}$ to $NS_{max}$ 2001 and 2002 (0.29 and 0.35, respectively) compared to 2003 (low [L]: 0.54; high [H]: 0.49).

In 2003, not only the dry weight of the flowerstalks was determined, but also the number of seed capsules was counted. Capsule numbers were earlier used as estimate for seed production by Weber et al. (1995) and Webb and Smith (1996). In 2003, ten mature capsules from 5 different *Striga* plants were sampled in each sub-plot. No infestation density or host plant genotype effect on seed weight per capsule was found, indicating that capsule number is a reliable estimate for seed production. Counting of capsules is however a time consuming and therefore expensive method. This study showed that a very high correlation exist between *Striga* seed capsule number and total aboveground *Striga* dry weight or, even more accurate, flowerstalk dry weight (Figure 4). This confirms the broad applicability of relations between seed production and plant biomass as found by Samson and Werk (1986) and Thompson et al. (1991). The linearity of this relation and its independency from genotype makes total aboveground or flowerstalk dry weight a reliable measure for *Striga* seed production.

A major constraint for the identification of genotypes that facilitate less *Striga* reproduction seems to be the high contribution of the environmental variance component to the phenotypic variation. The repeatability of capsule number was found to be low ($R$=0.34 to 0.48). *Striga* reproduction is an indirect genotypic trait, as it can only be measured at the *Striga* plants parasitizing the specific genotype. Therefore the phenotypic expression of the trait is subject to various factors. Deviations in rankings between years are most probably not due to differences in infestation level between the different years as in 2003 no significant genotype × infestation level interaction was found for either capsule production or flowerstalk dry weight. These deviations must therefore be caused by other environmental factors. Although the general genotype categorization in the various experiments was not affected, multiple location and multiple year testing for screening of genotypes that support low *Striga* reproduction is recommended.

### *Host plant genotype effects on Striga seed production*

The results clearly show a strong significant effect of host plant genotype on *Striga* number, biomass and flowerstalk dry weight. Rankings for the various characteristics within an experiment were largely identical, with N13 as the variety with the lowest number and weight of *Striga* plants and CK60-B with the highest plant number and weight. Resistance thus proved to be important in reducing *Striga* reproduction. Several authors (Doggett, 1988; Hess and Haussmann, 1999; Ejeta et al., 2000) already suggested an effect of host plant resistance on *Striga* reproduction. Both capsule number in 2003 and flowerstalks dry weight in 2001 and 2003 were significantly affected by genotype. Absence of this effect in 2002 ($P$=0.086) may be due to the overall high infection levels, levelling out differences between genotypes due to density effects. Total aboveground dry weight, also a good indicator for capsule production, was significantly affected by genotype in all years and at all infestation levels.

Variability in the number of aboveground *Striga* plants (both maximum and generative numbers) is the main reason for differences in *Striga* reproduction between host plant genotypes. This is shown by the highly significant correlations between $NS_{max}$ (and $NS_{gen}$) and $DW_{stalks}$ in all years as well as between $NS_{max}$ (and $NS_{gen}$) and $NR_{caps}$ in 2003. These observations confirm suggestions from Carsky et al. (1996), Kling et al. (2000) and Haussmann et al. (2001b). The majority of the genotypes supporting low *Striga* reproduction in this study (e.g. IS9830, SRN39 and N13) also showed low infection levels. These genotypes were classified as resistant in earlier studies (Maiti et al., 1984; Vasudeva Rao, 1984; Ramaiah, 1984, 1987b; Olivier et al., 1991; Ejeta et al., 2000; Heller and Wegmann, 2000; Omanya et al., 2004; Rodenburg et al., 2005). Additionally, genotypes with very high *Striga* numbers (CK60-B and E36-1) supported high *Striga* reproduction. High *Striga* numbers result in high aboveground *Striga* biomass and consequently high capsule production.

Comparison between genotypes shows that similar infection levels do not necessarily result in equal reproduction, whereas equal reproduction may be obtained as a result of different infection levels (Figures 2A-D and Figure 3A). Hence resistance is not the only genotypic factor determining *Striga* reproduction. From the results of this study it appeared that the differences in *Striga* reproduction between genotypes were also related to single *Striga* plant dry weight (data not shown), the fraction of aboveground plants that reached the generative stage and flowerstalk dry weight per emerged *Striga* plant. These last two parameters showed largely identical trends, indicating that one of the main reasons for a low *Striga* flowerstalk production per emerged plant was the fact that fewer plants reached the reproductive phase. The aforementioned traits seem not to be linked to resistance, as they all showed variation among genotypes that could not be explained by differences in infection level. Genotypes with low flowerstalk dry weight per emerged *Striga* plant or a low fraction generative plants were found among the susceptible genotypes (E36-1, Serena and Seredo), but also among those classified as moderately resistant (Framida and CMDT39).

Time, particularly first emergence time of *Striga* relative to the crop, has been suggested to have a major effect on *Striga* reproduction ( Weber et al., 1995; Kim and Adetimirin, 1997a), as it determines the total time for development and seed setting.

Emergence date depended on seed bank density, as shown by the significant later emergence in 2003L compared to 2003H, as well as on genotype, as shown in the experiments of 2002 and 2003L. Genotype dependency of emergence date was previously reported by (Doggett, 1988; Olivier et al., 1991a; Webb and Smith, 1996; Adetimirin et al., 2000c; Ast et al., 2000; Haussmann et al., 2001b). In general, late emergence was observed on genotypes with a high level of resistance (e.g. SRN39, IS9830, N13 and Framida). The significant negative correlations between emergence date and aboveground *Striga* numbers ($r = -0.25$ with $P<0.05$ in 2001; -0.27, -0.51 and -0.24 in 2002, 2003L and 2003H respectively, with $P<0.01$) confirm the entanglement between *Striga* development and resistance that was earlier found by Ast et al (2000).

Despite the significant negative correlations between emergence or flowering dates and flowerstalk dry weights in 2002 and 2003 ($r$ = -0.42 [$P<0.01$], -0.47 [$P<0.001$] and –0.34 [$P<0.01$] for $E_{date}$-$DW_{stalks}$ and –0.33 [$P<0.05$], -0.67 [$P<0.001$] and –0.29 [$P<0.01$] for $F_{date}$-$DW_{stalks}$, for 2002, 2003L and 2003H respectively) the variation in emergence and flowering time among genotypes could not always explain observed variation in *Striga* reproduction. In 2003, among the genotypes supporting low *Striga* reproduction only Serena and N13 showed a significantly delayed *Striga* development compared to genotypes supporting high *Striga* reproduction such as CK60-B and E36-1. In 2002, *Striga* flowering of N13 was not significantly later than on CK60-B, while *Striga* flowerstalk dry weight of N13 was still much lower than that of CK60-B. In 2003H, Seredo supported rather high seed production while *Striga* flowered relatively late whereas *Striga* on SRN39 combined low reproduction with early development dates. As there are many inconsistencies in genotype rankings based on development dates throughout the years it may be concluded that differences in development rate of *Striga* on different host plants may be only one, among several factors, determining *Striga* reproduction.

### *Density effects on seed production*

The experiment in 2003, conducted with two *Striga* infestation levels, revealed clear evidence of the existence of a density dependent relation between *Striga* number and *Striga* reproduction. A five times higher infestation level in the high density plots, resulted for most of the genotypes in a five times higher number of emerged *Striga* plants. At the same time, this increase in number of emerged *Striga* plants only resulted in a 2.5 to 3.5 times increase in flowerstalk dry weight and capsule number. It was observed that at the highest infestation level average *Striga* plant dry weight remained smaller, indicating the presence of intra-specific competition. On top of that, a smaller fraction of dry matter was allocated to the reproductive organs. This last aspect can partly be attributed to the smaller fraction of generative plants at the highest infestation level. In this study, density dependence thus mainly resulted from intra-specific competition of emerged *Striga* plants. Density dependence was previously reported by Smith and Webb (1996), but they observed this phenomenon between seed bank density and *Striga* emergence. This type of density dependence was only observed with the most susceptible genotypes CK60-B and E36-1, for which only a three-fold increase in number of emerged *Striga* plants was observed between 2003L and 2003H. It can thus be concluded that density dependence is able to manifest itself in more than one stage. Secondly, the expression of density dependence showed to be genotype specific, with the more susceptible genotypes showing this phenomenon in an earlier development stage of the parasite.

In many of the observed density dependency relations, N13 formed an exception on the rule. Instead of the generally observed decrease, this genotype showed an increase of *Striga* plant weights, generative fractions and flowerstalk dry weights per plant, with increasing aboveground *Striga* numbers. This may be caused by the extremely low numbers and the entanglement of these low numbers with time of emergence and generative development (e.g. mean first emergence at N13: 50.3 DAS compared to overall mean 41.7 DAS and mean first flowering at N13: 96.7 DAS compared to overall mean of 89.8 DAS). Consequently, the relation between individual *Striga* plant dry weight and infestation level is not a continuously descending curve; rather it is an optimum curve. At below optimum infestation levels few *Striga* plants emerge and these plants emerge relatively late and are not able to make up for the lost number of growing days. At infestation levels above the optimum, too many individuals emerge and in that situation intra-specific competition causes individual *Striga* plant dry weight to remain below the maximum.

### *Striga seed production after crop harvest*

*Striga* seed production continued beyond crop harvest. The magnitude of the additional seed production after harvest depended on seed bank density. Continued *Striga* reproduction beyond harvest contributed significantly (39%) to the final reproduction under low infestation, whereas under high infestation the final capsule production was already almost reached at harvest (only 8% was produced after harvest). As a result, differences in capsule production between low and high-infested plots decreased between harvest and the end of the *Striga* life-cycle. The difference in *Striga* development between low and high infestation levels is likely to be one of the major reasons for the differences in seed production pattern. In the low infestation plots, first emergence of the parasite and first flowering were on average delayed with 9.5 days. The additional time after crop harvest offers the opportunity for late emerged *Striga* plants to complete their life cycle and this is particularly relevant for the low infestation plots. Hence manifestation of the density effects on *Striga* reproduction increases with time, reducing the initial differences between infestation levels.

### *Host plant genotype effects on Striga seed bank*

In this study, estimated *Striga* seed number per generative plant averaged per genotype and infestation level ranged between 6,700 and 26,500. Maximum estimated seed number per generative plant found in a single observation plot was 72,000. These estimates are higher than those of Webb and Smith (1996) who estimated a range of 5,000 to 11,000, but within the range of Stewart (1990) who recorded up to 85,000 seeds per plant.

Increases in soil seed banks of 270% (Murdoch and Kunjo, 2003) and 340% (Delft et al., 1997) through newly produced *Striga* seeds within one cropping season have been reported. In this study the average (averaged over genotypes) estimated seed production per $m^2$ was 334 % (2003H) to 785 % (2003L) of the seed bank density at the onset of the experiments. Adetimirin et al. (2000c) and Haussmann et al. (2000b), suggested that reduction of the *Striga* seed bank of infested soils can be accomplished through the use of *Striga* resistant cultivars, as these lower the seed input through a reduced seed production rate. From this study, it appeared that resistant genotypes, those supporting fewer attachments or aboveground *Striga* infections, indeed affect *Striga* reproduction negatively. However, after multiplication of the capsule production per host plant with the estimated mean number of seeds per capsule (536 seeds $capsule^{-1}$) and the sorghum plant density (3.125 plants $m^{-2}$ in 2003), it appeared that for an initial seed bank of 30,000 seeds $m^{-2}$ (as in 2003L) a production of 18 capsules per host plant would be sufficient to completely replace the original seed bank. For an initial seed-bank of 150,000 seeds $m^{-2}$ (as in 2003H) a production of 90 capsules per host plant would be enough. In fact these values represent an upper limit to the required capsule production per host plant. Only in the situation of a complete depletion of the soil seed bank during the cropping season, these reproduction rates are required to just balance the seed bank. Rather than a complete depletion, Delft et al (1997) observed depletion rates of 50-70% depending on soil depth, whereas Murdoch and Kunjo (2003) found depletions rates of 46%. Based on the most conservative depletion rate (46%) , a host plant genotype in the 2003L plots of this study should not support *Striga* to produce more than eight (46% of 18) capsules and in the 2003H plot not more than 41 (46 % of 90) capsules to just balance the seed bank. This confirms earlier statements by Delft et al. (1997) that only a few *Striga* plants per $m^2$ would be enough to balance or increase the seed bank. Out of the ten genotypes used in this study, only the capsule production rate of N13 in the low infestation plots at harvest did not surpass the estimated upper limit. From these results and calculations it is concluded that only the use of extremely resistant varieties on fields that still have a very low seed bank density may prevent an increase of the seed bank density over time. At the same time, the results indicate that even with N13 not removing the *Striga* plants at crop harvest time would already be sufficient to initiate a further increase in *Striga* density. The calculations thus show that *Striga* problems easily increase and just the use of resistant genotypes is not enough to reduce the seed bank once the initial seed bank already surpassed a certain level.

# CHAPTER 6

# General discussion

## Orientation of the study

*Striga hermonthica* is an important and persistent problem in cereal production of the semi-arid tropics. It is important as a problem because of its wide dispersion throughout this climatic zone, and because it seriously lowers crop yields thereby threatening the livelihood of many subsistence farmers. It is persistent because it seasonally produces thousands of tiny but viable and long-lived seeds per plant that cause a gradual increase of infection levels if suitable host plants remain to be grown in the same field. Hence, control options against *Striga* should reduce yield losses and at the same time minimize or prevent future infestations. This may be achieved through proper host plant defence mechanisms such as resistance and tolerance. Resistance reduces or prevents infection and reproduction (Shew and Shew, 1994), while tolerance lowers or prevents yield losses or damage due to infection (Caldwell et al., 1958). The use of crop varieties with improved resistance and tolerance against *Striga* is believed to be one of the most useful control options against this parasitic weed. For smallholder farmers the advantage of improved varieties compared to other options is that these varieties do not require extra work or additional inputs (such as pesticides) that can be costly or have undesired side-effects on environment and health (e.g. Hess and Haussmann, 1999). Ever since the early work on plant resistance by Williams (1959), breeders and *Striga* researchers have been working on breeding for resistance and tolerance against *Striga* (e.g. Ramaiah, 1987a; Hess and Ejeta, 1992; Olivier et al., 1992; Efron, 1993; Kim, 1994; Kim et al., 1998; Adetimirin et al., 2000c). Success of these breeding efforts depends largely on the availability of practical and cost efficient screening techniques that make use of selection measures. that are precise, reliable and discriminative (Hess and Haussmann, 1999).

Host resistance and tolerance are intensively studied as control options against biotic stresses (e.g. Orton, 1909; Schafer, 1971; Clarke, 1986; Trudgill, 1991). Resistance and tolerance against *Striga* have been studied since the late 50's up to date (e.g. Williams, 1959; Obilana, 1984; Haussmann et al., 2000a; Wilson et al., 2000; Gurney et al., 2002a). Work on host plant defence against *Striga* can roughly be classified as studies on mechanisms behind resistance or tolerance (e.g. El Hiweris, 1987; Vogler et al., 1996; Arnaud et al., 1999; Gurney et al., 2002a) and studies on selection measures and methods such as the design of screening trials and *Striga* infestation techniques (e.g. Cubero et al., 1994; Adetimirin et al., 2000b; Haussmann et al., 2000b; Omanya et al., 2004). However, studies in which the two aspects are studied in an integrated way are rare. The present study combined both aspects, as the objective was to enhance efficiency of selection for tolerance and resistance against *Striga* through better understanding and proper characterization of these mechanisms.

## Resistance

Resistance against *Striga* has been widely studied and good measures for this defence mechanism are available. Resistance can be quantified based on the number of aboveground *Striga* plants at a specific moment in time (Adetimirin et al., 2000b; Omanya et al., 2004), the maximum number of *Striga* plants that emerged aboveground (Wilson et al., 2000), or the integration of regular *Striga* counts (Haussmann et al., 2000b). All these measures are based on aboveground *Striga* plants. For practical reasons aboveground measures are preferred over belowground measures. Likewise, selection measures that can be used in the field are preferred over those that require laboratories or pot experiments, as this environment resembles most the actual environment of a farmers' field. Furthermore some studies found inconsistencies between results from the field and those from other test environments (Haussmann et al., 2000b; Omanya et al., 2000).

Results of the current study support the suggestion that aboveground measures are adequate because they were found to reflect the number of belowground attachments reasonably well. Haussmann et al. (2000b) proposed the use of the Area under the *Striga* Number Progress Curve (*ASNPC*) as a suitable resistance measure. It provides a fair representation of the infection throughout the cropping season. In this study, the maximum aboveground *Striga* number ($NS_{max}$) was found to be as good as the *ASNPC*. It was objective, as it takes into account the genotypic differences in host development, and proved discriminative, very consistent over years and easy in use. Its advantage over the *ASNPC* is that it requires less time and labour, because counting can start later (just before the maximum number is expected) and stop earlier (as soon as numbers for all genotypes start to decrease).

Other measures that have been proposed for screening for resistance were *Striga* vigour (Haussmann et al., 2000a,b) and aboveground *Striga* dry weights (Kulkarni and Shinde, 1985). However, numbers are considered better for a variety of reasons. Compared to vigour scores, they are more objective and therefore less dependent on the person performing the screening. Numbers are also thought to be a more unambiguous resistance measure because they have less interaction with tolerance. For a *Striga* plant to be vigorous or to gain dry weight, it needs a sufficiently tolerant host plant that is able to provide it with the required carbohydrates. Furthermore, contrary to dry weights, counts do not require drying and weighing facilities.

This study showed that selection for resistance based on numbers implies a risk, if infestation levels are high. Relatively low *Striga* infection levels, compared to those on other genotypes, can be the result of a lower maximum attainable infection level. This may be due to a limited number of establishment sites on the host root (a resistance mechanism), or a limitation of the carrying capacity of the host (caused by sensitivity of the host plant) and subsequent intra-specific competition among *Striga* plants. Due to this limitation of the carrying capacity the infestation – infection curve shows an optimum, beyond which infection numbers start to decrease. The current study revealed two examples of genotypes showing such an optimum infection curve with increasing infestation (CK60-B and Tiémarifing). This typical interaction between susceptibility, sensitivity and intra-specific competition was earlier reported by Kim et al. (1998) and Haussmann et al. (2000b). They observed that susceptible or sensitive genotypes often support fewer emerged *Striga* due to reduced host vigour and underground competition.

Hence the number of infections is not only a result from resistance but may be the outcome of a complex interaction between resistance, tolerance and intra-specific competition. To avoid this entanglement with tolerance it was recommended to conduct resistance screening at low infestation levels. This study showed that aboveground *Striga* numbers obtained at low infestation levels, representing the initial slope of the infestation - infection curve, is the most discriminative screening measure for resistance (Chapter 3). Lower initial infection response to infestation may be the result of resistance mechanisms discovered in earlier studies, such as a low germination stimulant production (Hess et al., 1992; Olivier and Leroux, 1992), germination inhibitors (Weerasuriya et al., 1993), mechanical resistance hampering penetration of host root cells (Maiti et al., 1984; Olivier et al., 1991b; Ejeta and Butler, 1993) or reduced metabolite flow from the host to the parasite in the early belowground stages (Arnaud et al., 1999).

Complete resistance is defined as resistance that prevents growth and reproduction of the pathogen (Shew and Shew, 1994). Resistance as found against *Striga* is not complete, as it still allows some *Striga* plants to parasitize and hence reproduce. It has been hypothesized that despite the absence of complete resistance against *Striga*, resistance can lower the *Striga* seed production (Doggett, 1988; Ejeta et al., 2000). Resistance against *Striga* indeed proved an important factor to lower seed production. However, large variation in *Striga* reproductive efforts among equally resistant genotypes exist (Chapter 5). While *Striga* numbers were more relevant than dry weight for the assessment of resistance, *Striga* dry weight may be very useful to screen for genotypes supporting less *Striga* reproduction (Chapter 5). Seed production correlates very well with plant biomass (Samson and Werk, 1986; Thompson et al., 1991). This study showed that this is also true for *Striga* seed production and *Striga* dry weight. These measures can either be determined around crop harvest or at the end of the *Striga* life cycle. However if growth duration of genotypes under consideration varies a lot, an assessment at the end of the life cycle of *Striga* seems to result in a more fair comparison. In that way, at all genotypes *Striga* plants on all genotypes will have about the same development time, independent of the development time of the host genotype.

Carsky et al. (1996) assumed that host plant varieties could also reduce *Striga* reproductive efforts through early host maturity. However, *Striga* continues to reproduce after removal of the aboveground parts of the host plant (Chapter 5) and there were no significant correlations between crop harvest time and seed production. The effect of early host maturity on *Striga* reproduction seems to be overruled by other effects such as host susceptibility. Main constraint for post-harvest *Striga* reproduction seems to be the water availability to the *Striga*, determined by the water retention of the soil and the rooting density and depth of the host. Magnitude of the post-harvest reproduction depends on the initial seed bank density. Due to delayed development in plots with low initial seed bank densities, *Striga* reproduction after harvest makes up a very significant part of the total reproduction. As a result of this compensational time the difference between seed production under low and high initial seed bank densities reduces towards the end of the *Striga* life cycle (Chapter 5).

In the field, density dependent reduction in seed production mainly resulted from intra-specific competition between aboveground *Striga* plants. In pot experiments with much higher infestation levels than in the field, the relation between *Striga* infestation and *Striga* infection was also found to be density dependent, confirming the earlier conclusion of Smith and Webb (1996). However, in the field experiments this was only evident for the most susceptible genotypes, CK60-B and E36-1 (Chapter 5). Hence the density dependency between infestation and infection only becomes apparent when infection levels can reach sufficiently high levels.

## Yield loss and tolerance

Average estimated sorghum yield losses of 50% and more have been reported in *Striga* infested fields (Last, 1960; Bebawi and Farah, 1981). In this study (Chapter 2) relative yield loss estimates from the field ranged from 0 to 85 %. In the low infested fields mean relative yield loss over all genotypes was around 25% and in the high infested fields mean relative yield loss was just below 50%. Dogget (1965) estimated 2-3 kg yield loss ha$^{-1}$ 1000 *Striga* plants$^{-1}$. In the field experiments of this study this estimate ranged from 0 to 10 kg yield loss ha$^{-1}$ 1000 *Striga* plants$^{-1}$ in the low infested fields with estimated aboveground *Striga* densities ranging from 5,000 to 500,000 plants ha$^{-1}$. In the high infested fields, with estimated aboveground *Striga* densities of 80,000 to 2,900.000 plants ha$^{-1}$ the estimated yield loss ranged from 0 to 3 kg ha$^{-1}$ 1000 *Striga* plants$^{-1}$. This lower average yield loss per 1000 *Striga* plants at higher *Striga* densities demonstrates that yield loss is not proportional to *Striga* density.

Compared to resistance against biotic stresses or tolerance against abiotic stresses relatively few studies have focussed on tolerance against biotic stresses. This may have various reasons. Tolerance still allows the pathogen or the parasite to attack, develop and reproduce. Therefore *Striga* tolerance in itself is not considered a desirable defence mechanism, as it would cause a build-up of the seed bank and hence an aggravation of the problem in future cropping seasons. However, tolerance as an additional defence mechanism in a resistant host genotypes may be very useful (Ramaiah and Parker, 1982; Haussmann et al., 2000b, 2001a). Tolerance against *Striga* is especially required since to date no immunity against this parasite has been found. Hence parasites may still be able to attack crops and cause severe damage once resistance is combined with sensitivity. Another reason for the lower attention for tolerance against biotic stresses may be its entanglement with resistance. In plants, resistance and tolerance co-exist and may be represented at different degrees (Barker, 1993). In the separate quantification of both resistance and tolerance, this entanglement plays a complicating role. In general, selection for tolerance against abiotic stresses (such as salinity, heat or cold) is less complicated, as all genotypes in a selection trial can easily be exposed to the same stress level. In contrast, for biotic stresses, exposing host plants to equal disease or parasite pressure, a prerequisite for screening for tolerance according to Schafer (1971), proves difficult due to differences in levels of resistance against the disease or parasite (Chapter 3; Clarke, 1986).

This study showed that it is extremely difficult to get overlapping ranges of infection levels if the genotypes differ widely in resistance level. An extremely wide range in infestation levels would be needed for such an overlap, which is too laborious and not practical for use in the field (Chapter 3). Another theoretical solution would be to rely on interpolation techniques to correct the tolerance measure (e.g. relative yield loss) for differences in *Striga* infection levels, found among genotypes. This requires the relation between infection and relative yield loss to be known and preferably also to be the same for all genotypes. In the pot experiments of this study, despite the wide range of infestation levels, for none of the genotypes the complete relation between infection and relative yield loss could be resolved.

To explore relations between infestation, infection and yield loss in an integrated way, the three-quadrant figure, modified from the one introduced by de Wit (1953) for the analysis of fertilizer fate, was used. It shows the relation between *Striga* infestation and *Striga* infection (quadrant IV), *Striga* infestation and (relative) yield loss (quadrant II) and *Striga* infection and yield loss (quadrant I). Some of the above-mentioned problems related to tolerance can be illustrated by this representation.

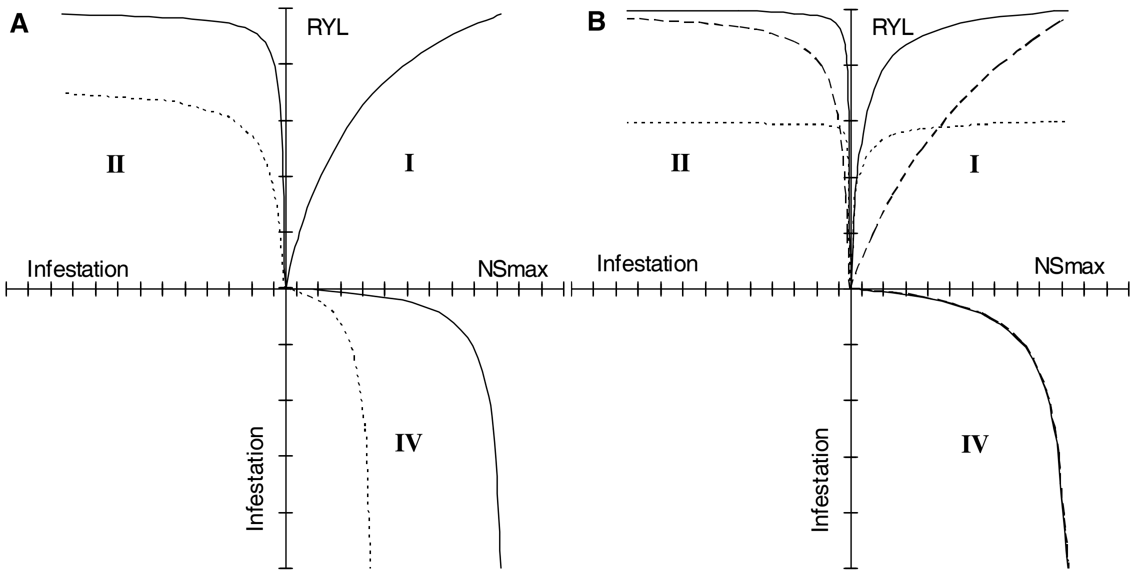

Figure 1 Three-quadrant representation of three relations: (1) between *Striga* infestation and *Striga* infection ($NS_{max}$: maximum aboveground *Striga* numbers; quadrant IV), (2) between *Striga* infection ($NS_{max}$) and relative yield loss (*RYL*; quadrant I) and (3) between *Striga* infestation and relative yield loss (quadrant II). Figure 1A shows these relations for a fictive resistant (dotted line) and susceptible genotype (solid line) with equal tolerance levels. Figure 1B shows genotypes with equal resistance that differ in sensitivity to *Striga* infection; genotypes are either sensitive (solid line) or contain tolerance resulting in a lower maximum yield loss level (dotted line) or a lower yield loss per *Striga* plant (discontinuous line).

In Figure 1A, two fictive genotypes with equal tolerance levels (same relation $NS_{max}$ and $RYL$) but different resistant levels are shown. Quadrant IV (Infestation level – $NS_{max}$) shows that a resistant genotype (dotted line) has very limited overlapping infection levels with a susceptible genotype (solid line), making a direct comparison for tolerance between those two genotypes extremely difficult. Due to the low infection levels, relative yield loss of the resistant genotype will not surpass a certain level, and is basically determined by the maximum number of attachments, whereas yield loss of the susceptible genotype may easily reach 100%. For the resistant genotype no information can be acquired on the maximum yield loss at high infection levels, whereas for the susceptible genotype, it proved very difficult to retain information on the initial slope of the relation between $NS_{max}$ and $RYL$ (Chapter 3). At the same time, it is not known whether the mechanism responsible for a lower initial slope is identical to the mechanism that is responsible for a reduced maximum yield loss. Tolerance could thus be based on a single mechanism, or on two separate mechanisms of which one causes a lower yield loss per *Striga* (initial slope), and the other a lower maximum attainable yield loss.

Figure 1B shows both tolerance mechanisms. The figure represents genotypes with equal resistance but different tolerance levels. The solid line represents a sensitive genotype, characterized by a steep initial increase and a high (100%) maximum yield loss. For the other lines either the initial slope is less steep (discontinuous line) or the maximum yield loss is less high (dotted line). The intersections of the different curves show that it depends on the actual infection level which of these tolerance mechanisms is most efficient and consequently which of these genotypes would be selected in a screening trial. Obviously, a combination of a reduced initial slope and a reduced maximum yield loss level would yield the best tolerance. In case both expressions of tolerance are based on one and the same mechanism, such a combination would automatically be obtained through selection.

It was concluded that for resistant genotypes, tolerance can be quantified as a reduced relative yield loss per aboveground *Striga* plant and for susceptible genotypes the maximum relative yield loss can be used (see 1A). One approach could be to make two separate groups of genotypes, one resistant and one susceptible group. This pre-selection could than be followed by two separate screenings for tolerance. For the group with resistant genotypes, the initial slope of the infection level-relative yield loss can be used as selection measure for tolerance, while for the susceptible genotypes one could use the maximum relative yield loss. Selected material from both groups could then be used in breeding programs, either in combination or as separate traits, depending on the objective and ease and costs of gene-localisation and transfer.

Yield based measures have at least one main obstacle. Due to the large genotypic variation in uninfected crop yields, resulting from differences in yielding ability or differences in adaptability to the local screening environment, yield under *Striga*-infested conditions can not simply be used as screening measure. The presence of controls therefore remains an indispensable requirement when using a measure of tolerance based on grain yield. Consequently, alternative selection measures for tolerance, without this requirement, are desired. This study investigated the use of alternative measures that were based on possible mechanisms of tolerance. *Striga* infection lowers host plant photosynthesis, and this reduction was also shown to be reflected in chlorophyll fluorescence measurements. Tolerant genotypes appeared less affected than sensitive ones. Differences in *Striga* effects on chlorophyll fluorescence among genotypes were earlier found by Gurney et al. (2002a). Chlorophyll fluorescence measurements proved to be suitable as screening measure for abiotic stresses, such as drought or cold (e.g. Havaux and Lannoye, 1985; Schapendonk et al., 1989a; Nogues et al., 1994; Fracheboud et al., 1999; Olsovska et al., 2000). The current study strongly suggests that chlorophyll fluorescence measurements can also be used as an alternative screening measure for tolerance to *Striga*. Based on the results of this study the most suitable measurement for selection for *Striga* tolerance seemed to be photochemical quenching (*Pq*) and electron transport (*ETR*). Comparative advantage of these measurements, over yield-based selection measures, is the possibility to screen in the absence of control plots, as values of *Pq* an *ETR* of unstressed plants at comparable phenological stages showed to be rather stable among genotypes (Chapter 4).

Whether the infestation level for tolerance screening should be high or low depends on the genotypes in the selection trials and the screening objective. For screening based on yield response as well as for screening based on a physiological response the differences between genotypes are most discriminative at high infestation levels (Chapter 3 and 4). This would confirm the earlier recommendations of Kim (1991). However, in view of the general objective of developing highly resistant varieties with high levels of tolerance, selection of tolerant parental lines may best be carried out at low levels of *Striga* infection. Since superior resistant genotypes guarantee low levels of infection, the desired tolerance is the one that is able to prevent yield loss at low infection levels. Hence, if the aim is to use tolerance as an additional defence to superior resistance, its selection measure could well be the initial relative yield loss per *Striga* infection. The maximum relative damage level (e.g. maximum relative yield loss) would be less useful as tolerance measure, simply because infection levels of superior resistant genotypes will never become high enough to attain the maximum relative yield loss. Furthermore, in the initial trajectories of the relation between infection and relative yield loss or chlorophyll fluorescence reduction, one can assume a nearly linear slope as was observed with Framida. This assumption would facilitate the calculation of losses or reductions per *Striga* infection, which can be used as a tolerance measure. If variation in resistance among genotypes is not considerable, one infestation level would probably be enough.

## Implications for breeding

Host plant resistance or tolerance is often believed to be one of the most promising solutions to *Striga* (e.g. Kim, 1996; Gurney et al., 1999). However, this study showed that, relative yield losses under field situations could still reach more than 22% in very tolerant and resistant genotypes (Chapter 2). Also, *Striga* may still be able to reproduce at very resistant genotypes and thereby completely replenish or even increase the seed bank (Chapter 5). Hence even with the use of improved varieties problems related to *Striga* persist and may even increase.

It is therefore recommended that farmers combine the use of varieties with improved resistance and tolerance with agronomic *Striga* control options such as hand weeding before flowering, the use of trap crops in crop rotations or intercropping schemes (e.g. Hess and Dodo, 2004) and possibly biological control options such as the use of AM fungi as proposed by Lendzemo and Kuyper (2001) and Lendzemo et al. (2005). Such an integrated *Striga* management approach is probably the best solution to the problem. It means however that each component of this integrated control should be optimised. Hence, breeding efforts should be further enhanced to develop better varieties that prevent or highly reduce *Striga* infection and reproduction and yield well either in the absence and the presence of *Striga*. The idea of this study was that the separation of resistance and tolerance in definitions, selection measures and methods could result in the selection of separate breeding material with either superior levels of resistance or superior levels of tolerance. Through subsequent crossings of these selections new varieties could be developed that combine superior levels of each mechanism. The combination of disease resistance and tolerance was earlier suggested by Stakman and Christensen (1960), and later for *Striga* by Ramaiah and Parker (1982), Kim (1991), Haussmann et al. (2001a,b), Pierce et al. (2003) and many others.

The conventional selection and breeding approach, as proposed in this study with improved methods and measures may be enhanced by combining it with other improved or more advanced methods or breeding strategies. Possibilities are to include wild relatives with natural resistance or tolerance in the breeding programme (Burdon, 1997; Wilson et al., 2000; Gurney et al., 2002b; Wilson et al., 2004), to pyramid genes for different resistance mechanisms in order to obtain more stable, polygenic resistance, or to transfer resistance or tolerance genes into well-adapted genotypes. The role of marker-assisted selection in these breeding strategies against *Striga* is very promising as it is a powerful tool for the incorporation of genes from selected genotypes or wild relatives into improved varieties (Tanksley et al., 1989). These additional techniques can, however, never completely replace the classical breeding (Hess and Haussmann, 1999).

One of the remaining constraints to breeding for defence against *Striga* is the large error variation and consequently rather low repeatabilities of the selection measures (this study). It is therefore necessary to use enough replications within each experiment and to replicate experiments over years. Haussmann et al. (2000b) recommended the use of at least 4 replications in screening trials. Also the high genetic variation of *Striga* should be taken into consideration in breeding programmes (Verkleij and Pieterse, 1994), as well as the need to exclude effects caused by typical genotype × environment interactions. Another problem is that most of the resistant and tolerant genotypes are poorly adapted and have low yields at locations outside their region of origin (Hess and Haussmann, 1999). For these reasons screening should be done at multiple sites, in order to test the broad adaptability of the genotype and stable performance of the defence (Ramaiah, 1987a).

Selection for genotypes that prevent or reduce *Striga* infection should be done in the field at low *Striga* infestation levels (around 25,000 viable *Striga* seeds $m^{-2}$) and can be based on maximum aboveground *Striga* numbers. It requires the breeder to start frequent *Striga* counts around 70 days after sowing. Additionally, for an adequate estimation of the reproductive effort of *Striga* on a genotype, total aboveground *Striga* dry weights or *Striga* flowerstalk dry weights should be assessed. Preferably the breeder regularly collects dead *Striga* plants from a known surface, including a number of host plants, and continues this collection until all *Striga* plants are collected (the end of the *Striga* life cycle). If time is sparse, and genotypes do not differ much in season length the breeder could decide to do a single sampling of all aboveground *Striga* material (dead or alive) at crop harvest. Slightly more work but also more accurate would be to collect dead *Striga* plants in two or more rounds (e.g. around crop harvest and subsequently at the end when all *Striga* plants are dead).

Selection for genotypes that endure *Striga* infection and maintain high crop yields should be done in the field. If this selection is based on yield response to *Striga* infestation, incorporation of *Striga*-free control plots is required. Alternatively a selection that does not require control plots can be carried out with a measurement system that is able to quantify photochemical quenching or electron transport rate through photosystem II. Considering that the objective is to find genotypes with tolerance that will eventually be combined with superior resistance, ensuring low infection levels, the infestation levels for tolerance screening can be kept relatively low. If the objective is to find superior tolerance that needs to stand on its own, high infestation levels (at least 300,000 viable seeds $m^{-2}$) are recommended, while the best bet might be to screen at two (low and high) infestation levels or with two groups of genotypes (susceptible and resistant). The latter solutions enable identification of possible different types of tolerance, one with expression at low infection and one with expression at high infection levels that could than both be incorporated in a superior resistant or adapted genotype.

Finally, for varieties to be acceptable to farmers, they have to meet a whole range of other criteria than yielding ability, disease resistance and agro-climatic stability alone (Defoer et al., 1997). Criteria such as grain colour, taste and cooking qualities proved to be both region and gender specific. Understanding these criteria, early incorporation of these criteria in the breeding program, and tailoring varieties to local needs could enhance adoption of improved varieties by farmers (Kamara et al., 1996; Bengaly and Defoer, 1997; Defoer et al., 1997).

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# Summary

*Striga hermonthica* (Del. Benth) is a parasitic weed on tropical cereals, such as sorghum (*Sorghum bicolor* [L.]), millet (*Pennisetum glaucum* [L.] R. Br. or *P. americanum* [L.] K. Schum), maize (*Zea mays* [L.]) and rice (*Oryza glaberrima* [Steudel] and *O. sativa* [L.]). It seriously reduces crop yields and is therefore one of the main biotic constraints to cereal crop production in the semi-arid tropics, endangering the livelihood of many subsistence farmers. *Striga* negatively affects its host by subtracting host assimilates, water and nutrients and by changing the plant hormone balance, which in turn alters host plant allometry (leaf/stem ratio) and lowers the photosynthetic rate of the host. Several control options have been proposed but none of these measures on its own is both sufficiently effective as well as practical and accessible for resource-poor farmers. Integration of various control options is thought to be the best approach to combat *Striga*. In integrated *Striga* management the role of crop varieties with improved resistance and tolerance is indispensable. For the development of such improved varieties the identification and selection of superior breeding material is of vital importance. This study focussed on the effects of *Striga* on host physiology and production and on the effects of host genotype on the *Striga* infection and reproduction rate with the aim of enhancing the understanding of their interaction and developing suitable tools for field selection of resistant and tolerant breeding material.

Between 2001 and 2004, three field and two pot experiments were conducted in Samanko (Mali) and two pot experiments were conducted in a greenhouse in Wageningen (The Netherlands). In the three field experiments, 10 different sorghum genotypes (CK60-B, CMDT39, E36-1, Framida, IS9830, N13, Seredo, Serena, SRN39 and Tiémarifing) were grown in the presence and absence of *Striga* seeds, and in the last year *Striga* plots were infested at two different levels (‘low’ and ‘high’). In 2001 and 2003 previously infested fields were used and *Striga*-free plots were achieved through ethylene gas injections with a backpack ethylene gas injector, while existing *Striga* plots received additional *Striga* seeds. In 2002, a non-contaminated field was used and *Striga* plots were achieved through artificial infestation, while avoiding contamination of the *Striga*-free plots. Small dikes surrounding the different plots prevented the *Striga*-free plots from contamination (through water flow) by escaping *Striga* seeds from neighbouring *Striga* plots. In three of the four pot experiments a selection of four of the 10 genotypes (CK60-B, E36-1, Framida and Tiémarifing) were grown under different *Striga* infestation levels. Each year sorghum seeds were multiplied through self-pollination for use in the subsequent year. *Striga* seeds used in all experiments were derived from sorghum plants grown in Samanko. In all

experiments, routine observations and measurements were done: *Striga* emergence counts, *Striga* dry weights and sorghum grain yield. More detailed observations, depending on the experiment, included photosynthesis and chlorophyll fluorescence of sorghum plants and flowering dates, flowerstalk dry weights, number of reproductive plants and seed production of *Striga*.

In the first study of this thesis (Chapter 2), field selection measures for resistance and tolerance were evaluated and discussed, based on results of the three field experiments and one pot experiment in Samanko with all 10 genotypes. Both resistance and tolerance are important yield determining traits under *Striga* infestation. Under low infestation, tolerance was relatively more important for yield than resistance, whereas resistance was more important under high infestation. The area under the *Striga* number progress curve (*ASNPC*) and the maximum number of aboveground *Striga* plants ($NS_{max}$) were discriminative and consistent measures for resistance. It proved more difficult to find a satisfactory measure for tolerance. Genotype differences in resistance and the non-linearity of the relation between *Striga* infection and yield loss are the main reasons for this.

In Chapter 3 an attempt was made to resolve the relationship between *Striga* infection and sorghum yield loss in order to find a suitable selection measure for tolerance against *Striga*. Data from three pot experiments, one in Samanko (2003) and two in the greenhouse in Wageningen (2003 and 2004) with CK60-B, E36-1, Framida and Tiémarifing, were used for this purpose. There were significant genotype, infestation and genotype × infestation effects on sorghum yield. The relation between infestation level and infection level was density dependent. As a result, the wide range of infestation levels resulted in a relatively narrow range of infection levels for each individual genotype. In the 2004 experiment the range of infestation levels was even further extended to obtain at least a narrow range of identical infection levels for all four genotypes. The relationship between *Striga* infection level and relative yield loss showed to be non-linear. The results suggested that for resistant genotypes tolerance could best be quantified by the reduction of relative yield loss per aboveground *Striga* plant, whereas for less resistant genotypes the maximum relative yield loss could best be used. Whether both expressions of tolerance are interrelated remained unresolved. Despite the identification of these tolerance measures a main bottle neck of selection for tolerance to *Striga* based on yield data remained the requirement of control plots.

Chapter 4 explored options for the use of photosynthesis or related measurements in screening for tolerance to *Striga hermonthica*. This work was based on the results from two pot experiments conducted in a greenhouse in Wageningen with CK60-B, E36-1, Framida and Tiémarifing. The aim was to find a better measure for tolerance without the requirement of control plots and various infestation levels.

$CO_2$ assimilation rate of sorghum plants was significantly reduced by *Striga* infection. This was accompanied by a reduced stomatal conductance, which was shown not to be the main cause of the reduction in photosynthetic rate. Other processes related to photosynthesis that were affected by *Striga* infection were transpiration rate, photochemical quenching and non-photochemical quenching, electron transport and photosynthesis per electron transport. Sensitive genotypes were affected earlier, more severe and at lower infestation levels than tolerant genotypes. Tiémarifing, earlier identified as the most tolerant variety, was the only genotype showing no significant *Striga* effect on any parameter at any measurement time. Consequently, *Striga* tolerant genotypes may be identified through photosynthesis or related measurements. Particularly suitable for this purpose seemed measurements of photochemical quenching and electron transport rate through photosystem II. These parameters facilitate screening at one single infestation level and without the requirement of *Striga*-free control plots. It was recommended to screen between first *Striga* emergence and sorghum flowering and at infestation levels of at least 300,000 *Striga* seeds $m^{-2}$.

The objective of Chapter 5 was to study the genotype effects on *Striga* reproduction and to find a suitable selection measure for *Striga* seed production. Data for this study were derived from the three field experiments in Mali with 10 sorghum genotypes. There were significant genotype and infestation level effects on aboveground *Striga* numbers, aboveground *Striga* dry weights and *Striga* seed production. There were significant correlations between aboveground *Striga* numbers and seed production and highly significant correlations between aboveground *Striga* dry weights and *Striga* seed production. Aboveground *Striga* dry weight and *Striga* flowerstalk dry weight were found to be good indicators for *Striga* reproduction.

An increase in infestation level in the field generally resulted in a proportional increase in infection level. Exceptions were the most susceptible genotypes (CK60-B and E36-1), for which high infestation levels resulted in a less than proportional increase in number of emerged *Striga* plants. Increasing infestation levels resulted in a disproportional increase in *Striga* dry weights (total and flowerstalks) and seed production for all genotypes. The relations between *Striga* infestation and *Striga* infection and between *Striga* infection and reproduction were both density and genotype dependent. Density dependence however was observed at much lower infestation levels for the second relationship (infection - reproduction) than for the first relationship (infestation - infection), where it only appeared at relatively high infestation levels. *Striga* reproduction continued after crop harvest. Differences in *Striga* seed production between *Striga* infestation levels decreased between harvest and the end of the *Striga* life-cycle. There were no significant genotype effects on seed dry weight per seed capsule.

In this study, suitable selection measures were found for resistance against *Striga* parasitism and reproduction as well as for tolerance against *Striga* infection. Maximum aboveground *Striga* numbers is a reliable selection measure for resistance. *Striga* flowerstalk dry weight can be used to identify genotypes supporting low *Striga* reproduction. Screening for tolerance showed to be more complicated. For susceptible genotypes, the highest relative yield loss that was attained is a suitable selection measure for tolerance, whereas for more resistant genotypes, the relative yield loss per *Striga* infection seems more appropriate. However, *Striga*-free control plots are indispensable for selection of tolerant genotypes when selection is based on host plant yield. Chlorophyll fluorescence parameters, and especially photochemical quenching (*Pq*) and electron transport (*ETR*) were identified as promising alternative screening measures for tolerance, particularly since with the use of these measures tolerance can potentially be identified without the presence of *Striga* free controls.

Host plant genotype choice affects *Striga* reproduction efforts. Differences in *Striga* seed production among sorghum genotypes can to a large extent be explained by differences in resistance level of the host plants. Resistance was responsible for a 70 to 93% reduction in *Striga* seed production in this study. To reduce the *Striga* seed bank, additional control options such as hand weeding before harvest are required.

# Samenvatting

*Striga hermonthica* (Del.) Benth is een onkruid dat parasiteert op tropische graangewassen zoals sorghum (*Sorghum bicolor* [L.]), gierst (*Pennisetum glaucum* [L.] R. Br. of *P. americanum* [L.] K. Schum), mais (*Zea mays* [L.]) en rijst (*Oryza glaberrima* [Steudel] en *O. sativa* [L.]). Het reduceert de opbrengst van zijn gastheer aanzienlijk en is daarom één van de meest belangrijke biotische problemen voor graanproductie in de semi-aride tropen en een groot gevaar voor de bestaanszekerheid van vele zelfvoorzienende boeren. *Striga* benadeelt zijn gastheer door onttrekking van assimilaten, water en nutriënten en doordat het de hormoonbalans van de gastheer verstoort, waardoor de allometrie van de plant (verhouding blad/stengel/wortel) verandert en de fotosynthesesnelheid afneemt. Verscheidene beheersmaatregelen zijn voorhanden, maar geen van deze maatregelen is zowel voldoende effectief als praktisch en toegankelijk voor arme boeren. Integratie van meerdere beheersmaatregelen lijkt daarom de beste benadering om *Striga* te bestrijden. In zo'n geïntegreerde aanpak is de rol van gewasvariëteiten, met verhoogde tolerantie en resistentie tegen de parasiet, essentieel. Het ontwikkelen van dergelijke variëteiten vereist het identificeren en selecteren van geschikt uitgangsmateriaal voor veredeling. Het doel van deze studie was het verkrijgen van een beter inzicht in de gastheer-*Striga* relatie om bruikbare methoden en selectiecriteria te ontwikkelen voor het verkrijgen van goed uitgangsmateriaal voor de verdere veredeling van rassen met een hoge mate van tolerantie en resistentie tegen *Striga*. Dit onderzoek concentreerde zich op het bestuderen van *Striga* effecten op de fysiologie en productie van zijn gastheer, alsmede op de effecten van het gastheer-genotype op *Striga* parasitisme en reproductie.

Tussen 2001 en 2004 zijn drie veldexperimenten en twee potexperimenten uitgevoerd in Samanko (Mali) en twee potexperimenten in de tropische kas in Wageningen (Nederland). In de drie veldexperimenten werden 10 verschillende sorghum genotypen (CK60-B, CMDT39, E36-1, Framida, IS9830, N13, Seredo, Serena, SRN39 en Tiémarifing) geteeld op zowel *Striga*-vrije als *Striga*-besmette velden. In het laatste veldseizoen (2003) werden de *Striga*-velden op twee besmettingsniveaus aangelegd ('laag' en 'hoog'). In 2001 en 2003 werden reeds besmette velden gebruikt, waarin *Striga*-vrije velden werden gecreëerd door middel van ethyleengas injecties, terwijl aan *Striga* velden extra *Striga* zaden werden toegevoegd. In 2002 werd een onbesmet veld gebruikt waarbinnen *Striga* velden werden gecreëerd door handmatige toediening van *Striga* zaad. Dijkjes om de verschillende velden beschermden *Striga*-vrije velden tegen besmetting (door afstromend water) met *Striga* zaad uit naastgelegen velden. In drie van de vier potexperimenten werd een selectie van vier van de 10 genotypen (CK60-B, E36-1, Framida en Tiémarifing) gebruikt bij een reeks van *Striga* besmettingsniveaus. Elk jaar werd sorghumzaad vermenigvuldigd door middel van zelfbestuiving, voor gebruik in het daaropvolgende jaar. Het *Striga* zaad dat in de experimenten gebruikt werd was afkomstig van sorghumplanten die in Samanko (Mali) geteeld waren. In alle experimenten werden routinewaarnemingen en -metingen gedaan, waaronder *Striga* opkomst-tellingen en de bepaling van het *Striga* drooggewicht en de korrelopbrengst van sorghum. In sommige experimenten werden meer gedetailleerde waarnemingen verricht, zoals fotosynthese- en chlorofylfluorescentiemetingen aan sorghumplanten alsmede bloeitijdstip en zaadproductie karakteristieken van *Striga* planten.

In hoofdstuk 2 werden selectiecriteria voor resistentie en tolerantie geëvalueerd aan de hand van gegevens van drie veldexperimenten en een potexperiment uitgevoerd in Samanko met alle 10 genotypen. Zowel resistentie als tolerantie bleken belangrijke opbrengstbepalende eigenschappen van sorghum in *Striga*-besmette velden. Onder lage besmettingsniveaus bleek tolerantie relatief belangrijker voor opbrengst dan resistentie, terwijl resistentie meer bepalend was onder hoge besmettingsniveaus. Het oppervlak onder de *Striga*-aantallen ontwikkelings-curve (*ASNPC*) en de maximale bovengronds zichtbare *Striga*-aantallen ($NS_{max}$) waren onderscheidende en consistente criteria voor resistentie. Het ontwikkelen van geschikte criteria voor tolerantie bleek moeilijker. De belangrijkste oorzaken hiervan waren de bestaande verschillen in resistentie tussen genotypen en het gegeven dat de relatie tussen *Striga*-infectie en het relatieve opbrengstverlies niet lineair is.

In het derde hoofdstuk is gepoogd de relatie tussen *Striga*-infectie en het relatieve opbrengstverlies op te helderen om zodoende een gepast selectiecriterium voor tolerantie tegen *Striga* te vinden. Deze studie was gebaseerd op gegevens van een potexperiment in Samanko (2003) en twee potexperimenten in de tropische kas in Wageningen (2003 en 2004) met CK60-B, E36-1, Framida en Tiémarifing. Er werden significante genotype-, besmettings- en genotype × besmetting effecten op de sorghumopbrengst gevonden. De relatie tussen besmettings- en infectieniveau bleek dichtheidsafhankelijk. Als gevolg hiervan resulteerde de brede reeks aan besmettingsniveaus in de experimenten van 2003 in een relatief smalle reeks aan infectieniveaus per ras. Hierdoor bleef een overlap in infectieniveaus, die een directe vergelijking tussen de vier genotypen mogelijk zou maken, uit. Om deze reden werd er in het experiment van 2004 gebruik gemaakt van een nog bredere reeks aan besmettingsniveaus, waardoor in ieder geval een smalle reeks van overeenkomstige infectieniveaus voor alle vier de genotypen werd verkregen. De relatie tussen *Striga*-infectieniveau en het relatieve opbrengstverlies bleek niet lineair. De resultaten suggereren dat voor resistente genotypen tolerantie het best kan worden gekwantificeerd als een gereduceerd relatief opbrengstverlies per bovengronds *Striga* plant, terwijl voor minder resistente genotypen het maximale relatieve opbrengstverlies kan worden gebruikt. Of beide maten van tolerantie aan elkaar gerelateerd zijn blijft onduidelijk. Ondanks de vaststelling van deze tolerantiematen blijft selectie op tolerantie tegen *Striga* gebaseerd op de sorghum korrelopbrengst het nadeel houden dat *Striga*-vrije controlevelden vereist zijn voor een goede onderlinge vergelijking.

In hoofdstuk 4 werden mogelijkheden voor het gebruik van fotosynthese, of eraan gerelateerde metingen, in de selectie voor *Striga* tolerantie onderzocht. Hierbij werd gebruik gemaakt van de gegevens van de twee potexperimenten in de kas in Wageningen, met een selectie van vier sorghumrassen (CK60-B, E36-1, Framida en Tiémarifing). Het doel van deze proef was het vinden van een beter selectiecriterium voor tolerantie tegen *Striga*, zonder verdere vereisten, zoals *Striga*-vrije controlevelden en meerdere *Striga* besmettingsniveaus. De $CO_2$-assimilatiesnelheid van sorghum werd door *Striga*-infectie significant gereduceerd. Dit ging gepaard met een daling van de stomataire geleidbaarheid. Andere aan fotosynthese gerelateerde processen die de reductie in fotosynthese door *Striga* infectie konden verklaren waren de transpiratiesnelheid, fotochemische en niet-fotochemische uitdoving van PSII, electronentransport door PSII en de verhouding tussen fotosynthese en electronentransport. Bij gevoelige genotypen traden deze negatieve effecten reeds in een eerder stadium, in sterkere mate, en bij een lager besmettingsniveau op dan bij tolerante genotypen. Tiémarifing, eerder geïdentificeerd als tolerant, was het enige genotype waarbij voor geen van deze parameters een significant *Striga*-effect werd waargenomen. Hieruit valt af te leiden dat tolerantie voor *Striga* via fotosynthese-gerelateerde metingen kan worden aangetoond. Met name fotochemische uitdoving en electronen transportsnelheid door fotosysteem II lijken hiervoor geschikt te zijn. Deze metingen maken het mogelijk om een selectie uit te voeren bij slechts één besmettingsniveau, zonder de verplichte aanwezigheid van *Striga*-vrije controleplanten. Selectie tussen opkomst van *Striga* en de bloei van sorghum en daarnaast op besmettingsniveaus van ten minste 300.000 levensvatbare *Striga* zaden per vierkante meter lijkt het meeste perspectief te bieden.

Doelstelling van het in hoofdstuk 5 beschreven onderzoek was het kwantificeren van het effect van genotype op de *Striga* reproductie alsmede een geschikte selectiemaat te vinden voor *Striga* zaadproductie. Hiervoor werden gegevens van drie veldexperimenten en van alle 10 genotypen gebruikt. Er waren significante effecten van genotype en besmettingsniveau op bovengrondse *Striga* aantallen, bovengrondse *Striga* drooggewichten en *Striga* zaadproductie. Bovendien waren er significante correlaties tussen bovengrondse *Striga* aantallen en zaadproductie en zeer significante correlaties tussen bovengrondse *Striga* drooggewichten en *Striga* zaadproductie. Drooggewichten van totale bovengrondse *Striga* biomassa en van *Striga* bloeiwijzen werden als goede indicatoren voor zaadproductie aangemerkt.

In het veld resulteerde een toename in besmettingsniveau van *Striga* veelal in een proportionele toename in infectieniveau. De twee meest vatbare genotypen (CK60-B en E36-1) vormden hierop een uitzondering. Bij deze rassen bleef het infectieniveau bij hogere besmettingsniveaus achter bij de verwachting. Een toename in besmettingsniveau leidde bij alle rassen tot een minder dan evenredige toename in bovengronds *Striga* drooggewicht (zowel totaal als alleen de bloeiwijzen) en zaadproductie. De relatie tussen *Striga* infectie en zaadproductie was naast dichtheidsafhankelijk ook afhankelijk van het sorghum genotype. De *Striga* reproductie ging in alle gevallen door na de oogst van het gewas en was, vooral bij lage besmettingsniveaus, aanzienlijk. Verschillen in *Striga* zaadproductie tussen besmettingsniveaus werden zodoende steeds kleiner in de periode tussen oogst en het einde van de *Striga* levenscyclus. Er waren geen significante effecten van sorghum genotype op *Striga* zaadgewicht per zaadcapsule.

In deze studie zijn geschikte selectiecriteria gevonden voor resistentie van de gastheer tegen *Striga* parasitisme, tegen *Striga* reproductie alsmede voor tolerantie van het gewas die optreedt na *Striga* infectie. Het maximum aantal bovengrondse *Striga* planten is een betrouwbaar selectiecriterium voor resistentie, terwijl het drooggewicht van *Striga* bloeiwijzen kan worden gebruikt om genotypen te identificeren die weinig *Striga* reproductie toestaan. Het vinden van een goed selectiecriterium voor tolerantie bleek het meest gecompliceerd. Voor vatbare genotypen is het hoogst verkregen relatieve opbrengstverlies een geschikt selectiecriterium voor tolerantie. Voor meer resistente genotypen lijkt het relatieve opbrengstverlies per opgekomen *Striga* plant beter geschikt als tolerantie criterium. Echter, als de selectie gebaseerd wordt op de opbrengst van de gastheerplant, zijn *Striga*-vrije controles onmisbaar voor selectie van tolerante genotypen. Een geschikt alternatief selectiecriterium voor tolerantie bleek te bestaan uit waarden afgeleid van chlorofylfluorescentiemetingen en dan in het bijzonder de fotochemische uitdoving en de electronentransportsnelheid. Een groot voordeel van het gebruik van chlorofylfluorescentiemetingen is dat tolerantie kan worden geïdentificeerd zonder de aanwezigheid van *Striga*-vrije controlevelden.

De sorghum rassenkeuze beïnvloedt de reproductie van *Striga*. Verschillen in *Striga* zaadproductie tussen sorghumrassen kunnen voor een groot deel toe worden geschreven aan verschillen in resistentie. In dit onderzoek resulteerde het gebruik van resistente genotypen in een reductie in *Striga* zaadproductie van 70 tot 93% ten opzichte van vatbare genotypen. Echter, om de *Striga* zaadbank te reduceren zijn additionele maatregelen nodig zoals handmatig wieden voor de oogst.

# Résumé

*Striga hermonthica* (Del. Benth) est une plante adventice parasite des céréales tropicales, telles que le sorgho (*Sorghum bicolor* [L.]), le mil (*Pennisetum glaucum* [L.] R. Br. ou *P. americanum* [L] K. Schum), le maïs (*Zea mays* [L]) et le riz (*Oryza glaberrima* [Steudel] et *O. sativa* [L]). Elle réduit sérieusement les rendements des cultures et constitue par conséquent l'une des principales contraintes biotiques à la production des cultures dans les zones tropicales semi-arides, fragilisant les moyens de subsistance des petits paysans. Le *Striga* pénalise son hôte en lui prélevant des assimilats, de l'eau et des nutriments et en modifiant l'équilibre des phytohormones qui à son tour modifie l'allométrie (ratio feuille/tige) de la plante hôte et réduit les taux de photosynthèse. Plusieurs moyens de lutte ont été proposés, mais aucun n'est tout à la fois suffisamment efficace, pratique et accessible pour les paysans à faible revenue. L'association de plusieurs moyens de lutte semble être la meilleure approche pour combattre le *Striga*. Dans la gestion intégrée du *Striga,* le rôle des variétés améliorées, résistantes et tolérantes, est indispensable. Pour le développement de ces variétés améliorées, l'identification et le choix de matériel végétal performant est d'une importance vitale. La présente étude s'est focalisée sur les effets du *Striga* sur la physiologie et la production de l'hôte ainsi que les effets du génotype de l'hôte sur le taux d'infection et de reproduction du *Striga*. Tout ceci dans le but de mieux apprécier leur interaction et de développer des outils appropriés pour la sélection au champ de matériel végétal résistant et tolérant.

Entre 2001 et 2004, trois expérimentations au champ et deux cultures en pots au Mali et deux cultures en pots en serre aux Pays-Bas ont été réalisées. Dans les trois expérimentations au champ, 10 différents génotypes de sorgho (CK60-B, CMDT39, E36-1, Framida, IS9830, N13, Seredo, Serena, SRN39 et Tiémarifing) ont été cultivés en présence et en absence de graines de *Striga,* et pour la dernière année les parcelles de *Striga* ont été infestées à deux niveaux ('bas' et 'élevé'). En 2001 et 2003, des champs préalablement infestés ont été utilisés et des parcelles indemnes de *Striga* ont été obtenues à la suite d'injection de gaz éthylène à l'aide d'un injecteur portable de, tandis que les parcelles déjà infestées ont bénéficié d'apports complémentaires de graines. En 2002, dans un champ non contaminé une infestation artificielle contrôlée a permis d'installer des parcelles *Striga* tout en évitant de contaminer les parcelles indemnes. De diguettes entourant les différentes parcelles ont empêché les parcelles indemnes d'être contaminées par les graines de *Striga* provenant (via le ruissellement de l'eau de pluie) des parcelles infestées avoisinantes. Dans trois des quatre cultures en pots, une sélection de quatre des dix génotypes (CK60-B, E36-1, Framida et Tiémarifing) a été cultivée sous différents degrés d'infestation par le *Striga*. Chaque

année, les semences de sorgho ont été multipliées par autofécondation pour être utilisées l'année suivante. Les graines de *Striga* utilisées pour ces études ont été collectées sur des plants de sorgho cultivés à Samanko (Mali). Dans toutes les expérimentations, des observations et mesures de routine ont été faites: comptage de levée des plantes de *Striga*, poids de matière sèche du *Striga* et rendement en grains du sorgho. Selon l'expérimentation, des observations plus détaillées ont été réalisées: la photosynthèse et la fluorescence chlorophyllienne des plants de sorgho et les dates de floraisons, le poids de matière sèche des hampes florales de plantes de *Striga* ainsi que le nombre des plants en phase de reproduction et la production de graines de *Striga* par comptage de capsules de graines.

Dans la première étude de cette thèse (chapitre 2), des critères de sélection au champ pour la résistance et la tolérance ont été évalués et comparés sur la base des résultats des trois expérimentations au champ et d'une culture en pot au Mali avec tous les dix génotypes. La résistance comme la tolérance du sorgho sont des déterminants importants du rendement dans le cas d'infestation de *Striga*. En condition de faible infestation, la tolérance est relativement plus importante que la résistance pour le rendement, tandis que la résistance est plus importante dans le cas de fortes infestations. L'*ASNPC* (la surface en dessous de la courbe de progression du nombre de plants de *Striga*) ainsi que le $NS_{max}$ (le nombre maximum de plants de *Striga* émergé) étaient discriminants et fiables pour les critères de résistance. Il a été plus difficile de trouver un critère satisfaisant pour la tolérance. Les différences de résistance entre les génotypes et la relation non linéaire entre l'infection par le *Striga* et la perte de rendement en sont les principales explications.

Le chapitre 3, avait pour objectif de démontrer la relation entre l'infection par le *Striga* et la perte de rendement pour obtenir un critère approprié de sélection pour la tolérance au *Striga*. Les données de trois expérimentations en pots, une au Mali (2003) et deux en serre aux Pays-Bas (2003 et 2004) avec CK60-B, E36-1, Framida et Tiémarifing, ont été utilisées à cet effet. Il y avait des effets significatifs sur le rendement du sorgho pour les génotypes, pour les infestations et pour l'interaction génotype × infestation. La relation entre le niveau d'infestation et le niveau d'infection était dépendant de la densité. Par conséquent, la large gamme des niveaux d'infestation n'a entraîné qu'une petite gamme de niveau d'infection pour les quatre génotypes dans les expérimentations de 2003, sans avoir des infections identiques pour tout les génotypes. L'expérimentation de 2004 a été conçue pour obtenir au moins une petite gamme d'infection identique pour tous les quatre génotypes. La relation niveau d'infection par le *Striga* et perte relative de rendement n'était pas linéaire. Les résultats montrent que pour les génotypes résistants, la tolérance pouvait être mieux évalué par la diminution de la perte relative de rendement reliée au nombre de plants de *Striga* emergés, tandis que pour les génotypes moins résistants, la perte maximale de rendement était le meilleur indicateur. L'hypothèse selon laquelle les deux expressions de tolérance étaient liées n'est pas confirmée. Il a été conclu qu'un critère de tolérance sur la base du rendement nécessite toujours la présence de témoins.

Le chapitre 4 explore les options d'utilisation de la photosynthèse ou des mesures s'y rapportant dans le criblage pour la tolérance au *Striga hermonthica*. Ce travail était basé sur les résultats des deux cultures en pots conduits aux Pays-Bas avec CK60-B, E36-1, Framida et Tiémarifing. L'objectif était de trouver un meilleur critère de criblage pour la tolérance avec moins d'exigences, telles la présence de parcelles témoins et de différents niveaux d'infestation. L'assimilation du $CO_2$ du sorgho a été réduit significativement par l'infection du *Striga*. Cette diminution était accompagnée par une diminution de la conductance stomatique qui toutefois n'était pas la raison principale de la diminution de l'assimilation du $CO_2$. Les autres processus importants affectés par *Striga* étaient le taux de transpiration, l'extinction photochimique et non photochimique, le transport d'électrons et la photosynthèse par transport d'électrons. Les génotypes sensibles ont été affectés plus tôt et à des niveaux d'infestation plus faibles que les génotypes tolérants. Tiémarifing, identifiée auparavant comme la variété la plus tolérante, était le seul génotype ne montrant aucun effet de *Striga* significatif pour tout les paramètres mesurés à différentes dates. En conséquence, les génotypes tolérants au *Striga* peuvent être détectés par des mesures de photosynthèse. Les mesures de l'extinction photochimique et du transport d'électron au photosystème II semblent particulièrement être adaptées à cet objectif. Elles facilitent le criblage à une période donnée, à un niveau d'infestation unique et sans parcelles témoins exemptes de *Striga*. Il a été recommandé d'effectuer le criblage entre la première émergence de *Striga* et la floraison du sorgho et à des niveaux d'infestation d'au moins 300 000 graines viables de *Striga* par $m^2$.

L'objectif du chapitre 5 était d'étudier les effets des génotypes sur la reproduction du *Striga* et de trouver un critère approprié de sélection pour la production de graines de *Striga*. Les données utilisées pour cette étude proviennent des trois expérimentations au champ au Mali avec tous les dix génotypes. Il y avait des effets significatifs des génotypes et de niveau d'infestation sur le nombre de *Striga* émergés du sol, sur les poids de matière sèche de *Striga* émergés et sur la production de graines de *Striga*. Il y avait également des corrélations significatives entre le nombre de *Striga* émergés et la production de graines et des corrélations très significatives entre le poids de matière sèche de *Striga* émergés et la production de graines de *Striga*. Les poids de matière sèche de *Striga* émergé du sol et de hampes florales de *Striga* sont apparus comme de bons indicateurs pour la reproduction du *Striga*.

Généralement une augmentation du niveau d'infestation au champ augmente proportionnellement le niveau d'infection (le nombre de plants de *Striga* émergés de la terre), exception faite pour les génotypes les plus susceptibles (CK60-B et E36-1), pour lesquels les hauts niveaux d'infestation ont conduit à une augmentation non proportionnelle du niveau d'infection. Une augmentation du niveau d'infestation a conduit à une augmentation non proportionnelle du poids de matière sèche de *Striga* (total et hampe florale) et de la production de graines pour tous les génotypes. La relation entre l'infection par le *Striga* et la production de graines semble être dépendant à la fois de la densité et du génotype. La reproduction du *Striga* a continué après la récolte de la culture. Les écarts de production de graines de *Striga* entre les deux niveaux d'infestation par le *Striga* ont baissé entre la récolte et la fin de cycle du *Striga*. Il n'y avait pas d'effet significatif des génotypes sur le poids sec des graines par capsule.

Dans cette étude, des critères appropriés de criblage ont été trouvés pour la résistance de la plante hôte au parasitisme et à la reproduction du *Striga* ainsi que pour la tolérance à l'infection par le *Striga*. Le nombre maximum de *Striga* émergés du sol est un critère fiable de criblage pour la résistance. Le poids de matière sèche des hampes florales de *Striga* peut être utilisé pour identifier les génotypes qui supportent une faible reproduction du *Striga*. Comme le montre cette étude, le criblage de la tolérance est plus compliqué. Pour les génotypes susceptibles, la perte maximale relative de rendement semble être un critère de criblage approprié pour la tolérance. Pour les génotypes plus résistants, la perte relative de rendement par infection de *Striga* semble plus adéquate comme mesure de tolérance. Les parcelles témoins sans *Striga* sont indispensables pour la sélection des génotypes tolérants lorsque la sélection est basée sur les composantes du rendement de l'hôte. Un critère alternatif fiable pour la tolérance semble être les mesures de fluorescence chlorophyllienne comme l'extinction photochimique (*Pq*) ou le transport d'électron (*ETR*). Avec l'utilisation des mesures de la fluorescence chlorophyllienne, la tolérance peut être potentiellement identifiée en absence de témoins sans *Striga*.

Le choix des génotypes affecte les efforts de reproduction du *Striga*. De façon générale les écarts de production de graines de *Striga* entre génotypes de sorgho peuvent être expliqués par les écarts de résistance de la plante hôte. La résistance était responsable de 70 à 93 % de la réduction de la production de graines de *Striga* dans le cadre de cette étude. Pour réduire la banque des graines de *Striga* dans le sol, des moyens supplémentaires de lutte telles que le sarclage manuel avant la récolte, sont nécessaires.

# Publications

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

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# Curriculum vitae

Jonne Rodenburg was born on July 9, 1975 in Hilversum, The Netherlands. He attended the Stichtse Vrije School in Zeist as secondary school and obtained his VWO diploma at the Teisterbant College in Culemborg in June 1994. In September 1994 he started his MSc studies Tropical land use at Wageningen Agricultural University (WAU). He specialized in agronomy and soil fertility and graduated at Wageningen University (WU) in 1999. For his studies he conducted on-farm research on the use and effects of compost and rock phosphate in sorghum production systems in Burkina Faso for a rural development project financed by the Dutch Directorate-General for International Cooperation (DGIS), in Koudougou. In Indonesia he studied the effects of slash-and-burn practices on soil erosion and soil fertility in rice-rubber agro-forests in Jambi, Sumatra, under supervision of Meine van Noordwijk (ICRAF, Bogor, Indonesia), Bert H. Janssen and Nico de Ridder (WAU, Wageningen, The Netherlands). After his graduation he worked on temporary basis at the research station of Boomteelt Praktijkonderzoek, in Horst, Limburg. In the fall of 2000 he started his PhD research at Wageningen University within the Group of Crop and Weed Ecology on defence mechanisms in sorghum against the parasitic weed *Striga hermonthica*. During three cropping seasons he collected data for his PhD thesis at the research station of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), in Mali. He is currently working at Africa Rice Center (WARDA) in Cotonou, Benin, as agronomist in the Inland Valley Consortium. This APO position is financed by DGIS.