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Field Crops Research 93 (2005) 34–50
Field Crops Research
www.elsevier.com/locate/fcr

How can field selection for *Striga* resistance and tolerance in sorghum be improved?

J. Rodenburg[a,*], L. Bastiaans[a], E. Weltzien[b], D.E. Hess[c]

[a]*Department of Plant Sciences, Wageningen University, P.O. Box 430, 6700 AK Wageningen, The Netherlands*
[b]*International Crops Research Institute for the Semi-Arid Tropics, B.P. 320, Bamako, Mali*
[c]*Department of Agronomy, Purdue University, 915 W. State Street, West Lafayette, IN 47907-2054, USA*

Received 14 June 2004; received in revised form 2 September 2004; accepted 7 September 2004

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 below-ground 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 above-ground *Striga* number (NS_{max}) turned out to be discriminative and consistent selection measures. Both measures also corresponded well with the expression of resistance during below-ground 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.

Keywords: *Sorghum bicolor*; *Striga hermonthica*; Parasitic weeds; Screening methodologies

* Corresponding author. Tel.: +31 317 483519; fax: +31 317 485572.
E-mail address: j.rodenburg@cgiar.org, jonne.rodenburg@wur.nl (J. Rodenburg).

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doi:10.1016/j.fcr.2004.09.004

1. 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 above-ground *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 below-ground stages (e.g. germination, attachment, below-ground 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., 2001a). 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 *S. hermonthica* in sorghum, using *Striga*-free next to *Striga*-infested plots.

2. Material and methods

2.1. 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 *S. hermonthica* (Table 1). *Striga* seed for field and pot infestation, was collected in Samanko (all experiments) and Doumba, 80 km north-east of Samanko (agar-gel-assays only) and harvested from plants that parasitised sorghum.

2.2. 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 southwest 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 (2001–2003) 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

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. (2001b)
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
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) and 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

	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		

(2002 and 2003) with 45,000 (2001), 200,000 (2002), 30,000 and 150,000 viable *Striga* seeds m^{-2} (2003). 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 to 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.

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).

Above-ground *Striga* numbers were counted every 2 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., 2000). 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

Table 3
Information on field experiments in 2001–2003

Parameter	Year		
	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 45000	0 and 200000	0, 30000 and 150000
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

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 above-ground *Striga* plants at harvest ($NS_{harvest}$); (2) maximum number of above-ground *Striga* plants (NS_{max}); (3) area under the above-ground *Striga* number progress curve (ASNPC); (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 above-ground *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. (2000) was calculated as:

$$\text{ASNPC} = \sum_{i=0}^{n-1} \left[S_i + \frac{S_{(i+1)}}{2} \right] (t(i+1) - ti) \quad (1)$$

where n is the number of *Striga* assessment dates, S_i the *Striga* number at the ith assessment date, t_i the days after sowing at the ith 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):

$$\text{RYL} = \frac{Y_c - Y_s}{Y_c} \quad (2)$$

In an additional measure the RYL was divided by the maximum number of above-ground *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.

2.3. 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 6 replicates, with 10 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 above-ground *Striga* plants (NS_{bg} and NS_{ag}, respectively) were counted at 77 DAS.

2.4. Laboratory trial

Two agar-gel assays were conducted, in 2002 in a laboratory of Wageningen University, in Wageningen, The Netherlands, with 10 sorghum genotypes and *Striga* seeds from 2 different locations in Mali (Samanko and Doumba) in 8 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 5 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.

2.5. Statistical analyses

An analyses 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 below-ground 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. 413–426).

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 Section 3) genetic correlations could not be calculated.

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

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

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. 136–137). Repeatabilities set an upper-limit to the heritability of a selection measure.

3. Results

3.1. 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 2003 (H), 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 2003 H. 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 the three lowest resistant genotypes at the expense of Seredo. The three most resistant genotypes, based on NS_{max} and ASNPC, throughout the 3 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.

3.2. Below-ground information

A pot trial was conducted to determine the extent to which the number of emerged *Striga* plants (above-ground: NS_{ag}) reflects the number of attached *Striga* plants (below-ground; 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

Table 4
Means, rankings (1–10) and repeatabilities (*R*) of different measures used to express resistance in the field in 2001, 2002 and 2003 (L and H). Mean *Striga* number at harvest ($NS_{harvest}$), maximum above-ground *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		
2003 (L)[d]	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					
2003 (H)	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).

[d] In 2003, (H) means high *Striga* infestation level, (L) means low *Striga* infestation level.

Repeatability (*R*), the upper-limit for heritability, calculated according to Falconer and Mackay (1996).

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 number of attached or emerged *Striga* plants as observed in the pot experiment ($r(\mathrm{GS} - \mathrm{NS_{bg}}) = 0.304$; $r(\mathrm{GS} - \mathrm{NS_{ag}}) = 0.072$).

These data showed low stimulation of germination (GS) and low numbers of attachments and emergence ($\mathrm{NS_{bg}}$ and $\mathrm{NS_{ag}}$) 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 $\mathrm{NS_{bg}}$ and $\mathrm{NS_{ag}}$ were relatively high, whereas at N13, GS was high but $\mathrm{NS_{bg}}$ and $\mathrm{NS_{ag}}$ very low. Serena, Seredo, Tiémarifing and CMDT39 held an intermediate position in every stage.

3.3. 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 above-ground *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 above-ground *Striga* plants ($\mathrm{NS_{max}}$, 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 the lowest yielding genotypes. IS9830 and Framida belonged consistently to the highest yielding genotypes under *Striga*-infested conditions, except for Framida in 2003 H. Tiémarifing was a rather constant intermediate genotype, concerning Y_s. Only in 2003 H 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

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

Correlated traits		Year (level)			
		2001	2002	2003 (L)	2003 (H)
$NS_{harvest}$	NS_{max}	0.975*	0.462 ns[a]	0.977*	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.

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

Table 6
Means, standard errors (S.E.) or 95% confidence intervals (95% CI), repeatability (R) and rankings (1–10) of fraction of germinated *Striga* seeds (GS) and maximum germination distance (GD, in 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

Genotype	Germination							
	GS[a]	S.E.			GD (mm) [b]	95% CI		
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							
	NS_{bg} [b]	95% CI			NS_{ag} [b]	95% CI		
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			

Data are expressed per sorghum plant or sorghum seedling.
[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 third 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 the 10 sorghum genotypes for grain yield (kg ha^{-1}) under *Striga* (Y_s) and control (Y_c), relative yield loss due to *Striga* (RYL) and relative yield loss per *Striga* infection (a_{linear}) in 2001, 2002 and 2003 L (low *Striga* infestation level: L) and 2003 H (high *Striga* infestation level: 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.[c]	307.0			315.8						
	R[d]	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						
2003 (L)	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						
2003 (H)	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 ($P < 0.001$). No genotype effect was revealed at the $P < 0.01$ level of significance for Y_c 2001 ($P = 0.096$) and Y_s 2001 ($P = 0.037$). Degrees of freedom are: 36 (2001), 63 (2002) and 45 (2003 L and H).

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

[c] Standard error's of differences (S.E.D.).

[d] Repeatability (R), the upper-limit for heritability, calculated according to Falconer and Mackay (1996).

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, 2003 L (low *Striga* infestation level: L) and 2003 H (high *Striga* infestation level: H)

Correlated traits		Year (level)			
		2001	2002	2003 (L)	2003 (H)
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.

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 the 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.

3.4. 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.

4. Discussion

4.1. 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 × 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, 1987; Haussmann et al., 2000; 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.

4.2. 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, 1997; 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 is it 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 above-ground *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 above-ground *Striga* numbers, the a_{linear} decreases drastically (e.g. 2001 versus 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 above-ground 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 2003 L) but deviated significantly at higher infection levels (2002 and 2003 H). 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 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.

4.3. 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. (2000) 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 above-ground 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 above-ground *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 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}.

4.4. Usefulness of below-ground observations

Ejeta et al. (2000) and Kim (1996) stressed the importance of below-ground *Striga* observations in the assessment of resistance. Because these kind of observations is difficult to make in the field, one has to find other media, such as Petri dishes and pots to study below-ground 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. (2000) 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 below-ground resistance mechanism in a very specific stage (germination) are not necessarily identified by above-ground 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 Ejeta et al. (2000) and Kim (1996).

Combination of above-ground 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 number 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, 1987), 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).

5. Conclusions

Maximum number of above-ground *Striga* plants showed to be a reliable measure for resistance as a reasonable correspondence between number of below-ground 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 above-ground *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.

Acknowledgements

Financial assistance for this study was made possible through the beneficence of the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

We are grateful for contributions and support of WUR and ICRISAT-Mali. We especially thank Ana Amosse Dolo, Ibrahima Sissoko, the late Idrissa Sangare and Badara Diallo of ICRISAT. Professor Dr. Martin Kropff and Aad van Ast of Wageningen University are gratefully acknowledged for their input and advice.

We would like to thank Jacques Withagen and Dr. Niels Dingemanse for advice on statistics and quantitative genetics. This article is dedicated to the memory of the late Idrissa Sangare.

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