



The Use of Genetically Tolerant Maize (*Zea mays* L.) in the Control of *Striga hermonthica* in Northern Côte d'Ivoire

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Authors' contributions

This work was carried out in collaboration between all authors. Author LA designed the study and critically reviewed the first draft. Author CKK wrote the protocol, laid out the experiment; compiled the study results, performed the statistical analysis; wrote the first draft. Author IAZB supervised the study. Author RA critically reviewed the protocol. Author HAND helped a lot during field work and contributed to the results discussion. All authors read and approved the final manuscript.

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ABSTRACT

Aim: To use host plant tolerant maize (*Zea mays* L.) to control *Striga hermonthica* in northern Côte d'Ivoire and to test the infectivity of seeds of *S. hermonthica* populations on maize.

Study Design: Two-way factorial experiment on a randomized complete block design with three replications.

Place and Duration: Ferkessédougou research station of the National Center of Agricultural Research (CNRA), one year in 2011.

Methodology: The first factor was maize variety with two levels (IWD STR and GMRP-18). The second factor was *S. hermonthica* populations with six levels (StMi1, StMi2, StMa1, StSo, StMa2 and StMa3). A plot consisted of 2 rows, 5 m long, spaced 0.80 m apart with 0.50 m spacing between plants within the row. Data were collected on 18-maize competitive plants per plot.

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Results: The *Striga*-tolerant IWD STR produced up to 51% more grain ($P < .001$) than the susceptible variety. Three out of the six populations tested were able to significantly reduce grain yield ($P = .005$) by 38.5 to 58.7%. The difference in virulence of *S. hermonthica* populations followed a north-south gradient, with the highly virulent populations coming from the Northern Sudan Savanna zone. There was no strain specialization in the *S. hermonthica* populations tested.

Conclusions: Host plant tolerance is a useful control measure to combat the menace of *S. hermonthica* infestation in Côte d'Ivoire. The genetic development of *Striga* tolerant maize can be done without developing tolerant varieties to a particular strain of the parasite. Further studies should be carried out to determine the genetic diversity of *S. hermonthica* in Côte d'Ivoire and to understand the difference in virulence among populations.

Keywords: Maize; *striga*; genetic control; tolerant; virulence.

1. INTRODUCTION

Maize (*Zea mays* L.) is a major cereal staple food for rural and urban areas of the savanna zone in Côte d'Ivoire. It ranks second after rice in terms of consumption. The crop is essential in maintaining food security and improving farmers' income. More than 60% of maize cultivated areas are grown in the northern part of the country. However, yields recorded in the farmers' fields are very low and varying between 500 and 1000 kg ha⁻¹ (Kouakou et al. personal communication). This low yield is caused by several constraints, including *Striga* infestation. *Striga hermonthica* (Del) Benth. Of the Orobanchaceae family is the most widespread and is economically important biological constraint to maize production in Northern Côte d'Ivoire. It is estimated that about 108,159.1 hectares in maize production are severely infested by *S. Hermonthica* (Kouakou et al. personal communication). Complete yield losses occurred in *Striga* hot spots, obliging farmers to abandon heavily infested fields [1]. In order to reduce losses due to *Striga* infestation, many integrated control methods and growing of *Striga* tolerant maize varieties in association/rotation with trap crops have been practiced in *Striga*-infested endemic regions in Northern Côte d'Ivoire from 1999 to 2002 [2] before being suspended in 2002 due to the political instability.

Today, *Striga* infestation has become a national scourge and a threat on food security in endemic areas. Extensive management actions should be conducted to curb its attacks. Several control methods have been recommended, including genetic, [3], weeding [4], intercropping with trap and catch crops [5,6] application of high doses of nitrogen fertilizers [7], fallow, seed treatment and biological control [8]. These control measures are either impractical or labour intensive to the capital deficient farmers [9]. However, the use of genetic resistance is the most economical and environmentally sustainable way to control *Striga* [10]. Of this, host plant resistance or tolerance is considered the most affordable for poor farmers [11] since resistant cultivars can be grown without additional inputs [12]. Genetic resistance to *Striga* has been reported in maize plant [13,14]. Resistance to *Striga* refers to the ability of the host plant to stimulate the germination of the *Striga* seeds while preventing the attachment of the parasite to its roots, or kill the attached parasite [15]. The resistant maize has fewer *Striga* attachments, delayed parasitic development and higher mortality of attached parasites compared with the susceptible variety. The critical step is marked by the penetration of by haustorial cells of *Striga* into the host root tissues and eventually connecting the parasite to the vascular system of the host. Histologically, haustorial ingress on the resistant variety was often stopped at the endodermis. Parasites able to reach resistant host xylem vessels showed low haustorial development relative to

those invading susceptible roots [15]. *Striga* tolerance denotes the ability of host plants to withstand the effects of the parasites already attached. A *Striga* tolerant variety germinates and supports as many *Striga* plants (endures these infections) as compared to the susceptible variety but produces more grain and stover, therefore shows few symptoms of infestation [3]. *Striga* resistance or tolerance is quantitatively inherited [16] and the most appropriate traits for screening maize for *Striga* resistance are host plant damage score, grain yield under *Striga* infestation and *Striga* emergence [11]. The first two traits exhibit moderate inheritance (0.37 and 0.4, respectively) but heritability for *Striga* emergence is low (0.11). These characters are controlled predominantly by additive gene action, though non-additive gene action could also be important [17,18].

The more practical method of controlling *Striga* is to grow resistant maize varieties, but the cultural methods have been used because of the lack of resistant maize varieties [9]. In the absence of a resistant variety, Kim [3] has recommended the adoption of tolerance. Tolerant open pollinated varieties produced 2.0- 2.5 times the yield of susceptible varieties, especially under high *S. hermonthica* infestation [19].

The objectives of this study, therefore, were (i) to use host plant tolerant maize (*Zea mays* L.) in the control of *Striga hermonthica* in northern Côte d'Ivoire (ii) to test the infectivity of seeds of *S. hermonthica* populations on two maize host varieties (tolerant and susceptible).

2. MATERIALS AND METHODS

2.1 Experimental Site

The study was conducted at Ferkessédougou Station (9°36' N; 5°12' W; 330 m altitude with average annual rainfall of 1332 mm) under artificial *Striga* infestation. The soils of the station were gravelly red ferrallitic soils on shallow weathered schists with low effective cation exchange capacity and small amounts of total exchangeable bases. The level of available phosphorus was also frequently very low. Drainage was not hampered [20]. Rain falls during one well-defined wet season, from June to October [21]. The average annual temperature in the area was 27.1°C. Potential evapotranspiration reached 1847 mm. The vegetation belongs to the Sudanian Savanna zone [22].

2.2 Maize Varieties and *Striga* Populations

Two maize varieties of different genetic backgrounds and contrasting reactions to *Striga* were evaluated. The varieties were the *Striga*-tolerant/resistant (STR) open pollinated maize variety IWD STR, white and medium maturing (100 days), (developed by the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria), and the susceptible variety GMRP-18, yellow-grained and early (95 days), developed by the Centre National de Recherche Agronomique (CNRA), Côte d'Ivoire. The latter variety was derived from the CIMMYT QPM (Quality Protein Maize) gene pool designated as Pool 18.

The *Striga* seeds used for artificial infestation were collected from maize, millet and sorghum fields at the end of the previous growing season. Six samples or populations of *S. hermonthica* were collected from three locations, i.e., Tengréla, Ferkessédougou and Korhogo. The first location belongs to the agro-ecological zone called Sudan Savanna, and the last two belong to the Subsudan Savanna [22]. The six *S. hermonthica* populations were as follows:

- StMi1: population collected under millet at Kodolkaha, Korhogo;
- StMa1: population collected under maize at Katiofi, Korhogo;
- StMi2: population collected under millet at Maniasso, Tengréla ;
- StSo: population collected under sorghum at Zanasso, Tengréla ;
- StMa2: population collected under maize at Pégatienvogo, Ferkessédougou (Ferké);
- StMa3: population collected under maize at Tchélogokaha, Ferké.

2.3 Field Layout, Experimental Design and Trial Management

The technique for artificial infestation of *S. hermonthica* [11] was used. *Striga* seeds were mixed with finely sieved sand in the ratio of 1:9. The sand served as carrier material and provided adequate volume for rapid and uniform infestation. About 3000 germinable *Striga* seeds were placed in each planting hole of 8 cm depth and 10 cm diameter. Three maize seeds were placed in the same hole. The maize plants were thinned to one per hill two weeks after emergence to give a final plant population density of 25,000 plants ha⁻¹. Fertilization by 15-15-15 NPK of the artificially *Striga*-infested maize plots was carried out at the rate of 150 kg ha⁻¹. Half of the fertilizer was applied the day of planting and the other half 35 days later. Regular removal of weeds other than *Striga* was manually done.

A 2-way factorial experiment, laid out on a randomized complete block design with three replications, was set up in 2011. The first factor was maize variety with two levels (IWD STR and GMRP-18). The second factor was *S. hermonthica* populations with 6 levels (StMi1, StMi2, StMa1, StSo, StMa2 and StMa3). A plot consisted of 2 rows, 5 m long, spaced 0.80 m apart with 0.50 m spacing between plants within the row. This relatively wide spacing was adopted to reduce the number of hills for artificial infestation and to minimize the movement of *Striga* seeds into the adjacent hills. Two rows of each entry were separated by a 1.5 m alley to minimize the movement of *Striga* seeds from one population to other plots. The plots were arranged in a serpentine fashion. There were 22 plants per plot.

2.4 Data Collection and Statistical Analysis

Data were collected on 18-maize competitive plants per plot. Observations used in the *Striga* resistance-tolerance evaluation trials [11] were recorded, including grain yield, ear number, ear rot, husk cover, plant and ear heights, days to 50% anthesis and silking, anthesis-to-silking interval (difference between 50% silking and anthesis) percentage root lodging (percentage of plants leaning more than 30° from the vertical), stalk lodging (percentage broken at or below the highest ear node). In addition, host plant damage syndrome ratings and the number of emerged *Striga* were made 10 weeks after planting. The host plant damage syndrome ratings (STRA) were scored per plot on a scale of 1 to 9, where 1 = no symptoms, indicating normal plant growth and high tolerance and 9 = all maize plants dead or dying (i.e., highly susceptible). Maize *Striga* damage syndrome was used to calculate the “*Striga* severity” (STRSV), using the following modified formula [23]:

$$\text{STRSV} = \frac{\sum_{i=1}^9 (\text{STRA}_i \times n_i) \times 100}{\text{STRA}_{\max} \times N}$$

where n is the number of maize plants with the i th damage syndrome rating (STRA_i), STRA_{\max} is the host plant damage syndrome rating highest score, and N is the total number

of observations (maize plants). Additional variables measured were *Striga* incidence on maize, number of *S. hermonthica* attached seedlings (subterranean attached *Striga* plants, i.e., *Striga* plants which are attached to the roots but have not emerged above ground) and *Striga* vigor. Assessment of parasite vigor (0-9) took into account the following parameters similar to Haussmann et al. [24]: *Striga* height and the number of branches, where 0 indicates no emerged *Striga* plant (least vigor) and 9 the highest vigor. Data were collected on several traits but only those on the most important traits in the studies were presented here.

Data were computed on plot means of the individual characters with Gen Stat Discovery Edition 4 VSN International Ltd. A log transformation {log (counts+1)} was used on all *Striga* data prior to analysis, to ensure normal distribution of the error component before analysis of variance (ANOVA).

Least significant difference (LSD 0.05) values based on the analysis of variance were used for pair-wise multiple comparisons among means to identify significant differences among the means.

3. RESULTS AND DISCUSSION

3.1 Results

3.1.1 Performance of *Striga* tolerant maize variety for grain yield and other agronomic characters in a *Striga* environment

Under *Striga*-infested conditions, mean squares of all traits were significant for the two maize genotypes (G) Table 1. On the other hand, mean squares for *S. hermonthica* populations (Str) were significant for grain yield and plant height with the exception of anthesis-to-silking interval, root lodging and maize damage score at 10 weeks after planting (WAP). Mean squares of all characters were not significant for maize genotypes x *S. hermonthica* populations (GxStr). Variety IWD STR had high grain yield value (2736 kg.ha⁻¹) and low values for *Striga* damage syndrome ratings (3.27), root lodging (12.4%) an thesis-to-silking interval (3.56 days) and showed a normal plant height (131 cm). The STR variety produced up to 51% more grain than the susceptible variety.

Table 1. Comparison between the two maize varieties in grain yield, plant height, damage score, root lodging and anthesis-to-silking under *Striga*-infested conditions

| Host maize varieties | Grain yield (kg ha ⁻¹) | Plant height (cm) | Maize damage score 10 WAP (1-9) | Root lodging (%) | Anthesis -to-silking interval (days) |
|----------------------|------------------------------------|-------------------|---------------------------------|------------------|--------------------------------------|
| GMRP-18 | 1806 | 113.2 | 4.30 | 28.2 | 4.67 |
| IWD STR | 2736 | 131.0 | 3.27 | 12.4 | 3.56 |
| Grand mean | 2271 | 122.1 | 3.78 | 20.3 | 4.11 |
| LSD (0.05) | 307.7 | 5.70 | 0.505 | 12.02 | 0.948 |
| <i>P-var</i> | <.001 | <.001 | <.001 | .012 | .016 |
| <i>P-str</i> | .005 | .044 | .586 | .450 | .204 |
| <i>P- var x str</i> | .586 | .255 | .618 | .968 | .164 |

P-var: probability of F for variety; *P-str*: probability of F for *Striga*; *P-var x str*; Probability of F for cultivar x *Striga*; WAP: week after planting

The six *S. hermonthica* population samples used were different in terms of their pathogenicity effect on both maize genotypes for grain yield and plant height Table 2. *S. hermonthica* populations from Tengréla region were the most aggressive populations against the two maize varieties tested.

Table 2. Effects on maize grain yield, plant height, damage score, root lodging and anthesis-to-silking of *S. hermonthica* populations collected in three locations

| Grain yield and other agronomic traits of two maize varieties | | | | | |
|---|------------------------------------|-------------------|---------------------------------|------------------|-------------------------------------|
| <i>Striga hermonthica</i> population origin | Grain yield (kg ha ⁻¹) | Plant height (cm) | Maize damage score 10 WAP (1-9) | Root lodging (%) | Anthesis-to-silking interval (days) |
| Tengréla | 1875a | 115.9a | 4.01a | 26.0a | 4.58a |
| Ferké | 2458b | 124.2b | 3.73a | 19.4a | 4.17a |
| Korhogo | 2479b | 126.1b | 3.62a | 15.5a | 3.58a |
| LSD (0.05) | 395.1 | 7.08 | 0.290 | 14.89 | 1.059 |
| <i>P-values</i> | .005 | .015 | .390 | .354 | .170 |

Means with the same letter within a line are not significantly different from each other ($P=.05$) according to LSD test

The effects of the six *S. hermonthica* populations on the tolerant and susceptible maize varieties (IWD STR and GMRP-18) are presented in Table 3. Average percent grain yield and plant height reductions for both varieties due to these *Striga* populations were 38.5 – 58.7% and 9.7–20.5%, respectively. The *S. hermonthica* population collected on millet (StMi2) at Tengréla showed consistency in the reduction of grain yield of both maize varieties. Three of the six populations tested were able to significantly reduce grain yield ($P\text{-var} < .001$; $P\text{-str} = .005$) of the tolerant and susceptible maize varieties (IWD STR and GMRP-18). These *S. hermonthica* populations were collected on sorghum and millet (StSo and StMi2) in Tengréla region and on maize (StMa2) at Pegatienvogo, Ferké.

S. hermonthica population StSo was found to reduce significantly the height (13%) of the susceptible maize variety; followed by StMi2, StMa2 and StMa1 (3-4%). A significant ($P\text{-str} = .044$) but also lower reduction in plant height (1-6%) of the tolerant maize variety was observed between *S. hermonthica* populations StMi2, StMa2, StMa1 and StSo. All six *S. hermonthica* populations were not significantly ($P\text{-str} = .586$) different for their effects on the tolerant maize genotype in terms of maize damage score at 10 WAP, ($P\text{-str} = .450$) root lodging and ($P\text{-str} = .204$) anthesis-to-silking interval with the exception of StSo, and also StMa3 and StMa2 on the susceptible maize genotype.

3.1.2 *Striga* infection indices and severity on maize host plant

S. hermonthica population infection indices (number of underground *Striga* attachments, number of emerged *Striga* plants and *Striga* vigor) and severity on maize are presented in Table 4. The highly aggressive *S. hermonthica* populations (5.76 ± 1.28 parasite stems per maize plant; 13.06 ± 3.31 subterranean attached *Striga* plants; 43.92 ± 2.80 severity of *Striga* infection) seemed to come from the northern Sudan Savanna zone in Tengréla region. The virulence of the parasite seemed to be medium at Ferké in the southern Sudan Savanna zone (2.04 ± 0.47 parasite stems per maize plant; 10.55 ± 2.78 subterranean attached *Striga* plants; 40.84 ± 2.18 severity of *Striga* infection) and relatively lower in the northern SubSudan Savanna in Korhogo zone (1.94 ± 0.70 parasite stems per maize plant; 7.44 ± 1.93

subterranean attached *Striga* plants 38.64±1.72 severity of *Striga* infection). *Striga* vigor were approximately the same for *S. hermonthica* populations from Tengréla and Ferké, and relatively higher for *S. hermonthica* populations sampled at Korhogo. However, there was no significant difference in infection indices and severity among populations from any of the agro-ecological zones for the following traits: ($P=.355$) numbers of emerged *Striga*, ($P=.081$) subterranean attached *Striga* plants, ($P=.602$) *Striga* vigour and ($P=.200$) severity of parasite infection.

Table 3. Specific effects of six *S. hermonthica* populations collected from various crops: maize, pearl millet and sorghum on grain yield, plant height, damage score, root lodging and anthesis-to-silking and other agronomic traits on two maize varieties

| Host maize varieties (Traits) | <i>S. hermonthica</i> population origin | | | | | |
|---|---|--------------------|--------------------|--------------------|--------------------|---------------------|
| | Korhogo | | Ferké | | Tengréla | |
| | Ex-maize (StMa1) | Ex-Millet (StMi1) | Ex-maize (StMa2) | Ex-maize (StMa3) | Ex-millet (StMi2) | Ex-sorghum (StSo) |
| Grain yield | | | | | | |
| GMRP-18 | 1875a | 1958b | 1583a | 2292b | 1708a | 1417a |
| IWD STR | 3125cd | 2958c | 2583b | 3375d | 2042a | 2335a [§] |
| LSD (0.05) | 303.8 var | 526.2 str | | | | |
| <i>P-values</i> | <.001 var | .005 str | | | | |
| Plant height | | | | | | |
| GMRP-18 | 117.3b | 119.9c | 110.5b | 122.5c | 109.5b | 99.3a |
| IWD STR | 131.7a | 135.6b | 130.2a | 133.5b | 122.9a | 132.1a [§] |
| LSD (0.05) | 5.62 var | 9.74 str | | | | |
| <i>P-values</i> | <.001 var | 0.044 str | | | | |
| Maize damage score 10 WAP (1-9) | | | | | | |
| GMRP-18 | 4.07a | 4.10a | 4.57a | 3.80a | 4.13a | 5.13b |
| IWD STR | 3.20a [§] | 3.10a [§] | 3.37a [§] | 3.17a [§] | 3.57a [§] | 3.20a |
| LSD (0.05) | 0.499 var | 0.864 str | | | | |
| <i>P-values</i> | <.001 var | .586 str | | | | |
| Root lodging (%) | | | | | | |
| GMRP-18 | 17.5a | 32.7a | 24.8a | 23.2a | 18.4a | 52.6b |
| IWD STR | 4.2a [§] | 7.5a [§] | 16.0a | 13.5a | 20.4a | 12.8a |
| LSD (0.05) | 12.02 | 20.82 | | | | |
| <i>P-values</i> | .012 var | .450 str | | | | |
| Anthesis-to-silking interval (day) | | | | | | |
| GMRP-18 | 3.33a | 3.33a | 5.00b | 5.33bc | 4.33a | 6.67c |
| IWD STR | 4.00a | 3.67a | 3.33a | 3.00a | 3.33a [§] | 4.00a |
| LSD (0.05) | 0.880 var | 1.523 str | | | | |
| <i>P-values</i> | .016 var | .204 str | | | | |

- Means with the same letter within line of the same host maize variety are not significantly different from each other ($P = .05$) according to LSD test. Means with the same letter within column of the two host maize varieties are not significantly different from each other ($P = .05$). Means with the following symbol 'a[§]' within column of the two host maize varieties are significantly different from each other ($P = .05$).

- *P-var*: Probability of F for maize varieties; *P-str*: Probability of F for *Striga* populations

Table 4. *S. hermonthica* population infection indices and severity on maize host plants

| Parasite origin | | Emerged <i>Striga</i> counts (SE) | <i>Underground Striga</i> counts (SE) | <i>Striga</i> vigor (SE) | Severity of <i>Striga</i> infection (SE) |
|---|----------|-----------------------------------|---------------------------------------|--------------------------|--|
| Agro-ecological zone | Location | | | | |
| Northern Sudan Savanna | Tengréla | 5.76 (1.28) | 13.06 (3.31) | 2.67 (0.51) | 43.92 (2.80) |
| Southern Sudan Savanna | Ferké | 2.04 (0.47) | 10.55 (2.78) | 2.73 (0.69) | 40.84 (2.18) |
| Northern Subsdan Savanna | Korhogo | 1.94 (0.70) | 7.44 (1.93) | 1.83 (0.32) | 38.64 (1.72) |
| Probability of <i>F</i> for <i>Striga</i> | | .355 | .081 | .602 | .200 |

SE: Standard error of mean

3.1.3 Host-specificity in *S. hermonthica* populations: intracrop specialization (strain specialization to a maize variety)

Both tolerant and susceptible maize varieties were successfully infested by all six *S. hermonthica* populations tested Table 5. None of the populations of this species showed specificity to maize variety according to the parasite origin in terms of numbers of emerged *Striga* stems per host plant. Similarly, no specificity was observed for *S. hermonthica* populations sampled from plants parasitizing the different hosts, i.e., maize, pearl millet and sorghum. There was no significant difference in susceptibility of both tolerant and susceptible maize genotypes ($P= .658$) among the six *S. hermonthica* populations ($P= .239$) in terms of number of emerged *S. hermonthica* stems per one host plant.

Table 5. Susceptibility of two maize host varieties to *S. hermonthica* populations collected from various crops: maize, pearl millet and sorghum in three locations in Côte d'Ivoire. Mean (\pm SE) number of emerged *S. hermonthica* stems per one host plant at 10 weeks after sowing

| Host maize varieties | Parasite origin | | | | | |
|----------------------|-----------------|-----------------|----------------|----------------|-----------------|-------------|
| | Korhogo | | Ferké | | Tengréla | |
| | Ex-maize var 1 | Ex-Millet var 1 | Ex-maize var 2 | Ex-maize var 3 | Ex-millet var 2 | Ex-sorghum |
| GMRP-18 | 3.00 (1.32) | 0.25 (0.14) | 2.92 (1.45) | 1.25(0.72) | 6.08 (1.61) | 6.88 (2.97) |
| IWD STR | 4.25 (1.66) | 0.25 (0.14) | 2.00 (0.38) | 2.00 (1.15) | 4.50 (3.56) | 5.56 (3.25) |
| <i>P-values</i> | .658 var | | .239 str | | | |

P-var: Probability of *F* for maize varieties; *P-str*: Probability of *F* for *Striga* populations.

3.2 Discussion

Results showed that IWD STR variety produced up to 51% more grain yield than the susceptible variety. Such good performance under diverse *Striga*-infested population conditions confirmed that cultivar IWD STR was tolerant to *Striga* while variety GMRP-18 was susceptible. The absence of Genotype x *Striga* infestation interaction for grain yield,

host plant response (damage symptoms) and other agronomic traits also suggested that the two maize varieties were different for their horizontal resistance level. These results showed the merits of growing *Striga* tolerant maize varieties (STR) in *Striga* endemic zones rather than using susceptible varieties. This corroborates the findings of Badu-Apraku et al. [25], who observed STR varieties to have the highest grain yield, and *Striga* susceptible varieties to have the lowest grain yield under a *Striga*-infested environment. These results were also in agreement with the findings of Abdulai et al. [25] who reported that STR varieties grown in sole cropping produced up to 70% more than the farmers' maize variety, which was the susceptible check.

Furthermore, our results showed that growing a STR variety could lead to 625 - 1083 kg more gain than growing a *Striga* susceptible variety. Khan et al. [26] reported that revenue generated by the farmers is influenced by the amounts of crop yield obtained and the prices the product can fetch in the nearby markets. In Côte d'Ivoire, maize prices fluctuated between 0.2 - 0.6 USD per kg, so that the total income arising from sale of product from the STR variety could be estimated at 125 to 217 USD per hectare or 375 to 650 USD more. Consequently, there was a general increase in the amount of income in *Striga*-tolerant maize monocrop. Thus, host plant tolerance is a useful control measure to combat the menace of *S. hermonthica* infestation in Côte d'Ivoire. It could contribute to poverty alleviation through food security and income generation of farmers in *Striga* endemic areas. Moreover, it is considered to be the most economical, affordable, effective, and environmentally sustainable approach for controlling *Striga* in Africa for poor farmers [11].

S. hermonthica populations collected on sorghum and millet (StSo and StMi2) from Tengréla region in the northern Sudan Savanna zone were the most aggressive populations in terms of maize-grain yield reduction, especially the millet population. These were followed by the population collected on maize at Pegatienvogo, Ferké in the southern Sudan Savanna zone. This study revealed that there is a difference in virulence of *S. hermonthica* populations, with the highly virulent populations coming from the northern Sudan Savanna zone and the relatively less virulent in the southern Sudan Savanna zone of Côte d'Ivoire. This agrees with Kouakou et al. (personal communication) who reported the same observations. The hypothesis supporting the increasing of *Striga* infestations in Côte d'Ivoire according to a north-south gradient was confirmed. In a related study, Reda et al. [27] found variability on *S. hermonthica* populations originating from different geographical areas. Our results clearly identify different *S. hermonthica* populations occurring in northern Côte d'Ivoire, which are capable of reducing maize grain yield between 38.5 and 58.7%. Our findings will allow the National Agency Support of Rural Development (ANADER) and NGOs in charge of distributing *Striga* control technologies to take appropriate precautionary measures on the promotion and distribution of improved varieties in general and *Striga*-tolerant maize varieties in particular.

All six *S. hermonthica* populations tested showed no specificity to maize. There was no strain specialization to a variety of crop species in these populations. A similar conclusion was drawn by Johnson et al. [28] who pointed out that there is either no intracrop nor intercrop (strain specificity to crop species) specialization in *S. hermonthica* from Côte d'Ivoire. In contrast, King and Zummo [29] reported the existence of physiological specialization in *S. hermonthica* from West Africa. Rasha et al. [30] also reported host specificity and existence of two distinct strains on sorghum and millet. One of the applications of our results is that it provides information on the extent to which no difference in host preference exists among *S. hermonthica* from Côte d'Ivoire. Such information suggested that rotations of one susceptible cereal species with another leads to the

continuous build up of *S. hermonthica* populations. Farmers in Côte d'Ivoire should therefore use appropriate crops in their cropping systems in *Striga* endemic zones. Furthermore, breeding resistant varieties in the national program could easily be done without the necessity of developing varieties resistant to a particular strain of the parasite.

4. CONCLUSION

This study showed that the *Striga*-tolerant variety (STR) IWD STR produced up to 51% more grain than the susceptible variety under diverse *Striga*-infested population conditions, amounting up to 650 USD of income for a hectare of farmland. These results prove the merits of growing *Striga* tolerant maize varieties in *Striga* endemic zones rather than using susceptible varieties. Therefore, host plant tolerance is a useful control measure to combat the menace of *S. hermonthica* infestation in Côte d'Ivoire. It could contribute to poverty alleviation through food security and income generation of farmers in *Striga* endemic areas. No strain specialization to a variety of a crop species in *S. hermonthica* populations was found. Further studies are needed to determine the genetic diversity of *S. hermonthica* in Côte d'Ivoire and to understand the difference in virulence among populations.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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