

Genotype-Dependent Strigolactones Effect on Stimulation of *Striga hermonthica* (Del.) Benth Seed Germination and Induced Systemic Resistance Indicators in Reducing *Striga* Weed Population

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ABSTRACT

Purpose: To identify the presence of GR24 and other strigolactones in 27 maize genotypes in experiments 2 and 3 m – derived from a 7 x 7 full diallel single crossing of *Striga* resistant and susceptible maize genotypes including their parents and two checks varieties in experiment 1 – using an LC/MS/MS analytical procedure, as well as the level of stimulation of *Striga* seed germination by each genotype in a germination assay.

Research Method: Four different concentrations of prepared root exudates (0, 2, 4, and 6 mg/ml) were collected from 10 seedlings each of 27 genotypes for LCMS analysis and germination assay hydroponically through freeze drying. GR24 standard was used as a positive control.

Findings: The LC/MS/MS analysis revealed that only two genotypes namely SUWAN X SAMMAZ 17 and Check GWG111 produced a detectable amount of a similar compound as that of the standard GR24 (*m/z* 321). In the germination assay, all genotypes showed varied degrees of *Striga* seed germination stimulation at all applied concentrations of each genotype, with GR24 at 6 mg/ml and 4 mg/ml giving the highest *Striga* seed germination counts of 68.83 and 47.00 respectively, while TZSTR 190 at 2 mg/ml had the least *Striga* seeds germination counts of 2.00.

Research Limitations: The paucity of funds to acquire different strigolactone standards and repetition of the LCMS analysis using other concentrations of the samples.

Originality/Value: This research paves the way for the utilization of the freeze-drying method to concentrate exudates without degrading strigolactones.

Keywords: Germination assay, GR24, LC-MS-MS, Open pollinated varieties maize, *Striga*, strigolactone.

INTRODUCTION

Many seed germination stimulants have been extracted and identified in parasitic weeds host and non-host plants (Li *et al.*, 2020). Among the germination stimulants of parasitic weeds in host plants are three distinctive classes of compounds, which include dihydroquinones, strigolactones, and sesquiterpene lactones (Li *et al.*, 2020).

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Strigolactones were formerly believed to be biochemical sesquiterpene lactone compounds but later reclassified as apocarotenoids with the discovery of the ABC part (tricyclic part of lactones) derived from carotenoid, which is most likely from the action of carotenoid cleaving enzyme (Yoshimura *et al.*, 2020; Sanchez *et al.*, 2018).

The actual biosynthetic pathway for strigolactone biosynthesis is still to be resolved completely (Akiyama *et al.*, 2010; Xie *et al.*, 2013). However, all the strigolactones identified so far are intermediate carlactones (CL) derived from sequential catalyst reaction synthesis of β -carotene by three biosynthesis enzymes, which remain the most important (Khetkam *et al.*, 2014).

The biosynthesis enzymes, as reported by Yoshimura *et al.* (2020), include: Carotenoid Cleavage Dioxygenase 7 (CCD7), Carotenoid Cleavage Dioxygenase 8 (CCD8), and cis-trans Isomerase Dwarf 27 (D27). The D-ring connecting the ABC part through the enol-ether bridge with little changes has been suggested to be responsible for the biological activities of strigolactones in plants and the rhizospheres (Sanchez *et al.*, 2018).

Strigolactones play numerous vital functions in plant response to stress, development, and interaction with microorganisms in the rhizosphere of plants (Kohlen *et al.*, 2011; Proust *et al.*, 2011; Stauder *et al.*, 2018). It serves as a signaling molecule for the germination of some parasitic weed seeds like *Striga*, *Phelipanche* and *Orobanche* and signals the presence of a host plant to symbiotic arbuscular mycorrhizal (AM) fungi in the rhizosphere (Akiyama *et al.*, 2010).

It, in addition, inhibits branching of plant shoots as well as tillering ability of plants (Cardoso *et al.*, 2014). At present, close to twenty-five varied chemical structures and biosynthesis have been identified under this biochemical group and still counting, as many plant species are yet to be explored (Charnikhova, 2017). Strigolactones (strigol and strigyl acetate), which stimulate *Striga* seed germination, were first isolated from cotton, a non-host plant, in 1966. Different strigolactones have been identified in different plant species.

Ent-2'-epi-5-deoxystrigol and orobanchol were identified in rice (Xie *et al.*, 2013), Sl-like1 or methyl carlactonoate in *Arabidopsis* and heliolactone in sunflower (Stauder *et al.*, 2018). Heliolactones show similarity with SLlike 1 from *Arabidopsis* in structure

because of the absence of ABC-ring structure (Stauder *et al.*, 2018). A new novel strigolactone, 7 α - and 7 β -Hydroxyorobanchyl acetate stimulating parasitic weed germination in addition to 12 pre-existing ones, was reported by Khetkam *et al.* (2014) in cucumber.

Orobanchol, an *Orobanche* germination stimulant; alectrol and putative didehydro-orobanchol have been isolated from red clover, sorgolactone from sorghum and alectrol from cowpea. Strigol has also been identified in the root exudates of host plant sorghum, maize and millet (Charnikhova *et al.*, 2017; Yoneyama *et al.*, 2016).

Maize plant produces at least two strigolactones, strigol and sorgolactone (Xie *et al.*, 2010; Jatto *et al.*, 2024a; Jatto *et al.*, 2024b). Jamil *et al.* (2011) in their work reported some common SLs like sorgomol and 5-deoxystrigol and some yet to be named putative SLs, SL1 and SL2 with molecular mass of 348 and 376 respectively in maize. However, studies by Charnikhova *et al.* (2017) have shown the presence of seven unidentified SLs and 2 new structures were identified in maize.

Interestingly, these new structures carry unique non-canonical 4,4-dimethyltetrahydrofuran-2-one motif as A-ring structures instead of the classic canonical (di) methyl cyclohexane structure consisting of tricycle lactone (ABC-ring) and essential butenolide ring (D-ring) found in other SLs (Charnikhova *et al.*, 2017; Sanchez *et al.*, 2018). When isolated, they were found to stimulate the germination of *Striga hermonthica* seeds. Consequently, these structures identified were later named as Zealactones 1a and 1b (Charnikhova *et al.*, 2017; Jamil *et al.*, 2011).

Several novel strigolactones have been isolated from root exudates of various species of plants, however, many are still yet to be identified. Different varieties or cultivars within the same species may differ in the production of major strigolactones or germination stimulants (Yohannes *et al.*, 2016).

Strigolactones produced by individual plants are usually unstable and very low in concentration for isolation and characterization using ODS-HPLC separation (Xie *et al.*, 2010). Recovery in a culture filtrate using this method is put at as low as 2% thereby making it unfit for low strigolactone-producing plants like maize. However, the use of a simple and fast analytical tool known as HPLC-tandem mass spectrometry (LC/MS/MS) has been reported for adequate identification, isolation, characterization and

quantification of biomolecules in samples (Ismail *et al.*, 2019; Jamil *et al.*, 2011; Motmainna *et al.*, 2021; Araujo *et al.*, 2020). The quantity of strigolactone produced by plants has been reported to determine the amount of *Striga* weed germination. The higher the quantity produced, the higher the stimulated *Striga* seed germination.

Those plants that produce fewer levels of the stimulants tend to be useful in reducing *Striga* weed population in the field. Different varieties or cultivars within the same species may differ in the production of major strigolactones or germination stimulants (Yohannes *et al.*, 2016). The plant variety that produces fewer amounts of strigolactone will stimulate fewer germinations of *Striga* seeds, hence useful in managing and controlling *Striga* weed population. This present study aims to identify the presence of strigolactones in some selected hybrids of maize and their parents identified with high, low and moderate *Striga* infestation in a potted glasshouse experiment using LC/MS/MS and germination assay. The study also examines the relationship between the strigolactone production and *Striga* seed germination stimulation in maize for reduction in the weed population and control in the field.

MATERIALS AND METHODS

Planting Material

Forty-two hybrids (F_1 's and Reciprocals) obtained from a 7×7 full diallel crossing procedure, seven parental lines and three check varieties, giving a total of 52 genotypes, were screened for *Striga* resistance in *Striga* inoculated pot soils in Experiment 1. This experiment was conducted in a glasshouse located at Ladang 15 of the Faculty of Agriculture, University Putra Malaysia. Approximately 10 kilograms of topsoil mixed with lime and poultry manure was used to fill (16 cm × 16 cm) plastic pots. A total of 312 pots were used with 156 inoculated and 156 non-inoculated (control) arranged in a split-plot design and replicated three times (Fig. 5.1).

The *Striga* inoculated pots were mixed with a mixture of 100–150 sterilized viable *Striga* seeds and fine dry river sand at the ratio of 1:99 by weight (1 g of *Striga* seeds to 99 g of river sand) to achieve even distribution. The mixture was placed at 6–12 cm deep and pre-conditioned for 14 days before sowing of the *maize* seeds. Two seeds each of the 52 genotypes (42 crosses, 7 parents and 3 checks) were planted in the *Striga*-seed-inoculated potted soil and non-inoculated potted

soil, each at 4 cm deep and thinned to one plant per pot at one week after planting.

Controlled irrigation was practiced using a drip irrigation system according to requirements. Weeding was done frequently to keep the potted plant competition-free with other weeds. NPK 15:15:15 fertilizer was applied at the rate of 40N, 40P, and 40K at two weeks and four weeks after planting, and the *Striga* count was recorded at 7 and 10 weeks after planting.

Seeds of twenty-seven (27) genotypes, comprising nine crosses and their reciprocal hybrids (18 hybrids) out of the 42 hybrids, their seven parents and two check varieties screened with different reactions to *Striga* infestation, were selected from the potted glasshouse experiment and used for LCMS strigolactone detection and germination assay.

The crosses and their reciprocals selected include: recip. SUWAN × SAMMAZ 16, cross SAMMAZ 14 × SUWAN, TZRST 190 × TZSTR 193; TZSTR 190 × SAMMAZ 14, SAMMAZ 17 × TZSTR 190 and SAMMAZ 14 × TZSTR 193, SUWAN × TZSTR 193, SUWAN × SAMMAZ 17, SAMMAZ 16 × TZSTR 190, the parents, TZSTR 190, TZSTR 192, TZEI 114, SAMMAZ 14, SAMMAZ 16, SAMMAZ 17 and SUWAN, and the check varieties 5005 and GWG 111 (Table 1). The seeds of *maize* and *Striga* used in the experiment were supplied by the International Institute for Tropical Agriculture, Ibadan, Nigeria, and Green World Genetics (GWG) Seed Company.

Exudate Extraction Procedure and Sample Preparation for LC-ESI-MS/MS

The exudate extraction was carried out at the Weed Science Lab of the Crop Science Department of the Faculty of Agriculture, the Central Lab, and the Physiology Lab of the Institute of Tropical Agriculture and Food Security, University Putra Malaysia. Seeds from 27 *maize* genotypes selected from Experiment 1 (Table 1) were sterilized for 2 minutes in 70% ethanol (EtOH) and then for 5 minutes in 1% sodium hypochlorite (NaOCl). The seeds were thoroughly rinsed in distilled water. We germinated the seeds in Petri dishes with moistened filter paper for 7 days at 28°C in the dark (Figure 1A).

Ten germinated seedlings from each variety were transferred into Nalgene (115 mL filter units with 0.8 µm pore size) containing 2 cm glass wool fibre in the filter unit and moistened with 1 mL half-strength

Table 1: Descriptions of materials used

S/No	Genotype	Reaction to <i>Striga</i> Infestation
1	TZSTR 190	Resistant
2	TZSTR 193	Resistant
3	TZEI 114	Susceptible
4	SAMMAZ 14	Susceptible
5	SAMMAZ 16	Resistant
6	SAMMAZ 17	Susceptible
7	SUWAN	Highly susceptible
8	SAMMAZ 14 × TZSTR193	Highly susceptible
9	TZSTR193 × SAMMAZ 14	Resistant
10	TZSTR193 × SUWAN	Tolerant
11	SUWAN × TZSTR193	Highly susceptible
12	SUWAN × SAMMAZ 17	Highly susceptible
13	SAMMAZ 17 × SUWAN	Resistant
14	SAMMAZ 14 × SUWAN	Highly susceptible
15	SUWAN × SAMMAZ 14	Highly susceptible
16	SAMMAZ 16 × SUWAN	Highly susceptible
17	SUWAN × SAMMAZ 16	Resistant
18	TZSTR190 × SAMMAZ 16	Resistant
19	SAMMAZ 16 × TZSTR190	Tolerant
20	SAMMAZ 17 × TZSTR190	Resistant
21	TZSTR190 × SAMMAZ 17	Tolerant
22	TZSTR190 × TZSTR193	Resistant
23	TZSTR193 × TZSTR190	Tolerant
24	TZSTR 190 × TZEI 114	Susceptible
25	TZEI 114 × TZSTR 190	Resistant
26	Check 5005	Resistant
27	Check GWG 111	Highly susceptible

Hoagland's nutrient solution as culture medium (Figures 1B and 1C). The culture medium in each filter was removed by suction and replaced with a fresh solution at two-day intervals for three weeks. The setups were placed under inflorescence illumination and maintained at $25 \pm 1^\circ\text{C}$.

The exudates were collected by washing the filter with 150 mL of sterile water after 24 hours, and fresh sterile water was added. We extracted the collected root exudates three times using 100% LCMS GRADE acetone and kept them stored at -20°C . The acetone extracts were combined and washed using 0.2 M K_2HPO_4 (pH 8.4), dried over anhydrous MgSO_4 , stored at -80°C (Figure 2A), and later concentrated using a freeze dryer (Figure 2B).

A 4 mg/mL solution of the freeze-dried acetone extracts (powder) from each sample was prepared using 55% LCMS GRADE methanol, vortexed, and filtered through 0.2 μm spin columns into sterile glass vials for LC-QTOF-MS/MS analysis. This procedure adopted was a modification of protocols presented by Jamil *et al.* (2011).

LC-ESI-MS/MS Analysis of Samples

LC-ESI-MS/MS analysis was carried out on root extract exudates from 27 different genotypes by measuring 2 $\mu\text{g/mL}$ samples from sub-section and GR24 standard. A Thermo Scientific Ultimate 3000™ Q Exactive™ Hybrid Quadrupole Orbitrap mass spectrometer with an ESI attached to a UHPLC binary pump auto sampler (Macherey-Nagel, Düren,

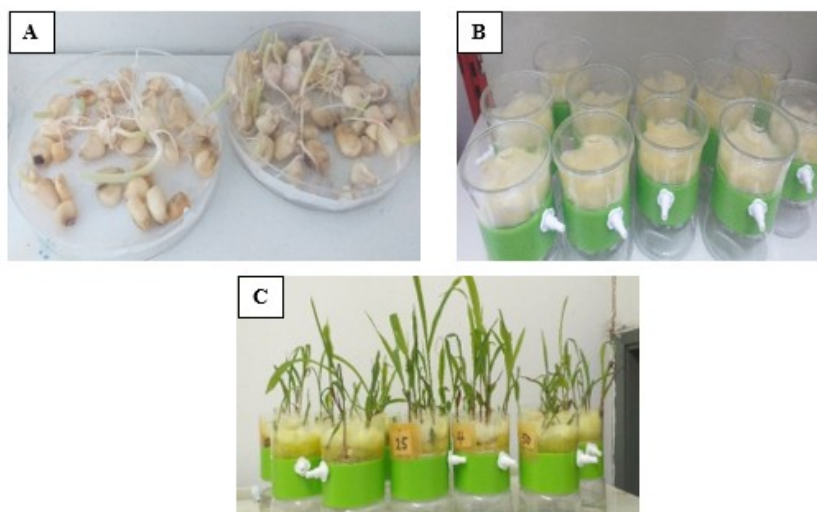


Figure 1: Picture showing strigolactone extraction process.

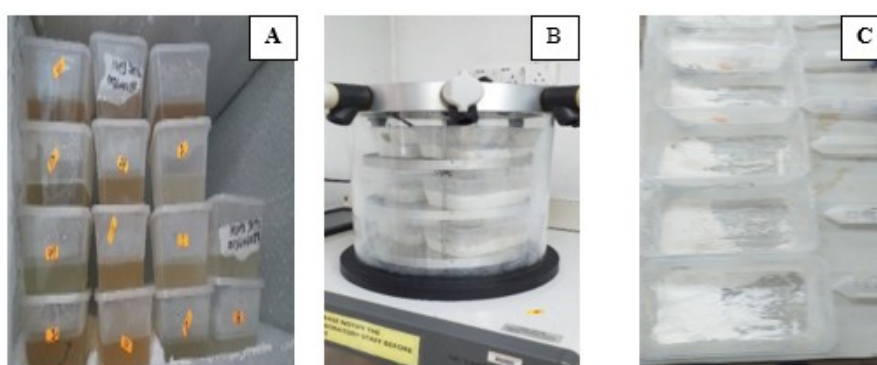


Figure 2: Extraction procedure and sample preparation for LC/MS analysis and *Striga* seed germination assay.

Germany) was used. Separation was performed using a Waters Acquity UPLC™ BEH C18 reversed-phase column (100 mm × 2.1 mm, 1.9 μm) (Ireland). The mobile phase was: A – 0.1% formic acid in water, and B – 0.1% formic acid in methanol, with a flow rate of 0.5 mL/min and an injection volume of 5 μL. The PDA range was 190–600 nm. The gradient elution program was as follows:

- 0–11 minutes: 95% A, 5% B
- 12–15 minutes: 10% A, 90% B
- 15–17 minutes: 95% A, 5% B

It remained isocratic at 95% A and 5% B until 20 minutes. The mass acquisition was operated in both negative and positive switch modes, with a voltage of 4.0 kV, capillary temperature of 350°C, a sheath gas flow rate of 80 arbitrary units, and a scan range of m/z 150 to 2000. Data acquisition was performed using Xcalibur 2.2 SP 1.48 (Thermo Fisher Inc) software.

***Striga* Seeds Germination Assay**

Pre-conditioning of *Striga* seeds: Germination assay experiments were conducted twice at the Weed Science Laboratory, Faculty of Agriculture, Institute for Tropical Agriculture and Food Security's Central and Physiology Laboratory, University Putra Malaysia. Under sterile conditions, *Striga* seeds were surface sterilized in 2% sodium hypochlorite containing 0.02% (v/v) Tween 20 for 5 minutes and rinsed thoroughly with distilled water.

The seeds were dried for 30 minutes in a laminar airflow cabinet. Approximately 100–150 seeds were spread on a glass fibre filter paper (GFFP) disc (9 cm diameter) and placed in sterilized Petri dishes (9 cm diameter), covered with a Whatman filter paper as described by Jamil *et al.* (2011). The setup was wetted with 2.7 mL of distilled water, sealed with parafilm, and incubated in darkness at 28°C for 12 days.

The setups were checked regularly, and water was added when necessary. After pre-conditioning, 1 g

of the preconditioned seeds was dissolved in 99 mL of distilled water (1:99), and 100 μ L containing approximately 75 seeds was pipetted into Petri dishes containing folded tissue papers.

Root Exudates Preparation: Four different concentrations: 0 mg/mL (Blank 55% methanol) as negative control, 2 mg/mL, 4 mg/mL, and 6 mg/mL of freeze-dried acetone exudates from each sample and GR24 standard (positive control) were prepared in 55% methanol.

Ten μ L of each sample solution was pipetted into each Petri dish containing *Striga* seeds in triplicates (three replications) arranged in a Completely Randomized Design (CRD), sealed using parafilm to maintain moist conditions, and incubated in the dark at room temperature ($25 \pm 1^\circ\text{C}$) for five days. This experiment was repeated twice and results were recorded accordingly.

Data Collection: The number of *Striga* seedlings and germination percentage at five days after incubation were recorded.

Data Analysis: The collected data were subjected to analysis of variance (ANOVA), and the means were separated using Fisher's Least Significant Difference (LSD) at the 5% level of significance. The germination percentage was calculated using the following formula 1.

RESULTS AND DISCUSSION

Table 2 presents the mean interaction for *Striga* germination count averaged in a split-plot potted maize experiment at 7 and 10 weeks after planting.

Mean Performance of Parent

The mean performances of the parents (per se performance) are presented in Table 2. The means are ranked according to their significance levels for *Striga* germination count at 7 and 10 weeks after planting. SAMMAZ 16 recorded the least average of *Striga* emergence/count at week 7 with an average of 0.08, followed by SUWAN (0.17), TZSR 190 (0.25), SAMMAZ 17 (0.25), TZEI 114 (0.67), SAMMAZ 14 (0.92), while the highest was recorded in TZSR 193 (1.17). TZSR 190 had the least *Striga* count at week 10 with an average of 0.08, followed by TZEI 114 (0.33), TZSR 193 (0.42), SAMMAZ 17 (0.50), SAMMAZ 14 (0.75), SUWAN (1.00), while SAMMAZ 16 had the

highest *Striga* count of 1.33 at week 10.

For *Striga* damage at week 7, the greatest damage was recorded in TZEI 114 (2.42), followed by TZSR 193 (1.92), SAMMAZ 14 (1.75), SAMMAZ 16 and SUWAN (1.65 each), while TZSR 190 had the least *Striga* damage rate. Similarly, TZSR 190 recorded the least *Striga* damage of 1.33 at week 10, followed by SAMMAZ 16 (2.25), TZSR 193 (2.33), SUWAN (2.42), SAMMAZ 17 (2.75), SAMMAZ 14 (2.83), while TZEI 114 was worst damaged (4.17) by *Striga* at week 10. The results show significant differences existing between all the genotypes (crosses and reciprocals) derived from the seven parents and three check varieties. This indicates that the genotypes were amenable to selection procedures (Bahari *et al.*, 2012; Fasahat, 2016).

For *Striga* count at week 7, the cross TZSR 190 $\times$ SAMMAZ 16 recorded the least *Striga* count/emergence of 0.08, followed by the cross SAMMAZ 17 $\times$ SUWAN (0.17), recip. SAMMAZ 17 $\times$ SAMMAZ 14 (0.17), check 5005 (0.17), cross TZEI 114 $\times$ SAMMAZ 16 (0.25), and recip. SAMMAZ 17 $\times$ TZSR 190 (0.25), while recip. SAMMAZ 14 $\times$ TZSR 193 had the highest *Striga* count of 2.58 at week 7, followed by recip. SUWAN $\times$ TZSR 193 (2.17), recip. SAMMAZ 16 $\times$ SAMMAZ 14 (1.75), and cross SAMMAZ 14 $\times$ SAMMAZ 17 (1.67).

For *Striga* count at week 10, recip. SUWAN $\times$ SAMMAZ 16 and cross SAMMAZ 14 $\times$ SUWAN recorded the least *Striga* count of 0.33 each, followed by cross TZSR 190 $\times$ TZSR 193 (0.50), cross TZSR 190 $\times$ SAMMAZ 17 (0.50), check 5005 (0.58), cross SAMMAZ 16 $\times$ SAMMAZ 17, TZSR 193 $\times$ SAMMAZ 17 and TZSR 190 $\times$ SAMMAZ 14 all recorded 0.67 each, while the highest *Striga* count of 2.83 was recorded in recip. SAMMAZ 14 $\times$ TZSR 193, followed by recip. SUWAN $\times$ SAMMAZ 17 (2.75), recip. SAMMAZ 17 $\times$ TZSR 193 (2.17) and recip. SAMMAZ 17 $\times$ TZSR 190.

Recip. SAMMAZ 17 $\times$ TZSR 190 and cross SAMMAZ 14 $\times$ SUWAN recorded the least *Striga* damage of 1.17 each at week 7, followed by cross TZSR 190 $\times$ SUWAN, cross TZSR 193 $\times$ TZEI 114, TZEI 114 $\times$ TZSR 193, and check 5005 with 1.25 each. TZSR 190 $\times$ TZSR 193 and TZSR 190 $\times$ SAMMAZ 16 also recorded 1.50 *Striga* damage each at week 7, while check GWG 111 recorded the highest *Striga* damage of 3.00 at week 7, followed by recip. SUWAN $\times$ TZSR 193 which recorded 2.67, and recip. SUWAN $\times$ SAMMAZ 17 and cross SAMMAZ 14 $\times$ SAMMAZ

$$\text{Germination Percentage} = \left(\frac{\text{Number of germinated } \textit{Striga} \text{ seeds}}{\text{Total number of } \textit{Striga} \text{ seeds}} \right) \times 100 \quad (1)$$

17 which recorded 2.42 each.

For *Striga* damage at week 10, recip. SAMMAZ 17 × TZSR 190 had the least *Striga* damage rate of 1.58, followed by cross TZSR 190 × TZSR 193 (1.67), recip. SAMMAZ 16 × TZSR 190 (1.83), recip. TZSR 193 × TZSR 190 (2.00), cross TZSR 193 × TZEI 114 (2.00), cross TZSR 190 × SAMMAZ 16 (2.00), and check 5005 (2.00), while check GWG 111 was the most damaged by *Striga* parasite (4.42), followed by recip. SAMMAZ 14 × TZSR 193 (4.25), check 888 (4.17), cross SAMMAZ 14 × SAMMAZ 17 (3.92), and SUWAN × TZSR 193 (3.67).

It is interesting to note that some hybrids such as TZSR 190 × SUWAN with low *Striga* counts were greatly damaged by *Striga* due to subterranean germination of the parasites without emerging at the surface, while others such as recip. SAMMAZ 14 × TZSR 193 and SUWAN × TZSR 193 with high *Striga* counts equally showed a great damage rate by *Striga* due to their high susceptibility to *Striga* evasion.

Some hybrids such as SAMMAZ 17 × TZSR 190 with high *Striga* counts had little or no damage due to their tolerance to the parasites, whereas resistant hybrids such as cross SAMMAZ 14 × SUWAN, cross TZSR 190 × TZSR 193, recip. TZSR 193 × TZSR 190, cross TZSR 190 × SAMMAZ 16, recip. SAMMAZ 16 × TZSR 190, and check 5005 showed little or no *Striga* count with low *Striga* damage and also performed greatly in terms of yield and yield components.

Similar trends were reported by Badu-Apraku *et al.* (2015); Gowda *et al.* (2021); Sangaré *et al.* (2018). Rodenburg *et al.* (2017) insisted that genotypes that exhibit low *Striga* counts and high *Striga* damage are not useful in breeding for *Striga* resistance programs.

This was in line with the reports of Shaibu *et al.* (2021) who reported a reciprocal effect on strigolactone production in maize plants.

LCMS Analysis of Samples

The LCMS analysis on the standard showed the value of GR24 to be *m/z* 321.07 on the full scan (Figure 3A).

The MS/MS fragment analysis showed fragments at *m/z* 321, *m/z* 224, and *m/z* 11 at a retention time of 3.95 minutes. This result agrees with the report of Rial *et al.* (2019).

The only genotypes that showed the same compounds as the standard at 3.95 minutes retention time were the hybrid reciprocal SUWAN × SAMMAZ 17 and the check GWG 111. The full mass scan of the hybrid reciprocal SUWAN × SAMMAZ 17 and the check GWG 111, as well as the MS/MS fragments at *m/z* 321, *m/z* 224, and *m/z* 11, are shown in Figures 3B and 3C. This result is also in agreement with the report of Rial *et al.* (2019).

Striga Seeds Germination Assay

The analysis of variance for *Striga* seed germination at 5 days: The analysis of variance for mean squares of *Striga* seed germination at 5 days for the combined analysis results for *Striga* seed germination assay arranged in a two-factor design is presented in Table 2. The mean squares from the analysis of variance in a combined season, as well as the mean interaction of treatment × concentration of the methanol-based root exudates from 27 maize genotypes and analogue synthetic Standard GR24 in a *Striga* seed germination assay, are presented in Table 2 and Table 3, respectively.

The result in Table 3 shows that the effects of treatment, concentration and their interactions on the germination of *Striga* seeds were highly significant. This indicates that the germination of *Striga* seeds is dependent on the treatment (genotypes) and the concentration of strigolactones in the root extracts formulation. This is in line with the findings of Mohamed *et al.* (2018) and Motmainna *et al.* (2021). Also, the combined analysis shows a highly significant difference in the repeated experiment. This could be a result of an increase in the duration of *Striga* seeds conditioning. The longer the period of pre-conditioning, the higher the germination of *Striga* seeds. This is in line with the work reported by Charnikhova *et al.* (2017) and Jamil *et al.* (2011).

Table 2: Mean interaction for Striga resistance characters of forty-two hybrids (crosses and reciprocals), seven parents and three varieties of maize in Striga inoculated potted experiment.

SOV	SCT7	SCT10	SDM7	SDM10
Inf. treatment				
Inoculated	1.53a	2.23a	2.47a	4.49a
Non inoculated	0.00b	0.00	1.00b	1.00b
Mean	0.77	1.12	1.74	2.75
CV	196.48	154.73	58.57	43.96
LSD	0.52	0.93	0.18	0.34
Genotype – Parents				
P1	0.25	0.08	1.33	1.33r
P2	1.17	0.42	1.92	2.33
P3	0.67	0.33	2.42	4.17
P4	0.92	0.75	1.75	2.83
P5	0.08	1.33	1.67	2.25
P6	0.25	0.50	1.50	2.75
P7	0.17	1.00	1.67	2.42
Genotype – Crosses				
P1 × P2	0.33	0.50	1.50	1.67
P1 × P3	1.08	1.75	1.58	2.50
P1 × P4	0.83	0.67	1.67	2.92
P1 × P5	0.08	0.92	1.50	2.00
P1 × P6	1.08	0.50	2.00	2.25
P1 × P7	0.33	0.83	1.25	2.42
P2 × P3	0.58	1.25	1.25	2.00
P2 × P4	0.25	1.42	1.50	2.58
P2 × P5	0.42	1.08	1.67	2.58
P2 × P6	0.83	0.67	1.58	3.25
P2 × P7	1.17	0.75	2.00	2.58
P3 × P4	1.58	1.58	2.17	3.58
P3 × P5	0.25	0.92	1.42	2.17
P3 × P6	0.42	1.33	1.67	2.67
P3 × P7	1.08	1.00	1.75	2.75
P4 × P5	0.83	1.42	1.50	2.33
P4 × P6	1.67	1.25	2.42	3.92
P4 × P7	0.50	0.33	1.17	2.92
P5 × P6	0.67	0.67	2.00	3.25
P5 × P7	1.20	1.30	1.50	2.67
P6 × P7	0.17	1.00	1.75	2.50
Genotype – Reciprocals				
P2 × P1	0.58	1.58	1.50	2.00
P3 × P1	0.50	0.83	1.67	2.33

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SOV	SCT7	SCT10	SDM7	SDM10
P3 × P2	0.50	1.25	1.25	2.75
P4 × P1	1.08	1.33	2.08	3.08
P4 × P2	2.58	2.83	2.08	4.25
P4 × P3	1.42	1.50	1.67	3.00
P5 × P1	1.33	1.33	1.58	1.83
P5 × P2	0.75	1.25	1.58	3.17
P5 × P3	0.58	1.08	1.58	2.17
P5 × P4	1.75	0.75	2.33	3.75
P6 × P1	0.25	2.00	1.17	1.58
P6 × P2	0.92	2.17	1.58	2.83
P6 × P3	1.08	0.83	1.67	2.50
P6 × P4	0.17	1.83	1.42	2.08
P6 × P5	1.08	1.08	1.83	3.33
P7 × P1	0.50	1.33	1.42	2.67
P7 × P2	2.17	0.67	2.67	3.67
P7 × P3	0.42	1.25	2.17	3.42
P7 × P4	0.42	1.75	1.58	2.92
P7 × P5	0.50	0.33	1.50	2.25
P7 × P6	1.08	2.75	2.42	2.92
Checks				
CHECK1	0.58	0.92	3.00	4.42
CHECK2	0.17	0.58	1.25	2.00
CHECK3	0.67	1.33	2.17	4.17
Mean	0.77	1.12	1.74	2.74
LSD	0.14	0.16	0.82	0.97
CV	236.29	203.69	77.78	85.01

SCT7 = Striga count at 7 weeks, SCT10 = Striga count at 10 weeks, SDM7 = Striga damage at 7 weeks, SDM10 = Striga damage at 10 weeks.

Table 3: Analysis of variance for *Striga* germination at 5 days after treatment in combined season.

Source of variation	df	MS
Season	1	363.15**
Treatment	27	825.71**
Concentration	3	24450.82**
Treatment × Season	27	159.86**
Treatment × Concentration	81	142.23**
Treatment × Season × Concentration	84	34.42**
Error	224	
Total	335	

** highly significant at p=0.001

Table 4: Mean interaction for treatment and concentration for *Striga* seed germination at 5 days after treatment for combined season

Treatment/Conc	0 mg/mL	Germ.%	2 mg/mL	Germ.%	4 mg/mL	Germ.%	6 mg/mL	Germ.%	Mean	Germ.%	LSD
GR24	0.00	0.00	24.00	32.00	47.00	62.67	68.83	91.77	34.96	46.61	5.77
TZSTR190	0.00	0.00	2.00	2.67	7.67	10.23	19.33	25.77	7.25	9.67	3.92
TZSTR193	0.00	0.00	18.83	25.11	34.67	46.23	43.17	57.56	24.17	32.23	10.42
TZEI114	0.00	0.00	5.50	7.33	14.67	19.56	21.00	28.00	10.29	13.72	3.44
SAMMAZ 14	0.00	0.00	11.50	15.33	20.83	27.77	28.00	37.33	15.08	20.11	3.81
SAMMAZ 16	0.00	0.00	15.50	20.67	23.50	31.33	32.50	43.33	17.88	23.84	3.50
SAMMAZ 17	0.00	0.00	9.83	13.11	17.00	22.67	24.83	33.11	12.92	17.23	2.90
SUWAN	0.00	0.00	16.00	21.33	25.67	34.23	33.00	44.00	18.67	24.89	5.01
SAMMAZ 14 × TZSTR193	0.00	0.00	13.33	17.77	22.33	29.77	30.00	40.00	16.42	21.89	3.66
TZSTR193 × SAMMAZ 14	0.00	0.00	3.67	4.89	10.00	13.33	18.83	25.11	8.13	10.84	2.93
TZSTR193 × SUWAN	0.00	0.00	7.00	9.33	14.50	19.33	19.17	25.56	10.17	13.56	2.52
SUWAN × TZSTR193	0.00	0.00	15.33	20.44	27.67	36.89	30.00	40.00	18.25	24.33	4.98
SUWAN × SAMMAZ 17	0.00	0.00	7.50	10.00	13.50	18.00	20.67	27.56	10.42	13.89	2.28
SAMMAZ 17 × SUWAN	0.00	0.00	13.50	18.00	21.17	28.23	30.33	40.44	16.25	21.67	6.82
SAMMAZ 14 × SUWAN	0.00	0.00	6.33	8.44	21.17	28.23	28.83	38.44	14.08	18.77	4.60
SUWAN × SAMMAZ 14	0.00	0.00	3.33	4.44	12.50	16.67	18.17	24.23	8.59	11.45	2.34
SAMMAZ 16 × SUWAN	0.00	0.00	13.67	18.23	21.50	28.67	32.00	42.67	16.79	22.39	8.41
SUWAN × SAMMAZ 16	0.00	0.00	11.17	14.89	17.00	22.67	27.67	36.89	13.96	18.61	4.87
TZSTR190 × SAMMAZ 16	0.00	0.00	10.67	14.23	19.83	26.44	26.17	34.89	14.17	18.89	5.75
SAMMAZ 16 × TZSTR190	0.00	0.00	5.00	6.67	13.67	18.23	17.50	23.33	9.04	12.05	3.83
SAMMAZ 17 × TZSTR190	0.00	0.00	8.00	10.67	20.83	27.77	31.00	41.33	14.96	19.94	6.17
TZSTR190 × SAMMAZ 17	0.00	0.00	10.67	14.23	24.00	32.00	34.33	45.77	17.25	23.00	6.07
TZSTR190 × TZSTR193	0.00	0.00	7.33	9.77	15.33	20.44	21.83	29.11	11.13	14.84	5.65
TZSTR193 × TZSTR190	0.00	0.00	3.50	4.67	12.33	16.44	20.67	27.56	9.13	12.17	3.05
TZSTR190 × TZEI114	0.00	0.00	7.50	10.00	13.33	17.77	20.17	26.89	10.25	13.67	3.06
TZEI114 × TZSTR190	0.00	0.00	4.17	5.56	10.50	14.00	16.50	22.22	7.79	10.39	3.16
CHECK 5005	0.00	0.00	7.83	10.44	19.17	25.56	24.33	32.44	12.83	17.11	3.13
CHECK GWG 111	0.00	0.00	14.33	19.11	23.17	30.89	43.67	58.23	20.29	27.05	7.57
Mean	0.00	0.00	9.89	13.19	19.45	25.93	27.95	37.27	14.32	19.09	0.72
LSD	0.00		3.76		4.73		6.12		2.11		2.29

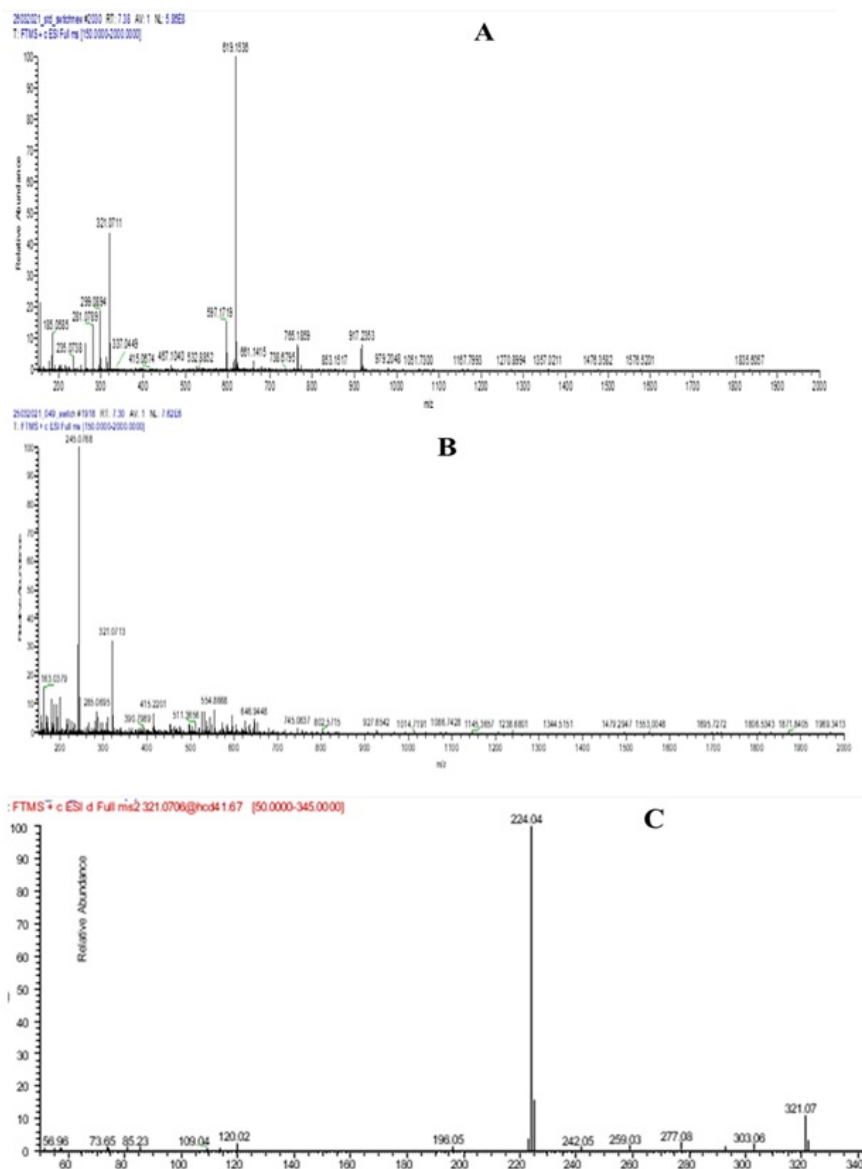


Figure 3: LC-MS analysis showing peak for the of strigolactone in sample. MS/MS fragmentation of standard strigolactone GR24 (A) and strigolactone in hybrid recip. SUWAN X SAMMAZ 17 (B) and Check GWG 111 (C).

Mean Interaction Effects of Treatment $\times$ Concentration on Striga Seed Germination

GR24 has the highest number of germinated *Striga* seeds

The mean interactions between treatment and exudates concentration on *Striga* seed germination as shown in Table 4 indicates that GR24 at 6 mg/mL and 4 mg/mL had the highest *Striga* seed germination of 68.83 (Figure 4A) and 47.00 representing 91.77% and 62.67%, respectively, followed by check GWG111 (43.67) 58.23% at 6 mg/mL (Figure 4E) and parent TZSTR 193 (43.17) 57.56% at 6 mg/mL (Figure 4D). While TZSTR 190 at 2 mg/mL had the least *Striga* seed germination of 2.00 representing 2.67%.

However, there was no significant difference with the control at a 0 mg/mL concentration. This was followed by SUWAN $\times$ SAMMAZ 14 (3.33) 4.44%, TZSTR 193 $\times$ TZSTR 190 (3.50) 4.17% and TZSTR 193 $\times$ SAMMAZ 14 (3.67) 4.80% at concentration 2 mg/mL. The overall mean showed that

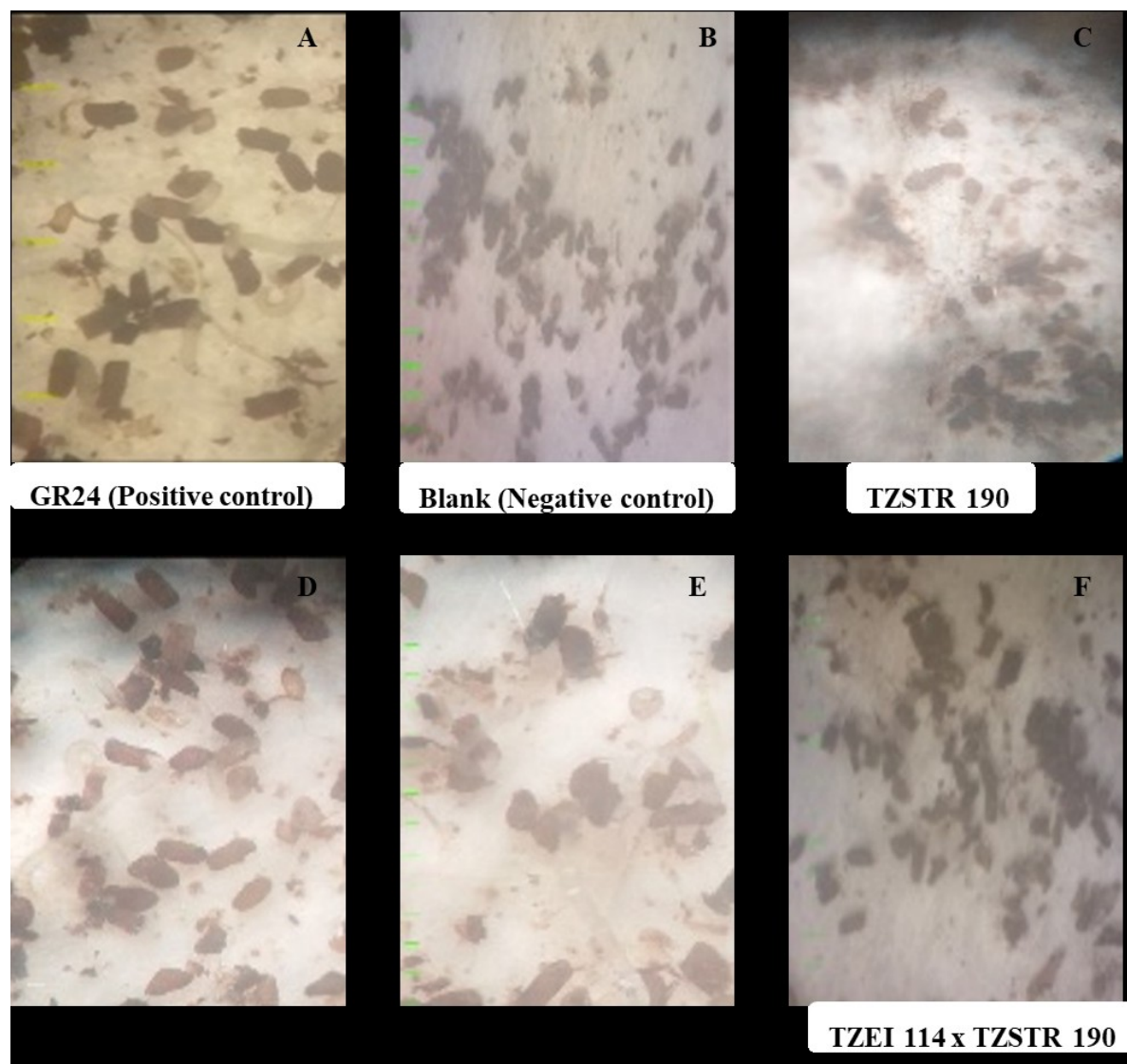


Figure 4: Striga seeds stimulated germination in GR24 and exudates from some maize genotypes.

at 34.96, representing 46.61%, which was significantly different from TZSTR 193, which has the second highest *Striga* seed germination of 24.17, representing 32.23%.

This was closely followed by Check GWG 111 (20.29) 27.05%, SUWAN (18.67) 24.89%, SUWAN $\times$ TZSTR 193 (18.67) 24.33% while TZSTR 190 has the least overall *Striga* seed germination of 7.25 representing 9.67% followed by TZEI 114 $\times$ TZSTR 190 with 7.79 (10.39%). However, there was no significant difference in the germination counts between the TZSTR 190 and TZEI 114 $\times$ TZSTR 190; the two genotypes with the least in the overall *Striga* seed germination are TZSTR 193 $\times$ SAMMAZ 14 (8.13) 10.84% and SUWAN $\times$ SAMMAZ 14 (8.59) 11.45%.

The result also shows that an increase in concentration of the root exudate solution across all genotypes and Standard GR24 gave a corresponding increase in *Striga* seed germination except TZSTR 190 at 0 mg/mL and 2 mg/mL, TZSTR 193 and SUWAN $\times$ TZSTR 193 at 4 mg/mL and 6 mg/mL, respectively, as well as SAMMAZ 16 $\times$ SUWAN at 2 mg/mL and 4 mg/mL. It is interesting to note that there was a significant difference in the *Striga* seeds germination between most crosses and their reciprocals when considering

the overall mean of the treatments, indicating that there could be reciprocal or maternal effects in the inheritance of strigolactones production by the maize plants.

CONCLUSION

Root extract exudates of two genotypes, namely SUWAN X SAMMAZ 17 and Check GWG111 produced a detectable amount of strigolactone compound under the conditions used in this study. However, all the genotypes stimulated the germination of *Striga* seed germination in various degrees at different concentrations of the root extract solution in a germination assay conducted. This may be due to either the amounts produced by the other genotypes were too small to be detected or there are other forms of strigolactones present in the roots. Some F1s and reciprocal produced from the cross between susceptible and resistant parental lines stimulated less *Striga* seed germination when compared to their *Striga* susceptible parents, which showed induced systemic resistance as a result of hybridization. However, it may be concluded that the different genotypes produced different mixtures of stimulants at different concentrations, which could be very low for detection by the procedure

used in this study. Further studies using different higher concentrations of the root extracts in an LC/MS/MS analysis should be conducted to identify stimulants present in samples.

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