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RESEARCH ARTICLE

Suicidal germination as a control strategy for *Striga hermonthica* (Benth.) in smallholder farms of sub-Saharan Africa

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Societal Impact Statement

Infestation by the parasitic plant *Striga hermonthica* is a severe threat to food security in sub-Saharan Africa, impacting the production of the major staple crops pearl millet and sorghum, equating to 7–10 billion \$ losses. Using *Striga* seed dependency on host-released germination stimulants, we have developed and validated a method for addressing the problem of accumulated parasite seedbanks—the major obstacle in combating *Striga* infestation in African rain-fed fields. Application of our method promises to alleviate the problem posed by this pernicious weed by increasing crop production for smallholder farmers.

Summary

- The root parasitic plant *Striga hermonthica* is a major threat to global food security, causing enormous losses in yields of the main staple crops in sub-Saharan Africa, which include pearl millet, sorghum, maize and rice.
- Sustainable *Striga* control should ideally lead to the depletion of the vast, long-lived *Striga* seedbank, and this can be achieved by inducing suicidal seed germination through application of strigolactone (SL) analogs in the absence of host plants. However, this “suicidal germination” strategy has not been evaluated under the natural rain-fed conditions that prevail in *Striga*-prone regions.
- We have developed and validated a protocol for suicidal germination in laboratory and natural conditions in *Striga*-infested rain-fed African fields. Three SL analogs were tested and these resulted to between 65% and 55% reduction in *Striga* emergence in pearl millet and sorghum fields, respectively.
- We conclude that suicidal germination is an effective method for reducing the *Striga* seedbank. Moreover, the minimal demands of our protocol, in terms of water consumption and amount of selected SL analogs, make it affordable and applicable at a large scale in African rain-fed agriculture, holding promise for sustainable cleaning of heavily *Striga*-infested fields in sub-Saharan Africa.

KEYWORDS

application protocol, farmers' field, methyl phenlactonoates, *Striga* spp., strigolactone analogs, suicidal germination, sustainable *Striga* management

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1 | INTRODUCTION

The root parasitic plants *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze are the most economically important weeds in the rain-fed agriculture of sub-Saharan Africa, infecting pearl millet, sorghum and other cereal crops (Haussmann, Hess, Welz, & Geiger, 2000; Kountche et al., 2013; Parker, 2009, 2012; Rispail et al., 2007). It is estimated that over 50 million ha of the sub-Saharan African arable land are infested with *Striga* spp., causing enormous yield losses that range from 40% to complete crop failure (Dörr, 1997; Ejeta, 2007; Gressel et al., 2004; Parker, 2012; Rodenburg, Bastiaans, Weltzien, & Hess, 2005; Venne, Beed, Avocanh, & Watson, 2009; Westwood et al., 2012). *Striga* damage has been reported to be exacerbated by low soil fertility and drought, the typical prevailing conditions in *Striga*-prone regions (Oswald, 2005). *Striga* is thus considered to be one of the greatest biotic constraints to food production in Africa, adversely affecting the livelihood of 300 million people, especially subsistence farmers, and aggravating food insecurity and poverty (Pennisi, 2010). Hence, the control of *Striga* is an important factor in ensuring food security in these regions (Ejeta, 2007; Rodenburg et al., 2005).

Striga is an obligate root hemi-parasite plant that cannot survive in the absence of a suitable host plant. A single *Striga* plant can produce 10,000–200,000 minute seeds under optimal conditions (Hearne, 2009). Indeed, these seeds germinate only in the presence of host-derived chemical signals, generally strigolactones (SLs), which is usually preceded by a period of pre-conditioning that requires warm weather and moist soil (Bouwmeester, Roux, Lopez-Raez, & Bécard, 2007; Ejeta, 2007).

SLs are a novel group of carotenoid derived plant hormones that regulate different developmental processes, such as the establishment of shoot and root architecture, and which are involved in plants' responses to biotic and abiotic stress (Al-Babili & Bouwmeester, 2015; Decker et al., 2017; Screpanti et al., 2016; Zwanenburg & Blanco-Ania, 2018; Zwanenburg & Pospíšil, 2013). In addition, SLs released by roots are key mediators of biotic interactions in the rhizosphere, inducing seed germination in *Striga* and related species of parasitic plant (Bouwmeester et al., 2007; Tank, Beardsley, Kelchner, & Olmstead, 2006), and triggering hyphal branching in mycorrhizal fungi to initiate AM symbiosis (Akiyama, Matsuzaki, & Hayashi, 2005). In this widespread mutualistic interaction, plants obtain minerals and water through the fungal hyphae and provide the fungal partner with photosynthetic products (Akiyama & Hayashi, 2006; Akiyama et al., 2005; Bonfante & Genre, 2010).

Strigol was the first natural SL isolated from roots of cotton, a non-host of *Striga* (Cook, Whichard, Turner, Wall, & Egley, 1966). Since then, the number of isolated SLs has increased steadily. Today, there are more than 25 known natural SLs (Ćavar, Zwanenburg, & Tarkowski, 2015; Xie, 2016) characterized by a common structure consisting of butenolide ring (D-ring) coupled in *R*-configuration via an ethol ether bridge to a tricyclic lacton (ABC-ring) in canonical SLs, such as strigol, or to a less conserved moiety in non-canonical

ones (Al-Babili & Bouwmeester, 2015; Jia, Baz, & Al-Babili, 2018). Stereoconfiguration of the B/C junction, modifications of the ABC ring and structural variations of non-canonical SLs give rise to the diversity of natural SLs (Al-Babili & Bouwmeester, 2015; Jia et al., 2018; Zwanenburg & Pospíšil, 2013).

A diverse array of control approaches have been pursued individually or in an integrated way to address the challenge presented by *Striga*. These approaches aim to improve soil fertility or directly target the parasite by chemical or mechanical means and include the use of resistant varieties as well as cultural measures (reviewed by Teka, 2014). Although these methods have helped in reducing the impact of this pernicious weed, they have not addressed the *Striga* seed problem effectively (Ransom, 2000). Thus, the extensive seedbank of *Striga* in infested-fields remains an impediment (Parker, 2012). As long as the *Striga* seedbank is not controlled adequately, the need to apply means to control the parasite will persist.

Suicidal germination is a promising option in combating *Striga*. This strategy refers to decreasing the seedbank in infested soils by applying synthetic germination stimulants in the absence of the host, and has been the subject of intense discussion for decades (Eplee, 1975; Kgosi, Zwanenburg, Mwakaboko, & Murdoch, 2012; Neffkens, Thuring, Beenackers, & Zwanenburg, 1997; Wigchert et al., 1999; Zwanenburg, Mwakaboko, & Kannan, 2016; Zwanenburg, Mwakaboko, Reizelman, Anilkumar, & Sethumadhavan, 2009). However, few studies have tested this strategy under field conditions (Samejima, Babiker, Takikawa, Sasaki, & Sugimoto, 2016; Zwanenburg et al., 2016). One such example has been the use of ethylene gas, a plant hormone that induces parasitic seed germination, in North Carolina to eradicate *S. asiatica*, through injection using special, sophisticated equipment (Eplee, 1975). However, this approach cannot be applied in sub-Saharan Africa where the income of subsistence farmers is usually too low to afford such technology (Ransom, 2000). Therefore, application of SLs or SL analogs appears attractive owing to their decomposition in the soil within a short period of time (Kannan & Zwanenburg, 2014; Zwanenburg et al., 2016). The use of natural SLs for this purpose is not a realistic alternative because chemical synthesis of these compounds is very laborious. In addition, plants produce and release SLs in very low amounts, even under phosphate starvation that triggers both processes (Halouzka, Tarkowski, Zwanenburg, & Ćavar, 2018; Matusova, 2005; Stewart & Press, 1990; Sugimoto, Wigchert, Thuring, & Zwanenburg, 1998; Wigchert et al., 1999; Xie, Yoneyama, & Yoneyama, 2010). Although significant success has been achieved in the development of a wide array of SL analogs (Jia et al., 2016; Kondo et al., 2007; Mwakaboko & Zwanenburg, 2011a, 2011b; Zwanenburg & Pospíšil, 2013), the practicability of the SL-based suicidal germination strategy has been rarely explored in field trials (Zwanenburg et al., 2016, 2009).

A series of SLs analogs can be used to develop a protocol for implementing the suicidal germination strategy for combating *Striga* in sub-Saharan Africa, such as the GR series, e.g., GR5 and GR7 (Johnson, Gowda, Hassanali, Knoz, & Monaco, 1981), Nijmegen-1

(Nefkens et al., 1997), analogs derived from ketones and cyclic keto enols (Mwakaboko & Zwanenburg, 2011a, 2011b) and analogs recently developed, derived from methyl phenlactonoates (MP series) (Jamil et al., 2018). Only a few of these SL analogs have been tested in soil, including GR5 (Johnson et al., 1981), Nijmegen-1 (Zwanenburg et al., 2016, 2009), analogs derived from tetralone and hydroxycoumarin (Kgosi et al., 2012). However, in addition to efficient stimulants, the suicidal germination approach requires a practical and economically affordable protocol. To the best of our knowledge, such a practical suicidal germination protocol that suits African rain-fed agriculture has not been established. Following an account of successful control of a related parasitic plant, *Orobancha ramosa*, infesting tobacco, we sought to test Nijmegen-1 in laboratory and field experiments (Zwanenburg et al., 2016, 2009), along with MP1 and MP3 from the MP series, which we selected based on their simple structure and attractive germination profile (Jamil et al., 2018), and because they do not negatively impact mycorrhization (Kountche et al., 2018).

In this study, we assessed the efficiency of these three selected, formulated SL analogs under laboratory, greenhouse and field conditions, and developed and validated a practical suicidal germination application protocol in Burkina Faso. Our protocol can be applicable at a large scale in African rain-fed agriculture, promising a new means of sustainable cleaning of heavily *Striga*-infested pearl millet and sorghum fields in West Africa.

2 | MATERIALS AND METHODS

2.1 | Synthesis and formulation of SL analogs

The synthetic germination stimulants viz., Nijmegen-1 (MW = 343.29), MP1 (MW = 319.27) and MP3 (MW = 274.27), and GR24 (MW = 298.29) were prepared as previously described in (Nefkens et al., 1997), (Jamil et al., 2018) and (Malik, Rutjes, & Zwanenburg, 2010), respectively (Figure 1). For germination bioassays, SL analogs were dissolved in acetone to prepare 10 mM

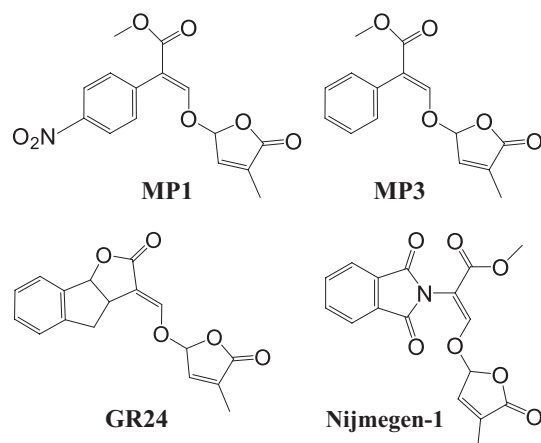


FIGURE 1 Chemical structure of selected SL analogs MP1, MP3, Nijmegen-1 and GR24

stock solution that was diluted with water to reach the required concentrations prior application. To formulate SL analogs, we used Atlas G-1086, a polyoxyethylene sorbitol hexaoleate (CRODA Company, Netherlands), dissolved in cyclohexanone at 1:4 ratio (see Zwanenburg et al., 2016, 2009).

2.2 | Plant materials

Seeds of *Striga hermonthica* were collected during 2012 from sorghum fields near Wad Medani, Sudan and kindly provided by Dr Abdel Gabbar Babiker. The highly *Striga*-susceptible rice cultivar "IAC-165" (Gurney, Slate, Press, & Scholes, 2006; Jamil et al., 2011) used in the pot experiments was obtained from Africa Rice Tanzania (Courtesy of Dr Jonne Rodenburg and Dr Mamadou Cissoko). Local susceptible pearl millet (Idipiéni, 11°55'32"N, 0°17'49"E) and sorghum (Itoyari, 11°58'53"N, 0°19'43"E) varieties were used to test the suicidal germination protocol in farmers' fields.

2.3 | In vitro *Striga* bioassays

We assessed the germination-inducing activity of selected SL analogs on *S. hermonthica* seeds using the protocol described by Jamil et al. (2011). To investigate the effect of the formulation agent on seed germination activity, SL analogs were applied, in both formulated and non-formulated form, at three concentrations (0.05, 0.5 and 5 μ M). The synthetic SL analog (GR24) and double sterile MilliQ water were used as positive and negative control, respectively. The germination ratio in % (GR%) was calculated for each replicate using the formula: $GR\% = (N_{gs}/N_{ts}) \times 100$, where N_{gs} is the number of germinated seeds per disc and N_{ts} is the total number of seeds per disc.

2.4 | Protocol development

To allow practical on-farm application of the suicidal germination approach, we developed a simple protocol where rainfall was used as the only source of water. Three different experiments were conducted in pots, mini-fields and farmers' fields. In both pots and mini-fields trials, irrigation water was supplied to mimic rainfall. In farmers' field experiments, plants were grown solely with rainfall. The protocol, illustrated in Figure 2, involves three main stages and was conducted as follows:

2.4.1 | Seeds pre-conditioning

Striga seeds were pre-conditioned for 10 days under moist conditions in order to respond efficiently to germination stimulants. For this purpose, three rains were simulated at three days interval starting from the experiment set up day (D0) where 20 mm rainfall (20 L/m²) was mimicked, followed by two simulated 10 mm rainfalls on D3 and D6, respectively. In field trials, a minimum of 6 weeks after the first rain (>10 mm) was set to allow adequate seeds preconditioning.

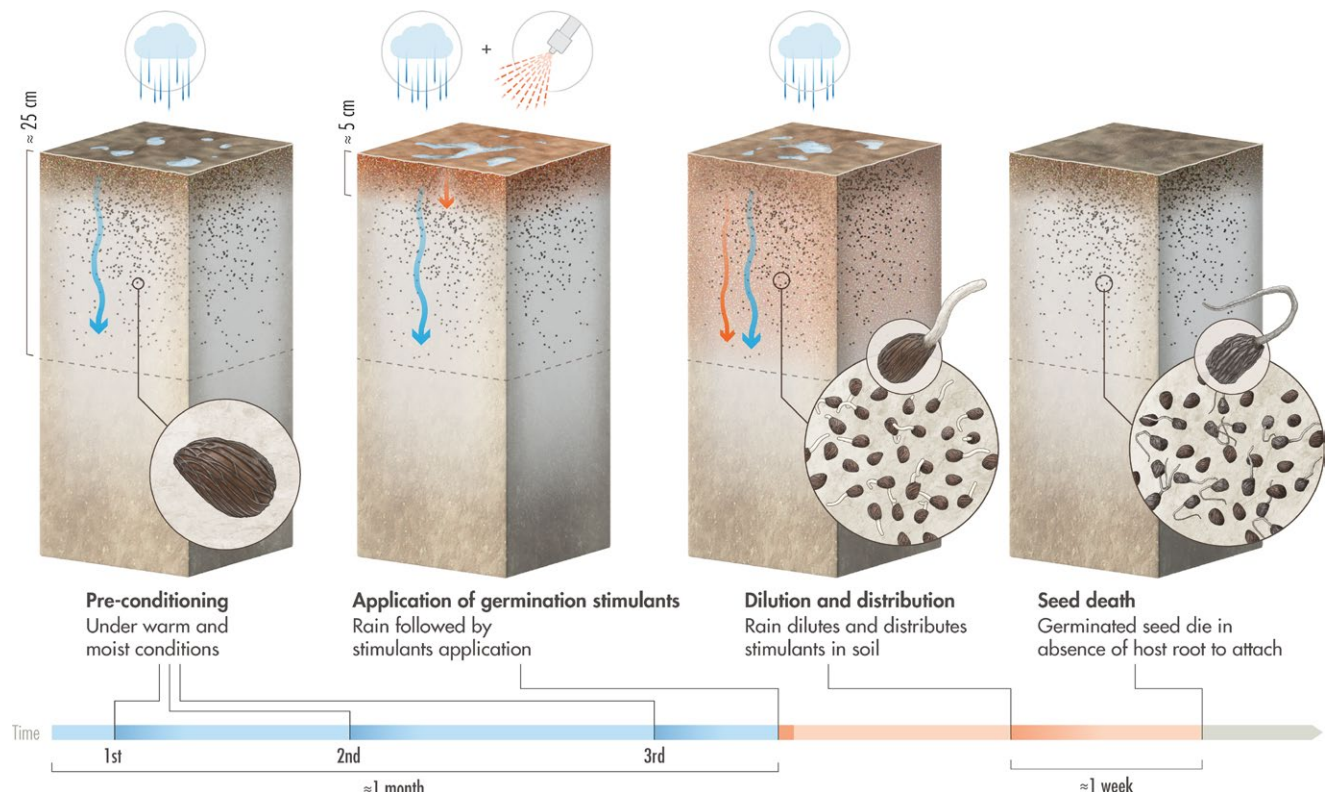


FIGURE 2 Schematic summary of the validated field protocol for suicidal germination application. In the first step, (pre-conditioned) *Striga* seeds become responsive to germination stimuli under moisture and warm stratification that prevail with the start of the rainy season. After this prerequisite step, formulated SL analog is applied in a concentrated form on moist soil, following a rainfall (≥ 10 mm). Soil moisture resulting from rainfall dilutes and distributes the applied SL analog that stimulates *Striga* seed germination. Germinated *Striga* seedlings cannot survive in the absence of a host and will then die in subsequent days

2.4.2 | Application of SL analogs

On the tenth day of pre-conditioning (D10), 10 mm rain was simulated. After 3 hr, SL analogs were applied in concentrated (400 μ M) and formulated form. In field trials, compounds were applied after a minimum of 10 mm rain. SL analogs were applied at 5×10^{-7} mol/L (0.5 μ M) estimated final concentration in a total of 20 mm rain received before and after application.

2.4.3 | Siphoning SL analog into the soil

To further dilute and distribute the SL analog in the top layer of the soil where the *Striga* seeds were placed, 10 mm rain was simulated one day after SL application (D11). Under field conditions, we relied on the next rain following application to dilute and distribute the germination stimulants. Effectiveness of the protocol and performance of formulated SL analogs were ascertained by estimating the germination rate and *Striga* emergence under pot, mini-field and field experiments.

2.5 | Pot experiment

The feasibility of the developed protocol was first evaluated under pot conditions using a randomized complete block design with five replications (pots) per treatment. Pots of 380 cm² of area and 5 L

capacity were filled with a mixture of silver sand (Hanson, UK) and soil (Stender, Germany) at 1:1 ratio. In each pot, about 4,500 *Striga* seeds were then mixed with the sand/soil substrate. All pots were kept in the greenhouse under natural light conditions at 35/28°C for Day/Night time, respectively. *Striga* seed preconditioning and SL analog application were performed following the protocol described above. Two one-week-old rice seedlings were sown in each pot 10 days after SL application. The potential of SL analogs was assessed by counting the number of emerged *Striga* plants per pot. Data on host-plant (rice) growth were recorded for plant height at the harvest.

2.6 | Mini-field experiment procedures

Efficacy of SL analogs and the feasibility of the protocol were further assessed under mini-field conditions by examining their germination activity on *Striga* seeds placed in Eplee bags. The mini-field consisted of a box of 1 × 1 m with 40 cm depth. Two independent experiments, differing in soil type, were conducted during the 2017 off-season at INERA-Kamboinsé research station (Ouagadougou, Burkina Faso). In the first experiment (mini-field 1), each box was filled with soil, characterized by a high clay content, collected from *Striga*-infested field near INERA-Kamboinsé research station (Ouagadougou, Burkina Faso). In the second experiment (mini-field 2), we used a mixture

(1:1 ratio) of this clay-containing soil and river sand, to assess the possible effect of soil type on the germination activity of SL analogs. About 50–100 cleaned *Striga* seeds were evenly spread on a glass fiber filter paper disc, which was then transferred into an Eplee bags. In total, nine bags were placed at 10 cm depth and spaced with 20 × 20 cm distance in each box. Randomized complete block design with three replications (boxes) per treatment was used in each experiment. Activity of SL analogs was determined by counting the percentage of germinated seeds under the microscope at day 3 after application. This was followed by a simulated 10 mm rain, to maintain soil moist and so maximize the exposure of seeds to the formulated SL analog for the second counting that was performed at day 6 after compound application.

2.7 | Field experimental procedures

Experiments in naturally infested fields were performed in two farmers' fields located near Kouaré research station (11°58'49"N, 0°18'30"E) (Fada N'Gourma, Burkina Faso). Fields were sown with widely used local pearl millet "Idipiéni" and sorghum "Itoyari" varieties, which were described as highly susceptible to *Striga* by farmers, and were collected and grown in field 1 (11°55'32"N, 0°17'49"E) and field 2 (11°58'53"N, 0°19'43"E), respectively. Each experiment was conducted in a randomized complete block design with four replications. Each plot consisted of two ridges of 3 m length and spaced with one ridge between rows. The hills within a single ridge were spaced from 0.50 m (7 hills per row), and the distance between plots was spaced with one ridge in order to provide enough space for *Striga* counting and to avoid border effects. About 15 cereal seeds were sown per hill. Seedlings were then thinned to two plants per hill three weeks after emergence.

Selected SL analogs (25 ml/m² at 400 µM) and the negative control (water) were applied in formulated form twice in each *Striga* sick-plot, following rains (≥10 mm). Crops were sown at least 1 week after the second application. Data on the number of emerged *Striga* plants at three counting dates were collected on a plot basis. The three *Striga* counts were then used to calculate the average number of emerged *Striga* plants throughout the season. Efficiency of the developed

protocol and performance of SL analogs were determined by comparing the mean number of emerged *Striga* of each SL analog to the mean number of emerged *Striga* of the control (water). Performance of each SL analog expressed in percentage decrease in *Striga* emergence ($D\%$) was calculated following the formula: $D\% = \left[\left\{ \frac{(\bar{X}_t - \bar{X}_w)}{\bar{X}_w} \right\} \times 100 \right]$, where $D\%$ is the percentage decrease for the treatment, $\bar{X}_t$ is the mean number of emerged *Striga* in t formulated SL analog treated plots, $\bar{X}_w$ is the mean number of emerged *Striga* of the formulated water used as control.

2.8 | Statistical analysis

Data collected from each experiment were analyzed following one-way analysis of variance (ANOVA). Conceptually, the statistical model used to perform the analysis of data recorded under each validation experiment is described as follows: $Y_i = \mu + \alpha_i + \varepsilon_i$, where Y_i is the observed performance of the treatment; μ is the overall mean, α_i is the effect of i^{th} treatment and ε_i is the random experimental error. Treatment means were further compared using the Tukey Honesty Significance Difference Test (HSD) package implemented in R software.

3 | RESULTS

3.1 | Formulated SL analogs exhibit moderate to high germination activity under lab conditions

First, we assessed the germination activity of MP1, MP3 and Nijmegen-1 (Nij1) on *S. hermonthica* seeds in bioassays conducted under lab conditions and determined the effect of the formulation on this activity. Analogs were applied in formulated and non-formulated form at 0.05, 0.5 and 5 µM concentrations. At 5 µM concentration, we observed high germinating activity with all tested SL analogs (Figure 3a). At a 10-fold lower concentration (0.5 µM), the mean germination percentage of MP1 (61%) was slightly below that of the positive control GR24 (66%) and higher than that of Nij1 (54%) and MP3 (44%) (Figure 3b). The differences between the three

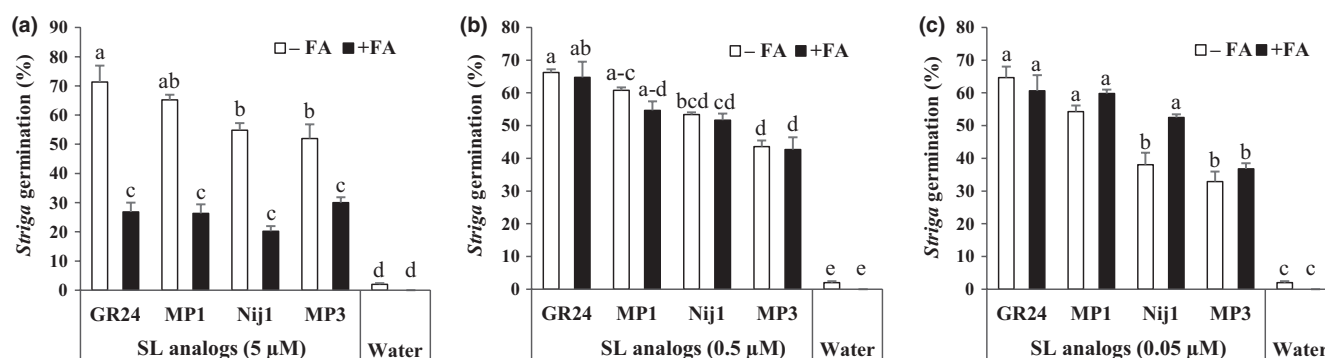


FIGURE 3 In vitro *Striga* germination bioassays of MP1, MP3 and Nijmegen1 (Nij1). (a) Effects of formulated (+FA) and non-formulated (-FA) SL analogs at concentrations of 5 µM; (b) 0.5 µM; and (c) 0.05 µM are shown in black and white bars, respectively. GR24 and sterile water were used as positive and negative controls respectively. Means sharing the same letter in either the black or white bars are not significantly different according to Tukey's HSD ($p < 0.05$)

compounds were more pronounced when applied at the low concentration of 0.05 μM . Application of GR24 and MP1 led to a germination rate of 65% and 54%, respectively, while Nij1 and MP3 induced significantly lower germination in treated seeds, with a rate of 38% and 33%, respectively (Figure 3c).

At 5 μM concentration, formulation of the compounds resulted in an obvious decrease in germinating activity (Figure 3a). This negative effect was not detected at the lower concentration of 0.5 μM . At 0.05 μM concentration, the formulation led even to a significant increase in the activity of Nij1 (Figure 3c). We also observed slightly elevated activity of MP1 and MP3 at 0.05 μM concentration upon formulation. However, this effect was not statistically significant (Figure 3c).

3.2 | Formulated SL analogs induce suicidal germination in pots under greenhouse conditions

Next, we evaluated the ability of SL analogs in inducing suicidal germination of *Striga* seeds in soil under greenhouse conditions at KAUST, using the highly *Striga*-susceptible rice cultivar "IAC-165" as host. Based on their availability at the time of the experiment, Nij1, MP1 and GR24 were selected as stimulants and applied at an estimated final concentration of 0.5 μM in formulated form to artificially *Striga*-infested pots. We sowed IAC-165 seeds 10 days after application, thus allowing the surviving *Striga* seeds to germinate and attach to host plant roots. This treatment led to a considerable decrease on average in the number of emerged *Striga* plants in pots treated with GR24 and MP1 (0.50 and 0.25 plants, respectively), compared to the control (6 plants) (Figure 4a). The application of Nij1 also reduced the number of emerged *Striga* plants, but this decrease was statistically non-significant and less pronounced when compared to the application of GR24 and MP1 (Figure 4a). In order to determine the impact of reducing *Striga* infestation on host performance, we collected data on rice plant height. As expected, the growth of the host plants was correlated negatively with the number of emerged *Striga* plants. Accordingly, the average plant height was significantly higher

in GR24 and MP1 treated pots (73–74 cm) compared to water and Nij1 treated pots (30–42 cm) (Figure 4b, c). These results suggest that MP1 was more active in inducing suicidal germination of viable seeds, thereby reducing the damage on host plant growth.

3.3 | Suicidal germination activity of formulated SL analogs under mini-field conditions

Next, we investigated the germination activity of formulated SL analogs on *Striga* seeds in two independent mini-field experiments performed at Kamboinsé research station (Ouagadougou, Burkina Faso). The aim of these experiments was to validate the feasibility of the developed protocol and to determine whether the soil type affects the germination stimulating activity of SL analogs. In both experiments, the protocol proved to be successful in breaking *Striga* seed dormancy and making them responsive to applied SL analogs, as demonstrated by changes in the germination rates (Figure 5). In the first experiment conducted in a soil with high clay content, MP1 showed high germination activity that was measured on day 3 (61%) and 6 (69%) after application. This activity was at least in the range of that of the positive control GR24. By contrast, Nij1 and MP3 effect was similar to that of water used as a negative control (Figure 5a). In the second experiment, in which we used a sand/soil mixture, we also observed highest activity for MP1 and the positive control GR24 on day 3 and 6 after application, although at a level significantly lower than in experiment 1. Interestingly, the activity of Nij1 was moderate but significantly higher than that of the negative control (water). Activity of MP3 was slightly higher, but not significantly different from that of the negative control (Figure 5b). Despite high temperatures (40°C average), we detected moderate (14%, Figure 5b) to high (up to 69%, Figure 5) *Striga* seed germination with MP3, Nijmegen-1, and MP1 in the mini-field experiments conducted during the off-season. This result indicates that these compounds can remain stable for at least a week and are fortunately still active under such harsh conditions. Taken together, these results confirm that SL analogs are also active in African soil

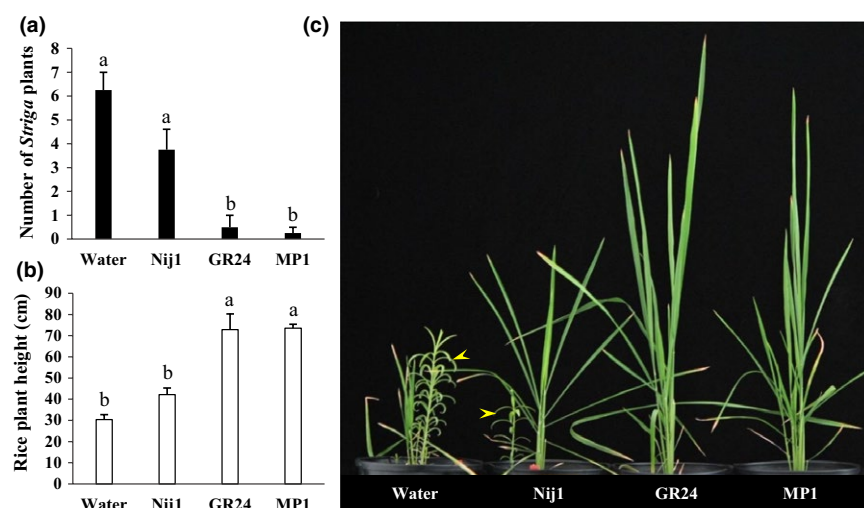
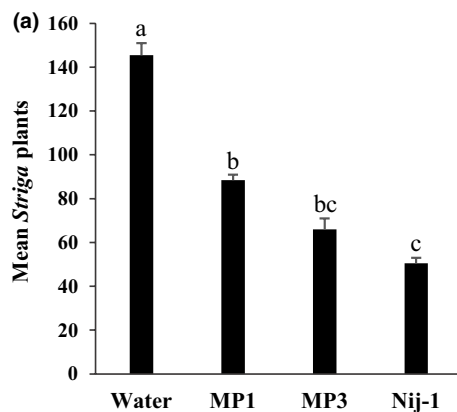
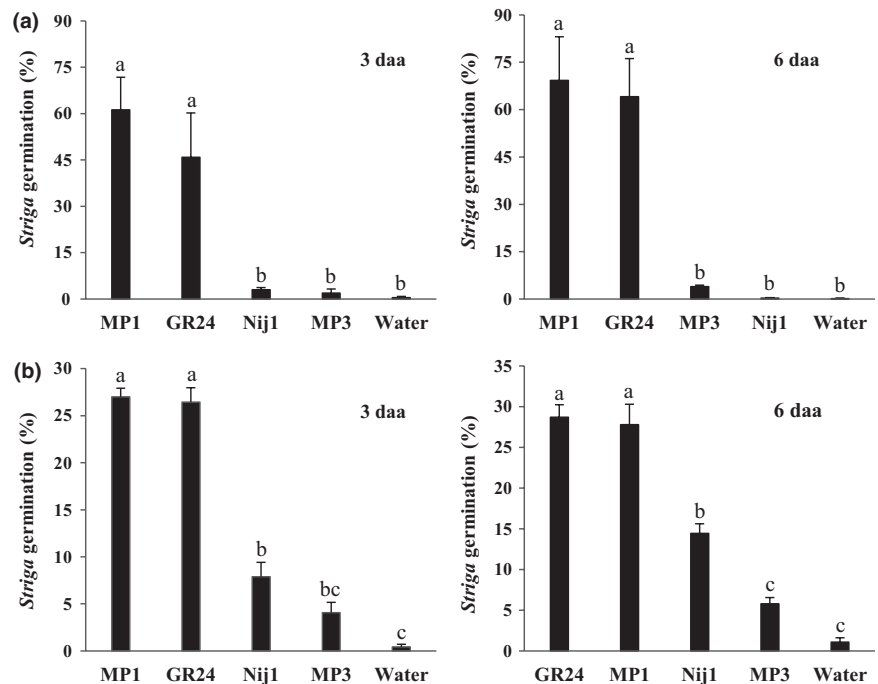


FIGURE 4 Suicidal germination activity of formulated SL analogs in pots. (a) Number of emerged *Striga* plants; (b) host-plant height; and (c) *Striga* damage on host-plant growth. Arrows in yellow show *Striga* plants invading rice. Bars represent mean $\pm$ SE ($n = 4$). Bars showing different letters display significant differences following Tukey's HSD ($p < 0.05$)

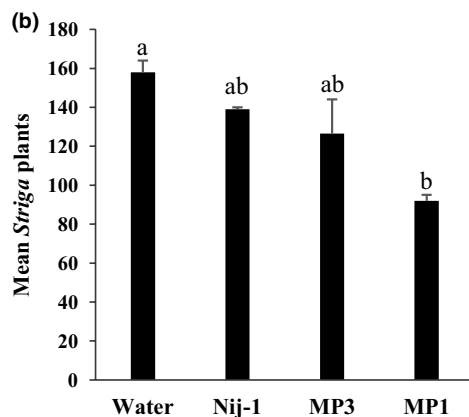
FIGURE 5 Effect of formulated MP1, MP3 and Nijmegen1 (Nij1) on *Striga* seed germination under mini-field conditions. Mean germination rates are shown for mini-field 1 (a) and mini-field 2 (b) conducted during of offseason 2017. Activity of selected SL analogs was compared to that of GR24 at two countings 3 and 6 days after application (daa). Bars represent means $\pm$ SE ($n = 9$). Different letters indicate significant differences between treatments following Tukey's HSD ($p < 0.05$)



Nij-1 treated plot



Water control plot



MP1 treated plot



Water control plot

FIGURE 6 Suicidal germination activity of formulated MP1 and Nijmegen1 under farmer's field conditions. Performance of formulated SL analogs on *Striga* emergence in the two farmer's fields grown with pearl millet (a) and sorghum (b) are shown. Water in formulated form was used as control. Values represent average number of emerged *Striga* plants. Means sharing different letters indicate significant difference according to Tukey's HSD ($p < 0.05$). Photographs show plots treated with the best performing SL analogs and the corresponding water-treated controls

and climate, and that soil type may affect the germination activity of SL analogs.

3.4 | Formulated SL analogs induce suicidal germination in *Striga*-infested farmer's fields

We further evaluated the developed protocol (Figure 2) for the application of SL analogs in rain-fed agriculture and validated it during the 2017 rainy season under farmers' field conditions. During the 2017 cropping season, we observed, in general, high *Striga* infestation in the region where we conducted the field experiments. Figure 6 shows the performance of formulated SL analogs in inducing suicidal germination in the two field experiments. In pearl millet grown field (field 1), number of emerged *Striga* plants was on average significantly lower in plots treated with formulated Nij1 (51 ± 2.5), MP3 (66 ± 5.0) and MP1 (89 ± 2.5) compared to the control plot (146 ± 5.5) that was treated with formulated-water. In other words, treatment with Nij1, MP3 and MP1 led to 65%, 55% and 39% reduction of *Striga* emergence, respectively (Figure 6a). In the sorghum field (field 2), the mean number of *Striga* plants was significantly lower (92 ± 3.0) in MP1 treated plots compared to control plots (158 ± 6.0). On average the number of *Striga* in MP3 (127 ± 17.5) and Nij1 (139 ± 1.0) treated plots were also lower compared to control plots, however, these differences were statistically non-significant (Figure 6b). This study also revealed variation in the potential of MP3 and Nij1 across the two field conditions.

4 | DISCUSSION

4.1 | Effectiveness and potential of the suicidal germination application protocol to contribute to integrated *Striga* control

For over 4 decades, suicidal germination has been advocated a powerful approach to combat the root parasitic weeds of the family Orobanchaceae, because it offers the possibility to rapidly decrease the significant seedbank. However, the technology has not been applied owing to the lack of suitable germination stimulants and practical application protocol. In the past decade, an increasing number of SL analogs have been developed, including compounds that could be used to deplete *Striga* seedbank in infested soil (Jamil et al., 2018; Samejima et al., 2016; Zwanenburg et al., 2016, 2009). Here, we report, for the first time, the development of a protocol for suicidal germination application (depicted in Figure 2) that can be used by smallholder farmers to significantly decrease the enormous *Striga* seed reservoir in infested-fields. Generally, validation experiments should demonstrate that the developed protocol is reliable for the intended application. Evaluations under pot, mini-field and farmers' field conditions using at least four replicates proved to be effective for validating the feasibility of the developed suicidal germination application protocol. Our work demonstrates that the objective of the rainfall mimic protocol—breaking seeds dormancy and making them responsive to formulated synthetic SL analogs with

minimal amount of water—is largely attained in all validation experiments, especially under farmers' field conditions. On the other hand, selection of appropriate formulation of the potential SL analogs is needed to facilitate large-scale on-farm application. Characteristics of a good formulation include, but are not limited to, enhancing the efficacy of the SL analog, increasing its shelf-life and reducing the required end-use amount, as summarized by Zwanenburg et al. (2016). These authors have successfully used Atlas G-1086, a polyoxyethylene sorbitol hexaoleate mixed in cyclohexanone, as an emulsifier to formulate Nijmegen-1 applied in tobacco fields parasitized by *Orobanche ramosa*. In this study, the same formulation was used which showed a positive effect on the activity of the stimulant under pot, mini-field and farmers' field conditions, thereby facilitating the validation of the developed protocol. In vitro, we observed an inhibitory effect of the formulation at 5 μ M concentration, which might be caused by toxic side effects of this high stimulant concentration stabilized by the emulsifier.

4.2 | Appropriateness of selected SL analogs for on-farm suicidal germination application

In this study, three synthetic SL analogs including MP1, MP3 and Nijmegen-1 were selected based on their simple structure and high bioactivity in inducing parasitic seed germination. To assess the performance of these compounds as potential candidates for parasitic weed control, we combined in vitro bioassays, pot, mini-field and farmers' field-based experiments. Indeed, results from the in vitro bioassays confirmed that MP1, MP3 and Nijmegen-1 are all potent in inducing *Striga* seed germination. Nefkens et al. (1997) and Wigchert et al. (1999) showed that Nijmegen-1 exhibits moderate germination stimulatory on seeds of *S. hermonthica*. More recently, we have shown that unformulated MP3 and MP1 display moderate to high bioactivity in stimulating *Striga* seed germination compared with that of the standard SL analog (GR24) (Jamil et al., 2018). These results are in line with those obtained with these analogs upon formulation. It is noteworthy that formulation of relatively high-concentrated SL analogs (5 μ M) resulted in significant decrease in their activity (Figure 3a) but showed an opposite effect on low-concentrated (0.05 μ M) Nijmegen-1 (Figure 3c).

The variation in MP3 and Nijmegen-1 activities between the two experiments may be attributed to the difference in soil type. MP3 and Nijmegen-1 displayed very weak activity in high clay soil (mini-field 1) and showed relatively moderate one in mixture soil (mini-field 2). Nijmegen-1 also showed weak activity in suppressing *Striga* emergence in the pot experiment performed in greenhouse at KAUST. In addition, the performance of MP3 and Nijmegen-1 was not consistent across the two farmers' fields, showing a considerable 55% and 65% reduction in *Striga* emergence in pearl millet grown-field (field 1, sandy soil), but only 20% and 12% in sorghum grown-field (field 2, soil with high clay content), respectively. This difference may be influenced by several variables, including soil type, degree of moisture and different host-adapted *Striga* populations. Our results suggest that MP3 and Nijmegen-1 may perform better under sandy soil conditions.

MP1, on the other hand, exhibited consistent performance under both experimental conditions. Importantly, Samejima et al. (2016) have demonstrated the practicability of the suicidal germination approach using the synthetic SL analog T-010. These authors reported up to 33% reduction in *Striga* emergence under artificial infestation. However, this result was achieved using irrigation for compound distribution and by applying significantly higher amounts (100 to 10,000 g/ha) of the SL analog than in the present study where application of only 32 g a.i. ha⁻¹ (MP1, MW = 319.27) has resulted in 39% decrease in *Striga* emergence in naturally infested, rain-fed farmers' field (Figure 6). Results from both studies demonstrate that low amounts of SL analogs may be sufficient for successful suicidal germination application.

Lab experiments show that increasing the concentration of the SL analogs from 0.5 to 5 μ M did not lead to a significant improvement in seed germinating activity. Therefore, we used the germination stimulants at 0.5 μ M concentration in mini-field and field trials, which might be recommended for future application. However, determining the optimal concentration of a germination stimulant requires a dose response curve established based on a wide range of concentrations, which should be a main goal for further refinement of our protocol. In addition, structure optimization and cost-effectiveness studies are needed, combined with the development of large-scale synthesis, to make the suicidal germination technology accessible and affordable for on-farm application.

It should be emphasized that, under field conditions, viable *Striga* seeds do not break their dormancy in a synchronized manner, resulting in continuous seed germination and *Striga* plant emergence throughout the cultivation season. In this context, a single application of germination stimulant during the rainy season would not be enough to reduce the *Striga* seedbank effectively. In our study, SL analogs were applied only twice, which resulted in significant decrease in viable *Striga* seeds under field conditions. However, continuous application of formulated SL analogs would very likely increase the effectiveness of the treatment, leading to much higher depletion of the seedbank. Repeated treatment over the course of several years would very likely eliminate *Striga* seeds in infested fields.

In this study, we used local pearl millet and sorghum varieties susceptible to *Striga*, according to farmers. To determine the effect of host resistance and susceptibility on the success of the suicidal germination application, screening different genotypes, which include control varieties with defined *Striga* resistance profile, is needed.

4.3 | Pathway towards implementing the validated suicidal germination protocol

Our results clearly demonstrate the effectiveness of the developed protocol as well as the potential of the synthetic germination stimulants to suppress *Striga* emergence in highly infested fields up to 65%. These findings suggest that deployment of the technology in the field can significantly decrease the *Striga* seedbank. However, a

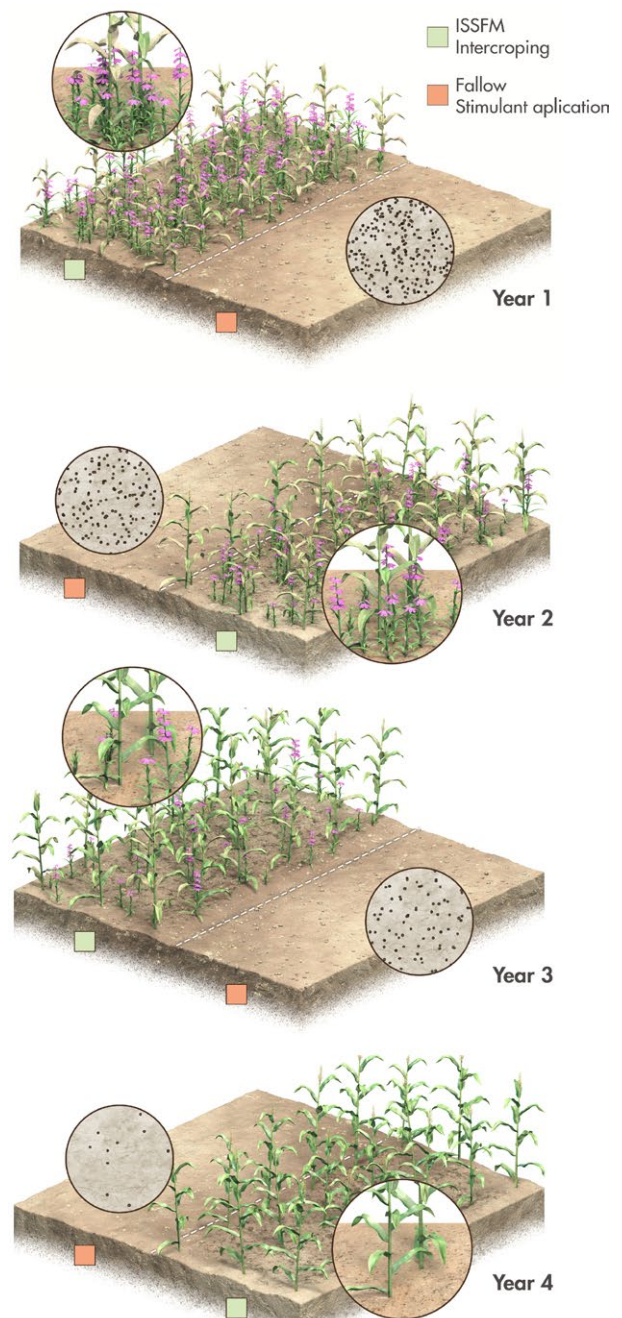


FIGURE 7 Proposed pathway towards implementing suicidal germination technology in farmers' field

successful and sustainable *Striga* management system must be based on combination of different control methods with suicidal germination as a principal component (Kountche, Al-Babili, & Haussmann, 2016). The farming systems in which parasitic weeds represent a major problem are subject to a variety of crop production systems. The impact of the diversity of farm management practices on the suicidal germination approach has not been evaluated yet. The next step in combating parasitic weeds would be to consider how to integrate the suicidal germination approach in different crop management systems.

Given the scale and the persistence of the *Striga* problem, collective efforts are needed to deploy available, routinely used *Striga* control methods and agricultural good practice effectively. Farmers' practices include, but are not limited to, fallow, crop rotation and intercropping (Emeghebe et al., 2004; Hess & Dodo, 2004). In fact, rotation has been also practiced and refers to the division of the field into separate sections, each devoted to a given crop or fallow during a growing season. Considering the limited resources of small-scale subsistence farmers in sub-Saharan Africa, we propose an integrated path that combines in a single farmer's field:

1. A section (fallow) in which the fit-for-purpose suicidal germination technology can be applied without any planting of the host crop, enabling the stimulant to hydrolyse slowly in the soil. In parallel to the treatment and to increase the suicidal germination rate, this section may be planted with non-host, high-value crops, such as cowpea or sesame;
2. An intercropping, staple crop and cowpea/sesame system in the other section of the field. This strategy, called "integrated *Striga* and soil fertility management" (ISSFM), has been extensively used in the last few decades (Samaké, Stomph, Kropff, & Smaling, 2006).

In addition to being the most effective and least expensive method to improve soil fertility, a rotation of this scheme over several years (Figure 7) is expected to drastically reduce or even eliminate the parasitic seedbank in infested fields of sub-Saharan Africa.

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AUTHOR CONTRIBUTIONS

SA, BAK, and JM designed and conceptualized the project; TA, DBA and BZ synthesized and provided the strigolactone analogs; BZ designed the mini-field experiment; BAK and JM conducted *Striga* germination bioassays and pot experiment; BAK, JM, DY, and PN performed the mini-field and farmer's field experiments; BAK was responsible for compiling all data and conducting data analysis. BAK and SA wrote the manuscript.

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