COMPARATIVE ANALYSIS OF STRIGOLACTONE PRODUCTION IN BAMBARA GROUNDNUT AND COWPEA GENOTYPES

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ABSTRACT

This study examined strigolactones (SLs) in 12 Bambara groundnut root exudates. A mixture of three strigolactones, orobanchol, orobanchyl acetate, and fabacyl acetate, were detected by LC-MS/MS in the root exudates of all Bambara groundnut genotypes investigated. Fabacyl acetate was not detected over ten days of P-starvation. Two of these strigolactones, orobanchol and orobanchyl acetate, were previously identified in cowpeas. The levels of orobanchol and orobanchyl acetate secreted varied significantly between genotypes ($p<0.001$) and ($p<0.04$), respectively. Over 21 days of P-starvation, meagre amounts of fabacyl acetate (< 10-12 M) were detected in Bambara groundnut root exudates, and there were no significant differences between genotypes. Among all the genotypes studied, Mana was the highest producer of the strigolactones detected, while DodR was the genotype whose exudates

contained the lowest amount of strigolactones. The relative proportion of orobanchol contained in the strigolactone mixture of root exudates was very high across all 12 genotypes. These detected SL mixtures induced the germination of *A. vogelii* seeds at concentrations as low as 10-12 M but did not lead to *S. gesnerioides* germination, suggesting that *A. vogelii* is more sensitive to SL induction than *S.gesnerioides* and therefore differences inSL quantity maybe a key factor determining host specificity of parasitic plants. Although Alectrabutnot Striga parasitized the 12 BGN genotypes studied in a separate TETFund IBR grant awarded to the Federal Polytechnic Ekowe, genotypes with lower concentrations of SL mixtures result in lower *Alectra* shoot counts, suggesting that Bambara groundnut may be resistance/tolerance to root parasitic plants based on reduced SL production.

Keywords: *Bambara groundnut, Alectra vogelii, Striga generioides, strigolactones, orobanchol, orobanchyl acetate, fabacyl acetate.*

INTRODUCTION

Legumes such as cowpeas (*Vigna unguiculata* L.), groundnuts (*Arachis hypogaea* L.) and Bambara groundnut (*Vigna subterranea* L.) are important food crops for millions of people in the tropics, especially in sub-Saharan African countries where more than 200 million people depend on them for food security, income generation, improved nutrition and enhancing soil fertility.

Cowpeas and groundnuts are particularly important, accounting for about 14 million metric tons in sub-Saharan Africa (FAO2012). The current yield estimates for cowpeas and groundnuts in a typical SSA farmer's field are about 0.5t/ha and 1.01t/ha, respectively. These data suggest significant yield gaps (>50%) in farmers' fields and experimental conditions.

While drought is a significant abiotic stress that can severely reduce crop plant productivity and quality in groundnuts, cowpeas are continuously plagued by a host of

parasitic weeds (Singh & Emechebe, 1997; Parker, 2012).

The major parasitic weeds damaging cowpea plants and causing substantial yield losses are Allegra *vogelii* (Benth.) and *Striga gesnerioides* (Willd.) Vatke.

Bambara groundnut is a native African legume crop which has the potential to meet the demand for food and nutritional security in Africa because it is nutrient-dense and resilient to climate change agriculture.

However, the root-parasitic plants *Striga gesnerioides* and *Alectra vogelii* severely damage crop productivity and can adversely affect yield by up to 100% (Kamara *et al*., 2008; Mbega *et al*., 2016).

*A. vogelii*parasitizes more host legumes, including cowpea (*V. unguiculata*), Bambara groundnut (*V. subterranean*), groundnut (*Arachis hypogaea*), soybean (*Glycine max*), common bean (*Phaseolus vulgare*) and mung bean (*Vignaradiata*) throughout large parts of sub-Saharan Africa (Riches et al., 1992; Phiri *et al*., 2019). Indeed, both parasites can occur in the same cowpea field (Singh & Emechebe, 1991). However, cowpea cultivars that are resistant or moderately resistant to *Striga* are also found to be susceptible to *Alectra* as in the case of APL-1, 87-2, IT82D-849, Suvita-2, IT97K-205-8 and IT98K-1092-1(Singh & Emechebe,1997; Omoigui *et al*., 2010).

Such successful parasitism on highly drought-tolerant legumes such as Bambara groundnut and cowpea suggests that *Alectra* in Africa has the potential to undermine the struggle to attain food, nutritional and environmental security. Parasitism by *Alectra* on different host species depends on the perception of specific chemical signals called strigolactones (SLs).

The host roots exude these molecules into the rhizosphere (Yoneyama *et al*., 2009). SLs are highly active parasitic seed germination stimulants (Bouwmeester *et al*., 2003), inducing germination at concentrations as low as 10-12 M (Xie *et al*., 2010) and also enabling symbiotic arbuscular mycorrhizal fungi to detect their host plant (Akiyama *et al*., 2005).

The mechanisms by which these parasitic plants identify and associate with host plants have been studied, and crop cultivars

that exude low SL levels are resistant to *Striga* in cereals (Jamil *et al*., 2011; Mohemed *et al*., 2016) and broom rape species in legumes (Fernandez-Aparicio *et al*., 2014; Pavan *et al*., 2016).

Therefore, host-plant tolerance or resistance to parasitism by parasitic plants is a manifestation of one or more potential mechanisms, and one of the better-understood mechanisms of resistance against witch weeds is a reduction in SL exudation (Samejima & Sugimoto, 2018).

Resistance to *A. vogelii* and *S. gesnerioides based* on low SL germination stimulant production was investigated in this study, and reduced production of parasite seed germination stimulants is the best characterised of all possible resistance mechanisms.

Crops such as cowpea and sorghum, which are highly drought tolerant, are known to exude stimulants that induce parasitic weed germination, particularly under poor soil conditions lacking in phosphorus and nitrogen. The increased levels of stimulating compounds may represent an attempt to promote symbiosis with mycorrhizal fungi (Jamil *et al*., 2013). SL exudation under phosphate starvation was reported to increase orobanchol exudation in red clover (Yoneyama *et al*., 2007a), Arabidopsis (Kohlen *et al*., 2011) and orobanchol and 5-deoxystrigolinrice (Jamil et al., 2012), several SL sintomato (Lopez-Raez*etal*.,2008).

It was further demonstrated that phosphate-based seed priming down-regulates the production of strigolactones in the rhizosphere (Jamil *et al*., 2013), and also high phosphate availability decreased the extent of AM symbiosis by reducing SL production in roots (Bouwmeester *et al*., 2007). These studies prove that SL synthesis is induced by internal phosphate deficiency in plants.

However, soil phosphate levels may also play a role since SL synthesis is positively regulated in low phosphate conditions. Among the SLs reported to be present in cowpeas, groundnut, common bean, and soybean are orobanchol and its acetate (orobanchyl acetate), which are known as germination stimulants for *A. vogelii* and *S. gesnerioides*and are also regarded as significant SLs of *Fabacea*plants (Xie *et al*., 2008; Ueno *et al*., 2011).

The key objective of this TETFund IBR-funded project was to identify Bambara groundnut and cowpea genotypes that are resistant/tolerant to the root parasitic plants based on low germination stimulant production and an enhanced capacity to deploy resistance traits into breeding programmes effectively.

This germplasm characterisation for resistance to Alectra and *Striga gesnerioides* based on low strigolactone production will contribute to developing improved Bambara groundnut cultivars with resistance to parasitic plants. The key objectives of this TETFund IBR grant awarded to the PI at the Federal Polytechnic Ekowe were achieved for Bambara groundnut, and this report focused on the identification and quantification of SLs in Bambara groundnut genotypes which are resistant to *S.gesnerioides* but susceptible/ tolerant to Alectra.

MATERIALS AND METHODS

Plant material

Twelve out of thirteen genotypes of Bambara groundnut originating from different African locations were used in the experiments (Figure 1). These genotypes were obtained from the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria. Seeds of yellow witchweed (*Alectra vogelii* Benth.) were obtained from Henderson Research Station, Zimbabwe, via Dr Admire Shanyako, University of KwaZulu-Natal, South Africa. Dr. Ousmane Boukar, IITA cowpea breeder in Kano station, supplied the seeds of cowpea witchweed (*Striga gesnerioides*(Willd.) Vatke.

Figure 1: Seeds of the thirteen Bambara groundnut genotypes obtained from the International Institute of Tropical Agriculture (IITA) showing variation in testa colour.

Aeroponicculture of Bambara groundnut and root exudates collection

Bambara groundnut seeds were surface sterilized in sodium hypochlorite (70%) for 5 minutes. After thoroughly rinsing with demineralized water, the seeds were sown in 96 modules trays containing a mixture of sand and compostinaratio of 1:1(v/v) for 7 days. Eight healthy seedlings from each genotype were grown on a custom-made aeroponics system operating with 4 litres of modified half-strength Hoagland solution with 100% phosphorus (P; 0.4 mM), replacing the nutrient solution twice a week. The experiments were conducted in a completely randomized design with three biological replicates under controlled greenhouse conditions (28oC/25oC;450uM.m-2.s-1; 6h/8h photoperiod; and 60% relative humidity). The plants were continuously supplied with half-strength Hoagland solution for 14 days, after which phosphorus(P) deficiency (by using half-strength Hoagland solution without phosphorus, KH2PO4) was introduced to induce the production of SLs (Lopez-Raez *et al*., 2008). Root exudates (2 litres) were collected after 10 and 21 days of

PO-deficiency treatment (Figures 2 and 3), refreshing the nutrient solution 24 h before collection to remove all accumulated strigolactones. The nutrient solution from the aeroponics container was concentrated using C-18 columns (Grace, C18-fast/5000mg) to analyze SL levels in the root exudates.

Figure2: Bambara groundnut plants at 10-days of P-starvation in aeroponics containers

Figure3: Bambara groundnut plants at 21-days of P-starvation in aeroponics containers

STRIGO LACTONE CHARACTERIZATION OF ROOT EXUDATES

The LC-MS/MS analysis of strigo lactones was performed by comparing the retention time and mass transitions with those of 12 major authentic strigolactones standards (5DS, *epi*-5DS, orobanchol, *ent*-2'-*epi*-orobanchol, strigol, *epi*-strigol, solanacol, orobanchyl acetate, sorgolactone, sogomol, oxo-orobanchol and 7α-hydroxyorobanchol) according to the method described by Kohlen *et al.*, 2012 with some modifications.

The mass spectrometer was operated in positive electrospray ionization mode. Cone and desolvation gas flows were set to 50 and 1000 L h^{-1}, respectively. The capillary voltage was set at 3.0 kV, the source temperature at 150°C, and the desolvation temperature at 650°C. The cone voltage was optimized for each standard compound using the Waters Intelli Start MS Console.

MRM was used for identification of strigo lactones by comparing retention times and MRM mass transitions with standards. Data acquisition and analysis were performed using MassLynx 4.1 (combined with TargetLynx) software (Waters).

GERMINATION BIOASSAY

Alectra and *S. gesnerioides* seeds (300 mg) were surface sterilized with 2% (v/v) NaOCl containing 0.02% Tween 20 for 5 min. After rinsing 3-5 times with Milli-Q water and surface drying for 1 h in a laminar hood, *Alectra* and *S. gesnerioides* seeds were pretreated (conditioned) on moistened glass-fibre filter paper (Whatman, Maidstone, Kent, UK) in Petri dishes for 9-11 days at 30oC before use. Preconditioned seeds were treated with aliquots of the synthetic strigolactone analogue (GR24), sorghum root exudate (SRN39), ora100-fold diluted, C18-purified root exudates.

The treated seeds were incubated at the same temperature as conditioning and were microscopically examined for germination (radicle protrusion) after 48 h. Each treatment was replicated at least three times, and the germination percentage of *Alectra*and *S. gesnerioides* was checked. Distilled water was used as a negative control. Sorghum (SRN39) root exudate was used as a second positive control in addition to GR24 (10-6 M).

STATISTICAL ANALYSES

Data were subjected to analysis of variance (ANOVA) using the GENSTAT for Windows 19th Edition (VSN International Ltd, Hemel Hempstead, UK) to observe the difference between genotypes and strigolactone production, and to test for significance.

RESULTS AND DISCUSSION

Strigolactone production

A mixture of three strigolactones-orobanchol, orobanchyl acetate, and fabacyl acetate were detected by LC-MS/MS in the root exudates of all Bambara groundnut genotypes under investigation (Figure1,4). Fabacylacetate was not detected over 10-days of P-starvation. Two of these strigolactones, orobanchol and orobanchyl acetate, were previously identified in cowpea (Muller *et al*.,1992; Ueno *et al*.,2011), a close relative of Bambara groundnut and host of *Alectra* and *S. gesnerioides*.

Figure 4 shows MRM chromatograms of root exudates from genotypes "Mana" and "DodR". For all Bambara groundnut genotypes, the MRM chromatograms showed two peaks at retention times of 4.56 and 7.23 min, and they were identified as orobanchol and orobanchy lacetate, using an external calibration curve of orobanchol and corrected by an internal standard (GR24). In addition, a peak eluted

at a retention time of 6.55 min from exudates under 21- days P-starvation was identified as fabacyl acetate.

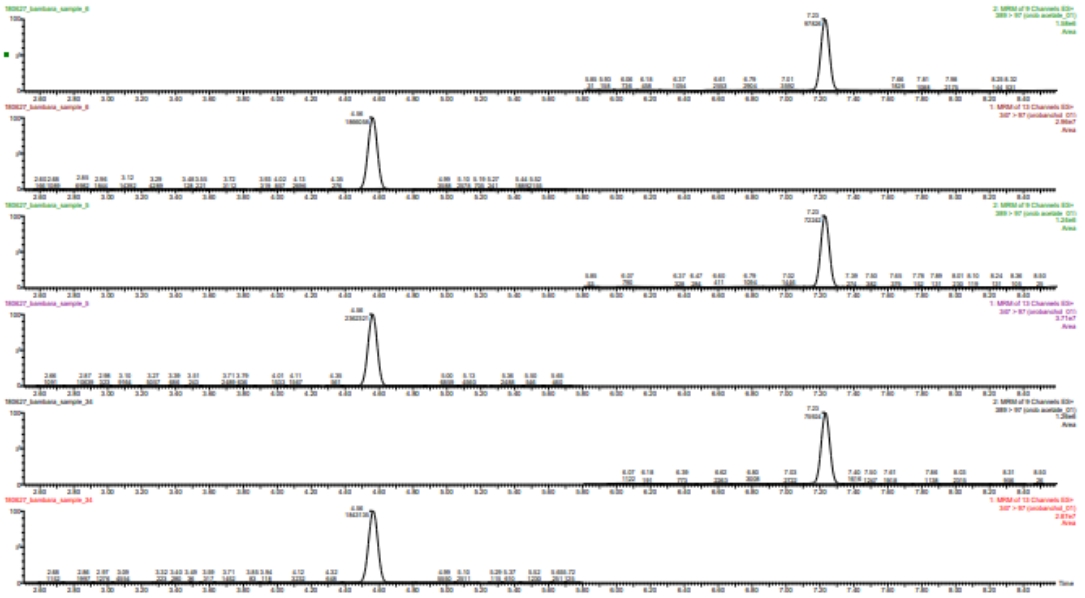

Figure 4: MRM chromatograms of root exudates from the genotypes, Mana(a) and DodR (b). The transitions monitored were *m/z* 405>231 for fabacyl acetate, *m/z* 389>97 for orobanchyl acetate, and *m/z* 347>97 for orobanchol.

The levels of orobanchol and orobanchyl acetate secreted varied significantly between genotypes ($p<0.001$) and ($p<0.04$), respectively. Over 21 days of P-starvation, meagre amounts of fabacylacetate(< 10-12 M) were detected in Bambara groundnut root exudates, and there was no significant difference between genotypes.

Among all the genotypes studied, Mana was the highest producer of the strigolactones detected, while DodR was the genotype whose exudates contained the lowest amount of strigolactones (Figure 5a).

The relative proportion of orobanchol contained in the strigolactone mixture of root exudates was very high across all 12 genotypes. The ratio of all three strigolactone mixtures exuded by each genotype appears fixed according to their decreasing levels: orobanchol, orobanchyl acetate, and fabacyl acetate.

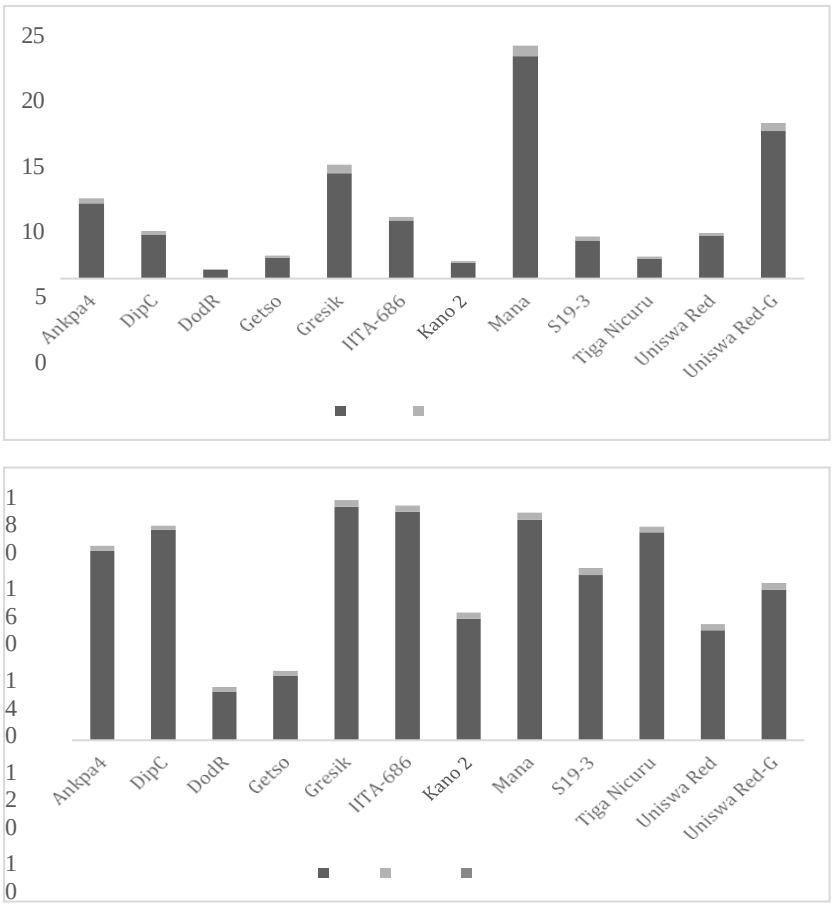

Figure 5: Levels of the three strigolactones, orobanchol (black filled), orobanchyl acetate (light), and fabacyl acetate (dark), detected in 12 Bambara groundnut root exudates over 10- days of P-starvation (a) and 21 days of P-starvation (b)

Effects of P-starvation on strigolactone exudation by genotypes

There were significant differences ($p<0.001$). As the number of days of P- P-starvation was increased from 10 to 21, the amount of orobanchol and orobanchyl acetate detected were very high, and in strigolactone exudation by all the 12 Bambara groundnut genotypes in response to phosphorus deficiency fabacyl acetate that was not detected over ten days of P-starvation was now detected in very low amounts (Figure 5a, 5b).

The germination-inducing activity of Bambara groundnut root exudates

Germination stimulation activity of root exudates of 21 days P starved Bambara groundnut plants (1 in 100 dilutions) are shown in Figure 6. Bambara groundnut root exudates with orobanchol and orobanchyl concentrations lower than 10-12 induced the germination of *Alectra vogelii* seeds, but there were no significant differences in germination stimulation activities.

Bambara groundnut root exudates failed to stimulate *S. gesnerioides* seed germination. Similar to the non-inducing activity of Bambara groundnut root exudates toward *S. gesnerioides*, the negative control (demineralised water), as well as the synthetic SL (GR24) and sorghum cultivar (SRN39) root exudates did not induce the germination of *A. vogelii* seeds.

However, the root exudates of sorghum (SRN39), used as a second positive control, elicited the germination of approximately 80% of *S. gesnerioides* seeds. Interestingly, this sorghum genotype produced a high amount of orobanchol (Mohemed *et al*., 2018), a germination stimulant that is required at 1 nM concentration to induce reasonable germination of *S. gesnerioides* seeds (Uen*oet al*., 2011).

These results indicate that a mixture of two significant SLs, orobanchol and orobanchyl acetate, at deficient concentrations (<10-12M) are essential in root exudates to induce the germination of *Alectra* seeds, and a much higher level of orobanchol (10-9 M) will be needed to induce an appreciable germination of *S. gesnerioides* seeds.

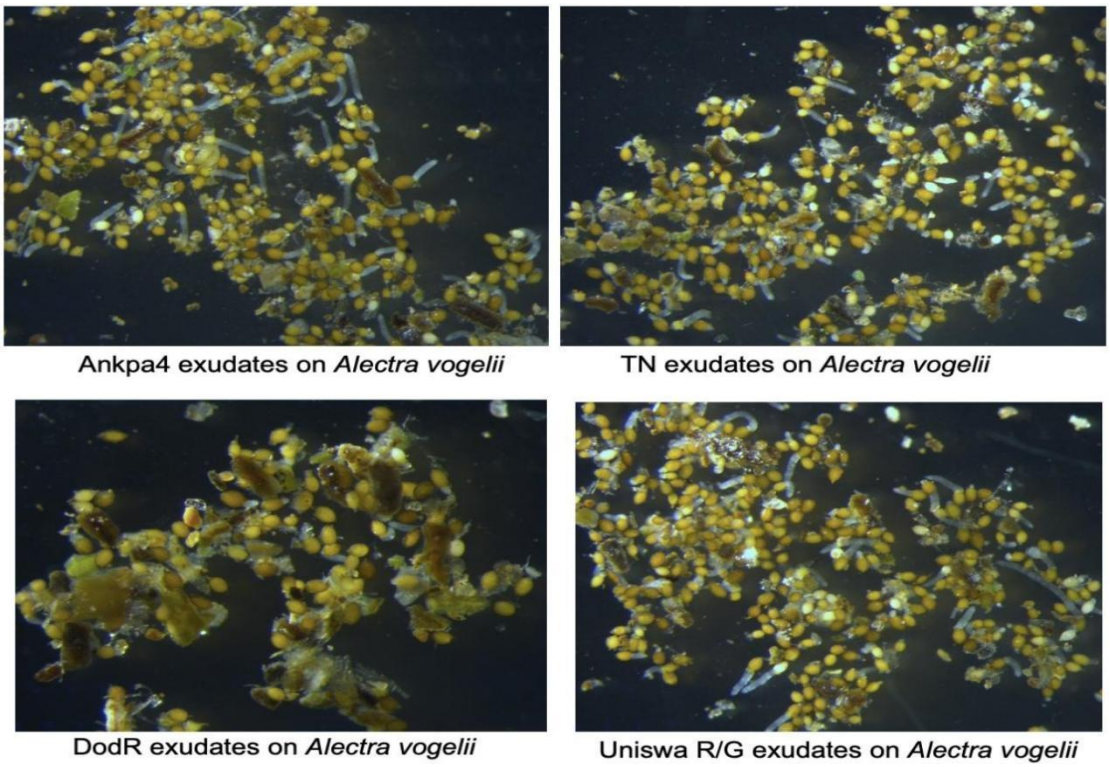

Figure 6: Effects of Bambara groundnut pure root exudates on the germination of *Alectra vogelii* seeds

CHALLENGES/DIFFICULTIES, IF ANY IN IMPLEMENTING THE PROJECT:

In the work reported here, the difficulties encountered were in obtaining enough Bambara groundnut seeds for the required number of replications and seeds of the parasitic weeds from collaborating research partners needed to arrive earlier for the germination assay. Funding was a significant challenge (due to the massive fall in the value of the naira) in collaboration with an advanced Lab (University of Amsterdam, Netherlands) on such a highly technical research project. Due to limited funding we focused on SLs analysis on only Bambara groundnut genotypes.

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