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VARIABILITY OF VOLATILE ORGANIC COMPOUNDS EMITTED BY SEEDLINGS OF SEVEN AFRICAN MAIZE VARIETIES WHEN INFESTED BY ADULT *CICADULINA STOREYI* CHINA LEAFHOPPER VECTORS OF MAIZE STREAK VIRUS

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ABSTRACT

Maize (*Zea mays* L.) is an important source of energy for the people in sub-Saharan Africa. Unfortunately, maize production is under the threat of Maize streak virus (MSV) (Geminiviridae: genus Mastrevirus), an endemic pathogen of native African grasses. This virus is acquired and transmitted in a persistent manner, by *Cicadulina* spp. leafhoppers (Homoptera: Cicadellidae) .One possibility for controlling the virus and the vectors is to exploit volatile semiochemicals released by plants following insect herbivory. A study was conducted on herbivore-induced volatile organic compounds (VOCs) of seven African maize (*Zea mays* L.) varieties in the presence of the leafhopper (*Cicadulina storeyi* China, Homoptera: Cicadellidae) an important vector of maize streak virus (MSV) with a view of developing novel leafhopper control strategies in sub-Saharan Africa. VOCs are known to repel herbivory and also serve as cues for parasitoids to locate their hosts. Volatiles were collected from young maize seedlings of 7 varieties after entrainment with or without infestation of leafhoppers in 0 - 24, 24 - 48, 48 - 72 and 72–96 hr periods and combined and subsequently analysed by gas chromatography. Analysis of the VOCs collected from the seven elite African varieties shows high interspecific VOC variability. Gas chromatography (GC) and coupled GC-mass spectrometry (GC-MS) led to the identification of (*z*)-3-hexen-1-ol, heptanal, (z)-2-pentenyl acetate, MHO, octanal, myrcene, (*z*)-3-hexen-1-yl acetatate, (*E*)-3-hexen-1-yl acetatate, nonanal Linalool, DMNT, (*E*)-2-decen-1-ol, Methyl salicylate, DMNT, Phenethyl acetate, Indole, *cis*-jasmone, α-copaene, Geranyl acetone, β-caryophyllene, α-bergamotene, (E)-β-farnesens, TMTT, and Humulene from infested seedlings. Of these, methyl salicylate, (E)-caryophyllene, (E)-β-farnesene and TMTT were identified previously as volatile semiochemicals involved in plant defense against other sucking insect pests. TZB-SR seedlings emitted 22 compounds in the presence of leafhoppers, compared with 5 by uninfested seedlings; while BR9943-DMR.SR emitted only seven compound in the presence of leafhoppers compared with 6 by uninfested seedlings. The compounds emitted by the seven maize varieties after herbivory were in the following descending order: TZB-SR > TZBR.ELD3.C3 > AMA.TZBR = 8338-1> GUSAU 81.POOL16-SR = 9021-18.STR > BR9943-DMR.SR. Although these varieties were bred for resistance to MSV and other production constraints like downy mildew and stem borers, the variability being reported would have significant ecological implications in utilising plant induced volatiles as repellents for leafhoppers in controlling MSV and underscores the need to breed for varieties that produce volatiles which are very attractive to biological control agents and repellent to leafhoppers. This is the first report of variability of maize genotypes on herbivores-induced volatiles from an African pest/pathogen complex and is in conformity with previous studies that maize shows relatively high genetic and VOC variability, both intrinsically and in herbivore-induced emissions.

Key Words: Herbivores-induced volatile organic compounds, *Zea mays*

RÉSUMÉ

Le maïs (*Zea mays* L.) est une importante source d'énergie du peuple d'Afrique sub-saharienne. Malheureusement, sa production est affectée par la striure brune du maïs (MSV) (Geminiviridae: genus Mastrevirus), un pathogène endémique originaire d'herbes africaines. Ce virus est acquis et transmis de manière persistante par la Cicadelle (Homoptera: Cicadellidae). Pour contrôler ce virus et ses vecteurs, il est possible d'exploiter les produits semiochimiques émis par les plantes infestées par les insects. Une étude était effectuée sur des composés organiques volatiles émis par sept variétés de maïs (*Zea mays* L.) losrqu'infectées par la cicadelle (*Cicadulina storeyi* China, Homoptera: Cicadellidae), un vecteur important du virus de la striure de maïs (MSV) afin de développer des stratégies de contrôl de la cicadelle en Afrique sub-saharienne. Les VOCs servent comme signaux pour les parasitoïdes afin de localiser leurs hôtes. Les volatiles étaient collectés des jeunes plants des sept variétés après introduction ou pas d'infestation de la cicadelle à des périodes de temps allant de 0 - 24, 24 - 48, 48 - 72 and 72–96 heures et combinée, plutard analysés à l'aide du gaz chromatographique. L'analyse des VOCs issus de sept variétés africaines élites montre une variabilité interspécifique des VOCs. Le gaz chromatographique (GC) et la combinaison GC- masse spéctrométrie (GC-MS) ont permis l'identification de (*z*)-3-hexen-1-ol, heptanal, (z)-2-pentenyl acetate, MHO, octanal, myrcene, (*z*)-3-hexen-1-yl acetatate, (*E*)-3-hexen-1-yl acetatate, nonanal Linalool, DMNT, (*E*)-2-decen-1-ol, Methyl salicylate, DMNT, Phenethyl acetate, Indole, *cis*-jasmone, α-copaene, Geranyl acetone, β-caryophyllene, α-bergamotene, (E)-β-farnesens, TMTT, et Humulene dans des plants infestées. De tous ces produits précités, seuls methyl salicylate, (E)-caryophyllene, (E)-β-farnesene et TMTT étaient auparavant identifiés comme volatiles semiochemiques impliqués dans la défence des plants contre d'autres pestes d'insectes suceurs des plantes. Les plants TZB-SR ont émis 22 composés en présence de la cicadelle en comparaison avec 5 plants non infestés; alors que BR9943-DMR.SR ont émis seulement sept composés en présence de la cicadelle en comparaison de 6 plants non infestés. Les composés émis par les sept variétés de ma¿s après infestation de la cicadelle étaient classes comme suit par ordre descendant: TZB-SR > TZBR.ELD3.C3 > AMA.TZBR = 8338-1> GUSAU 81.POOL16-SR = 9021-18.STR > BR9943-DMR.SR. Bien que ces variétés étaient dotées de résistance au MSV et autres contraintes à la production comme le mildew et le stem borers, la variabilité manifestée pourrait avoir des implications écologiques significatives dans l'utilisation des composés volatiles émis des plantes comme moyen de repousser les cicadelles dans le contrôl du MSV. Ceci souligne le besoin d'entreprendre des études d'amélioration génétique des variétés pouvant émettre des composés volatiles comme agent de contrôl biologique et repulsif de la cicadelle. Ceci constitue le premier rapport sur la variabilité des génotypes de ma¿s eu égard aux composés volatiles organiques émis à partir du complexe de peste/pathogène africain. Ceci est en conformité avec des études antérieures qui montrent une relative variabilité génétique et des VOCs, tous intrinséquement dans des émissions induites des herbivores.

Mots Clés: Composés organiques volatiles émis par des herbivores, *Zea mays*

INTRODUCTION

Maize (*Zea mays* L.) is the third major cereal crops in the world, after wheat and rice. It is the most important crop in sub-Saharan Africa, where it has gradually displaced native food crops such as sorghum and millet. It is grown for human consumption, animal feed and several industrial uses. The greatest constraints to higher yields are pests, diseases and parasitic weeds (Efron *et al.*, 1989). Maize can supply 50% of the caloric intake in sub-Saharan Africa, but in certain years, a farmer's entire crop can be wiped out by Maize streak virus (MSV) (Geminiviridae: genus Mastrevirus), an endemic pathogen of native African grasses (Thottappilly *et al.*, 1993). This virus is acquired and transmitted in a persistent manner, by *Cicadulina* spp. leafhoppers (Homoptera: Cicadellidae) (Oluwafemi *et al.*, 2007).

One possibility for controlling the virus and the vectors is to exploit volatile semiochemicals released by plants following insect herbivory. These are naturally-occurring behaviour and development-modifying chemicals, which can deter herbivore colonisation, while at the same time attracting insects antagonistic to herbivores, such as parasitoids and predators (Dicke *et al.*, 1993; 2003; Karban and Baldwin, 1997). Knowledge of the induced plant defense chemistry in maize upon leafhopper damage could lead to the selection and/or development of varieties with more durable resistance, through enhanced constitutive or induced plant defense (Bernasconi *et al.*, 1998; Stout and Davis, 2009). This study examined the chemical ecology of the interaction between maize and *C. storeyi*, which is a major vector of MSV in Africa (Oluwafemi *et al.*, 2007). The study also provides information on the uniformity/variation among maize varieties in the release of volatile organic compounds.

MATERIALS AND METHODS

Insects and plant materials. *Cicadulina storeyi* China (Homoptera: Cicadellidae) leafhoppers, free of MSV, were collected from the mass rearing colony of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, and reared on pearl millet, *Pennisetum americanum* (= typhoides) in a quarantine growth facility (23±2 °C, 40% RH, 16:8 h, L:D) at Rothamsted Research, Harpenden, Hertfordshire, UK as reported before (Oluwafemi *et al*., 2011). The following seven maize varieties were supplied by Dr. S.O. Ajala, of the Maize Improvement Programme of IITA, Ibadan: AMA.TZBR-WC2B; BR9943-DMR.SR; TZB-SR; TZBR.ELD3.C3; 9021-18.STR; 8338-1; and GUSAU 81.POOL16-SR, and grown under controlled conditions at Rothamsted Research (25±1 °C; 16:8 hr, L:D; 150 µE.m-2.s-1).

Volatile organic compound (VOC) collection. Air entrainment was carried out following standard procedures (Agelopoulos *et al*., 1999; Oluwafemi *et al*., 2011) using 10 to 12 day-old maize seedlings. Seeds were pre-germinated and then planted singly in 13 cm plastic pots inside a growth chamber (25 °C, 16:8 hr, L:D). For each collection, a single seedling was enclosed in a glass vessel (22 cm high × 6.5 cm internal diam) open at the bottom with two collection ports at the top (one for inlet and the other for outlet). The bottom was closed without pressure around the plant stem by using two semicircular aluminium plates with a hole in the centre to accommodate the stem. The plates were clipped to a flange on the open end of the glass vessel. Air, purified by passage through an activated charcoal filter, was pumped into the vessel through the inlet port at 700 ml min^{-1} (flow rate controlled by a needle valve and measured by a flow meter). Air was drawn out at 600 ml min^{-1} through Porapak Q (50 mg) in a 5-mm diam glass tube (Alltech Associates, Camforth, Lancashire, UK). The difference in flow rates created a slight positive pressure to ensure that unfiltered air did not enter the system; thus removing the need for an airtight seal around the stem.

All connections were made with polytetrafluoroethylene (PTFE) tubing (Alltech Associates) with brass ferrules and fittings (North London Valve, London, UK) and sealed with PTFE tape (Gibbs & Dany, Luton, UK). Glassware, metal plates, and other equipment were washed with Teepol detergent (Herts County Supplies, Herts, UK) in an aqueous solution, acetone, and distilled water, and then baked overnight at 180 °C. Porapak Q tubes were conditioned before use by washing with redistilled diethyl ether (1 ml) and heated to 132 °C for 2 hr under a stream of constant nitrogen. Charcoal filters (BDH, 10–14 mesh, 50 g) were conditioned before use by purging with nitrogen inside an oven (150 °C) for a minimum of 2 hr.

Once conditioned, filters were sealed using Swagelok cap fittings and left to cool to ambient temperature prior to use. VOCs collected on Porapak Q were eluted with freshly distilled diethyl ether (750 ml). Eluted samples were then concentrated to ca. 100 ml under a gentle stream of nitrogen, and stored in tightly capped microvials in a freezer (-20 °C) until required for use. Plants were entrained for 7 days, but the Porapak Q tubes were changed daily, ensuring 24 hr entrainment periods. VOCs were collected from clean and *C. storeyi* infested maize seedlings. For the latter, seedlings were infested with 50 adults per plant, and allowed to settle for 1 hr prior to commencement of VOC collection. Entrainments from clean and infested plants were replicated 3 times.

Gas Chromatography (GC) and Coupled GC-Mass Spectrometry (GC-MS). VOCs were analysed on a Hewlett-Packard 6890 GC equipped with a cool-oncolumn injector, a flame ionisation detector (FID), and a non-polar HP-1 bonded phase fused silica capillary column (50 m×0.32 mm i.d., film thickness 0.52 µm). The oven temperature was maintained at 30 °C for 1 min, and programmed at 5 °C min^{-1} to 150 °C and held for 0.1 min, then 10 °C min^{-1} to 230 °C. The carrier gas was hydrogen. Four µl of each eluted sample were injected into the injector port of the GC instrument. Data were analysed using HP Chemstation software.

GC-MS analysis of collected VOCs was performed using a fused silica capillary column (50 m×0.32 mm i.d., film thickness 0.52 µm, DB-1), attached to a cool on-column injector, which was directly coupled to a magnetic sector mass spectrometer (Autospec Ultima, Fisons Instruments, Manchester, UK). Ionisation was by electron impact (70 eV, source temperature 250 °C). Helium was the carrier gas. The oven temperature was maintained at 30 °C for 5 min, and then programmed at 5 °C min^{-1} to 250 °C. Tentative identifications were made by comparison of spectra with mass spectral databases (NIST, 2005). Identifications were confirmed by peak enhancement on GC using authentic compounds (Pickett, 1990).

Chemicals. Porapak Q (80/100 mesh) was purchased from Alltech (PA, USA). Diethyl ether (purris.) was purchased from Sigma Aldrich. Hexane (95% pesticide residue) was purchased from Fisher Scientific (Loughborough, Leicestershire, UK) and distilled prior to use.

RESULTS

The volatile compounds from the seven African varieties, with or without leafhoppers are presented in Table 1. Analysis of the odour

TABLE 1. List of volatile organic compounds emitted by seven African varieties of *Zea mays* upon infestation by *Cicadulina storeyi*

Compounds	V1		V2		V3		V4		V5		V6		V7	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
(*z*)-3-hexen-1-ol					+									
Heptanal					+									
(z)-2-pentenyl acetate					+									
MHO	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Octanal					+		+							
Myrcene					+									
(*z*)-3-hexen-1-yl acetatate	+	+	+	+	+	+	+	+	+		+	+	+	+
(*E*)-3-hexen-1-yl acetatate					+		+							
Nonanal	+	+	+	+	+	+	+	+	+	+	+	+		+
Linalool	+		+	+	+		+	+	+		+		+	
DMNT					+		+							
(*E*)-2-decen-1-ol					+		+							
Methyl salicylate	+		+	+	+	+			+		+	+	+	
Decanal					+		+							
Phenethyl acetate					+		+							
Indole	+				+		+		+	+	+	+	+	
cis-jasmone					+		+							
α-copaene					+									
Geranyl acetone	+	+	+	+	+	+	+		+	+			+	
β-caryophyllene	+										+	+	+	
α-bergamotene	+		+				+		+		+	+	+	
(E)-β-farnesens	+				+				+		+	+	+	
TMTT					+									
Humulene					+						+			
Total number of compounds	10	4	7	6	22	5	14	4	9	4	10	8	9	3

A = with leafhoppers; B = without leafhoppers; V1 = AMA.TZBR-WC2B; V2 = BR9943-DMR.SR; V3 = TZB-SR; V4 = TZBR.ELD3.C3; V5 = 9021-18.STR; V6 = 8338-1; V7 = GUSAU 81.POOL16-SR blends, which were collected in 0-24, 24–48, 48–72, and 72–96 hr periods and combined, using GC and coupled GC-MS showed variation among the varieties. Many more compounds were also emitted by the maize seedlings when infested with leafhoppers than by uninfested, intact seedlings. TZB-SR seedlings emitted 22 compounds in the presence of leafhoppers, compared with 5 by uninfested seedlings; while BR9943-DMR.SR emitted only 7 compounds in the presence of leafhoppers compared with 6 by uninfested seedlings. Tentative identifications included (*z*)-3-hexen-1-ol, heptanal, (z)-2-pentenyl acetate, MHO, octanal, myrcene, (*z*)-3-hexen-1-yl acetatate, (*E*)-3-hexen-1-yl acetatate,, nonanal Linalool, DMNT, (*E*)-2-decen-1-ol, Methyl salicylate, DMNT, Phenethyl acetate, Indole, *cis*-jasmone, α-copaene, Geranyl acetone, β-caryophyllene, α-bergamotene, (E)-β-farnesens, TMTT and Humulene from infested seedlings.

MHO was the only compound emitted by all seven varieties, by both uninfested and infested seedlings. Linalool was always produced by all seven varieties in the presence of the leafhoppers. Only one variety, TZBR.ELD3.C3, did not emit methyl salicylate in the presence of leafhoppers. Three varieties (BR9943-DMR.SR; TZB-SR and 8338-1) emitted methyl salicylate by both uninfested and infested seedlings. β-caryophyllene was produced by three varieties (AMA.TZBR-WC2B, 8338-1, GUSAU 81.POOL16-SR) in the presence of leafhoppers; while one variety (8338-1) emitted it by intact, uninfested seedlings. α-Bergamotene was produced by six varieties except TZB-SR in the presence of leafhoppers while 8338-1 intact, uninfested seedlings also emitted it. (*E*)-b-farnesens was produced by five varieties in the presence of leafhoppers while 8338-1 emitted it by intact uninfested maize seedlings. Linalool and humulene were the only additional compounds emitted by 8338-1 in the presence of leafhoppers as compared to uninfested seedlings. Octanal, DMNT and Phenethyl acetate were produced only in the presence of leafhoppers by TZB-SR and TZBR.ELD3.C3.

DISCUSSION

Analysis of the VOCs collected from seedlings of seven African varieties when infested with *C. storeyi* by gas chromatography (GC) and coupled GC-mass spectrometry (GC-MS), showed that the VOC profile was similar to those reported earlier by the same leafhopper for the European maize cultivar (cv. Delprim) (Oluwafemi *et al*., 2011) and those induced by the leafhopper, *Euscelidius variegatus* (Erb, 2009), and *Spodoptera* spp. caterpillers (*S. littoralis* and *S. exigua*) (Hoballah *et al*., 2002; 2004; Schmelz *et al*., 2003; Hoballah and Turlings, 2005; Gouinguene *et al*., 2003; 2005; Farag *et al*., 2005). Tentative identifications included (*z*)-3-hexen-1-ol, heptanal, (z)-2-pentenyl acetate, MHO, octanal, myrcene, (*z*)-3-hexen-1-yl acetatate, (*E*)-3-hexen-1-yl acetatate, nonanal Linalool, DMNT, (*E*)-2-decen-1-ol, Methyl salicylate, Phenethyl acetate, Indole, *cis*-jasmone, α-copaene, Geranyl acetone, β-caryophyllene, α-bergamotene, (E)-β-farnesens, TMTT and Humulene, from infested seedlings. Replication of volatile collections from clean and infested plants confirmed a consistent pattern in VOC profiles.

The VOC profile of the seedlings was altered markedly when plants were infested with *C. storeyi*. The results show wide variation in the quality of the emissions among the seven African varieties, compared with the European cultivar (Delprim) earlier reported (Oluwafemi *et al*., 2011). TZB-SR emitted more volatiles than others upon leafhoppers infestation. However, this variety did not emit β-caryophyllene and α-bergamotene which were emitted by cv. Delprim and reported to be repellent to *C. storeyi* (Oluwafemi *et al*., 2011). Only one variety, TZBR.ELD3.C3, did not emit methyl salicylate in the presence of leafhoppers. Three varieties (BR9943-DMR.SR; TZB-SR and 8338-1) emitted methyl salicylate by both uninfested and infested seedlings. The strong induced emission of methyl salicylate following *C. storeyi* infestation from African varieties agrees with our earlier report (Oluwafemi *et al*., 2011) on cv.

The strong emission of methyl salicylate by maize seedlings when leafhoppers feed on them may be very important as this compound has been demonstrated to act as a critical mobile signal in plants to mediate systemic immunity against viral and bacterial diseases (Park *et al*., 2007; Vlot *et al*., 2008). Leafhoppers damage maize crops not only through feeding but critically through transmission of MSV. Inoculation of MSV during feeding is followed by systemic development of MSV disease as symptoms start to appear from the next sets of leaves and further growth of the plant is hindered. It is possible that this strong induction of emission of methyl salicylate contributes to systemic immunity against MSV infection as these African varieties of maize (under study) have been developed to be resistant to MSV and other African pathogens and pests such as downy mildew and stem borers.

Previous studies that compared induced odour blends emitted by different cultivars of the same plant species attacked by the same herbivores, indicated considerable variation. Gouinguene *et al.* (2001) and Degen *et al.* (2004) showed that total amounts and quality of volatiles released by different maize cultivars varied significantly when emissions were induced by mechanical damage and oral secretions of *Spodoptera littorallis* (Lepidoptera: Noctuidae). Turlings *et al.* (1998) also showed differences in the induced odour blend of two maize cultivars LG11 and Iowa sweet corn. The volatiles induced by the mite *Tetranicus urtiae* (Acari: Tetranychidae) varied between two apple cultivars and these differences were considerably larger than differences for one apple cultivar infested by two different mites species (Takabayashi *et al*., 1996). Large differences in terpenoid emissions were also reported by Krips (2000) with odour emissions among four gerbera (Asteraceae) cultivars after spider mite attack.

The behavioural activity of induced volatile semiochemicals against *C. storeyi* leafhoppers have potential for use in leafhopper control (Oluwafemi *et al*., 2011), and may reduce the prevalence of plant diseases through reduced vector activity, either as outright repellents, or as attractants of natural enemies such as hymenopterous parasitoids (Moya- Raygoza *et al*., 2006). However, the release of such materials, either as slow-release formulations, or *via* genetically transformed plants (Beale *et al*., 2006), is going to be very challenging for resource-poor farmers based in Africa. Future studies will examine the behavioural responses of *C. storeyi* to different odours emitted by these African varieties and seek to relate the data for potential use in the control of these vectors. A major area of emphasis in future studies would be the identification of the behaviourally active components in leafhopper- induced emissions and their optimal combinations for attractiveness of predators and parasitoids. As we earlier reported for cv. Delprim (Oluwafemi *et al*., 2011), the behavioural responses of *Cicadulina* to African varieties would be examined.

This study shows that elite African maize cultivars have high variability in herbivore-induced emissions, as reported for cultivars from Europe and North America (Turlings *et al*., 1995; Gouinguene *et al*., 2001; Degen *et al*., 2004). This interspecific variability may imply that breeding efforts should be focused on cultivars that are not only resistant to MSV (and other major pathogens) but also that produce volatiles which are repellent on the vectors while at the same time attractive to biological control agents of the vectors. Repellent semiochemicals such as methyl salicylate, (E)-β-farnesene, and TMTT, which are being reported should be investigated further among cultivated African varieties and developed for use in the manipulation of leafhoppers. The observed variability also suggests that African maize varieties would differ in their attractiveness to natural enemies of leafhoppers. This could also exploited by breeding varieties that are very attractive to biological control agents of leafhoppers which are important vectors of MSV.

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