Electrophysiological and behavioural responses of sweetpotato weevil, *Cylas formicarius* Fab. to sweetpotato varieties

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Electrophysiological and behavioural studies coupled with field experiments were conducted to analyse the olfactory responses of sweetpotato weevil (SPW), *Cylas formicarius* Fab. to six varieties of sweetpotato, in order to understand how the olfactory system of the weevil distinguishes between volatiles from the susceptible and resistant varieties. Female SPW recorded significantly highest attraction ($P < 0.01$) towards 'Kishan' volatiles and lowest towards 'Gouri'. SPW infestation was highest in 'Kishan' (82.33%), whereas it was lowest in 'Gouri' (33.73%) at field level. A greater electrophysiological response was recorded by male and female SPW antenna to leaf and flower volatiles respectively. Males showed higher depolarization (amplitude) and lesser recovery time compared to females, particularly to leaf volatiles. The comparative study of electroantennographic analysis, olfactometry and infestation data indicated that 'Kishan' is the most susceptible variety, attracting a large number of weevils; while 'Gouri', is the resistant variety.

Keywords: *Cylas formicarius*, electroantennography, infestation, resistance, sweetpotato.

SWEETPOTATO, *Ipomoea batatas* (L.) is a major food crop, grown circumglobally in tropical and subtropical latitudes and ranks seventh among all food crops worldwide, with an annual production of 111 million metric tonnes[1]. Sweetpotato weevil (SPW), *Cylas formicarius* Fab. has been recorded as the most serious pest of sweetpotato, causing extensive damage to the storage root, thereby leading to significant reduction in crop yield and economic loss. The feeding of SPWs on the storage root induces terpenoid production, making the root unpalatable for humans and cattle[2]. *C. formicarius* is difficult to control with conventional chemical insecticides because of cryptic larvae and pupae, in spite of using non-infested planting material. The development of resistant cultivars to this weevil, has been a major challenge for plant breeders. The criteria used to assess and select individual traits are an obstacle for the development of a resistant cultivar. All cultivars show varying degrees of susceptibility to weevil damage. The production of insect-resistant cultivars has eliminated the annual application of over 3 lakh tonnes of insecticides in the US (ref. 3).

The use of plant volatiles can lead to identification of resistant cultivar[4]. Plant–plant and plant–insect communication are well understood through biologically active volatile plant chemicals, which helps in the selection of a resistant variety. Plant volatiles play an important role in plant–insect interaction[5]. The study of insect behaviour towards the plant and its volatiles has become necessary for safeguarding the plant and to deter the insects[6]. This indicates inter-plant difference which makes the degree of attraction of weevils also different[4,7]. Also, different plant parts produce an entirely unique set of semiochemicals which has profound influence on the behaviour of weevil and its reproductive biology. Wang and Kays[8] reported variation in volatile compounds between foliage and roots. Qualitative and quantitative differences in volatile semiochemicals are related to the expression of resistance in sweetpotato to SPW. *C. formicarius* responds differently to different sweetpotato varieties due to changes in chemical constituents among these varieties[7,8], resulting in variation in initial attraction, host choice, success of weevils in utilizing different plants, or a combination of these factors[9].

The electroantennogram (EAG) method records antennal olfactory responses of insects to a given odour[10]. This electrophysiological method indicates the sensitivity of the main olfactory system by estimating the receptor potentials of the antennal olfactory neurons. The use of insect antennae as an odour detector could be one of the most sensitive techniques for detection of responsiveness to different sweetpotato plant varieties[4,7]. Antennae have been used in simplified and sensitive odour environments to detect specific volatile compounds; for instance, those emanating from unhealthy potatoes[11], measuring cross-sectional relative concentration differences across plumes[12]. Insect antenna responds differently to volatiles with varied depolarization levels and measuring the amplitude and recovery time, leading to identification of structural differences between these compounds[13]. The present study is designed to understand the differential response of SPW to volatile extracts of six popular sweetpotato varieties using electrophysiological and behavioural assays.

The sweetpotato genotypes, viz. Kalinga, Sourin, Goutam, Kishan, Shankar and Gouri were planted at a distance of 60 × 20 cm in a 3 m × 2 m plot (five ridges times 10 plants per ridge) in the farm of ICAR-Central Tuber Crops Research Institute, Regional Centre, Bhubaneswar, during 2012 and 2013 in a randomized block design with three replications in red loamy soil with different varieties on separate plots. Irrigation was done at every 15 days interval and weeding at 30 and 50 days after planting (DAP). Field infestation of SPW on these genotypes was recorded at 60 DAP. Destructive sampling was done for estimation of weevil infestation in vines (stem) and

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storage roots. Five plants were randomly selected and entirely rooted out; their vines and storage roots were cut open for counting grubs and adults.

Storage roots were collected from the experimental field and maintained in BOD incubator at 28°C for SPW emergence. The young weevils were segregated based on their sex and maintained separately. Two-day-old healthy and active weevils were selected for different bioassay purposes. Weevils provided with honey solution until use and starved for 48 h prior to different bioassays. For weevil infestation pattern, the number of SPWs in storage roots of five plants was transformed per unit weight.

Extracts from leaves, flowers and storage roots of each variety on 60 DAP were collected through solvent extraction. Three hundred number of sweetpotato flowers (150 g) were transferred into a jar, to which redistilled *n*-hexane (99% pure) was dispensed in the ratio 1 : 3 (M/V). Similarly, leaves (150 g) from top, middle and bottom portion of sweetpotato plants (1 : 1 : 1) were added into another jar containing redistilled hexane (1 : 3 M/V). Redistilled hexane (3 : 1 V/M) was added to a separate jar containing sweetpotato storage root periderm (150 g). The extracts were then filtered thrice through Whatman No. 1 filter paper and volatile extracts were collected through vacuum rotary evaporator (Heidolf, Germany) at 50°C at 100 rpm and condensed to 10 ml. These extracts were stored in separate vials at 4°C for further use in bioassays.

The antennal responses of adults of both the genders to the volatile extracts were studied by EAG. One antenna of each test weevil was excised and finely cut on both ends. The antenna was held onto the metal electrodes in a constant humidified air stream (50 ml min^{-1}) generated by a stimulus controller (model CS-55, Syntech Ltd, Germany). The olfactory stimuli were obtained by impregnating 50 µl of each of the extracts onto separate filter paper (Whatman No. 1) strips of 6 cm × 0.5 cm size. The solvent was allowed to evaporate for 1 min before placing this filter paper inside the glass Pasteur pipette (14 cm long). By injecting a puff of purified air (0.2 sec), odour stimulation was administered, amplified and recorded using EAG software (EAG Pro, Syntech, Germany), linked to a computer system coupled with IDAC-2 (data acquisition interface board; Syntech). One-minute interval was allowed between successive stimulations for antennal recovery. Since the antennal responses diminished throughout an experiment, the responses (amplitudes and duration of signals) to the test extracts are expressed as mean of all recorded antennal depolarizations.

A modified dual-choice olfactometry bioassay[7] was used to compare the responsiveness of weevils to leaf, flower and storage root extracts collected from the six genotypes. The olfactometer comprised of a *Y*-shaped glass tube with three terminals attached to removable glass lids (5 cm long, 3 cm diameter), separately. These lids were named as treatment chamber, control chamber and main chamber according to the purpose they served. The former two were attached to the top two arms of the *Y*-tube, whereas the latter one at the basal end. Each of the three arms of the *Y*-tube was 20 cm long and 3 cm in diameter. A copper wire of 3 mm diameter ran through the three arms. Test extract (50 µl) and control (*n*-hexane 50 µl) were impregnated onto separate filter papers (Whatman No. 1, 6 cm × 6 cm size), allowed to evaporate and then placed in treatment and control chambers, respectively. Purifed air @100 ml/min was pumped from upstream control and treatment chamber using mini aquarium pumps. Thirty 2-day-old weevils were released into the main chamber one after the other. Weevils found in any arm just after 2 cm of the junction point were regarded as having chosen that arm. The *Y*-tube was rotated by 180° once, to avoid directional influence. A black cloth was spread below the *Y*-tubes and the room was maintained dark to avoid any visual cues. The olfactometer set-up was rinsed with mild soap solution and then with hexane followed by air drying, for every new extract and a new set of weevils.

To find whether any significant difference exists between the responses of male and female weevils to a volatile extract, data were analysed with two-tailed Student's *t*-test ($P \leq 0.05$); Analysis of variance (ANOVA) was performed to know the differential response of male and female *C. formicarius* across the extracts and their means were compared with Tukey's multiple comparison test. The chi-square test was conducted to determine the choice of the weevils moving towards or away from the extract under the assumption of independence.

The male SPWs showed high EAG response than females to leaf volatiles and vice versa to flower volatiles. The male and female weevils exhibited different EAG response profiles to the odourants of these six varieties. Employing EAG studies in the identification of host-plant volatiles that modify the behaviour of insect pests, understanding of host-plant resistance to pests mediated by plant volatiles and identification of resistance in sweetpotatoes against *C. formicarius* have been successful in the past[4,7]. Developing a theoretical framework to study the degree of plant defence against herbivores has become important. The resistance of plants to insects is a relative property which depends on the comparative reaction of resistant and susceptible plants, grown under similar conditions, to pest insects[14]. Plants with constitutive defence possess genetically inherited qualities, resulting in a plant of one cultivar being less damaged than a susceptible plant lacking these qualities[15]. Susceptibility is governed by differential volatile emissions[4] and production of cyclopropane fatty acid esters[7] to which *C. formicarius* respond differently. Hence, EAG can record responses to a broad range of volatile compounds from host plants and is an efficient odour discrimination method[16,17] such as insect attraction using the powerful

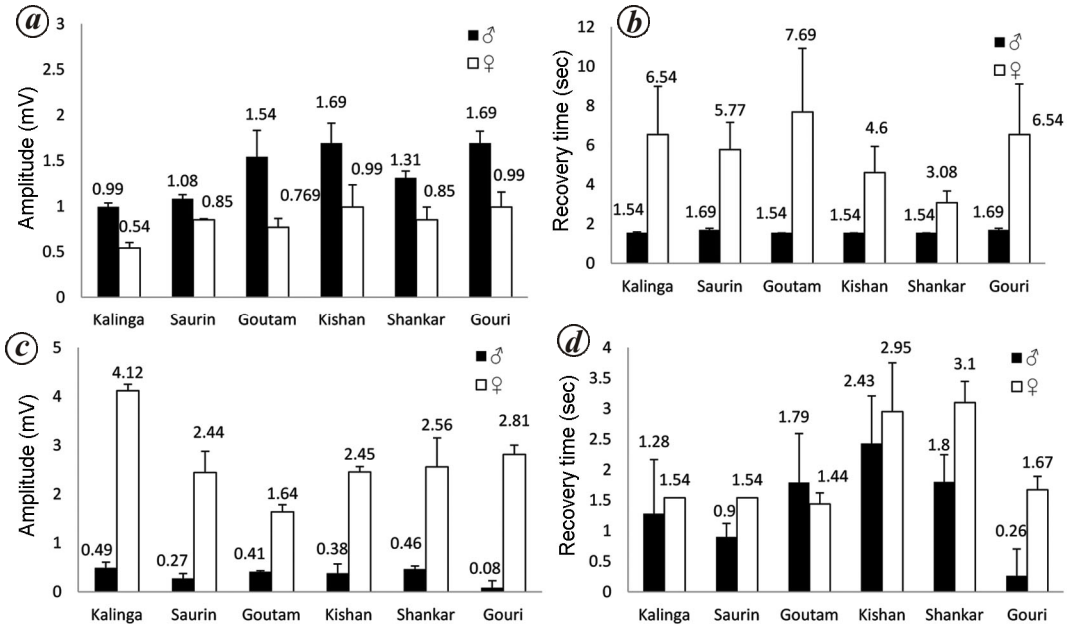

Figure 1. Electrophysiological responses of *Cylas formicarius* Fab. to leaf volatile extracts (***a*** and ***b***), and flower extract (***c*** and ***d***) of sweetpotato varieties.

insect olfactory system[18,19] and identification of plant varieties with SPW resistance[4,7]. The corroboration of the EAG data demonstrates the specific physiological role of various volatiles from different plant varieties in SPW *in vivo*. The female antennal responses elicited by each of the flower extracts have shown similar pattern obtained by Changwei and co-workers[20]. The amplitude and recovery time of SPW antenna to leaf extracts to reach the resting potential were inversely proportional, indicating that higher the amplitude, lesser the recovery time and vice versa (Figure 1). The ability of both sexes to detect leaf and flower volatiles is probably due to their similar habitat, which requires the use of same clues to locate host plants for survival and reproduction. Significantly different EAG responses were recorded to different extracts as well as to both genders[21]. It appears to be a general phenomenon among phytophagous insects that females and males can detect the same range of volatiles, but females have greater sensitivity to certain compounds[4,21,22]. From the perspective of chemical ecology, volatile compounds produced by plants serve as olfactory cues for herbivore host location[23].

Behavioural assays indicated the presence of significantly higher attraction ($P < 0.01$) of females to flower and storage roots compared to males, and more males to leaf. In leaf odour choice test, a significant difference has been observed in the attraction of male weevils to the varieties (F5, 15 = 8.93, $P < 0.01$), but not in females. Male weevils were attracted significantly higher, almost double, than those of females to 'Kishan' ($t = -9.09$, $df = 6$, $P < 0.01$) and 'Shankar' extracts ($t = -3.97$, $df = 6$, $P < 0.01$). In the flower-odour choice test, a significant difference has been observed in the attraction of female SPWs across the varieties (F5, 15 = 12.16, $P < 0.01$). In storage root-odour choice test, a significant difference has been observed in the attraction of both males (F5, 15 = 10.27, $P < 0.01$) and females (F5, 15 = 42.22, $P < 0.01$) across the tested varieties. Overall, significantly the highest number of weevils moved towards 'Kishan' and the lowest number towards 'Gouri' variety. 'Kishan' recorded the presence of the highest female weevil and the lowest male weevil in flower and root respectively, but the reverse in leaf. The difference between the means of all pairwise combinations was compared with the HSD (honestly significant difference) to find if any significant difference existed between them. Volatile extracts from storage roots and aerial parts (especially flower) were attractive to female SPWs, the former being substantially greater. According to our results, male SPWs were attracted in the order of leaf > flower > root volatiles, the order being same with field infestation data. The preference of weevils to an extract was completely gender-dependent. SPWs have significantly preferred leaf, flower and storage root of 'Kishan' and 'Shankar', but not that of 'Gouri' (χ^2 test, $N = 30$, $P < 0.05$) (Table 1).

Stems and storage roots across the six sweetpotato varieties have shown significant difference in infestation levels by SPW (Table 2). The average weevil infestation was maximum in 'Kishan' (8.62 grubs/five plants) and minimum in 'Gouri' (2.04 grubs/five) variety, indicating 'Kishan' as highly susceptible while 'Gouri' shows some degree of resistance to SPW (Table 2).

The storage root damage and yield are directly proportional (correlation coefficient, $r = 0.86$) with highly

Table 1. Behavioural response (%) of sweet potato weevil *Cylas formicarius* (Fab.) to leaf, flower and storage root extracts in a dual-choice olfactometer.

	Attraction (%) of weevils ($N = 30$) to leaf extracts				Attraction (%) of weevils ($N = 30$) to flower extracts				Attraction (%) of weevils ($N = 30$) to storage root extracts			
Variety	Male	Female	t, d$f = 6$	χ^2 value (P-value)	Male	Female	t, d$f = 6$	χ^2 value (P-value)	Male	Female	t, d$f = 6$	χ^2 value (P-value)
Kalinga	45.00^{a} ± 3.34	27.50^{a} ± 11.98	–2.51*	11.99 (0.0025)*	20.83^{a} ± 8.77	27.50^{ab} ± 5.00	-1.53^{NS}	4.174 (0.124)	20.83^{abcde} ±1.67	26.67^{abc} ± 3.85	–3.21*	1.35 (0.510)
Saurin	33.33^{b} ± 3.85	30.00^{b} ± 14.14	-0.53^{NS}	1.41 (0.495)	20.00b ± 8.16	40.00^{acd} ± 8.61	–3.89**	13.61 (0.001)*	15.00^{a} ± 1.93	21.67^{de} ± 1.92	–5.65**	3.66 (0.161)
Goutam	34.17^{c} ± 3.19	30.00^{c} ± 13.47	-0.50^{NS}	2.764 (0.251)	22.50^{c} ± 7.39	33.33^{e} ± 2.72	–3.18*	6.78 (0.033)*	15.00^{b} ± 1.93	20.83^{fg} ± 1.67	–5.29**	3.43 (0.179)
Kishan	49.17^{bcd} ± 3.19	25.83^{d} ± 5.00	–9.09**	15.179 (0.0005)*	27.50^{d} ± 6.87	43.33^{bfg} ± 6.09	–3.99**	16.01 (0.0003)*	11.64^{c} ± 1.92	40.83^{adfh} ± 3.19	18.09**	17.67 (0.000145)*
Shankar	43.33^{e} ± 12.17	18.33^{e} ± 7.94	–3.97**	17.68 (0.0001)*	28.34^{e} ±21.86	22.5^{cf} ± 3.19	0.61^{NS}	7.00 (0.03)*	15.00^{d} ± 1.93	35.84^{begi} ± 1.67	–18.86**	13.89 (0.0009)*
Gouri	27.50^{ade} ± 1.66	25.00^{f} ± 13.47	-0.43^{NS}	0.2105 (0.900)	16.67^{f} ± 5.44	19.17deg ± 3.19	-0.92^{NS}	0.94 (0.625)	15.00^{e} ± 1.93	20.00^{chi} ± 2.72	–3.46*	1.42 (0.492)
F5, 15	8.93**	0.54^{NS}			0.75^{NS}	12.16**			10.27**	42.22**		

Letters following the values represent results of ANOVA followed by Tukey's multiple comparison test. Values followed by the same letters are significantly different. Table value: $t = 3.707$, d$f = 6$, $P < 0.01$ denoted by **, $t = 2.447$, d$f = 6$, $P < 0.05$ denoted by *; NS, Non-significant. Table value: F5, 15 = 4.56, P<0.01 denoted by **, F5, 15 = 2.9, $P < 0.05$ denoted by *. *χ^2 Test: P-value < 0.05.

Table 2. Infestation pattern of weevil *Cylas formicarius* (Fab.) in sweet potato genotypes

Variety	Number of grubs/five plants		Average number of weevils in both stem and storage roots of five plants	Average number of weevils per kg of storage roots
	Stems	Roots		
Kalinga	$3.00^{a} \pm 1.00$	$0.67^{a} \pm 0$	3.80	58.27
Saurin	$5.00^{bc} \pm 2.00$	$1.33^{b} \pm 1.00$	4.92	60.89
Goutam	$2.67^{d} \pm 0.58$	$2.33^{c} \pm 0.58$	3.76	39.44
Kishan	$8.00^{abdef} \pm 1.00$	$3.33^{d} \pm 1.15$	8.62	108.46
Shankar	$3.30^{e} \pm 0.58$	$3.00^{e} \pm 1.00$	4.89	92.94
Gouri	$2.33^{cf} \pm 0.58$	$0.00d^{e} \pm 0$	2.04	33.79
F5, 10	15.51**	3.41*		

Table value: F5, 10 = 5.64, $P < 0.01$ denoted by **, F5, 10 = 3.33, $P < 0.05$ denoted by *; NS, Non-significant. Letters following the values represent results of ANOVA followed by Tukey's multiple comparison test. Values followed by the same letters are significantly different.

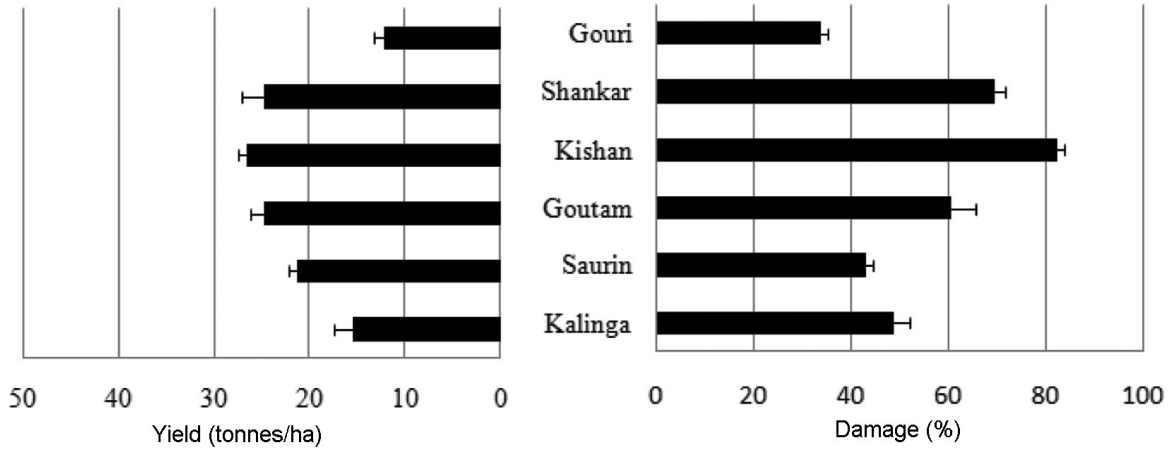

Figure 2. Sweetpotato weevil, *Cylas formicarius* Fab., per cent damage and yield (tonnes/ha).

susceptible variety ('Kishan') recording 26.68 t ha^{-1}, and the resistant variety ('Gouri') 12.5 t ha^{-1} (Figure 2). In this study, the variety showing comparatively higher degree of resistance to SPW produced less yield, indicating that sweetpotato plants adjust their physiology either to produce more or to defend more. Plants divert their biomass for production of defence compounds against herbivores resulting in lower yields[24]. The resistant variety, which has shown low yield, has also recorded low levels of insect infestation; probably because these varieties are generally not preferred by SPW either because of the production of anti-nutritional factors or behaviour modifying chemicals like repellents, or production of lesser quantities of attractants. In 'Kishan', there was a significant difference in infestation pattern compared at 90 and 120 DAP as well as 60 and 120 DAP in stem, while for all comparisons the infestation pattern was significantly different in storage roots, indicating preference of weevils towards roots than stem. This may be due to the favourable conditions and availability of required nutrients for weevil sustenance and multiplication in storage roots but not in stem. The results suggest that 'Gouri' contains compounds that might not be much preferred by SPW. Variation in the response of plants to SPW is due to alteration in chemical constituents among varieties, which could result in the variation in initial attraction, host choice, success of weevils in utilizing different plants or a combination of these factors[12]. The highest SPW damage was observed in the storage roots of 'Kishan' (82.33%), whereas the lowest was observed in 'Gouri' (33.73%; Figure 2). The average number of weevils per unit weight of storage roots was highest in 'Kishan' and lowest in 'Gouri', similar to the trend of per cent damage. This indicates that chemical factors might be involved in determining the preference of weevils towards particular varieties[4,9].

There was a significantly greater response of females than males to flower extracts in both olfactometry and electroantennography, whereas it was the reverse in leaf extracts. Thus, the highest weevil attraction towards specific variety by olfactometric studies, electrophysiological response, field infestation data and maximum damage in the storage roots implies that 'Kishan' appears to be highly susceptible to *C. formicarius*, whereas 'Gouri' is

the least susceptible or highly resistant. Moreover, the SPW olfactory system shows similar and highest amplitude to volatiles from both resistant (Gouri) and susceptible (Kishan) varieties, with a variation across varieties. The higher depolarization in the antennae is possibly because of the greater tendency of the weevils to get attracted towards or repelled by the varieties, which thereby refers to either susceptibility or resistance. This implies that higher EAG amplitude may not indicate either susceptibility or resistance; rather, it can be an indicator of both. The olfactory receptor system on weevil antennae responds similarly to volatiles that govern resistance or susceptibility of sweetpotato varieties. In the selection process for plants producing high levels of resistance against insects, those varieties which have repelled the highest number of and attracted the lowest number of SPWs and also having highest amplitude can be considered as resistant. Measurement of insect damage to plants is usually more useful than that of insect growth or population development on plants, because reduced insect damage to plants and the resulting increase in yield or quality are the ultimate goals of most crop improvement programmes. The real mechanism of odour perception by olfactory receptors in sweetpotato weevil would provide scope for future studies.

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