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HOST ASSOCIATED VARIATIONS IN NEONICOTINOID SUSCEPTIBILITY IN *BEMISIA TABACI* AND CORRELATION WITH *CYTP450*

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ABSTRACT

Neonicotinoid susceptibility of five populations of *Bemisiatabaci* (Gennadius) from two major cotton growing regions of India was evaluated. These included- North region: Sriganganagar (Rajasthan), Ludhiana (Punjab) and New Delhi and Central region: Khandwa (Madhya Pradesh) and Amravati (Maharashtra). To establish a correlation between neonicotinoid susceptibility and populations, LC_{50} (imidacloprid, thiamethoxam and acetamiprid), and activity of cytochrome P450 was explored. Bioassay revealed that population from Amravati recorded the maximum lethal concentration with least susceptibility to neonicotinoids with LC_{50} values ranging from 1317.21 to 1448.22 mg/L, whereas New Delhi population was the most susceptible (LC_{50} values ranging from 328.18 to 552.51 mg/L). This was also evident from level of cytochrome P450 levels. The difference in cytochrome P450 monooxygenase activity was observed to be non- significant. New Delhi population was taken as a unity to compare fold increase in cytochrome P450 activity with fold increase in the range of 1.90 to 2.39 for cotton, 2.12 to 3.11 for brinjal and 1.87 to 3.08 for tomato as a host.

Key words: *Bemisiatabaci*, **neonicotinoids, cotton, brinjal, tomato, Sriganganagar, Ludhiana, New Delhi, Khandwa, Amravati, cytochrome P450, susceptibility,**

Whitefly *Bemisiatabaci* (Gennadius) (Hemiptera: Aleyrodidae) is the most devastating pest of global significance. Its wide scale adaptation can be attributed to its polyphagous nature and development of resistance. Polyphagous nature of *Bemisia* with more than 600 documented host plants and variations in detoxifying enzymesis known (Oliveira et al., 2001). Complex interaction exists between host plants and phytophagous insects affecting the organisms at both trophic levels (Whitham et al., 2006). Plants produce a wide variety of defense compounds to counteract the herbivore attack, and herbivores in turn respond and evolve the various physiological mechanisms with detoxification enzymes to overcome host defense. This complex interaction between host plant and insect will be operating like see saw referred to as co-evolution (Schoonhoven et al., 2005; Howe and Jander, 2008; John and Graeme, 2008). Association of detoxifying enzymes with insecticide resistance has been well documented (Owusu et al., 1995; Li et al., 2007; Alon et al., 2008) and host plants are known to affect the activity and expression of these enzymes in insects (Liang et al., 2007; Wang et al., 2010; Xue et al., 2010; Xie et al., 2011). Further, there are reports that confirm the responses of different herbivores, not only changes between the host plants species, but also intraspecific variations (Iida et al., 2009; Xie et al., 2011; Yan et al., 2011).

Neonicotinoid insecticides represent quarter share in world insecticide usage for management of sucking pests, which stands same in Indian context as well, being widely used for whitefly management in cotton ecosystem. Hence the present study on the status and level of susceptibility to neonicotinoids in various populations of *B. tabaci* along with role of cytochrome in imparting tolerance, in *B.* populations reared on cotton, brinjal and tomato.

MATERIALS AND METHODS

The populations of *B. tabaci*were collected from cotton crop of five different locations falling under two major cotton growing regions of India, North region: Sriganganagar (Rajasthan, 29°55’12” N; 73°52’48” E), Ludhiana (Punjab, 30°36’0.338” N;74°47’41.719” E) and Delhi (28°38’5.940” N; 77°09’6.750” E); Central region; Khandwa (Madhya Pradesh, 21°48’56” N; 76°22’11” E) and Amravati (Maharashtra, 20°58’715” N; 77°46’437” E).The collections were made in August-September months in 2014 following Zee

walk mode. Adult whiteflies were collected early in the morning using an aspirator; green leaves were plucked to collect immature stages. The insects were transferred in ventilated cages containing leaflets inserted into wet sponges. Collected populations were kept in rearing cages for the emergence of fresh adults and the 'puparia' were sampled for valid species authentication (Martin, 1987). Population genetic group was confirmed using *mtCOI* gene amplification. The respective populations were raised in insecticide free exposure conditions on cotton (*Gossypium hirsutum* L), brinjal (*Solanum melongena* L), tomato (*Lycopersiconesculentum* Mill) seedlings, at 27±2°C temperature, 14:10 h (L:D) photoperiod and 60-70% relative humidity in insect rearing chamber at Division of Entomology, ICAR-IARI, New Delhi.

The required amount of technical grade insecticides, imidacloprid (98%), thiamethoxam (98%) and acetamiprid (96.5%) were weighed (w/w), diluted in acetone and subsequently, different concentrations of insecticides were prepared by serial dilution in deionized water containing 0.1% of non-ionic wetting agent, triton X-100. Bioassays were performed through the leaf dip method with slight modification (Naveen *et al*., 2011). Leaves with petiole from fifteen to twenty days old seedlings were immersed in serially diluted solutions for 20 sec, and allowed to air dry on paper towel, and these were placed after inserting the petiole in agar slant (2%) in Petri plate (90mm x 15mm), leaves dipped in emulsifier water were used as control. The adults were momentarily anaesthetized using CO_2 and transferred in batches of 30-40 on to the treated leaves; the plates were sealed with ventilated lids. All such assays were replicated three times for each concentration, a minimum of five concentrations for each insecticide were used for bioassay. Mortality observations were recorded at 24 hours after treatment wherein, adults showing no sign of movement were scored as dead. Mortality data for all five populations in combination with all three neonicotinoids were recorded for further calculation of LC_{50} value.

Cytochrome P450 activity was quantified and expressed in terms of general oxidase level, an indirect measure of cytochrome P450, using heme peroxidation method which is considered as a reliable tool for comparing differences in general oxidase levels based on hemeprotein levels. In this heme peroxidation, TMBZ was used as a substrate and H_2O_2 as co-substrate. With the presence of H_2O_2,the microsomal oxidases use the TMBZ and develops two oxidized TMBZ molecules (Brogdonet al., 1997; Penilla et al., 2007).

For general oxidase assays, five flies were separated in three replications and homogenates were prepared using a hand held homogenizer with a plastic pestle in 50 µl ice-cold potassium phosphate buffer (0.625 M, pH 7.2), containing 0.1% (w/v) Triton X-100. The reaction mixture consisted of 80 µl of 0.625 M potassium phosphate buffer (pH 7.2), 20 µl of enzyme source (homogenate), 200 µl TMBZ solution, 25 µl of H_2O_2 (3.0%) with a final volume of 325 µl. The substrate solution was prepared by dissolving 2 mg of TMBZ in 2.5 ml of methanol and 7.5 ml of 0.25 M sodium acetate buffer (pH 5.0). Absorbance was read at 620 nm against blanks (wells containing all reaction components, except the enzyme source) in a GEN5absorbance microplate reader after 5 min. of incubation. A standard curve for heme peroxidase activity was prepared using different concentrations of cytochrome C. The activity of cytochrome P450 (general oxidase) obtained from plate reading was expressed as nano moles of cytochrome P450 per milligram of protein by using the standard curve of cytochrome C.

The total protein content of homogenate was determined using the Coomassie brilliant blue G-250 dye (CBBG) methodwith bovine serum albumin (BSA) as the standard. Absorbance was recorded at 595 nm (Bradford, 1976). Bioassay data were analysed to calculate the LC_{50} values using log–dose probit analysis (Finney, 1971) using Polo Plus 2.0 (LeOra Software, Petaluma, CA). Activities of general oxidase among the different populations were compared using Tukey's test ($P<0.10$).

RESULTS AND DISCUSSION

Host plantsand neonicotinoids

Host plant influence on susceptibility of *B. tabaci*to insecticide has been studied in various cropping systems under greenhouse and field populations showing considerable variations. In the present study, *B.tabaci* populations collected from five different locations were reared on three different host plants in the laboratory (cotton,brinjal and tomato) for six to eight generations so that insects can adapt on a particular host plant and its derived secondary metabolites also. The populations were bio-assayed with neonicotinoids (imidacloprid, acetamiprid and thiamethoxam). Significant variations were observed across the populations with respect to median lethal concentration (LC_{50}) but were not significant across the hosts within same population (Table 1). Population from Amravati recorded the maximum lethal concentration of 1400.09, 1424.75 and 1448.22 mg/L for imidacloprid, acetamiprid and

Table 1. Neonicotinoids susceptibility of *B. tabaci*vs hosts

Population	N	Slope ±SE	χ^2	LC_{50} value (mg/l)	Fiducial limit in mg/l (CI 95%)
			Amaravati		
Imidacloprid					
Cotton	273	4.02±1.08	0.19	1400.09	1138.81-1546.63
Brinjal	321	4.02±0.98	0.05	1317.21	1078.25-1451.15
Tomato	299	3.83±0.97	0.14	1349.77	1124.99-1485.35
Acetamiprid					
Cotton	277	4.97±1.11	0.05	1424.75	1252.08-1542.75
Brinjal	331	5.57±1.04	0.70	1339.52	1191.37-1438.18
Tomato	280	4.86±1.08	0.58	1330.20	1125.05-1450.89
Thiamethoxam					
Cotton	273	4.93±1.11	0.10	1448.22	1292.78-1568.45
Brinjal	360	4.57±1.02	0.24	1341.68	1166.48-1449.66
Tomato	320	4.59±1.00	0.17	1328.84	1152.97-1439.80
			New Delhi		
Imidacloprid					
Cotton	376	1.57±0.44	2.35	552.51	397.44-810.68
Brinjal	331	1.46±0.32	0.92	378.58	252.04-482.97
Tomato	380	1.56±0.45	2.58	440.87	268.77-606.72
Acetamiprid					
Cotton	354	1.58±0.45	2.45	476.08	313.14-664.15
Brinjal	345	1.89±0.32	1.87	328.18	239.59-402.28
Tomato	378	1.77±0.46	1.50	385.91	235.79-510.02
Thiamethoxam					
Cotton	249	1.70±0.35	0.47	488.69	366.03-619.91
Brinjal	357	1.68±0.30	0.36	390.83	298.89-477.42
Tomato	406	1.34±0.39	0.10	361.61	176.13-511.44
			Ludhiana		
Imidacloprid					
Cotton	259	3.58±0.88	1.77	1354.69	1210.29-1618.23
Brinjal	255	4.02±0.92	1.41	1019.27	842.58-1133.10
Tomato	350	3.93±1.06	0.29	1086.77	889.69-1242.69
Acetamiprid					
Cotton	273	4.05±0.86	0.70	1162.89	1047.50-1295.07
Brinjal	298	3.39±0.94	0.84	967.56	707.88-1097.85
Tomato	245	4.78±0.95	0.61	928.28	786.89-1023.46
Thiamethoxam					
Cotton	236	3.24±0.89	1.08	1314.84	1152.02-1629.83
Brinjal	274	3.57±0.80	0.39	935.35	775.37-1045.82
Tomato	346	3.98±1.05	0.72	929.69	693.96-1068.13

		Sriganganagar			
Imidacloprid					
Cotton	302	2.52±0.79	0.11	1361.84	1177.58-1855.89
Brinjal	261	3.36±0.89	0.39	1090.75	925.49-1230.52
Tomato	261	2.90±0.87	0.50	1188.38	1000.06-1403.05
Acetamiprid					
Cotton	289	3.84±0.83	1.75	1086.32	952.12-1200.70
Brinjal	252	4.55±0.87	1.29	1029.78	909.13-1127.20
Tomato	257	4.08±0.92	0.61	963.93	806.18-1068.97
Thiamethoxam					
Cotton	312	2.98±0.80	0.17	1380.09	1217.88-1792.28
Brinjal	279	2.87±0.73	0.75	1103.78	938.26-1272.67
Tomato	235	3.22±0.87	1.10	1167.58	987.65-1352.16
		Khandwa			
Imidacloprid					
Cotton	261	3.27±0.70	0.01	1104.63	975.64-1340.83
Brinjal	305	3.60±0.65	2.17	954.00	856.80-1059.86
Tomato	319	3.05±0.66	1.14	846.73	712.13-951.65
Acetamiprid					
Cotton	254	3.16±0.70	0.39	921.37	790.12-1053.87
Brinjal	272	2.88±0.63	0.75	847.97	691.99-968.42
Tomato	291	3.66±0.69	0.72	777.81	657.99-867.57
Thiamethoxam					
Cotton	287	2.82±0.66	0.05	1136.52	993.66-1421.29
Brinjal	314	3.31±0.64	1.64	960.55	858.78-1079.21
Tomato	309	2.83±0.65	1.80	823.63	676.30-936.13

thiamethoxam respectively when reared on cotton. However median lethal values recorded on other two hosts were 1317.21, 1339.52, 1341.68 mg/L on brinjal and 1349.77, 1330.20, 1328.84 mg/L on tomato for imidacloprid, acetamiprid and thiamethoxam respectively (Table 1).

Populations from New Delhi recorded the lowest LC_{50} values of 552.51, 476.08, 488.69 mg/L in cotton; 378.58, 328.18, 390.83 mg/L in brinjal and 440.87, 385.91, 361.61 mg/Lin tomato for imidacloprid, acetamiprid and thiamethoxam respectively (Table 1). Results showed that intermediate values of median lethal dose were observed in the populations from other three locations viz., Ludhiana, Sriganganagar and Khandwa. Studies on resistance monitoring conducted by Castle et al.(2009) in Imperial Valley for *B. tabaci* populations collected from broccoli, cantaloupes and cotton crops showed significant host plant influence with broccolipopulations being tolerant compared to populations of cantaloupes and cotton. Similar we also found cotton populations to be more tolerant compared to tomato and brinjal. Robertson et al.(1994) was of opined that phytophagous insects acquire plant allelochemicals and show resistance to particular insecticide group. In our study as well, cotton populations showed relatively higher neonicotinoid tolerance may be due to secondary metabolites or allelochemicals of cotton acquired by whitefly that might have played role in imparting tolerance. The same response towards insecticides can be obtained through consumption of plant allelochemicals incorporated in artificial diet (Hunter et al., 1994). Similarly, Howe and Jander (2008) explained that host plant and their secondary metabolite are closely related to development of resistance in *B. tabaci*. The defensive compounds of host plant such as toxins and defensive proteins target insect physiological processes induce the insecticide resistance in herbivorous insects. The effect of host associated variations on susceptibility to insecticides was also reported by Sivasupramaniam et

al.(1997) when they sampled populations of *B. tabaci* from various crops in Arizona and bioassayed with bifenthrin and observed that *B. tabaci* populations were most tolerant which were collected from broccoli.

Susceptibility of different populations of *B. tabaci* against three neonicotinoids was compared taking New Delhi population as unity. The relative susceptibility values of neonicotinoids for Amravati population were in the range of 0.33 to 0.40 on cotton, 0.25 to 0.29 on brinjal and 0.27 to 0.33 on tomato. Populations from Ludhiana also followed the same trend with the relative susceptibility values of 0.37 to 0.41 on cotton, 0.34 to 0.42 on brinjal and 0.39 to 0.42 on tomato. Closer values were observed in case of Sriganganagar population with the relative susceptibility ranging between 0.35 to 0.44, 0.32 to 0.35 and 0.31 to 0.40 on cotton, brinjal and tomato respectively (Table 2). From the findings it is evident that host plant has definite role to play in imparting relative tolerance to neonicotinoids in *B. tabaci* but susceptibility variation was found to be more evident across the locations rather than across host plants.

Host plants and cytochrome P450 (cyt P450) activity

Host plants play an important role in induction of detoxification enzyme system in insects (Saha et al., 2012). The encountering of *B. tabaci* to wide range of plant allelochemicals and efficient performance of detoxification enzymes probably has a crucial role in its resistance against insecticides.In the present study, a significant difference was observed in the cytochrome P450 monooxygenase activity among different populations reared on three different host plants (cotton,brinjal and tomato). Li et al. (2002) showed that cytochrome monooxygenase production is induced by activation of jasmonate and salicylate pathways in herbivores that plays crucial role in enhancing the production of detoxifying enzymes like cytochrome. The population from Amravati recorded highest enzyme activity (739.02 nmol/mg on cotton,664.37 nmol/mg on brinjal and 680.32 nmol/mg on tomato) on all the three hosts as well as a highest median lethal dose for all the three neonicotinoids tested.

Populations from Ludhiana, Sriganganagar and Khandwa recorded the cytochrome values of 654.74, 609.16 and 587.76 nmols/mg of protein, respectively when the populations were reared on cotton.It was also reflected in their susceptibility towards neonicotinoids where cotton recorded highest tolerance level. Populations from Ludhiana, Sriganganagar and Khandwa recorded the cytochrome values of 462.32, 451.98 and 463.42 nmols/mg of protein, respectively when reared on brinjal but the differences were insignificant. Whereas, on tomato population from Khandwa, a slightly lower value (413.65 nmols/mg of protein) of cytochrome was recorded when compared with that of Ludhiana and Sriganganagar populations which had cytochrome values of 458.32 and 446.69 nmols/mg of protein. New Delhi population showed the lowest cytochrome value on all the hosts which was also reflected in its susceptibility towards neonicotinoids. New Delhi population recorded cytochrome values

Table 2. Relative toxicity and susceptibility of *B. tabaci* to neonicotinoidsvs hosts

Insecticides	Relative susceptibility*				
	New Delhi	Khandwa	Ludhiana	Sriganganagar	Amravati
			Cotton		
Imidacloprid	1	0.50	0.41	0.41	0.40
Thiamethoxam	1	0.43	0.37	0.35	0.34
Acetamiprid	1	0.52	0.41	0.44	0.33
			Brinjal		
Imidacloprid	1	0.40	0.37	0.35	0.29
Thiamethoxam	1	0.41	0.42	0.35	0.29
Acetamiprid	1	0.39	0.34	0.32	0.25
			Tomato		
Imidacloprid	1	0.52	0.41	0.37	0.33
Thiamethoxam	1	0.44	0.39	0.31	0.27
Acetamiprid	1	0.50	0.42	0.40	0.29

*Relative susceptibility= LC_{50} of Delhi strains/ LC_{50} of each population

Table 3. Cytochrome P450 in populations of *B. tabaci*

Population	Cotton		Brinjal		Tomato	
	Cytochrome P450 monooxygenase (nmol/mg of protein ±SE)	RA	Cytochrome P450 monooxygenase (nmol/mg of protein ±SE)	RA	Cytochrome P450 monooxygenase (nmol/mg of protein ±SE)	RA
New Delhi	308.77±41.40[a]	1	213.68±28.56[a]	1	221.05±20.99[a]	1
Ludhiana	654.74±40.46[b]	2.12	462.32±9.35[a]	2.16	458.32±12.43[a]	2.07
Sriganganagar	609.16±48.85[b]	1.97	451.98±56.21[a]	2.12	446.69±11.26[a]	2.02
Amravati	739.02±56.09[a]	2.39	664.37±50.52[a]	3.11	680.32±24.94[a]	3.08
Khandwa	587.76±17.25[b]	1.90	463.42±32.88[a]	2.17	413.65±7.19[a]	1.87

Values compared across hosts within the population; Values followed by same letters not significantly different (p= 0.10- Tukey's HSD test); RA= Relative activity

of 213.68, 308.77 and 221.05 nmols/mg of protein on brinjal, cotton and tomato respectively (Table 3).

Cotton host recorded the highest value for all the five populations evaluated for cytochrome activity. However, cytochrome values recorded on Brinjal and tomato were found to be on par except for Khandwa population wherein tomato recorded slightly lower values of cytochrome. New Delhi population was taken as a unity to compare fold increase in activity and it was observed that the fold increase was in the range of 2.12 to 3.11 on brinjal, 1.90 to 2.39 for cotton and 1.87 to 3.08 for tomato as a host (Table 3).

Li et al. (2002) studied host associated variations involving two host plants change activities of GST and P450 and relative tolerance towards acetamiprid and abamectin in *B. tabaci*. Xie et al.(2011) studied induction effect of host on insecticide susceptibility and detoxification enzymes of *B. tabaci*. They investigated induced changes through bioassay and biochemical studies on five different hosts viz., cabbage, poinsettia, cucumber, cotton and tomato. They observed significantly higher glutathione-S-transfarase and cytochrome P450 activity in *B. tabaci* of poinsettia population compared to that of cucumber population. They also reported the sensitivities of *B. tabaci* cucumber population to acetamipid were significantly higher than that of poinsettia population.Cabbage exhibited significantly higher enzyme activity compared to that of poinsettia, cucumber, cotton and tomato.Thus, the variations in susceptibility were more evident due to difference in populations of whiteflies rather than the host and this is attributed to variation in levels of cytochrome P450 in these populations.

Feng et al. (2010) explained that resistance mechanism of *B. tabaci*to neonicotinoids results from enhanced detoxification by cytochrome P450. In our study for each population enzyme activity was maximum on cotton as a host followed by brinjal and tomato. The enzyme activity of each population also differed which can be correlated with lethal toxicity of neonicotinoids. The population from Amravati recorded highest enzyme activity on all the three hosts as well as a highest median lethal dose for all the three neonicotinoids tested. New Delhi population recorded the lowest cytochrome value on all the hosts which was also reflected in its susceptibility towards neonicotinoids. Cytochrome levels of Ludhiana, Sriganganagar and Khandwa populations reared on cottonwere significantly different from cytochromelevels of brinjal and tomato reared populations. The cytochrome activity of different populations of *B. tabaci* were compared with New Delhi population and fold increase in activity for Amravati population was 2.39, 3.11 and 3.08 folds on cotton,brinjal and tomato respectively. The other three populations *viz*., Ludhiana, Sriganganagar and Khandwa recorded 2.12, 1.97 and 1.90 folds, respectively on cotton, 2.16, 2.12 and 2.17 folds, respectively on brinjal and 2.07, 2.02 and 1.87 folds on tomato respectively (Table 3).

The present findings indicate that feeding on different host plant may cause sensitivity changes to neonicotinoids in *B. tabaci* by affecting the activities of cytochrome P450. Our results were supported by various studies who reported the role of cytochrome P450 in detoxification of host phytochemicals and xenobiotics (Despreset al., 2007; Li et al., 2007; Alon et al., 2010; Castaneda et al., 2009; Zhou et al., 2010; Schuler 2011; Deng et al., 2013). For all the five populations, susceptibility to all three neonicotinoids can be very well correlated with cytochrome. Though some of the possible reasons responsible for it have been studied and validated, Kontsedalov et al.(2008)

and Ghanim and Kontsedalov (2009) explained that the host plant induction effect on activity levels of detoxifying enzymes and insecticide susceptibility are not so simplified. They explained that responsiveness to insecticide could be affected by inherent factors such as presence and densities of bacterial symbionts in *B. tabaci*. Therefore, our results may also be related to types and densities of bacterial symbionts in five different populations of *B. tabaci* adapted to three different host plants during future course of work.

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