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Non-preference (Antixenosis) parameters in tomato genotypes and their effect against whitefly, *Bemisia tabaci* under controlled condition

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Abstract
Whitefly, *Bemisia tabaci* is one of the major constraints for tomato production worldwide both by direct damage of desapping the plant phloem content and indirectly by transmitting plant viruses especially begomoviruses. Vectoring capability of *B. tabaci* vary widely all over the Indian sub-continent. Exploration of resistant tomato genotypes is very much important for the effective and environmentally safer management of whitefly and its spread of tomato leaf curl virus (ToLCV) on tomato. Among the three plant resistance mechanisms, presence of non-preference (Antixenosis) mechanism is crucial in checking virus spread for certain plant viruses like ToLCV, which will limit the selection of host plants for feeding and oviposition by the vector insects. Selected tomato which performed better from field and glasshouse screening experiments were evaluated in laboratory condition for its antixenotic fitness by conducting leaf surface test for egg laying preference, trichome density and wax concentration test. The genotypes EC-631364 (4.67 and 5.33), EC-620389 (5.67 and 3.33), EC-520078 (4.67 and 2.33) and EC-315477 (9.33 and 2.33) notably had the lowest mean number of *B. tabaci* eggs in the abaxial surface and abaxial surface of leaves. The highest mean number of eggs on both abaxial and abaxial surface of tomato leaves was observed to be in EC-620370, EC-620372, EC-538153 and EC-620427. Comparatively the preference for egg laying was more in the abaxial surface of the test genotypes held. The genotype EC-520078 recorded the lowest number of trichomes (114/cm^2) followed by EC-620389 (125.33/cm^2) and PKM1 (150/cm^2). The highest content of epicuticular wax was observed in genotypes *viz.*, EC-520078 (64.2 mg), EC-620389 (56.9 mg) and EC-315477 (48.1 mg), while it was the least on the genotypes EC-620372 (2.7 mg) and EC-620417 (10.57 mg). Overall, the genotypes *viz.*, EC-520078, EC-631364, EC-315477 and EC-620389 were noted as highly resistant against whitefly with non-preference plant resistance mechanism and may need additional laboratory studies before making incorporation into resistance breeding strategies for *B. tabaci* and their vectoring capabilities of ToLCV on tomato.

Keywords: whitefly, *B. tabaci,* tomato genotypes, plant resistance mechanism, non-preference or antixenosis

Introduction
The cultivation of tomato (*Solanum lycopersicum* L., 2n=24, Family: Solanaceae), is practiced in almost all parts of India covering an area of 7.78 lakh hectares and annually accounting a total production of 193 lakh tonnes, with a productivity of 24 tonnes per ha [1]. The production of tomato is hampered by an array of abiotic and biotic stresses and among these issues, the problems associated to pests and diseases are very critical. Out of an array of insect pests reported on tomato, the plant sap feeding insects such as thrips, whiteflies and aphids cause severe damage to the crop mainly by involving themselves in transmission of virus diseases rather than their direct feeding damages [2] and hence, these tiny insects are considered very critical in tomato cropping system. The polyphagous sweet potato whitefly, (*Bemisia tabaci* Gen.) (Aleyrodidae: Hemiptera), the most devastating and one among the economically important agricultural insect pests, has invaded a wide range of cropping systems causing considerable damage to cultivated crops [3]. *B. tabaci* is a cryptic population and is highly complex with 44 biotypes being reported and out of these biotypes of *B. tabaci* H, P, K, G, and B biotypes have been reported from India [4]. *B. tabaci* is the known vector of begomoviruses and transmits tomato leaf curl virus (ToLCV), which is predominantly caused by Biotype B in India [5] even though other biotypes are also involved in their transmission [6].

The cultivation of agronomically superior but at the same time whitefly susceptible tomato genotypes in the field had led to strong buildup of huge numbers of whitefly population and also was the root cause for major spread of begomoviruses in tomato ecosystem [7]. Farmers are depending on insecticides heavily to manage the whitefly to safe guard their crop from virus incidence [8], which had practically not happened, but at the same time caused a set of different problems like insecticide resistance development among the whitefly population [9], residues on the crop produce [10], ecologically imbalance, health hazards to the growers, *etc*. For the effective check over whitefly population build up and thereby the prevention of spread of viral diseases such as ToLCV, host plant resistance (HPR) technique is an important option, and hence it is important to look for the presence of natural resistance among the tomato genotypes and warrants continuation of screening of germplasm from time to time owing to the variations happening among the *B. tabaci* population and also the ToLCV as well [11]. The tolerance or resistance offered by a genotype may be from any one or combinations of the three basic resistance mechanisms *viz.*, nonpreference, antibiosis and plant tolerance [12]. HPR is a strong alternative method of control and are highly effective, sustainable and environmentally safe which may help in mitigating development of diverse biotypes of whiteflies that plague crops in different geographical and crop production environments [13].

A resistant plant may influence the host selection process of an insect and such plant may be avoided by the insect involved in host selection process, deter oviposition and feeding, impact survival and development of insect, and may recover from the damage caused from insect populations which otherwise would greatly damage other plants of the same species under similar environmental conditions [14]. In a plant-insect-virus interaction context, resistance offered by a host plant may greatly differ the interference with virus uptake and transmission abilities of the vectoring insect [15]. The feeding biology of the insect plays a major role in virus transmission on host plants and therefore an important area of research in plant virus management strategies [16]. The non-preference or antibiosis mechanism of resistance, therefore, has a significant role in checking plant virus transmission and spread among cultivated crops [17]. In this context, the mechanism of resistance in tomato genotype against whitefly, *B. tabaci* especially antixenosis (nonpreference) was studied and reported in the present paper.

Materials and Methods

Plant material

The tomato genotypes (50 nos.) received from NBPGR (National Bureau of Plant Genetic Resources, New Delhi) were first field screened in a farmer holding at Linganayakanpati, Usilampatti Taluk, (Coordinates: 9.9651ºN, 77.7885ºE), Madurai district, Tamil Nadu, India hot spot location for the ToLCD incidence, under natural infestation of *B. tabaci* and ToLCV. Twenty three genotypes were selected based on their performance in field and taken to further screening along with susceptible check (Arka Vikas) and moderately resistant check (PKM 1) that included in glasshouse facility, Centre of Innovation, Agricultural College and Research Institute, Tamil Nadu Agricultural University (TNAU), Madurai, Tamil Nadu, India during Oct., 2019.

The selected tomato genotypes from field and glasshouse screening were further evaluated under laboratory for their antixenotic fitness against *B. tabaci*. Laboratory experiments were conducted unless otherwise specified at Agricultural College and Research Institute, Tamil Nadu Agricultural University (TNAU), Madurai, Tamil Nadu, India (Coordinates: 9.9699° N, 78.2040° E).

Whitefly culture

The whitefly culture used for the screening were predominantly collected from cotton (*Gossypium* spp.) crop at the fields of Agricultural College and Research Institute, Madurai, Tamil Nadu and cultured in the greenhouse of Insectary on host plants *viz.*, cotton (*cultivar* ARBH 1401), tomato (*cultivar*, Arka Vikas) and Black night shade (*Solanum nigrum* L.) (*cultivar* Local). The mtCOI based molecular analysis revealed that *B. tabaci* population used in the present study was aligning to *B. tabaci* complex sp. Asia I mitochondrion GenBank ID: KJ778614.1 with 99.56% homology. The plants were grown on coirpith and soil medium with proper fertilizers and regular watering. The plants were maintained in cages (150cmx150cmx150cm) that were covered with 100µ mesh paint-filter cloth on all the sides. Every fortnight pest free fresh plants aged 30-40d was regularly introduced inside the culture cages for continuity of cultures. Naive and newly emerged fresh whitefly adults needed for experiments were collected by separate caging of whitefly infested plants after vigorous shacking of plants to remove the feeding adults after 3 - 4 d, from 100µ mesh cloth cages using borosilicate glass test tubes of size 25 × 220 mm connected to an aspirator.

Non-preference (Antixenosis): Resistance mechanism studies

Ovipositional preference: Leaf surface test

Ovipositional preference among the selected entries was checked out by undergoing leaf surface test with suitable methods. To analyze leaf surface resistance for egg laying, modified petri dish (9 cm dia. x 1.5 cm depth) method was used and the petri dishes were prepared as described hereafter. Evenly spaced 2 cm circular openings were created @ four numbers per plate in the bottom plates of each fresh plastic petri dish at a circumference of 4cm from the centre of the dish. The top lids of each petri dish were lined with Whatman No.4 filter paper upon which tomato leaflets were arranged for the test as described hereafter. A total of four fully opened uniform sized leaflets selected and detached from each plant of every genotype were carefully arranged in the prepared petri dishes with two of them placed with their upper leaf surface facing upward in opposite ends, while the remaining two selected leaflets placed with the lower leaf surface facing upward opposed each other in a criss-cross fashion. The arranged leaflets were central in alignment with the four openings of bottom plates of the dish and both plates of the dish were closed oppositional way. The filter paper was saturated with distilled water. Then, a second lid with a 4cm opening at the centre was placed on the top of the petri dish. Rubber bands were perpendicularly roped to each other around the top and bottom lids to hold them together. Twenty adult females of *B. tabaci* introduced into the petri dish cage at the central 4cm hole of top second lid with the help of an aspirator and the entrance was plugged with tissue paper. After 48 h, the number of *B. tabaci* eggs deposited on the four leaflets was counted and recorded [18] (Plate 1).

Trichome density assay

The method suggested by Maiti, Bidinger [19] was used for trichome density analysis on different tomato genotype taken. Leaf samples were taken from the third fully opened leaf from each plant of genotypes to complete the analysis. Three replicates were maintained for each leaf sample collected randomly, which were cut into leaf bits of one cm^2 at random from the selected leaflets @ three replicates/plant of each genotype. Then, the leaf bits were boiled in test tubes containing 20 ml of water for 15 min at 85 °C using hot water bath and then the water was drained off. The leaf bits were again boiled in 20 ml of 96% ethyl alcohol for 20 min at 80 °C and then the alcohol was drained off. Boiling with alcohol and draining process was repeated until all chlorophyll pigments were completely bleached off from the leaves. Afterwards, 90% lactic acid was added to the test tubes, were stoppered and heated at 85 °C for approximately 30-45 min. until leaf segments were fully cleared. Then, after sufficient cooling leaf segments were taken out from the test tubes and mounted on clean glass slides using a drop of lactic acid. Under a stereozoom microscope (STEMI 508) at 45 X magnification by image analyzer, number of trichomes per cm^2 area was counted and recorded for each leaf sample (Plate 2).

Extraction of epicuticular wax

The method described by [20, 21] was adopted to estimate the epicuticular wax of tomato leaves. The individual healthy leaves of uniform size and weight (100mg) from different genotypes were taken for the study. The leaves were immersed completely in 25 ml of chloroform in pre-weighed clean glass petri dishes (size: 15 mm × 80 mm) and agitated twice for 1 min under a fume hood. The setup was left undisturbed for 10 minutes. Then, the extracts were allowed to completely evaporate at room temperature. The final weight of each petriplate was weighed with the condensed epicuticular wax smeared in and around the petri plate surfaces. The experiment was replicated thrice.

The wax concentration (mg/leaf) was calculated using the formula of Yin, Bi [22], where wax concentration = $(W_1 – W_0)$, given W_1 is the final weight of the petriplate with condensed epicuticular wax (mg), and W_0 is the initial weight of the fresh petriplate (mg).

Statistical analysis

Data from the experiments were subjected to one-way analysis of variance (ANOVA) and PROC GLM analysis [23]. The data on population numbers were transformed with square root transformation ($\sqrt{x}$) before statistical analysis. When significant, the differences between genotype means, were separated employing Duncan's Multiple Range Test (DMRT) [24] (P=0.05).

Results

Ovipositional preference: Leaf surface test

The results of the leaf surface test indicated significant differences between the tested tomato genotypes. The mean number of *B. tabaci* eggs laid in the abaxial surface of leaves of tomato genotypes indicated that the least number of eggs were found in genotypes EC-631364, EC-620389 and EC-520078 with 4.67, 5.67 and 4.67 nos. respectively and were on par with each other. The highest number of *B. tabaci* eggs was recorded in EC-620370 (10.67 nos.) and EC-620372 (11.67 nos.) that were on par with each other. The adaxial surface of leaves recorded the lowest number of eggs in EC-315477, EC-520078, EC-620389 and PKM1 with 2.33, 2.33, 3.33 and 4.33 nos. respectively and were on par with each other. The highest number of eggs on adaxial surface was observed in EC-538153 and EC-620427 (9.33 and 10.67 nos., respectively) and were found to be on par. The susceptible check Arka vikas recorded 10.33 nos. of eggs in abaxial surface and 16 nos. of egg in adaxial surface. The preference of egg laying was high on abaxial surface in the genotypes *viz.*, EC-620372 (11.67 nos.), EC-620370 (10.67 nos.), EC-620417(10.33 nos.), EC-315477 (9.33 nos.), EC- 620401 (9.00 nos.), EC-3176 (8.33 nos.), EC-165690 (7.67 nos.), PKM1 (7.33 nos.), EC-620389 (5.67 nos.), and in EC-520078 (4.67 nos.) (F= 29.85; df=13; Pr > F= < 0.0001) The adaxial surface was highly preferred for egg laying by *B. tabaci* in the genotypes *viz.*, EC-620427 (10.67 nos.), EC-538153 (9.33 nos.) and EC-631364 (5.33 nos.) and (F= 28.09; df=13; Pr > F= < 0.0001). Comparatively the preference for egg laying was more in the abaxial surface of the test genotypes held (Table 1).

Trichome density

The trichome density assessment per cm^2 for the genotype was done with the stereo zoom microscope image analyzer. The highest number of trichomes were recorded in the genotype EC-620401 with 454.33 nos. followed by EC-315477 (406.67) and EC-538153 (397.67). The susceptible check Arka vikas recorded the overall highest number of trichomes with 571.67. The genotype EC-520078 recorded the lowest among all the screened genotype with 114 nos. followed by EC-620389 with 125.33 and PKM1 with 150 trichomes. The remaining genotypes *viz.*, EC-620417, EC-620370, EC-620427, EC-631364, EC-165690, EC-3176 and EC-620372 had registered 386.33, 348.33, 316.67, 249.33, 220.00, 207.33 and 175.67 per cm^2 respectively (Fig. 1).

Leaf epicuticular wax content

The results of the experiment conducted indicated that the presence of wax ranged from 2.7 to 64.2 mg per leaf with significant differences among the genotypes. The highest concentration of wax was in the tomato genotype EC-520078 with 64.2 mg followed by EC-620389 (56.9 mg) and EC-315477 (48.1 mg). The least amount of epicuticular wax was recorded in the genotype EC-620372 with 2.7 mg followed by EC-620417 with 10.57 mg. The susceptible check Arka vikas recorded 2.2 mg of epicuticular wax. The other tested tomato genotypes *viz.*, EC- 620401, PKM1, EC-EC-3176, EC-165690, EC-620427, EC-620370 and EC-538153 had registered 37.7, 34.3, 31.6, 29.5, 14.3, 13.5 and 11.5 mg per leaf level of epicuticular wax respectively (Fig. 1).

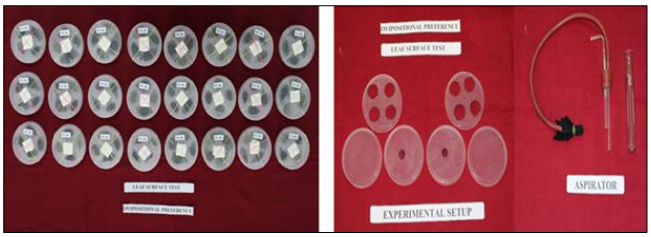

Plate 1: Experimental setup for leaf surface test organized to assess the ovipositional laying preference of whitefly, *B. tabaci* adults on different tomato genotypes

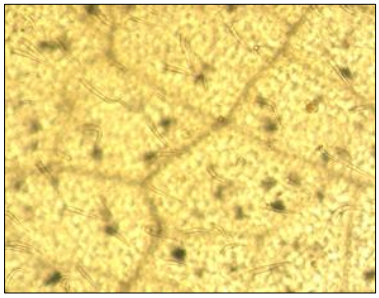

Plate 2: Trichome density assay of tomato genotypes used to study non-preference (antixenosis) plant resistance against whitefly, *B. tabaci*: Genotype EC-620372 at 45 X magnification

Table 1: Number of eggs laid by whitefly *B. tabaci* on different tomato, *Solanam lycopersicum* genotypes in leaf surface test under laboratory condition

Genotypes	Mean number of eggs ± SE per leaf disc	
	Abaxial surface	Adaxial surface
EC- 620401	9.00±0.13 (3.00)^{cd}	5.67±0.15 (2.38)^{cde}
EC-315477	9.33±0.07 (3.06)^{ed}	2.33±0.07 (1.53)^{a}
EC-520078	4.67±0.07 (2.16)^{a}	2.33±0.07 (1.53)^{a}
EC-620389	5.67±0.07 (2.38)^{a}	3.33±0.07 (1.82)^{ab}
EC-631364	4.67±0.07 (2.16)^{a}	5.33±0.07 (2.31)^{bcd}
EC-538153	8.00±0.00 (2.83)^{bc}	9.33±0.15 (3.05)^{fg}
EC-620417	10.33±0.07 (3.21)^{ef}	6.33±0.19 (2.52)^{cde}
EC-3176	8.33±0.07 (2.89)^{bcd}	6.67±0.26 (2.58)^{de}
EC-165690	7.67±0.07 (2.77)^{b}	5.00±0.13 (2.24)^{bcd}
EC-620370	10.67±0.15 (3.27)^{fg}	7.00±0.22 (2.65)^{de}
EC-620427	8.00±0.00 (2.83)^{bc}	10.67±0.07 (3.27)^{g}
EC-620372	11.67±0.15 (3.42)^{g}	7.67±0.15 (2.77)^{ef}
PKM1	7.33±0.07 (2.71)^{b}	4.33±0.07 (2.08)^{abc}
Arka Vikas	10.33±0.07 (3.21)^{ef}	16.00±0.22 (4.00)^{h}
SEd	0.5634	0.9677
CD(.05)	1.1542	1.9824

* Mean of three replications
Values in the parantheses are square root transformed values
In a column, the mean followed by the same letter are not significantly different from each other and were separated using, Duncan's Multiple Range Test (DMRT) [24] (P =0.05)
SE: Standard Error of difference

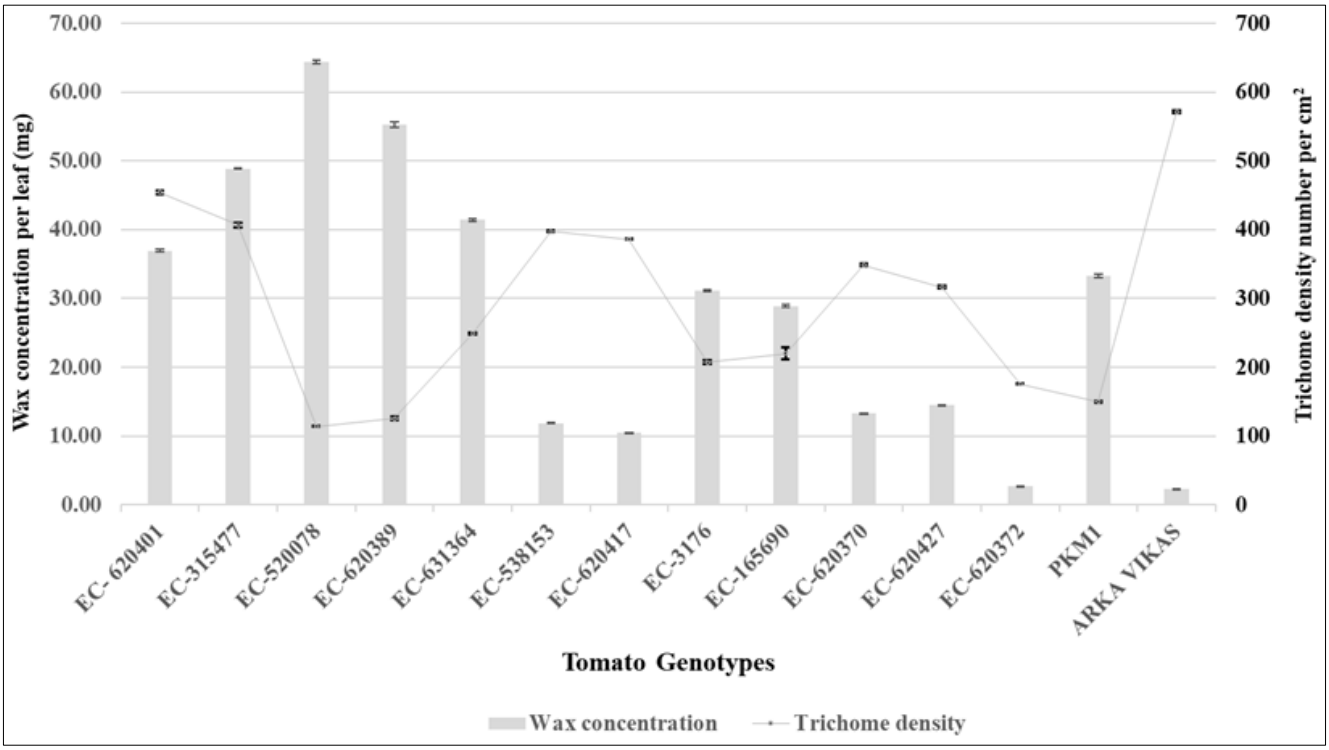

Fig 1: Leaf epicuticular wax content and trichome density assessed on different tomato *Solanum lycopersicum* genotypes used in assay on non-preference plant resistance against whitefly, *B. tabaci* under laboratory condition

Discussion

The ToLCV is a phloem-restricted virus infecting tomato. The effective stylet activities of the whitefly *B. tabaci* in phloem sieve elements determine ToLCV inoculation [25]. In order to reduce the primary, spread of the ToLCV by *B. tabaci* adults, the non-preference of *B. tabaci* over the tomato plants is the important aspect in the host selection process for egg laying and feeding prospects. In context to this, the nonpreference study on egg laying on different genotypes under controlled laboratory conditions revealed that the mean number of *B. tabaci* eggs laid in the abaxial surface of tomato leaf was more comparatively than the eggs laid on the adaxial surface. The egg laying on abaxial surface also indicated that the preference was more in EC-620372 followed by EC-620370 and the preference were found least in the genotypes EC-631364 and EC-520078. The adaxial surface preference was found more in EC-620427 and EC-538153. The results of the studies are in line with [18] where 19 tomato genotypes were studied for their ovipositional preference by leaf surface test and reported that genotypes COTLCVRH 1 and LE 1165 were with the lowest mean number of eggs on both the surfaces whereas genotype LE 231 had the lowest number of eggs only on adaxial surface. The results are related to the number of trichomes and other phytochemicals that are present over the host plant surfaces on leaves.

Leaf trichomes play a very crucial role in many whitefly-host plant relationships. There has been a positive linear relationship reported between trichome density and their type with the whitefly egg laying in various studies. The rate of oviposition was higher on leaves with trichomes at greater density in plants such as cotton [26-29], soybean [30], brinjal [31, 32] and tomato plants [17, 33, 34]. The lack of suitable egg laying sites by the absence or less number trichomes, which are normally used by *B. tabaci* adults to glue their eggs had led to the rejection of non-hairy leaved varieties of plants [35], and may also be the part of evolutionary responses to selection pressures exerted by parasitoids and predators and the natural enemies of whitefly showed better efficiency in searching on glabrous leaves rather than densely trichomed lines [36-38].

A more suitable microclimate for oviposition under high pubescence lines might be an added reason [39]. Therefore, an important criterion for whitefly resistance predictions might be pointed towards glabrous leaves of host plants. Further, the type of trichomes also had a profound influence on whitefly preference [40] and in tomato genotypes antixenosis for oviposition was related to presence of more type IV glandular trichomes, however a high level of ovipositional preference by *B. tabaci* adults was shown to be on genotypes that possessed a high density of type V nonglandular trichomes on leaf surfaces.

In the present study, assessment of trichomes among the test genotypes recorded the highest level on genotype EC-620401 with (454.33) no followed by EC- 315477 (406.67) and EC-538153 (397.67) whereas the lowest be on EC-520078 (114) per cm^2. The least preferred tomato genotypes with most resistance to *B. tabaci* had recorded high densities of glandular type IV trichomes and at the same time with none or low densities of type V trichomes. Associations between whitefly resistance and trichome type were found in tomato species *viz., S. galapagense* [33, 41], and *S. habrochaites* [42, 43]. The species that are closely related to cultivated tomato and readily used for introgression in cultivable tomato *viz., S. galapagense* (genotypes VI063177 and VI037239) *S. cheesmaniae* (genotype VI037240) and *S. pimpinellifolium* (genotype VI030462) were reported expressing whitefly resistance based on choice and no-choice bioassays. There was reduced numbers of whitefly adults, nymphs, puparium, and eggs recorded in the choice bioassay and there was also high adult whitefly mortality noticed in the no-choice bioassay on these genotypes and the genotypes had the high densities of type IV trichomes and low densities of type V trichomes Therefore, whitefly-resistant genotypes could be selected rapidly based on trichome analysis at the beginning followed by choice and no-choice assays When different genotypes are being tested [17].

The surface property of host plant leaves hinders the attachment of the legs of insects and also egg deposits, since epicuticular waxes present on leaf surfaces and their chemistry influences the fine structure of the cuticular surface. The locomotion of insects and access of insects to different plant parts are unfluenced by physical and chemical characteristics of the epicuticular waxes and are considered responsible for initiating rejection behaviour in insects. The tactile and chemical cues of the phylloplane of the host plant surface is evaluated by *B. tabaci* while landing on host plants with small amounts of watery saliva which would dissolve plant surface epicuticular waxes, and thereby suitability of the site for feeding and oviposition is determined [44]. Hence, epicuticular waxes are important in *B. tabaci* host selection process. The wax concentration (mg) results of the experiment indicated the highest concentration of wax in EC-520078 with 64.2 followed with 56.9 in EC-620389 and EC-315477 with 48.1. The least amount of epicuticular wax concentration was found to be in the genotype EC-620372 with 2.7 mg followed by EC-620417 with 10.57mg (Fig 2). The significant differences between the genotype indicated the direct correction of resistance towards *B. tabaci*. The best performed genotypes at field and glasshouse screening [45] and in the present investigation had a significant wax concentration compared to the other genotypes taken for study.

The plant surface waxy compounds consists of long-chain alkanes, alcohols, carboxylic acids, and also secondary metabolites such as quinones and flavonoids, which have a role in insect feeding stimulation [46].

The presence of cuticular waxes make whitefly attachment difficult to plant surfaces and act as physical barrier which limits the entry of pathogens, and also acts as a basin of signals to trigger the plant defense responses [47, 48]. The n-alkanes, 2-methylalkanes, 3-methylalkanes and branched hydrocarbons, which are part of epicuticular waxes of tomato (*S. lycopersicum*), related wild species and their interspecific hybrids [49] influenced *B. tabaci* with different effects [50], even reported to cause mortality [51]. The cuticular waxes acted as first line of defense against whiteflies and thus the leaf curl virus. Crops with natural defensive strategies such as longer trichomes, inorganic salts with increased concentration of cuticular waxes, that acted as armoury against whiteflies, leaf curl virus and other pathogens widely [52-54].

Resistance for virus transmission may also emerge due to the lack of feeding by the vector or avoidance by the vector therefore, genotypes displaying natural resistance in the form of non-preference are handy even though such phenomena may not be resistant to its transmittable virus. In real, resistance can be determined by introducing these resistant genotypes in controlled inoculation conditions were the vector and virus are in quantifying numbers [55]. Hence, the resistant lines with the best non-preference plant resistance mechanism

reported in the present investigation may need additional laboratory studies before making incorporation into resistance breeding strategies for *B. tabaci* and their vectoring capabilities of ToLCV on tomato.

Conclusion

The genotypes *viz.*, EC-520078, EC-631364, EC-315477 and EC-620389 notably had the highest non-preference mechanism of plant resistance against whitefly, *B. tabaci* as compared to the other genotypes tested in the present study and may be used for resistance breeding of varieties and genetic studies for ToLCV management.

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