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CHARACTERIZING THE DENSITY AND TYPE OF LEAF TRICHOMES IN TOMATO FOR RESISTANCE TO YELLOW LEAF CURL DISEASE

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SUMMARY

Global tomato (*Solanum lycopersicum* L.) production faces a major threat of tomato yellow leaf curl disease (TYLCD), transmitted by the whitefly (*Bemisia tabaci*). However, the resistance to TYLCD can gain enhancement by managing the vector. In tomatoes, the trichomes act as physical barriers against whiteflies. Developing tomato cultivars with specific trichome types in higher density works as a promising alternative to insecticides. The presented study investigated the relationship between trichome types, their density, and resistance to TYLCD by inoculating the cultivated tomatoes with the whitefly transmission method. The trichomes' analysis also succeeded under a compound light microscope, aiding the selection of cultivars with high trichome density and TYLCD resistance. A negative correlation appeared between the glandular trichome type VI density and TYLC virus (TYLCV) resistance. Highly resistant tomato accessions (KKU-T23157, KKU-T23160, KKU-T23163, and KKU-T23164) and moderately resistant accessions (KKU-T23152, KKU-T23154, and KKU-T23172) displayed all five types of trichomes, with type VI density of 32–55/mm² and 32.67–42/mm², respectively. Susceptible tomato cultivars had only three trichome types, with type VI density of 9–19/mm². The presence of high glandular trichome type VI density, *Ty-2*, and *Ty-3* resistance genes contributed to the TYLCD resistance. These selected tomato cultivars proved valuable for future tomato breeding programs.

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Keywords: Tomato (*Solanum lycopersicum* L.), tomato yellow leaf curl disease (TYLCD), *Bemisia tabaci*, insect resistance, trichome morphology, *Ty-2* and *Ty-3* genes

Key findings: Tomato (*Solanum lycopersicum* L.) genotypes observed with the highest trichome density, particularly of glandular trichomes type VI, demonstrated considerable resistance to TYLCD via a mechanism that encompasses resistance to the viral transmission by *Bemisia tabaci*. The *Ty-2* and *Ty-3* genes' presence enhanced the resistance to TYLCV.

INTRODUCTION

Improving cultivated tomato (*Solanum lycopersicum* L.) cultivars for consumer suitability has resulted in maintaining less than 5% of the genetic variability (Miller and Tanksley, 1990). As a result, the important host characteristics, such as disease and pest resistance, were lost due to genetic erosion in wild cultivars (Sade *et al*., 2020; Resende *et al*., 2021). Thus, cultivated cultivars are at risk of yield loss from diseases and insect pests.

Tomato yellow leaf curl disease (TYLCD) impacts tomato production, especially in tropical and subtropical countries (Segbefia *et al*., 2015). The management of the virus comes from the whitefly (*Bemisia tabaci*) (Mahfouze and Mahfouze, 2019). The TYLCD symptoms on tomato plants include leaf curling, yellowing, stunted growth, and, eventually, reduced fruit yield. In unprotected fields, the disease may reach 100% incidence, causing yield losses and rendering the crop unsuitable for harvest (Picó *et al*., 1996; Riley and Srinivasan, 2019). The mitigation of the TYLCV yield losses requires the use of tomato-resistant cultivars as a viable approach (Lapidot and Friedman, 2002; Czosnek, 2007). The resistance against TYLCD often arises in the genotypes by having the *Ty* gene derived from wild species (Lapidot *et al*., 2001; Legarrea *et al*., 2015). The resistant tomato cultivars can delay the disease symptoms and reduce the disease severity (Srinivasan *et al*., 2012). The resistant cultivars can still serve as reservoirs for whiteflies, function as inoculum sources of TYLCD, and subsequently influence the disease virus epidemics (Polston and Lapidot 2007; Legarrea *et al*., 2015).

Apart from the resistance conferred by the *Ty* gene, it has also been noteworthy that TYLCD resistance correlated with hostility to insect vectors in tomato (Bellotti and Arias, 2001). Thus, the use of tomato-resistant cultivars with the management of whitefly with insecticides and reflective mulch has become a recommendation (Polston and Lapidot, 2007; Riley and Srinivasan, 2019). However, whiteflies can alter the toxicity of insecticides, causing immunity development to various types of insecticides (Horowitz *et al*., 2005; Gilbertson *et al*., 2015). Plant defense traits, such as trichomes, may induce non-preference predator responses in insects, causing whiteflies to avoid that plant as a host and transmission source (Channarayappa *et al*., 1992; Glas *et al*., 2012). Such types of studies present another option that may provide alternatives to insecticide use and whitefly control methods, potentially increasing production costs (Pandey *et al*., 2023).

Trichome is the hair that the tomato develops from the epidermis, serving as a physical barrier against insects (Schilmiller *et al*., 2008). Generally, subdividing trichomes can have two categories. The first comprised non-glandular trichomes (types II, III, V, and VIII) without glands at the tip that act as physical barriers to movement and feeding of insects. The second included glandular trichomes (types I, IV, VI, and VII) with glands at the tip that serve to synthesize, store, and secrete natural insecticides, such as terpenoids, phenylpropanoids, flavonoids, alkaloids, and acyl sugar (Goffreda *et al*., 1989; Glas *et al*., 2012; Pott *et al*., 2012; Dhaliwal *et al*., 2020). Several annual and perennial plants of the genus *Alfalfa* also have those characteristics (Zhang *et al*., 2020).

Trichomes and their highest density have significant correlations with insect resistance, serving as vectors of disease in tomatoes (Zhang *et al*., 2020). Especially glandular trichomes type I, IV, and VI containing acylsugar and zingiberenoids, which are the allelochemical of sesquiterpene. These compounds significantly reduce the feeding, oviposition, survival rates, and growth of whiteflies (Lucini *et al*., 2015; Fan *et al*., 2019; Dawood and Snyder, 2020; Vendemiatti *et al*., 2021; Pandey *et al*., 2023).

At present, the initiative to develop tomato cultivars resilient to both whitefly infestation and TYLCD has encountered limited success in maintaining desired consumer attributes. The latest study's design sought to scrutinize whether the type and density of trichomes exert influence on TYLCD resistance via the inoculation of TYLCD virus with the whitefly transmission method on tomatoes with consumer-preferred characteristics. Studying the qualities and density of trichomes under a compound light microscope proceeded to select accessions with high trichome density along with resistance to TYLCV for use as genetic resources to develop tomato cultivars resistant to TYLCV and whiteflies.

MATERIALS AND METHODS

Tomato accessions and procedure

Nine tomato accession seedlings cultivated together with susceptible cultivars commenced in a net house for three weeks. Afterward, the seedlings' transplanting followed into 60-hole trays for the whitefly transmission process. The TYLCD's transmitting to the tomato plants used the whitefly transmission method. Healthy whitefly (*Bemisia tabaci*) reared on non-infected Thai eggplant plants (*Solanum virginianum* L.) succeeded in transferring to source plants infected with TYLCD for 48 h. These infected whiteflies then proceeded to transfer to 21-day-old tomato seedlings for virus transmission for 48 h, after which the use of insecticides eliminated them. The seedlings' transplanting into 4-inch pods continued with their placing in a net house to assess the disease symptoms. The disease symptoms bore weekly recording for six weeks, following the methodology of Lapidot *et al*. (2001), i.e., 0% disease index (HR—highly resistant), 1%–20% disease index (R—resistant), 21%–40% disease index (MR—moderately resistant), 41%–60% disease index (S—susceptible), and 61%–100% disease index (HS—highly susceptible). Leaf samples collected after four weeks of infection sustained examination for the presence of TYLCV and resistance genes (*Ty-2* and *Ty-3*) using PCR techniques with specific primers (Table 1). The obtained data on various parameters then underwent statistical analysis for compilation and concluding the results.

Determination of type and density of the trichome

Leaf samples of different tomato accessions gathered from the experimental fields underwent assessment at the Khon Kaen University, Thailand. The third leaf from the top of each genotype was the selected part for analysis. The density and shape of trichomes on tomato leaves incurred investigation under the compound light microscope (Nikon model ECLIPSE Ci-L with microscope digital camera DS-Fi3) at 4× magnification in a 1-sq mm region.

Table 1. Molecular markers used for tomato yellow leaf curl virus (TYLCV) resistance genes.

Markers	R Gene	Forward primer / Reverse primer	Molecular size of band (bp)		Reference
			R allele	S allele	
P1-16	*Ty-2*	CACACATATCCTCTATCCTATTAGCTG/ CGGAGCTGAATTGTATAAACACG	300	600	Nevame *et al*. (2020)
P6-25	*Ty-3*	GGTAGTGGAAATGATGCTGCTC/ GCTCTGCCTATTGTCCCATATATAACC	660, 630, 450	320	Nevame *et al*. (2020)
CP	*Begomovirus*	CGGGATCCATGTCGAAGCGTCCAG/ CCCAAGCTTTTAATTCGTCACTGAG	+	-	Krupeu *et al*. (2020)

Figure 1. Three tomato accessions with susceptibility to TYLCV. HR: highly resistant; R: resistant; MR: moderately resistant; MS: moderately susceptible; S: susceptible; and HS: highly susceptible.

Statistical analysis

The analysis of variance (ANOVA) ensued using a randomized complete block design. The comparison of means employed the new Duncan's multiple range test (DMRT), with a confidence level of 95%, and the correlation coefficients, as calculated, engaged IBM SPSS Statistics 28.0.0.0 software. For correlation graph representation, the data visualization used OriginLabPro 2024.

RESULTS

With the whitefly transmission method, the 11 tomato accessions bore inoculations with the TYLCD virus, with disease symptoms observed seven days post-inoculation for the tomato accessions KKU-T11006, KKU-T23174, and KKU-T12002. Upon completion of the evaluation, these accessions exhibited different levels of susceptibility. The tomato accessions KKU-T11006 and KKU-T23174 showed susceptibility (DI = 45% and 56.67%) with the *Ty-2* and *Ty-3* resistance genes. Conversely, the accession KKU-T12002 (susceptible cultivar) demonstrated the highest susceptibility (DI = 91.67%) with no resistance genes (Figure 1).

For the 35 days post-inoculation, accessions KKU-T23152, KKU-T23154, KKU-T23167, and KKU-T23172 exhibited varied responses to TYLCD. The three accessions KKU-T23152, KKU-T23154, and KKU-T23172 displayed resistance and demonstrated disease indexes of 10%, 6.67%, and 1.67%, respectively. Meanwhile, the accession KKU-T23167 exhibited moderate resistance, with a disease index of 25%. Additionally, the evaluation further revealed no viral disease symptoms resulted in the four tomato accessions, i.e., KKU-T23157, KKU-T23160, KKU-T23163, and KKU-T23164, which exhibited the highest resistance (DI = 0%) (Figure 2).

In the molecular marker analysis for resistance genes, the tomato accessions with only the *Ty-3* gene exhibited a disease response with resistance (DI = 1.60%–10.00%). The tomato accessions carrying both *Ty-2* and *Ty-3* genes showed a disease response ranging from susceptible to highly resistant (DI = 0.00%–56.67%). In contrast, the susceptible tomato cultivars lacked resistance genes and demonstrated a disease response with the greatest susceptibility (Table 2).

In 11 tomato accessions, the trichome characteristics evaluation revealed trichome types totaling five. From the five types, three were non-glandular types: II, III, and V (Figure 3), and two were glandular types: IV and VI (Figure 4). However, types V and VI were the most common, with the heaviest density in all the tomato accessions. Types II and III were also common, found in all the accessions except in the accession KKU-T23172. The type IV only appeared in the accessions KKU-T23152 and KKU-T12002 (the susceptible cultivars) (Table 3).

The HR group comprised four tomato accessions: KKU-T23157, KKU-T23160, KKU-T23163, and KKU-T23164. These accessions

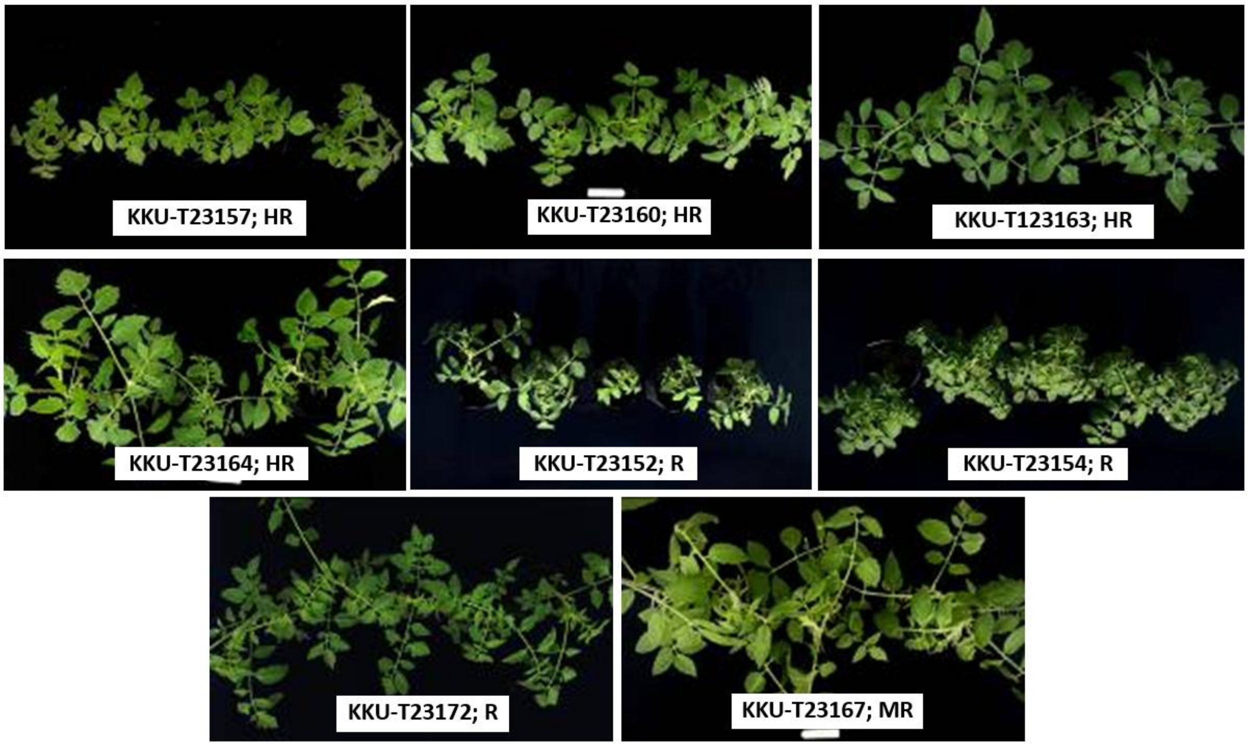

Figure 2. Eight tomato accessions with the resistance to TYLCV. HR: highly resistant; R: resistant; MR: moderately resistant; MS: moderately susceptible; S: susceptible; and HS: highly susceptible.

Table 2. The disease index, disease response, and resistance gene in 11 tomato accessions.

Accessions	Disease index (%)						Disease response	Resistance gene
	7 dpi	14 dpi	21 dpi	28 dpi	35 dpi	42 dpi		
KKU-T23152	0.00	0.00	0.00	0.00	3.33	10.00	R	*Ty-3*
KKU-T23154	0.00	0.00	0.00	0.00	6.67	6.67	R	*Ty-2, Ty-3*
KKU-T23157	0.00	0.00	0.00	0.00	0.00	0.00	HR	*Ty-2, Ty-3*
KKU-T23160	0.00	0.00	0.00	0.00	0.00	0.00	HR	*Ty-2, Ty-3*
KKU-T23163	0.00	0.00	0.00	0.00	0.00	0.00	HR	*Ty-2, Ty-3*
KKU-T23164	0.00	0.00	0.00	0.00	0.00	0.00	HR	*Ty-2, Ty-3*
KKU-T23167	0.00	0.00	0.00	0.00	25.00	25.00	MR	*Ty-2, Ty-3*
KKU-T23172	0.00	0.00	0.00	0.00	1.67	1.67	R	*Ty-3*
KKU-T11006	21.67	23.33	23.33	26.67	36.67	45.00	S	*Ty-2, Ty-3*
KKU-T23174	3.33	3.33	1.67	18.33	41.67	56.67	S	*Ty-2, Ty-3*
KKU-T12002[1]	41.67	41.67	48.33	58.33	71.67	91.67	HS	-
F-test[2]	**	**	**	**	**	**		
C.V.%	33.06	23.86	23.35	16.57	19.19	12.6		

[1]susceptible cultivar; HR = highly resistant; R = resistant; MR = moderately resistant; MS = moderately susceptible; S = susceptible; HS = highly susceptible; and dpi = days post inoculation.

exhibited four distinct types of trichomes, viz., III, IV, V, and VI. All four accessions also showed types V and VI. The density of type V and type VI ranged from 32.67 to 93.67/mm² and 32 to 55/mm², respectively. Type III was evident in the three accessions: KKU-T23157, KKU-T23160, and KKU-T23163, with a density range of 0.33–3.00/mm². The accession KKU-T23163 had the type IV characteristics, with a density of 0.67/mm². The R group, comprising

Figure 3. Non-glandular trichomes under a stereo microscope.

Figure 4. Glandular trichomes under a stereo microscope.

three accessions: KKU-T23152, KKU-T23154, and KKU-T23172, exhibited four distinct types of trichomes, i.e., II, III, V, and VI. All three accessions displayed types V and VI. The density of type III ranged from 0.33 to 1.00/mm^2, and type V had a density of 47.33-55.00/mm^2. The accession KKU-T23152 had type II characteristics, with a density of 0.33/mm^2.

The MR group comprised the single accession KKU-T23167, which exhibited two kinds of trichomes (V and VI), with densities of 69.00 and 25.33/mm^2, respectively. The S group had two accessions: KKU-T11006 and KKU-T23174. These accessions revealed three distinct types of trichomes: III, V, and VI. Both accessions also showed types V and VI. Type V had a density of 62.33-22.00/mm^2, and type VI gave a density of 22.00 and 19.00/mm^2, respectively. The HS group, comprising the single accession KKU-T12002 (susceptible cultivar), exhibited three distinct types of trichomes: IV, V, and VI, with densities of 0.33, 10.00, and 9.00/mm^2, respectively (Table 3).

The aforementioned results demonstrated that comparing trichome types and density in tomato-resistant groups with susceptible groups tends to reveal the trichome types found in each accession to relate to the trichome types III, V, and VII's density with disease resistance. Particularly, types V and VI, found in all the tomato accessions, showed a noticeable difference in density compared with the susceptible cultivar with the highest disease index (DI).

Correlation coefficients indicated the moderately positive association between the density of trichomes type III and V, with a significance at a 0.01 level and correlation value of 0.746. Similarly, such results suggested trichome type V has an increasing density proportional to the density of trichome type III. It implies the trichome type V density increased proportionately compared with trichome III. Additionally, a significant

Table 3. The density of all five trichome types and the disease response in 11 tomato accessions.

Accessions	Trichome types					Disease response
	II	III	IV	V	VI	
KKU-T23152	0.33	1.00	0.00	47.33	36.67	R
KKU-T23154	0.00	0.33	0.00	52.33	32.67	R
KKU-T23157	0.00	3.00	0.00	93.67	33.33	HR
KKU-T23160	0.00	1.00	0.00	59.67	38.00	HR
KKU-T23163	0.00	0.33	0.67	41.33	55.00	HR
KKU-T23164	0.00	0.00	0.00	32.67	32.00	HR
KKU-T23167	0.00	0.00	0.00	69.00	25.33	MR
KKU-T23172	0.00	1.00	0.00	55.00	42.00	R
KKU-T11006	0.00	0.00	0.00	62.33	22.00	S
KKU-T23174	0.00	3.00	0.00	86.67	19.00	S
KKU-T12002[1]	0.00	0.00	0.33	10.00	9.00	HS

[1] susceptible cultivar

HR: highly resistant; R: resistant; MR: moderately resistant; MS: moderately susceptible; S: susceptible; HS: highly susceptible; and dpi: days post inoculation.

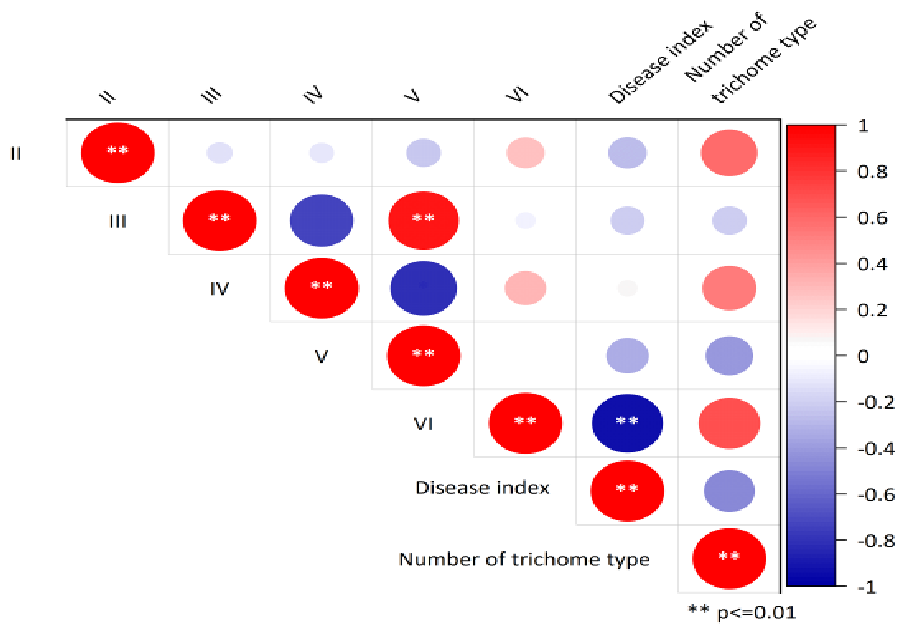

Figure 5. Correlation coefficient graph between trichome density, disease response, and the number of trichome types.

negative correlation existed between the density of trichome type VI and the disease index at a significance level of 0.01 and a correlation coefficient of -0.860. These findings also implied that a rise in a higher density of type VI shows an association with a decrease in disease index, and accordingly, an increased TYLCD resistance in tomatoes (Figure 5).

DISCUSSION

Tomato accessions inoculated with TYLCD virus resulted in the first appearance of disease symptoms between seven and 35 days post-inoculation. After the onset of the disease symptoms, the disease index either increased or remained stable until the completion of the evaluation. Accessions showing resistance started to manifest symptoms 35 days after inoculation (MR and R) or remained asymptomatic until the conclusion of the evaluation (42 days, HR). These results were greatly analogous to past findings, wherein the same method used revealed resistant plants exhibited the disease symptoms 14–21 days post-inoculation (Lapidot, 2007). Consequently, to fully express symptoms and obtain the accurate evaluation results, a minimum duration of five weeks was essential for disease evaluation in tomatoes.

For resistance genes, the molecular marker analysis revealed tomato accessions carrying at least one of the genes (*Ty-2* or *Ty-3*) exhibited the highest resistance to TYLCD compared with the susceptible genotype without the said resistance genes. The *Ty* genes have been shown to reduce the viral replication and mitigate the disease symptoms' expression (Lapidot *et al*., 2001; Legarrea *et al*., 2015). Nevertheless, some tomato accessions containing resistance genes still displayed susceptibility to the TYLCD. These results suggested the resistance to TYLCD may also have influences from the mechanism related to insect resistance. Plants could develop physical barriers, such as a thicker cuticle, glossy leaf surfaces, and specific types of trichomes, inhibiting insect vectors from landing and feeding (Bellotti and Arias, 2001). These characteristics could reduce the likelihood of the plant being selected as a host, thereby limiting viral transmission through vector insects.

By analyzing tomato trichome characteristics (Glas *et al*., 2012), the presented study detected five distinct trichome types. By comparing trichome density across the different disease responses, it was notable that non-glandular trichomes (II, III, and V) had no association with the TYLCD resistance, even though type V had the highest density. Although an association between glandular trichomes (IV and VI) and disease resistance in glandular trichome type VI appeared, it exhibited the second-highest density on tomato leaves. Glandular trichome type IV, found only in a few tomato accessions with low density, did not associate with disease resistance levels. The results indicated glandular trichomes have a considerable role in TYLCD resistance compared with non-glandular trichomes. This discovery was consistent with the past research by Almeida *et al*. (2023), which disclosed that wild tomatoes with a high density of trichomes, particularly glandular types, proved resistant to whiteflies and caterpillars. Conversely, the tomato with a lower density of glandular trichomes emerged more susceptible.

The trichome types have a significant impact on insect resistance; however, a sufficient density is necessary to effectively resist the whiteflies and TYLCD. Among the various trichome types, glandular trichome type IV has had reports of being most strongly associated with whitefly resistance due to its production of acylsugars, which inhibit feeding, oviposition, survival, and growth more effectively than other trichome types (McDowell *et al*., 2011; Pandey *et al*., 2023). Furthermore, this trichome type has been proven to reduce TYLCD virus transmission by nearly threefold versus hybrids without acylsugars (Marchant *et al*., 2020). Despite its functional significance, glandular trichome type IV is less abundant, whereas glandular trichome type VI is the predominant type present on tomato leaves and stems (Bergau *et al*., 2015).

Aside from producing acylsugars, the glandular trichome type VI stores catecholic phenolic compounds (Kang *et al.,* 2010) and synthesizes zingiberenoids, which serve as key sesquiterpene allelochemicals involved in whitefly resistance (Schilmiller *et al.,* 2009; Oliveira *et al.,* 2020). Thus, the tomato accessions KKU-T23157, KKU-T23160, and KKU-T23164, which lack the glandular trichome type IV but possess the glandular trichome type VI at densities of 32–38/mm², exhibited high resistance (HR). They were comparable to KKU-T23163, containing the glandular trichome types IV at 0.67/mm² and VI at 55/mm². Similarly, accessions KKU-T23152, KKU-T23154, KKU-T23172, and KKU-T23167, which also lack the glandular trichome type IV but have the glandular trichome type VI at slightly lower densities (25.33–42/mm²), displayed moderate to high resistance (MR-R).

In contrast, accession KKU-T12002, having glandular trichome types IV at 0.33/mm² and VI at only 9/mm², was highly susceptible to TYLCD.

The relationship between trichome density and resistance suggests that glandular trichome type VI density could play a more critical role in resistance than the presence of glandular trichome type IV, which is less prevalent and occurs at lower densities. Correlation analysis further supports this finding, as only glandular trichome type VI exhibited a significant negative correlation (-0.860) with the disease index, whereas the total trichome number showed a weaker negative correlation (-0.18). The negative correlation indicates a lower disease index corresponds to a higher resistance to TYLCD. These results signify that high glandular trichome type VI density has a stronger association with resistance than trichome type diversity. This finding aligns with previous studies indicating that trichome density is a more critical determinant of resistance than trichome type (Channarayappa *et al*., 1992; Zhang *et al.,* 2020).

Most commercially available tomato cultivars lack resistance to whitefly, leading to high oviposition rates due to a low glandular trichome density (Marchant *et al*., 2020). Increasing trichome density, particularly glandular trichome type VI, can enhance the whitefly resistance and reduce the TYLCD virus infection risk. However, trichomes could not stop TYLCD virus replication post-infection. Once the virus transmission reaches the phloem, it spreads similarly to susceptible cultivars without trichomes (Marchant *et al*., 2020). After infection, the resistance to TYLCD has *Ty* genes' management, which functions by reducing disease expression and viral replication (Lapidot *et al*., 2001; Legarrea *et al*., 2015). Thus, an effective breeding method may combine the physical barrier of high glandular trichome density with *Ty*-resistance genes. The timely study identified tomato accessions with TYLCD resistance. Notably, the four tomato accessions, KKU-T23157, KKU-T23160, KKU-T23163, and KKU-T23164, showed no disease symptoms throughout the evaluation and exhibited the highest density of the glandular trichome type VI. These tomato accessions presented valuable genetic resources for future breeding programs aimed at reducing the risk of TYLCD outbreaks in tomato cultivation.

CONCLUSIONS

Whiteflies are the primary vectors for the transmission of tomato yellow leaf curl disease (TYLCD) virus, and the trichomes act as physical barriers that reduce the whitefly preference, contributing to TYLCV resistance. A higher density of glandular trichome type VI, alongside the presence of diverse trichome types, has shown associations with increased resistance to TYLCV. However, the trichomes primarily deter the insect vector, with post-infection resistance conferred by the presence of *Ty* genes. The tomato accessions, such as KKU-T23157, KKU-T23160, KKU-T23163, and KKU-T23164, exhibited the high density of trichome type VI, which also demonstrated a considerable resistance and offered valuable genetic resources for future breeding programs.

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