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Incidence of *Bemisia tabaci* in wild tomato germplasm and its relationship with antioxidant compounds.

Incidencia de *Bemisia tabaci* en germoplasma silvestre de jitomate y su relación con compuestos antioxidantes.

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ABSTRACT

In the gene pool of native and wild populations of tomatoes, natural defenses represent an alternative for generating insect-resistant or tolerant varieties. The study aimed to evaluate the incidence of *Bemisia tabaci* and its relationship with antioxidant compounds in tomatoes. Two wild species (*Solanum habrochaites* and *S. pimpinellifolium*), eight Mexican natives, and the commercial variety Río Grande (control) were examined. The number of nymphs (Nn) and eggs (Ne) was recorded in a no-choice test. The content of phenolic compounds (PC) and DPPH antioxidant activity (Aaox) in plants with incidence (PWI) and lacking incidence (PLI) of *B. tabaci* were analyzed spectrophotometrically. Significant differences were found between genotypes in Nn + Ne ($p < 0.004$) and PC ($p < 0.0001$). Differences between PLI and PWI in PC ($p < 0.0001$) and Aaox ($p < 0.0001$) indicate variations in the synthesis of antioxidant compounds among populations. The correlations of Nn + Ne with Aaox (-0.44**), PC with Aaox (0.31**), and Nn + Ne with PC (-0.23) suggest the involvement of antioxidant molecules to varying degrees. *S. habrochaites*, with the lowest insect incidence, and the native Ojo de Venado 21207, with the highest PC content, show potential in breeding programs.

KEY WORDS: *Bemisia tabaci*, DPPH antioxidant activity, phenolic compounds, native tomato varieties.

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RESUMEN

En el acervo genético de poblaciones nativas y silvestres de jitomate, las defensas naturales representan una alternativa para generar variedades resistentes o tolerantes a insectos. El objetivo fue evaluar la incidencia de *Bemisia tabaci* y su relación con compuestos antioxidantes en jitomate. Se examinaron dos silvestres (*Solanum habrochaites* y *S. pimpinellifolium*); ocho nativos mexicanos y la variedad comercial Río Grande (testigo). En ensayo de no elección se registró el número de ninfas (Nn) y de huevos (Ne). Se analizaron, mediante espectrofotometría, el contenido de compuestos fenólicos (PC) y la actividad antioxidante DPPH (Aaox), en plantas con incidencia (PWI) y sin incidencia (PLI) de *B. tabaci*. Hubo diferencias entre genotipos en Nn + Ne ($p < 0.004$) y en PC ($p < 0.0001$). Diferencias de PLI a PWI en PC ($p < 0.0001$) y Aaox ($p <0.0001$) indican variaciones en la síntesis de los compuestos antioxidantes entre poblaciones. Las correlaciones de Nn + Ne con Aaox (-0.44**), PC con Aaox (0.31**) y Nn + Ne con PC (-0.23), señalan la participación de moléculas antioxidantes en diferentes grados. *S. habrochaites* con la menor incidencia insectil y el nativo ojo de venado 21207 con el mayor contenido de PC demuestran potencial en mejoramiento genético.

PALABRAS CLAVE: *Bemisia tabaci*, actividad antioxidante DPPH, compuestos fenólicos, variedades nativas de jitomate.

Introduction

The tomato crop (*Solanum lycopersicum* L.) is susceptible to pests such as the whitefly *Bemisia tabaci* (Genn.) (Narita *et al*., 2023). This polyphagous insect represents a threat to the tomato crop and world agriculture (Ortega-Arenas & Carapia, 2020; Joshi & Srivastava, 2022). *B. tabaci* decreases tomato fruit yield and quality by directly damaging plant sap-sucking and indirectly through virus transmission (Perring *et al*., 2018; Rodríguez-López *et al*., 2020; Narita *et al*., 2023). For its control, insecticides are frequently used, inappropriate pesticide use leads to the resistance development of insects (Perier *et al*., 2022). An alternative is to generate insect-resistant or tolerant tomato varieties (Narita *et al*., 2023) by exploring and utilizing the natural defenses of plants (Kumar *et al*., 2020). In this sense, genetic variability in wild and native populations of tomatoes constitutes an important source of alleles useful for increasing resistance to biotic and abiotic factors in commercial varieties (Marin-Montes *et al*., 2019).

In plant resistance, the combination of different defensive features, both constitutive and induced, can reduce the success of an insect as a parasite on a given plant species (Firdaus *et* *al*., 2012; Zunjarrao *et al*., 2020; Yactayo-Chang *et al*., 2020; Shree *et al*., 2021). For instance, mechanical barriers such as morphological structures in leaves, and biochemical compounds naturally present or induced in plant tissues, including alkaloids, terpenoids, cyanogenic glycosides, digestive enzyme inhibitors, and phenols, can exhibit antifeedant (antibiosis-type resistance) or repellent (antixenosis-type resistance or non-preference) effects on arthropods (Alvarez, 2015; War *et al*., 2020).

Allelochemicals present in wild tomato populations participate in interactions with arthropods and confer resistance through antibiosis and antixenosis, such as methyl ketones, sesquiterpenes, and acylsugars (Álvarez, 2015; Dawood & Snyder, 2020; Rodríguez-López *et al*., 2020), which are mainly stored in glandular trichomes and are absent in cultivated tomato (Andrade *et al.,* 2017). However, other research refers to the participation of secondary metabolites, such as phenolic compounds (PC) in the defense mechanisms and resistance to whitefly stress in tomatoes (Yao *et al*., 2019; Pal *et al*., 2021). Phenolic compounds have been associated with plant defense against insects, such as coumarins and flavonoids (Yao *et al*., 2019; Yang *et al*., 2023), hydrolyzable tannins and condensed tannins, which, due to their toxic accumulation in leaves, cause insect-repellency or preference towards their host. Others indirectly mediate in the lignin and suberin synthesis that strengthen cell walls (Dar *et al*., 2017; Rashad *et al*., 2020). Wagay *et al*. (2020) further note the antioxidant potential of phenolic compounds against Reactive Oxygen Species (ROS).

ROS are implicated in various plant physiological responses; however, they also induce oxidative damage to proteins, lipids, and nucleic acids (Nafees *et al*., 2019; Sperdouli *et al*., 2022), particularly under stress conditions such as insect feeding (Wagay *et al*., 2020; Sperdouli *et al*., 2022). Nevertheless, plants mitigate the oxidative stress induced by ROS through enzymatic and non-enzymatic antioxidant molecules, thereby inducing tolerance (Orabi & AboU, 2019), as evidenced in response to insect incidence in tomatoes (Dieng *et al*., 2011; El-Zohri *et al*., 2020).

Identifying wild or native tomato germplasm exhibiting tolerance to whitefly incidence could facilitate its utilization as a genetic resource. Thus, this research aimed to assess the incidence of *Bemisia tabaci* in native Mexican and wild tomato germplasm and its correlation with phenolic compound content and antioxidant activity.

Material and Methods

Location of the experiment

The experiment was conducted at the facilities of the Colegio de Postgraduados (19º 30’N and 98º 53’W, altitude 2250 m), located in Montecillo, Texcoco, State of Mexico, in the summer-autumn cycle 2021.

Plant material

Eleven tomato populations were assessed, comprising eight Mexican native varieties displaying varying degrees of domestication from diverse geographical regions of Mexico, two introduced accessions of wild tomato relatives, and the commercial variety Río Grande utilized as a control (Table 1).

Table 1. Characteristics, origin, and species of the evaluated tomato populations (*Solanum spp.*) for the whitefly (*B. tabaci*) incidence assessment and its correlation with antioxidant compounds.

Genotype	Type	Origin/Coordinates	Species
Native Mexican tomatoes			
21201	Arriñonado	Santa Cruz Xitla, Oax. 16°19′00″N 96°40′00″W	*S. lycopersicum* var. *lycopersicum*
21202	Chino criollo	Tehuacán, Pue. 18°27′46″N 97°23′39″W	*S. lycopersicum* var. lycopersicum
21203	Ojo de Venado	Xicotepec, Pue. 20°18′00″N 97°58′00″W	*S. lycopersicum* var. lycopersicum
21204	Ojo de Venado	Huatusco, Ver. 19°08′56″N 96°58′03″W	*S. lycopersicum* var. lycopersicum
21206	Cherry	Teotitlán de Flores Magón, Oax. 18°08′00″N 97°05′00″W	*S. lycopersicum* var. *cerasiforme*
21207	Ojo de Venado	Tehuacán, Pue. 18°27′46″N 97°23′39″W	*S. lycopersicum* var. *lycopersicum*
21208	Arriñonado	Malinalco, Edo. Méx.18°57′N 99°30′W	*S. lycopersicum* var. *lycopersicum*
21209	Cherry	Tejupilco, Edo. Méx. 18°54′21″N 100°09′10″W	*S. lycopersicum* var. *cerasiforme*
Wild relatives of tomatoes			
21205	Cherry	U. D. C. Germplasm Bank*.	*S. pimpinellifolium* LA1602
21211	Ojo de Venado	U. D. C. Germplasm Bank*.	*S. habrochaites* LA1777
Commercial variety			
21210	Saladette	Commercial Rio Grande Pomodoro	*S. lycopersicum* L.

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Insect population

An isolated *B. tabaci* population, previously characterized in the Phytosanitary Program - Entomology of the Colegio de Postgraduados, was used. Adults of *B. tabaci* were maintained in pots of tomato plants var. Rio Grande for more than 10 generations in entomological cages (60 x 40 x 60 cm) covered with organza fabric. The whitefly colony was maintained until the beginning of the germplasm evaluation.

Establishment of the experiment and agronomic management

Two trial types were conducted under greenhouse conditions: With and Lacking whitefly incidence (PWI and PLI, respectively). In both trials, the genotypes were arranged in a randomized complete block experimental design with five replicates per population for PWI and three replicates per population for PLI. The experimental unit consisted of one plant. Seeds were germinated in peat moss (Peat moss®, Kekkilä) in 200-cavity trays. 36 days after sowing (das), seedlings were transplanted into 7-inch black plastic pots filled with a mixture of peat moss (Peat moss®, Kekkilä) and perlite (Multiperl) in a ratio of 2:1. Plants were nourished via drenching with Steiner's solution (1984), maintaining a pH between 5.5 and 6.0, at concentrations of 25 % (~20 to 25 days after transplanting, dat), 50 % (~26 to 40 dat), 75 % (~41 to 60 dat), and 100 % (~61 dat forwards).

Plants were supported with wooden stakes, and those in the PLI and PWI trials were enclosed in separate organza fabric cages (6 x 3 x 2.5 m), with lateral shoots removed from the onset of cultivation and the main meristem eliminated at 60 dat. Insecticides (imidacloprid and cypermethrin) were applied at crop beginning, and liquid soap was used for maintenance until just before whitefly infestation. Additionally, to prevent mildew, preventive fungicides, Captan® and Ridomil Gold® were applied.

Whitefly infestation (no-selection test)

40 days after transplanting (dat), in the plants with Infestation (PWI) treatment, two leaflets were selected from the middle third of each plant for each repetition (5 repetitions). A 4 cm diameter polyurethane entomological cage was attached to each leaflet, where approximately 20 adults of *B. tabaci* (aged 1 to 6 days and fasting for 2 hours) were introduced through a hole using a manual aspirator. The adults were confined within the cages for 72 hours to allow oviposition. Afterward, the entomological cages and whitefly adults were removed to prevent future infestations. Seven days later, the number of eggs was recorded in a 10 mm^2 area at the center of the underside of each leaflet. Subsequently, the eggs and nymphs were monitored every three days. 35 days after infestation, when the IV instar nymphs appeared, they were counted in a 10 mm^2 area at the center of the underside of the leaflets using the methodology proposed by Ortega-Arenas *et al*. (2006). The total count of whitefly incidence (eggs and nymphs) included data from both leaflets to obtain a total count per population. Plants lacking whitefly incidence (PLI) (3 per population) were kept isolated in another independent cage covered with organza fabric and free of insects.

Extraction and analysis of phenolic compounds (PC)

The phenolic compounds content was determined using the Folin-Ciocalteu (FC) method as described by Singleton *et al*. (1999).

At 75 dat, 1 g of leaflets was collected from the middle layer of both plants without whitefly incidence and plants with whitefly incidence. The samples were macerated in 40 mL of methanol (80 %) and incubated at 60°C for 60 min. Subsequently, the mixture was filtered using a Kitasato flask with a vacuum pump to separate and preserve the supernatant at 4°C. For analysis, 0.2 mL of the sample supernatant was mixed with 0.5 mL of FC reagent and 2.5 mL of 10 % Na_2CO_3 solution, and the volume was adjusted to 4.0 mL with distilled water. The mixture was then left in darkness for 30 min on an orbital shaker.

The spectrophotometer blank consisted of 80 % methanol. Absorbance readings were taken at 760 nm using a spectrophotometer (Thermo Fisher Scientific Oy, Ratastie 2, FI-01620 Vanta, Finland). A calibration curve was prepared using gallic acid (10 mg in 10 mL of 80 % methanol) as a standard, with concentration intervals of 0.010 mg. Each sample was analyzed in triplicate. The results were expressed as milligrams of gallic acid equivalents per gram of fresh sample weight (mg GAE g^{-1} FSW).

Extraction and analysis of DPPH antioxidant activity (Aaox)

The antioxidant activity was determined using the 1,1-diphenyl-2-picryl-hydrazyl (DPPH) method according to Abe *et al*. (1998).

The extraction method was carried out on the same leaflet samples collected for the phenolic compounds' determination. A solution of DPPH at 50 µM in 80 % methanol (19.72 mg in 1000 mL of 80 % methanol) was prepared. To 2.750 mL of the DPPH solution, 0.250 mL of the supernatant of the tomato leaflet extract was added and left on an orbital shaker for 30 min in the dark.

Absorbance readings were taken at 517 nm using a spectrophotometer (Thermo Fisher Scientific Oy, Ratastie 2, FI-01620 Vanta, Finland). The spectrophotometer blank consisted of 80 % methanol. A calibration curve was constructed using Trolox (10 mg in 10 mL of 80 % methanol) as a standard, with concentration intervals of 0.001 mg. Each sample was analyzed in triplicate. The results were expressed as µg of Trolox equivalents per gram of fresh sample weight (µg Trolox g^{-1} FSW).

Statistical analysis

The data were analyzed using analysis of variance (ANOVA) with a significance level of $\alpha = 0.05$, followed by Tukey's mean comparison test ($\alpha = 0.05$) using statistical software from the R Core Team (2021). Multiple correlation analysis was also conducted. For the calculation of variances, the insect incidence data were transformed using the square root (x + 1).

Results and Discussion

Whitefly incidence

The analysis of variance (Table 2) revealed highly significant differences in the occurrence of nymphs ($p \leq 0.001$) and nymphs + eggs ($p \leq 0.004$), but not for eggs ($p = 0.13$). The mean nymphs

+ eggs (Nn + Ne) ranged from 2.1 to 4.5 between the wild accession *Solanum habrochaites* (21211) and the commercial variety Rio Grande (21210), respectively (Table 3). Upon comparing the means of total eggs plus nymphs (Nn + Ne), *S. habrochaites* (21211) formed one group exhibiting the lowest whitefly population density, while another group comprised the commercial variety Rio Grande 21210, with the highest averages. The remaining Mexican native varieties (21201, 21202, 21203, 21204, 21206, 21207, 21208, and 21209) and the wild accession of *Solanum pimpinellifolium* (21205) formed a third group (Table 3).

The no-choice test, indicated by the absence of statistical differences in egg numbers, left *Bemisia tabaci* adults with no alternative in selecting a given population for oviposition. However, after egg hatching, at the nymph stage, statistical differences (Table 2) suggest intrinsic variations among populations in defense mechanisms, which are crucial for the presence or survival of the insect. These results align with Alcantar-Acosta *et al*. (2020), suggesting that natural variation enables the existence of host resistance to different levels of whitefly infestation. In other plant species, Ortega-Arenas *et al*. (2006) report differences in whitefly population density (eggs and nymphs) in different genotypes only up to evaluation in the no-choice test.

Table 2. Sum of squares of the sources of variation, averages, and standard deviation of seven variables of 11 tomato genotypes infested with *Bemisia tabaci.*

Variable	Sources of variation (SS)			CV (%)	Df			Mean
	Genotypes	Block	Error		Genotypes	Block	Error	
Ne	6.2	8.0**	15.5	33	10	4	40	1.9
Nn	10.1**	3.5*	11.3	19	10	4	40	2.8
Ne + Nn	16.5**	4.8	20.6	22	10	4	40	3.3
PC (PLI)	224.8**	41.7**	67.1	16	10	2	20	10.9
PC (PWI)	519.1**	14.7	130.9	17	10	4	40	11.2
Aaox (PLI)	0.3	2.3**	0.54	1.4	10	2	20	11.6
Aaox (PWI)	4.3	0.6	11.6	4.4	10	4	40	12.0

**$p \leq 0.01$; SS: Sum of Squares; CV: Coefficient of Variation, Df: degrees of freedom. Ne: Eggs, Nn: Nymphs, Ne + Nn: Eggs + Nymphs, PC (PLI) and Aaox (PLI): Phenolic compounds and antioxidant activity lacking whitefly incidence; PC (PWI) and Aaox (PWI): Phenolic compounds and antioxidant activity with whitefly incidence.

Table 3. Comparison of means of the concentration of phenolic compounds (mg GAE g^{-1} FSW) and antioxidant activity (µg Trolox g^{-1} FSW) in germplasm of native Mexican and wild tomatoes and the commercial variety Rio Grande, 75 days after transplanting in plants lacking incidence (PLI) and with incidence (PWI) of whitefly *Bemisia tabaci*, 2021.

Genotype	Ne	Nn	Nn + Ne	PC (PLI)	PC (PWI)	**Aaox(PLI)**	**Aaox(PWI)**
Mexican natives							
21201 (Arriñonado)	1.95^{a}	3.27^{a}	3.68^{ab}	9.66^{b}	10.83^{bc}	11.60^{a}	12.15^{a}
21202 (Criollo chino)	1.93^{a}	3.25^{a}	3.7^{a}	11.75^{b}	11.05^{bc}	11.60^{a}	12.19^{a}
21203 (Ojo de Venado)	1.77^{a}	2.64^{ab}	3.02^{ab}	10.53^{b}	10.36^{bcd}	11.67^{a}	12.13^{a}
21204 (Ojo de Venado)	1.72^{a}	2.84^{ab}	3.19^{ab}	12.07^{b}	10.38^{bcd}	11.71^{a}	12.08^{a}
21206 (cherry)	1.76^{a}	2.54^{ab}	3.08^{ab}	12.38^{b}	9.56^{bcd}	11.70^{a}	12.01^{a}
21207 (Ojo de Venado)	1.93^{a}	3.03^{ab}	3.46^{ab}	18.74^{a}	19.43^{a}	11.86^{a}	12.30^{a}
21208 (Arriñonado)	1.86^{a}	2.79^{ab}	3.24^{ab}	10.24^{b}	9.02^{cd}	11.67^{a}	12.20^{a}
21209 (cherry)	1.86^{a}	2.73^{ab}	3.17^{ab}	10.5^{b}	$10.05b^{cd}$	11.51^{a}	12.12^{a}
Wild relatives							
21205 *S. pimpinellifolium* (cherry)	1.87^{a}	2.81^{ab}	3.29^{ab}	8.81^{b}	9.24cd	11.52^{a}	12.30^{a}
21211 *S. habrochaites* (Ojo de Venado)	1.45^{a}	1.88^{b}	2.15^{b}	10.04^{b}	13.17b	11.63^{a}	12.08^{a}
Commercial variety							
21210 var. Rio grande (saladette)	2.88^{a}	3.6^{a}	4.52^{a}	9.08^{b}	6.83^{d}	11.5^{a}	11.23^{a}
Mean	1.91	2.85	3.32	11.2^{A}	10.9^{A}	11.64^{A}	12.07^{B}
LSD	1.3	1.1	1.5	5.4	3.9	0.5	1.16

Ne: Eggs, Nn: Nymphs, Nn + Ne: Nymphs + Eggs, PC (PLI): Phenolic compounds lacking incidence of *B. tabaci*, PC (PWI) = Phenolic compounds with incidence of *B. tabaci*; Aaox (PLI): Antioxidant activity lacking incidence of *B. tabaci*, Aaox (PWI): Antioxidant activity with incidence of *B. tabaci*. LSD: Least Significant Difference. Means with equal lowercase letters, between columns, are not statistically different (Tukey $p \leq 0.05$). Overall means between columns with equal capital letters are not statistically different (Tukey $p \leq 0.05$).

Within this natural variation, cultivated varieties regularly show a higher incidence of whiteflies than wild populations of tomatoes (Baldin *et al*., 2005; García-Sánchez *et al*., 2023). According to Sánchez-Peña *et al*. (2006), this is because wild tomato populations are exposed to selective pressure imposed by the whitefly, which would explain their higher levels of resistance against the insect. Such is the case for the resistance of *S. habrochaites* (21211) to *B. tabaci*, already reported by other authors (Kortbeek *et al*., 2019; García-Sánchez *et al*., 2023), which coincides with the findings of this research showing a low insect incidence. Additionally, future evaluations could include the Mexican native Ojo de Venado Xicotepec 21203, cherry Teotiltán 21206, and cherry Tejupilco 21209, which, after *S. habrochaites* (Table 3), presented the lowest values of nymph incidence. According to Zeist *et al*. (2021), native populations of tomato, being part of the intraspecific variability of *S. lycopersicum*, represent a more convenient source of resistance to pests in selection and hybridization than those derived from interspecific crosses.

Phenolic compounds (PC)

Significant statistical differences in phenolic compound (PC) content were found among the evaluated tomato germplasm, both in plants lacking whitefly incidence (PLI) ($p < 0.0002$) and with whitefly incidence (PWI) ($p < 0.0001$) (Table 3). In PLI, *Solanum pimpinellifolium* (21205) recorded the lowest PC content (8.81 mg GAE-g^{-1} PF), while 'ojo de venado' Tehuacán (21207) had the highest (18.74 mg GAE-g^{-1} FSW). In PWI, the Río Grande variety recorded the lowest PC concentration (6.83 mg GAE-g^{-1} FSW), and 'ojo de venado' Tehuacán (21207) had the highest (19.43 mg GAE-g^{-1} FSW).

From PLI to PWI conditions, the differences in PC content were significant ($p < 0.0001$). *S. habrochaites* (21211) showed an increase in PC content from PLI to PWI of nearly double (73 %; $p < 0.02$). The Mexican native varieties arriñonado Santa Cruz (21201) (12.11 %; p < 0.49) and Ojo de Venado Tehuacán (21207) (3.7 %; $p < 0.9$), as well as the wild accession *S. pimpinellifolium* (4.8 %; $p < 0.4$), also showed increases, although these were not significant. In contrast, the commercial variety Rio Grande (21210) showed a 25 % ($p < 0.01$) decrease in PC content from PLI to PWI. Other Mexican natives, such as 21203 (-1.6 %; $p < 0.9$), 21202, 21204, 21208, 21209, and 21206 (-22.8 %; $p < 0.1$), also showed decreases in PC content; however, these changes were not significant.

Although herbivorous insects are responsible for large losses in agriculture (Kortbeek *et al*., 2019), plants employ various defense mechanisms, both constitutive and induced, for pest protection (Zunjarrao *et al*., 2020; Yactayo-Chang *et al*., 2020), involving both physical and chemical barriers (Mostafa *et al*., 2022). These chemical defenses include products of primary metabolism, such as antioxidant enzymes (Dieng *et al*., 2011), and molecules of secondary metabolism, such as phenolic compounds (Kundu & Vadassery, 2019; Alcantar-Acosta *et al*., 2020), which reduce insect attacks (Perier *et al*., 2022).

In this study, the presence and variation in phenolic compound (PC) content among tomato germplasm suggests differential modulation among genotypes. Wild genotypes (*S. habrochaites* and *S. pimpinellifolium*) and the Mexican native varieties arriñonado Santa Cruz (21201) and Ojo de Venado Tehuacán (21207) showed an increase in PC content. In contrast, the commercial variety Río Grande and the other Mexican natives showed a decrease in this metabolite. Variations in phenolic compound content in tomatoes are reported by Pal *et al*. (2021) and indicate a higher concentration in those resistant to whitefly. Su *et al*. (2018) report the role of PC as a defense response in tomato plants infested with whitefly. However, other studies in tomatoes indicate that variations in PC content depend on plant age, genotype, tissues, season, growing conditions, and the time of exposure to a specific type of stress (Kisa *et al*., 2019; Dadáková *et al*., 2020).

The significant increase in phenolic compound (PC) content from PLI to PWI in the wild accession of *S. habrochaites* (21214), contrasted with the significant decrease in the commercial variety Río Grande (21210), along with the variations in PC content among native germplasm, highlight differences in the phenolic compounds synthesis between wild and cultivated tomato populations. This calls for future research on the defensive role of phenolic compounds. War *et al*. (2020) suggest that the synthesis and induction of secondary metabolites, such as phenolic compounds, is a common plant response to insect herbivory. Such induced resistance can be exploited as a tool for pest management (Shree *et al*., 2021). In other *Solanaceae* infested with *B. tabaci* and *T. vaporariorum,* the content of phenolic compounds significantly increased relative to control plants (Zhang *et al*., 2017). Populations of tomatoes, such as the Mexican native 'Tehuacan Ojo de Venado' (21207), which constitutively present a high PC concentration, may have an ecological advantage by synthesizing these compounds constitutively. This contrasts with populations that induce changes in PC, which often represent a greater investment of resources to maintain the active synthesis of secondary metabolites (Kerchev *et al*., 2012). Paudel *et al*. (2019) suggest that trait selection during domestication and selective breeding in plants, such as tomatoes, could alter resource allocation, with plants selected for higher yield allocating resources to defense only when attacked.

Phenolic compounds, such as flavonoids (Yao *et al*., 2019), chlorogenic acid (Zhang *et al*., 2017; Kundu & Vadassery, 2019), tannins, lignin, and suberin (Rashad *et al*., 2020), catechin, caffeic acid, rutin, p-coumaric acid, and ferulic acid (Zhang *et al*., 2017), among others, can act as agents in plant protection. They are involved in cell wall strengthening, toxic accumulation in leaves, and insect repellency (Dar *et al*., 2017; Rashad *et al*., 2020). They may also contribute to the desiccation and/or detachment of eggs on leaves (Hilker *et al*., 2016). However, their role in plant growth and development is more diverse (Wagay *et al*., 2020; Tak & Kumar, 2020).

DPPH antioxidant activity (Aaox)

The antioxidant activity (Aaox) of the evaluated germplasm was similar in both PLI ($p < 0.39$) and PWI ($p < 0.18$) conditions (Table 3). However, from PLI to PWI, Aaox registered an average increase of 3.7 % ($p < 0.0001$). The Mexican native varieties arriñonado Santa Cruz (21201) showed a 4.74 % increase ($p < 0.02$), Ojo de Venado Xicotepec (21203) a 3.94 % increase ($p < 0.02$), arriñonado Malinalco (21208) a 4.5 % increase ($p < 0.005$), and cherry Tejupilco (21209) a 5.25 % increase ($p < 0.01$). Similarly, the wild *S. pimpinellifolium* (21205) recorded a 6.75 % increase ($p < 0.02$) and *S. habrochaites* (21211) a 3.8 % increase ($p < 0.04$) in Aaox from PLI to PWI, suggesting the involvement of antioxidant molecules during plant-insect interaction.

The increase in Aaox from PLI to PWI in other Mexican natives such as 21202 (5.05 %, $p < 0.08$), 21204 (3.17 %, $p < 0.12$), 21206 (2.6 %, $p < 0.06$), and 21207 (3.6 %, $p < 0.23$) was not significant. This could indicate the participation of other defense mechanisms against the insect. In contrast, Aaox in the commercial variety Rio Grande (21210) decreased from PLI to PWI ($p < 0.5$), which could represent a capacity loss in plants to respond to stress through this mechanism. This decrease can be attributed to the loss of genetic functions due to the selection processes performed during its creation (Kulus, 2022).

In plant-insect interactions, ROS such as singlet oxygen (O^1_2), superoxide radical (O^{2-}), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH^-), can be either harmful or helpful depending on their cellular concentration (Sachdev *et al*., 2021; Dvořák *et al*., 2021). At low concentrations, ROS activates multiple intracellular signaling components to promote defense responses; conversely, at high concentrations, they increase stress damage (Satyabrata *et al*., 2021). However, plants have enzymatic and non-enzymatic antioxidant mechanisms to counteract oxidation caused by ROS, which is enhanced under biotic and abiotic stresses (El-Zohri *et al*., 2020).

The significant increase in Aaox in some tomato populations suggests the involvement of antioxidant molecules that neutralize ROS during plant-insect interaction and/or possibly in the defensive gene activation. In this regard, Kerchev *et al*. (2012) highlight a reprogramming of gene expression during insect herbivory, where ROS plays a central role as signaling molecules. El-Zohri *et al*. (2020) associate an increase of H_2O_2 concentration with insect tolerance, as it triggers defensive responses.

The loss of genetic variability in modern tomato cultivars increases susceptibility to pests and diseases (Kulus, 2022), which could explain the decrease in Aaox in the commercial variety Rio Grande 21210, contrary to what was observed in the wild *S. habrochaites* and *S. pimpinellifolium*. Orabi and Abou (2019) suggest that under prolonged stress, plants with higher antioxidant potential have better-developed ROS scavenging pathways or detoxification mechanisms to mitigate the adverse impact of oxidative stress and induce tolerance. Therefore, the redox state of the plant can be considered an indicator of its resistance, which is achieved through the elimination of ROS generated, for example, by increasing antioxidant molecules in tomato plants after insect presence (El-Zohri *et al*., 2020). Thus, plants with the ability to counteract stress conditions, such as whitefly (*B. tabaci*) feeding, through an increase in antioxidant activity, could present a greater antioxidant potential and induce defense mechanisms or counteract the ROS generated.

Correlation analysis

The negative and significant correlations between insect incidence, particularly nymphs (r = -0.28**), eggs (r = -0.50**), and nymphs plus eggs (r = -0.44**), with antioxidant activity (Aaox) indicate the involvement of antioxidant molecules in tomato populations due to the presence of the whitefly *B. tabaci* (Table 4). Although the main source of ROS is produced during photosynthesis, the whitefly can reduce the carbon fixation and photosynthetic rate of its hosts. Such alteration could interfere with the production of ROS involved in the signaling cascade in response to the insect, resulting in the inactivation of defensive genes, whereby this phenomenon is harnessed by the whitefly (El-Zohri *et al*., 2020).

Furthermore, the significant correlation between phenolic compounds (PC) and antioxidant activity (Aaox) (r = 0.31*) highlights the role of these metabolites as antioxidant molecules in tomato samples. These results are consistent with those reported by Tak and Kumar (2020), who described that phenolic compounds have several functions in mitigating various stress conditions. For instance, their role as antioxidants within the non-enzymatic mechanism in plants (Orabi & Abou, 2019), aligns with the significant association observed between these two variables.

Table 4. Pearson correlation matrix of five variables in tomato germplasm evaluated for whitefly incidence.

	Aox (PWI)	**PC (PWI)**	**Nn**	**Ne**	**Nn + Ne**
Aox PWI	1				
Cf PWI	0.31*	1			
Nn	-0.28*	-0.2	1		
Ne	-0.5**	-0.2	0.46**	1	
Nn+ Ne	-0.44**	-0.23	0.88	0.82	1

Ne: Eggs, Nn: Nymphs, Nn + Ne: Nymphs + Eggs; PC (PWI) and Aaox (PWI): Phenolic compounds and antioxidant activity with incidence of *B. tabaci.* * Significant (p ≤ 0.05); **Highly significant (*p* ≤ 0.01).

Plant responses to insect herbivory depend on various factors such as plant species, the number and species of herbivores, and the infestation duration (El-Zohri *et al*., 2020). The negative, but not significant, correlation between PC and *B. tabaci* incidence suggests a generally limited role of these metabolites in defense mechanisms against whiteflies, indicating the potential involvement of other defensive strategies. Previous research has identified PC as part of the defense mechanism against whiteflies (Alcantar-Acosta *et al*., 2020). Additionally, phenolic compounds, beyond their role in neutralizing ROS, are implicated in responses to various other stress types not evaluated in this study (Bacha *et al*., 2017; Dar *et al*., 2017; Awan *et al*., 2018; Yao *et al*., 2019).

Conclusions

The presence of *B. tabaci* subsequently egg-laying in the evaluated tomato populations suggests the activation of the antioxidant system of plants. The positive and significant correlation between antioxidant activity (Aaox) and phenolic compounds (PC) likely indicates the activation of defensive genes responsible for the synthesis of products that neutralize ROS and mitigate insect damage. *S. habrochaites*, with the lowest incidence of *B. tabaci*, and the Mexican native Ojo de Venado Tehuacán 21207, with the highest PC content, show promise for inclusion in breeding programs aimed at enhancing pest resistance. The role of phenolic compounds in the antioxidant defense system during plant-insect interactions is significant, though other defense mechanisms may also play a role in counteracting and repelling *B. tabaci*. Exploring natural plant defenses as a pest resistance strategy is crucial for developing environmentally friendly approaches to whitefly control.

Author contribution

Work conceptualization: author 1, author 2, author 7. Methodology development, author 1, author 2, author 3, author 5. Software management, author 1, author 2, author 6. Experimental validation, author 3, author 4, author 6, author 7. Analysis of results, author 1, author 2, author 3, author 6, author 7. Data management, author 1, author 3, author 4, author 7. Manuscript writing and preparation, author 1, author 7. Writing, revising and editing, author 1, author 3, author 6, author 7. Manuscript writing and preparation, author 1, author 7. Drafting, revising, and editing, author 1, author 3, author 6, author 7. Project manager, author 2, author 5. Fund acquisition, author 2.

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The study does not require ethical approval.

Statement of Informed Consent

Not applicable for this research.

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Conflict of interest

The authors declare that they have no conflicts of interest.

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