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Can *Capsicum* spp. genotypes resist simultaneous damage by both *Phytophthora capsici* and *Bemisia tabaci*? Can natural enemies of *Bemisia* complement plant resistance?

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Capsicum (Solanaceae) includes peppers and chilies. *Phytophthora capsici* (Peronosporaceae) and *Bemisia tabaci* (Hemiptera: Aleyrodidae) are two relevant problems in the production of this genus. Among the sustainable alternatives for disease and pest control, plant resistance and biological control stand out. The main objective of this research was to evaluate the resistance of *Capsicum* genotypes to damage by *P. capsici* and infestation by *B. tabaci*, as well as to diagnose whether the action of predators and parasitoids against *B. tabaci* could complement the resistance of the plants. The progression of disease caused by *P. capsici* and infestation by *B. tabaci* was estimated in 23 *Capsicum* genotypes, corresponding to the species: *Capsicum annuum*, *Capsicum baccatum*, *Capsicum chinense*, *Capsicum frutescens* and *Capsicum. pubescens*, from the GenBank of the National Institute of Agricultural Research (INIAP-Ecuador). Three genotypes: ECU-11993 (*C. baccatum*), ECU-11991 and ECU-2244 (*C. pubescens*) showed high susceptibility to both *P. capsici* damage and *B. tabaci* infestation. *C. baccatum*, *C. chinense* and *C. frutescens* genotypes showed the highest resistance to both pests, suggesting multiple resistance. Six taxa of predators and parasitoids reduced *B. tabaci* populations that developed in the most infested genotypes. Plant resistance is a control alternative that could allow the use of biological control, making it environmentally friendly. These results provide the basis for breeding programs in *Capsicum*.

1 Introduction

The genus *Capsicum* (Solanaceae) is native to the Americas in a region that extends from Mexico to the south of the Andes and consequently Ecuador is part of the center of origin and domestication of species of this genus (Barboza et al., 2022). *Capsicum* spp. includes approximately 43 species of chilies and peppers, some of which are cultivated and represent economically important vegetables worldwide (Barboza et al., 2022). *Capsicum annuum* L., *Capsicum baccatum* L., *Capsicum frutescens* L., *Capsicum pubescens* Ruiz & Pav., *Capsicum chinense* Jacq. make up the five cultivated species among which *C. annuum* is the most economically important in the world (Barboza et al., 2022). *Capsicum* crops can be affected by pest and disease problems caused by various arthropods and pathogens. Diseases include root and crown rot and stem blight caused by *Phytophthora capsici* Leonian (Peronosporaceae) (Retes-Manjarrez et al., 2020; Vélez-Olmedo et al., 2020) and damage caused by the whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (Singh and Joshi, 2020).

Phytophthora capsici is a highly destructive pathogen that causes leaf and stem blight, root and crown rot, and fruit rot (Retes-Manjarrez et al., 2020), which has caused severe epidemics in more than 50 plant species, mainly from the Solanaceae, Cucurbitaceae, and Fabeaceae families (Foster and Hausbeck, 2010; Quesada-Ocampo and Hausbeck, 2010; Lamour et al., 2012; Truong et al., 2012). Barchenger et al. (2018) reported that worldwide losses due to this pathogen are estimated at over $100 million annually. *Bemisia tabaci* causes direct damage through sap extraction and indirect damage through the growth of sooty mold produced by saprophytic fungi such as *Capnodium* spp. However, the most serious damage caused by *B. tabaci* is the transmission of viruses, especially the genera *Begomovirus*, *Carlavirus*, *Crinivirus*, *Ipomovirus*, and *Torradovirus* (Navas-Castillo et al., 2011). The direct and indirect damages caused by *B. tabaci* can lead to losses ranging from 20 to 100% of crop yield, amounting to millions of dollars (Sani et al., 2020).

The use of local genotypes of *Capsicum* is an alternative for the management of *P. capsici* and *B. tabaci*. Several candidate genes that could be involved in resistance to *P. capsici* have been identified, which interact in a complex way depending on the genotype and the *Capsicum* species (Rolling et al., 2020; Ro et al., 2022). However, few genotypes have been reported as sources of resistance in *C. annuum* (Criollo de Morelos-334 [CM334], PI 201232 and PI 201234 85 from Mexico; AC2258 from Central America, and Perennial from India) (Quirin et al., 2005); although more resistant genotypes might be found in other cultivated species of the genus. Likewise, physicochemical characteristics such as cuticle thickness, pubescence, trichomes (Ballina-Gomez et al., 2013), and secondary metabolites (Kariñho-Betancourt, 2018) are also mechanisms of resistance in plants against *B. tabaci*. Additionally, biological control exerted by predators and parasitoids has been successful in reducing the damage caused by *B. tabaci* in many countries (Kheirodin et al., 2020; Yang et al., 2022).

Agroecosystems are a simplified version of natural ecosystems. They are an economic process involving living organisms such as plants and animals, developed and produced within a generally complex environmental setting. The ecological nature of the process makes it dependent on the trophic interactions of the producing organisms (plants) with their biotic and abiotic components. The abiotic components, such as climate and soil, condition the interaction of the biotic components, including insects, microbes, and other plants (Noman et al., 2020).

Tri-trophic interactions refer to the interconnections that link plants (first trophic level), herbivores or phytophagous (second trophic level), and carnivores such as predators, parasitoids, or entomopathogens (third trophic level) (Price et al., 2011). Herbivores rely on plants as primary producers to obtain vital resources for their development and reproduction, generating plant-herbivore interactions. Plants defend themselves from herbivores to survive, and through co-evolution, these interactions induce changes in herbivores for the same purposes (Burghardt and Schmitz, 2015). The second trophic level includes insects, other arthropods, as well as pathogens both aboveground and below ground (Van der Putten et al., 2001). Carnivores at the third trophic level obtain nutrients from herbivores, whose efficiency could influence cascading effects that reduce plant damage (Burghardt and Schmitz, 2015).

Utilizing trophic interactions and plant defense mechanisms against insects and pathogens, as well as the activity of parasitoids and predators, can be employed as alternatives for managing two significant issues caused by *B. tabaci* and *P. capsici* in genotypes of *C. annuum*, *C. baccatum*, *C. frutescens*, *C. pubencens*, and *C. chinense*. Therefore, the objective of this research was to assess the resistance of Ecuadorian genotypes of *Capsicum* spp. to damage caused by *P. capsici* and infestations by *B. tabaci*, as well as to estimate the impact of predators and parasitoids on *B. tabaci* populations.

2 Materials and methods

2.1 Location

This study was carried out at the Experimental Campus of the Faculty of Agricultural Engineering (FIAG) of the Technical University of Manabí (UTM), located in the Province of Manabí, Ecuador. The damage caused by *P. capsici* and *B. tabaci* was evaluated on 23 *Capsicum* genotypes (Table 1) from the gene bank of the National Institute of Agricultural Research (INIAP) (Santa Catalina Experimental Station, Quito-Ecuador); accessions were collected from different provinces of the three continental regions of Ecuador (Monteros et al., 2018).

2.2 *Phytophthora capsici*

Isolate Pc3 of *P. capsici* was used as inoculum for pathogenicity tests (Vélez-Olmedo et al., 2020). The pseudo-fungus was cultured in V8 agar culture medium (20%) at room temperature 24 ± 2 °C and under constant fluorescent light (Foster and Hausbeck, 2010). To obtain inoculum, the pathogen was sown in an Oat-Agar culture medium for the abundant production of mycelium (Saltos et al., 2020). When the colonies reached five days of age, 15 mm toothpicks were placed on top of the *P. capsici* colonies for colonization; 10-day-old cultures were used for inoculation.

TABLE 1 Genotypes of the different *Capsicum* species evaluated in this study and the province of collecting.

Genotype	Species	Province	Genotype	Species	Province
ECU-2254 A	*C. annuum*	El Oro	ECU-12975	*C. frutescens*	Morona Santiago
ECU-2254 B	*C. annuum*	El Oro	ECU-2244	*C. pubescens*	El Oro
ECU-2255	*C. annuum*	Loja	ECU-11991	*C. pubescens*	Carchi
ECU-12860	*C. annuum*	Los Ríos	ECU-2240	*C. chinense*	Manabí
ECU-11993	*C. baccatum*	Imbabura	ECU-9122	*C. chinense*	Napo
ECU-12840	*C. baccatum*	Loja	ECU-12969	*C. chinense*	Morona Santiago
ECU-12841	*C. baccatum*	Loja	ECU-12970 A	*C. chinense*	Morona Santiago
ECU-12857	*C. baccatum*	Loja	ECU-12972 A	*C. chinense*	Morona Santiago
ECU-12862	*C. baccatum*	Loja	ECU-12979	*C. chinense*	Morona Santiago
ECU-2251	*C. frutescens*	El Oro	ECU-12985	*C. chinense*	Morona Santiago
ECU-5360	*C. frutescens*	No data	ECU-12989	*C. chinense*	Pastaza
ECU-12970 B	*C. frutescens*	Morona Santiago			

ECU is the code for INIAP's gene bank.

Plants of the 23 genotypes of *Capsicum* spp. were planted in 50-well seedling trays, with a substrate previously sterilized (121°C and 1.5 atm) for two consecutive days and composed of a 1:1 ratio of sandy-loam soil and rice husks. During inoculation *Capsicum* spp. plants were decapitated following the procedures described by Pochard et al. (1976), and immediately, a wooden toothpick, colonized by the mycelium of the pathogen, was inserted into the apical meristem of the 45-day-old plants (V5 vegetative stage) (De La Torre et al., 2009). These plants were maintained under greenhouse conditions at 25±4°C and ~80% relative humidity. Plants were kept with field capacity humidity and fertilized weekly with a chemical mixture based on macronutrients (NPK 20-20-20, YaraTera Kristalon®) and foliar sprays of micronutrients (Evergreen®). The treatments comprised 23 *Capsicum* genotypes as aforementioned (Table 1). These were distributed in a completely randomized design with three replicates, where each replicate consisted of three plants.

The severity of the disease was quantified based on measurements of the length of stem necrosis with a ruler (Koc and Üstün, 2012). Symptoms were measured four days after inoculation (dai), and then every 48 h until 14 dai. To determine the cumulative advance of the symptom in the genotypes, the calculation of both the daily advance produced by *P. capsici*, as well as the time in which the maximum speed of advance the accumulated symptom were registered. Plants without of symptoms were classified as resistant, while plants that showed an accumulated lesion length between 1< and< 10 cm were categorized as moderately resistant, and plants with a lesion length > 10 cm were classified as susceptible.

2.3 Bemisia tabaci

Capsicum plants were transplanted into a greenhouse 30 days after sowing. Plants were placed at a distance of 1.30 m between rows and 0.70 m between plants. A randomized block design with four replicates was used, with five plants of each genotype planted per replicate. To accelerate the establishment of whitefly populations, pesticide sprays were applied at the beginning, following the methodology of Chirinos and Geraud-Pouey (1996). Fifteen days after plants were transplanted, profenofos (doses: 0.8 L.ha^{-1}; 500 g active ingredient.L^{-1} (a.i.)) was applied and in the following two weeks, abamectin (doses: 0.75 L.ha^{-1}, 18 g.L^{-1} a.i. (once a week). No more pesticide applications were done after. Sampling began one week later, taking four leaves per plant (two from the top layer and two from the middle layer) from two randomly selected plants per genotype for each replicate.

Leaf samples were collected in transparent plastic bags and taken to the Entomology Laboratory, FIAG-UTM and observed under a Carl-Zeiss® stereoscope (magnification: 10–40X), counting the number of eggs, first to third instar nymphs, and fourth instar nymphs of *B. tabaci*. Parasitized nymphs and predated nymphs of *B. tabaci* were also counted. The parasitized nymphs were identified by the larva or the pupa of the parasitoid that was observed through the integument. The predated ones were recognized because they were deflated or dry (without hemocoel content). Samplings were carried out at weekly intervals for 24 weeks. The percent (%) mortality in *B. tabaci* nymphs was calculated according to Equation 1.

(Equation 1)

$$Mortality\ (\%) = \frac{Parasited\ nymphs\ +\ predated\ nymphs}{Total\ nymphs} x100$$

Parasitized nymphs were placed individually in N° 2 transparent gelatin capsules until the emergence of adults, which were mounted on slides using Hoyer's medium for subsequent identification to species with the keys of Polaszek and Evans (1992). The plates with the parasitoids were observed under an Olympus CX21® microscope at 4 - 100X magnification. Predatory coccinellids were identified to genus with the diagnostic

characters outlined by Gonzalez (2015). Larvae of lacewings were identified to genus level by characteristics provided by Tauber et al. (2000).

2.4 Data analysis

Tests of normality (Shapiro-Wilk test) and homogeneity (Barllett's test) of variances were performed on the numerical data of the evaluated variables; when necessary, the data were transformed using $\sqrt{y \text{ obs} + 0.5}$. Analysis of variance (ANOVA) followed by the Scott-Knott clustering test ($p < 0.05$) was also used. A linear regression fit was performed to analyze the temporal progression of the disease and the cumulative progression of symptoms produced by *P. capsici*. For *B. tabaci*, the Friedman test was used to compare populations by genotype ($p < 0.05$). For genotypes where whitefly populations developed, a log regression analysis was performed between the percentage mortality and the number of nymphs ($p < 0.05$). A cluster analysis based on Euclidean distance was developed including the variables number of eggs, nymphs and severity of *Phytophthora* stem blight. Statistical analysis and preparation of graphs were performed in SAS version 9.4 (2018), Graphpad Prism software (version 8.0.2, San Diego, CA, USA) (2019), and the 'fact extra', 'ggplot2' and 'ExpDes.pt' packages available in R software version 4.3.0 (R Core Team, 2023).

3 Results

3.1 Phytophthora stem blight symptoms

The speed of onset of Phytophthora stem blight symptoms caused by *P. capsici* varied among genotypes and *Capsicum* species.

Genotypes such as ECU-11991 showed stem blight symptoms from the first day after inoculation (dai), with a daily progress of stem necrosis of 1.8 cm per day resulting in plants completely destroyed at 15 dai (Figure 1). Theses genotypes were classified as highly susceptible according to the methodology used. In genotypes such as ECU-12970B and ECU-12669, symptoms were observed from two dai, with a slow progression of stem necrosis of 0.41 and 0.47 cm per day, respectively (Figure 1). Theses genotypes were categorized as moderately resistant. The progression of Phytophthora stem rot showed a linear behavior with time, according to the regression fit.

3.2 Phytophthora stem blight severity

The final severity of Phytophthora stem blight caused by *P. capsici* was higher in genotypes ECU-11991 of *C. pubescens*, ECU-11993 of *C. baccatum* and ECU-2251 of *C. frutescens*, which exhibited stem necrosis length of 21.7, 21.2 and 18.1 cm, respectively (Figure 2). In ECU-2244, ECU-12857 and ECU-2255 genotypes of *C. pubescens*, *C. baccatum* and *C. annuum*, respectively, stem necrosis sizes exceeded 15 cm, these genotypes were classified as the second more susceptible group to infection by *P. capsici*. On the other hand, the genotypes with the lowest expression of symptoms were ECU-12841, ECU-12862 (*C. baccatum*), ECU-12985, ECU-12970A, ECU-12972B and ECU-12969 (*C. chinense*) and ECU-12970B (*C. frutescens*), whose average size of stem necrosis was 6.6 cm, being classified as moderately resistant (Figure 2). Overall, all genotypes developed symptoms of Phytophthora stem blight, suggesting no qualitative (vertical) resistance to the disease was present.

Species presented significant differences ($p < 0.05$) in response to infection of Phytophthora stem blight. The highest resistance
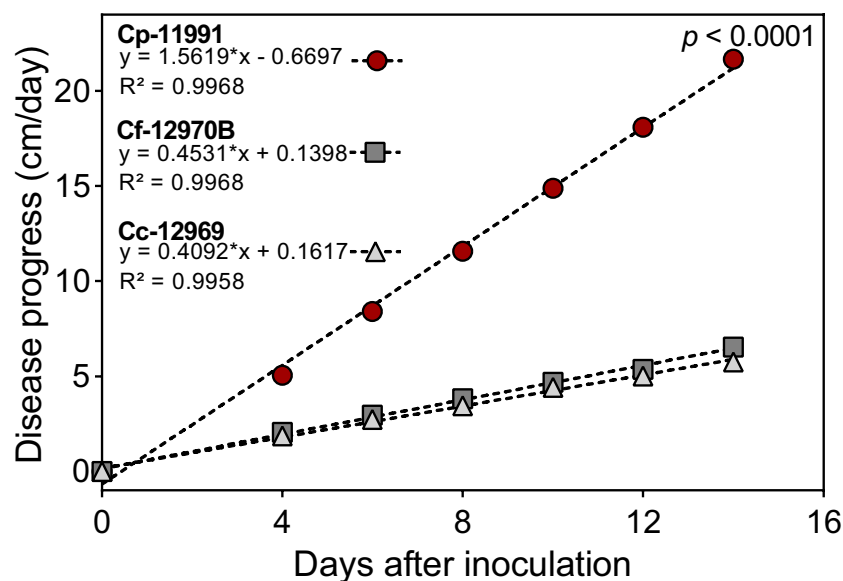

FIGURE 1
Differences in the progress of *Phytophthora* stem blight caused by *Phytophthora capsici* between highly susceptible (Cp-11991) and moderately resistant genotypes (Cf-12970B y Cc-12969) of *Capsicum* spp. *Statistical significance for the regression model according to the F test ($p < 0.0001$). Cc, *C. chinense* Cf, *C. frutescens* and Cp, *C. pubescens*.
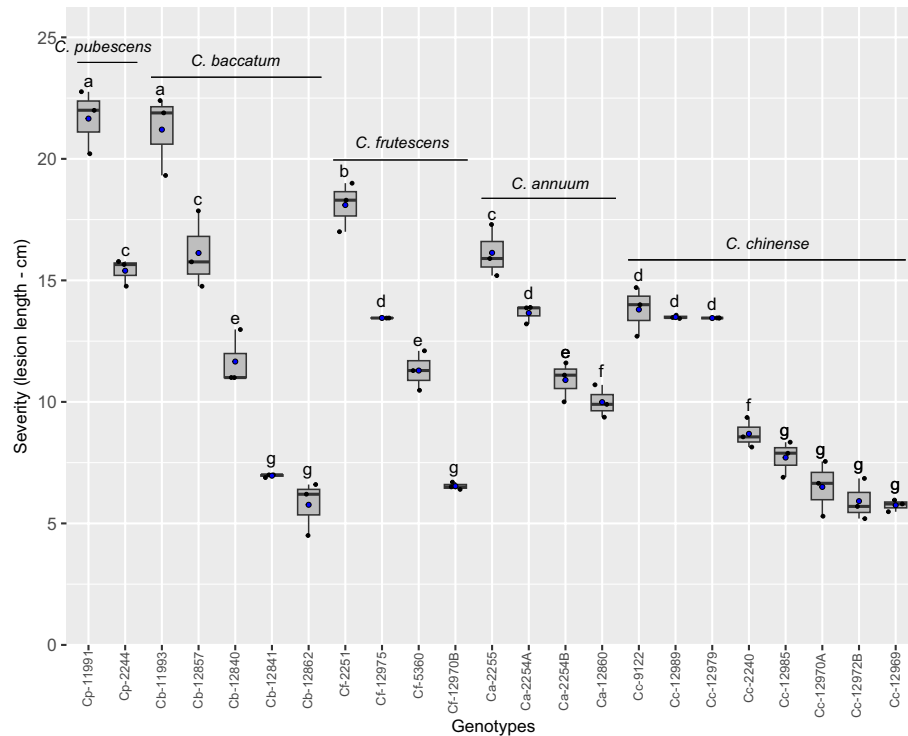
FIGURE 2
Phytophthora stem blight severity in *Capsicum* genotypes infected by *Phytophthora capsici*. Boxes with the same letters do not differ statistically from each other according to the Scott-Knott test ($p < 0.05$). Black and blue points represent the distribution and mean of the observations ($n = 3$), respectively. Ca, *C. annuum*. Cb, *C. baccatum*, Cc, *C. chinense* Cf, *C. frutescens* and Cp, *C. pubescens*.

responses were exhibited by *C. annuum*, *C. baccatum*, *C. chinense* and *C. frutescens* with mean stem lesion severity of 9.4, 12.3, 12.4 and 12.6 cm, respectively (Figure 3), while *C. pubescens* exhibited a higher degree of severity of the disease with 18.5 cm on average. The temporal progress of Phytophthora stem blight showed a linear growth through time in the five species evaluated, supported by the high statistical significance ($p < 0.0001$) of the regression fit.

3.3 Eggs and nymphs of *Bemisia tabaci*

Eggs and nymphs of *B. tabaci* were abundant on four *Capsicum* genotypes (Figures 4, 5). The Friedman test showed that both, the number of eggs and nymphs of *B. tabaci*, were significantly higher in ECU-11993 (*C. baccatum*), with average values of 73 and 38 eggs and nymphs per leaf, respectively. Genotypes ECU-11991 and ECU-2244 (*C. pubescens*) were the second most infested, followed by ECU-12860 (*C. annuum*). Likewise, in three genotypes, two of *C. chinense* (ECU-12970A and ECU-12969), and one of *C. frutescens* (ECU-5360) no eggs were detected. Regarding the nymphs, in addition to these genotypes, this phase was not found in ECU-12862 of *C. baccatum*. The number of eggs on genotype ECU-11993 varied from 0 to 500, while in ECU-11991 and ECU-2244 the eggs fluctuated from 0 to 170 and 200, respectively (Figure 4).

Our results showed that four genotypes had high infestation rates and in the other 19 genotypes, low numbers of *B. tabaci* eggs and nymphs were detected. On ECU-12857 (*C. pubescens*) and

ECU-2255 (*C. annuum*) eggs and nymphs did not exceed two individuals. In the remaining 17 genotypes, the average number of nymphs and eggs was even lower, reaching values ranging from 0 to 0.4 individuals.

3.4 Mortality on *Bemisia tabaci* nymphs

The densities of *B. tabaci* nymphs together with the mortality percentage were plotted for the four most infested genotypes (Figure 5). *Bemisia tabaci* nymphs reached their highest number on the fifteenth week of evaluation for ECU-11993 and ECU-2244 genotypes with approximately 300 and 180 nymphs per leaf, respectively; while genotype ECU-11991 had the highest density on the sixteenth week, with 140 nymphs per leaf. The largest population of *B. tabaci* in ECU-12860 was observed on the eleventh week with 90 nymphs per leaf.

Between the fourteenth and sixteenth week of evaluation, predators and parasitoids became notorious which decimated the populations of *B. tabaci* with maximum mortality percentages varying from 85 to 100% depending on the genotype (Figure 5). Thus, the increase in the percentage of mortality was associated with the decrease in the densities of *B. tabaci* nymphs in the most infested genotypes. This was corroborated by the logarithmic regression equations calculated in which the decrease in the densities of *B. tabaci* nymphs was explained by an increase in the percentage of mortality with an $R^2 > 0.89$ (Figure 6). Three taxa of
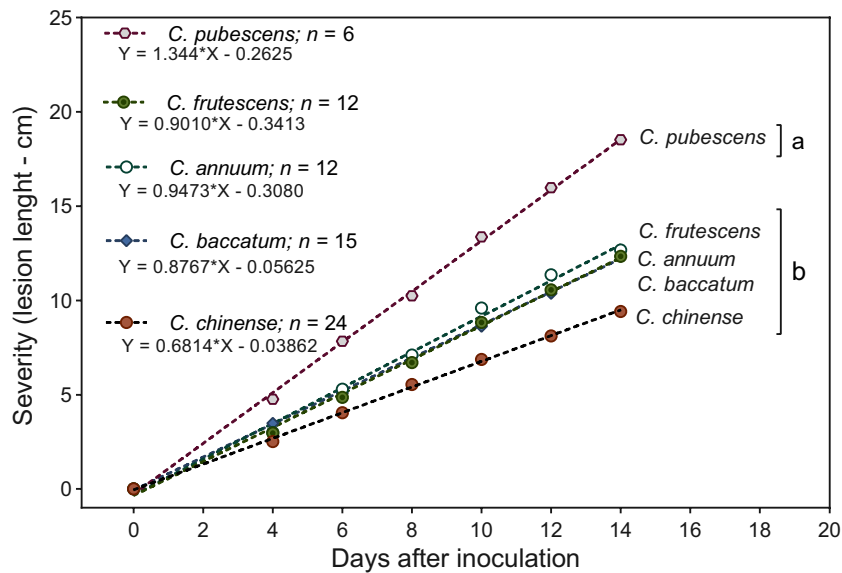
FIGURE 3
Temporal severity of *Phytophthora* stem blight in five *Capsicum* species. Species grouped with different letters differ statistically by the Scott-Knott test ($p < 0.05$). * Statistical significance for the regression model according to the F test ($p < 0.0001$).

predators and three species of parasitic wasps caused the death of *B. tabaci* (Figure 7). The predators were among the genera *Nephaspis* sp. and *Delphastus* sp. (Coleoptera: Coccinellidae), and the genus *Ceraeochrysa* sp. (Neuroptera: Chrysopidae). Parasitoid species found attacking *B. tabaci* nymphs were *Encarsia formosa* Gahan, *Encarsia nigricephala* Dozier and *Encarsia pergandiella* Howard (Hymenoptera: Aphelinidae).

3.5 *Capsicum* genotypes clustered according to incidence and damages caused by *Bemisia tabaci* and *Phytophthora capsici*

Capsicum genotypes were grouped into three distinctive clades based on the severity of Phytophthora stem blight and the level of

FIGURE 4
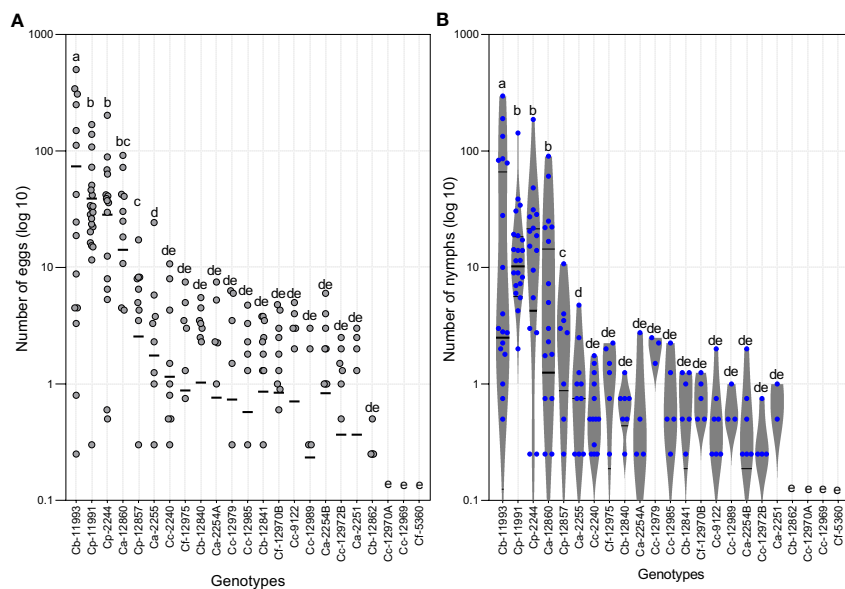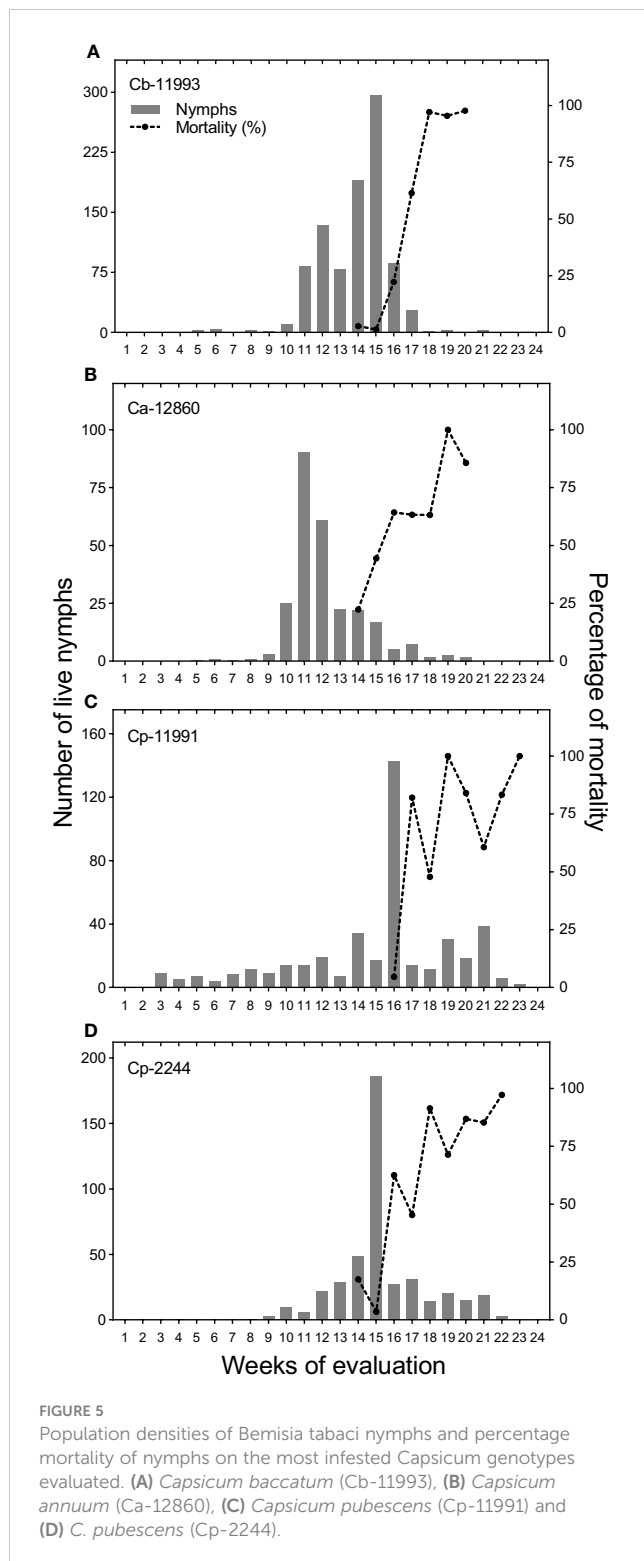**(A)** Numbers of eggs and **(B)** Number of nymphs of *Bemisia tabaci* on the genotypes of *Capsicum spp.* evaluated. Ca, *Capsicum annuum*; Cb, *Capsicum baccatum*; Cc, *Capsicum chinense*; Cf, *Capsicum frutescens*; Cp, *Capsicum pubescens*. The horizontal lines represent quartile 1, median and quartile 3. Means of equal letters do not differ significantly. Friedman test (p < 0.05).

FIGURE 5
Population densities of Bemisia tabaci nymphs and percentage mortality of nymphs on the most infested Capsicum genotypes evaluated. **(A)** *Capsicum baccatum* (Cb-11993), **(B)** *Capsicum annuum* (Ca-12860), **(C)** *Capsicum pubescens* (Cp-11991) and **(D)** *C. pubescens* (Cp-2244).

infestations by *B. tabaci* using Euclidean distance with a cut-off point of 2.93 based on the Majena method. A first clade was made up of the ECU-11993 genotype, a second clade grouped *C. pubescens* genotypes ECU-11991 and ECU-2244, both groups showed high susceptibility to Phytophthora stem blight and *B. tabaci*. A third clade was comprised of the 20 remaining genotypes, which presented variable responses to infection by *P. capsici* and

B. tabaci, however, they showed greater resistance in relation to the first two groups (Figure 8).

4 Discussion

Our findings showed that genotypes *C. pubescens* (ECU-11991 and ECU-2244) as well as *C. annuum* genotype (ECU-2255), *C. baccatum* (ECU-11993); and, *C. frutescens* (ECU-2251) showed high susceptibility to Phytophthora stem blight, with a faster progression of symptoms (stem necrosis). Regarding susceptibility at a species level, *C. pubescens* could be considered a susceptible, in relation to *C. annuum*, *C. baccatum*, *C. chinense* and *C. frutescens*, which could be classified as moderately resistant. There are reports in which genotypes moderately resistant to *P. capsici* show progression of stem necrosis length of around 1.95 cm at 3 days after inoculation (dai), while susceptible genotypes express nearly double the magnitude of *P. capsici* symptoms, with 3.5 cm lesions (Maillot et al., 2022). These results are similar to those found in our trial, where genotypes with high levels of resistance significantly delayed the progression of symptoms, to the point of stopping the infectious process. Barchenger et al. (2018) indicate that *Capsicum* plants with resistance to *P. capsici* quickly recognize and activate mechanisms related to defense in comparison with susceptible plants. Interactions between partially resistant *Capsicum* spp. plants with *P. capsici* adapted isolates showed little or no progress of the pathogen in infected tissue, possibly due to the activation of a detoxification system associated with the expression of phytoalexins in the plants (Maillot et al., 2022). Additionally, Zhang et al. (2013) reported that CaRGA2-like genes increased their expression during *P. capsici* infection. Therefore, resistant genotypes present higher levels of transcription of R genes in relation to the susceptible ones (Xia et al., 2013; Barraza et al., 2022).

Different varieties of *Capsicum* spp. have been identified as containing resistance genes against *P. capsici* (Candole et al., 2010). Until now, the best source of resistance against *P. capsici* has been found in the Morelos Creole genotype (CM-334) of *C. annuum* (Glosier et al., 2008; Ro et al., 2022). Other sources of resistance have been identified in varieties such as "PI 188476", "PI 201232", "PI 201234", "Chile Ancho San Luis", "Fyuco" and "Línea 29" (Kimble and Grogan, 1960; Walker and Bosland, 1999; Roig et al., 2009; Candole et al., 2010) and Dokyachunhchung (Glosier et al., 2008; Ro et al., 2022). However, despite the fact that CM-334 is an old source of resistance, it is the reference genotype in relation to its response capacity against various *P. capsici* isolates from different hosts and geographical regions (Oelke et al., 2003; Sarath et al., 2011; Sy et al., 2005). Genotype CM-334 presents at least two resistance genes against *P. capsici*, but this phenomenon has been associated with more genes (Walker and Bosland, 1999; Thabuis et al., 2003; Sy et al., 2005); however, Kim and Hur (1990) and Saini and Sharma (1978) indicate the presence of a single dominant gene. The moderate resistance of *Capsicum* spp. to *P. capsici* could be modulated by a multi-gene additive system (Lefebvre and Palloix, 1996). Our findings suggest the presence of potential sources of quantitative resistance, as genotypes such as ECU-12969, ECU-
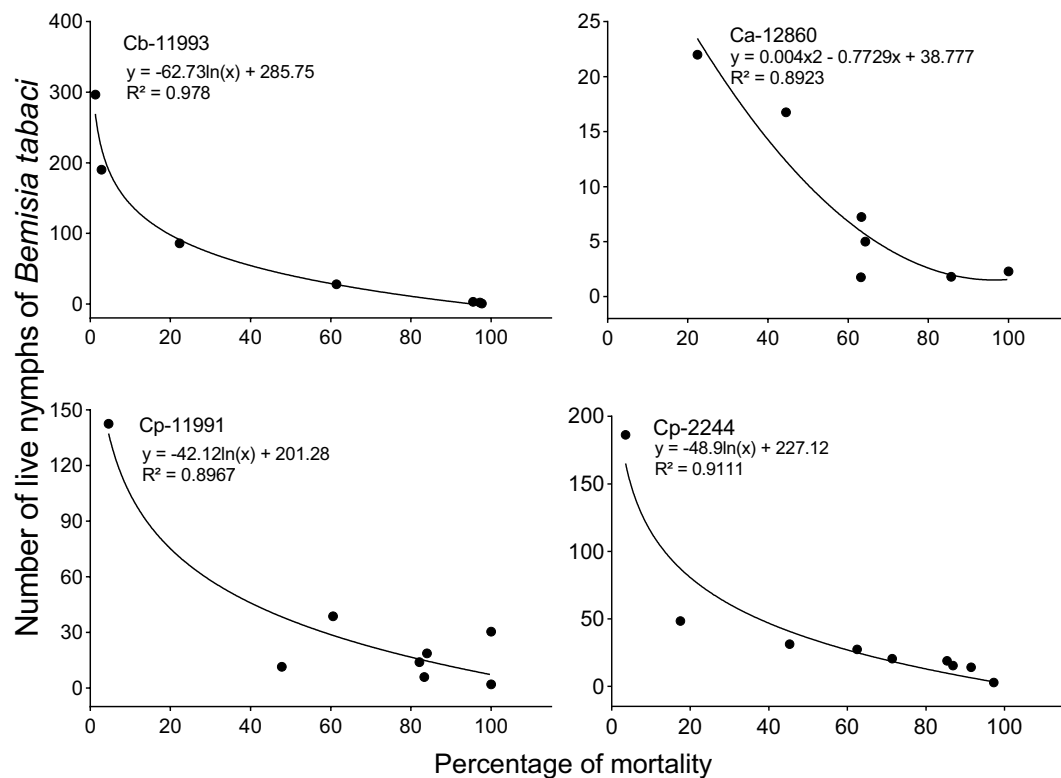
FIGURE 6

Logarithmic regression equations between the percentage of mortality (X) and *Bemisia tabaci* nymphs (Y). Ca, *Capsicum annuum*; Cb, *C. baccatum* and Cp, *C. pubescens*.

12972b, ECU-12970a, ECU-12985, and ECU-12970b showed mild symptoms but did not succumb to the infection caused by *P. capsici*. Therefore, this phenomenon could be associated with the combined action of various genes governing resistance in the aforementioned genotypes (Naegele and Hausbeck, 2020). In Ecuador, the presence of *P. capsici* has been reported as the causal agent of root and crown rot (Vélez-Olmedo et al., 2020) and the evaluation of resistance in commercial pepper cultivars to the pathogen (Saltos et al., 2020). However, the resistance of *Capsicum* germplasm with resistance to *P. capsici* has not been explored.

Ro et al. (2022) reported that accessions of *C. chinense* (PI 439449) and *C. frutescens* (PI82005) have exhibited moderate resistance to *P. capsici*, while accessions of *C. baccatum* did not show any type of resistance. Similarly, our results showed high levels of resistance in *C. chinense* genotypes, highlighting ECU-12969, ECU-12972B, ECU-12970A and ECU-12985 genotypes; and, *C. frutescens* ECU-12970B. In contrast with Ro et al. (2022), we also detected resistance against *P. capsici* in *C. baccatum* genotypes ECU-12941 and ECU-12862. These findings highlight the genetic diversity available in *Capsicum* and its potential for the development of varieties resistant to this pathogen.

For *B. tabaci* three instances were found depending on the population densities of *B. tabaci* in the genotypes. One in which at least one genotype of *C. annuum*, *C. baccatum* and *C. pubescens* reached high infestations, while the rest of the genotypes of these species showed incipient infestations indicating susceptibility and resistance within the same species. In the other, all the evaluated

genotypes of *C. chinense* and *C. frutescens* exhibited little or no infestation, evidencing resistance against *B. tabaci*.

Evaluation of *C. annuum* genotypes in other regions has also shown differential resistance. For example, the Amaxito and Simojovel genotypes of *C. annuum* were tested against *B. tabaci* infestation among 15 native genotypes from Chiapas and Yucatán, Mexico, and both showed low oviposition and high nymphal mortality (Hernández-Alvarado et al., 2019). Chan et al. (2014) evaluated adult attraction and oviposition preference of *B. tabaci* to 14 local genotypes of *C. annuum* collected in Chiapas, Tabasco, and Yucatán. The Maax ik genotype from Yucatán was the least attractive for oviposition compared to Jalapeño, a commercial genotype susceptible to attack by this insect (Chan et al., 2014).

In Thailand, free-choice trials showed that the Keenu (*C. frutescens*) and Karang (*C. chinense*) cultivars were more attractive to *B. tabaci* adults for both feeding and oviposition (Sripontan et al., 2022), which contrasts with our results, since the genotypes of these species showed low or no infestation by *B. tabaci*. Firdaus et al. (2011) examined the resistance to *B. tabaci* infestations of 44 genotypes of *C. annuum*, *C. baccatum*, *C. chinense* and *C. frutescens*; the results showed one genotype of *C. annuum*, two of *C. baccatum*, five of *C. chinense* and one of *C. frutescens* were susceptible. Our results are similar for the first two species; however, they differ for the *C. frutescens* and *C. chinense* genotypes classified as susceptible, since resistance was detected in our study.

Differential levels of infra-species infestations by *B. tabaci* are probably related to the wide genetic variability within species.
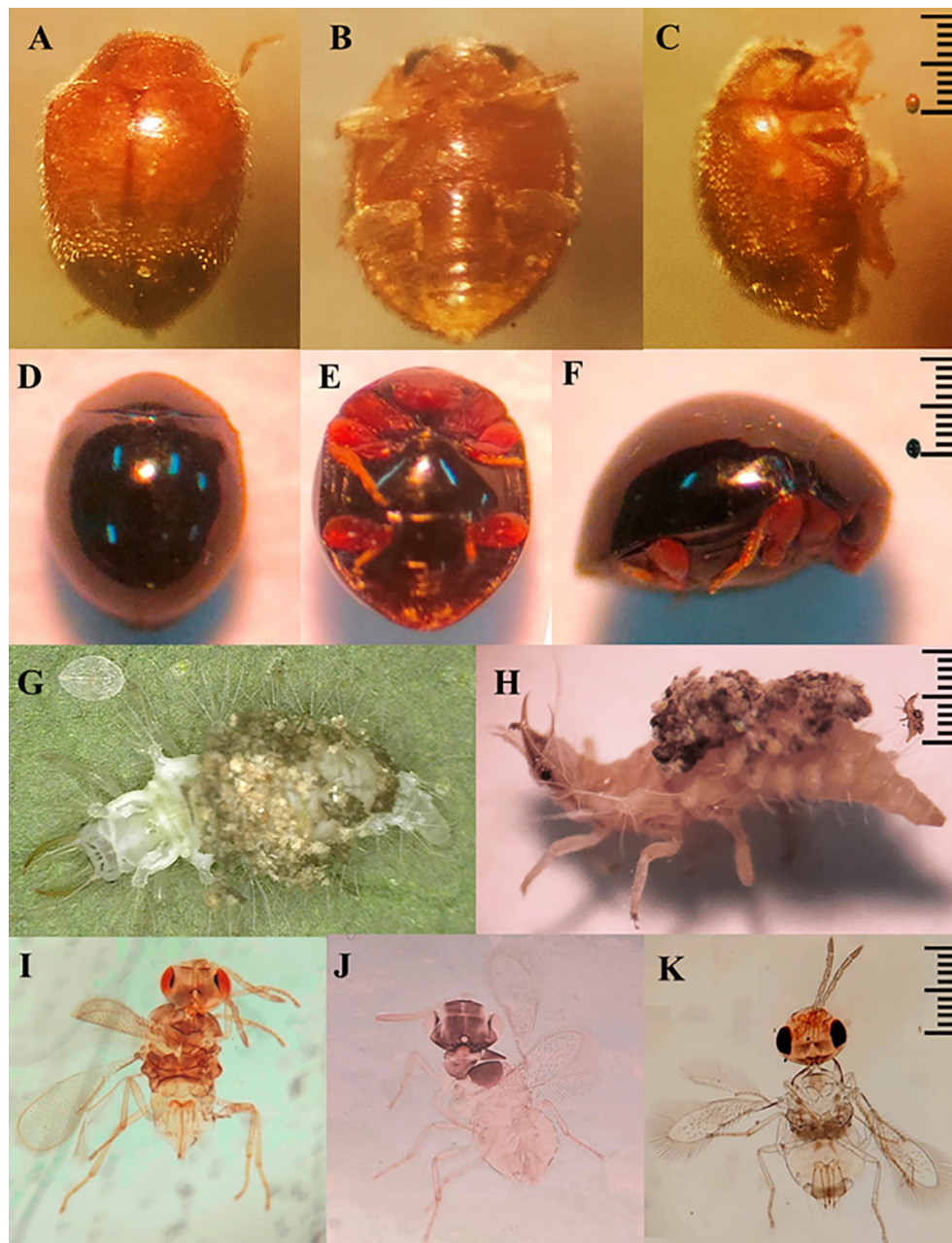
FIGURE 7
Predators: *Nephaspis* sp. **(A–C)**, *Delphastus* sp. **(D–F)**, *Ceraeochrysa* sp. **(G, H)**. Parasitoids: *Encarsia formosa* **(I)**, *Encarsia nigricephala* **(J)** y *Encarsia pergandiella* **(K)**.

Genetic variability has been detected in *Capsicum* hybrids resulting in distinct morphological and molecular characteristics (Tripodi and Kumar, 2019; Barboza et al., 2022). In those genotypes that were hardly or not infested, resistance could be associated with antixenosis, which is a mechanism of plant resistance to deter colonization by an insect including morphological changes, such as variations in the plant surface, color changes, flavor, waxy or pubescent leaves, as well as gummy or resinous exudations (Kogan and Ortman, 1978). However, the antibiosis (mechanism of resistance) of the plant on the nymphs of *B. tabaci* is not ruled out.

The predator taxa detected in this study have been observed in Ecuador and other regions attacking whiteflies and other sucking insects. *Nephaspis* and *Delphastus* species have been reported preying on whiteflies in Ecuador (González, 2009). Gonzalez (2015) points out that an unspecified species of *Nephaspis* was found attacking whiteflies and hard scales on coconut, lemon and mango trees. Likewise, *Delphastus* species attacks whiteflies (Gonzalez, 2015). *Ceraeochrysa* sp. attacks leafhoppers and aphids in sugarcane, and the Asian psyllid in citrus (Cevallos et al., 2021). Kheirodin et al. (2020) report that *Delphastus* and *Nephaspis* species have shown effectiveness in regulating *B. tabaci*. Arno et al. (2010)
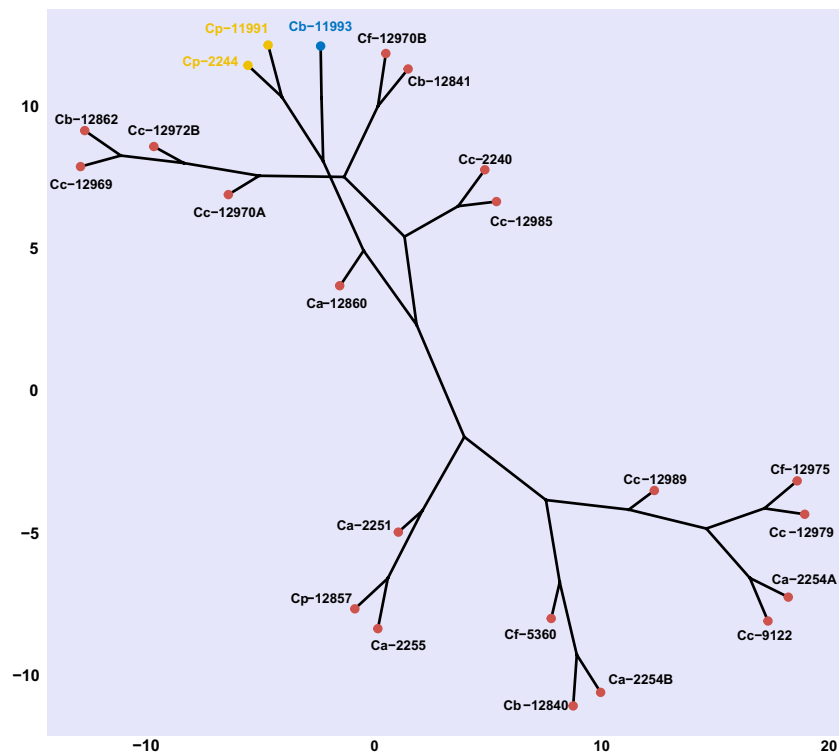
FIGURE 8
Cluster analysis (Euclidean method) based on phenotypic variables (number of eggs, number of nymphs and disease severity) of response against *Bemisia tabaci* and *Phytophthora capsici* in *Capsicum* genotypes. Ca, *Capsicum annuum*. Cb, *C. baccatum*, Cc, *C. chinense* Cf, *C. frutescens* and Cp, *C. pubescens*. Genotypes with the same font color belong to the same clade according to Majena's method grouping (k = 1.25).

point to a species of *Ceraeochrysa* as an effective predator of *B. tabaci* eggs and nymphs.

Regarding parasitoids, the identified species of *Encarsia* have been referred to as important biological control agents of *B. tabaci* in various crops. Yang et al. (2022) indicate that the genera *Encarsia* and *Eretmocerus* have been successfully used for biological control of *B. tabaci* in many countries. In Ecuador, *E. formosa* has been the subject of biological control programs for tomato whitefly (Castillo et al., 2020). *Encarsia nigricephala* and *E. pergandiella* have been reported to attack *B. tabaci* nymphs on melon and cotton (Zambrano et al., 2021; García-Vélez et al., 2023).

In several pepper-producing areas in Ecuador, at least two weekly organo-synthetic pesticide sprays have been carried out during a crop cycle to control pests, without taking into account the confidence intervals before harvest (Chirinos et al., 2020). In contrast, our results show the existence of biological control agents that have demonstrated effectiveness in reducing *B. tabaci* populations, one of the main pests of *Capsicum*. Given the existence of beneficial entomofauna that shows effectiveness in reducing insect pest populations, the implementation of conservation biological control programs is necessary. Chirinos et al. (2021) indicated that the two main strategies of conservation biological control consist of modifying the habitat to increase the survival, longevity, and reproduction of natural enemies, as well as reducing the exposure of these beneficial insects to pesticides.

Based on these results, 15 genotypes of *Capsicum* spp. showed susceptibility to *P. capsici* (Figure 2), while four genotypes

developed high populations of *B. tabaci* (Figures 4, 5). Of these, three genotypes: ECU-11993 (*C. baccatum*); ECU-11991 and ECU-2244 (*C. pubescens*), exhibited susceptibility to both *P. capsici* infection and *B. tabaci* infestation. On the other hand, eight *Capsicum* genotypes showed resistance to both *P. capsici* and *B. tabaci*. The latter could be a mechanism of multiple resistance expressed in such genotypes.

Phytophthora capsici and *B. tabaci* are important phytosanitary problems in Solanaceae, causing devastating losses in pepper worldwide (Lamour et al., 2012; Li et al., 2021). Thus, the use of cultivars resistant to both biotic problems represent a less impactful measure for disease and pest management compared to the use of synthetic pesticides (Firdaus et al., 2012; Barchenger et al., 2018).

Multiple resistance to pests and diseases has been reported, although not frequently. In tomato, resistance to the root-knot nematode, *Meloidogyne* spp., aphids and whitefly has been found and attributed to the expression of the Mi-1.2 gene (Nombela et al., 2003). Similarly, multiple resistance against *P. capsici* and *Verticillium dahliae* Kleb. has been detected in the Grif 9073 genotype of *C. annuum* (Gurung et al., 2015). Multiple resistance mechanisms against various pests in *Solanum pennellii* Correll were associated with the presence of type IV glandular trichomes and secreted acyl sugars (Gentile and Stoner, 1968).

The use of resistant cultivars in integrated pest management programs, along with other control methods, favors the presence of natural enemies of both *B. tabaci* and *P. capsici*. The exploration of plant genetic resources to identify sources of resistance to diseases

and pests is a critical task in the plant breeding process (Srivastava and Mangal, 2019). By identifying sources of resistance and understanding the mechanisms involved in plant responses to biotic factors, it is possible to develop varieties that are adapted to local conditions. Advances in the genetic improvement of this vegetable not only contribute to the development of more productive *Capsicum* varieties, but also provide long-term solutions for disease and pest management in sustainable production systems.

4.1 The tri-trophic interaction: plant - herbivores – predators

The base of the trophic chain is composed of "green" plants, which are organisms that synthesize organic matter from carbon dioxide, oxygen, water and solar energy, which becomes metabolically more complex with the participation of mineral nutrients found in the soil. Consumers (heterotrophic organisms) obtain vital nutrients from the plant that they cannot produce on their own. Consumer food chains constitute different trophic levels (phytophagous, carnivorous and saprophagous) (Price et al., 2011), which form structurally and functionally complex networks. Additionally, some individuals can be found sharing functions in more than one trophic level (Price et al., 2011; Centeno-Parrales et al., 2022). In this complexity lies the dynamic stability of biotic communities. Then, at the base of the trophic chain would be the genotypes of *Capsicum* spp., while *B. tabaci* and *P. capsici* constitute the second trophic level and the natural enemies of *B. tabaci* the third level (Figure 9).

Within this context, plants have generated a diversity of mechanisms to defend themselves against herbivory, ranging from structural defenses such as spines or hard or difficult to chew tissues, to chemical defenses consisting of toxic compounds (Burghardt and Schmitz, 2015). It has been proposed by several researchers that plant-herbivore co-evolution has contributed significantly to the diversification of plant defense mechanisms that in turn generate evolutionary changes in herbivores (Luckmann and Metcalf, 1975; Johnson et al., 2015).

Three basic strategies frame plant resistance: deterrence (antixenosis), resistance (antibiosis) and tolerance (Kant et al., 2015). Antixenosis prevents colonization by the herbivore and involves constitutive characters, including morphological changes, such as subtle variations in plant surface, changes in color, taste, waxy or hairy leaves, as well as exudations of colored gums or resins (Kogan and Ortman, 1978). In antibiosis, the herbivore feeds on the plant, but the plant has adverse effects on the biology and can kill the herbivore or slow its development and reproduction (Painter, 1951; Shi et al., 2023). In tolerance, plant traits do not interact negatively with the herbivore, but compensate for damage caused by changes in assimilation rate, compensatory growth, phenological changes, resource allocation or morphological changes (Tiffin, 2000; Pérez-Hedo et al., 2015). Additionally, preformed structural characters constitute barriers that are referred to as constitutive defenses while induced defenses are triggered in response to herbivore attack (Kant et al., 2015).

As mentioned, we estimate that the resistance of the 19 *Capsicum* spp. genotypes that had low or no infestation by *B. tabaci* is related to antixenosis due to low oviposition and low abundance of nymphs found in these genetic materials, in which constitutive characters of the genotypes prevented the colonization of the insect. On the other hand, induced defenses could participate in the low damage of *P. capsici* on *Capsicum* spp. genotypes that resisted the progress of the disease caused by this pathogen.

Regarding the herbivore-carnivore interaction, in this study and despite the susceptibility of four *Capsicum* spp. genotypes to infestations by this insect, when carnivores (predators and parasitoids) attacked, *B. tabaci* populations were dramatically reduced in those susceptible *Capsicum* genotypes.

Burghardt and Schmitz (2015) indicated that, in the absence of predators, plant abundance is limited by herbivore consumption. However, predators can reduce herbivore abundance and consequently have an indirect effect on plants through cascading effects and can reduce plant damage, which is called trophic cascade (Burghardt and Schmitz, 2015). This could also be contributed by plant traits that attract natural enemies of herbivores, such as predators and parasitoids. Figure 9 is a representation of the effect of *P. capsici* and *B. tabaci* on resistant and susceptible genotypes of *Capsicum* spp. and the action of natural enemies on *B. tabaci* populations and its indirect effect on the plant.
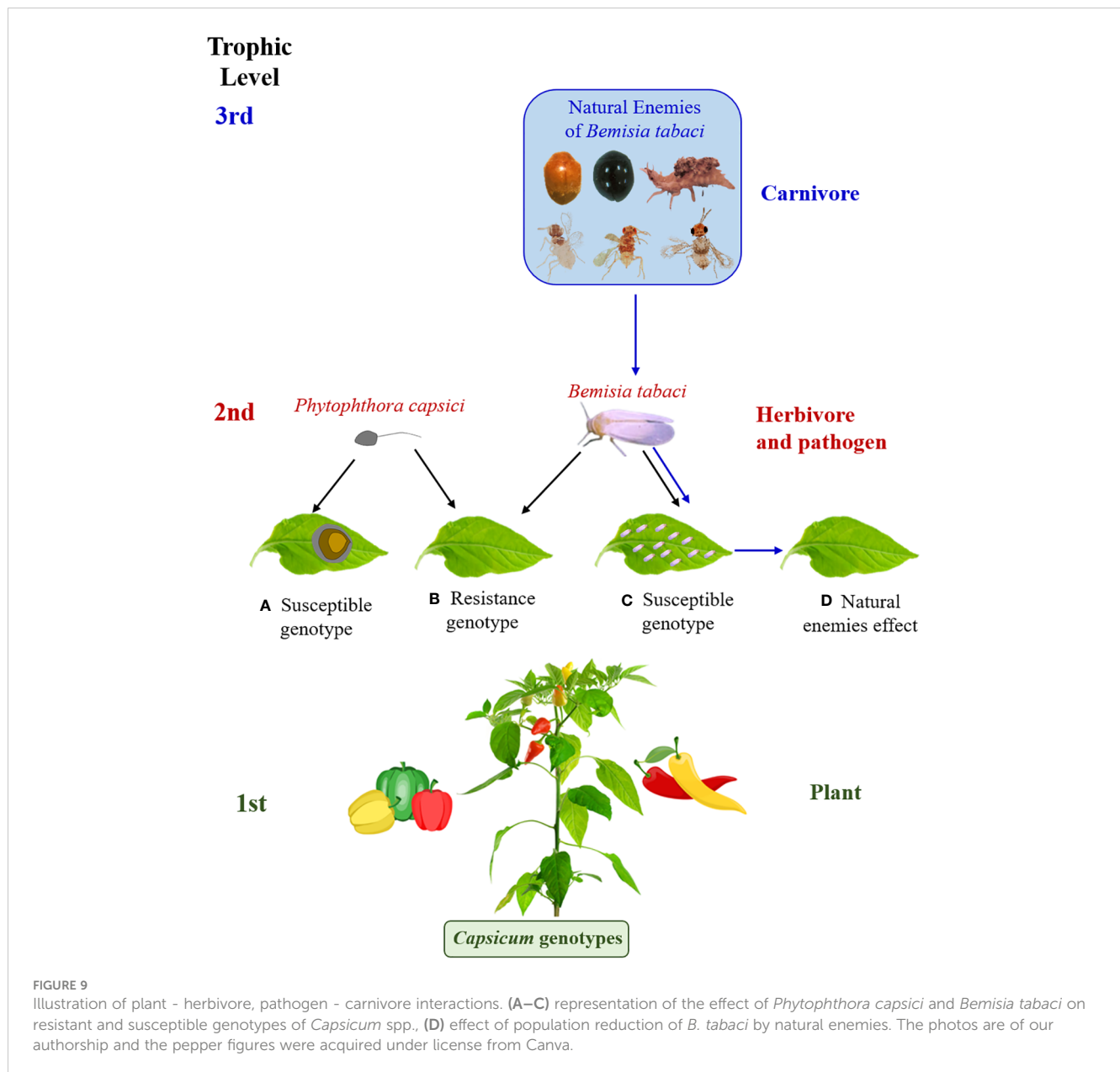
Kant et al. (2015) reported that indirect plant defense consists of traits that enhance the attraction of natural enemies of the herbivore, such as predators and parasitoids, among which plant odor would be used by predators as an orientation to locate prey. Population reduction of *B. tabaci* by predators and parasitoids was corroborated in the four most infested genotypes. Thus, when efficient herbivory regulation by predators and parasitoids occurs, the increase in plant biomass "dilutes" the effects of consumption, mitigating the significance of damage.

In this research, the same genotypes that resisted *B. tabaci* infestations also resisted damage by *P. capsici*. This suggests multiple defense strategies of *Capsicum* spp. plants against an aerial herbivore and a soil-borne pathogens. Furthermore, the action of predators and parasitoids may contribute to the reduction of *B. tabaci* abundance.

Plant resistance is considered an alternative for managing these two phytosanitary problems. For *B. tabaci*, our results show that resistance and the existence of natural enemies could complement each other in the management of this pest. Starks et al. (1972) indicated that a marked resistance effect of the plant against a phytophagous insect is not essential, since moderate effects can be enhanced in combination with other factors such as natural enemies, such as the predators and parasitoids identified in this study.

5 Conclusions

Nineteen genotypes of *Capsicum* spp. showed resistance to *Bemisia tabaci* infestations while eight genotypes were moderately resistant to *Phytophthora capsici*. Consequently, eight genotypes exhibited resistance to both types of harmful organisms. This research constitutes unprecedented work in the detection of multiple resistance of *Capsicum* spp. genotypes to two of the

FIGURE 9
Illustration of plant - herbivore, pathogen - carnivore interactions. **(A–C)** representation of the effect of *Phytophthora capsici* and *Bemisia tabaci* on resistant and susceptible genotypes of *Capsicum* spp., **(D)** effect of population reduction of *B. tabaci* by natural enemies. The photos are of our authorship and the pepper figures were acquired under license from Canva.

main biotic problems that affect *Capsicum* species, such as *Bemisia tabaci* and *P. capsici*, which generate severe losses in crop yield in the main producing areas of the world. The introduction of promising genotypes in productive systems could substantially improve the management of these phytosanitary problems, making pepper and chili pepper cultivation a sustainable and economically viable activity for the farmer.

The finding of predators and parasitoids at the third trophic level that dramatically suppressed *B. tabaci* populations represents a fundamental aspect for implementing biological control programs.

Future studies should focus on determining the genetic factors involved in plant resistance, as well as estimating the functional and numerical responses of the main natural enemies of *B. tabaci* to establish further biological control programs.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for this study because the arthropods found in this research are associated with pepper crops, previously and widely reported in Ecuador so they were not collected in protected forests. Massive collections were not carried out, but rather they were observed on the sampled pepper leaves and consequently their presence was determined.

Author contributions

LC-Q: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing, Funding acquisition, Project administration. DC: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing, Visualization. LS-R: Formal analysis, Investigation, Supervision, Visualization, Writing – original draft, Writing – review & editing. AM-A: Conceptualization, Investigation, Methodology, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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