Genetic effects on resistance to *Phytophthora capsici* in chile of agua (*Capsicum annuum* L.)

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ABSTRACT

Objective: Genotypes of chile de agua (*Capsicum annuum* L.) were evaluated under greenhouse conditions to identify resistance to *Phytophthora capsici*.

Design/methodology: The experiment was arranged as a randomized complete block design (RCBD) with two replications and two treatments (inoculated and non-inoculated). Twenty-one single-cross F_1 hybrids were generated using Griffing's diallel method II (parents and F1s). With the seven parents and 21 F_1 crosses, a total of 28 genotypes were assessed.

Disease severity was rated, and the Disease Index (DI) and the Area Under the Disease Progress Curve (AUDPC) were computed.

Results: Analysis of variance (ANOVA) revealed significant differences among genotypes. Crosses 1×5, 4×6, and 6×7 exhibited the lowest DI and AUDPC values. Diallel analysis indicated significant general combining ability (GCA) and specific combining ability (SCA) effects. Parents 3, 5, and 8, together with the crosses, are promising sources for breeding programs targeting resistance to *P. capsici*.

Findings/conclusions: The study was conducted in Saltillo, Coahuila, Mexico, in 2024.

Keywords: genetic resistance, general combining ability, heterosis, *Phytophthora capsici*.

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INTRODUCTION

The cultivation of chili pepper (*Capsicum annuum* L.) holds substantial importance in Mexico, a country recognized for its extensive genetic diversity, attributable to its status as the center of origin and domestication of this species (Arroyo-Vargas *et al.*, 2013; Luna Ruiz *et al.*, 2018). Within this species, the chile de agua landrace, endemic to the Central Valleys of Oaxaca, stands out due to its pronounced economic and cultural relevance in the region (Montaño-Lugo *et al.*, 2014; SIAP, 2023). *Phytophthora capsici* L. is an oomycete first reported infecting *Capsicum annuum* in 1922 in New Mexico, USA, and subsequently in Mexico by Galindo (1960) in crops from Chapingo. This pathogen

induces root, crown, and fruit rot, leading to sudden wilting and, under favorable environmental conditions, yield losses that may reach 80-100% (Mendoza, 1999; Pérez *et al.*, 2003). It is regarded as one of the principal soilborne pathogens affecting chili pepper, alongside *Fusarium oxysporum* f. sp. *capsici*, *Rhizoctonia solani*, and *Ralstonia solanacearum*, all of which are associated with the wilting syndrome (Vásquez-López *et al.*, 2009). In Mexico, its impact is particularly severe in irrigated production areas such as Chihuahua, Zacatecas, and Sinaloa, where recurrent incidence compromises yield stability and crop sustainability. Conventional management strategies, including crop rotation and fungicide application, have demonstrated limited effectiveness due to the prolonged survival of oospores and the pronounced genetic variability of the pathogen (Barchenger *et al.*, 2018). Moreover, the intensive use of chemical inputs entails environmental risks and a progressive decline in efficacy. Consequently, genetic resistance constitutes the most sustainable alternative for disease management. Notably, the Criollo de Morelos 334 (CM334) variety has been identified as a prominent source of resistance, along with diverse native and wild accessions that have exhibited partial resistance under field conditions (Oelke *et al.*, 2003; Sy *et al.*, 2008; Gómez-Rodríguez *et al.*, 2017). Nevertheless, the complex inheritance of resistance encompassing recessive and dominant genes, as well as polygenic control with epistatic interactions has hindered its effective incorporation into breeding programs (Chunthawodtiporn *et al.*, 2019; Siddique *et al.*, 2019). Diallel analysis constitutes a fundamental approach for partitioning genetic variation into general combining ability (GCA) and specific combining ability (SCA). General combining ability (GCA) reflects the average performance of a parent across multiple crosses and is primarily associated with additive genetic effects. In contrast, specific combining ability (SCA) quantifies the particular deviation of a given cross from the value expected based on the GCA of its parents and is related to dominance and/or epistatic effects (Sprague & Tatum, 1942; Griffing, 1956). In Griffing's Method II, Model I, which includes parents and all direct crosses under a fixed-effects framework, inferences are restricted to the evaluated set; conversely, a random-effects approach is appropriate when parents represent a sample from a broader population (Griffing, 1956). For resistance-related traits (*e.g.*, disease index or area under the disease progress curve [AUDPC]), negative GCA values indicate parental donors of alleles that reduce disease severity, whereas negative SCA values in a cross suggest heterosis and favorable non-additive effects. In *Capsicum*, empirical evidence supports the utility of the GCA/SCA framework for complex traits. Martínez *et al.* (2005) reported significant GCA in parental lines and significant SCA for yield, highlighting opportunities for hybrid development and trait-specific selection. Pech May *et al.* (2010) identified a predominance of additive effects for yield, modulated by environmental conditions, recommending hybridization to enhance productivity and inbreeding combined with selection for plant and fruit traits. In guajillo chili, Hernández-Mendoza *et al.* (2021) found highly significant GCA and SCA effects for fruit number and yield, identifying outstanding heterotic crosses. Collectively, these findings substantiate the estimation of GCA and SCA for resistance to *Phytophthora capsici* and inform strategic decisions: line selection when GCA predominates and hybrid development when SCA exerts a greater influence (Martínez *et al.*, 2005; Pech May *et al.*, 2010; Hernández-Mendoza *et al.*, 2021). The aim of this research was to elucidate the genetic effects of seven creole populations of chile de agua (*Capsicum annuum* L.) and their F_1 crosses under controlled artificial inoculation with *Phytophthora capsici* in greenhouse conditions. This information provides a robust foundation for initiating a breeding program for this landrace, aimed at developing cultivars specifically adapted to the agroecological and productive conditions of the Central Valleys of Oaxaca.

MATERIALS AND METHODS

The experiment was conducted during the fall of 2024 in Greenhouse Seven at the Universidad Autónoma Agraria Antonio Narro (UAAAN), located in Saltillo, Coahuila, Mexico. Seven parental genotypes (creole populations) of chile de agua (*Capsicum annuum* L.) were used, all collected from villages in the Central Valleys of Oaxaca. Each accession was designated according to its community of origin. Seeds were obtained from fruits harvested directly under field conditions.

Sowing was carried out in 200-cell trays containing a commercial substrate. Two sowing dates, spaced one week apart, were implemented to ensure an adequate number of plants. Twenty seeds were sown per genotype (28 genotypes in total: 7 parents + 21 crosses), resulting in eight trays overall. Thirty-five days after germination, when seedlings exhibited 5-6 true leaves, they were transplanted into 12 oz expanded polystyrene cups containing the same substrate. Prior to transplantation, both the working surfaces and containers were thoroughly washed and disinfected with a household chlorine solution to ensure sanitary conditions. The greenhouse operated under temperatures ranging from 26 to 32 °C. Irrigation was applied by flooding. As the study focused exclusively on the seedling stage, fertilization was provided only at the tray stage (starter fertilization), with no subsequent applications after transplantation. No fungicides were applied that could interfere with the experimental infection process. A total of 28 genotypes were evaluated: 7 parental lines and 21 simple F_1 crosses. The number of crosses corresponded to $n(n-1)/2=7\times6/2=21$, in accordance with Griffing's diallel design, Method II, Model I (fixed effects, without reciprocals).

Preparation of the culture medium and inoculum

The *Phytophthora capsici* isolate was provided by the Centro de Investigación en Alimentación y Desarrollo (CIAD), Culiacán, Sinaloa, Mexico, by Dr. Raymundo Saúl García Estrada and his research team. A V8 agar culture medium was used. To prepare 500 mL, 100 mL of V8 juice were filtered, transferred to a 1 L Erlenmeyer flask, and mixed with 400 mL of distilled water, 10 g of bacteriological agar, and 1.5 g of calcium carbonate ($CaCO_3$). The mixture was homogenized on a shaker and sterilized in an autoclave at 15 psi for 15-20 min. Subsequently, the medium was cooled and poured into Petri dishes under sterile conditions. Isolate 20 of *P. capsici* was reactivated by placing a mycelial plug in the center of Petri dishes and incubating them at 27 °C for eight days. To increase inoculum production, the methodology described by Fernández-Pavía *et al.* (2004) was followed with modifications. The absence of contaminants was confirmed, and 20 mL of sterile distilled water were added to each plate, which were then incubated for 72 h to promote sporangial formation. Plates were subsequently subjected to a thermal shock by alternating 4 °C and 27 °C for 30 min at each temperature to induce zoospore release. The resulting suspension was collected in a sterile flask, and zoospore concentration was quantified using a Neubauer hemocytometer (Neubauer-imp®, Marienfeld, Germany), adjusting the final concentration to 10^5 zoospores mL^{-1}.

Greenhouse conditions and inoculation

The experiment was established using a randomized complete block design (RCBD) in a split-plot arrangement, with two blocks, two replicates, and two treatments (T1=non-inoculated; T2=inoculated). Inoculation was performed using a 20 mL syringe, applying 1 mL per plant of the suspension at 1×10^5 zoospores mL^{-1}. After transplantation, plants were maintained under adequate moisture conditions to favor infection.

Disease assessment

Evaluation of the response to *P. capsici* began six days after inoculation and was repeated every three days, for a total of eight assessments. Healthy, diseased, and dead plants were recorded using the severity scale proposed by Glosier *et al.* (2008), where 0=healthy plant, 1=leaf yellowing without stem necrosis, 2=slight stem necrosis, 3=moderate necrosis and slight wilting, 4=severe necrosis with marked wilting, and 5=dead plant. For genetic and severity analyses, only T2 (inoculated) was considered, as T1 did not develop symptoms and served as the negative control.

Calculation of disease index (DI) and area under the disease progress curve (AUDPC)

Using the severity-scale data, the disease index (DI) was calculated as:

$$IE=\left[\frac{\sum_{i=1}^{n}\frac{X_i}{n}}{n}\right](100)$$

where: X_i=disease severity in the *i*-th seedling; n=number of plants evaluated.

Using these indices, the area under the disease progress curve (AUDPC) was calculated according to Shaner and Finney (1977):

$$AUDPC=\sum_{i=1}^{n}\left[\frac{X_{(i+1)}+X_i}{2}\right]\left(T_{(i+1)}-T_i\right)$$

where: X_i=proportion of disease at the *i*-th observation; $T_{(i+1)}-T_i$ =time interval between two consecutive assessments; n=number of evaluations.

Statistical models

ANOVA (split-plot design)

Data were analyzed using analysis of variance (ANOVA) to evaluate the effects of sowing dates, treatments, genotypes, and their interactions on disease severity. Missing data were imputed using a general linear model (GLM) with fixed effects for the parental lines:

$$Y_{\{rfg\}} = \mu + F_f + R(F)_{\{rf\}} + G_g + (GF)_{\{gf\}} + \varepsilon_{\{rfg\}}$$

where: F_f: Sowing dates (fixed; main plot); $R(F)_{\{rf\}}$: Replication within sowing dates; G_g: Genotypes (fixed; subplot); $(GF)_{\{gf\}}$: Fixed interaction (genotype × sowing date); $\varepsilon_{\{rfg\}}$: Residual error.

Diallel analysis (Griffing, Method II, Model I)

A general combining ability (GCA) and specific combining ability (SCA) analysis was performed based on Method II proposed by Griffing (1956), which includes both parents and F_1 hybrids.

Additive linear model:

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + y_k + \varepsilon_{ijk}$$

where: Y_{ijk}=observed phenotypic value of the cross; μ=overall mean of all observations; g_i, g_j=general combining ability (GCA) effects of parents i and j; s_{ij}=specific combining ability (SCA) effect of the cross ($i \times j$); y_k=effect of the k-th replication; ε_{ijk}=experimental error associated with observation i_{jk}.

Software and packages

Analyses were performed in R (R Core Team, 2025), using RStudio and the tidyverse, agricolae, and DiallelAnalysisR packages.

RESULTS AND DISCUSSION

Table 1 presents the mean squares from the analysis of variance, in which significant differences were observed among genotypes in their response to inoculation with *Phytophthora capsici*.

Significant effects ($p<0.01$) were detected for both evaluation dates and genotypes, indicating substantial variation in disease progression (Table 1). The genotype × date interaction was not significant, suggesting that disease progression was consistent across the evaluated genotypes. The observed differences can be attributed to the genetic variability of the creole materials collected from different communities in the Central Valleys of Oaxaca. The delayed onset of symptoms (after day six) and the slower progression observed in some genotypes suggest the possible presence of major genes and/or mechanisms of partial resistance.

According to Van der Plank (1984), delayed disease onset is associated with vertical resistance (*i.e.*, major genes), whereas slow disease development is related to a reduced rate

Table 1. Mean squares from the analysis of variance for the reaction of parental genotypes and F_1 hybrids to inoculation with *Phytophthora capsici*.

Source of variation	Degrees of freedom	Middle squares
Evaluation dates	7	8924**
Replications/Dates	7	262
Genotypes	27	6060**
Genotype × Dates	189	186
Error	216	849
Total	447	
CV (%)		82.9

Highly significant at 0.01.

of disease increase. Previous studies have reported similar patterns. Martínez (2011) found no significant differences among chile mirador collections, although symptom progression was more rapid. Hernández (2009) evaluated 128 materials and reported that only one accession (118) maintained resistance for 10 weeks.

Retes-Manjarrez *et al.* (2020) identified six highly resistant local races when evaluating 32 *Capsicum* accessions under controlled conditions, with clear differences in the phenotypic expression of the disease. Table 2 presents the results for the disease index (DI) and the area under the disease progress curve (AUDPC), which enable the identification of genotypes exhibiting distinct levels of resistance to *P. capsici*.

According to Ristaino (1990), only materials with a disease index (DI) between 0 and 20 can be considered resistant. Under this criterion, only the parent San Andrés (DI=19.38) and the cross San Andrés × San Pablo (DI=5.31) were classified as resistant, highlighting their value for genetic improvement. The lowest area under the disease progress curve (AUDPC) value also corresponded to this cross (1282.5%·days), followed by La Raya × Ocotlán and San Andrés × Santa Cruz, both with 116.25. Although the values below 100% reported by Martínez (2011) as indicative of high resistance were not achieved, these combinations exhibited moderately resistant performance. According to Van der Plank (1984), this partial resistance is attributable to horizontal resistance of a polygenic genetic nature, which does not prevent disease development but rather slows its progression. This was evident in crosses such as San Andrés × Ocotlán (DI=11.17; AUDPC=455.29) and San Pablo × Zimatlán (DI=27.31; AUDPC=525). In contrast, Zimatlán × Vigallo and Ocotlán × Vigallo showed the highest DI (60 and 58.28) and AUDPC (1275 and 1154.88) values, indicating high susceptibility. Among the parents, Zimatlán and La Raya were the most susceptible, whereas San Andrés, San Pablo, and Santa Cruz exhibited lower disease progression, suggesting the presence of horizontal-resistance genes. Although this resistance is complex to fix, it is stable and durable (Van der Plank, 1984; Shaner & Finney, 1977). Overall, these results are consistent with Cíntora Portuguez (2016), who emphasized the utility of AUDPC as a key criterion for identifying resistant genotypes.

Overall, disease progress exhibited a steady increase throughout the evaluation period, as shown in Figure 1. Parental lines displayed higher AUDPC values than their corresponding F_1 crosses, indicating greater severity and more rapid infection development.

Table 2. Means of the disease index (DI) and area under the disease progress curve (AUDPC) in parental lines and F_1 crosses of chile de agua inoculated with *Phytophthora capsici*.

Genotype	Type	Disease Index (%)	Distribution of the area under the disease progress curve (%·days)
San Andrés	Parent	19.38	427.5
San Pablo	Parent	29.38	611.25
La Raya	Parent	30.94	615
Santa Cruz	Parent	41.41	926.25
Ocotlán	Parent	49.38	1106.25
Zimatlán	Parent	76.56	1635
Vigallo	Parent	78.13	1687.5
San Andrés × Santa Cruz	Cross F_1	9.58	116.25
La Raya × Ocotlán	Cross F_1	36.41	116.25
Ocotlán × Zimatlán	Cross F_1	52.5	207
San Pablo × Vigallo	Cross F_1	32.03	234.55
Santa Cruz × Vigallo	Cross F_1	51.31	288.75
Santa Cruz × Zimatlán	Cross F_1	48.75	318.75
San Andrés × Ocotlán	Cross F_1	11.17	455.29
San Pablo × Zimatlán	Cross F_1	27.31	525
San Pablo × La Raya	Cross F_1	21.68	571.875
San Andrés × La Raya	Cross F_1	7.97	573.45
La Raya × Zimatlán	Cross F_1	38.75	712.5
San Pablo × Ocotlán	Cross F_1	26.88	735
La Raya × Vigallo	Cross F_1	39.38	765
San Andrés × Zimatlán	Cross F_1	15.16	776.25
San Pablo × Santa Cruz	Cross F_1	23.28	791.25
La Raya × Santa Cruz	Cross F_1	32.81	986.25
Santa Cruz × Ocotlán	Cross F_1	44.69	1095
San Andrés × Vigallo	Cross F_1	15.78	1098.75
Ocotlán × Vigallo	Cross F_1	58.28	1154.88
Zimatlán × Vigallo	Cross F_1	60	1275
San Andrés × San Pablo	Cross F_1	5.31	1282.5

Nevertheless, parents 3 and 5 stood out, as their AUDPC values were comparable to —or lower than— those observed in some crosses, suggesting relatively higher resistance. These findings confirm the presence of genetic variability in resistance to *Phytophthora capsici* among the evaluated materials and support the selection of parental lines with favorable additive effects for genetic improvement. Table 3 presents the effects of general combining ability (GCA) and specific combining ability (SCA) on the disease index (DI), enabling the identification of parents with favorable additive effects and cross combinations exhibiting significant non-additive interactions.

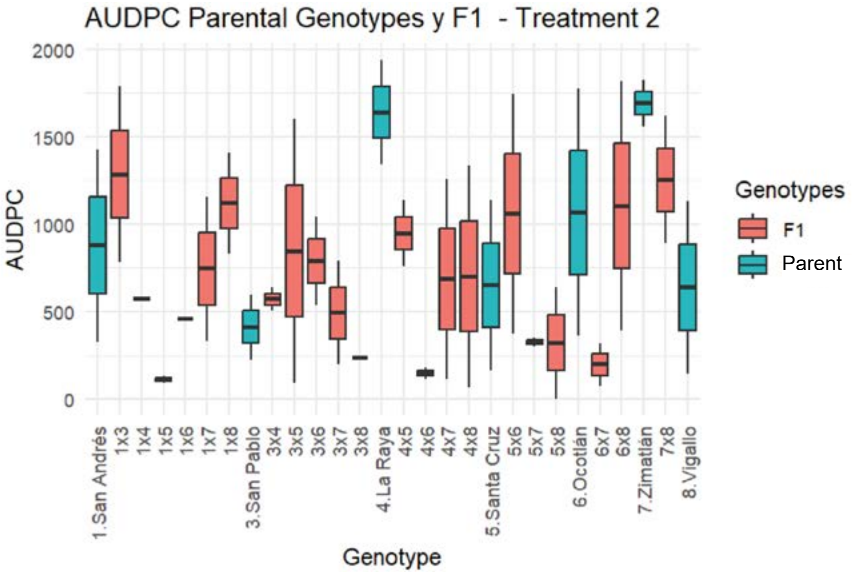

Figure 1. Distribution of the area under the disease progress curve (AUDPC) for parental lines and F_1 crosses of chile de agua inoculated with *Phytophthora capsici*.

Table 3. General combining ability (GCA) and specific combining ability (SCA) effects on the disease index (DI) in 21 F_1 crosses of chile de agua inoculated with *Phytophthora capsici*.

F_1 Crosses	Disease index (%)	General combinatorial ability	General combinatorial ability	Specific combining ability
1×3	60	0.54	−4.78	29.09 **
1×4	27.31	0.54	4.85	−13.22 *
1×5	5.31	0.54	−5.58	−24.79 **
1×6	21.68	0.54	−0.49	−13.52 *
1×7	36.4	0.54	5.53	−4.81
1×8	52.5	0.54	−0.07	16.88 **
3×4	26.87	−4.78	4.85	−8.34
3×5	39.37	−4.78	−5.58	14.59 *
3×6	38.75	−4.78	−0.49	8.87
3×7	23.28	−4.78	5.53	−12.62
3×8	11.16	−4.78	−0.07	−19.14 **
4×5	44.68	4.85	−5.58	10.28
4×6	7.96	4.85	−0.49	−31.54 **
4×7	32.81	4.85	5.53	−13.50 *
4×8	30.93	4.85	−0.07	−7.12
5×6	48.75	−5.58	−0.49	19.67 **
5×7	15.15	−5.58	5.53	−19.94 **
5×8	15.78	−5.58	−0.07	−13.72 *
6×7	9.58	−0.49	5.53	−30.61 **
6×8	51.31	−0.49	−0.07	16.72 *
7×8	58.28	5.53	−0.07	17.66 **

**, *, very significant 0.01, significant 0.05, resp.

In the GCA and SCA analysis of the 21 simple F_1 crosses of chile de agua, the negative GCA values of parents 3 (−4.78) and 5 (−5.58) highlight their additive potential to reduce the disease index, making them promising candidates for parental-line selection. However, strongly negative SCA effects revealed the most heterotic combinations. Crosses such as 1×5 (SCA=−24.79; DI=5.31%), 4×6 (SCA=−31.54; DI=7.96%), and 6×7 (SCA=−30.61; DI=9.58%) exhibited reductions in severity far greater than expected based on the GCA of their parents, suggesting favorable gene interactions (dominance and/or epistasis) that could be exploited to develop highly resistant hybrids. In contrast, crosses such as 1×3, 7×8, and 1×8 showed positive SCA effects and DI means close to 60%, indicating particularly susceptible combinations. Overall, these results suggest that an effective breeding program should integrate the selection of parents with favorable GCA and the identification of specific crosses with strongly negative SCA to maximize resistance to *P. capsici*.

CONCLUSIONS

The evaluation of 27 chile de agua crosses revealed significant genetic variability in response to *Phytophthora capsici*. Crosses 1×5, 4×6, and 6×7 exhibited the lowest disease index (DI) and AUDPC values, indicating moderately resistant performance. Parents 3 and 5 showed favorable additive effects (negative GCA), whereas specific combinations with highly negative SCA suggest useful non-additive gene interactions for the development of resistant hybrids. These results support the use of parents with strong GCA in combination with high-performing specific crosses, as an effective strategy for breeding chile de agua resistant to *P. capsici*.

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