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Heterosis and combining ability analysis of *Phytophthora capsici* induced root rot resistance and horticultural traits in *Capsicum annuum*

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Phytophthora capsici **causes severe root rot in chili crop, leading to significant global yield losses. Effective resistance screening across various environments is crucial to identify stable resistant genotypes with superior horticultural traits. This study aimed to investigate the resistance response of different chili genotypes and their crosses, along with their agronomic performance in diverse screening conditions. The controlled greenhouse environment enabled precise genotype screening, with AVPP-0206 and Turkey-1 demonstrating notable resistance. Screening under field conditions revealed high susceptibility in genotypes like A-132 and Wiz-21. Male fertile lines showed varying susceptibility, with Wiz-21 being highly susceptible, whereas AVPP-0206 and VRI-YP showed moderate resistance. Crosses involving resistant lines resulted in hybrids exhibiting moderate to strong resistance, while hybrids from susceptible lines showed high susceptibility. Heterosis estimates indicated that crosses such as A-441 × Turkey-1, A-512 × AVPP-0206, A-512 × VRI-YP, A-512 × Turkey-1, and A-512 × Turkey-14 exhibited positive commercial heterosis for fruit yield and negative heterosis for disease incidence. These crosses also showed significant specific combining ability (SCA) effects for fruit yield and disease resistance traits, which were consistent across all tested environments. These selected lines and crosses provide valuable genetic resources for breeders, offering a foundation for developing robust, high-yielding chili cultivars with enhanced root rot resistance and superior horticultural traits.**

Keywords Chili, Root rot, *Phytophthora capsici*, Heterosis, Gene action, Hybrids, Screening

Chili (*Capsicum annuum* L.) belongs to the Solanaceae family[1] and was domesticated 6,000 years ago in Central and South America[2]. It is used as a fresh vegetable, dried powder, or pickled form in different cuisines worldwide[3]. Capsaicin, a volatile compound in chili, is widely used in pharmaceutical industry due to its antioxidant, anti-inflammatory and metabolic benefits[4]. Moreover, it is showing growing industrial applications in food preservation, active packaging, functional foods and cosmeceutical formulations[5,6]. Chili is prone to numerous abiotic stresses like high temperatures, drought, etc.[7–9] and susceptible to various viral, bacterial, and fungal infestations[10]. Among these, *P. capsici*, a soil-borne oomycete, is a very serious threat to chili production worldwide[11]. It infects chili at different growth stages and different plant organs[12] causing root rot, collar rot, stem rot[13,14], foliar blight, and crown rot[15,16]. *P. capsici* causes root rot disease in Solanaceae, Fabaceae, and Cucurbitaceae family[17]. It ranks among the top five most destructive oomycetes globally with annual economic losses estimated up to $100 million[18] and up to 100% yield losses in chili in open field and greenhouse cultivation worldwide[19]. Cultural practices like controlled irrigation, crop rotation, chemical control[20–22] and biological control[23] to counter this disease have proven ineffective[24], leaving breeding for resistant cultivars the simple,

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cost effective[25] and environmentally friendly[26–28]. However, very limited information is available about host defense mechanisms and the inheritance of traits conferring resistance to *P. capsici* induced root rot[29]. Moreover, resistance-based germplasm characterization and cataloging for this disease have been limited[10,19,20]. Few landraces exhibiting varying degrees of resistance to this devastating chili pathogen have been reported[10,30] like CM-334, AC2258, PI201232, and PI201234[14,31–33], but cultivars with stable resistance to *P. capsici* have yet to be bred[10].

Most of the resistant cultivars identified are lacking in agronomic traits[16], like CM334[34], which limit their use in the development of high yielding chili cultivars coupled with economically important horticultural traits and disease resistance[10,35]. Moreover, studies aiming at the identification of resistant genotypes to *P. capsici* induced root rot along with good horticultural traits are limited[28]. Hence, the hunt for new resistant genotypes with good performance in other horticultural traits has become the prime objective of chili breeders[35].

The resistance behavior of available cultivars varies significantly under different field conditions[36], depending upon genotype, plant age, temperature, inoculation method, temperature, etc. Moreover, different chili genotypes vary in their resistance response to *P. capsici* infection with inoculation method[37]. Many commercially available resistant cultivars vary in their resistance response to root rot under different field conditions[10]. Hence, screening for resistance behavior under different environmental conditions is essential for the effective selection of *P. capsici*-resistant genotypes. Moreover, the genetics of resistance to *P. capsici* is a complex trait due to variation in genetic material and pathogen isolates. Studies on *P. capsici* induced root rot resistance inheritance in chili have reported single gene[38], two genes[39] and multiple gene systems, which have made its genetics controversial[12].

This study aims to identify chili hybrids and parental genotypes resistant to *P. capsici*-induced root rot while possessing favorable horticultural traits through line × tester analysis. Line × tester analysis has been previously used to study inheritance patterns of resistance to anthracnose in cassava[40], rust in cowpea[41], cercospora leaf spot in brinjal[42], late wilt and downy mildew in maize[43], and blast in rice[44]. Male sterility based line × tester mating designs have been widely adopted in different crops due to their high sensitivity in detecting both general and specific combining ability effects for yield and stress-resistance traits[45]. Combining ability enables breeders to select suitable parental genotypes with desired combination of horticultural and resistance traits, along with an understanding of inheritance pattern. This information facilitates the choice of a suitable breeding strategy to meet the desired breeding objective. By crossing genetic male sterile lines with fertile lines and screening the resulting hybrids and their parents under different conditions, this research seeks to contribute valuable insights into resistance mechanism of *P. capsici* induced root rot and support the development of high-yielding, and disease-resistant chili cultivars with desired horticultural traits.

Materials and methods

Location, weather and soil conditions

This study was conducted at Vegetable Research Institute, Faisalabad, and Department of Plant Pathology, University of Agriculture, Faisalabad, during the period of 2020-22. Faisalabad is located at an altitude of 184.4 m at outskirt of tropics, 31°26 latitude and 71°06 longitude[46]. It experiences a semi-arid climate characterized by long, hot, and humid summers extending from mid-April to October, followed by cool, dry winters from November to early February[47]. The soil at the experimental site is classified as loamy, with low organic matter (1.40%) content and an alkaline 8.1 pH.

P. capsici culture collection

The *P. capsici* isolate used in this study was obtained from our previous research[48], where it was originally isolated and maintained. Molecular identification of the isolate was already conducted by sanger sequencing, and the sequence has been submitted to GenBank under the accession number (OQ472606).

Development of F_1 hybrids

Three Genetic Male Sterile (GMS) lines and six male fertile restorer lines were obtained from Vegetable Research Institute, Ayub Agricultural Research Institute (AARI), Pakistan, and Asian Vegetable Research and Development Center, Taiwan (Table 1). No ethics approval was required as no wild or endangered plant species were studied and no formal herbarium voucher for the plant germplasm was deposited, as all lines were sourced from authenticated institutional breeding collections. The GMS lines were chosen for their stable male sterility expression and previous performance in preliminary evaluations by Vegetable Research Institute, Faisalabad, while the testers represented genetically diverse and agronomically important lines (unpublished data / field observations). Seeds of the parental lines were sown in 72-cell plastic seedling trays filled with peat moss pre-mixed with Dynasty® fungicide (containing 37.5 g/L mefenoxam, 12.5 g/L fludioxonil, and 75 g/L azoxystrobin) at a rate of 5 mL per kg of substrate. Two seeds were placed in each cell. Upon emergence of the first true leaf, seedlings were fertigated with a 0.5% solution of Nitrophos (20:20:0 NPK). One week later, fertigation was continued using a 1.0% Nitrophos solution until the three-leaf stage, followed by a 1.5% solution up to the four- to five-leaf stage. Once the seedlings reached a height of 4–5 leaves, they were transplanted into a plastic-covered tunnel. During the flowering stage, the tunnel was covered with insect net to controlled pollination. Manual crossing was performed between three female lines and six male lines, resulting in 18 F_1 hybrids following a Line x Tester design. The fruit was harvested when it turned red, air-dried, and the seed was extracted manually.

Screening for *P. capsici* resistance

The eighteen crosses along with nine parental lines and one commercial hybrid "Golden Hot" were screened for resistance to *P. capsici* in three different screening conditions i.e. Greenhouse conditions (GH) under polythene bags, in field artificially inoculated (AIF) with *P. capsici* culture at Department of Plant Pathology, University of

	Genotype	Pedigree/source	Institute
Genetic male sterile lines	A-132	*Forever F_1 / F_2 → F_8 (Sibbing pair A "FrA1")	Vegetable Research Institute, Ayub Agricultural Research Institute (AARI), Pakistan
	A-441	*Forever F_1 / F_2 → F_8 (Sibbing pair B "FrB1")	
	A-512	*(A3 × Sardar) F_1 / F_2 (Sib.1) → F_6	
Male fertile lines	Wiz-21	Local selection, registered with Federal Seed Certification and Registration Department (FSC&RD), Pakistan	
	Shahzadi	P6 F_1 / F_2 → F_8	
	VRI-YP	Selection, registered with Federal Seed Certification and Registration Department, Pakistan as "YP-M8"	
	Turkey-1	Quick Mirch F_1 / F_2 (P1) → F_8	
	Turkey-14	Registered with Federal Seed Certification and Registration Department, Pakistan as "VRIHP-03"	
	AVPP-0206	Germplasm collection	Asian Vegetable Research and Development Center, Taiwan
Standard	Golden Hot	East West Seeds, International	Imported and marketed by Haji Sons (Pvt.) Ltd. Pakistan

Table 1. Detail of parental lines and commercial check of *Capsicum annuum* L. used in the study.

Agriculture, Faisalabad and under natural field conditions (NC) with no artificial disease pressure at Vegetable Research Institute, Ayub Agricultural Research Institute, Faisalabad.

Inoculum preparation

P. capsici culture was used as a source of inoculum. To induce sporulation in *P. capsici*, a 10-days old culture plate was taken and flooded with autoclaved distilled water. Sterilized L-shaped spreading rod was used to dislodge sporangia from culture plate. To promote the release of zoospores from *P. capsici* culture, the prepared sporangial suspensions were incubated for 30–45 min at room temperature. Hemocytometer was used to quantify the zoospore suspension and diluted at a concentration of 1×10^6 zoospores/mL[49].

Screening in greenhouse

The purpose of this greenhouse experiment was to estimate the resistance level to Phytophthora root rot for selected chili germplasm under controlled conditions. A total of 28 genotypes, including six parental lines, eighteen F_1 crosses, and one standard hybrid cultivar "Golden Hot" were tested in this experiment. Seeds of each genotype were treated with a fungicide solution and sown in the seedling trays containing peat moss. Forty-five days old seedlings were taken, and roots were dipped in prepared inoculum of *P. capsici* for 30 s. After inoculation the treated seedlings and their controls (seedlings without inoculum treatment) were shifted into plastic bags containing sterilized soil with good nutrient profiles[49].

Experiment was conducted by using a randomized complete block design with three replications. Each plant was inoculated with 2 mL of zoospore suspension of *P. capsici* at a concentration of 1×10^6 zoospores/mL that was pipetted adjacent to the plant on the surface of the potting media. Plants were rated for incidence of mortality at multiple time points. Mortality was defined as total plant wilting or necrosis of all shoot tips. Ratings were recorded at 6 time points after a 7-days interval up to 42 days after inoculation (DAI).

Screening in artificially inoculated field

For the establishment of an inoculated field, two successive applications of prepared *P. capsici* inoculum with 10 days intervals were carried out on an area of 300 m^2 before transplanting the most susceptible varieties of chili pepper i.e., Desi and Maxi in the field. Before transplanting of these susceptible varieties, 35 days old seedlings were taken from the seedling trays with peat moss and dipped into the inoculum solution of *P. capsici* for 30 s and shifted into the already prepared inoculated field. After the establishment of characteristic symptom of root rot in inoculated field, the root samples were brought to the lab for the detection of *P. capsici*. After verification, the diseased plants were ploughed in the soil and irrigated to enhance the decomposition of plant debris and creating conditions for maximum *P. capsici* growth. Forty-five days old healthy seedlings of experimental genotypes were taken and shifted in inoculated field (Fig. 1). Experiment was conducted using randomized complete block design with three replications. Plants were rated for incidence of mortality at multiple time points. Ratings were recorded at 6 time points after a 7-days interval up to 42 days after inoculation (DAI).

Screening in natural field conditions

This field trial was conducted to record the level of resistance of experimental genotypes against *P. capsici* under natural field conditions without any artificial disease pressure. One commercial hybrid, 3 female, 6 male, and 18 F_1 entries were screened in this trial. Forty-five days old healthy seedlings were taken and shifted in field in a triplicated randomized complete block design. Plants were rated for incidence of mortality at multiple time points. Ratings were recorded at 6 time points after a 7-days interval up to 42 days after inoculation (DAI).

Data collection

Disease symptoms on chili plants were examined every 7 days of interval by using 0–5 disease rating scale. Disease incidence (DI) was calculated by using the following formula as described by Asghar et al.[50].

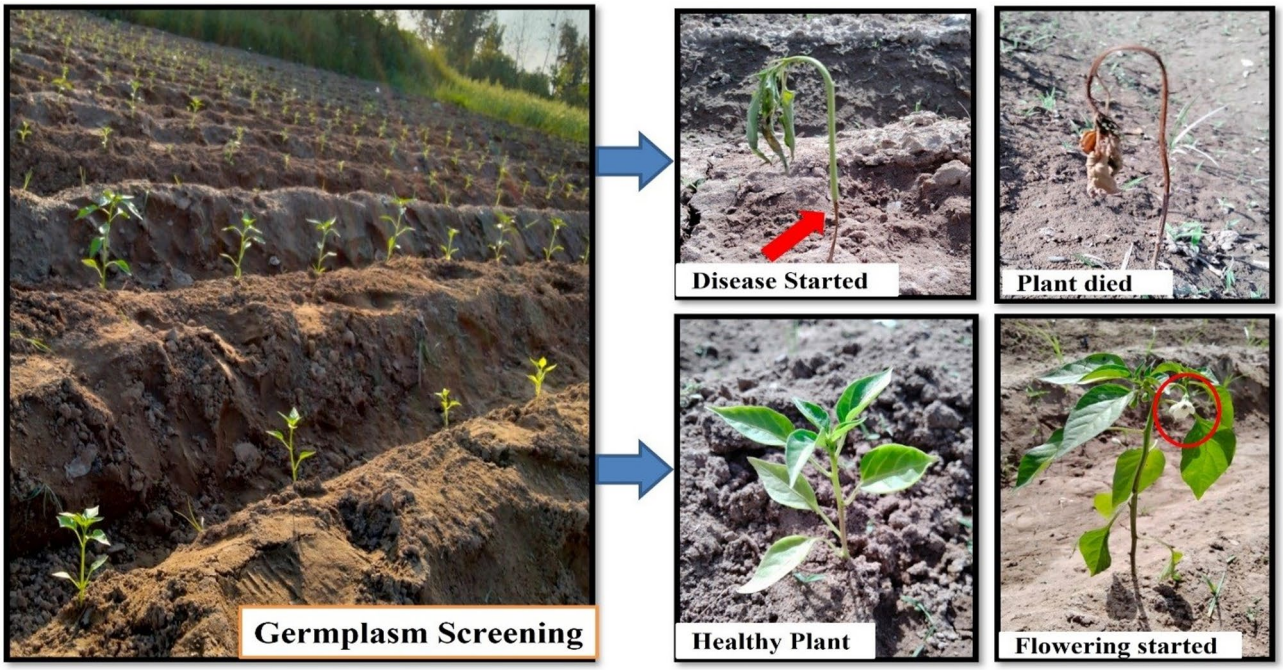

Fig. 1. Chili germplasm screening trial at *P. capsici* inoculated field showing, how disease progress in highly susceptible entries from wilting to complete plant death while resistant genotypes remain healthy (this is for visual demonstration of field symptoms, not the disease rating scale).

$$\text{Disease incidence } (\%) = \frac{\text{Number of infected plants}}{\text{Total number of plants}} \times 100$$

The genotypes were categorized based on disease incidence as follows: Resistant (R) with 1–9%, Moderately Resistant (MR) with 10–19%, Moderately Susceptible (MS) with 20–29%, Susceptible (S) with 30–39%, and Highly Susceptible (HS) with over 40% disease incidence.

Data on agronomic parameters and yield components were also recorded. Plant height and plant spread were measured at maturity using a measuring tape[51]. During peak flowering in the first week of May, 20 freshly opened flowers were tagged on each selected plant. A flower was considered to have set fruit if it remained intact on the plant 12 days after anthesis[52]. The fruit setting percentage was calculated as the ratio of set flowers to total tagged flowers, expressed as a percentage, using the following equation[52]:

$$\boldsymbol{Fruit\ setting\ percentage}\ (\%) = \frac{\boldsymbol{No.\ of\ set\ flowers}}{\boldsymbol{Total\ number\ of\ flowers\ tagged}} \times 100$$

Fruit parameters and yield were recorded following method described by Hong et al.[53] and Barchengar et al.[54]. Ten fresh red fruits were randomly picked and weighed to calculate the average fresh fruit weight (FFW) in grams. Fruit length (FL) in centimeters was measured with a measuring tape, and fruit width (FW) in millimeters was measured using a digital vernier caliper. These fruits were then sun-dried and weighed again to determine the dry fruit weight (DFW). The moisture content of the fruit (MCF) was calculated using the following equation:

$$\boldsymbol{Moisture\ contents\ of\ fruit}\ (\%) = \frac{\boldsymbol{Fresh\ fruit\ weight}\ (g) - \boldsymbol{Dry\ fruit\ weight}\ (g)}{\boldsymbol{Fresh\ fruit\ weight}\ (g)} \times 100$$

Fresh fruit pericarp thickness (FPT) and dry fruit pericarp thickness (DPT) were recorded and averaged from five randomly selected red fruits from three plants in each replication. Seeds were manually extracted from ten dry red fruits, counted, weighed, and averaged to calculate the number of seeds per fruit (SpF) and the thousand seed weight (TSW). To estimate yield (t/ha), fresh red fruits were harvested and weighed from each replication in two pickings: the first picking during the last week of May 2021, and the second picking during the last week of June 2021. The yield was extrapolated on replication area basis to calculate the fresh red fruit yield in tons per hectare (t/ha) using following formula[54].

$$Yield\ (t/ha) = \frac{plot\ yield\ (kg) \times 10000}{plot\ size\ (m^2) \times 1000}$$

Statistical analysis

Data was analyzed using line into tester analysis to estimate combining abilities of parental lines and their crosses[55] using procedure outlined by Nadarajan et al.[56] through TNAUSTAT-Statistical package[57]. Estimates of additive variance ((σ^2_A)) and dominance variance (σ^2_D) were calculated with inbreeding coefficient (F) value of 0. Degree of dominance was estimated using following equation described by Kumari et al.[58].

$$Degree\ of\ dominance = \left(\frac{2\sigma^2_D}{\sigma^2_A}\right)^{1/2}$$

RStudio[59] was used to make bar graphs of general and specific combining ability effects of parents and their crosses for *P. capsici* disease incidence under different screening conditions.

Commercial heterosis was calculated as described by[60]

$$Commercial\ heterosis = \frac{Hybrid\ performance - Standard\ performance}{Standard\ performance} \times 100$$

.

Golden Hot, a widely cultivated commercial hybrid in Punjab, Pakistan, was used as the standard check to estimate commercial heterosis.

Ethical compliance statement

No ethics approval was required as no wild or endangered plant species were studied and no formal herbarium voucher for the plant germplasm was deposited, as all lines were sourced from authenticated institutional breeding collections.

Results

Heatmap for agronomic traits and yield components

Mean performance of parental lines along with their crosses and standard cultivar are presented in Fig. 2A. Among the female parents, A-132 has the highest mean values for several parameters, including plant height (76.9 cm), plant spread (146.0 cm), fresh fruit weight (15.5 g), dry fruit weight (3.8 g), fruit setting percentage (74.0%), and number of seeds per fruit (109.7). On the other hand, A-512 has the highest mean values for fruit length (7.7 cm), moisture contents of fruit (88.4%), fresh pericarp thickness (1.5 mm), thousand seed weight (3.6 g), and yield (14.5t/ha).

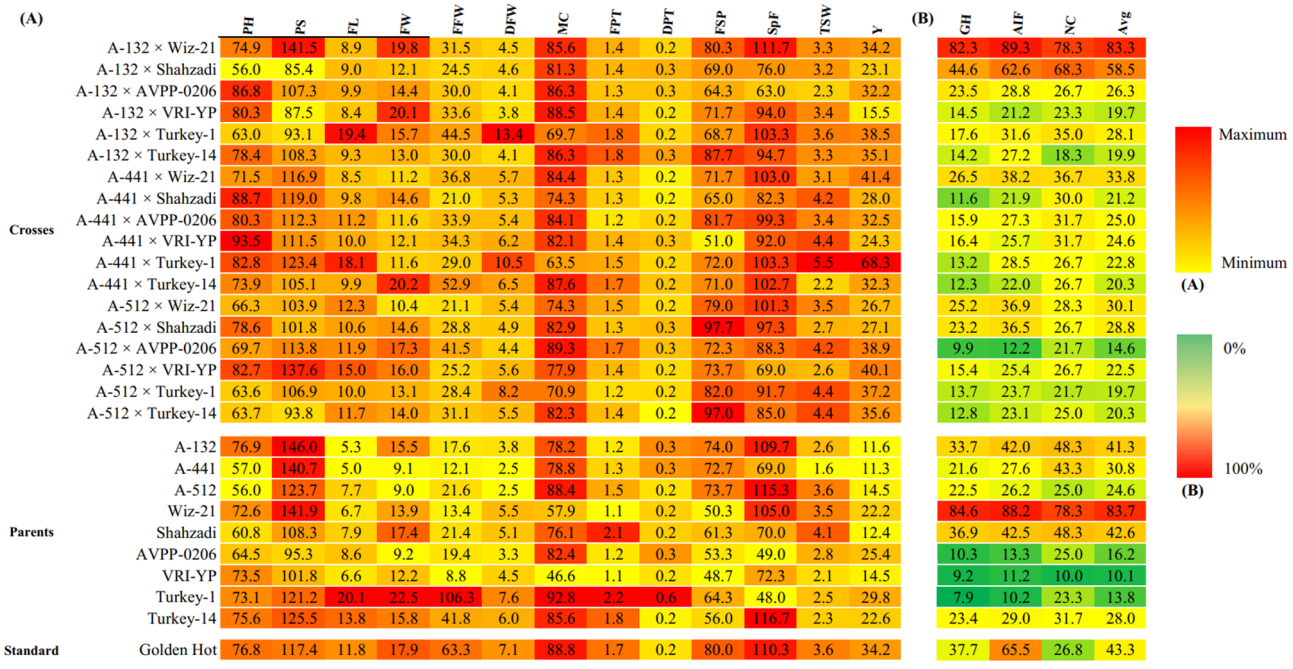

Fig. 2. Mean performance of chili parental lines and their crosses along with standard cultivar for (**A**) various agronomic parameters and yield components *PH* Plant height (cm), *PS* Plant spread (cm), *FL* Fruit length (cm), *FW* Fruit width (mm), *FFW* Fresh fruit weight red (g), *DFW* Dry fruit weight red (g), *MC* Moisture contents of fruit (%), *FPT* Fresh pericarp thickness red (mm), *DPT* Dry pericarp thickness red (mm), *FSP* Fruit setting percentage (%), *SpF* Number of seeds per fruit, *TSW* Thousand seed weight (g) and (**B**) disease incidence of *P. capsici* induce root rot under different screening conditions. *GH* Greenhouse conditions, *AIF* Artificially inoculated field conditions, *NC* Natural conditions, *Avg* Average disease incidence percentage.

Among the male parents, Wiz-21 stands out with the highest mean value for plant spread (141.9 cm). Shahzadi leads in thousand seed weight (4.1 g), while AVPP-0206 has the highest mean value for yield (25.4t/ha). eAmong the crosses, A-441 × VRI-YP has the highest mean value for plant height (93.5 cm), while A-512 × VRI-YP leads in plant spread (137.6 cm). The cross A-132 × Turkey-1 has the highest mean value for fruit length (19.4 cm), and A-132 × Wiz-21 leads in fruit width (19.8 mm). A-441 × Turkey-14 has the highest mean value for fresh fruit weight (52.9 g), and A-132 × Turkey-1 leads in dry fruit weight (13.4 g). A-512 × AVPP-0206 excels in moisture contents of fruit (89.3%). The crosses A-132 × Turkey-1 and A-132 × Turkey-14 share the highest mean value for fresh pericarp thickness (1.8 mm), while multiple crosses share the highest mean value for dry pericarp thickness (0.2 mm). A-512 × Shahzadi stands out with the highest mean values for fruit setting percentage (97.7%) and number of seeds per fruit (97.3). Finally, A-441 × Turkey-1 has the highest mean values for thousand seed weight (5.5 g) and yield (68.3t/ha).

Means heatmap for *P. capsici* disease incidence

The evaluation of *P. capsici* resistance across different screening conditions revealed distinct patterns of susceptibility and resistance among the genetic male sterile (GMS) lines, male fertile restorer lines, and their F_1 hybrids (Fig. 2B). The GMS line A-132 consistently exhibited high susceptibility, particularly under natural field conditions with a disease incidence of 48.3% and under artificial inoculation with 42.0%. In the greenhouse, it was categorized as susceptible with a 33.7% incidence. A-441 also showed high susceptibility in the natural field (43.3%) but was moderately susceptible in both greenhouse (21.6%) and artificial field conditions (27.6%). In contrast, A-512 was moderately susceptible in all environments, with incidences ranging from 22.5 to 25.0%.

Among the male fertile restorer lines, Wiz-21 was highly susceptible across all conditions, with incidences between 78.3% and 88.2%. Shahzadi mirrored this high susceptibility under field conditions but was slightly less affected in the greenhouse. AVPP-0206 demonstrated moderate resistance, particularly in the greenhouse (10.3%) and artificial field (13.3%), though it was moderately susceptible in the natural field (25.0%). VRI-YP consistently showed moderate resistance with low disease incidences. Turkey-1 varied from resistant in the greenhouse (7.9%) to moderately susceptible in the field. Turkey-14's response ranged from moderately susceptible to susceptible, depending on the environment.

The F1 hybrids displayed diverse responses, influenced by the resistance status of the parental lines. Hybrids of A-132 with Wiz-21 and Shahzadi were highly susceptible across all conditions, while crosses with AVPP-0206, VRI-YP, Turkey-1, and Turkey-14 showed moderate resistance to moderate susceptibility. Hybrids of A-441 generally exhibited moderate resistance to susceptibility, except when crossed with Wiz-21 and Shahzadi, which resulted in higher susceptibility. Hybrids of A-512 showed better resistance profiles when crossed with AVPP-0206, VRI-YP, Turkey-1, and Turkey-14, demonstrating moderate resistance to moderate susceptibility. The commercial hybrid Golden Hot was consistently susceptible, with incidences ranging from 26.8 to 65.5% across all conditions.

Analysis of variance for lines × testers including parents

Genotypic mean squares were highly significant for all agronomic and yield components while replication mean squares were non-significant for most traits except for plant spread, fresh fruit weight, number of seeds per fruit, thousand seed weight, and yield (Table 2). Mean squares for parents and crosses were significant for all traits, except for the crosses mean squares for dry pericarp thickness. Mean squares for lines were non-significant for fruit length and fruit setting percentage, whereas the testers' mean squares for plant height were non-significant. Additionally, for the interaction between crosses and parents, mean squares for fruit width and fresh fruit pericarp thickness were non-significant.

The analysis of variance for disease incidence of *P. capsici* in chili under various screening conditions revealed significant genetic variability among genotypes, parents, crosses, lines, and testers (Table 3). Replication mean squares were non-significant across all conditions (greenhouse (GH), artificially inoculated field (AIF), natural conditions (NC), and average disease incidence (Avg)). Genotypes, parents and crosses exhibited highly significant mean squares for all conditions, reflecting substantial genetic variation for disease incidence. The interaction between lines and testers was significant only under GH conditions, Comparing crosses to parents revealed highly significant differences in GH and Avg conditions, significant differences in NC, but non-significant differences in AIF, indicating varying responses depending on the environment.

Analysis of variance for combining ability

The traits for which the mean squares were highly significant for lines, testers, and their interactions include plant height (PH), plant spread (PS), fresh fruit weight (FFW), moisture content of fruit (MCF), thousand seed weight (TSW), and yield (Table 2). For these traits, lines, testers and their interaction have significant contribution towards total variance of crosses. This indicates that both additive and non-additive gene actions are important for the inheritance of these traits. For fruit length (FL) and fruit width (FW), the significance was observed in testers and interaction components, but not in lines. For fresh pericarp thickness (FPT), only lines and testers were significant, while interaction was not."

In case of dry fruit pericarp thickness, mean squares for both lines and their interaction with testers were significant,. Likewise, for dry fruit weight, only the mean squares for testers were significant,.

The combining ability analysis showed significant contributions from lines, testers, and their interactions to the total variance of crosses for disease incidence (Table 3), with lines contributing 21.6–21.3%, testers 44.3–42.5%, and lines × tester interactions 34.1–36.2%. These findings suggest both additive and non-additive gene actions are important for the inheritance of *P. capsici* disease incidence in chili.

Analysis of variance for lines × testers including parents														
Source of variance	**d.f**	**PH**	**PS**	**FL**	**FW**	**FFW**	**DFW**	**MCF**	**FPT**	**DPT**	**FSP**	**SpF**	**TSW**	**Yield**
Replication	2	30.4	75.8**	2.4	3.7	24.0*	0.5	8.7	0	0	0	46.8**	0.6**	2.5*
Genotypes	26	303.3**	876.1**	45.1**	38.3**	989.6**	16.0**	322.5**	0.2**	0.5**	481.1**	1093.0**	2.4**	446.8**
Crosses (C)	17	308.7**	686.3**	30.1**	29.1*	194.5**	18.2**	160.0**	0.1**	0.1	391.1**	501.3**	2.2**	356.9**
Parents	8	204.1**	990.4**	71.2**	61.4**	2782.8**	8.6**	665.9**	0.6**	0.1**	308.7**	2335.0**	1.9**	139.7**
Lines (P)	2	418.3**	408.1**	6.7	41.4**	69.2**	1.6**	97.9**	0.1**	0.0**	1.4	1916.3**	3.0**	9.5**
Tester (P)	5	105.2	886.3**	85.9**	62.8**	4032.2**	6.3**	944.4**	0.8**	0.1**	114.1**	2431.8**	1.8**	129.0**
Lines (P) vs. tester (P)	1	269.8**	2675.5**	126.7**	94.7**	1963.2**	34.4**	409.5**	0.4**	0	1896.3**	2688.2**	0.6	454.**
Crosses vs. parents	1	1006.5**	3188.5**	91.6**	8.6	161.4**	39.4**	338.3**	0	0.1**	3389.4**	1216.9**	10.4**	4432.6**
Error	52	29.5	15.8	4.7	8.1	7	0.2	15.4	0	0	14.2	12.7	0.2	0.7
Analysis of variance for combining ability														
Line (C)	2	601.5** (22.9%)	531.6** (9.1%)	5.9 (2.3%)	25.2 (10.2%)	125.6** (7.6%)	4.9 (3.2%)	72.5** (5.3%)	0.09 (11.4%)	0.006** (18%)	1036.7** (31.2%)	350.0** (8.2%)	2 (10.8%)	290.5** (9.6%)
Tester (C)	5	321.7** (30.7%)	443.2** (18.9%)	46.7** (45.7%)	11.1 (11.2%)	195.3** (29.5%)	48.8** (79.1%)	402.2** (73.9%)	0.08 (26.9%)	0.001 (9.3%)	377.4** (28.4%)	726.9** (42.7%)	2 (27.3%)	563.3** (46.4%)
Lines × tester (C)	10	243.6** (46.4%)	838.7** (71.9%)	26.6** (52%)	38.9** (78.6%)	207.9** (62.9%)	5.5 (17.7%)	56.3* (20.7%)	0.09 (61.6%)	0.005** (72.7%)	268.8** (40.4%)	418.8** (49.1%)	2.3 (61.9%)	266.9** (44%)
Error	34	24.6	16.5	6	8.3	7.3	0.2	5	0	0.003	15	13.4	0.1	0.7

Table 2. Analysis of variance for various agronomic characters and yield components in chilies under natural field conditions. *Significance at $P \leq 5\%$, ** Significance at $P \leq 1\%$, *d.f* Degree of freedom, *PH* Plant height (cm), *PS* Plant spread (cm), *FL* Fruit length (cm), *FW* Fruit width (mm), *FFW* Fresh fruit weight red (g), *DFW* Dry fruit weight red (g), *MCF* Moisture contents of fruit (%), *FPT* Fresh pericarp thickness red (mm), *DPT* Dry pericarp thickness red (mm), *FSP* Fruit setting percentage (%), *SpF* Number of seeds per fruit, *TSW* Thousand seed weight (g). Values in parenthesis are percent contribution of lines, testers and lines × testers interaction to total crosses variance.

Analysis of variance for lines × testers including parents					
Source of variance	**d.f**	**GH**	**AIF**	**NC**	**Avg**
Replication	2	3.6	49.5	16	11.6
Genotypes	26	1118.4**	1155.5**	870.6**	1006.8**
Crosses (C)	17	883.1**	938.9**	737.5**	820.2**
Parents	8	1678.3**	1759.9**	1214.1**	1501.7**
Lines (P)	2	135.5**	229.9**	452.8**	215.7**
Tester (P)	5	2621.9**	2723.7**	1752.2**	2316.4**
Lines (P) vs. Tester (P)	1	45.9*	1.4	46.3	0.2
Crosses vs. parents	1	638.2**	0.1	385.8*	220.5**
Error	52	2.8	7.6	85.9	10.7
Analysis of variance for combining ability					
Line (C)	2	1621.2* (21.6%)	1667.6** (20.9%)	1296.3** (20.7%)	1487.4** (21.3%)
Tester (C)	5	1328.9* (44.3%)	1471.6** (46.1%)	874.1** (34.9%)	1184.6** (42.5%)
Lines × tester (C)	10	512.6* (34.1%)	526.9** (33%)	557.4** (44.5%)	504.5** (36.2%)
Error	34	3.2	6.9	84.6	11

Table 3. Analysis of variance for disease incidence of *P. capsici* in chilies under various screening conditions. *Significance at $P \leq 5\%$, ** Significance at $P \leq 1\%$, *d.f* Degree of freedom, *GH* Greenhouse conditions, *AIF* Artificially inoculated field conditions, *NC* Natural field conditions, *Avg* Average disease incidence percentage.

Lines	PH	PS	FL	FW	FFW	DFW	MCF	FPT	DPT	FSP	SpF	TSW	Yield
A-132	− 2.01	− 5.6**	− 0.5	1.3	0.2ns	− 0.3*	2.3**	0.1*	0.02	− 1.7	− 1.7	− 0.4**	− 4.2**
A-441	6.5**	5.3**	− 0.1	− 1	2.5**	0.6**	− 1.3*	− 0.05	− 0.01	− 6.6**	5.0**	0.3**	3.9**
A-512	− 4.5**	0.2	0.6	− 0.3	− 2.8**	− 0.4**	− 1.0	− 0.03	− 0.01	8.3**	− 3.3**	0.1	0.3
Testers													
Wiz-21	− 4.4*	11.4**	− 1.4	− 0.7	− 2.3*	− 0.8**	0.8	− 0.05	− 0.02	1.7	13.2**	− 0.3	0.2
Shahzadi	− 0.9	− 7.3**	− 1.5	− 0.8	− 7.4**	− 1.1**	− 1.1	− 0.1*	0	1.9	− 6.9**	− 0.2	− 7.9**
AVPP-0206	3.7*	1.7	− 0.3	− 0.1	3.0**	− 1.4**	5.9**	− 0.02	0.01	− 2.5	− 8.6**	− 0.2	0.6*
VRI-YP	10.2**	2.8*	− 0.2	1.5	− 1.1	− 0.8**	2.2**	− 0.02	0	− 9.9**	− 7.1**	− 0.1	− 7.3**
Turkey-1	− 5.6**	− 1.6	4.5**	− 1.1	1.9*	4.7**	− 12.6**	0.03	− 0.01	− 1.1	7.3**	0.9**	14.0**
Turkey-14	− 3.3	− 7.0**	− 1.0	1.2	5.9**	− 0.6**	4.8**	0.2**	0	9.9**	2	− 0.2	0.4

Table 4. General combining ability effects of genetic male sterile lines and male fertile testers for various agronomic characters and yield components. *Significance at $P \leq 5\%$, ** Significance at $P \leq 1\%$, *PH* Plant height (cm), *PS* Plant spread (cm), *FL* Fruit length (cm), *FW* Fruit width (mm), *FFW* Fresh fruit weight red (g), *DFW* Dry fruit weight red (g), *MCF* Moisture contents of fruit (%), *FPT* Fresh pericarp thickness red (mm), *DPT* Dry pericarp thickness red (mm), *FSP* Fruit setting percentage (%), *SpF* Number of seeds per fruit, *TSW* Thousand seed weight (g).

GCA effects for agronomic and yield components

Among the genetic male sterile female lines, A-132 exhibited significant positive GCA effects for moisture contents of fruit and fresh fruit pericarp thickness whereas significant negative GCA effects for plant spread, dry fruit weight, thousand seed weight and yield (Table 4). Conversely, A-441 has significant positive GCA effects for plant height, plant spread, fresh fruit weight, dry fruit weight, number of seeds per fruit, thousand seed weight and yield with notable negative GCA effects for moisture contents of fruits and fruit setting percentage. A-512 displayed significant positive GCA effects for fruit setting percentage alongside negative effects for plant height, fresh fruit weight red, dry fruit weight red and number of seeds per fruit.

Among the male fertile tester genotypes, Wiz-21 exhibited significant positive GCA effects for plant spread and number of seeds per fruit, while showing negative effects for plant height, fresh fruit weight and dry fruit weight. Shahzadi, in contrast, displayed significant negative GCA effects for plant spread, fresh fruit weight red, dry fruit weight red, fresh fruit pericarp thickness, number of seeds per fruit, and yield. AVPP-0206 showcased significant positive GCA effects for plant height, fresh fruit weight red, moisture contents of fruit, and yield, but negative effects for dry fruit weight and number of seeds per fruit. VRI-YP demonstrated significant positive GCA effects for plant height, plant spread and moisture contents of fruit with significant negative GCA effects for dry fruit weight, fruit setting percentage, number of seeds per fruit and yield. Turkey-1 displayed significant positive GCA effects for fruit length, fresh fruit weight, dry fruit weight, number of seeds per fruit, thousand seed weight and yield along with significant negative GCA effects for plant height and moisture contents of fruits. Turkey-14 exhibited significant positive GCA effects fresh fruit weight, moisture contents of fruit, fresh

fruit pericarp thickness and fruit setting percentage while notable negative GCA effects for plant spread and dry fruit weight.

General combining ability effects for *P. capsici* disease incidence

Figure 3 presents the general combining ability (GCA) effects of parental genotypes of chili for disease incidence of *P. capsici* under three screening conditions: Greenhouse (GH), Artificially infected soil (AIF), and Natural conditions (NC), as well as the average disease incidence (Avg). Among the female parents, A-132 exhibited the highest significant positive GCA effects for disease incidence across all conditions, with values of 10.9** (GH), 11.1** (AIF), 9.33** (NC), and 10.4** (Avg). Conversely, A-512 showed the lowest significant negative GCA effects, with values of − 5.1** (GH), − 6** (AIF), − 7.4** (NC), and − 6.2** (Avg). Among the male parents, Wiz-21 demonstrated the highest significant positive GCA effects for disease incidence under all conditions, with values of 22.8** (GH), 22.5** (AIF), 15.4** (NC), and 20.3** (Avg). In contrast, Turkey-14 exhibited the lowest significant negative GCA effects, with values of − 8.7** (GH), − 8.2** (AIF), − 9** (NC), and − 8.7** (Avg). These results highlight the potential of A-512 and Turkey-14 for breeding programs aimed at reducing disease incidence of *P. capsici* in chili, while A-132 and Wiz-21 represent genotypes with notable susceptibility across the tested conditions.

Specific combining ability effects for agronomic and yield components

The specific combining ability (SCA) effects of chili hybrids for various agronomic traits and yield components are presented in Table 5. A-132 × Wiz-21 displayed significant positive SCA effects for plant height, plant spread, fruit weight, fruit setting percentage, number of seeds per fruit, and yield, without any negative SCA effects. Conversely, A-132 × Shahzadi had significant negative SCA effects for plant height, plant spread, fruit setting percentage, and the number of seeds per fruit, but a significant positive SCA effect for yield. Similarly, A-132 × AVPP-0206 showed significant positive SCA effects for plant height and yield, with significant negative SCA effects for fresh fruit weight, fruit setting percentage, number of seeds per fruit, and thousand seed weight. The hybrid A-132 × VRI-YP exhibited positive SCA effects for moisture content of fruit, fruit setting percentage, and the number of seeds per fruit, but had significant negative SCA effects for plant spread, dry fruit weight, and yield. A-132 × Turkey-1 demonstrated positive SCA effects for fruit length, fresh fruit weight, dry fruit weight, and the number of seeds per fruit, but had negative SCA effects for plant spread, thousand seed weight, and yield. A-132 × Turkey-14 showed positive SCA effects for plant height, plant spread, dry pericarp thickness, and yield, with negative SCA effects for fruit width, fresh fruit weight, and dry fruit weight.

For A-441 × Wiz-21, significant positive SCA effects were recorded for fresh fruit weight, moisture content of fruit, and yield, while plant height, plant spread, the number of seeds per fruit, and thousand seed weight had negative SCA effects. A-441 × Shahzadi showed positive SCA effects for plant height, plant spread, and thousand

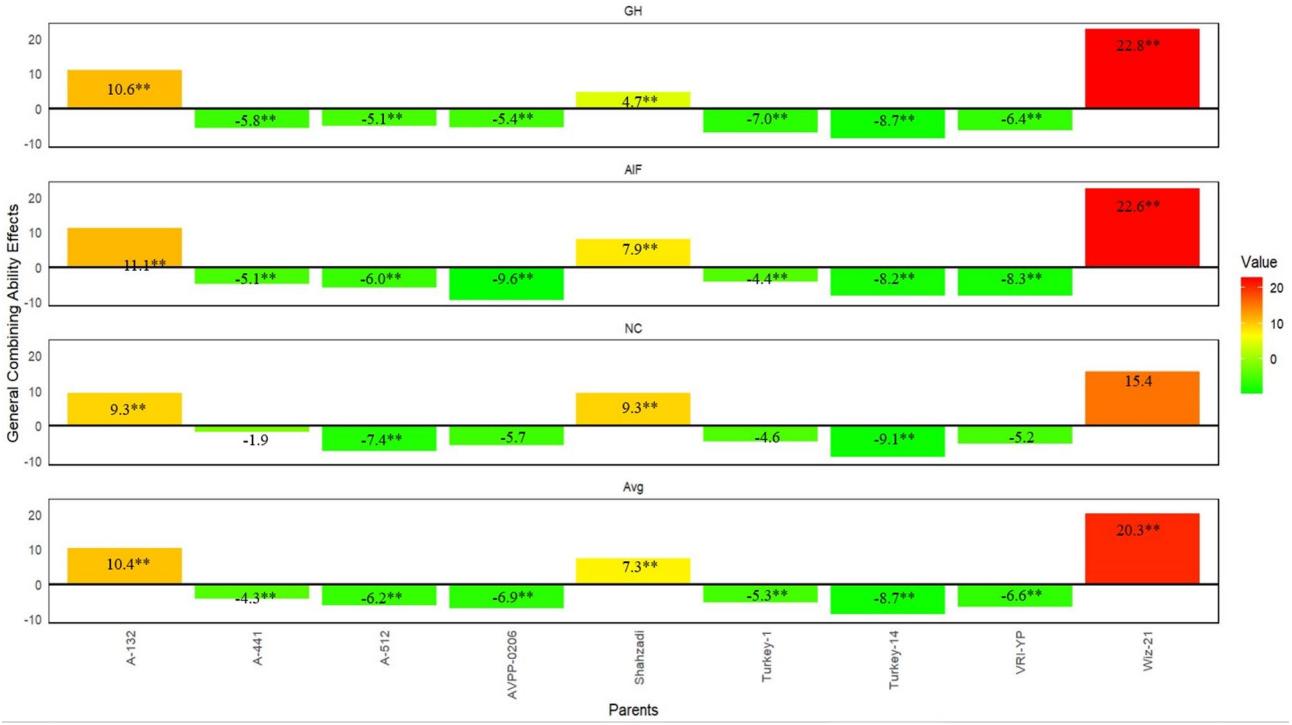

Fig. 3. General combining ability (GCA) effects of parental genotypes of chili for *P. capsici* induce root rot disease incidence under different screening conditions. *GH* Greenhouse conditions, *AIF* Artificially inoculated field conditions, *NC* Natural field conditions, *Avg* Average disease incidence percentage. *Significance at $P \leq 5\%$, **Significance at $P \leq 1\%$.

Crosses	PH	PS	FL	FW	FFW	DFW	MCF	FPT	DPT	FSP	SpF	TSW	Yield
A-132 × Wiz-21	5.9*	26.3**	− 0.5	4.7**	1.5	− 0.5	1.8	− 0.1	− 0.01	5.0*	8.0**	0.4	4.3**
A-132 × Shahzadi	− 16.4**	− 11.1**	− 0.3	− 2.9	− 0.5	− 0.1	− 0.6	− 0.03	0	− 6.5**	− 7.6**	0.2	1.2*
A-132 × AVPP-0206	9.9**	1.7	− 0.6	− 1.4	− 5.4**	− 0.3	− 2.6	− 0.2	− 0.01	− 6.7**	− 18.9**	− 0.7**	1.8**
A-132 × VRI-YP	− 3.2	− 19.2**	− 2.3	2.7	2.3	− 1.1**	3.4*	− 0.1	− 0.03	7.9**	10.7**	0.3	− 6.9**
A-132 × Turkey-1	− 4.8	− 9.2**	4.1**	0.9	10.3**	2.9**	− 0.6	0.2	− 0.02	− 3.9	5.6*	− 0.5*	− 5.3**
A-132 × Turkey-14	8.4**	11.5**	− 0.5	− 4.0*	− 8.2**	− 1.0**	− 1.4	0.1	0.1*	4.2	2.2	0.4	4.9**
A-441 × Wiz-21	− 5.9*	− 9.2**	− 1.3	− 1.6	4.5**	− 0.1	4.3**	− 0.03	− 0.01	1.3	− 7.3**	− 0.5*	3.4**
A-441 × Shahzadi	7.8**	11.6**	0.1	1.8	− 6.3**	− 0.2	− 3.9**	0.01	− 0.03	− 5.6*	− 7.9**	0.6*	− 1.9**
A-441 × AVPP-0206	− 5.1	− 4.1	0.3	− 1.8	− 3.8*	0.1	− 1.2	− 0.2*	− 0.01	15.5**	10.8**	− 0.2	− 5.9**
A-441 × VRI-YP	1.5	− 5.9*	− 1.0	− 2.9	0.8	0.4	0.6	0.1	0.04	− 7.9**	2.0	0.7**	− 6.2**
A-441 × Turkey-1	6.5*	10.3**	2.4	− 0.9	− 7.5**	− 0.8**	− 3.2*	0.03	0.01	4.4	− 1.1	0.7**	16.4**
A-441 × Turkey-14	− 4.7	− 2.6	− 0.3	5.5**	12.3**	0.6*	3.5**	0.1	0	− 7.6**	3.6	− 1.4**	− 5.9**
A-512 × Wiz-21	− 0.1	− 17.1**	1.8	− 3.1	− 5.9**	0.5	− 6.1**	0.1	0.02	− 6.3**	− 0.7	0.1	− 7.7**
A-512 × Shahzadi	8.7**	− 0.6	0.2	1.1	6.8**	0.3	4.5**	0.02	0.03	12.2**	15.4**	− 0.7**	0.7
A-512 × AVPP-0206	− 4.8	2.4	0.3	3.2	9.2**	0.2	3.8**	0.3**	0.02	− 8.7**	8.1**	0.8**	4.1**
A-512 × VRI-YP	1.7	25.2**	3.3*	0.3	− 3.1	0.7**	− 3.9**	0	0	− 0.1	− 12.7**	− 0.9**	13.1**
A-512 × Turkey-1	− 1.7	− 1.1	− 6.5**	− 0.02	− 2.8	− 2.1**	3.9**	− 0.2*	0.01	− 0.5	− 4.4*	− 0.2	− 11.1**
A-512 × Turkey-14	− 3.8	− 8.8**	0.8	− 1.4	− 4.1*	0.5	− 2.1	− 0.2**	− 0.1*	3.5	− 5.8**	0.9**	0.9

Table 5. Specific combining ability effects of crosses among genetic male sterile lines and male fertile testers for various agronomic characters and yield components. * Significance at $P \leq 5\%$, ** Significance at $P \leq 1\%$, *PH* Plant height (cm), *PS* Plant spread (cm), *FL* Fruit length (cm), *FW* Fruit width (mm), *FFW* Fresh fruit weight red (g), *DFW* Dry fruit weight red (g), *MCF* Moisture contents of fruit (%), *FPT* Fresh pericarp thickness red (mm), *DPT* Dry pericarp thickness red (mm), *FSP* Fruit setting percentage (%), *SpF* Number of seeds per fruit, *TSW* Thousand seed weight (g).

seed weight, but negative effects for fresh fruit weight, moisture content of fruit, fruit setting percentage, number of seeds per fruit, and yield. A-441 × AVPP-0206 had positive SCA effects for fruit setting percentage and the number of seeds per fruit, with negative effects for fresh fruit weight, fresh red fruit pericarp thickness, and yield. Conversely, A-441 × VRI-YP exhibited negative SCA effects for plant spread, fruit setting percentage, and yield, with positive effects only for thousand seed weight. A-441 × Turkey-1 had positive SCA effects for plant height, plant spread, thousand seed weight, and yield, but negative effects for fresh fruit weight, dry fruit weight, and moisture content of fruit. Similarly, A-441 × Turkey-14 showed positive SCA effects for fruit width, fresh fruit weight, dry fruit weight, and moisture content of fruit, with negative effects for fruit setting percentage, thousand seed weight, and yield.

For A-512 × Wiz-21, significant negative SCA effects were observed for plant spread, fresh fruit weight, moisture content of fruit, fruit setting percentage, and yield, with no positive SCA effects. A-512 × Shahzadi exhibited positive SCA effects for plant height, fresh fruit weight, moisture content of fruit, fruit setting percentage, and the number of seeds per fruit, but negative effects for thousand seed weight. A-512 × AVPP-0206 had positive SCA effects for fresh fruit weight, moisture content of fruit, fresh red fruit pericarp thickness, the number of seeds per fruit, thousand seed weight, and yield, with negative effects only for fruit setting percentage. A-512 × VRI-YP showed positive SCA effects for plant spread, fruit length, dry fruit weight, and yield, with negative effects for moisture content of fruit, the number of seeds per fruit, and thousand seed weight. A-512 × Turkey-1 had positive SCA effects only for moisture content of fruit, with negative effects for fruit length, dry fruit weight, the number of seeds per fruit, and yield. A-512 × Turkey-14 exhibited positive SCA effects only for thousand seed weight, with negative effects for plant spread, fresh fruit weight, fresh red fruit pericarp thickness, dry red fruit pericarp thickness, and the number of seeds per fruit. These hybrids, distinguished by their significant positive SCA effects across multiple traits, signify their potential for enhancing agronomic performance and yield in chili hybrid breeding programs.

Specific combining ability effects for *P. capsici* disease incidence

The specific combining ability (SCA) effects of crosses among genetic male sterile lines and male fertile testers for disease incidence of *P. capsici* in chili under various screening conditions are summarized in Fig. 4. These effects provide insights into the performance of different hybrid combinations in response to varying degree of disease pressure.

Under greenhouse conditions, all crosses had significant SCA effects except A-512 × AVPP-0206. Significant negative SCA effects were observed in A-512 × Wiz-21 (− 14.00**), A-441 × Wiz-21 (− 12.3**), A-132 ×VRI-YP (− 11.9**), A-132 × Turkey-14 (− 9.9**), A441 × Shahzadi (− 9.0**), A-132 × Turkey-1 (− 8.2**) and A-132 × AVPP-0206 (− 3.9**). Similarly, significant negative SCA effects were predominant under artificially inoculated field condition. Hybrids such as A-132 × AVPP-0206 (− 5.0**), A-132 × VRI-YP (− 14.0**), A-132 × Turkey-1 (− 7.4**), A-132 × Turkey-14 (− 8.0**), A-441 × Wiz-21 (− 11.6**), A-441 × Shahzadi (− 13.2**), A-512 × Wiz-21 (− 12.0**) and A-512 × AVPP-0206 (− 4.5**) exhibited notable negative SCA effects while all other crosses

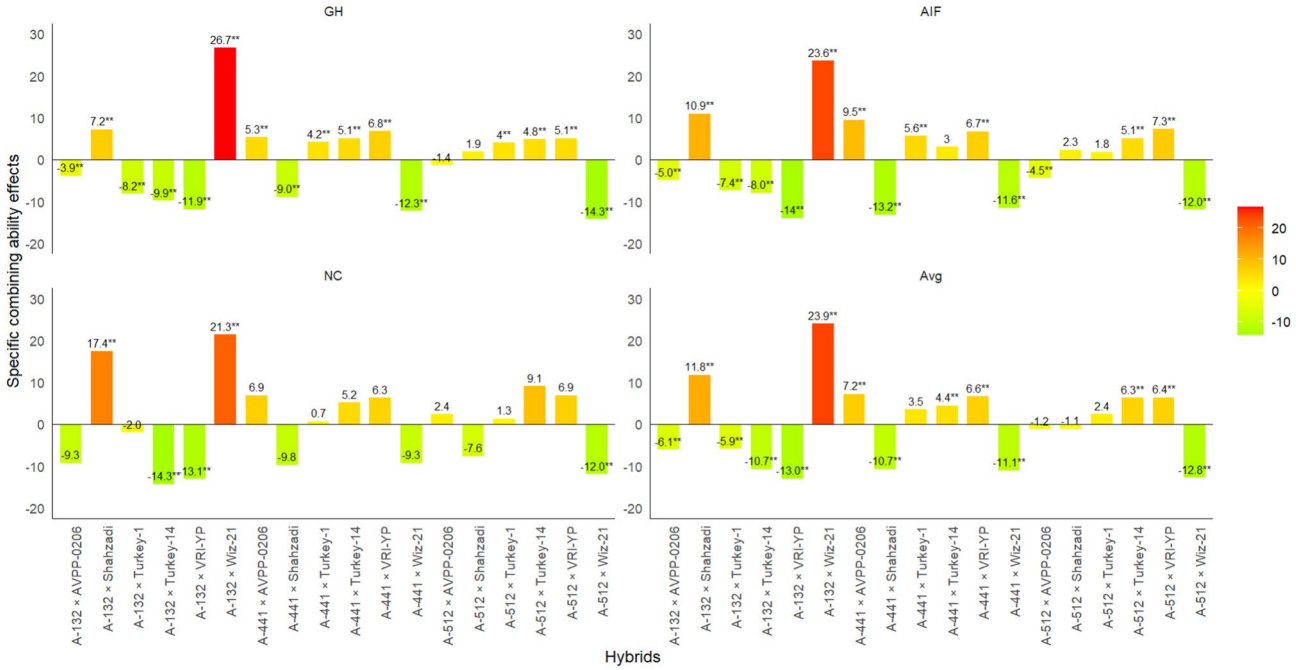

Fig. 4. Specific combining ability (SCA) effects chili crosses for *P. capsici* induce root rot disease incidence under different screening conditions. *GH* Greenhouse conditions, *AIF* Artificially inoculated field conditions, *NC* Natural field conditions, *Avg* Average disease incidence percentage. *Significance at $P \leq 5\%$, ** Significance at $P \leq 1\%$.

had significant positive SCA effects. Under natural disease pressure, key hybrids with significant negative SCA effects include A-132 × VRI-YP (– 13.1**), A-132 × Turkey-14 (v14.3**) and A-512 × Wiz-21 (– 12.8**) whereas significant positive SCA effects were recorded in A-132 × Wiz-21 (21.3**) and A-132 × Shahzadi (17.4**). Across screening conditions, hybrids with consistent significant negative SCA effects include A-132 × VRI-YP (– 13.0**), A-132 × Turkey-14 (– 10.7**) and A-512 × Wiz-21 (– 12.8**). Conversely, hybrids, A-132 × AVPP-0206, A-132 × Turkey-1, A-441 × Wiz-21 and A-441 × Shahzadi had significant negative SCA effects under greenhouse and artificially infected soil with non-significant negative SCA effects under natural field conditions but significant negative SCA effects on average. Overall, the results suggest that specific crosses exhibit significant negative SCA effects, indicating reduced disease incidence across various screening conditions. These findings highlight the potential of certain hybrids to mitigate *P. capsici* infection in chili crops, offering valuable insights for disease-resistant breeding programs.

Estimation of genetic parameters

The Table 6 presents genetic parameters related to various plant traits, providing insights into their genetic control through the degree of dominance. For traits like dry fruit weight and moisture contents of fruit, the degree of dominance is moderate (around 3), indicating that both additive and non-additive genetic variances contribute significantly to trait expression. Low degrees of dominance suggest that additive effects are more significant, allowing effective selection based on parent line performance. Traits such as fruit setting percentage, plant height, fruit width, yield, and dry fruit pericarp thickness show strong dominance levels, with degrees of dominance ranging between 6 and 10. This suggests that heterozygous combinations significantly influence these traits more than additive effects alone. High degrees of dominance indicate that non-additive effects are substantial, requiring consideration of specific parent combinations for breeding. For plant spread, fruit length, fresh fruit weight, fresh fruit pericarp thickness, number of seeds per fruit, and thousand seeds weight, the degree of dominance is exceptionally high, exceeding 10. This indicates that non-additive genetic effects, such as dominance or overdominance, are the primary drivers of trait expression, implying that heterozygous combinations greatly surpass both homozygous parents for these traits. Very high degrees of dominance suggest that hybrid vigor might be a significant factor, benefiting from hybrid breeding programs to fully exploit these dominance effects.

Regarding *P. capsici* disease incidence in chili under various screening conditions, the table showed that the degree of dominance varies depending on the screening environment. Under greenhouse conditions, the degree of dominance is 5.53, indicating that non-additive genetic effects play a significant role, but additive effects are also important. This conclusion is supported by the consistently low σ^2A/σ^2D ratios across environments; 0.07 (greenhouse), 0.07 (green house), and 0.03 (natural field), indicating a predominant role of dominance variance over additive variance. The GCA variances (Cov. H.S Avg) were relatively low across conditions: 11.11, 12.35, and 5.40, while the SCA variances (Cov. F.S) were much higher: 372.57, 392.70, and 269.48, respectively. Under all three screening environments, the full-sib covariances (Cov. F.S) were substantially higher than the half-sib

Parameters	Cov. H.S (line)	Cov. H.S (tester)	Cov. H.S (average)	Cov. F.S	σ^2_A	σ^2_D	σ^2_A / σ^2_D	Degree of dominance
Agronomic and yield parameters								
Plant height	19.88	8.67	1.95	119.49	7.81	291.99	0.03	8.65
Plant spread	17.06	43.95	4.57	200.57	18.29	1096.29	0.02	10.95
Fruit length	1.15	2.24	0.1	0.7	0.42	27.45	0.02	11.43
Fruit width	0.77	3.09	0.29	5.9	1.18	40.89	0.03	8.32
Fresh fruit weight	4.57	1.4	0.4	56.72	1.6	267.47	0.01	18.28
Dry fruit weight	0.03	4.81	0.38	6.12	1.52	6.99	0.22	3.03
Moisture contents of fruit	0.9	38.43	3.11	54.22	12.42	68.38	0.18	3.32
Fresh fruit pericarp thickness	0.0004	0.001	0.0001	0.02	0.0005	0.1	0.01	20.00
Dry fruit pericarp thickness	0.0001	0.0004	0	0.0004	0.0001	0.003	0.03	7.75
Fruit setting percentage	42.67	12.07	3.67	178.33	14.67	338.41	0.04	6.79
Number of seeds per fruit	3.82	34.24	2.48	159.25	9.9	540.49	0.02	10.45
Thousand seeds weight	0.02	0.03	0.003	0.66	0.01	2.85	0.00	23.87
Yield	1.31	32.93	2.7	121.61	10.79	355.01	0.03	8.11
P. capsici disease incidence								
Green house conditions	61.59	90.70	11.11	372.57	44.44	679.19	0.07	5.53
Artificially inoculated field conditions	63.37	104.97	12.35	392.70	49.42	693.37	0.07	5.30
Natural field conditions	41.05	35.19	5.40	269.48	21.60	630.39	0.03	7.64
Average	54.61	75.57	9.47	339.82	37.86	657.96	0.06	5.90

Table 6. Gene action governing inheritance of various agronomic and yield components and *P. capsici* disease incidence in chili. *Cov* Covariance, *H.S* Half sib, *F.S* Full sib, σ^2_A Additive variance, σ^2_D Dominance variance.

covariances (Cov. H.S), for instance, under greenhouse conditions, Cov. F.S was 372.57 while Cov. H.S was only 11.11. This large difference indicates that dominance variance is the major contributor to the inheritance of disease resistance. However, the non-zero values of Cov. H.S also confirm that additive genetic variance plays a minor but significant role, implying that both types of gene actions (additive and non-additive) are involved in governing resistance to *P. capsici*.

Estimation of commercial heterosis

The Table 7 presents the commercial heterosis of 18 chili crosses for various agronomic and yield components and *P. capsici* disease incidence, compared to the standard commercial hybrid "Golden Hot." In terms of plant height, the highest positive and significant commercial heterosis was exhibited by A-441 × VRI-YP, followed by A-441 × Shahzadi and A-132 × AVPP-0206, while negative significant heterosis was found in hybrids A-132 × Shahzadi, A-132 × Turkey-1, A-512 × Turkey-1, A-512 × Turkey-14, and A-512 × Wiz-21. Plant spread showed positive significant heterosis in A-132 × Wiz-21 and A-512 × VRI-YP, with most of the crosses exhibiting significant negative heterosis, including A-132 × Shahzadi and A-132 × VRI-YP. For fruit length, A-132 × Turkey-1 and A-441 × Turkey-1 showed positive significant heterosis, whereas several crosses displayed negative but non-significant heterosis, such as A-441 × Wiz-21 and A-132 × VRI-YP. Fruit width predominantly exhibited negative heterosis, with eight hybrids having significant negative commercial heterosis of which A-512 × Wiz-21 and A-441 × Wiz-21 showing maximum reductions. In case of fresh fruit weight, all the hybrids had significant negative commercial heterosis whereas dry fruit weight also generally showed negative significant heterosis, with notable decreases in crosses like A-132 × VRI-YP and A-132 × AVPP-0206 whereas A-132 × Turkey-1 and A-441 × Turkey-1 had significant positive commercial heterosis for dry fruit weight. Moisture content of fruit demonstrated negative significant heterosis in several crosses, including A-441 × Turkey-1 and A-132 × Turkey-1. In terms of fresh pericarp thickness, none of hybrids displayed notable positive heterosis. Conversely, nine hybrids exhibited significant negative heterosis, with the hybrid A-441 × AVPP-0206 showing the most pronounced negative heterosis, suggesting thinner pericarps in these crosses. Regarding dry pericarp thickness, seventeen out of eighteen hybrids had positive heterotic values with only one hybrid, A-132 × Turkey-14, exhibiting significant positive heterosis implying a thicker pericarp after drying. Fruit setting percentage saw positive significant heterosis in A-512 × Shahzadi, A-512 × Turkey-14 and A-132 × Turkey-14, while eight hybrids had significant negative commercial heterosis for fruit setting percentage. For number of seeds per fruit, seventeen out of eighteen crosses had significant negative commercial heterosis. Maximum significant positive heterosis for yield was observed in A-441 × Turkey-1 followed by A-441 × Wiz-21, A-512 × YP, A-512 × AVPP-0206, A132 × Turkey-1, A-512 × Turkey-1 and A-512 × Turkey-14. Conversely negative significant heterosis for yield was observed in hybrids A-132 × VRI-YP, A-132 × Shahzadi, A-441 × VRI-YP, A-512 × Wiz-21, A-512 × Shahzadi, A-441 × Shahzadi, A-132 × AVPP-0206, A-441 × Turkey-14 and A-441 × AVPP-0206. For disease incidence under natural conditions, positive significant heterosis was noted in A-132 × Wiz-21 and A-132 × Shahzadi, indicating increased disease incidence, whereas negative significant heterosis, indicating reduced disease incidence, was observed in eleven out of eighteen crosses i.e. A-132 × AVPP-0206, A-441 × Turkey-1, A-441 × Turkey-14, A-512 × Shahzadi, A-512 × VRI-YP, A-441 × Shahzadi, A-512 × Turkey-14, A-132 × VRI-YP, A-512 × AVPP-0206, A-512 × Turkey-1 and A-132 × Turkey-14.

Crosses	PH	PS	FL	FW	FFW	DFW	MCF	FPT	DPT	FSP	SpF	TSW	Yield	DI.NC
A-132 × Wiz-21	− 2.48	20.5**	− 24.65	11.19	− 50.29**	− 36.62**	− 3.61	− 16.50	16.67	0.42 ns	1.21	− 7.48	0.09	80.77**
A-132 × Shahzadi	− 27.10**	− 27.21**	− 23.80	− 32.28*	− 61.28**	− 35.21**	− 8.41**	− 18.45*	33.33	− 13.75**	− 31.12**	− 11.21	− 32.27**	57.69**
A-132 × AVPP-0206	13.11*	− 8.63**	− 15.58	− 19.59	− 52.60**	− 42.25**	− 2.70	− 20.39*	33.33	− 19.58**	− 42.90**	− 36.45**	− 6.05**	− 38.46*
A-132 × VRI-YP	4.65	− 25.48**	− 28.90	12.50	− 46.97**	− 46.48**	− 0.23	− 14.56	16.67	− 10.42*	− 14.80**	− 4.67	− 54.68**	− 46.15*
A-132 × Turkey-1	− 17.89**	− 20.70**	64.87**	− 12.31	− 29.66**	89.20**	− 21.41**	0.97	16.67	− 14.17**	− 6.34*	0.93	12.66**	− 19.23
A-132 × Turkey-14	2.17	− 7.73*	− 21.25	− 27.05*	− 52.55**	− 42.25**	− 2.74	6.80	66.67**	9.58*	− 14.20**	− 7.48	2.72	− 57.69**
A-441 × Wiz-21	− 6.86	− 0.40	− 28.05	− 37.31**	− 41.92**	− 19.25**	− 4.92*	− 22.33*	− 0.00	− 10.42*	− 6.65*	− 13.08	20.94**	− 15.38
A-441 × Shahzadi	15.50**	1.39	− 17.00	− 18.28	− 66.91**	− 24.88**	− 16.27**	− 24.27*	− 0.00	− 18.75**	− 25.38**	17.76	− 18.04**	− 42.31*
A-441 × AVPP-0206	4.65	− 4.29	− 4.53	− 35.07**	− 46.50**	− 24.41**	− 5.18*	− 30.10**	16.67	2.08	− 9.97**	− 3.74	− 4.98*	− 26.92
A-441 × VRI-YP	21.80**	− 4.97	− 15.01	− 32.28*	− 45.82**	− 13.15*	− 7.48**	− 16.50	33.33	− 36.25**	− 16.62**	24.30*	− 28.86**	− 26.92
A-441 × Turkey-1	7.86	5.11	54.11**	− 35.26**	− 54.18**	48.36**	− 28.40**	− 14.56	16.67	− 10.00*	− 6.34*	54.21**	99.59**	− 38.46*
A-441 × Turkey-14	− 3.78	− 10.48**	− 15.86	13.25	− 16.51**	− 7.98	− 1.24	− 0.97	16.67	− 11.25**	− 6.95*	− 37.38**	− 5.56**	− 38.46*
A-512 × Wiz-21	− 13.63*	− 11.45**	4.82	− 41.79**	− 66.65**	− 24.41**	− 16.27**	− 14.56	16.67	− 1.25	− 8.16**	− 2.80	− 21.84**	− 34.62
A-512 × Shahzadi	2.34	− 13.32**	− 9.63	− 18.28	− 54.55**	− 31.46**	− 6.50**	− 22.33*	33.33	22.08**	− 11.78**	− 23.36*	− 20.87**	− 38.46*
A-512 × AVPP-0206	− 9.21	− 3.04	1.42	− 3.17	− 34.40**	− 37.56**	0.68	0.97	33.33	− 9.58*	− 19.94**	18.69*	13.83**	− 50.00**
A-512 × VRI-YP	7.69	17.24**	28.05	− 10.26	− 60.18**	− 21.60**	− 12.21**	− 18.45*	16.67	− 7.92	− 37.46**	− 26.17**	17.14**	− 38.46*
A-512 × Turkey-1	− 17.19**	− 8.89**	− 15.30	− 26.49*	− 55.13**	15.96**	− 20.10**	− 26.21**	16.67	2.50	− 16.92**	23.36*	8.66**	− 50.00**
A-512 × Turkey-14	− 16.98**	− 20.08**	− 0.57	− 21.46	− 50.81**	− 22.54**	− 7.21**	− 20.39*	− 16.67	21.25**	− 22.96**	23.36*	4.08*	− 42.31 *

Table 7. Estimates of commercial heterosis for various agronomic and yield components and *P. capsici* disease incidence in Chili under natural field conditions. *Significance at $P \leq 5\%$, ** Significance at $P \leq 1\%$, *PH* Plant height, *PS* Plant spread, *FL* Fruit length, *FW* Fruit width, *FFW* Fresh fruit weight red, *DFW* Dry fruit weight red, *MCF* Moisture contents of fruit, *FPT* Fresh pericarp thickness red, *DPT* Dry pericarp thickness red, *FSP* Fruit setting percentage, *SpF* Number of seeds per fruit, *TSW* Thousand seed weight, *DI.NC* Disease incidence under natural conditions.

Discussion

Root rot caused by *P. capsici* is the most damaging disease[25] of chili crop worldwide[10] which cause significant yield losses[27,61,62]. Screening under different environments and disease pressure is essential for the effective selection of *P. capsici* resistant genotypes. Screening under greenhouse conditions offers a controlled environment that minimizes external variables, allowing for precise assessment of genotype resistance[63] for specific isolate of pathogen[64]. The results from the greenhouse screening showed clear differentiation among genotypes with AVPP-0206 (10.3%) and Turkey-1 (7.9%) displaying notable resistance. These conditions are particularly useful for early-stage selection and for identifying genetic lines with inherent resistance[65,66] before further testing under field conditions.

The evaluation for *P. capsici* resistance in different chili germplasm lines and their F_1 hybrids across three distinct screening conditions i.e. greenhouse, artificially infected soil, and natural field conditions, revealed significant variability in susceptibility and resistance behavior[37]. Among the GMS lines, A-132 exhibited the highest susceptibility across all screening conditions, particularly in the natural field (48.3%) and under artificial inoculation (42.0%). Its susceptibility in the greenhouse (33.7%) further underscores its vulnerability to *P. capsici* infection. A-441 showed a similar pattern but with slightly lower incidences, being highly susceptible in the field (43.3%) and moderately susceptible in both greenhouse (21.6%) and artificial field conditions (27.6%). A-512, on the other hand, displayed moderate susceptibility consistently across all conditions, indicating a relatively more stable resistance profile compared to A-132 and A-441.

The male fertile restorer lines demonstrated a broader range of responses. Wiz-21 was highly susceptible across all conditions, indicating its unsuitability for breeding resistant hybrids. VRI-YP consistently demonstrated moderate resistance, making it a promising candidate for breeding programs. Previous studies have also shown that genotypes resistant to *P. capsici* in greenhouse conditions also tend to exhibit resistance in natural field conditions[64]. Foster and Hausbeck[67]Wyatt, et al.[68] and Parada-Rojas and Quesada-Ocampo[64] has also used both green house and field screening to identify chili genotypes with stable resistance against *P. capsici*. However, highly resistant genotypes have more or less similar response to isolate specific screening under both natural conditions and greenhouse conditions[64]. Rabuma, et al.[10] screened 233 diverse chili genotypes and identified five as highly resistant to *P. capsici* infection based on field performance and genetic diversity analysis, along with 22 resistant and 17 moderately resistant genotypes. Katoch and Singh[27] screened 86 chili genotypes at the seedling stage under greenhouse conditions and identified three resistant and three moderately resistant genotypes. Jo, et al.[70] reported varying degree of resistance response of 100 commercial chili cultivars to different isolates of *P. capsici* under controlled conditions with only six genotypes exhibiting stable resistance to all six isolates.

The F_1 hybrids exhibited diverse resistance profiles influenced by the resistance status of their parental lines. Notably, hybrids of A-512 demonstrated better resistance profiles, particularly when crossed with AVPP-0206, VRI-YP, Turkey-1, and Turkey-14, indicating that A-512 can contribute positively to resistance when paired with moderately resistant or resistant male lines[39].

The commercial hybrid Golden Hot was consistently susceptible, with incidences ranging from 26.8 to 65.5% across all conditions. This underscores the necessity for breeding programs to prioritize the development of hybrids with enhanced resistance[10,71].

Crosses between resistant parents typically produce hybrids with moderate to strong resistance across different conditions. When resistant lines are crossed with susceptible lines, the resistance of the resulting hybrids varies but tends to be intermediate. For example, hybrids involving resistant lines such as A-512 with susceptible lines like Wiz-21 or Shahzadi showed moderate resistance to susceptibility. This suggests that while some level of resistance is inherited from the resistant parent, the susceptibility of the other parent can weaken the overall resistance. Crosses between two susceptible parents generally result in hybrids with high susceptibility. Hybrids involving highly susceptible lines, such as A-132 with Wiz-21 and Shahzadi, exhibited high susceptibility across all conditions. This pattern confirms that resistance to *P. capsici* is a dominant trait with one or two major genes[39,72,73] with epistatic interaction[39]. Sy, et al.[72] has reported 3:1 resistant to susceptible segregation ratio in the F_2 progeny of a cross between *P. capsici* resistant and susceptible chili genotypes, suggesting the involvement of a single dominant gene. When both parents lack resistance, hybrids are highly vulnerable to disease. Breeding programs should focus on utilizing resistant lines like A-512, AVPP-0206, and VRI-YP to enhance resistance in hybrids. Crosses involving resistant x resistant or resistant x susceptible parents exhibit varying resistance responses under different conditions. For example, hybrids of A-512 with AVPP-0206, VRI-YP, Turkey-1, and Turkey-14 showed better resistance profiles, yet the degree of resistance varied across different environments. Similar varied resistance response of chili genotypes to *P. capsici* under different screening conditions has also been reported by Dunn, et al.[69] and Dunn and Smart[74]. Naegele, et al.[75] has reported that even resistant genotypes can show some level of susceptibility under high pathogen pressure or disease conducive environment. This variation may be attributed to complex nature of resistance inheritance[19,64,69,76,77] with involvement of single gene[38,72]two genes[39,78] or many genes[30,71,76] along with epistatic effects[79,80] and genotype-environment interactions[64,69]. Understanding these genetic and environmental interactions is crucial for breeding programs aiming to develop consistently resistant pepper varieties.

Estimation of genetic parameters to study genetic behavior of resistant genotypes and their inheritance is prerequisite for effective utilization of resistant germplasm in breeding program aimed at development of resistant cultivars[82]. The analysis of variance (ANOVA) for Lines × Testers, including parents, revealed significant genetic variability and inheritance patterns for agronomic and yield components in chili[83]. Most traits showed highly significant genotypic mean squares, indicating substantial genetic variation essential for breeding program[84].

The combining ability analysis indicated that both additive and non-additive gene actions are important for traits like plant height, plant spread, fruit length, fruit width, fresh fruit weight, moisture content, fresh pericarp thickness, thousand seed weight, and yield[83–85]. This suggests that breeding strategies should consider both general and specific combining abilities. For dry fruit pericarp thickness and dry fruit weight, additive gene action was predominant, facilitating more straightforward selection. Kamble, et al.[86]Do Rêgo, et al. [87] and [88] reported significant differences for GCA and SCA effects in most fruit parameters and yield components in chili. However, Sitaresmi, et al.[89] found significant differences for GCA effects on fruit weight and number of fruits per plant, but non-significant differences for SCA estimates.

The comparison of General Combining Ability (GCA) effects for agronomic traits and disease incidence in chili provided valuable insights into identifying suitable parental lines that excel in both agronomic performance and disease resistance[83,89–91]. Numerous researchers have emphasized the significance of combining ability effects in the efficient selection of parents for successful breeding program[81,86,90–92]. The high GCA effects of a genotype for a particular trait indicate preponderance of additive genes in that parent[89,91] whereas low GCA estimate translate to negative contribution of that genotype for that particular trait[93,94]. Likewise, in resistance breeding, negative GCA effects for disease incidence are desirable[95,96]. Among the female parents, A-441 emerged as a versatile performer with positive GCA effects for various agronomic traits, indicating its potential as a valuable contributor to overall plant productivity. A-512 demonstrated the lowest significant negative GCA effects for disease incidence, indicating its potential for imparting resistance to the disease. Similarly, among the male parents, Turkey-1 and AVPP-0206 stand out as a top performers for yield-related traits, while exhibiting potential for disease resistance, as indicated by significant negative GCA effects for disease incidence.

Comparison of GCA and SCA effects helps breeders to decide proper breeding strategy for crop improvement[93,97] in chili[98,99]. High SCA estimates are indicative of exceptional performance of cross than expected from parental means[84,100] and non-additive genetic effects[91] enabling breeders to select suitable cross combinations for next generation[100]. Hybrids exhibiting positive SCA effects for fruit quality and yield components should be selected for increasing fruit productivity in chili[84]. The hybrid A-132 × Wiz-21 is exceptional as it has positive SCA effects for numerous agronomic traits including yield, but a significant positive SCA effect for disease incidence under natural conditions, suggesting it may excel agronomically but could be vulnerable to disease. A-132 × VRI-YP, positive for fruit setting percentage and number of seeds per fruit, and negative for disease incidence, is a strong candidate for disease-resistant breeding programs with good agronomic potential. A-512 × AVPP-0206 and A-132 × Turkey-14 showed positive SCA effects for several agronomic traits including yield, and negative effects for disease incidence, making it highly promising for both yield and disease resistance. A-512 × AVPP-0206 and A-132 × Turkey-14 emerged as top-performing hybrids with positive SCA effects for key agronomic traits and yield, coupled with significant negative SCA effects for disease incidence. These hybrids are likely to provide both high yield and resilience against disease, making them valuable candidates for breeding programs focused on improving both productivity and disease resistance in chili crop through hybrid breeding[81].

The genetic analysis of yield components and disease incidence in chili revealed that both traits are influenced by a combination of additive and non-additive gene actions[84,87,101,102]. For yield, traits such as fruit setting percentage, plant height, and yield itself showed strong dominance levels, indicating that non-additive

effects, particularly dominance and overdominance, play a significant role[103,104]. This suggests that hybrid breeding strategies, which exploit heterozygous combinations, are essential to maximize chili productivity[85,105]. Conversely, the analysis of *P. capsici* disease incidence, with degrees of dominance ranging from 5.30 to 7.64 across different screening conditions, indicated that both additive and non-additive genetic effects are important. Yunianti, et al.[82] used diallel analysis to study the inheritance of *P. capsici* resistance in chili and reported that resistance is governed by group of positive genes with no epistatic and overdominance effects and high heritability estimates. Majid, et al.[108] has reported that chili has hypersensitive resistance genes for *P. capsici* infection which are induced by varying environments. This implies that a breeding strategy combining parent selection with negative GCA for additive effects and hybrid breeding to leverage non-additive effects is necessary for developing disease-resistant cultivars.

Heterosis estimates enable breeders to select parental genotypes to develop crosses with productive superiority and stress endurance[89]. Many previous researchers has reported significant heterotic effects for fruit quality and yield components in chili for genetic improvement through heterosis breeding[88,109–111]. Crosses, A-132 × Turkey-1, A-441 × Turkey-1, A-512 × AVPP-0206, A-512 × VRI-YP, A-512 × Turkey-1, A-512 × Turkey-14 had significant positive commercial heterosis for yield coupled with significant negative heterosis for *P. capsici* disease incidence. Likewise, hybrids like A-441 × VRI-YP, A-441 × Shahzadi, and A-132 × AVPP-0206 exhibit positive heterosis in traits such as plant height, fruit length, and yield, suggesting potential for enhanced commercial performance[84,113–115]. Female line A-512 tend to contribute to positive heterosis in yield and resistance to *P. capsici* disease while hybrids involving A-132 and A-441 often manifest negative heterosis, indicating the importance of female line selection. Male lines also played a significant role, with crosses featuring VRI-YP and Turkey-1 showing positive heterosis in various traits, while those with Wiz-21 and Shahzadi often exhibit negative heterosis. These findings underscore the complexity of heterosis expression and emphasize the need for comprehensive breeding strategies that consider both female and male line contributions with good performance[112,116] to optimize trait combinations for commercial success in chili hybrid breeding program[117–119].

Conclusion

In conclusion, utilizing diverse screening conditions is essential for effectively selecting *P. capsici* resistant genotypes in chili breeding programs. Key parental lines, such as A-512 and Turkey-14, and hybrids (A-441 × Turkey-1, A-512 × AVPP-0206, A-512 × VRI-YP, A-512 × Turkey-1, and A-512 × Turkey-14) showed significant potential, exhibiting high yield and strong disease resistance. The results also provide practical implications for hybrid development, suggesting that combining ability analysis under multiple screening conditions can be effectively used to select superior cross combinations. Future research should focus on validating these promising hybrids across additional environments and years, and on mapping quantitative trait loci (QTLs) associated with resistance and yield, to enable marker-assisted selection and accelerated cultivar development.

Data availability

The datasets used and/or analyzed during the current study available from the corresponding author on reasonable request.

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Author contributions

M.U.A. and M. M. conceptualized the study, designed and performed the experiments, statistical analysis, and wrote the initial manuscript draft. M. A. and R.M.A. provided technical support and contributed to manuscript revisions. M. U. and W.K. contributed to the greenhouse and field experimentations, as well as data collection and analysis. O.I. assisted in the statistical analysis and interpretation of results. N.A.R. supervised the overall research work, critically reviewed, and edited the manuscript. Q.A. secured funding, provided technical support, and contributed to manuscript revisions.All authors reviewed and approved the final version of the manuscript.

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Declarations

Competing interests

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Declaration ofof generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to improve language clarity and grammar of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

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