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Characterizing Sources of Resistance to Phytophthora Blight of Pepper Caused by *Phytophthora capsici* in North Carolina

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Abstract

Phytophthora blight, caused by *Phytophthora capsici*, is an important disease of peppers in the United States and worldwide. *P. capsici* causes crown, root, and fruit rot as well as foliar lesions in peppers. Field trials were conducted in 2015 and 2016 to evaluate 32 commercial and experimental pepper cultivars against a mixed-isolate inoculum in North Carolina. Cultivars Martha-R and Meeting were classified as highly resistant to *P. capsici*, and Paladin was classified as resistant. Intermediate resistance to *P. capsici* in the field was observed with Fabuloso, Revolution, Vanguard, Archimedes, Aristotle, Ebano-R, and Declaration. Greenhouse experiments were conducted to determine the response of 48 pepper cultivars when inoculated individually with two isolates from North Carolina and an isolate from Michigan. Isolates exhibited different levels of virulence in pepper cultivars screened for resistance. Landraces CM334 and Fidel as well as the cultivars Martha-R, Meeting, and Intruder were categorized as highly resistant or resistant to the three isolates tested. Overall, highly resistant cultivars tended to respond similarly to field mix inoculations and greenhouse single isolate inoculations.

Keywords: pepper, host resistance, *Phytophthora*, field and greenhouse vegetables

Pepper (*Capsicum annuum*) is an economically important vegetable cultivated worldwide (FAOSTAT 2016). Many cuisines throughout the world incorporate peppers as key elements in salads and as spice to food (Bosland and Votava 2012). In 2016, the United States planted 25,980 ha of bell and hot pepper with a total production value of more than $850 million (USDA-NASS 2017b). North Carolina (NC) contributed to national production by planting approximately 1,000 ha of bell peppers and producing a total value of more than $18 million in 2016 (USDA-NASS 2017a). Vegetable growers often suffer significant crop losses owing to plant diseases. Since 1948, the NC vegetable industry has been threatened every year by the soilborne oomycete *Phytophthora capsici* (Crossan et al. 1954). *P. capsici* is a destructive hemibiotrophic pathogen capable of causing disease on a broad range of plant families including solanaceous, cucurbitaceous, and fabaceous crops among others (Granke et al. 2012; Kousik et al. 2015; Quesada-Ocampo et al. 2009). Under favorable conditions, *P. capsici* infects the pepper plant at any growth stage. The disease, known as Phytophthora blight, appears as small water-soaked areas on the stem visible at the soil line. In moist conditions, the disease progresses to affect the roots, crown, foliage, and fruit (Lamour et al. 2012). In fruit, expanding lesions produce fresh sporangia over 5 days and appear as a distinctive white "powdered sugar" layer on the surface of the fruit, visible to the naked eye (Lamour and Hausbeck 2003).

Managing *P. capsici* on peppers relies on an integrated approach that combines multiple control tactics such as water management, crop rotation, fungicide applications, and host resistance (Granke et al. 2012). Weather patterns impose pressure on management strategies for *P. capsici*. Increasing rain events and flooding of fields seem to exacerbate disease incidence in all pepper growing areas in the United States (Bornt 2012; Quesada-Ocampo et al. 2011a). Identifying sources of resistance in pepper becomes highly important when combating Phytophthora blight. Currently, landrace peppers such as Criollo de Morelos 334 are used to breed for resistance to *P. capsici* (Xu et al. 2016). However, the genetics behind the resistance is complex, involving multiple genes that confer resistance to different disease symptoms (Naegele et al. 2014; Quesada-Ocampo et al. 2016). Because *P. capsici* exhibits high genetic and phenotypic diversity (Granke et al. 2011a, 2011b; Quesada-Ocampo et al. 2011b), breeding for resistance is challenging and relies on the knowledge of local pathogen populations, as well as environmental factors (Granke et al. 2012). Every year, pepper cultivars are evaluated for resistance to *P. capsici* (Dunn et al. 2013; Foster and Hausbeck 2010a; Wyatt et al. 2013). In fields trials conducted over 5 years, Dunn et al. (2014) reported bell pepper cultivars Archimedes, Aristotle, Intruder, and Paladin as the most resistant to a single isolate of *P. capsici* from New York. Greenhouse and field evaluations reported high levels of resistance in Aristotle, Intruder, Paladin, and Revolution (Foster and Hausbeck 2010a, 2010b; Wyatt et al. 2013). Variation in virulence among isolates of *P. capsici* has also been reported in peppers (Foster and Hausbeck 2010b), highlighting the importance of evaluating pepper cultivars across a panel of *P. capsici* isolates. Effective host resistance evaluations should integrate knowledge

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of the local population structure of *P. capsici* in order to deploy durable resistance (Granke et al. 2012).

In this context, we aimed to improve management of Phytophthora blight in pepper by characterizing resistance to *P. capsici* of bell and hot pepper cultivars. Specifically, we sought (i) to evaluate commercial and experimental lines of peppers for resistance to *P. capsici* under field and greenhouse conditions and (ii) to compare the level of resistance among different pepper cultivars against two current *P. capsici* isolates from NC and one isolate from Michigan under greenhouse conditions.

Isolate Selection and Inoculum Preparation

Table 1 details isolate information including their source, mating type, mefenoxam sensitivity, and host of origin. *P. capsici* isolates were transferred from long-term storage to unclarified V8 agar (16 g of agar, 3 g of $CaCO_3$, 160 ml of V8 juice, and 840 ml of distilled water) and maintained under constant fluorescent light at room temperature (21 ± 2°C) for 7 days. Before inoculum preparation, the isolates were inoculated on pepper fruits and then reisolated from the symptomatic tissue to ensure virulence (Quesada-Ocampo and Hausbeck 2010). For field and greenhouse inoculations, millet seed was used as a substrate to grow and deploy *P. capsici* in the soil or potting media. One-liter flasks were filled with 100 g of millet seed, 72 ml of distilled water, and 0.08 mg of L-asparagine. Flasks were autoclaved twice for 30 min on consecutive days. Ten 7-mm agar plugs from actively growing cultures of *P. capsici* were added to flasks, which were incubated for 21 to 28 days under constant fluorescent light at room temperature with daily mixing (Quesada-Ocampo and Hausbeck 2010).

Field Experiment

Twenty-two commercially available pepper cultivars and 10 experimental lines were planted to evaluate their resistance to a mix of *P. capsici* isolates (R377, R388, R328, R297, NC21064, and NC21810) in the summers of 2015 and 2016 (Table 2). A known highly resistant landrace pepper, Fidel, and a known highly susceptible cultivar, Red Knight, were included for comparison. Field experiments were located at the Sandhills Research Station, Jackson Springs, NC (35°11′44.2″N, 79°40′59.2″W). The field soil type is sandy. Pepper seedlings were grown in the greenhouse under natural light for 4 weeks in 72-cell flats filled with peat moss/vermiculite potting medium (Conrad Fafard, Agawam, MA). Seedlings were placed outside in a protected area to harden off for 3 days. Pepper seedlings were transplanted in raised beds on 11 June and 26 May for the 2015 and 2016 trials, respectively. Treatment plots consisted of 10 plants from each pepper cultivar, which were spaced 0.3 m apart in a single row by a mechanical transplanter that also applied a starter fertilizer (17N-17P-17K) at a rate of 224.17 kg/ha. Plots were 3 m long and spaced 0.6 m apart. To promote disease, plants were transplanted in bare ground soil and irrigated using overhead sprinklers. During the field season, weeds within plots were controlled by hand weeding, whereas weeds between rows were cultivated. Plots were arranged in a completely randomized block design with four replications. Plants were inoculated 2 weeks after transplanting by inserting 1 g of *P. capsici*–infested millet seed directly into the soil adjacent to each plant crown, avoiding root or crown injury.

Plants first were assessed for wilting and crown rot approximately 7 days after inoculation and consecutively thereafter every 3 days (n = 8). Disease severity estimation was based on a 0 to 5 scale, in which 0 = no disease symptom observed, 1 = 1 to 30% wilting in the older leaves, 2 = 31 to 50% minor wilting in the older and younger leaves or crown rot observed, 3 = 51 to 70% advanced wilting of the entire plant but green foliage color still observed, 4 = 71 to 90% advanced wilting and foliage discoloration observed, and 5 = >90% necrotic leaves, defoliation, or plant dead (Supplementary Fig. S1). The area under the disease progress curve (AUDPC) was calculated for each plant per plot and averaged to each cultivar and replication in each year according to the method of Shaner and Finney (1977). Weather data were downloaded from the NC Climate Retrieval and Observations Network of the Southeast Database during the two growing seasons. The weather station was located at the Sandhills Research Station 1 km from the field. Maximum air temperature (°C), daily air temperature (°C), and daily soil temperature (°C) were averaged for each growing season in 2015 and 2016 (Table 3). Total soil moisture (m^3/m^3) and total rainfall (mm) were summed over the growing season. Upon completion of each field trial, 10% of symptomatic plants were randomly selected for pathogen reisolation according to the methods of Quesada-Ocampo and Hausbeck (2010).

Greenhouse Experiment

Thirty commercial pepper cultivars and 18 experimental lines were screened for resistance to three *P. capsici* isolates (NC21810, 12889, and NCCP3) in a greenhouse under a 16-h light/8-h dark photoperiod. (Table 4). Among the cultivars tested, we included two landrace peppers, CM334 and Fidel, known for their high level of resistance to *P. capsici*. Four-week-old seedlings were grown in 72-cell flats filled with peat moss/vermiculite potting medium (Conrad Fafard) in a greenhouse under natural light. Four-week-old seedlings were transplanted into 6-inch-diameter 5.5-inch-depth pots filled with the same potting medium as described above. Plants were watered daily with care to avoid splashing and fertilized

TABLE 1
Eight *Phytophthora capsici* isolates used for field and greenhouse evaluations of resistance in pepper

Isolate	Source	State	Host	Year of isolation	Mefenoxam sensitivity[z]	Mating type	Evaluation
R377	Ristaino J.	NC	Pepper	1980s	S	A1	Field
R388	Ristaino J.	NC	Pepper	1980s	S	A1	Field
R328	Ristaino J.	NC	Pepper	1980s	S	A2	Field
R297	Ristaino J.	NC	Pepper	1980s	S	A2	Field
NC21064	Quesada L.	NC	Pepper	2015	IS	A1	Field
NC21810	Quesada L.	NC	Zucchini	2015	S	A2	Field and greenhouse
NCCP3	Quesada L.	NC	Squash	2015	S	A2	Greenhouse
12889	Hausbeck M.	MI	Pepper	2009	I	A1	Greenhouse

[z] S = sensitive; IS = intermediately sensitive; and I = insensitive.

with 1g of Osmocote (14N-6.2P-11.6K) per pot at transplanting. The experiment was designed as a split-plot arranged in a complete randomized block design with main plots referring to each of the isolates and control treatments and subplots as each of the cultivars. Five seedlings of the same cultivar were inoculated with each isolate. Five noninoculated seedlings were included as a control. The experiment was conducted once in 2015 and 2016.

One week after transplanting, seedlings were inoculated with each isolate by inserting 1 g of infested millet seed directly into the potting medium and close to the crown. Uninfested millet seed containing sterile V8 agar plugs was added to control plants. Plants were scored for Phytophthora blight symptoms every other day for 5 weeks according to a 0 to 5 scale, in which 0 = no disease symptom, 1 = 1 to 30% wilting in the bottom leaves, 2 = 31 to 50% wilting of the top and bottom leaves, 3 = 51 to 70% advanced wilting and discoloration, 4 = 71 to 90% advanced leaf discoloration and necrosis of bottom leaves, and 5 = >90% necrosis of top and bottom leaves or plant dead (Supplementary Fig. S2). AUDPC values were calculated for each plant according to the method of Shaner and Finney (1977). Approximately 10% of the symptomatic plants were randomly selected for reisolation of the pathogen according to the method of Quesada-Ocampo and Hausbeck (2010).

Statistical Analysis

Mean AUDPC values from field and greenhouse experiments were subject to analysis of variance (ANOVA) using the PROC GLIMMIX procedure of SAS version 9.4 (SAS Institute, Cary, NC). The generalized linear mixed model was selected and gamma

TABLE 2
Commercial and experimental pepper cultivars evaluated for resistance to a mix of *Phytophthora capsici* isolates during 2015 and 2016 field experiments[v]

Cultivar	AUDPC 2015[w]	AUDPC 2016[w]	Cultivar ranking[x]				Disease response[y]
			a (2015)	*b* (2016)	*c*	*d*	
Fidel	10.99 f	7.51 de	1	2	3	–3.40	HR
Martha-R	14.63 ef	3.46 e	2	1	3	–3.40	HR
Meeting	20.31 def	9.73 cde	3	3	6	–3.06	HR
Paladin	42.77 a–e	10.14 b–e	7	4	11	–2.50	R
EXP.9[z]	29.52 c–f	42.88 a	4	10	14	–2.16	R
Fabuloso	56.17 a–d	28.88 abc	10	6	16	–1.93	IR
Revolution	41.10 a–e	56.39 a	6	12	18	–1.70	IR
EXP.3[z]	45.68 a–e	39.26 a	9	9	18	–1.70	IR
EXP.8[z]	59.60 a–d	33.25 abc	11	7	18	–1.70	IR
Vanguard	43.41 a–e	58.39 a	8	14	22	–1.25	IR
Archimedes	73.59 abc	26.21 a–e	17	5	22	–1.25	IR
EXP.4[z]	67.36 abc	45.21 a	15	11	26	–0.79	IR
Aristotle	81.63 abc	36.35 ab	18	8	26	–0.79	IR
Ebano-R	34.99 b–f	63.34 a	5	22	27	–0.68	IR
Declaration	59.98 a–d	62.00 a	12	19	31	–0.23	IR
EXP.1[z]	62.96 a–d	61.93 a	14	18	32	–0.11	IR
PS09941819	83.12 abc	59.39 a	19	16	35	0.23	MS
EXP.6[z]	85.48 abc	58.70 a	20	15	35	0.23	MS
SV3198HJ	71.25 abc	62.89 a	16	20	36	0.34	MS
EXP.7[z]	62.20 a–d	71.44 a	13	25	38	0.57	MS
EXP.5[z]	88.36 abc	59.98 a	21	17	38	0.57	MS
Karisma	98.14 ab	57.83 a	26	13	39	0.68	MS
Revelation	89.47 abc	66.79 a	22	23	45	1.36	MS
EXP.2[z]	98.09 ab	71.24 a	25	24	49	1.81	MS
SV3782PP	94.76 abc	74.65 a	23	27	50	1.93	MS
Quattro	97.04 ab	71.84 a	24	26	50	1.93	MS
Camelot	112.85 a	63.33 a	30	21	51	2.04	S
Plato	109.46 ab	77.96 a	28	29	57	2.72	S
EXP.10[z]	100.79 ab	82.64 a	27	31	58	2.84	S
Red Knight	111.71 ab	78.64 a	29	30	59	2.95	S
Keystone	121.66 a	76.29 a	31	28	59	2.95	S
Bastille	123.79 a	83.49 a	32	32	64	3.52	HS

[v] Isolates used in the inoculum mixture are R377, R388, R328, R297, NC21064, and NC21810.

[w] Area under the disease progress curve (AUDPC) means within a column for each cultivar followed by the same letter are not significantly different ($P = 0.05$).

[x] The grand mean (G) of the rank sums (c) is 33; a = cultivar ranking based on AUDPC means from 2015; b = cultivar ranking based on AUDPC means from 2016; c = rank sum ($a + b$) for each cultivar; d = deviation from the grand mean (G) of the rank sums, $d = [(c - G)/\text{standard deviation}] \times 2$.

[y] Disease response identified by rank-sum classification method: HR = highly resistant; R = resistant; IR = intermediately resistant; MS = moderately susceptible; S = susceptible; and HS = highly susceptible.

[z] EXP.# refers to experimental lines tested in this study.

distribution assumed owing to nonnormal distribution of data, and the AUDPC values were a continuous-skewed response variable type (Stroup 2015). We used the post hoc Tukey–Kramer honestly significant difference test to examine significant differences (α = 0.05) among the means. AUDPC means were analyzed separately for each year and each experiment. To identify consistently resistant pepper cultivars screened in both field and greenhouse experiments, we used the rank-sum method as described by Afolabi et al. (2008) to classify them into different categories of resistance based on the AUDPC means of each cultivar. Positive deviations from the grand mean were rated susceptible, whereas negative deviations from the grand mean were rated resistant. Cultivars with deviations of 0 to 2, 2 to 3, and larger than 3 were classified as moderately susceptible, susceptible, and highly susceptible, respectively, whereas cultivars with deviations of 0 to –2, –2 to –3, and smaller than –3 were considered intermediately resistant, resistant, and highly resistant, respectively. To determine the correlation between the deviations from the grand mean of the ranks and the AUDPC means, we used the Spearman rank correlation test as described by Ariyo et al. (2010).

Evaluation of Resistance to *P. capsici* in Peppers

In field experiments, 1 week after inoculation with *P. capsici*–infested millet susceptible pepper plants showed wilting and crown rot symptoms that progressively developed into advanced wilting or death (Fig. 1). Significant differences (ANOVA, $P < 0.0001$) were detected for AUDPC means calculated among cultivars for both years. We observed significant differences between years (ANOVA, $P = 0.001$) with the 2015 field experiment exhibiting higher AUDPC means (61.56) than 2016 (42.40). The field trials revealed commercial and experimental pepper cultivars resistant to current NC isolates of *P. capsici* (Table 2). Cultivars Martha-R and Meeting, as well as the landrace Fidel, consistently exhibited the lowest AUDPC means during the two field seasons. The rank-sum analysis categorized Fidel, Martha-R, and Meeting as highly resistant to the NC isolates of *P. capsici* inoculated in the field during both seasons. Paladin and EXP.9 exhibited higher numerical AUDPC means when compared with Fidel during 2015 and 2016 and were consequently classified as resistant by the rank-sum analysis. In 2015, EXP.9 presented lower AUDPC means than in 2016, whereas Paladin presented higher AUDPC means in 2015 compared with 2016. During 2015 and 2016 field seasons, Bastille had the highest AUDPC mean among all cultivars, and it was categorized as a highly susceptible cultivar by the rank-sum analysis. AUDPC means for Keystone, Camelot, Red Knight, Plato, EXP.10, Karisma, EXP.2, Quattro, SV3782PP, EXP.5, EXP.6, EXP.7, Revelation, SV3198HJ, EXP.1, Declaration, Aristotle, EXP.4, Archimedes, Vanguard, EXP.8, EXP.3, Revolution, Fabuloso, and PS09941819 were not significantly different from Bastille (highly susceptible) for both years.

The rank-sum analysis separated cultivars with high AUDPC means into two categories: susceptible and moderately susceptible (Table 2). The AUDPC means for most of the susceptible cultivars were numerically higher for the 2015 than the 2016 growing season. Cultivars Fabuloso, Revolution, EXP.3, EXP.8, Vanguard, Archimedes, EXP.4, Aristotle, Ebano-R, Declaration, and EXP.1 displayed intermediate values of AUDPC means and were classified as intermediately resistant by the rank-sum analysis. Among the cultivars classified as intermediately resistant, Revolution, EXP.3, Vanguard, Declaration, and EXP.1 consistently presented intermediate AUDPC means during 2015 and 2016. AUDPC means for cultivars Fabuloso, Archimedes, EXP.4, Aristotle, and EXP.8 exhibited higher AUDPC means in 2015 than in 2016 and were also classified as intermediately resistant by the rank-sum analysis. In contrast, Ebano-R exhibited lower AUDPC means in 2015 than in 2016. Temperature, soil moisture, and rainfall varied between the 2015 and 2016 field trials (Table 3). The 2015 growing season was warmer with higher moisture based on mean air temperatures, mean daily soil temperature, total soil moisture, and total rainfall. In contrast, the 2016 growing season was relatively cooler and drier.

In greenhouse experiments, disease symptoms observed for inoculated pepper plants included wilting, crown rot, leaf necrosis, and plant death (Fig. 2). Initial symptoms of wilting and crown rot were evident 5 days after inoculation with isolate NC21810 in susceptible plants. Symptoms progressed and dead plants were first observed at 12 days after inoculation. We observed significant differences ($P < 0.0001$) among AUDPC means calculated for pepper cultivars, isolates, and their interaction. The significant interaction indicates that the cultivar response depends significantly on the isolate inoculated, and the isolate virulence is constrained by the cultivar it is exposed to. AUDPC means calculated for pepper cultivars inoculated with isolate 12889 were not significantly different between the experiments conducted in 2015 and 2016 ($P = 0.2277$). Cultivars inoculated with isolates NC21810 and NCCP3 exhibited higher AUDPC means in 2015 than in 2016 ($P < 0.0001$). Among the cultivars inoculated with isolate NC21810, Paladin, Revolution, Aristotle, and Plato exhibited higher AUDPC means during the 2015 experiment than in 2016. In contrast, Ebano-R presented a lower AUDPC mean in 2015 than in 2016 (Table 4). In both experiments, isolate NC21810 caused significantly higher severity (highest AUDPC means) than isolate 12889, and both caused significantly more disease than isolate NCCP3 (*data not shown*). Noninoculated control plants remained asymptomatic during both experiments.

Cultivars Martha-R and Meeting and landrace peppers CM334 and Fidel exhibited the lowest AUDPC means when challenged with the three *P. capsici* isolates during both experiments. Paladin, EXP.4, Archimedes, EXP.11, and Ebano-R exhibited significantly higher AUDPC means than CM334 when inoculated with NC21810 and 12889. Touchdown, Bastille, Pepper #1, Keystone, and Plato showed high AUDPC means during both experiments when challenged with NC isolates (NC21810 and NCCP3). When challenged with 12889, Bastille showed the highest AUDPC mean among all cultivars in 2015 and the third highest in 2016. Based on the rank-sum analysis, which ranks the AUDPC mean from each cultivar during both experiments, we determined the disease response of all 48 cultivars when challenged with two NC isolates and one isolate from Michigan (Table 4). Among all cultivars evaluated, 10 cultivars were found to be highly resistant or resistant to isolate NC21810, nine cultivars were highly resistant or resistant to isolate 12889, and 15 cultivars were resistant to isolate NCCP3. Pepper cultivars CM334, Fidel, Martha-R, Meeting, and Intruder were highly resistant to isolate NC21810. Intruder was classified as resistant to 12889 and NCCP3. None of the cultivars were categorized as highly resistant to NCCP3. About half of the cultivars

TABLE 3
Temperature, soil moisture, and rainfall for the 2015 and 2016 growing season during field experiments

Weather parameter	2015	2016
Mean maximum air temperature (°C)	32.94	31.24
Mean daily air temperature (°C)	27.16	25.53
Mean daily soil temperature (°C)	29.84	28.29
Total soil moisture (m^3/m^3), expressed as %	17.94	14.65
Total rainfall (mm)	221.80	193.30

TABLE 4
Commercial and experimental pepper cultivars evaluated for resistance in the greenhouse to three *Phytophthora capsici* isolates obtained from North Carolina (NC21810 and NCCP3) and Michigan (12889)

	AUDPC 2015[q]			AUDPC 2016[q]			Disease response[r]		
Cultivar	NC21810	12889	NCCP3	NC21810	12889	NCCP3	NC21810	12889	NCCP3
CM334[s]	0.10 d	0.10 g	0.10 d	0.10 h	0.10 j	0.10 e	HR	HR	R
Fidel[t]	0.10 d	0.10 g	0.10 d	0.10 h	0.10 j	0.10 e	HR	HR	R
Martha-R[u]	0.10 d	0.10 g	0.10 d	0.10 h	0.10 j	0.10 e	HR	HR	R
Meeting[u]	0.10 d	0.10 g	0.10 d	0.10 h	0.10 j	0.10 e	HR	HR	R
Intruder[v]	0.10 d	1.62 c–f	0.10 d	0.10 h	1.59 hi	0.10 e	HR	R	R
EXP.8[w]	18.22 bc	0.39 fg	0.10 d	9.58 f	1.08 hi	0.10 e	R	R	R
Paladin[x]	33.38 abc	17.56 abc	0.10 d	0.81 g	3.53 gh	0.10 e	R	IR	R
EXP.4[w]	27.11 abc	1.01 d–g	0.10 d	18.51 b–f	10.04 c–g	0.10 e	R	IR	R
Archimedes[y]	35.75 abc	11.25 a–d	0.10 d	17.22 c–f	26.54 a–d	0.10 e	R	IR	R
EXP.11[w]	40.21 abc	10.99 a–d	0.10 d	16.45 def	0.65 i	0.10 e	R	R	R
Ebano-R[w]	16.06 c	0.10 g	0.10 d	31.21 a–f	17.65 a–g	0.10 e	IR	R	R
SV3198HJ[y]	48.10 abc	40.31 ab	7.43 abc	27.87 a–f	18.09 a–f	5.91 ab	IR	IR	S
EXP.12[w]	54.42 abc	13.71 abc	0.10 d	37.10 a–e	16.06 a–g	0.27 de	IR	IR	MS
Vanguard[w]	60.55 abc	0.10 g	3.33 abc	34.56 a–f	3.69 fgh	0.10 e	IR	R	IR
EXP.1[w]	61.91 abc	24.45 ab	5.23 abc	34.23 a–f	17.66 a–g	0.10 e	IR	IR	IR
EXP.5[w]	68.24 abc	43.53 ab	0.10 d	24.92 a–f	21.96 a–d	0.10 e	IR	MS	R
Compadre[v]	56.99 abc	37.54 ab	0.10 d	38.07 a–e	17.46 a–g	0.10 e	IR	IR	R
Revolution[v]	71.74 abc	37.10 ab	2.74 abc	19.78 a–f	5.52 d–g	0.10 e	IR	IR	IR
EXP.13[w]	62.41 abc	45.63 ab	27.13 ab	37.98 a–e	40.12 abc	0.61 cde	IR	MS	S
EXP.3[w]	28.35 abc	0.63 efg	0.10 d	47.30 a–e	17.96 a–f	0.10 e	IR	IR	R
EXP.6[w]	53.19 abc	51.54 ab	1.30 bcd	42.17 a–e	19.30 a–e	0.10 e	IR	MS	IR
Fabuloso[u]	72.65 abc	36.63 ab	28.15 ab	31.00 a–f	14.31 a–g	0.10 e	IR	IR	MS
Aristotle[y]	82.97 abc	64.05 ab	15.92 ab	12.72 ef	16.05 a–g	0.10 e	IR	MS	IR
Declaration[v]	63.49 abc	11.21 a–d	0.10 d	40.24 a–e	13.27 b–g	0.10 e	IR	IR	R
EXP.15[w]	67.09 abc	49.78 ab	13.34 ab	40.53 a–e	36.66 abc	0.10 e	IR	MS	IR
EXP.14[w]	66.26 abc	6.73 b–e	0.40 cd	43.38 a–e	18.52 a–f	0.10 e	MS	IR	IR
Revolution[w]	68.32 abc	17.56 abc	0.43 cd	43.87 a–e	27.03 a–d	0.10 e	MS	IR	IR
EXP.2[w]	81.31 abc	47.44 ab	53.27 a	36.22 a–f	23.59 a–d	0.10 e	MS	MS	MS
Karisma[w]	77.18 abc	38.88 ab	3.55 abc	40.77 a–e	35.03 abc	1.94 a–d	MS	MS	S
EXP.7[w]	79.00 abc	54.33 ab	3.40 abc	39.84 a–e	17.81 a–g	0.10 e	MS	MS	IR
EXP.16[w]	68.73 abc	61.21 ab	43.26 a	51.80 a–d	53.49 ab	0.10 e	MS	S	MS
PS09941819[y]	76.99 abc	56.05 ab	8.76 abc	52.94 a–d	41.03 abc	6.33 ab	MS	MS	S
EXP.18[w]	80.83 abc	24.34 ab	9.74 abc	47.16 a–e	4.22 e–h	0.10 e	MS	IR	IR
Plato[y]	100.15 a	87.93 a	54.33 a	39.48 a–e	51.86 ab	1.28 bcd	MS	S	HS
Lafayette[v]	86.33 abc	52.72 ab	11.86 ab	49.23 a–d	53.49 ab	0.10 e	MS	MS	IR
EXP.17[w]	77.61 abc	66.25 ab	13.25 ab	66.68 ab	62.07 ab	0.10 e	MS	S	IR
SV3782PP[y]	87.22 abc	81.75 a	46.29 a	50.49 a–d	38.94 abc	0.10 e	MS	S	MS
Gridiron[v]	78.33 abc	75.10 ab	54.10 a	66.91 ab	65.34 ab	0.10 e	S	S	MS
Red Knight[y]	83.27 abc	64.92 ab	18.91 ab	57.26 a–d	38.25 abc	0.61 cde	S	MS	S
Keystone[z]	78.78 abc	71.62 ab	44.42 a	68.89 ab	67.68 a	1.91 a–d	S	S	HS
Pepper #1[v]	85.92 abc	66.45 ab	57.40 a	58.03 a–d	51.46 ab	2.42 abc	S	S	HS
Camelot[v]	92.49 ab	58.42 ab	37.09 a	56.06 a–d	37.86 abc	0.10 e	S	MS	MS
California W[z]	93.45 ab	83.17 a	36.01 a	54.46 a–d	53.20 ab	0.10 e	S	S	MS
Revelation[y]	87.35 abc	76.80 ab	28.51 ab	63.13 abc	43.49 abc	0.10 e	S	S	MS
Quattro[w]	90.49 ab	68.99 ab	37.87 a	59.18 a–d	47.30 abc	0.10 e	S	MS	MS
EXP.10[w]	90.84 ab	79.56 a	35.14 a	58.70 a–d	50.86 abc	1.14 bcd	S	S	S
Bastille[v]	92.74 ab	91.51 a	59.24 a	71.71 a	62.36 ab	17.25 a	HS	HS	HS
Touchdown[y]	94.73 ab	87.58 a	38.44 a	70.09 a	60.72 ab	2.05 a–d	HS	S	HS

[q] Area under the disease progress curve (AUDPC) means within a column for each cultivar followed by the same letter are not significantly different ($P = 0.05$).
[r] Disease response to each *P. capsici* isolate was determined according to the rank-sum method. Cultivar rankings were assigned from the AUDPC means for each cultivar inoculated with each isolate during 2015 and 2016 greenhouse trials. HR = highly resistant; R = resistant; IR = intermediately resistant; MS = moderately susceptible; S = susceptible; and HS = highly susceptible.
[s] Chile Pepper Institute.
[t] Dr. David Ritchie.
[u] Sakata.
[v] Clifton Seeds.
[w] Harris Moran.
[x] Syngenta.
[y] Seminis.
[z] Wyatt-Quarles.

tested against the three *P. capsici* isolates were classified as moderately susceptible, susceptible, or highly susceptible. The rank-sum analysis classified about 31, 29, and 25% of the cultivars as intermediately resistant when inoculated with NC21810, 12889, and NCCP3, respectively. Cultivars Paladin, EXP.4, and Archimedes were resistant to the two NC isolates but intermediately resistant to 12889. Interestingly, cultivars SV3198HJ and EXP.12 were categorized as intermediately resistant to NC21810 and 12889 but susceptible and moderately susceptible to NCCP3. Cultivars Revolution, EXP.14, and EXP.18 were intermediately resistant to isolates 12889 and NCCP3 but moderately susceptible to NC21810. AUDPC means significantly correlated with the deviations from the grand mean of the ranks as revealed by Spearman rank correlation with $R = 0.93$ for NC21810 in 2015 and $R = 0.94$ for NC21810 in 2016, $R = 0.96$ for 12889 both years, and $R = 0.89$ for NCCP3 in 2015 and $R = 0.74$ for NCCP3 in 2016 ($P < 0.0001$).

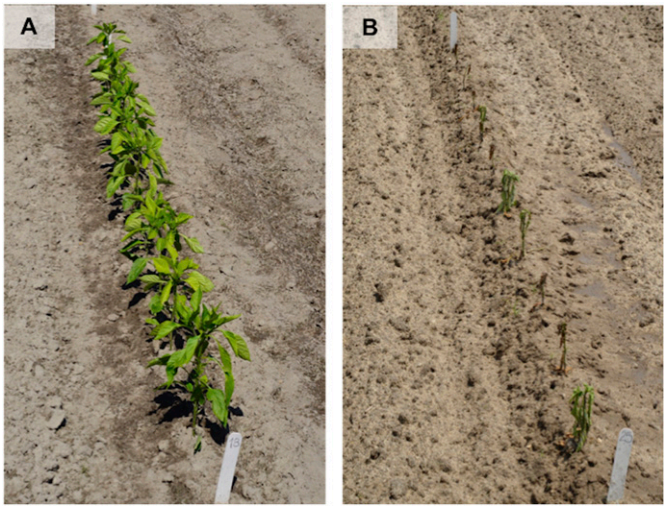

FIGURE 1

Cultivars at 3 weeks postinoculation in the 2015 field trial: **A,** Martha-R and **B,** Red Knight.

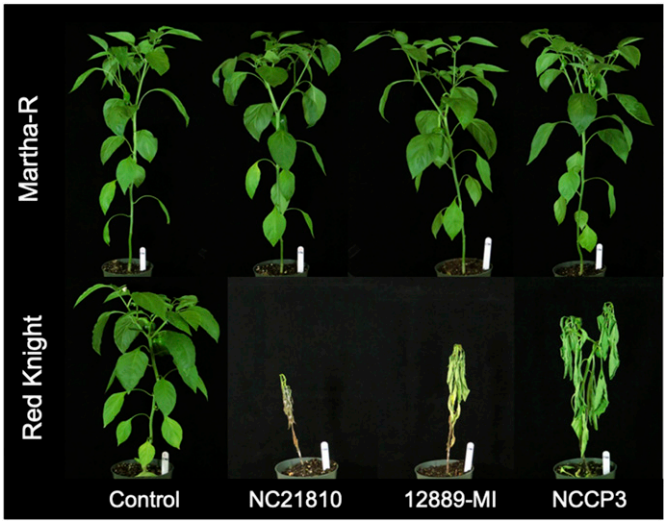

FIGURE 2

Response of cultivars Martha-R and Red Knight to the inoculation of three *Phytophthora capsici* isolates (NC21810, 12889, and NCCP3) and uninfested millet seed control under greenhouse conditions.

Deployment of resistant cultivars is one of the most sustainable and effective management strategies to control Phytophthora blight of peppers (Granke et al. 2012). In the present study, we evaluated a set of commercially available cultivars and experimental lines to identify resistance to *P. capsici* under field and greenhouse conditions. In our field trials, pepper cultivars exhibited variation of disease response during two growing seasons in 2015 and 2016. Dunn et al. (2014) reported similar variation when evaluating pepper cultivars for resistance to *P. capsici* over a 5-year field trial in New York. Our field studies identified a set of commercially available cultivars that were consistently resistant when challenged with a mix of current *P. capsici* isolates from NC and, thus, are more likely to perform consistently across the state.

Cultivars Martha-R and Meeting are sweet pepper hybrids commercially advertised as intermediately resistant and resistant to *P. capsici* (Sakata Seed America 2015); however, our results suggest that Martha-R and Meeting perform consistently as highly resistant cultivars under high disease pressure. Paladin, Archimedes, and Aristotle were regarded as resistant cultivars in the field to an isolate from New York (Dunn et al. 2014). Our field results confirmed resistance of Paladin to NC isolates of *P. capsici* and differed with respect to Archimedes and Aristotle, which exhibited higher AUDPC means and were classified by the rank-sum analysis as intermediately resistant. Dunn et al. (2013) reported high susceptibility for cultivars Revolution, Declaration, and Vanguard; however, in our field experiments, these cultivars exhibited intermediate values of AUDPC means and were classified as intermediately resistant to a mix of current isolates from NC. We observed a high number of cultivars that performed as moderately susceptible, susceptible, and highly susceptible based on the rank-sum analysis. Dunn et al. (2013) classified Karisma, Keystone, and Red Knight as highly susceptible cultivars to an isolate from New York under field conditions. Our field evaluations categorized Keystone and Red Knight as susceptible and Karisma as a moderate susceptible to the mix of NC isolates used in this study. The 2016 field season had cooler temperatures and lower rainfall, which may account for lower disease levels. The 2015 field season presented higher AUDPC means than the 2016 field season; we attributed the variation observed between years to environmental conditions. Dunn et al. (2014) experienced similar variation among field seasons and suggested that higher AUDPC means could be a result of the ability of *P. capsici* to grow, sporulate, and disperse under warm and wet conditions.

In addition to field evaluations, greenhouse assays are also helpful to identify resistance to plant pathogens among pepper cultivars, and they allow for single-isolate testing to dissect isolate-specific resistance. Our greenhouse study revealed different levels of virulence among two representative isolates from NC farms and one isolate from Michigan. Similarly, Quesada-Ocampo and Hausbeck (2010) reported variation in virulence among *P. capsici* isolates from Michigan used during tomato resistance evaluations. When comparing the response of pepper cultivars to inoculations with isolate 12889 in our study and Foster and Hausbeck (2010b), CM334, Karisma, Aristotle, Camelot, Plato, Revelation, and Red Knight exhibited the same disease response in both studies. However, Paladin, Revolution, and Declaration were classified as intermediately resistant to 12889 in our study, whereas Foster and Hausbeck (2010b) classified them as susceptible to the same isolate. According to the rank-sum analysis, Paladin and Archimedes exhibited resistance to NC21810 and NCCP3 but were intermediately resistant to 12889 from Michigan. Dunn et al. (2014) also reported resistance

of Paladin and Archimedes using a single isolate from New York under field conditions. Intriguingly, NCCP3 isolated from squash displayed the lowest virulence among the isolates tested; however, cultivars SV3198HJ and EXP.12 were susceptible and moderately susceptible to NCCP3. The rank-sum method classified these two cultivars in two different disease responses based on the AUDPC means rank for each cultivar across the 2 years. Therefore, it classifies a response with rank positions 1 and 37 for 2015 and 2016 as moderately susceptible in the case of EXP.12, even though the AUDPC values are 0.1 and 0.27, respectively.

Despite attempts to classify *P. capsici* isolates into races based on virulence to differential pepper genotypes (Glosier et al. 2008; Oelke et al. 2003), there is no formal race classification used by the *P. capsici* research community (Dunn et al. 2014). In fact, the genetic basis of virulence of *P. capsici* remains under investigation because specific effectors associated with isolates with a particular virulence phenotype have not been defined (Dunn and Smart 2015; Schornack et al. 2010). Identifying the genetic basis of resistance genes and effectors interacting during pepper infection by *P. capsici* could shed light on observations of isolate-specific resistance and physiological races indicated by our study and several past studies. As a soilborne oomycete, *P. capsici* stratifies by geography owing to its inability to disperse by air (Parada-Rojas and Quesada-Ocampo 2018; Quesada-Ocampo et al. 2011b) and reproduces sexually, generating new isolates with a broad range of virulence (Granke et al. 2011a). Results from our greenhouse study indicate substantial differences in virulence between *P. capsici* isolates from NC (NC21810 and NCCP3) and Michigan (12889), and between NC isolates NC21810 and NCCP3. Understanding the virulence composition of local pathogen populations, in combination with knowledge of specific major resistance genes and effectors involved in a compatible or incompatible interaction between *P. capsici* and pepper, could help accelerate breeding efforts by pointing to key isolates to use in resistance screenings and could inform host resistance deployment so that cultivars resistant to the local population are used.

In the past, several studies have suggested that *P. capsici* isolates display higher virulence on their host of origin than on an alternative host. Ristaino (1990) concluded that cucurbit isolates of *P. capsici* were less virulent on pepper than on cucurbits. Similarly, Lee et al. (2001) suggested that an underlying effector present in pumpkin isolates but absent in pepper isolates favors aggressiveness to pumpkin cultivars. In our experiment, isolate NC21810 obtained from zucchini produced significantly higher AUDPC means than isolate 12889 (Michigan) obtained from peppers. Our results contradict Lee et al. (2001) and Ristaino (1990), suggesting that virulence is isolate specific, and underlying effectors resulting in such virulence may not necessarily be predicted by host of origin.

Classification of pepper cultivars into different categories of resistance to *P. capsici* relies on several methods and input variables. Foster and Hausbeck (2010b) used a method that utilizes a disease rating scale to classify cultivars between resistant and susceptible. Sy et al. (2008) employed the χ^2 method to compare against a resistant control cultivar (CM334) to define disease response among pepper cultivars. In this study, we used the rank-sum method, which allows for nonnormal data, results in classification of cultivars within an experiment in categories that can then be compared across experiments, eliminates the need for previous knowledge of the genetic structure of the pepper cultivars, and utilizes continuous variables such as AUDPC means (Onyeka et al. 2005). We observed strong Spearman rank correlation between deviations from the grand mean of the ranks and the AUDPC means, indicating that the disease response categories obtained by the rank-sum method are consistent with the disease severity data typically used in similar studies. For isolate NCCP3 in Table 4, we observed discordance in the disease response when compared with the AUDPC values of other isolates for both years. It is crucial to remember that, because of the aforementioned nature of the rank-sum analysis, the same AUDPC value may be classified differently between cultivar-by-isolate combinations.

We identified a group of commercially available pepper cultivars with high levels of resistance to Phytophthora blight in NC. Cultivars Martha-R, Meeting, Intruder, Paladin, and Archimedes were classified as highly resistant and resistant when challenged with the three *P. capsici* isolates tested in the greenhouse. Foster and Hausbeck (2010b) reported complete susceptibility for commercial cultivars of peppers with only the landrace CM334 and breeding lines exhibiting high resistance or resistance to 12889. Our results also report a list of highly susceptible cultivars to *P. capsici*. Touchdown, Bastille, Pepper #1, Keystone, Plato, and Red Knight were consistently susceptible or highly susceptible to all isolates tested under greenhouse conditions. Our findings imply that the disease response of susceptible cultivars is consistent regardless of the variation in virulence among the three *P. capsici* isolates. Despite observing higher AUDPC means in the field than in the greenhouse, highly resistant cultivars tended to respond similarly to single (high and low virulent) *P. capsici* isolates and mixed isolate inoculations. Cultivars classified as highly resistant in the field such as Fidel, Martha-R, and Meeting were also highly resistant in the greenhouse, supporting our findings. Our data demonstrated that cultivars Archimedes and Ebano-R and experimental lines EXP.9 and EXP.4, classified as resistant in the greenhouse to all or two of the three isolates, performed as intermediately resistant cultivars under field conditions and mixed inoculum. This reiterates the importance of screening under local environmental conditions with a diverse isolate population.

In summary, our field evaluations expand the set of commercially available cultivars that can improve disease management of Phytophthora blight of peppers in NC. A group of cultivars consistently performed as highly resistant or resistant when challenged with a mix of current *P. capsici* isolates from NC. We observed high variation in the levels of virulence among *P. capsici* isolates. These virulence differences highlight the importance of including diverse isolates that represent the virulence spectrum of the pathogen when screening for resistance. Overall, cultivars identified here as highly resistant have a consistent response to mixed field inoculations and greenhouse single-isolate inoculations with a virulent isolate. Host resistance remains a promising management strategy to control *P. capsici* in pepper, and our study highlights the importance of accounting for pathogen diversity when screening for resistance.

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