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Research Article

Novel sources of resistance to powdery mildew (*Leveillula taurica* (Lév.) Arnaud) in pepper

Ivan-Ilich MORALES-MANZO[1], Adrián RODRÍGUEZ-BURRUEZO[1], Marisa JIMÉNEZ-PÉREZ[1], José J. LUNA-RUIZ[2], Alberto SAN-BAUTISTA[3], Ana FITA[1]*

[1]*Universitat Politècnica de València, Instituto de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV), Camino de Vera s/n, 46022, Valencia, Spain; ivmoman@posgrado.upv.es; adrodbur@upvnet.upv.es; majipe1@posgrado.upv.es; anfifer@btc.upv.es (*corresponding author)*
[2]*Universidad Autónoma de Aguascalientes (UAA), Centro de Ciencias Agropecuarias, Avenida Universidad 940, Aguascalientes, Aguascalientes 20100, Mexico; joselunaruiz11@yahoo.com.mx*
[3]*Universitat Politècnica de València, Centro Valenciano de Estudios sobre Riego – Dep. Producción Vegetal, Camino de Vera s/n, 46022, Valencia, Spain; asanbau@prv.upv.es*

Abstract

Peppers, a worldwide crop, are threatened by different pathogens. Powdery mildew, a biotroph fungal infection, can cause several damages directly on vegetative parts and indirectly on fruits. Despite some sources of resistance have been described, commercial genotypes only with partial resistance have been developed due to the complex nature of such resistance and variable genetic expression, which depends on the stage of the plants. In this paper 49 accessions from different *Capsicum* species and origins have been tested. Plants were grown in growth chambers inside of mini greenhouses. Repeated inoculations under pepper leaves were applied by spraying a suspension of 10^4 conidia ml^{-1}. Readings were made at 30 and 60 days after inoculation (DAI). Total number of leaves (TL), total number of affected leaves (LA), and maximum area affected (MAA) in the most damaged leaf were scored. In addition, a composite infection index (CII) was calculated on the basis of the three mentioned traits. Inoculated plants showed more severe symptoms at 30 DAI than at 60 DAI. Different response patterns were observed: from accessions suffering high leaf shedding to some others with local hypersensitive response, indicating different gene action. The use of CII prevented species bias and disease response. In the present work, four highly tolerant accessions were identified, including two chiltepins, *C. annuum* wild relatives, Ag-01 and Ag-02, and two *C. annuum* A-06 and A-23.

Keywords: chiltepin; high tolerance; oidium; chlorosis; complex control resistance; screening

Introduction

Peppers (*Capsicum* spp.) are one of the most important horticultural crops grown worldwide and adapted to a range of growing conditions, which are used as both fresh or processed (FAOSTAT, 2021). As a widespread crop it is threaten by different pathogens. Powdery mildew (*Leveillula taurica* (Lév.) Arn.) is one of them, mainly in cool and humid environments, as greenhouses and open fields in mid-latitudes during autumn

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and winter seasons (Parisi *et al.*, 2020). Infection of this obligate fungal endoparasite biotroph starts when airborne conidia (asexual spores) lands over upper leaf surface, germinates and hypha enters by stomata or any other aperture, developing his mycelium inside mesophyll leaves (Zheng *et al.*, 2013). First symptoms are yellow chlorotic spots in the oldest leaves. Later, the development of conidiophores on abaxial leaves (underside) provokes the characteristic white powder of this disease. Premature leaf shedding (or leaf abscission) is induced, affecting production by both decreasing photosynthesis and exposing fruits to sunscald (Molot *et al.*, 1990).

The biotroph nature of the fungus requires to maintain infected plants as a source of inoculum and limits the evaluation of accessions for resistance (Daubeze *et al.*, 1995; Lefebvre *et al.*, 2003; Blat *et al.*, 2005 and 2006). Evaluation usually is done in open fields at the fruiting stage, but it also can be done under controlled conditions (greenhouses or growth chambers) during early plant stages, where inoculation of accessions is done from 3-4 true leaves up to the fruiting stage (de Souza and Café-Filho, 2003; Zheng *et al.*, 2013). The response in early stages can differ from those in adult plants. For instance, some *C. annuum* L. commercial accessions have showed better responses against the infection in young plants (de Souza and Café-Filho, 2003). Three main inoculation techniques are commonly used: i) natural infection, ii) artificial inoculation by directly brushing conidia on leaves; iii) spraying conidia suspensions of variable concentration (10^5 – 2.5×10^4 ml^{-1}) with *Triton X 100* 1µl ml^{-1} (Molot *et al.*, 1990; Daubeze *et al.*, 1995; Zheng *et al.*, 2013; Albert *et al.*, 2017; Özer *et al.*, 2018; McCoy and Bosland, 2019). Controlled screenings have been performed using a wide range of temperatures (16-27 °C, Molot *et al.*, 1987; Zheng *et al.*, 2013), humidity (30-70% ± 15 RH, Bai *et al.*, 2003; Zheng *et al.*, 2012) and photoperiod (12-14 h light and 12-10 h dark, Molot *et al.*, 1987; Özer *et al.*, 2018). To evaluate properly the response to infection some authors have suggested semi-quantitative scoring system or variants (Molot *et al.*, 1987). Such methodology ranks the plants using a scale from 0 to 5, where 0 = to healthy plant (*i. e.*, no infested leaves) and 5 = 80-100% plant foliage infested. Daubeze *et al.* (1995) used a similar scoring system called sporulation intensity (Sp, 0-5 scale), but also evaluated the proportion of diseased leaf area per plant (Pr, 0-5 scale) using a semi-quantitative scale too.

Although some sources of tolerance to powdery mildew (PM) have been reported in peppers, no complete resistance has been found. One of the first and most resistant *C. annuum* accessions identified were H3 (a pungent small-fruited Ethiopian powdery mildew resistant accession) and HV-12, an accession obtained as haplodiploid from hybrids of H3 and cv. 'Vania' (Daubeze *et al.*, 1995; de Souza and Café-Filho, 2003; Zheng *et al.*, 2013). High tolerances have been found in other *Capsicum* species like *C. baccatum* L., *C. chinense* Jacq., *C. frutescens* L., and *C. pubescens* Ruiz & Pav. (Lee *et al.,* 2001; de Souza and Café-Filho, 2003; Blat *et al.*, 2005 and 2006). Despite *C. chinense* and *C. frutescens* are grouped within the *C. annuum* botanical complex, sexual incompatibility (both pre and postzygotic) has been reported on many occasions, depending on the accession (Manzur *et al.*, 2015). Therefore, the introgression of genes from other species into *C. annuum* is limited. Recently, McCoy and Bosland (2019) evaluated 152 accessions of *Capsicum spp.* under natural (not controlled) infection conditions in New Mexico fields. They putatively identified several *C. annuum* accessions and one accession of chiltepin (*C. annuum* var. *glabriusculum* (Dunal)), opening the possibility to find resistance genes in *C. annuum*. In this regard, screenings for PM resistance have not been conducted yet with sufficient accessions of *C. annuum* var. *glabriusculum*, a wild and semi-wild form of pepper, which has been described as a close ancestor of *C. annuum* (Aguilar-Meléndez *et al.*, 2009; Kraft *et al.*, 2013; Hayano-Kanashiro *et al.*, 2016; Pereira *et al.*, 2019). Several populations of wild and semiwild peppers are naturally distributed across Mexico (Luna-Ruiz *et al.*, 2018), and Kraft *et al.* (2013) assembled a collection of wild and semiwild peppers from Mexico and Southern USA, which may be good candidates to explore for additional sources of resistance to PM.

The objective of the present work was to screen, under controlled conditions, a wide range of *Capsicum* spp. accessions, including *C. annuum* var. *glabriusculum*, to identify possible novel sources of tolerance or resistance to PM.

Materials and Methods

Plant material and infection assay

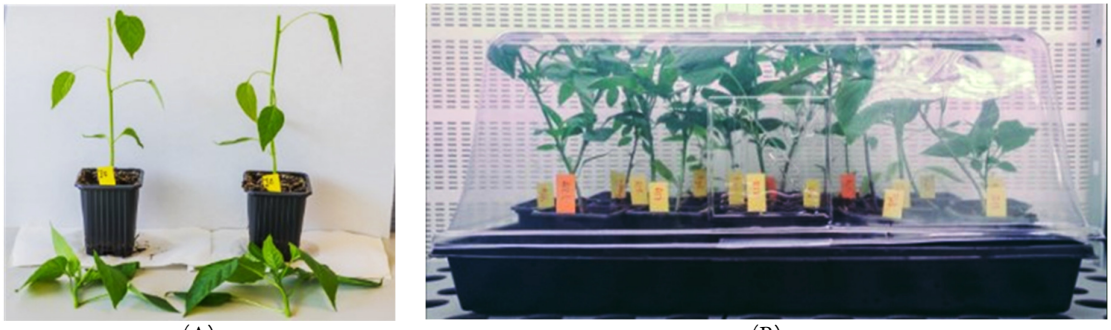
Forty-nine accessions of five different *Capsicum* taxa (22 *C. annuum* including some commercial cultivars, 5 *C. annuum* var. *glabriusculum*, 13 *C. baccatum*, 6 *C. chinense*, 1 *C. frutescens*. and 2 *C. pubescens*) were evaluated in two different trials (Table 1). In each trial three commercial accessions known for their good response against PM in field conditions (*C. annuum*: Co-0*) were included as controls. In addition, in the second trial four accessions selected from the first trial were re-evaluated to confirm their response against PM.

Table 1. Plant materials used, accessions names, abbreviations, origins and number of replicates in each trial tested

Accession	Abbreviation	Origin	No. replicates by trial	
Capsicum annuum			First	Second
Ací Sivri	A-09	Turkey	-	5
Acorde RZ F_1 (53-142)	Co-01	Rijk Zwaan, Spain	20	5
Ancho 101	A-10	Mexico, USA	-	5
Ancho Mulato	A-17	Mexico, USA	-	5
Bola	A-01	Murcia, Spain	5	-
California Wonder (r)	A-23	Breeding line COMAV, Valencia, Spain	-	5
California Wonder (y)	A-02	Breeding line, COMAV, Valencia, Spain	5	-
Carmagnola Rosso	A-12	Carmagnola, Italy	-	5
Chile Serrano 204D	A-03	Mexico/USA	5	-
Chile Serrano	A-04	Mexico/USA	5	-
Jalapeño Candelaria	A-13	Mexico/USA	-	5
Jalapeño Espinalteco 10397	A-21	Mexico/USA	-	5
Jalapeño M.	A-18	Mexico/USA	-	5
Kabuki F_1 (BF50820)	Co-02	Syngenta, Spain	20	5
Largo de Reus	A-05	Mascarell Seed Co., Spain	5	-
Largo Valenciano	A-14	Alicante, Spain	-	5
Mojo Palmero	A-22	La Palma, Spain	-	5
Nirvin RZ F_1 (35-150)	Co-03	Rijk Zwaan, Spain	10	5
Pasilla Bajío	A-06	Mexico/USA	5	-
Pimiento Valenciano	A-16	Valencia, Spain	-	5
Piquillo	A-07	Navarra, Spain	5	-
Serrano Criollo Morelos	A-08	Morelos, Mexico	5	-
C. annuum var. *glabriusculum*				
Arizona 1003	Ag-01	Arizona, USA	5	5
Chiapas 1333	Ag-03	Chiapas, Mexico	-	5
Nayarit 1411	Ag-04	Nayarit, Mexico	-	5
Oaxaca 1430	Ag-02	Oaxaca, Mexico	5	5
Veracruz 1196	Ag-06	Veracruz, Mexico	-	5
C. baccatum				
Bol – 103	B-04	Santa Cruz, Bolivia	5	-
Bol – 104	B-05	Santa Cruz, Bolivia	5	-
Bol – 106	B-11	Santa Cruz, Bolivia	-	5
Bol – 108	B-12	Santa Cruz, Bolivia	-	5
Bol – 111	B-13	Santa Cruz, Bolivia	-	5
Bol – 115	B-14	Santa Cruz, Bolivia	-	5
Bol – 117	B-07	Santa Cruz, Bolivia	5	-

Bol – 120	B-15	Santa Cruz, Bolivia	-	5
Bol – 134	B-01	Santa Cruz, Bolivia	5	-
Bol – 37R	B-03	Chuquisaca, Bolivia	5	-
Asta de Toro	B-02	Cochabamba, Bolivia	5	-
Bol – 67	B-09	Cochabamba, Bolivia	5	-
Bol – 71	B-10	Santa Cruz, Bolivia	5	5
C. chinense				
Aji dulce	C-01	Venezuela	5	-
Bol – 198	C-02	Santa Cruz, Bolivia	5	5
Ají Charapita	C-03	Amazonia, Peru	5	-
ECU-994	C-04	Ecuador	5	-
Habanero Rojo	C-06	Pennsylvania, USA	-	5
Ají Mochero	C-05	Valle de Moche, Peru	5	-
C. frutescens				
Bol – 144	F-01	Santa Cruz, Bolivia	5	-
C. pubescens				
Bol – 188	P-01	Chuquisaca, Bolivia	-	5
Bol – 59	P-02	Cochabamba, Bolivia	-	5

Seeds were sown in trays and one month later seedlings were transplanted to 7.5 × 7.5 cm pots. One week after transplanting, plants were trimmed to leave only three to four basal leaves (Figure 1A). Plants were then placed in mini greenhouses in a randomized block design (Figure 1B). Mini greenhouses were placed in climate chambers with an average temperature of 21 °C ± 2, and relative humidity of 80% ±5 (Bai *et al.*, 2003; Zheng *et al.*, 2012).



(A) (B)

Figure 1. Experiment setup
(A) 30 days old pepper plants decapitated ready to be inoculated; (B) mini greenhouses used to avoid spreading over inside climatic chamber of inoculum

Plants were inoculated and later reinoculated three times (at 7, 14 and 21 days after the first inoculation) by spraying the abaxial part of the leaves with a water suspension of 10^4 conidia ml^{-1} (maximum concentration obtained). *L. taurica* inoculum was obtained from infected leaves of peppers grown in commercial fields and kept *in vivo* in susceptible materials under controlled conditions. Plants were evaluated 30 and 60 days after the first inoculation (DAI).

Response evaluation

Due to the broad range of *Capsicum* species evaluated and to overcome the possible bias, a Composite Infection Index (CII) based in Daubeze *et al.* (1995) was used. The total number of leaves (TL) and the total number of leaves affected (LA) showing chlorotic spots were recorded in each evaluation date. Also, a LA/TL ratio, similar to "the sporulation intensity" of Daubeze, was calculated. The area affected in the most damaged

leaf, named maximum area affected (MAA), was also considered as Daubeze's "leaf area per plant". The MAA was recorded visually by scoring the proportion of leaf surface covered by chlorotic or sporulation spots (from 0.00 to 1.00 was used where 10% surface of chlorotic-sporulate spots was 0.10, 20% = 0.20... and 100% = 1.00). Our proposed CII (on a 0.00-1.00 scale) was calculated as follows:

$$CII = \frac{\left(\frac{LA}{TL}\right) + MAA}{2} \quad (1)$$

Statistical analysis

Five plants per accession were evaluated in both trials, except commercial accessions in the first trial (10 to 20 plants). Two-way factorial analysis of variance (ANOVA, $P < 0.05$) was performed using individual plant n-values to assess accession and block (mini greenhouses) effects (Hoshmand, 2020). In addition, Student-Newman-Keuls *post-hoc* multiple range test ($P < 0.05$) was used to detect significant differences among accessions means for all the evaluated traits. Data was standardized by z-score to compare within and between trials. All statistical analysis was performed using Statgraphics Centurion XVIII (18.1.13 ver., Statgraphics Technologies, VA, USA).

Results

First screening

The first trial infection produced the characteristic damage of PM in the plants. When assessing the performance of the 27 accessions tested in this trial, the ANOVA showed significant differences among them for all the evaluated traits ($P < 0.001$, Suppl. Table 1). As plants were organized in a randomized block design, the possible influence of the block was investigated. Also, the effect of the block contributed significantly to variation (Suppl. Table 1). This circumstance was considered on *post-hoc* analysis.

Infection intensity was higher at 30 than at 60 DAI (Table 2). Average LA TL^{-1} ratio was 0.32 at 30 DAI and decreased to 0.18 at 60 DAI; average MAA was 0.18 at 30 DAI and 0.23 at 60 DAI; average CII was 0.25 at 30 DAI and 0.20 at 60 DAI.

At 30 DAI the mean values of total number of leaves (TL) ranged from 7.85 (Co-02) to 20.38 (C-03), and accessions separate significantly in different groups, being Co-02, Co-01, A-02, A-07, Co-03, A-05 and B-10 the ones with the lowest number of leaves, whereas A-08, B-04, F-01, Ag-02, and C-03 showed the highest number (Table 2). The average number of leaves affected (LA) ranged from 0.36 (Ag-01) to 8.40 (C-03) and the accession Ag-01 differed significantly from the six most affected accessions (i.e., B-07, B-03, B-01, A-04, A-08 and C-03). For the ratio of affected leaves, mean values ranged from 0.07 (Ag-01) to 0.56 (A-02) and Ag-01 and C-05 significantly differed from the last three accessions (A-08, B-01 and A-02). For the MAA, mean values were comprised from 0.04 (Ag-01) to 0.42 (A-04), although only Ag-01 and C-05 were differed significantly from the two worst two accessions, A-02 and A-04. In the case of the composite infection index (CII), mean values ranged from 0.05 (Ag-01) as the most tolerant, to 0.44 (A-04), as the most susceptible. In this regard, the statistical test separates clearly Ag-01 and C-05 from the worst five accessions (B-10, B-01, A-08, A-02 and A-04) (Table 2).

At 60 DAI, the ANOVA detected significant differences among accessions in most traits, particularly in TL and LA (Suppl. Table 2). In TL, accessions grouped significantly like those at 30 DAI and, thus, the accessions with the highest number of leaves at 30 DAI also had high number of leaves at 60 DAI (Table 2). By contrast, this was not the case for the rest of parameters, indicating that the evolution of these traits from 30 to 60 DAP was different among the accessions. Thus, some accessions like A-06, Ag-01 and Ag-02 evolved with very low values of LA, LA/TL ratio, MAA and CII, C-02 showed moderate values in both 30 and 60 DAP, and C-03 and B-10 continued with high disease values (Table 2). On the contrary, some accessions like A-08, B-01,

B-03, A-04, B-05, which had very bad values in LA, LA/TL ratio, MAA and CII at 30 DAI, turned into very good performance at 60 DAI (Table 2).

Table 2. First trial mean values of total number of leaves (TL), leaves affected (LA), LA/TL ratio, maximum area affected (MAA) and composite infection index (CII) at 30 and 60 DAI

Acces.	TL		LA		LA/TL ratio		MAA		CII	
	30 DAI	60 DAI	30 DAI	60 DAI	30 DAI	60 DAI	30 DAI	60 DAI	30 DAI	60 DAI
Capsicum annuum										
A-01	12.02 ABCD	21.03 ABCDE	3.40 ABC	3.47 AB	0.30 ABC	0.17 A	0.13 AB	0.21 A	0.22 ABCD	0.19 A
A-02	9.12 AB	14.91 AB	4.28 ABC	3.29 AB	0.56 C	0.22 A	0.30 BC	0.21 A	0.43 D	0.21 A
A-03	12.64 ABCDE	23.30 ABCDEF	3.54 ABC	4.30 AB	0.29 ABC	0.17 A	0.18 AB	0.41 A	0.23 ABCD	0.29 A
A-04	16.56 CDEFG	40.10 G	6.46 CD	3.70 AB	0.45 ABC	0.11 A	0.42 C	0.17 A	0.44 D	0.14 A
A-05	9.52 AB	16.23 ABC	3.19 ABC	3.22 AB	0.33 ABC	0.19 A	0.11 AB	0.36 A	0.22 ABCD	0.27 A
A-06	13.68 ABCDEF	21.77 ABCDEF	2.41 ABC	2.58 A	0.19 ABC	0.11 A	0.13 AB	0.12 A	0.16 ABCD	0.12 A
A-07	9.17 AB	13.71 A	2.84 ABC	2.71 A	0.30 ABC	0.18 A	0.11 AB	0.34 A	0.20 ABCD	0.26 A
A-08	17.43 DEFG	35.49 EFG	8.16 D	2.29 A	0.51 BC	0.10 A	0.25 ABC	0.10 A	0.38 D	0.10 A
Co-01	9.00 AB	15.85 ABC	2.95 ABC	3.25 AB	0.35 ABC	0.20 A	0.15 AB	0.24 A	0.25 ABCD	0.22 A
Co-02	7.85 A	13.95 A	3.40 ABC	3.25 AB	0.45 ABC	0.25 A	0.14 AB	0.18 A	0.30 ABCD	0.21 A
Co-03	9.20 AB	14.70 AB	3.10 ABC	3.60 AB	0.35 ABC	0.27 A	0.27 ABC	0.21 A	0.31 ABCD	0.24 A
C. annuum var. *glabriusculum*										
Ag-01	14.92 BCDEFG	30.01 CDEFG	0.36 A	2.50 A	0.07 A	0.05 A	0.04 A	0.13 A	0.05 A	0.09 A
Ag-02	19.08 FG	36.59 FG	2.64 ABC	5.50 AB	0.10 AB	0.19 A	0.08 AB	0.17 A	0.09 ABC	0.18 A
C. baccatum										
B-01	12.56 ABCDE	22.84 ABCDEF	5.73 BCD	4.24 AB	0.53 C	0.18 A	0.22 ABC	0.11 A	0.37 D	0.14 A
B-02	16.64 CDEFG	36.56 FG	2.67 ABC	4.96 AB	0.17 ABC	0.20 A	0.16 AB	0.29 A	0.17 ABCD	0.24 A
B-03	13.92 ABCDEF	24.09 ABCDEF	5.66 BCD	2.91 A	0.38 ABC	0.12 A	0.28 ABC	0.16 A	0.33 BCD	0.14 A
B-04	18.28 DEFG	30.91 DEFG	3.54 ABC	4.49 AB	0.21 ABC	0.29 A	0.16 AB	0.26 A	0.18 ABCD	0.27 A
B-05	10.84 ABC	25.65 ABCDEFG	3.16 ABC	3.27 AB	0.37 ABC	0.14 A	0.26 ABC	0.17 A	0.32 ABCD	0.16 A
B-07	16.83 CDEFG	32.06 DEFG	5.27 BCD	5.93 AB	0.34 ABC	0.19 A	0.16 AB	0.39 A	0.25 ABCD	0.29 A
B-09	14.48 BCDEFG	34.74 DEFG	3.76 ABC	4.58 AB	0.29 ABC	0.12 A	0.21 ABC	0.25 A	0.25 ABCD	0.19 A
B-10	10.12 AB	19.86 ABCD	4.44 ABC	4.62 AB	0.48 ABC	0.25 A	0.21 AB	0.37 A	0.34 CD	0.31 A
C. chinense										
C-01	12.85 ABCDEF	25.08 ABCDEF	2.64 ABC	3.58 AB	0.20 ABC	0.15 A	0.14 AB	0.22 A	0.17 ABCD	0.18 A
C-02	13.35 ABCDEF	12.72 A	3.36 ABC	4.02 AB	0.26 ABC	0.29 A	0.12 AB	0.22 A	0.19 ABCD	0.25 A
C-03	20.38 G	35.39 EFG	8.40 D	7.43 B	0.41 ABC	0.20 A	0.20 AB	0.27 A	0.30 ABCD	0.24 A
C-04	16.48 CDEFG	28.88 BCDEFG	4.12 ABC	5.22 AB	0.31 ABC	0.17 A	0.14 AB	0.17 A	0.23 ABCD	0.17 A
C-05	17.14 CDEFG	29.80 CDEFG	1.86 AB	4.86 AB	0.08 A	0.20 A	0.04 A	0.19 A	0.06 AB	0.19 A
C. frutescens										
F-01	18.79 EFG	31.28 DEFG	3.91 ABC	5.74 AB	0.24 ABC	0.17 A	0.14 AB	0.27 A	0.19 ABCD	0.22 A
Mean	13.81	25.46	3.90	4.06	0.32	0.18	0.18	0.23	0.25	0.20

*Mean values with different letters within columns (ABCDEFG) are significantly different based on the Student-Newman-Keuls multiple range test at $p < 0.05$.

Second screening

Based on the results of the first screening, four accessions were selected to be included in the second screening, as they showed good response (Ag-01 and Ag-02), moderate response (C-02) and bad response (B-10), in both 30 and 60 DAI evaluations. Unfortunately, accession A-06 which showed a good performance in the first screening and was planned to be included as well, showed a poor germination (< 10%) and, consequently, it was discarded for the second screening.

The ANOVA found significant differences between accessions in most traits, with the only exception of MAA, and in most cases the effect of the block was also significant, which was considered when doing *post-hoc* analysis (Suppl. Table 3). On the whole, the severity of the symptoms at 30 DAI in all the accessions was higher on this second screening than those recorded in the first trial (Tables 2 and 3; Figure 2).

Table 3. Second trial mean values of total number of leaves (TL), leaves affected (LA), LA/TL ratio, maximum area affected (MAA) and composite infection index (CII) at 30 and 60 DAI

Acces.	TL		LA		LA/TL ratio		MAA		CII	
	30 DAI	60 DAI	30 DAI	60 DAI	30 DAI	60 DAI	30 DAI	60 DAI	30 DAI	60 DAI
Capsicum annuum										
A-09	7.04 $_{A}$	10.59 $_{A}$	6.03 $_{ABC}$	4.77 $_{AB}$	0.85 $_{ABC}$	0.62 $_{D}$	0.42 $_{A}$	0.18 $_{A}$	0.64 $_{AB}$	0.40 $_{B}$
A-10	10.18 $_{AB}$	21.13 $_{AB}$	5.70 $_{ABC}$	7.63 $_{AB}$	0.59 $_{ABC}$	0.36 $_{ABC}$	0.34 $_{A}$	0.20 $_{A}$	0.47 $_{AB}$	0.28 $_{AB}$
A-12	5.84 $_{A}$	19.87 $_{AB}$	3.75 $_{ABC}$	4.24 $_{AB}$	0.73 $_{ABC}$	0.21 $_{ABC}$	0.25 $_{A}$	0.14 $_{A}$	0.49 $_{AB}$	0.18 $_{AB}$
A-13	9.60 $_{AB}$	22.04 $_{AB}$	7.51 $_{ABC}$	5.96 $_{AB}$	0.74 $_{ABC}$	0.27 $_{ABC}$	0.37 $_{A}$	0.22 $_{A}$	0.56 $_{AB}$	0.24 $_{AB}$
A-14	5.93 $_{A}$	18.31 $_{AB}$	4.58 $_{ABC}$	6.49 $_{AB}$	0.84 $_{ABC}$	0.44 $_{BCD}$	0.30 $_{A}$	0.22 $_{A}$	0.57 $_{AB}$	0.33 $_{AB}$
A-16	3.57 $_{A}$	18.43 $_{AB}$	2.48 $_{AB}$	3.94 $_{AB}$	0.93 $_{ABC}$	0.24 $_{ABC}$	0.48 $_{A}$	0.13 $_{A}$	0.70 $_{AB}$	0.18 $_{AB}$
A-17	8.24 $_{A}$	25.27 $_{AB}$	5.95 $_{ABC}$	9.04 $_{AB}$	0.78 $_{ABC}$	0.35 $_{ABC}$	0.35 $_{A}$	0.22 $_{A}$	0.56 $_{AB}$	0.29 $_{AB}$
A-18	7.70 $_{A}$	19.77 $_{AB}$	5.10 $_{ABC}$	5.10 $_{AB}$	0.77 $_{ABC}$	0.40 $_{ABCD}$	0.39 $_{A}$	0.41 $_{B}$	0.58 $_{AB}$	0.41 $_{B}$
A-21	8.55 $_{A}$	17.69 $_{AB}$	7.38 $_{ABC}$	6.65 $_{AB}$	0.95 $_{BC}$	0.46 $_{CD}$	0.55 $_{A}$	0.17 $_{A}$	0.75 $_{B}$	0.31 $_{AB}$
A-22	10.35 $_{AB}$	26.56 $_{ABC}$	8.59 $_{ABCD}$	5.97 $_{AB}$	0.86 $_{ABC}$	0.23 $_{ABC}$	0.44 $_{A}$	0.24 $_{A}$	0.65 $_{AB}$	0.23 $_{AB}$
A-23	5.33 $_{A}$	18.86 $_{AB}$	2.90 $_{ABC}$	3.07 $_{AB}$	0.52 $_{AB}$	0.17 $_{ABC}$	0.18 $_{A}$	0.17 $_{A}$	0.35 $_{A}$	0.17 $_{AB}$
Co-01	7.15 $_{A}$	21.91 $_{AB}$	5.36 $_{ABC}$	4.46 $_{AB}$	0.74 $_{ABC}$	0.20 $_{ABC}$	0.43 $_{A}$	0.09 $_{A}$	0.58 $_{AB}$	0.14 $_{A}$
Co-02	3.59 $_{A}$	16.37 $_{AB}$	2.29 $_{A}$	4.27 $_{AB}$	0.75 $_{ABC}$	0.24 $_{ABC}$	0.25 $_{A}$	0.13 $_{A}$	0.50 $_{AB}$	0.19 $_{AB}$
Co-03	5.39 $_{A}$	20.67 $_{AB}$	3.32 $_{ABC}$	5.26 $_{AB}$	0.82 $_{ABC}$	0.27 $_{ABC}$	0.33 $_{A}$	0.20 $_{A}$	0.57 $_{AB}$	0.23 $_{AB}$
C. annuum var. *glabriusculum*										
Ag-01	23.29 $_{D}$	44.67 $_{CD}$	10.40 $_{CDE}$	8.09 $_{AB}$	0.51 $_{A}$	0.18 $_{ABC}$	0.30 $_{A}$	0.10 $_{A}$	0.41 $_{AB}$	0.14 $_{A}$
Ag-02	10.44 $_{AB}$	29.92 $_{ABCD}$	6.54 $_{ABC}$	8.32 $_{AB}$	0.71 $_{ABC}$	0.29 $_{ABC}$	0.25 $_{A}$	0.15 $_{A}$	0.48 $_{AB}$	0.22 $_{AB}$
Ag-03	7.45 $_{A}$	29.08 $_{ABCD}$	6.44 $_{ABC}$	8.61 $_{AB}$	0.89 $_{ABC}$	0.28 $_{ABC}$	0.42 $_{A}$	0.12 $_{A}$	0.65 $_{AB}$	0.20 $_{AB}$
Ag-04	16.72 $_{BC}$	30.34 $_{ABCD}$	10.13 $_{BCDE}$	9.73 $_{B}$	0.69 $_{ABC}$	0.30 $_{ABC}$	0.34 $_{A}$	0.18 $_{A}$	0.51 $_{AB}$	0.24 $_{AB}$
Ag-06	19.36 $_{CD}$	73.11 $_{E}$	15.37 $_{E}$	14.18 $_{C}$	0.80 $_{ABC}$	0.22 $_{ABC}$	0.33 $_{A}$	0.29 $_{AB}$	0.57 $_{AB}$	0.25 $_{AB}$
C. baccatum										
B-10	10.42 $_{AB}$	33.17 $_{BCD}$	7.45 $_{ABC}$	6.19 $_{AB}$	0.69 $_{ABC}$	0.18 $_{ABC}$	0.33 $_{A}$	0.21 $_{A}$	0.51 $_{AB}$	0.19 $_{AB}$
B-11	10.02 $_{AB}$	29.07 $_{ABCD}$	6.64 $_{ABC}$	4.71 $_{AB}$	0.75 $_{ABC}$	0.18 $_{ABC}$	0.26 $_{A}$	0.11 $_{A}$	0.51 $_{AB}$	0.15 $_{A}$
B-12	11.48 $_{AB}$	26.15 $_{ABC}$	9.29 $_{ABCD}$	5.33 $_{AB}$	0.77 $_{ABC}$	0.19 $_{ABC}$	0.50 $_{A}$	0.29 $_{AB}$	0.63 $_{AB}$	0.24 $_{AB}$
B-13	10.88 $_{AB}$	33.44 $_{BCD}$	10.38 $_{CDE}$	3.33 $_{AB}$	0.94 $_{ABC}$	0.10 $_{AB}$	0.37 $_{A}$	0.21 $_{A}$	0.65 $_{AB}$	0.15 $_{A}$
B-14	21.42 $_{CD}$	37.00 $_{BCD}$	14.62 $_{DE}$	6.96 $_{AB}$	0.72 $_{ABC}$	0.19 $_{ABC}$	0.34 $_{A}$	0.16 $_{A}$	0.53 $_{AB}$	0.17 $_{AB}$
B-15	11.65 $_{AB}$	24.96 $_{AB}$	7.17 $_{ABC}$	6.04 $_{AB}$	0.65 $_{ABC}$	0.24 $_{ABC}$	0.28 $_{A}$	0.21 $_{A}$	0.46 $_{AB}$	0.22 $_{AB}$
C. chinense										
C-02	4.22 $_{A}$	17.87 $_{AB}$	3.44 $_{ABC}$	5.31 $_{AB}$	0.97 $_{C}$	0.34 $_{ABC}$	0.36 $_{A}$	0.27 $_{AB}$	0.66 $_{AB}$	0.31 $_{AB}$
C-06	6.45 $_{A}$	26.81 $_{ABC}$	5.45 $_{ABC}$	5.85 $_{AB}$	0.89 $_{ABC}$	0.22 $_{ABC}$	0.41 $_{A}$	0.10 $_{A}$	0.65 $_{AB}$	0.16 $_{AB}$
C. pubescens										
P-01	10.98 $_{AB}$	45.73 $_{D}$	8.11 $_{ABC}$	2.74 $_{A}$	0.85 $_{ABC}$	0.10 $_{AB}$	0.45 $_{A}$	0.15 $_{A}$	0.65 $_{AB}$	0.12 $_{A}$
P-02	10.27 $_{AB}$	37.02 $_{BCD}$	6.19 $_{ABC}$	3.20 $_{AB}$	0.61 $_{ABC}$	0.08 $_{A}$	0.53 $_{A}$	0.16 $_{A}$	0.57 $_{AB}$	0.12 $_{A}$
Mean	9.78	27.44	6.85	6.05	0.77	0.26	0.36	0.19	0.57	0.22

*Mean values with different letters within columns ($_{ABCDEFG}$) are significantly different based on the Student-Newman-Keuls multiple range test at $p < 0.05$.

(A) (B) (C)

Figure 2. Results of the experiment; (A) Example tested plants; (B) Detail of Ag-01; (C) Detail of A-16 during the second trial at 30 DAI

TL mean values at 30 DAI ranged from 3.57 (A-16) to 23.29 (Ag-01) and showed significant differences according to the ANOVA ($P < 0.000$) (Suppl. Table 3). The statistical test separated a big group of fourteen accessions with the lowest values (A-16, Co-02, C-02, A-23, Co-03, A-12, A-14, C-06, A-09, Co-01, Ag-03, A-18, A-17, and A-21) from another group of four *C. annuum* var. *glabriusculum* and *C. baccatum* accessions (Ag-01, Ag-04, Ag-06, and B-14) showing the highest TL values (Table 3). Regarding LA, significant differences were found among accessions (ANOVA, $P < 0.000$) (Suppl. Table 3) and mean values ranged from 2.29 (Co-02) to 15.37 (Ag-06). The accessions differed statistically in a similar way to TL, with Co-02 and A-16 being the best accessions in one group and another group like the second group of TL (B-13, Ag-01, B-14 and Ag-06) (Table 3). The ANOVA also detected significant contribution of the accessions to the variation ($P < 0.003$) in the LA/TL ratio (ANOVA) (Suppl. Table 3) and mean values were comprised between 0.51 (Ag-01) and 0.97 (C-02) and the best accession Ag-01 differed significantly from the last two accessions (A-21 and C-02) (Table 3). As mentioned before, no significant differences were found in MAA (ANOVA, $P = 0.350$) (Suppl. Table 3) and the statistical test did not show significant differences among accessions, although mean values ranged 0.18 (A-23) to 0.55 (A-21) (Table 3). Finally, significant differences among accessions were found in CII (ANOVA, $P = 0.018$) (Suppl. Table 3), with the mean values being comprised between 0.35 (the best accession A-23) and 0.75 (A-21), which differed significantly (Table 3).

In general, according to the values recorded at 60 DAI, plants looked recovered from inoculation (Table 3). The ANOVA found a significant effect of the accessions in TL variation (ANOVA, $P < 0.000$) (Suppl. Table 4) and mean values ranged from 10.59 (A-09) to 73.11 (Ag-06), with A-09 being significantly worse than the group of accessions with the highest TL values, a mixture of *Capsicum* spp. (B-10, B-13, B-14, P-02, Ag-01, P-01 and Ag-06) (Table 3). For LA, also the ANOVA detected significant differences ($P< 0.000$) (Suppl. Table 4). Thus, mean values were comprised between 2.74 (P-01) and 14.18 (Ag-06), although only P-01 was significantly better than Ag-04 and Ag-06 (Table 3). Regarding the LA/TL ratio, mean values ranged from 0.08 (P-02) to 0.62 (A-09) and two groups of accessions differed significantly for this trait, with two *C. pubescens* and a *C. baccatum* (P-02, P-01 and B-13) showing LA/TL ratios considerably lower than the two *C. annuum* accessions A-21 and A-09 (Table 3). Significant differences were also found for MAA, and mean values ranged 0.09 (Co-01) to 0.41 (A-18), although only significant differences were found the 25 best accessions and the worst accession (A-18) (Table 3). Finally, significant differences were also found in CII (ANOVA, $P < 0.000$) (Suppl. Table 4), with mean values ranging from 0.12 (P-02) to 0.41 (A-18), and the best six accessions (P-02, P-01, Ag-01, Co-01, B-11 and B-13) differed significantly from the two worst accessions (Table 3).

Combined analysis of results

In order to have a general perspective of the performance of all the accessions evaluated, the z-score mean for CII was calculated for those accessions evaluated in the two trials (Suppl. Tables 5, 6 and 7). By plotting CII at 30 DAI against CII at 60 DAI it can be clearly observed that many genotypes had a consistent response against infection through the time. Thus, the CII z-score means of A-06, A-23, Ag-01, Ag-02 and C-05, had a consistent good response against the infection along the 30-60 DAI period (Figure 3, orange quadrant on the left), in contrast to the accession A-21, which showed a consistent bad response (Figure 3, orange quadrant on the right). In comparison, accessions like A-02, A-04 and A-08 showed high values of infection at 30 DAI, but good response (low CII values) at 60 DAI, suggesting a recovery of the plants. Finally accessions plotted at the left-top corner of the graph such as A-10 had worse values at 60 DAI than at 30 DAI (Figure 3, blue quadrant).

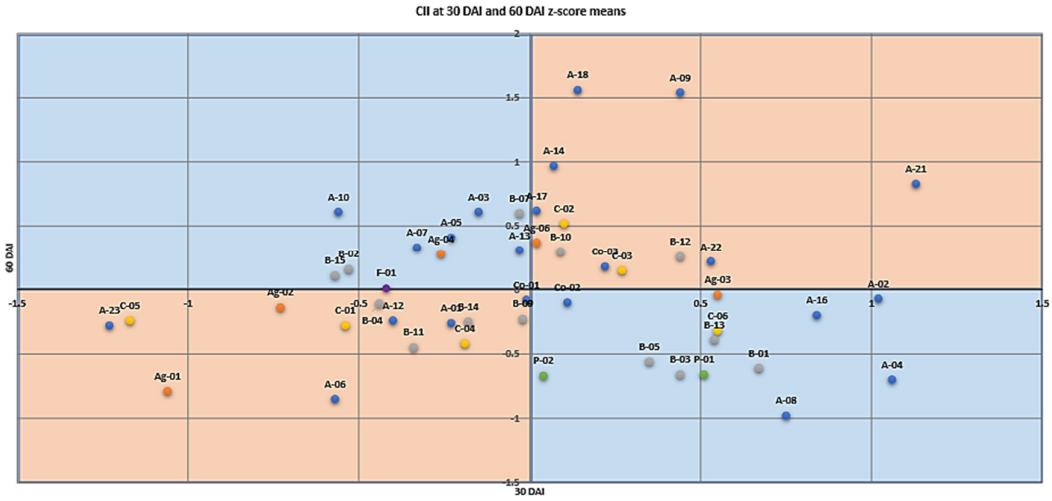


Figure 3. CII at 30 and 60 DAI z-score means

Color by *spp.* Red quadrants are steady responses, down-left as good, up-right as bad response. Blue quadrants are changing responses, up-left getting worst, and down-right getting better

Discussion

In this work, several *Capsicum* sp. accessions have been tested for their resistance to PM. Differences in the architecture, size, number of leaves and vigour among accessions could difficult the comparison of their level of tolerance. In addition, dichotomous evaluations for presence and absence of symptoms have been described as inefficient to properly define the resistance to *L. taurica* (Lin *et al.*, 2019). The use of a composite index mitigated those effects allowing a fair comparison.

Our findings indicate that responses to PM infection were highly dependent on the DAI readings. This agrees with other authors who found differences in the response to *L. taurica* inoculation according to the stage of development (de Souza and Café-Filho, 2003). In this study, plants had the most severe infection at 30 DAI while the responses at 60 DAI were variable among accessions. Some of them showed a remarkable recovery after a period with no inoculum pressure, while others showed similar symptoms and tolerance level at both evaluation times and, even, other accessions showed an increase in the symptoms at 60 DAI.

The resistance to PM is complex as it may be effective at different steps of the infection cycle, being also dependent on the plant age. Daubeze *et al.* (1995) estimated 2.6-3 genetic factors for seedlings and lighter inoculum pressure, and 5 genetic factors for older and strongest infection pressure. In this regard, leaf shedding is a common mechanism to deal with infection, that allows the plant to survive and sometimes recover. However, the production of photoassimilates is dramatically decreased during a period of time which can be

limiting for plant development and fruit setting. If defoliation takes place during the fruiting time, fruits can be exposed to excessive irradiation, increasing the risk of sunscald (Elad *et al.*, 2007; Sudha and Lakshmanan, 2009). Therefore, leaf shedding is considered as an indicator of susceptibility.

Other responses to PM infection are more valuable for hampering the development of the fungus, especially those which block the invasion of the host cells by the pathogen from the early stages. This is the action of the recessive genes *CaMlo1* and *CaMlo2* which are directly involved in cell death and formation of reactive oxygen species, thus avoiding appressorium establishment and germ tube penetration (Kim and Hwang, 2012). Or the classical response of the R-genes, as the PMR1 gene, a major nucleotide-binding site leucine-rich repeat-type gene (NBS-LRR) recently identified (Jo *et al.*, 2017) that detect pathogenic effectors and initiate immune responses. Even so, resistance to PM has a quantitative nature, from which, only some QTLs have been elucidated (Lefevre *et al.*, 2003; Eggink *et al.*, 2016; Gabor *et al.*, 2017).

As expected from the quantitative nature of the resistance to PM, our results showed a continuum of responses to *L. taurica* infection in the different accessions. To record the reaction at two different DAI allowed us to select accessions with a consistent response of low infection over the time, such as Ag-01, Ag-02, A-06, A-23, belonging to *C. annuum* and C-05, from *C. chinense*. On the contrary to other authors (Blat *et al.*, 2005 and 2006; McCoy and Bosland, 2019), our findings did not identified sources of resistance from the *C. baccatum* accessions tested here.

The best results of the experiments corresponded to Ag-01 in both trials, and other promising source of variation was Ag-02, although it showed a lower performance in the second trial. Both materials belong to *C. annuum* var. *glabriusculum* also known as chiltepins. This wild taxon, phylogenetically close to *C. annumm* (Pereira-Dias *et al.*, 2019), is a new source of resistance or tolerance genes only suggested previously by McCoy and Bosland (2019). Due to their cross- compatibility with *C. annumm* they offer the opportunity of easy introgressions of genes of interest by sexual hybridization, even easier than *C. chinense* or *C. frutescens* (Manzur *et al.*, 2015). In addition, the morphology of the leaves with higher hair density in Ag-01 than that observed in other accessions tested may suggest the presence of unexplored physical defense mechanism, as suggested in other species (Kono *et al.*, 2018).

Conclusions

The resistance to powdery mildew is controlled by several genes and the level of resistance vary with the age of the plant and the genetic background. Although some sources of resistance have been described previously, the search for novel tolerant accessions is still in course. Traditionally, high tolerance to powdery mildew has been found in other species than *C annuum*. However, here we have found high tolerance within the *C. annuum* taxon, in the var. *glabriusculum* which may facilitate the introgression of resistance genes into commercial varieties of common peppers. Further studies in adult plants, under several environment conditions and genetic analysis may confirm the potential of accessions of *C. annuum* var. *glabriusculum* as novel sources of resistance.

Authors' Contributions

Conceptualization: IIMM, ARB, JJLR and AF; Data curation: IIMM and AF; Formal analysis: IIMM and AF; Funding acquisition: IIMM, ARB and AF; Investigation: IIMM, ARB and AF; Methodology: IIMM, ARB and AF; Project administration: IIMM; Resources: ARB; Visualization: IIMM, MJP, JJLR and AF; Writing - original draft IIMM and AF; Writing - review and editing: IIMM, ARB, MJP, JJLR, ASB and AF.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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