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Phytophthora capsici resistance evaluation in pepper hybrids: Agronomic performance and fruit quality of pepper grafted plants

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Abstract

Phytophthora capsici has caused a major disease of pepper worldwide and only some partially resistant pepper cultivars are commercially available. In this work *P. capsici* resistance has been evaluated in the pepper hybrids Charlot and Foc, derived from pepper SCM 334, the most promising *P. capsici* resistance source. Inoculations with a highly virulent *P. capsici* isolate Pc-8 and the isolates Pc-448 and Pc-450 show that both hybrids have a level of tolerance that is similar to SCM 334. The measurement of the agronomic performance of both hybrids when used as rootstocks was made by comparing growth, yield, and the fruit quality of two commercial peppers (Coyote and Almuden) that were grafted onto Foc and Charlot. Comparisons were made with non-grafted and self-grafted plants. No differences were observed for growth since earliness in fruit maturity has been observed in Coyote grafted onto both Charlot and Foc rootstocks. Grafted plants produced a higher number of fruits per plant. However, higher commercial yields were only obtained in Coyote-grafted plants. Almuden-grafted and self-grafted plants showed a greater variability in fruit shape. Differences among Coyote- and Almuden-grafted plants are indicative of the importance of rootstock-scion interaction. Some fruit modifications such as changes in shape were observed in grafted and in self-grafted plants. Therefore, these modifications may be partially the consequence of the grafting process. Grafting onto both Foc and Charlot rootstocks did not modify the pericarp thickness and the mean number of lobes per fruit in Coyote and Almuden fruit. A slight increase in minerals and similar vitamin C content, a very important nutritional quality trait of peppers, were also obtained in the analysed fruit from grafted, self-grafted, and ungrafted plants.

Key words: *Phytophthora capsici*, grafting, pepper, interaction, quality, yield, rootstocks.

Introduction

Phytophthora root and crown rot caused by the oomycete *Phytophthora capsici* Leon has become a serious threat to pepper production and is a limiting factor for profitable production of many crops worldwide [1, 2]. Spain is the largest European pepper producer with 20,098 ha under cultivation in 2008 [3], and *P. capsici* is reported as potentially the most destructive disease affecting this crop [4]. Within the genotypes that exhibit resistance to *Phytophthora* root and crown rot, two pepper lines, Serrano Criollo de Morelos (SCM) 331 and 334 are the most promising [2, 5, 6]. Both have been used in breeding programs [7, 8], but no pepper cultivars with universal resistance to *Phytophthora* have been commercially released to date [9].

Grafting is a common technique that was developed in order to cope with soil-borne pathogens [10] and can be employed to enhance water or nutrient uptake [10-14] as well as for avoiding abiotic stresses such as low temperature [15] or salinity [16-19]. However, grafting may influence, positively or negatively, plant growth, yield, and the quality of scion fruit. This influence has been demonstrated in crops such as watermelon [20, 21].

Interest in pepper grafting worldwide has risen because of the increase in sustainable practices and the withdrawal of methyl bromide [22-25]. In these works, the use of rootstocks as part of the management of soil-borne pathogens has been proposed. Evaluation of some rootstocks in trials infected with *P. capsici* [26] or root knot nematodes [26, 27] were also reported.

The aim of this work was the evaluation of tolerance to *P. capsici* by Charlot and Foc pepper hybrids derived from SCM 334 [28] and the assessment of their agronomic performance (scion growth, yield, and fruit quality) when used as rootstocks. For this purpose we compared two commercial F1 pepper hybrids, Coyote (blocky type) and Almuden (rectangular type), grafted onto Charlot and Foc. Comparison was made with non-grafted and self-grafted plants.

Materials and Methods

P. capsici assessment: The *P. capsici* isolate Pc-8 from eastern Spain was chosen for an initial inoculation assay. This isolate has been shown as the most virulent of those previously assayed[28] and wilted 40% of SCM 334 inoculated plants. In this experiment each plant was irrigated with 5 ml of zoospores at 10^6 zoospores per ml (z.ml^{-1}). Zoospore suspensions were obtained for fungal inoculations in accordance with Larkin *et al.* [29]. Ten seedlings (five weeks old from seeding) of Charlot, Foc, SCM 334, PI 636424, Tresor, Almuden and Coyote were inoculated.

Charlot and Foc were hybrids obtained by Gisbert *et al.* [26]. Genotypes SCM 334 (PI 636424) and Chilcote (PI 201234) were provided by the UDSA Plant Genetic Resources Conservation Unit (USA), Coyote and Almuden F1 hybrids by Syngenta Seeds (the Netherlands) and Tresor-F1 by Nunhems Zaden (the Netherlands). In these experiments non-infected plants irrigated with soil drench were used as controls. This assay was conducted twice.

Before inoculation, all plants were watered to facilitate zoospore movement. Disease severity was rated for five weeks after inoculation. Plants affected by *P. capsici* were visually assessed and considered dead when they appeared irreversibly wilted. Five asymptomatic infected plants per genotype grew to maturity.

In a second assay the isolates Pc-448 and Pc-450 provided by F. Merino and J. Díez (University of A. Coruña) were used. In this assay, two replicates of 10 seedlings per genotype (Coyote, SCM 334, Charlot, and Foc) were inoculated as in the previous assay.

Grafting evaluation: The commercial hybrid pepper plants Almuden (A) and Coyote (C) were grafted onto Charlot (CH) and Foc (F) rootstocks using the cleft approach procedure described by Lee [10]. Non-grafted and self-grafted (A-A; C-C) plants of both commercial hybrids were used as controls. Almuden and Coyote commercial F1 pepper hybrids were chosen as representative of pepper hybrids cultivated in south-eastern Spain, the main sweet pepper producing area. Almuden is a Lamuyo-type pepper (rectangular shape) and Coyote a California-type (blocky shape) – both having three to four lobes.

Grafted (C-C, CH-C, F-C, A-A, CH-A, F-A) and ungrafted (A and C) pepper plants (fifteen to thirty plants per treatment) were transplanted in February 2008 to pots filled with non-fertilized coconut fibre substrate (Horticoco and Valimex, Valencia, Spain) and placed in a greenhouse (average 20ºC T max; 12ºC T min) in a completely random arrangement. Eight treatment combinations were made per triplicate (three rows). Plants were placed 0.4 m apart in rows separated by gaps of 1.7 m. They were watered using a drip irrigation system. Pressure compensated emitters that delivered 4 l/h were used for the drip irrigation. Final concentrations of the main anions and cations in the irrigation solution (ions in the irrigation water plus those supplied with the fertilizers) were: 11.66 mM NO_3^-, 1.50 mM $H_2PO_4^-$, 3.61 mM SO_4^{2-}, 0.50 mM HCO_3^-, 2.25 mM Cl^-, 1.00 mM NH_4^+, 5.50 mM K^+, 5.00 mM Ca^{2+}, 2.26 mM Mg^{2+}, 1.96 mM Na^+. Microminerals were supplied by adding the following salts to the irrigation water: 50 µM H_3BO_3, 10 µM FeEDTA, 4.50 µM $MnCl_2$, 3.80 µM $ZnSO_4$, 0.30 µM $CuSO_4$ and 0.10 µM $(NH_4)_6Mo_7O_{24}$. Excess water was applied in order to avoid salt build-up in the pots and to maintain a homogenous concentration of the nutrients and salts in the coconut fibre substrate. This hydroponic system was used in order to avoid the experimental error associated with differences in the soil heterogeneity and the availability of water resulting from cultivation in soil [30].

Growth of non-grafted and self-grafted plants as well as the appearance of flowers were visually observed weekly. Mean plant height (cm) was measured at 45 days when the first flowers appeared. The percentage of red fruit in the first and second harvests was used to determine earliness.

Fully mature fruit were harvested for two months, some 90 days, after transplanting. The fruit were weighed immediately after harvesting and visually classified as commercial or non-commercial quality (smaller and flattened fruit). Only the plants in the central row where sampled for the quality analysis. The number of seeds was indexed from zero (absence) to three (approximately the amount in the control fruit). Equatorial and longitudinal lengths (cm), pericarp thickness (mm) and the number of lobes were measured in 20 representative commercial-quality fruit per treatment. Ten to twenty representative marketable fruit pieces were collected at a similar maturity stage and analysed for quality parameters. The maturity stage was determined with reference to the CIEL*** coordinates using a Minolta CR-300 (Osaka, Japan) colorimeter. Fruit were dried in a forced-air oven at 80°C for 72 hours and weighed to determine the fruit dry matter (DM). For the quantification of total minerals (ash), 2 g of the dried samples was placed in a furnace at 450ºC for two hours, after which light coloured ash was weighed [calculated as 100 x (burnt weight/dry weight)] and expressed in g/100 g. Vitamin C was determined by titration with chloramine T using an automatic titration system equipped with a selective electrode (Titrino 702 SM in MEAS mode) (Metrohm, Herisau, Switzerland).

Data was statistically analysed using the analysis of variance (ANOVA) with two factors, grafting (non-grafted, self-grafted, CH-grafted and F-grafted) and scion (A and C), using the STATGRAPHICS software package. When statistical interaction of both factors was obtained, the ANOVA was carried out for each factor. Where the F-test proved significant ($p = 0.05$), means were compared using the Bonferroni test.

Results

P. capsici assessment: The susceptibility of seedlings to *P. capsici* isolate Pc-8 is shown in Fig. 1. Coyote and Almuden seedlings were highly susceptible and wilted quickly. *P. capsici* resistant SCM 334 displayed a greater resistance than Chilcote (15% vs. 35% wilted plants); and Tresor rootstock showed a high percentage of wilted plants (75%). Foc and Charlot demonstrated similar or even higher *P. capsici* resistance levels than SCM 334 (Fig. 1). The root dry weights (DW) of asymptomatic seedlings were compared in non-inoculated vs. inoculated plants and a DW reduction (mg) was observed in all inoculated plants (around 30% in SCM 334 and Charlot, 45% in Chilcote and Foc and 65% in Tresor). A sample of asymptomatic Tresor, Chilcote, SCM 334, Foc and Charlot inoculated plants was grown to adult stage (90 days post-inoculation, dpi). All Tresor plants wilted whereas the rest of peppers fructified – although showing a reduction in plant

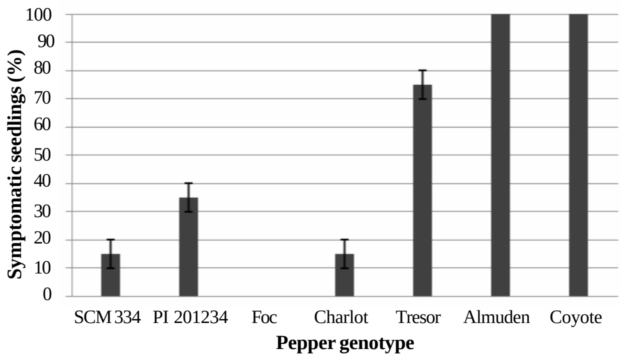

Figure 1. Percentages of symptomatic seedlings at five weeks post-inoculation with 5 ml of 10^6 z.ml^{-1} of the *P. capsici* isolate Pc-8. The values are the mean ± SE of two independent experiments (N = 10 seedlings inoculated per experiment).

height with respect to non-inoculated plants (35% in Chilcote and less than 20% in Foc, Charlot and SCM 334 plants).

Plants inoculated with the *P. capsici* isolates Pc-448 and Pc-450 did not die five weeks post-inoculation although a reduction of plant growth could be observed (Fig. 2). All the Coyote plants inoculated with both isolates suffered reduced growth when compared to non-inoculated plants by more than 50%. A reduction of 10% for SCM 334 and 23% for Charlot and Foc inoculated plants was observed (Fig. 2).

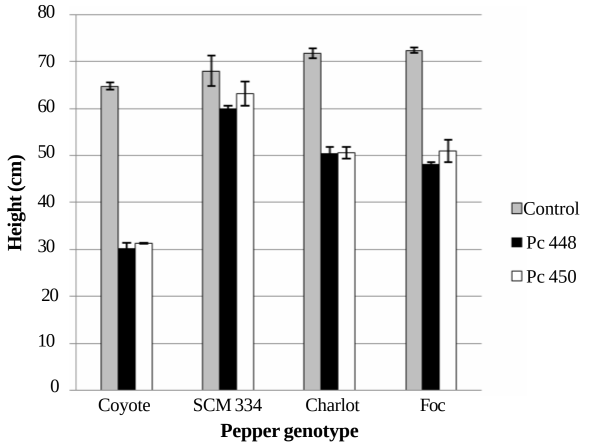

Figure 2. Plant height (cm) five weeks post inoculation with 5 ml of zoospores at 10^6 z.m^{-1} of the *P. capsici* isolates Pc-448 and Pc-450. The values are the mean ± SE of two independent experiments (N = 10 seedlings inoculated per experiment).

Grafting assay: Similar growth was observed independently of the treatment (non-grafted, self-grafted and grafted plants) for each pepper genotype during the vegetative period. The time elapsed between transplanting and anthesis of the first flowers was 45 days. Almuden plants were on average 112.61 ± 2.96 cm tall and those of Coyote were 99.67 ± 3.12 cm tall.

Harvest started three months after transplanting. The Coyote grafted plants (CH-C and F-C) produced twice as many ripe fruits as the C and C-C plants. Earliness was not observed in Almuden grafted plants. Harvested fruit were classified as commercial or non-commercial (smaller fruit or fruit with modified or flattened shapes). All the non-grafted Coyote plants were of commercial quality. Of the grafted plants 10.58, 8.72 and 7.91% of non-commercial quality fruit was harvested from C-C, CH-C and F-C plants, respectively. In the Almuden plants, non-commercial fruit was obtained in all treatments with percentages of 2.32, 12.5, 15.63 and 13.75 for A, A-A, CH-A and F-A, respectively.

Averages of the number of fruits per plant, fruit weight and yield are shown in Fig. 3. Differences for these parameters were observed in Almuden and Coyote treatments. The total number of fruit per plant was higher in grafted treatments than in non-grafted treatments (Fig. 3A). However, only in Coyote the number of commercial fruit was higher in the grafted plants. Fruit from CH and F-grafted plants showed a lower weight that those from non-grafted plants (Fig. 3B), mainly those from Almuden grafted plants – with a decrease in weight of 19-21% compared to fruit from ungrafted plants. Yield was higher for the total and commercial categories in Coyote grafted plants (CH-C and F-C) and lower in Almuden grafted plants when compared to non-grafted counterparts (Fig. 3C).

On average, commercial Almuden fruit measured 8.7 mm x 12.33 mm (width x length) corresponding to a rectangular shape and Coyote measured 7.9 mm x 9.0 mm with a blocky shape. A small but significant ($P \leq 0.001$) decrease in fruit length was produced in CH-A and F-A fruit. However, greater lengths were observed in Coyote fruit from self-grafted plants (Table 1). Small differences in fruit width were observed in all treatments. Fruit pericarp thickness was approximately 1 mm greater in Coyote than Almuden fruit; and these fruit had not suffered changes through grafting. The mean number of lobes per fruit (Table 1) remained unchanged. As a result of grafting, a large reduction in the number of seeds per fruit was observed in Almuden fruit from grafted plants (Table 1), mainly in those from F-A plants with more than 50% seedless fruit.

Representative samples of marketable fruit at a similar maturity stage were processed to determine the ascorbic acid and mineral content (ash). No significant differences among grafted treatments were recorded for the ascorbic acid content of the fruit (average 162.72 mg/100 mg fw). The result was strongly influenced ($P \leq 0.001$) by genotype scion with 148.2 mg/100 mg fw (on

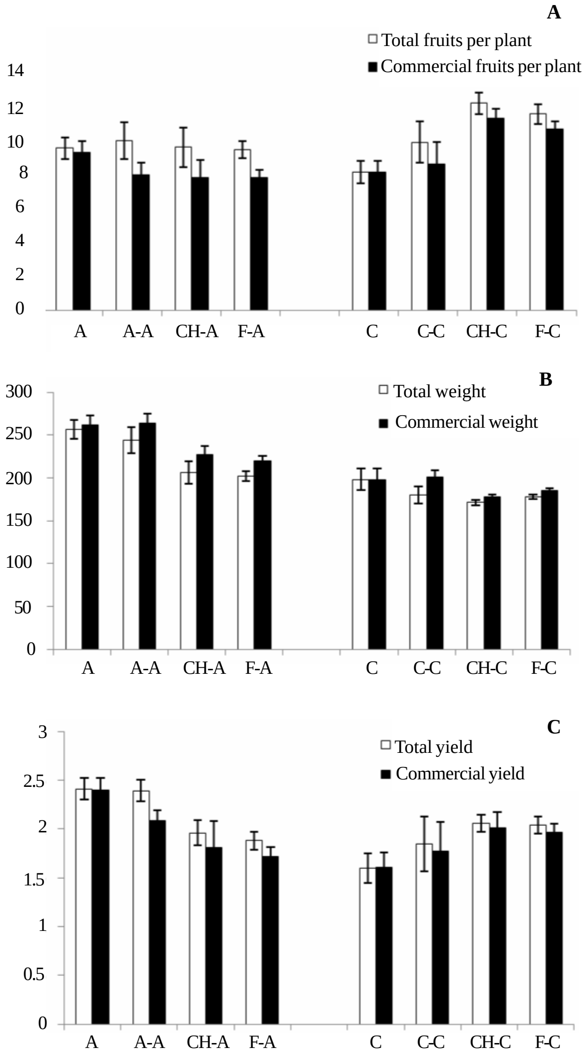

Figure 3. Means of: (A) the total (white bars) and commercial (dark bars) number of fruit per plant; (B) fruit weight (g) and (C) yield (kg) of Almuden (A) and Coyote (C) peppers, non-grafted (A, C), self-grafted (A-A, C-C) and grafted onto Charlot (CH-A; CH-C) and Foc (F-A, F-C) rootstocks. Error bars show standard errors of the mean of plant in each of the three rows (N = 5-10 plants for treatment in each row).

Table 1. Average values of quality Almuden (A) and Coyote (C) pepper fruit traits in non-grafted, self-grafted (A-A; C-C) and plants grafted onto Charlot (CH-A; CH-C) and Foc (F-A; F-C) rootstocks.

Treatment	Length (cm)	Width (cm)	Pericarp thickness (mm)	Number of lobes	Presence of seeds	Vitamin C (mg/100 g fw)	Ash (%)
A	12.67 d	8.72 cd	7.29 ab	3.38 abc	1.94 c	193.8c	0.126a
A-A	12.11 cd	8.40 abcd	7.35 abc	3.1 a	1.53 bc	155.3ab	0.124a
CH-A	11.40 c	8.36 bc	7.44 ab	3.28 ab	1.26 b	184.1bc	0.132ab
F-A	11.11 c	9.04 d	7.25 a	3.30 a	0.69 a	177.3bc	0.131a
C	8.28 a	7.95 ab	8.02 bcde	3.87 c	1.81 bc	142.6 a	0.136ab
C-C	9.62 b	8.17 abc	8.44de	3.39 abc	1.77 bc	150.2 a	0.149bc
CH-C	8.46 a	7.77 a	7.99 cd	3.58 bc	1.56 bc	154.4 a	0.154c
F-C	8.77 ab	7.98 ab	8.32 e	3.53 abc	1.73 c	145.3 a	0.136ab

Mean separation for each trait by Bonferroni multiple-range test at $P \leq 0.05$.

average) for Coyote and 171.6 mg/100 mg fw for Almuden fruit. There were significant differences for ash content among genotypes ($P \leq 0.001$) and the influence of grafting was lesser although significant ($P \leq 0.05$). An interaction graft-genotype measuring ($P \leq 0.05$) was observed. Analysis for each factor separately indicates significant differences for Coyote grafted onto CH rootstock that showed the highest ash content (Table 1).

Discussion

Tolerance to *P. capsici* (Fig. 1) has been shown by both Foc and Charlot pepper hybrids with similar or even higher tolerances than SCM 334, the main resistant *P. capsici* source [2, 5, 6]. SCM 334 displayed higher resistance than Chilcote – in agreement with previously reported research [31]. The commercial hybrid Tresor showed a lower *P. capsici* tolerance with 75% of wilted plants at 35 dpi and 25% of plants with delayed symptoms and unable to complete the culture cycle. As this hybrid has been described as *P. capsici* tolerant, our results could be associated with the high virulence of the *P. capsici* isolate used. In a previous assay, this isolate wilted more SCM 334 plants than the Pc-141 and Pc-196 isolates – both of which were described as more virulent than other isolates in the work reported by Silvar *et al.* [4]. Commercial Coyote and Almuden F1 hybrids were very susceptible and died quickly. Asymptomatic Chilcote, SCM 334, Foc and Charlot plants all grew to maturity although a 20-35% growth reduction was observed, probably associated with a decrease in the root system seen in seedling stage. Inoculations with Pc-448 and Pc-450 isolates did not result in dead plants five weeks after inoculation as occurred in the previous assay – probably because of a lesser virulence of these isolates. However, a height reduction in all Coyote plants and some plants of the other genotypes was observed this time – as occurred at a later stage in the previous experiment. A reduction greater than 50% was produced in Coyote plants and 10-23% in SCM 334, Charlot and Foc plants.

Low graft union and incompatibility have been reported in several works on pepper [27, 32, 33]. In our work, a good graft union and absence of primary incompatibility yielded survival rates of 95-98% for both the grafted sweet peppers used as scions.

A higher number of fruits per plant were harvested (Fig. 1A) in grafted plants – mainly in CH-C plants. This could be associated with a higher capacity for this rootstock in nutrient or water uptake, as described in other works [10-13]. Greater ash content was also obtained in fruit from CH-C plants (Table 1). The increase in the number of fruits per plant could be the cause of lower fruit weights from Coyote grafted plants, which suffered an average reduction of 11% when compared to fruit from ungrafted plants (Fig. 1). Fruit weight decreases of 19-21% for Almuden could also be explained by the great variability in fruit shapes and shorter commercial fruit lengths observed (Table 1). More and larger fruit were also reported in eggplant grafted onto tomato [34]. The fact that larger fruit were observed in C-C plants (Table 1) could indicate that this physiological change can also be induced by grafting. Non-commercial fruit were also obtained in self-grafted plants with percentages of 10.6% in C-C and 12.5% in A-A: confirming that grafting may be partially responsible for weight decreases and changes in fruit shapes. This observation also underlines the importance of using self-grafted as well as non-grafted plants as controls.

Earliness was observed in Coyote grafted onto both Charlot and Foc rootstocks. The advance in flowering and fruiting in grafted plants has been described in other works such as in melons grafted onto *Cucurbita* rootstocks [35, 36]. The fact that earliness was only observed in Coyote grafted plants (CH-C and F-C), whereas a considerable seed reduction (52% of seedless fruit) was only shown in fruit from Almuden grafted plants (Table 1) could indicate the existence of rootstock-scion interactions. As interactions among a particular rootstock-scion combination are common [18, 27, 36, 37] it is important for rootstock evaluations to use two or more scion genotypes.

Several changes in nutritional parameters as a result of grafting have been described in other species. For instance, in watermelon, positive (higher vitamin C content) and negative (lower soluble solids) modifications as a result of grafting were described by Proietti *et al*. [21] and López-Galarza *et al*. [38], respectively. In our work, the rootstocks Foc and Charlot have not modified fruit vitamin C content, a very important nutritional trait in pepper [39]. Fruit vitamin C content has neither been modified in Coyote nor in Almuden grafted plants. The vitamin C content, however, differed among Almuden and Coyote fruit – with a higher supply (23 mg more) in the first of each 100 g of fresh weight ingested pepper. This agrees with the results published in other works that reported high genotype dependence for this trait in pepper [40, 41].

Conclusions

The *P. capsici* tolerance of the experimental hybrids Foc and Charlot were demonstrated. Grafting results indicated a good graft union of Coyote and Almuden commercial hybrids on Foc and Charlot rootstocks. The importance of scion-rootstock interaction and the value of making comparisons with self-grafted plants was also shown. Some modifications such as variability in fruit shape could be due to the grafting process and not the rootstock used. A small decrease in fruit weight was obtained in grafted plants compared with non-grafted plants. However, a higher commercial yield was obtained in Coyote grafted plants. The absence of negative modifications for quality parameters, such as pericarp thickness, lobes per fruit, vitamin C and mineral content, indicate that these hybrids could be very suitable pepper rootstocks.

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