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Valérie Le Clerc, Anita Suel, A. Pawelec, Sabrina Marques, Sébastien Huet, et al.. Is there variety x isolate interaction in the polygenic quantitative resistance of carrot to *Alternaria dauci*?. *Euphytica*, 2015, 202 (2), pp.235-243. 10.1007/s10681-014-1279-x . hal-01392648

HAL Id: hal-01392648

<https://hal.science/hal-01392648v1>

Submitted on 13 Feb 2023

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Is there variety \times isolate interaction in the polygenic quantitative resistance of carrot to *Alternaria dauci*?

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Received: 19 May 2014 / Accepted: 10 October 2014 / Published online: 17 October 2014
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Abstract Horizontal and polygenic resistance is race-nonspecific and, therefore, more durable, unlike vertical resistance, which is race-specific and unstable. However, this division is perhaps not so obvious since some cultivar \times isolate interactions have already been observed for plant species with partial resistance. Carrot is known to be partially resistant to *Alternaria dauci*, but it is relevant for breeders to study cultivar \times isolate interactions in order to develop durable resistant varieties. For this purpose, 12 highly diverse carrot genotypes and one segregating population were inoculated in a tunnel or in a glass house with 11 isolates of *A. dauci* that also represented a high

diversity in terms of geographical origin, aggressiveness and genetic diversity. Disease severity values were assessed three times in the tunnel in a one-year experiment (2002) and twice in the glass house in an experiment over two consecutive years (2011 and 2012). The interaction of isolate with genotype was non-significant in the tunnel, and the same result was obtained in the glasshouse for both years of study except for the first scoring date in 2011, suggesting that the partial resistance of carrot to *A. dauci* is probably mainly explained by major QTLs that confer resistance to a large number of isolates and, potentially, some minor isolate-specific QTLs as well.

V. Le Clerc and A. Suel have contributed equally to this work.

Electronic supplementary material The online version of this article (doi:10.1007/s10681-014-1279-x) contains supplementary material, which is available to authorized users.

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Keywords *Daucus carota* · Partial resistance ·
Variety \times isolate interaction · Leaf blight

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Introduction

While for vertical resistance, it is admitted that the ranking of the cultivar according to disease severity may depend on the isolates used for testing the resistance; this ranking is independent of the isolates for horizontal resistance (Van der Plank 1963). Although this division was assumed by many scientists, it is probably not so clear. Indeed, small race-specific effects have been observed, for example, in the polygenic partial resistance of barley to barley leaf rust, considered to be of a race-nonspecific nature (Parlevliet and Van Ommeren 1985). Marcel et al. (2007) suggested a minor-gene-for-minor-gene interaction model to explain the small cultivar \times isolate interactions that they identified in the partial resistance of barley to *Puccinia hordei*. More recently, similar conclusions were drawn by Truong et al. (2012) in pepper when identifying isolate-specific resistance QTL to *Phytophthora capsici*.

Alternaria leaf blight is the most damaging foliage disease on carrot worldwide (Farrar et al. 2004). Different levels of carrot resistance to *A. dauci* have been identified by Strandberg et al. (1972) and Aguilar et al. (1986). Partial resistant varieties have been available for the last two or three decades, while scientific knowledge of the genetic determinism of carrot resistance to *A. dauci* is fairly recent. Vieira et al. (1991) estimated broad sense heritability at between 45.6 and 81.9 % in four populations of carrots. In a half-sib progeny, Boiteux et al. (1993) reported a narrow-sense heritability of 40 %, indicating a medium to low heritability of resistance. Based on a diallel analysis of American inbred lines, Simon and Strandberg (1998) identified a preponderance of additive variation in carrot resistance with some dominant gene actions. Le Clerc et al. (2009) confirmed this polygenic character with three QTL regions involved in carrot resistance to *A. dauci*, each QTL explaining between 10 to 23 % of the phenotypic part of the variation. Out of the three QTLs, only one was common to both tunnel and field environments and the two others were specific. These preliminary results suggest a differential response of carrot to *A. dauci* in different environmental conditions. These two environments were quite contrasted in terms of isolate composition, with a high diversity of isolates reported in the field (Philippe Simoneau, personal communication) versus one isolate tested in a tunnel. This high level of diversity for

A. dauci was confirmed by a high level of polymorphism using SSR (Benichou et al. 2009) and, more recently, by Boedo et al. (2012) in terms of aggressiveness and IGS polymorphism. In 2010, Rogers and Stevenson reported a differential interaction between *A. dauci* isolates, all from the northeastern USA, and three commercial varieties plus one wild accession. The three cultivars all belonged to the unique “cut and peel” Emperor-type used in the American processing industry. We can therefore ask ourselves about a possible putative differential interaction between carrot varieties and *A. dauci* isolates, taking a larger diversity of varieties and isolates into account. However, is it a relevant issue for this interaction for which polygenic resistance has been identified? To assess such putative race-specific effects in this differential response, additional information about the interaction between the plant and the pathogen would be valuable.

In the present study, the aim was to investigate cultivar \times isolate interaction with highly diverse varieties and a wide range of isolates from all over the world, representative of the diversity of the *A. dauci* species.

Materials and methods

Fungal and plant material

Eleven *A. dauci* isolates from a worldwide collection of 120 isolates (UMR IRHS, Fungisem team, Angers, France) were selected to represent high diversity according to their level of aggressiveness, the polymorphism of intergenic spacers (IGS), when available [evaluated by Boedo et al. (2012)], and their geographic origins (Table 1).

In a tunnel trial, 67F3 progenies from a segregating population for *A. dauci* resistance, their parental plants S269 and R268 (described in Le Clerc et al. 2009) and four other genotypes including two inbred lines, S270 and R266, and two commercial hybrids, Bolero and Presto (Table 2), were evaluated. S and R stand for susceptible and partially resistant line, respectively. Three isolates, i.e., FRA005, FRA017, two French isolates and USA001, an American isolate (Table 1), were inoculated individually.

In a glasshouse trial over two consecutive years, eight varieties or inbred lines were inoculated with nine isolates (Table 1). Varieties or lines were chosen

Table 1 Characteristics of 11 *Alternaria dauci* isolates inoculated on carrot genotypes in the tunnel (in bold) and/or in the glasshouse (in italics)

Isolate accession	Geographical origin	Year of isolation	IGS pattern ^a
<i>AUS001</i>	Australia	NA	C3
<i>BRA001</i>	Brazil	2006	NA
<i>FRA001</i>	France (Maine-et-Loire)	2000	C1
FRA005	France (Indre)	2000	C2
FRA017	France (Gironde)	2000	C1
<i>FRA018</i>	France (Gironde)	2000	n.a.
<i>GER001</i>	Germany	1989	C2
<i>ITA002</i>	Italy	2006	C3
<i>JPN002</i>	Japan	2007	C3
USA001	USA	1998	n.a.
<i>USA006</i>	USA	1992	C2

NA not available, n.a. not applicable

^a IGS pattern described in Boedo et al. (2012)

according to their susceptibility to *A. dauci*, based on several assessments in the field with natural infestation or in a tunnel after inoculation with isolate FRA017 (Pawelec et al. 2006; Le Clerc et al. 2009). Various geographic origins, root types and genetic backgrounds

represented by different breeding companies were also considered (Table 2).

Disease testing

Tunnel trial (2002)

In June, seeds were sown in a randomized complete block design (RCBD) with three blocks. Within each block, each progeny, parental line or variety was evaluated with 80 plants. The susceptible variety, Presto, was sown around each block to ensure uniform fungus development.

Glasshouse trials (2011 and 2012)

In mid-February, in a glasshouse with day/night temperatures of 20 ± 2 and 18 ± 2 °C, ten to 12 seeds per variety or line were sown in 7.5-L pots containing a peat moss (Tray substrate Klasmann)/sand (67:33, v/v) mixture. Until inoculation, three pots per variety were randomly distributed in the three replications of nine blocks, each block corresponding to one of the nine isolates to be inoculated (Online Resource 1). Thirty-six pots of cv. Presto were placed

Table 2 Characteristics of seven carrot genotypes and one segregating population evaluated in the tunnel with three isolates of *A. dauci*, and eight genotypes evaluated in the glasshouse with nine isolates of *A. dauci*

Plant material	Name of the genotype	Trial-Glasshouse (G); Tunnel (T)	Origin of the material	Root type	Level of resistance evaluated with isolate FRA017
Inbred line (S3)	H1	G	Scientific material	NA	Very low
Inbred line (S3)	S270	T	Breeding from an INRA population (PS-80)	Touchon	Very low
Commercial F1 hybrid	Presto	G/T	Breeding company (Vilmorin)	Nantais	Low
Parental line (S4)	S269	T	Vilmorin breeding program	Carentan	Low
Commercial F1 hybrid	Nerac	G	Breeding company (Bejo)	Nantais	Medium
Commercial F1 hybrid	Valor	G	Breeding company (Clause)	Nantais	Medium
Commercial F1 hybrid	Bolero	G/T	Breeding company (Vilmorin)	Nantais	High
Commercial F1 hybrid	Texto	G/T	Breeding company (Vilmorin)	Nantais	High
Inbred line (S2)	I2	G	Scientific material	Kuroda	High
Inbred line (S2)	K3	G	Scientific material	Kuroda	High
Parental line (S4)	R268	T	Vilmorin breeding program	NA	High
Inbred line (S3)	R266	T	Vilmorin breeding program	NA	High
67 F3 of a segregating population	S269 × R268	T	S269 and R268	Segregant	Segregant

NA not available

in and around each block. Thirty days after sowing, five plants per pot were kept for inoculation.

Inoculation

For conidia production, fungal isolates were grown in Petri dishes according to the procedure used by Boedo et al. (2012). Conidial suspensions were prepared as described in Pawelec et al. (Pawelec et al. 2006). Briefly, fungal cultures were flooded with sterile water and conidia were gently dislodged with a glass plate. Tween 20 was added to the suspension at a final concentration of 0.05 %. Mycelial and conidial suspensions were filtered through two layers of cheese-cloth. Spore density was counted using a haemocytometer and adjusted to $4\text{--}5 \times 10^3$ conidia per mL.

For the trial under the tunnel, a first inoculation was performed when plants showed three true leaves, and the second one was done 15 days later. Each block was sprayed until runoff with an atomizer, as described in Pawelec et al. (2006). A high relative humidity (95–100 % RH) was maintained for 48 h after inoculation.

Six weeks after sowing in the glasshouse, each block was sprayed with one of the nine inocula until runoff, using the same protocol as described for the tunnel. After that, each replication of each initial block was randomized in the glass house, and 12 pots of cv. Presto were placed in and surrounding each replication.

Disease assessment and data analysis

Disease severities (DS) in the tunnel were assessed three times, i.e., the first time, 1 month after the first inoculation and then every 15 days. From these DS, AUDPC were calculated for four inbred lines and two commercial hybrids (Online Resource 2).

For the two consecutive years in the glasshouse, disease severity was rated at 20 d.p.i. (referred to as 2011n1 and 2012n1) and 35 d.p.i. (2011n2 and 2012n2) by visual assessment based on a 0–9 scale (Pawelec et al. 2006) for each pot, with 0 corresponding to symptomless plants and nine to plants that were totally blighted.

For each experiment, disease severity values were subjected to analysis of variance performed with R software, version 2.14.0, after checking the assumptions. The normality of residues was evaluated with

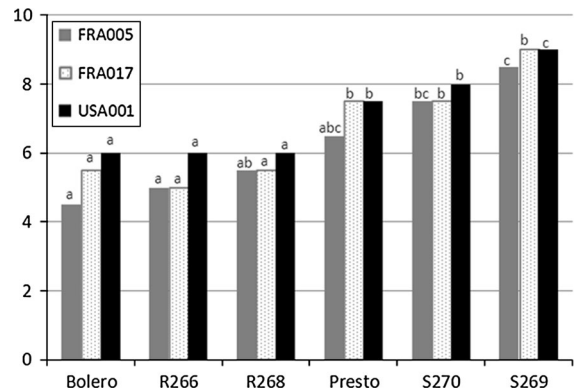


Fig. 1 Disease severity values obtained for six genotypes with three *Alternaria dauci* isolates in the tunnel for the third scoring date. For each isolate, Fisher's least significant procedure was used to discriminate among the means of disease severity values with $\alpha = 5.0$ %

skewness and kurtosis tests. For each score, total variation was broken down into isolate, genotype and residual effects.

Results

Tunnel trial (2002)

Regardless of the isolate, i.e., FRA005, FRA017 and USA001, the Bolero variety and the parental lines R266 and R268 were partially resistant, with DS values ranging from 4.5 to 6 for the third date rating, whereas the Presto variety and the parental lines S269 and S270 were susceptible, with higher DS values between 6.5 and 9 (Fig. 1). Isolate and genotype effects were significant, but interaction between isolate and genotype was not detected. The same conclusions were obtained for the segregating population evaluated with the same three isolates (Table 3).

Glasshouse trials (2011 and 2012)

In the glasshouse, regardless of the date and the year of scoring, isolate and genotype effects were highly significant, whereas no effect of genotype \times isolate interaction was observed, except a small one for score 2011n1 (Table 4).

For the sake of clarity, we only displayed the varieties we usually used as controls for the evaluation of *A. dauci*, i.e., Presto and Bolero (Fig. 2) and the scientific inbred lines H1, I2 and K3 (Fig. 3). Since the

Table 3 Analysis of variance of the effects of three *Alternaria dauci* isolates, carrot genotype and genotype \times isolate interaction on disease severity values for the tunnel trial

Source	Scoring date 1		Scoring date 2		Scoring date 3	
	F-ratio	P value	F-ratio	P value	F-ratio	P value
Genotypes						
Isolate	5.32	0.00	22.920	0.00	25.20	0.00
Genotype	4.03	0.04	4.790	0.02	4.17	0.03
Genotype \times isolate	0.58	0.81	1.250	0.33	0.37	0.95
Segregating population						
Isolate	4.01	0	5.33	0	3.53	0
Genotype	92.73	0	212.4	0	54.12	0
Genotype \times isolate	0.48	0.41	1.28	0.08	1.44	0.07

Table 4 Analysis of variance of the effects of nine *Alternaria dauci* isolates, eight carrot genotypes and genotype \times isolate interactions on disease severity values for the glasshouse trials

Source	df	Mean square	F	P > F
2011 n1				
Isolate	8	29.038	37.148	<0.001
Genotype	7	7.690	9.837	<0.001
Genotype \times isolate	56	1.306	1.671	<0.01
Residuals	142	0.782		
2011n2				
I isolate	8	15.88	14.851	<0.001
Genotype	7	8.708	8.144	<0.001
Genotype \times isolate	56	1.14	1.066	ns
Residuals	142	1.07		
2012n1				
Isolate	8	7.095	8.152	<0.001
Genotype	7	9.332	10.723	<0.001
Genotype \times isolate	56	0.526	0.604	ns
Residuals	144	0.87		
2012n2				
Isolate	8	4.89	4.175	<0.001
Genotype	7	16.444	14.039	<0.001
Genotype \times isolate	56	0.651	0.555	ns
Residuals	144	1.171		

ns not significant

results were very similar among the two intermediate varieties, Valor and Nerac, the first one was retained. Regardless of the date, the year of scoring and the isolate, Presto was still the most susceptible compared to the intermediate cultivar, Valor, and the partially resistant cultivar, Bolero (Fig. 2). While the differentiation between Bolero and Valor was less obvious for score 2011n2, it was clearer for score 2012n2. Like Presto, the same conclusions were drawn with the

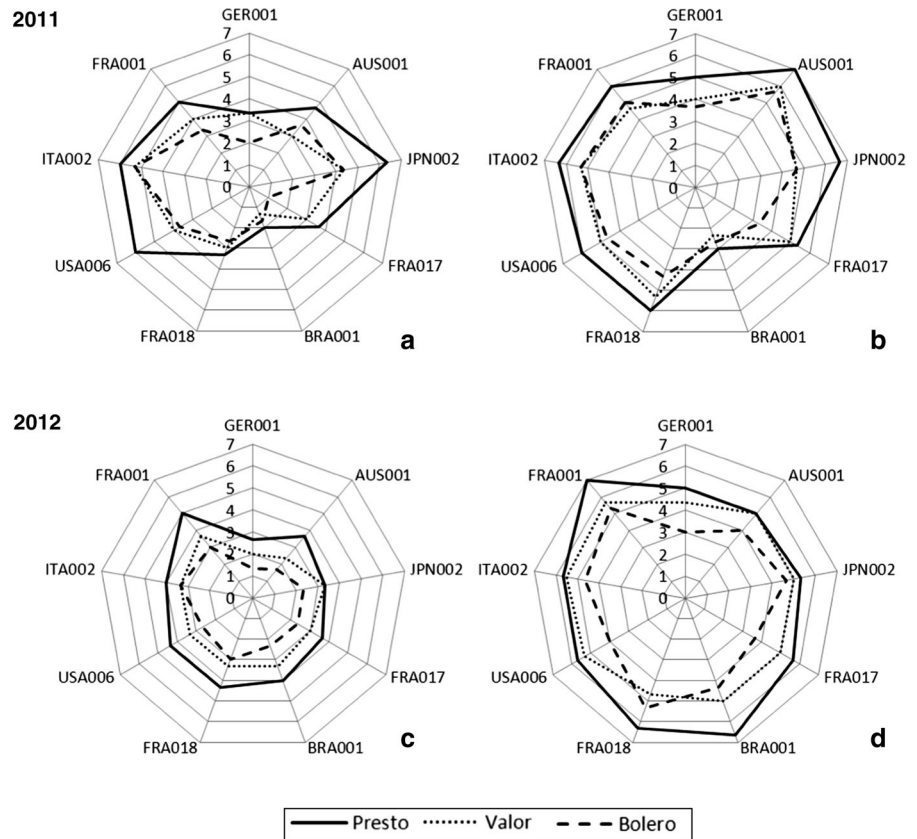
susceptible inbred line H1, compared to the two partially resistant genotypes I2 and K3 (Fig. 3). In 2011, with the isolate BRA001, regardless of the date of scoring, I2 and K3 were more susceptible than H1. For the same year, the isolate BRA001 was the less aggressive one.

In 2011, regardless of the isolate, mean disease severity values were comprised between 0.3 and 6.3 for score 2011n1, and increased between 2 and 6.7 for score 2011n2 (Online Resource 3). The same dynamic was observed in 2012 with values comprised between 1.3 and 6 for score 2012n1, and between 3 and 7 for score 2012n2. Even if the susceptibility ranking per isolate was not changed overall, the differentiation between susceptible and resistant genotypes was more or less obvious, depending on the scoring date. For example, for the first scoring in 2011 with the isolate FRA017, the Textovariety (DS = 3.7) was not differentiated from Presto (DS = 3.7) and was among the most susceptible genotypes, where as for the second scoring, Presto was more susceptible (DS = 5.3) than Texto (DS = 4.3); Texto was the most resistant, along with Bolero (DS = 3.3).

Discussion

Developing durable resistant varieties of carrot to *A. dauci* is one of the priorities for breeders today. In this context, selection for stability of varietal resistance in different environments is crucial. For this purpose, we need to characterize the response of different carrot varieties to different isolates of the pathogen to be sure that a resistant variety will be able to counteract all of the isolates it will encounter. When looking at a vertical resistance, the differential response of varieties to

Fig. 2 Disease severity values obtained for three commercial varieties, Bolero, Valor and Presto, with nine *Alternaria dauci* isolates in the glasshouse. **a**, **b**, **c** and **d** represent scoring dates 2011n1, 2011n2, 2012n1 and 2012n2, respectively



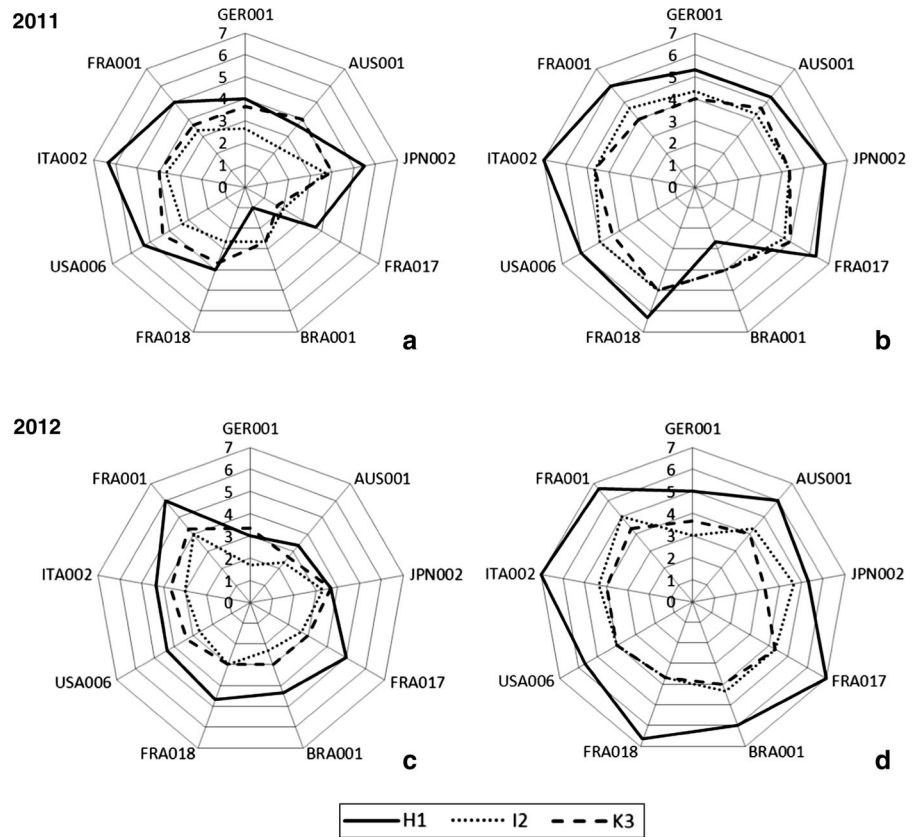
isolates belonging to different races is the rule, whereas in the case of partial resistance, this result is not expected. For one pathogen, it is assumed that polygenic resistance is generally controlled by broad-spectrum resistance factors that are effective against a large number of isolates. However, some studies have already identified isolate-specific resistance factors, suggesting that differential interaction between plant and isolate may be found in polygenic resistance (Caranta et al. 1997; Marcel et al. 2007; Truong et al. 2012).

In the present study, the ranking was the same for the parental lines and the segregating population evaluated under a tunnel with three isolates. This result suggests that the QTLs already detected in this population (Le Clerc et al. 2009) with the isolate FRA017 are broad spectrum QTLs or that the number of progenies tested was not enough to highlight isolate-specific QTLs with a lower effect on resistance. We were not able to check both hypotheses in 2002 since no QTL detection was manageable in this study due to the insufficient number of progenies

evaluated (63 progenies- no more seeds available for other progenies).

In the glasshouse, the interaction of isolate \times cultivar was non-significant for both years for the eight cultivars, except for the first scoring date in 2011. Indeed, except with the Brazilian isolate BRA001, no interaction was observed. This isolate was less aggressive than FRA017 in 2011 for both scoring dates, whereas in 2012, it was as aggressive as FRA017. When previously tested under a tunnel, it had also revealed itself to be more aggressive (data not shown), suggesting that its behavior in 2011 was not completely reliable. In any case, the ranking of the genotypes was similar, regardless of the isolate inoculated and the year. It is not excluded that the very small variations observed in the glasshouse for the level of resistance against different isolates may be partially due to isolate specificity of some QTLs, i.e., these QTLs may slightly modulate the response of the plant to different isolates.

Fig. 3 Disease severity values obtained for three inbred lines, H1, K3 and I2, with nine *Alternaria dauci* isolates in the glasshouse. **a**, **b**, **c** and **d** represent scoring dates 2011n1, 2011n2, 2012n1 and 2012n2, respectively



We suggest that the partial resistance of carrot to *A. dauci* is probably mainly explained by major QTLs that confer a resistance to a large number of isolates and, potentially, some minor isolate-specific QTLs as well. Depending on the genetic background of the variety, the presence of some isolate-specific QTLs may confer varying degrees of resistance in some environments. This would perhaps explain, at least in part, why our results differ from those of Rogers and Stevenson (2010) who revealed significant variety \times isolate interactions. Varieties, isolates and environmental conditions were very different than our material and conditions. According to their results, it seems that interactions were generally due to the behavior of their intermediate variety (“Enterprise”) that became significantly more susceptible than their susceptible one (“Heritage”) to three isolates among 22 isolates used for the inoculation.

One important consideration revealed by our results is the date when symptoms are scored. Indeed, for a

given isolate, the kinetics of disease development is very different from one genotype to another. This was particularly true for the genotypes I2, K3 and H1 in 2012. For the isolates that are the least aggressive for the first scoring date, i.e., GER001, AUS001 and JPN002, and, to a lesser extent, with the more aggressive ones, the differentiation between the susceptible genotype H1 and the partially resistant genotypes I2 and K3 was not possible or less obvious than for the second scoring date. This suggests that, depending on the isolate, some resistance mechanisms may be activated earlier or later or not at all. When the differentiation between resistant and susceptible varieties is observed very rapidly, it suggests that the activation of those resistance mechanisms may occur as soon as the early stages of recognition between the plant and the fungus are reached. The study of Boedo et al. (2010) supports this hypothesis since significant differences were observed between two partially resistant cultivars (Bolero and Texto) and one susceptible cultivar (Presto) when

considering the mean number of germ tubes per conidium produced *in planta* (isolate FRA017). The number of germ tubes was higher for the partially resistant cultivars, suggesting greater difficulty for the fungus to penetrate the host. Similar results were obtained for the two partially resistant genotypes (K3 and I2) and the susceptible one (H1) (Online Resource 4). Thus, unlike for the susceptible genotypes, the activation of resistance mechanisms within resistant genotypes is perhaps more rapid and intense because of this differential emission of germ tubes.

With isolates other than FRA017, these early resistance mechanisms are perhaps not activated in these resistant genotypes or more weakly so, giving way to the implementation of later resistance mechanisms. In this case, the difference between resistant and susceptible genotypes based on symptom scoring is also observed later. Therefore, depending on the date of scoring for the symptoms, conclusions about interaction between varieties and isolates may be slightly different.

In conclusion, no general interaction between varieties and isolates was detected in our study. This means that breeders could develop partial resistant varieties capable of counteracting a large number of isolates from all over the world. A high number of varieties are likely to carry broad-spectrum QTLs, which probably explains the huge proportion of carrot resistance to *A. dauci*. They could be involved in general and non-specific defense responses to a broader range of isolates, but isolate-specific QTLs are not excluded. Until now, we have detected QTLs with moderate to considerable individual effects on resistance (R^2 comprised between 10 and 29 %) after inoculation with one isolate (FRA017) or after infestation in the field in three different segregating populations (Le Clerc et al. 2009). Knowledge about the nature of quantitative resistance will undoubtedly contribute to the development of a strategy for the management of resistance durability.

Acknowledgments We are grateful to Gérard Simon (breeder from Vilmorin) who provided the inbred lines S269, S270, R266 and R268, Elodie Auperpin and Stéphanie Bersihand for their technical help in the glasshouse, our colleagues from INEM (Rémi Gardet and Jacky Granger, Agrocampus Ouest, Angers) involved in glasshouse experiments, and Gail Wagman for reviewing the English. This work was financed by the “Fonds de Compétitivité des Entreprises” (‘Création Variétale Potagère’ FCE project, 2007–2010).

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