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Evaluation of olive cultivars for resistance to *Verticillium dahliae*

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Abstract

Resistance of 23 important olive cultivars to *Verticillium dahliae* has been evaluated in four experiments under controlled conditions. Nine-month-old nursery olive plants were inoculated with a cotton non-defoliating (ND) (V4) or a cotton defoliating (D) (V117) isolate of *V. dahliae*. Resistance was evaluated by assessing symptom severity using a 0–4 rating scale and estimating the area under disease progress curves. The percentage of plants killed and of those which recovered from the disease were used as additional parameters for including a particular cultivar into a defined category. Most of the evaluated cultivars were susceptible, although at different levels, to both isolates of *V. dahliae*. All cultivars were more susceptible to the D pathotype than to the ND one. A group of 11 cultivars, including several important Spanish cultivars, were susceptible or extremely susceptible to both pathotypes of *V. dahliae*. A second group showed differences of resistance depending on the pathotype used. They were susceptible or extremely susceptible to the D pathotype but resistant or moderately susceptible to the ND one. Finally, 'Frantoio', 'Oblonga' and 'Empeltre' were moderately susceptible to the D isolate of *V. dahliae* and resistant to the ND one. The resistance of 'Empeltre' was evident by the plant ability to recover from infection with either isolates. 'Empeltre' is considered to be a valuable cultivar for inclusion in breeding programmes for resistance to Verticillium wilt.

Introduction

Verticillium dahliae is a major pathogen affecting olive orchards in the Mediterranean Basin (Al-Ahmad and Mosli, 1993; Blanco-López et al., 1984; Cirulli and Montemurro, 1976; López-Escudero and Blanco-López, 2001; Hiemstra and Harris, 1998; Rodríguez-Jurado et al., 1993; Serrhini and Zeroual, 1995; Thanassolopoulos et al., 1979). Disease incidence and severity are usually highest in young trees (Al-Ahmad and Mosli, 1993; Blanco-López et al., 1984; Serrhini and Zeroual, 1995; Wilhelm and Taylor, 1965). The new olive orchards established in Spain during the last 15–20 years have increased the importance of Verticillium wilt of olive. Spread of the disease is linked to planting olive trees in fields previously used for growing susceptible hosts to the pathogen (Blanco-López et al., 1984), or in those close to cotton fields infested by *V. dahliae* (Bejarano et al., 1996; López-Escudero and Blanco-López, 2001; Wilhelm and Taylor, 1965). Several characteristics of the pathogen make Verticillium wilt control difficult (Blanco-López and Jimenez-Diaz, 1995; Tjamos and Jimenez-Diaz, 1998). The pathogen can survive in the soil for long periods of time (Wilhelm, 1955), it has a wide host range (Heale, 1988; Sinclair et al., 1987; Vargas-Machuca, 1987), and chemical compounds are not effective. The use of cultivars resistant to wilt is, as with other wilt diseases (Blanco-López et al., 1998), likely to be effective for olive.

The problem is made more difficult by the presence of two groups of *V. dahliae* isolates that have been identified on cotton and olive: defoliating (D) and non-defoliating (ND) pathotypes (Schnathorst, 1973). The ND pathotype is moderately severe and the D one is highly virulent

in both hosts (Schnathorst and Sibbett, 1971; Rodriguez-Jurado, 1993; López-Escudero, 1999). In Spain, both pathotypes of *V. dahliae* were found infecting cotton (Bejarano-Alcázar et al., 1995; 1996; Blanco-López et al., 1989) and olive (López-Escudero and Blanco-López, 2001). They are present in olive areas planted with the Spanish cultivars 'Cornicabra', 'Hojiblanca', 'Manzanilla' and 'Picual'. The spread of the D pathotype of *V. dahliae* in Spain (Bejarano et al., 1996) and its presence in commercial olive orchards (López-Escudero and Blanco-López, 2001) make it necessary to determine which olive cultivars have higher resistance to *V. dahliae*.

The objective of this work was to evaluate the resistance of olive cultivars to D and ND pathotypes of *V. dahliae*, so that resistant cultivars can be identified and thus used for replanting, as rootstocks or as sources for resistance in future breeding programmes.

Materials and methods

Twenty-one olive cultivars were evaluated for resistance to *V. dahliae* in four experiments (R1–R4) in controlled conditions in a growth chamber, with 10 replications per experiment. Plant material consisted of 9-month-old rooted cuttings, obtained from the World Olive Germplasm Bank of CIFA, 'Alameda del Obispo' (Córdoba, Spain). Plants were inoculated with isolates of *V. dahliae*, V4 or V117, from the collection of the Plant Pathology Laboratory of the Agronomy Department, University of Cordoba. Isolate V4 represents a mild virulent, cotton ND strain, and V117 a highly virulent, cotton D isolate (Blanco-López et al., 1989). Both isolates maintain the same differential pathogenicity in olive (Rodríguez-Jurado et al., 1993). Two olive cultivars, 'Picual' and 'Oblonga', were included in each experiment as examples of known resistance. 'Picual' is very susceptible to the D and susceptible to the ND isolate, while 'Oblonga' is moderately susceptible to D and resistant to the ND isolate (Hartman et al., 1971; Rodríguez-Jurado, 1993).

The technique for plant inoculation was based on Rodriguez-Jurado et al. (1993). Inoculum was prepared from single-spore cultures of V4 and V117 isolates, maintained on potato dextrose agar (PDA) slants at 4 °C. Plants were inoculated by dipping their bare root systems in a suspension of 10^7 conidia/ml for 30 min. They were transplanted to sterile soil (1 : 1 : 1, peat : sand : lime) in pots and incubated in a growth chamber adjusted to 22 ± 2 °C. Plants remained in darkness and at 95% RH for 3 days after inoculation to reduce losses due to the transplanting and the inoculation process. Then, light and humidity were adjusted to a photoperiod of 14 h (216 μEm-2 s^{-1} fluorescent light) and 80% HR.

To evaluate wilt resistance, disease severity were assessed weekly for 10 weeks, starting 2 weeks after inoculation. A scale 0–4 was used according to the percentage of plant tissue affected by chlorosis, leaf and shoot necrosis or defoliation (0 = healthy plant or plant without symptoms; 1 = affected plant in 1–33%; 2 = 34–66%; 3 = 67–99%; 4 = dead plant). The percentage of dead plants (PDP), recovery from the disease (López-Escudero and Blanco-López, 2001; Hiemstra and Harris, 1998; Wilhelm and Taylor, 1965) and other symptoms such as marginal spots of leaves and irregular growth of twigs were also considered to estimate the severity of reactions. The area under the disease progress curve (AUDPC) was estimated for each cultivar considering its percentage with regard to the maximum possible value that could be reached in the 10 weeks period of assessment based on Campbell and Madden (1990): AUDPC = $[(t/2^*(S_2 + 2^*S_3 + \cdots + 2S_{i-1} + S_i)/4^*n]^*100$ (t = interval in days between observations; S_i = final mean severity; 4 = maximum disease rating; n = number of observations).

Plant infection was verified by the isolation of the fungus from affected shoots or leaf petioles of affected plants during the experiments. Isolations from shoots and branches were also made from all dead plants at the end of the experiments. Pieces of affected tissues were washed in running tap water, bark was removed and woody tissues surface disinfected in 0.5% sodium hypochlorite for 1 min. Chips of wood were placed onto PDA. Plates were incubated at 24 °C in the dark for 5–6 days.

Plants were arranged according to a split-plot completely randomised block design. The main-plot was the *V. dahliae* pathotype, and cultivars were assigned to sub-plots. The analysis of variance (ANOVA) of AUDPC of reference-cultivars ('Picual' and 'Oblonga') in each experiment were performed to determine the variability among experiments. In experiments where reactions of 'Picual' or 'Oblonga' were statistically different, values of AUDPC of cultivars included in these experiments were corrected regarding the percentage of the difference between the values of AUDPC for reference-cultivars in

significant and non-significant experiments. Statistical analysis were performed by Statistix 4.1 program (Analytical Software, Tallahase, USA). Mean values were compared by the Fisher's protected LSD at $P = 0.05$.

Results

Disease symptoms and virulence of isolates

Chlorosis was the most common symptom observed when the ND isolate was used. In plants inoculated with the D isolate, chlorosis was associated with cultivars showing certain level of resistance. Defoliation was also very frequent. It occurred, in the absence of chlorosis, in all susceptible cultivars inoculated with the D isolate, starting at 3–4 weeks after inoculation and intensifying from the seventh week after inoculation. Defoliation was intensive in susceptible cultivars such as 'Arbequina', 'Cobrancosa' and 'Picual', and slight and restricted to the middle of the main shoots of the plants in moderately resistant cultivars.

Sudden wilt or apoplexy, characterised by the progressive rolling inward and chlorosis of leaves, was also observed in plants inoculated with the D or the ND *V. dahliae* isolate. Leaves became necrotic and remained attached to the twigs. 'Oblonga' was more resistant than 'Picual', when it was inoculated with either ND or D isolates. The D isolate induced higher incidence of disease and symptom severity than the ND one, and earlier death of plants. Therefore, the D isolate caused between 70% and 100% of dead plants in 13 out of the 23 cultivars inoculated, whereas mortality was only observed in seven of them when the ND isolate was used (Table 1).

Table 1. AUDPC and PDP of olive cultivars inoculated with D and ND isolates of *V. dahliae*[1]

Cultivars	Defoliating		Cultivars	Non-defoliating	
	AUDPC[2]	PDP[2]		AUDPC	PDP
'Valanolia'	83.8	90	'Valanolia'	72.8	37.5
'Cornicabra'	75.8	85.7	'Villalonga'	53.4	0
'Arbequina'	72.2	100	'Negral'	41.1	12.5
'Manzanilla Sevilla'	71.8	100	'Manzanilla Piquito'	36.2	0
'Lechín de Granada'	71.1	100	'Hendeño'	34.9	0
'Ocal'	71.1	57.1	'Nevadillo Negro'	32.6	0
'Villalonga'	68.0	75	'Ocal'	26.7	0
'Picual'[3]	66.6	95	'Meski'	26.4	0
'Meski'	66.4	50	'Pajarero'	26.4	0
'Negral'	63.4	60	'Arbequina'	22.6	30
'Picudo'	61.5	100	'Cornicabra'	22.3	50
'Manzanilla Piquito'	61.4	50	'Leccino'	22.2	10
'Hendeño'	60.7	100	'Picual'	22.1	17.5
'Verdial Alcaudete'	60.5	88.8	'Hojiblanca'	19.9	20
'Pajarero'	58.8	77.7	'Picudo'	19.6	0
'Cobrancosa'	56.1	70	'Lechín de Granada'	15.9	0
'Nevadillo Negro'	52.7	25	'Frantoio'	13.2	0
'Hojiblanca'	52.6	60	'Morisca'	11.3	0
'Morisca'	50.1	60	'Cobrancosa'	11.1	0
'Leccino'	46.9	80	'Oblonga'	11.1	0
'Frantoio'	40.3	12.5	'Verdial Alcaudete'	8.7	0
'Empeltre'	30.9	0	'Empeltre'	8.4	0
'Oblonga'[3]	25.3	14.4	'Manzanilla Sevilla'	6.6	0

[1]Nine-month-old olive plants were inoculated with cotton-ND or cotton-D isolate of *V. dahliae*. Symptom severity was assessed weekly from 2 to 12 weeks after inoculation.
[2]AUDPC = area under the disease progress curve; PDP = percentage of dead plants.
[3]Values of reference-cultivars ('Picual' and 'Oblonga') are the mean of AUDPC of non-significant experiments: R1–R4 for the D isolate, and R2–R4 for the ND one.

Presence of the pathogen in olive shoots

The fungus was recovered from 60% of affected shoots in living plants at the middle of experiments and from 80% of dead plants at the end of them. The pathogen was also isolated from petioles of green leaves collected immediately after defoliation.

Disease progress and analysis of resistance

Disease symptoms were always more severe in inoculations with the D pathotype (Figure 1, Table 1). ANOVA of AUDPC for the reference-cultivars did not result in statistical differences between experiments, with the exception of inoculations with the ND pathotype in experiment R1, where 'Arbequina', 'Cornicabra' and 'Frantoio' were included. In this experiment, the average of AUDPC for 'Picual' and 'Oblonga' inoculated with the ND isolate reached 31.0% compared to 16.6% of the mean of experiments R2–R4 of the same value.

From the seventh week after inoculation, some cultivars showed recovery from the disease, expressed as a reduction in disease severity (Figure 1). This phenomenon mainly occurred in several cultivars inoculated with the ND isolate (Figure 1) and was associated with a certain level of resistance.

Categories of resistance

Cultivars were classified into resistance categories as shown in Table 2. Most of the evaluated cultivars were susceptible to V4 (ND) or V117 (D) isolate of *V. dahliae*. Moreover, all cultivars were more susceptible to the D pathotype than to the ND one.

Eleven of the 23 cultivars were susceptible or extremely susceptible to both pathotypes of *V. dahliae* (Table 2). This group includes the most important Spanish commercial cultivars, such as 'Picual', 'Hojiblanca', 'Cornicabra' and 'Arbequina'.

The second group was characterised by cultivars showing notable differences of resistance depending on the pathotype used (Tables 1 and 2). 'Cobrancosa', 'Manzanilla Sevilla', 'Morisca' and 'Verdial Alcaudete' were resistant to the ND, but extremely susceptible to the D isolate. The resistance of these cultivars to the ND isolate was similar

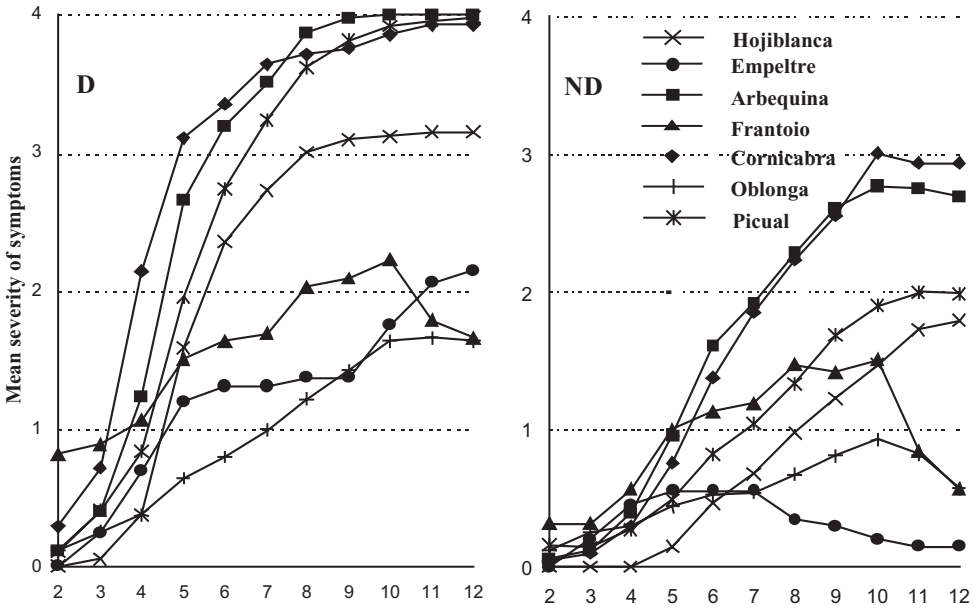

Figure 1. Progress of the severity of symptoms in several widespread olive cultivars inoculated with the D and ND isolates of *V. dahliae*. Severity of plant symptoms was weekly assessed for 10 weeks, starting at 2 weeks after inoculations, on a 0–4 rating scale according to percentage of plant tissue affected by chlorosis, leave and shoot necrosis, or defoliation (0 = healthy plant or plant without symptoms; 1 = affected plant in 1–33%; 2 = 34–66%; 3 = 67–99%; 4 = dead plant). For 'Picual' and 'Oblonga' the mean values of severity of symptoms of the experiments R1–R4 were used.

Table 2. Resistance of olive cultivars to Verticillium wilt caused by the D and ND isolates of *V. dahliae*

Susceptibility[1,2]		Cultivars
D	ND	
E	E	'Cornicabra', 'Valanolia'
E	S	'Arbequina', 'Hendeño', 'Hojiblanca', 'Manzanilla Piquito', 'Negral', 'Ocal', 'Picual', 'Villalonga'
S	S	'Nevadillo Negro'
E	MS	'Leccino', 'Lechín de Granada', 'Meski', 'Pajarero', 'Picudo'
E	R	'Cobrancosa', 'Manzanilla Sevilla', 'Morisca', 'Verdial Alcaudete'
MS	R	'Empeltre', 'Frantoio', 'Oblonga'

[1]R = resistant, MS = moderately susceptible; S = susceptible; E = extremely susceptible. Susceptibility has been determined according to values of AUDPC, PDP at 12 weeks after inoculation and others complementary criteria such as shape of AUDPC and recovery from the disease.
[2]Resistance categories correspond to following interval of values of AUDPC for the D/ND isolates of *V. dahliae*: HR = 0–10%/0–10%; R = 11–30%/11–30%; MS = 31–50%/31–40%; S = 51–70%/41–60%; E = 71–100%/61–100%.

to that expressed by the resistant cultivars 'Frantoio' and 'Oblonga' (Tables 1 and 2). Finally, 'Frantoio', 'Oblonga' and 'Empeltre' were moderately susceptible to the D isolate of *V. dahliae* and resistant to the ND one. 'Empeltre' resistance was manifested by the ability of its plants to recover from infection with either isolate, with final values of mean severity and dead plant similar, or even lower, to those of 'Frantoio' and 'Oblonga' (Figure 1, Table 1). Moreover, neither of the isolates caused death of 'Empeltre', while 'Frantoio' and 'Oblonga' reached percentages of mortality of 12.5% and 14.4%, respectively, in inoculations with the D pathotype (Table 1).

Discussion

Our method proved to be adequate for testing cultivar resistance to Verticillium wilt. Disease reaction showed by the reference-cultivars, 'Picual' and 'Oblonga', were effectively differentiated in our inoculations by the mean of values of AUDPC and PDP, and consistent with those observed in infested field (Martos-Moreno et al., 2001). Positive isolations of the fungus from affected plants during experiments demonstrated that plants were consistently infected, irrespective of the cultivar, pathotype and resistance level (Rodríguez-Jurado, 1993).

Almost all the evaluated cultivars have been catalogued as susceptible or extremely susceptible to both pathogenic variants of *V. dahliae*, including the most important Spanish cultivars, 'Picual', 'Cornicabra' and 'Hojiblanca' (Table 2). Moreover, all the cultivars were more susceptible and showed higher frequency of positive isolations of the pathogen from affected plant tissues when they were inoculated with the D pathotype than with the ND one. These results agree with studies of Hartman et al. (1971), Schnathorst and Sibbett (1971) and Rodríguez-Jurado (1993).

We have also demonstrated that 'Arbequina', a cultivar widely used nowadays in high-density orchards, shows the same susceptibility as 'Picual' (Tables 1 and 2). Also, 'Leccino' had similar susceptibility as 'Picual' and 'Hojiblanca' to the ND isolate (Tables 1 and 2), and tissues from affected plants yielded consistently cultures of the pathogen. This fact contrasts with the resistance recognised by Cirulli and Montemurro (1976) of this cultivar that was based on the low positive isolations of the pathogen from plants.

'Cobrancosa', 'Manzanilla Sevilla', 'Morisca' and 'Verdial Alcaudete' were extremely susceptible to the D isolate, but resistant to the ND one, with similar resistance to 'Frantoio' or 'Oblonga' (Tables 1 and 2). Probably, this differential reaction makes them appropriate candidates to be tried as rootstocks in soil infested with low inoculum densities of ND pathotypes of *V. dahliae*.

Resistance of 'Oblonga' and 'Frantoio' was reported by Hartman et al. (1971), Wilhelm and Taylor (1965) and Cirulli and Montemurro (1976). Symptoms of wilt were not observed in 'Frantoio' (Wilhelm and Taylor, 1965) after inoculating one-year-old plants with of a conidial suspension on roots at the time of planting, or by Cirulli and Montemurro (1976) in 79 plants inoculated with several isolates of *V. dahliae*. In this case, the fungus was isolated from 14 of these plants. In our experiments, 'Frantoio' showed only slight chlorosis or slight defoliation in inoculations with the ND and the D isolate, respectively, and this began to diminish from 10 weeks after inoculating with either isolates,

reaching very low final values of severity of symptoms (Figure 1). The similar reaction of 'Frantoio' and 'Oblonga' is consistent with the conclusion that these are the same cultivar, as demonstrated by Barranco et al. (2000) by molecular analyses.

Finally, our results indicate that 'Frantoio' (='Oblonga') and 'Empeltre' are resistant to *V. dahliae*, so that they could be used for replanting or tried as rootstocks for other susceptible cultivars. Furthermore, 'Empeltre' shows high productivity, excellent oil quality, early fruit maturation and easy mechanical harvesting (Barranco et al., 1996). Some disadvantages for commercial use of 'Empeltre' could be its problems of fruit set and susceptibility to frost injury in certain areas, but the main inconvenience for using it as a rootstock consists of its low rooting ability (Caballero and del Río, 2001). 'Empeltre' was the only cultivar in which neither of the isolates caused death of plants. All these reasons might justify the inclusion of this cultivar in breeding programmes for resistance to Verticillium wilt of olive.

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