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Recovery of young olive trees from *Verticillium dahliae*

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Abstract

Natural recovery from wilt disease symptoms was evaluated in young olive trees root dip inoculated with *Verticillium dahliae* in a growth chamber over a 12 week period and, later on, when the trees were transplanted in a *V. dahliae*-free soil in a lathhouse during a period of 127 weeks. Recovery in an individual tree was considered when a plant showed symptom remission after having reached a maximum value of symptom severity. Recovery accounted for 53% of 464 trees that showed wilt symptoms during observations in the two environments. The remaining trees died. Recurrent wilt symptoms were not observed in recovered trees, and recovery was usually accompanied by the production of new green tissues. Recovery was clearly higher in trees inoculated with a non-defoliating (ND) isolate (86.4%) of the pathogen than in those inoculated with a defoliating (D) isolate (23.9%). The percentage of recovery and the level of resistance were significantly correlated. Recovery accounted for 92.1% of the cases in resistant and moderately susceptible cultivars, reaching 100% in plants inoculated with the ND isolate (Table 2); meanwhile it was three times lower (30.1% of the plants) in susceptible and extremely susceptible diseased trees. In the lathhouse, periodical tissue isolations for monitoring the progress of infections over a period of 127 weeks in recovered trees, showed that the pathogen could only be isolated from trees 19 weeks after inoculation. Pathogen isolation was significantly higher from susceptible and extremely susceptible cultivars (84.6%) than from resistant and moderately susceptible ones (33.3%). Results showed that if a tree overcomes infection by pathogen from a single inoculation, and it is able to begin a recovery process, it will not express wilt symptoms again in a pathogen-free environment. The pathogen remained inactive or dead over time in recovered trees. Thus, new infections from rootlets would be necessary for new symptom expression. Recovery from *Verticillium* wilt is an important natural mechanism that occurs in a high percentage of infected olive trees, and can complement the resistance of the cultivar, particularly in conditions of low inoculum densities of low virulence isolates of the pathogen in the soil.

Introduction

Recovery is a natural phenomenon commonly associated with mechanisms that allow trees to overcome injury and decay (Shigo, 1984; Hiemstra, 1998), and can be activated after infections caused by vascular pathogens such as *Verticillium dahliae* (Tippet and Shigo, 1981). Recovery in woody hosts affected by *Verticillium* wilt has been reported in almond and peach (Ciccarese et al., 1990; Cirulli et al., 1998); apricot (Taylor and Flentje, 1968; Vigouroux and Castelain, 1969), ash and Norway maple (Hiemstra, 1995a, b), pistachio (Paplomatas and Elena, 1998), cocoa (Emechebe et al., 1974) and avocado (Latorre and Allende, 1983). In olive, natural recovery has been particularly observed under field conditions in olive orchards (Wilhelm and Taylor, 1965; Vigouroux, 1975; Blanco-López et al., 1990, Tjamos et al., 1991; López-Escudero and Blanco-López, 2001).

This phenomenon has been widely explained by the active response of the tree. The highly compartmentalised structure of the xylem in combination with cambial activity, producing new layers of tissue to replace the old or diseased xylem, facilitate plant recovery (Shigo, 1984). As reported by Wilhelm and Taylor (1965) and Tjamos et al. (1991), olive trees affected by *Verticillium* wilt are subjected to seasonal and transient infections by *V. dahliae*. This means that new infections should be necessary for new symptom development after a period of recovery, and enables control of the disease by preventing new invasions of rootlets by soil treatments, such as soil solarization (Tjamos et al., 1991; López-Escudero and Blanco-López, 2001), that reduce the inoculum density of *V. dahliae* in the soil around the tree.

In commercial olive orchards in Spain, natural recovery has been observed as a phenomenon that could play an important role in overcoming seasonal infections by *V. dahliae*, especially in young olive orchards, being more prevalent in soils with lower inoculum densities of non-defoliating (ND) pathotypes (Blanco-López et al., 1990; López-Escudero and Blanco-López, 2001; Martos-Moreno et al., 2001). Moreover, recovery has been also associated with the resistance level of the cultivar planted, as suggested by Resende et al. (1995) in cocoa. If this association also occurs in olive, it would be particularly important since in Andalucía (southern Spain) the integrated control and risk prediction systems of *Verticillium* wilt of olive are mainly based on the use of resistant cultivars, conditioned by the presence and spread of defoliating (D) isolates of the pathogen throughout new olive orchards (López-Escudero and Blanco-López, 2001; López-Escudero et al., 2004).

The phenomenon of recovery is difficult to evaluate since it is linked to the occurrence of asymptomatic infections, discontinuity and seasonal variations; this affects the feasibility of isolating the pathogen from infected plants. In olive trees, variations in pathogen isolation over time indicate that, in absence of continuous infections, the pathogen becomes occluded in vascular tissues and, presumably, becomes inactivated or dies (Wilhelm and Taylor, 1965; Rodríguez-Jurado, 1993).

The objective of the present work was to evaluate and quantify natural recovery from wilt disease symptoms in young olive trees, root dip inoculated under controlled conditions and, later on, in recovered plants after being transplanted in a *V. dahliae*-free soil. A second objective was to correlate plant recovery with pathogen virulence, cultivar resistance and infection.

Materials and methods

Disease progress and recovery of symptoms in the growth chamber

Studies were done using olive plant material inoculated in several experiments in controlled conditions with an ND or D isolate of *V. dahliae* (López-Escudero et al., 2004). The aim of this research was to assess the level of resistance of the cultivars to the infection by this pathogen. In these studies, severity of wilt symptoms was assessed weekly for 10 weeks, starting 2 weeks after inoculation. A scale of 0–4 was used according to the percentage of plant tissue affected by chlorosis, leaf and shoot necrosis or defoliation: 0 = healthy plant; 1 = 1–33% of plant affected (slight symptoms); 2 = 34–66% (moderate symptoms); 3 = 67–99% (severe symptoms); 4 = dead plant. Recovery from the disease in a given tree was considered when, after suffering a clear and consistent expression of wilt (equal or higher than value 1 in the disease scale, during more than 2 weeks), symptoms of disease stopped or consistently diminished after reaching a maximum value. Recovery was also considered when new green tissues, indicating disease resistance, were produced. Progress curves for incidence, percentage of dead plants, and percentage of plants that had started recovery over time were calculated for the entire period of the evaluation. The maximum value of symptom severity reached by each individual tree that had started recovery was also recorded.

Disease progress and recovery of symptoms in a lathhouse

Twelve weeks after inoculation, surviving olive trees were moved from the growth chamber to semi-controlled conditions in a lathhouse. Plants were transplanted to bigger plastic pots (25 cm high and 28 cm diam) filled up with a pathogen-free non-sterilised soil of the same composition as described previously. Disease progress was

observed during a period of time from the date of replacement of surviving trees from growth chamber to lathhouse, to one and a half years (for last replaced plants, inoculated in the fourth experiment) up to two and a half years (for first replaced ones, inoculated in the first experiment). Observations were made at variable intervals using the same disease scale described for the growth chamber period.

Statistical analyses

The percentage of plant recovery of different cultivars was correlated with the level of resistance shown by the cultivars using a Pearson correlation, using the programme Statistix 8.0 for Windows (Analytical Software, Tallahassee, FL). For this correlation, values 4, 3, 2 and 1 were assigned to the susceptibility classes resistant, moderately susceptible, susceptible and extremely susceptible, respectively. These classes had been previously assigned to the cultivars according to final values of the area under the disease progress curve and the percentage of dead plants after inoculation with *V. dahliae* (López-Escudero et al., 2004). Recovery was analysed separately for plants inoculated with each isolate.

Plant infection

Colonisation of plants by the pathogen was examined by isolations from affected twigs or leaf petioles from all plants showing wilt symptoms during the period in the growth chamber and from twigs and branches of all dead trees at the end of the experiments. In the first case, particularly in plants with slight and moderate symptom expression, 2–3 lateral diseased stems or petioles from green leaves recently defoliated were chosen, to avoid interference with the vegetative recovery of the main stem of these trees. Samples were washed in running tap water, peeled off the bark and surface disinfected in 0.5% sodium hypochlorite for 1 min. Wood chips or entire cross sections were placed onto Potato Destose Agar (PDA). Plates were incubated at 24 °C in the dark for 6 days.

The continuity of the presence of the pathogen in tissues of trees recovered from the inoculations in the growth chamber was assessed during the lathhouse period by complete and destructive isolations, carried out at 19, 69, 75, 106 and 127 weeks after inoculation. These consisted of isolations from secondary roots; crown (upper main root); lower and upper stem; medium, low and upper parts of the main twig; and low, medium and upper lateral twigs of each tree. Only trees with enough vegetative growth to allow this complete sampling were processed. Isolations from aerial parts of plants were done on PDA or PDA acidified, with three replications (plates) per part as explained above. Plates were incubated in the dark at 22–24 °C and, after 5 days of incubation *V. dahliae* colonies were identified and counted. For isolating the pathogen from roots, 0.4 g of fragments of secondary roots were chosen at random from the whole root, disinfested in 0.5% sodium hypoclorite for 1 min, and suspended in 10 ml of sterile distilled water in glass tubes. Fragments were ground in the suspension by a bench-top homogeniser (Polytron PT 10/35, Kinematica, GmbH, Luzern, Switzerland), for 1 min. Aliquots of 0.5 ml of dilutions 1:10 and 1:100 were placed onto Petri plates of PDA supplemented with 50 ppm of streptomycine sulfate, and 25 ppm of chloranphenicol and chlortetracycline, with 4 replications; plates were incubated as above.

Results

Disease progress and recovery of symptoms in growth chamber and lathhouse conditions

Infection in the growth chamber was very effective, since only 39 and 6 plants escaped from the inoculation with the ND and D isolates (Table 1). Disease symptoms started at the second week after inoculation and consisted of slight chlorosis and defoliation. From the fourth week, disease symptoms were more generalised and severe. Non-inoculated control trees remained free of disease symptoms. Percentage of trees that showed symptoms in the growth chamber experiment accounted for 91.2% of the plants and was higher for trees inoculated with the D isolate (97.7%) than for those inoculated with the ND isolate (84.5%) (Table 1); 11.3 and 66.9% of the symptomatic plants inoculated with the ND and the D isolate of *V. dahliae*, respectively, did not show recovery during controlled conditions and disease severity increased until the death of the plants (Table 1).

Table 1. Reaction of olive tree plants to inoculation with a non-defoliating or a defoliating isolate of *Verticillium dahliae*[a]

Inoculated trees	*V. dahliae* isolate[b]				Total	
	ND		D			
	N°	%	N°	%	N°	%
	252	100	257	100	509	100
Non symptomatic in growth chamber	39	15.5	6	2.3	45	8.8
Symptomatic in growth chamber	213	84.5	251	97.7	464	91.2
Dead in growth chamber	24	11.3	168	66.9	192	41.4
Recovered in growth chamber	158	74.2	47	18.8	205	44.2
Still recovered in lathhouse	158	100	47	100	205	100
Non recovered in growth chamber	31	14.5	36	14.3	67	14.4
Dead in lathhouse	5	16.1	23	63.9	28	41.8
Recovered in lathhouse	26	83.9	13	36.1	39	58.2
Total dead	29	13.6	191	76.1	220	47.4
Total recovered	184	86.4	60	23.9	244	52.6

[a]Plants were initially inoculated in four experiments under controlled conditions in a growth chamber, where resistance to *Verticillium* wilt of 23 olive cultivars was assessed (López-Escudero et al., 2004). Disease progress was evaluated in the growth chamber for 12 weeks after inoculations. Plants showing symptoms in the growth chamber were transferred to a lathhouse, and observations continued for two and a half years. Number and percentages of plants within the same rank, are additive in columns.
[b]ND = non-defoliating, D = defoliating.

Recovery started from the fourth week after inoculation, and occurred particularly in plants inoculated with the ND isolate (Figure 1) that showed slight symptoms, such as slight chlorosis, that diminished over time. Between the fifth and the sixth weeks after inoculation, maximum disease incidence was reached for plants inoculated with both isolates (Figure 1). Some of the non-recovered trees did not die in the growth chamber but still showed disease symptoms when they were moved to the lathhouse (Table 1).

New wilt symptoms were not observed during the lathhouse period in the trees that had started recovery in the growth chamber period (Table 1). For trees still symptomatic at the end of the growth chamber period, the chance of recovery of a given plant in the lathhouse depended on symptom severity level at the end of the period under controlled conditions. In plants showing high final severity of symptoms in the growth chamber, particularly those infected with the D isolate, chlorosis development, necrosis and defoliation continued in the lathhouse until the death of the plant; however, this only occurred in 5 and 23 plants infected with the ND and the D isolates, respectively. Meanwhile the remaining trees overcame the disease and did not show new symptoms (Table 1).

Recovery of the disease over time, both in the growth chamber and the lathhouse, was characterised by the production of new vegetative growth of twigs and leaves with no symptoms, that developed from healthy buds close to old affected tissues. In severely affected trees the production of new buds suckering from the base of the main stem was frequently observed. As result of the recovery, after a period of time new twigs were produced, that frequently enveloped completely old infected parts of the plant. Although there were no wilt symptoms, vegetative recovery in some trees was slow, and the production of new tissues or the regeneration of tissues previously wilted took more than one growing season.

Results of the observation of diseased progress in 464 symptomatic trees in the two environments therefore yielded global percentages of 52.6% of recovered trees and 47.4% of dead trees (Table 1). Recovery was clearly higher in plants inoculated with the ND than in those inoculated with the D isolates, accounting for 86.4 and the 23.9% of the symptomatic plants, respectively (Table 1). Disease recovery mainly occurred in plants in which maximum values of symptom severity were moderate and slight, respectively, for the D and the ND isolates (Figure 2).

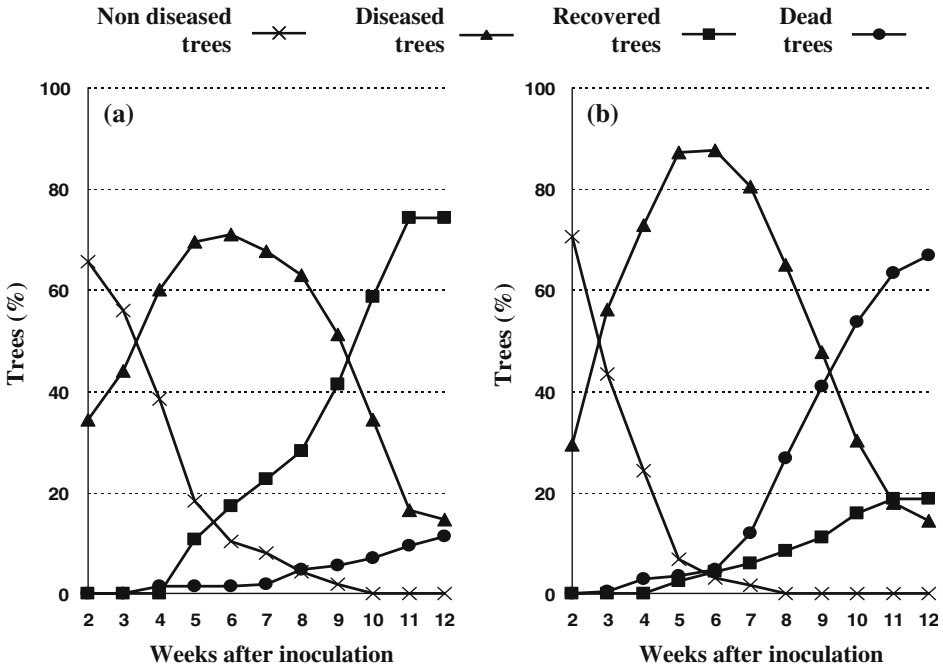

Figure 1. Disease progress and recovery from wilt disease in olive trees inoculated with ND (a) or D (b) isolates of *Verticillium dahliae* in the growth chamber. Curves correspond to the reaction of 464 olive trees, evaluated during 12 weeks in controlled conditions. During this period, 213 and 251 of the plants inoculated with the ND and D isolates of the pathogen, respectively, showed wilt symptoms (disease incidence). Non-diseased trees = asymptomatic trees; Diseased trees = diseased trees showing an increase in symptom development; Recovered trees = diseased trees that stopped or showed diminished wilt symptom development; Dead trees = trees that died after showing wilt symptoms.

Plant infection

Almost all trees showing symptoms during the growth chamber period yielded cultures of *V. dahliae*, demonstrating the consistency of infections. The pathogen was easier to isolate from plants with higher levels of symptom severity and, particularly, from plants inoculated with the D isolate at the end of experiments in controlled conditions. Similarly, *V. dahliae* was consistently isolated from tissues of dead plants.

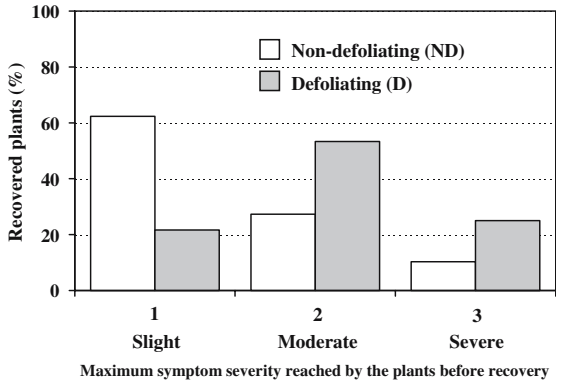

Figure 2. Percentage of recovered olive plants inoculated with ND or D isolates of *Verticillium dahliae* from the maximum symptom severity values reached by the plants before recovery phenomenon.

During the lathhouse period, *V. dahliae* could only be isolated from recovered plants 19 weeks after inoculation. By this time, tissues from 29 trees out of 35 yielded cultures of the pathogen. This corresponded to positive isolations from 17 plants inoculated with the ND isolate and 12 from those inoculated with D. The fungus was found more often in twigs than in roots, and all root isolations corresponded to positive isolations from aerial tissues of the same plants. Conversely, some of the positive isolations from twigs did not correspond to positive isolations from roots. The pathogen could not be isolated from crown tissues. The pathogen could not be isolated from trees during complete isolations performed from 69 to 127 weeks after inoculations. For these plants and sampling dates, there was only one exception in one plant of the cultivar 'Oblonga' inoculated with

the ND pathotype; in this case *V. dahliae* was isolated from root tissues 106 weeks after inoculation.

Relationship between recovery and cultivar resistance

The Pearson coefficient of correlation between the percentage of recovery and the level of resistance was highly significant, accounting for 0.61 and 0.92 for trees inoculated with the ND and the D isolates of the pathogen, respectively. Irrespective of the pathogen inoculated, the percentage of recovered trees was 86%, 77.5% and 13% in the moderately susceptible, susceptible and extremely susceptible plants, respectively. On the other hand, 100% of trees from resistant cultivars recovered from the disease in inoculations with the ND isolate. Therefore, in resistant and moderately susceptible cultivars (152 diseased trees), recovery accounted for 92.1% of cases (Table 2); it was nearly three times lower (33.3% of the plants) in susceptible and extremely susceptible diseased trees. With the exception of the moderately susceptible plants, the percentage recovery for each resistance class was significantly higher in the inoculations with the ND isolate than in inoculations with the D isolate (Table 2).

During the isolations carried out 19 weeks after inoculation, the pathogen was isolated in higher percentages from susceptible and extremely susceptible cultivars (84.6%) than from resistant and moderately susceptible ones (33.3%) (Table 2). In plants inoculated with the ND isolate, *V. dahliae* was only isolated from susceptible or extremely susceptible cultivars, that accounted for 71.4% of the processed plants. Nevertheless, the D pathotype was easily isolated from plants included in all resistance categories (85.7% of cases), although results indicated that susceptible and extremely susceptible plants were more consistently infected.

Discussion

We have shown that recovery occurred in a high percentage of olive plants after being inoculated with *V. dahliae*. In infected trees, the symptoms of the disease developed during a variable period, until the plant died or reached a maximum value of disease symptom severity. From this time, surviving trees started to recover from the disease. Recovery was usually expressed by the cessation of symptom development and the production of new vegetative growth. From the observations on disease progress it follows that recovery success clearly depends on the virulence of the *V. dahliae* isolate used to infect the plant, the level of severity of symptoms shown by the plant and the level of cultivar resistance.

In the present study we have quantified the differences in the capability of olive trees for overcoming infections caused by *V. dahliae* isolates differing in virulence. Thus, recovery from the disease was much higher in trees infected by the ND isolate than by D, resulting in percentages of 86.4% and 23.9%, respectively. Recovery from *Verticillium* wilt has also been clearly associated with the level of resistance of the olive cultivar, as demonstrated by Resende et al. (1995) in cocoa. Percentage of recovery in resistant and moderately susceptible diseased plants was three times higher than in susceptible and extremely susceptible diseased plants. In olive, both pathogen virulence and cultivar resistance seem to be connected with the capability of the plant to slow down pathogen development during colonisation, as suggested by Rodriguez-Jurado (1993) and López-Escudero et al. (2004). Levin et al. (2003) reported on natural recovery in the olive cv. Barnea (tolerant), but not in cv. Souri (susceptible) in a commercial olive orchard in Israel, where the soil was highly infested with *V. dahliae*.

In the current work, the symptom severity reached by a plant had a significant influence on its recovery, which started earlier and more successfully in plants with slight symptoms caused by the ND isolate. This is presumably due to limited or discontinuous colonisation by the less virulent isolate, that allowed plants to stop pathogen development early and start production of new tissues. Disease symptoms were overcome in plants inoculated with the D isolate from higher values of disease severity, and was usually slower, suggesting that infection by this isolate was faster, more extended and consistent. In some of the susceptible or extremely susceptible cultivars, such as Hendeño, Hojiblanca, Meski or Valanolia, recovery was expressed as a re-growth of the plants after reaching very high values of symptom severity. Thus, in these severely injured plants recovery from the disease had no agronomic value.

Table 2. Relationship between cultivar resistance and recovery of olive plants from inoculations with a non-defoliating or a defoliating isolate of *Verticillium dahliae*[a, b]

Isolate	Cultivar resistance	Diseased plants			Recovery (%)	Mean[d]
		N°	Recovered			
			N°	%[c]	Cultivar	
ND	R	66	66	100	'Cobrancosa' (100), 'Empeltre' (100), 'Frantoio' (100), 'Manzanilla Sevilla' (100), 'Morisca' (100), 'Oblonga' (100), 'Verdial Alcaudete' (100)	100
	MS	39	35	89.7	'Leccino' (88.8), 'Lechin de Granada' (100), 'Meski' (83.3), 'Pajarero' (100), 'Picudo' (80.0)	90.4
	S	90	73	81.1	'Arbequina' (87.5), 'Hendeño' (100), 'Hojiblanca' (66.6), 'Manzanilla Piquito' (100), 'Negral' (71.4), 'Nevadillo Negro' (100), 'Ocal' (83.3), 'Picual' (62.3), 'Villalonga' (100).	85.7
	ES	18	10	55.5	'Cornicabra' (50), 'Valanolia' (62.5)	56.2
D	R	0	0	0	-	0
	MS	47	39	82.9	'Empeltre' (100), 'Frantoio' (87.5), 'Oblonga' (79.7)	89.1
	S	8	3	37.5	'Nevadillo Negro' (37.5)	37.5
	ES	196	18	9.2	'Arbequina' (0), 'Cobrancosa' (20), 'Cornicabra' (0), 'Hendeño' (44.4), 'Hojiblanca' (22.2), 'Leccino' (20), 'Lechin de Granada' (0), 'Manzanilla Piquito' (14.3), 'Manzanilla Sevilla' (0), 'Meski' (20), 'Morisca' (10), 'Negral' (10), 'Ocal' (14.3), 'Pajarero' (0), 'Picual' (0), 'Picudo' (0), 'Valanolia' (10), 'Verdial de Alcaudete' (0), 'Villalonga' (12.5)	10.4

[a]ND = non-defoliating; D = defoliating.
[b]Resistance categories of olive cultivars according to López-Escudero et al. (2004). R = resistant, MS = Moderately susceptible; S = Susceptible; ES = Extremely susceptible.
[c]Total recovered plants after being inoculated with *V. dahliae*. Percentages of recovery were correlated (Pearson) with the level of resistance. Correlation coefficient was highly significant, accounting for 0.61 and 0.92 in trees inoculated with the ND and the D isolate of the pathogen, respectively.
[d]Mean recovery of cultivars from the same resistance category.

The only available quantitative data for recovery in olive can be extracted from untreated trees in field experiments with soil solarization in olive orchards carried out by Tjamos et al. (1991). Although their results demonstrate the important role of natural recovery from *Verticillium* wilt in the field, these might not be comparable with our results, since in their studies trees were subjected to continuous infections from a naturally infested soil. In the present study recovery occurred very frequently in young trees subjected to a single inoculation with *V. dahliae*, and continued after transplanting to a *Verticillium*-free soil. New infections might be limited from the residual inoculum in the rhizosphere (Lacy and Horner, 1966) or from microsclerotia generated in the original soil from mycelium growing close to this zone. However, in these conditions the probability of plants being re-infected is low due to the low saprophytic growth capability of *V. dahliae* (Schnathorst, 1981). Therefore, if a plant overcomes infection and colonisation by the pathogen, it will not express wilt symptoms again. These results confirm the hypothesis of Wilhelm and Taylor (1965) who suggested that, under field conditions, if new infections through rootlets did not occur, recovery of a tree was permanent. This could also explain the frequent natural phenomenon of recovery observed in field experiments with olive trees showing severe symptoms (Blanco-López et al., 1990; Tjamos et al., 1991; López-Escudero and Blanco-López, 2001).

Initial steps of recovery probably depend on the capability of the tree to occlude infected vessels, inactivate the viable fungus in the xylem and impede new infections, as reported by several authors (Wilhelm and Taylor, 1965; Talboys, 1968; Sinclair et al., 1981; Rodríguez-Jurado, 1993; Hiemstra, 1995a, b). Conclusions from this study agree with

this hypothesis, since *V. dahliae* could not be isolated (with one exception) from any of the examined trees 19 weeks after inoculation. Since recovery occured not only in the field but also in controlled conditions, it could be not only a passive inactivation caused by non-favourable environmental conditions, such as high temperature in the field, but as a result of the active response of the infected plant.

Recovery is an important natural mechanism that may be important in the field when cultivar resistance is high, the colonisation of the olive tree is partial and/or the inoculum density of *V. dahliae* in the soil is low, particularly in infested soils with isolates of the pathogen of low virulence.

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