EEET ECOLOGICAL ENGINEERING & ENVIRONMENTAL TECHNOLOGY

Ecological Engineering & Environmental Technology, 2026, 27(12), 509–540
https://doi.org/10.12912/27197050/241750
ISSN 2719–7050, License CC-BY 4.0

Received: 2026.09.19
Accepted: 2026.10.20
Published: 2026.11.02

Verticillium wilt of *Olea europaea*: A re-emerging pathogen threat under climate change and sustainable management

Sana El Haji[1,2*], Malak Sahnoun[1], Laila Rhazi[1], Redouan Qessaoui[2], Rachid Bouharroud[2], Aicha El Aissami[1], Soukaina Msairi[1]

[1] Laboratory of Botany and Valorization of Plant and Fungal Resources, Department of Biology, Faculty of Sciences, Mohammed V University in Rabat, 4 Avenue Ibn Battouta, B.P. 1014 RP, Rabat, Morocco
[2] Regional Center of Agricultural Research of Agadir, National Institute of Agricultural Research (INRA), Rabat, Morocco
* Corresponding author's e-mail: sana_elhaji@um5.ac.ma

ABSTRACT

Verticillium dahliae, a soil-borne fungus, is responsible for *Verticillium* wilt, one of the most serious vascular diseases affecting olive groves worldwide. This disease is prevalent mainly in the Mediterranean region, causing significant economic damage to olive orchards, particularly among highly susceptible varieties. The fungus penetrates the xylem tissue of the trees, leading to leaf drop and wilting; in severe cases, it can even kill the trees. Controlling *Verticillium* wilt is challenging due to the pathogen's long-term survival in the soil and its complex biological nature. The pathogen's pathogenic mechanism is highly intricate, as the pathogen can survive as microsclerotia in the soil for many years and has the ability to spread through plants and irrigation water. This review aims to provide up-to-date information on the biology of *V. dahliae*, including its strains, infection cycle, and epidemiology. Chemical control has proven relatively ineffective, while intensive cultivation and irrigation exacerbate the conditions conducive to disease development. This highlights the urgent need for sustainable and integrated disease management techniques. These techniques may include planting resistant varieties, such as Frantoio; biological control using agents such as *Trichoderma* species; solar soil sterilization; and improved drainage practices. Recent developments have emphasized the role of ecology and biotechnology in managing this disease through the application of microbial biostimulants. In this review, climate drivers of the disease are analysed in a dedicated section, the level of evidence of diagnostic and control approaches is graded (olive-specific versus other hosts), and an integrative framework linking pathogen biology, diagnostics and management is proposed together with the main knowledge gaps.

Keywords: *Verticillium dahliae*, *Verticillium* wilt, *Olea europaea*, climate change, sustainable agriculture, integrated disease management.

INTRODUCTION

Olea europaea subsp. *europaea* L., the cultivated olive tree, is an integral part of the socio-ecological structure of the Mediterranean region, promoting biodiversity and the economy and cultivated for thousands of years (FAO, 2020). Being native to this area, the tree has been cultivated by humans since ancient times, according to available evidence (Green, 2002, 2004; Connor, 2005). The high degree of tolerance of this tree, its longevity, and the good taste characteristics of the fruit, whether as olives or oil, make it a vital component of the Mediterranean agroecosystem. Mediterranean climate has served as one of the principal forces in the development of agriculture in the region, which has historically involved the cultivation of olives, cereals, and grapes (Ramos et al., 2025). As the leading producer of olives in the world with an area of more than 2.62 million hectares, Spain is responsible for about 45% of olive oil and 23% of table olives produced around the globe (FAOSTAT, 2021).

In the past, traditional propagation methods did not contribute to the loss of genetic diversity in the olive tree or to the adaptive evolution of the species. This limited effect resulted from low selection pressure in extensive cultivation systems and the strong geographic structuring of cultivar ranges, which tended to confine most varieties to their native regions (Barranco et al., 2017). Over recent decades, however, olive growing has undergone a "green revolution," shifting from extensive, traditional practices to high-density plantation systems (Connor et al., 2014; Montes-Osuna and Mercado-Blanco, 2020). While these changes increased productivity, they also made orchards more vulnerable to pathogens particularly *V. dahliae*, the agent of *Verticillium* wilt of olive (VWO). Combined with environmental stressors, the change in production systems has aggravated the incidence and severity of soil-borne and xylem-invading diseases, notably those caused by *V. dahliae* and *Xylella fastidiosa*, which today represent transboundary threats to olive production (Jiménez-Díaz et al., 2011; Schneider et al., 2020).

Verticillium wilt is now regarded as the most destructive disease of olive trees worldwide. First recorded in Italy in 1946, it has since become widespread across the Mediterranean region (Jiménez-Díaz et al., 2011). *Verticillium* wilt is caused by the soil-borne, xylem-colonizing ascomycete *V. dahliae Kleb.*, a vascular pathogen that produces severe wilting, defoliation, branch necrosis, reduced fruit yield, and, ultimately, tree death (Inderbitzin et al., 2011; López-Escudero and Mercado-Blanco, 2011; Jiménez-Díaz et al., 2012; Levin et al., 2003; Landa et al., 2019).

In Morocco, another significant olive-producing country within the Mediterranean region, the area devoted to olive production exceeds 560,000 ha and accounts for about 5% of national GDP. It is dominated by the Picholine Marocaine variety to the tune of 80-96% of the planted area. (Hadiddou et al., 2013; Bouymajane et al., 2020). This variety's popularity in Morocco can be attributed to several factors including its past prominence.

In contrast, 'Picual' is considered one of the most important cultivars in various Mediterranean nations because of its characteristics like precocity, high productivity, low fruit removal force (which is beneficial for mechanized harvest), and wide adaptability to various soils and climates (Barranco, 2008). However, another drawback of 'Picholine Marocaine' is that it is very vulnerable to the *Verticillium* wilt disease, putting olive production in the country in danger (Boutaj et al., 2020a,b). Due to the economic and environmental significance of this disease, *Verticillium* wilt management has become an important task for scientists and the olive oil industry around the globe (López-Escudero and Mercado-Blanco, 2011; Jiménez-Díaz et al., 2012; Tsror, 2011).

Previous review articles have already considered the biology of the pathogen and VWO management (López-Escudero and Mercado-Blanco, 2011; Jiménez-Díaz et al., 2012). The achievements of the past decade have been summarized as well (Montes-Osuna and Mercado-Blanco, 2020).This review (i) explores the effects of climate variables as an independent factor influencing the olive-*V. dahliae* pathosystem; (ii) assesses the evidentiary basis for the diagnosis and management of the disease and distinguishes olive-based data from that of other hosts; (iii) identifies the diagnostic assays validated for olive; (iv) develops an integrated concept of the relationship between biology, diagnostics, and management.

OLIVE CROP

The economic importance of olive cultivation worldwid

Olive oil is an essential product of the olive tree as well as a critical component of the Mediterranean cuisine. Apart from its nutritional value, it holds much cultural and economic importance throughout the area (Vossen, 2007; Mallamaci et al., 2021). As per International Olive Council, worldwide consumption of olive oil for the 2024/25 period is estimated to be approximately 3,064,500 tonnes, up by 10.0% from 2023/2024.

The planting of olives is primarily carried out in countries with high and medium incomes; 49% of the total area of olives grown is planted in high income countries, while around 44% is planted in countries with medium incomes (Villar and Pereira, 2018). Production is significantly concentrated in a few Mediterranean countries according to FAOSTAT (2025), (Figure 1). The largest producer is Spain, which produces about 5.10 million tons in 2023 (≈30.9% of total production), followed by Italy (2.39 million tons, 14.5%), Turkey (1.52 million tons, 9.2%), Portugal (1.19 million tons, 7.2%), Tunisia (1.08 million tons, 6.5%), and Morocco (1.05 million tons, 6.3%). Algeria and Syria produce about 0.90

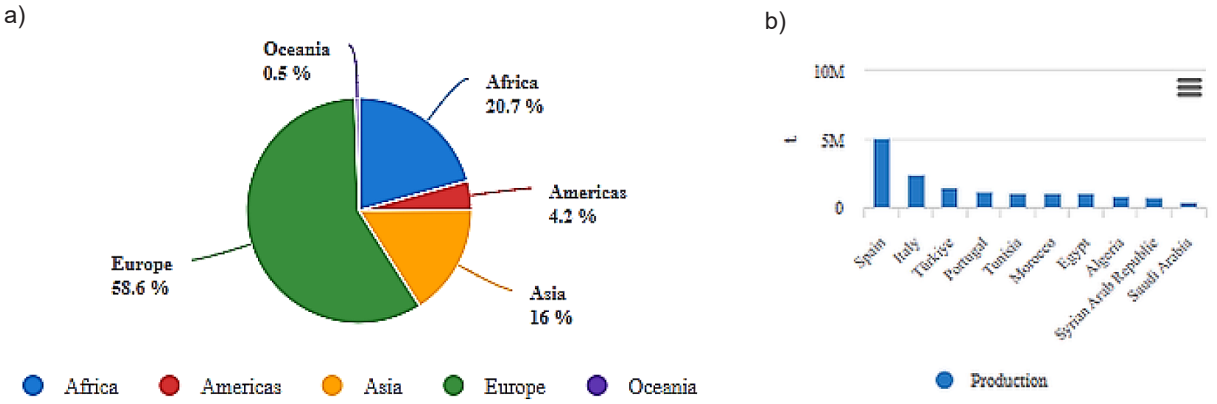


Figure 1. Olive production by regions (a) and top ten olive-producing nations globally in 2023 (b), (FAOSTAT, 2025)

million tonnes (5.5%) and 0.70 million tonnes (4.2%), respectively.

Geographically, the total area of land used for cultivating olive is 10,578,246 hectares with total production of about 19,464,495 tonnes (Al-Jaleely et al., 2025). The major producer of olives includes Europe with a share of 58.6 percent, while Africa contributes 20.7 percent, and Asia contributes 16.0 percent. Other parts include Americas (4.2%) and Oceania (0.5%). This geographic distribution indicates the significance of the Mediterranean region in the olive industry.

VERTICILLIUM WILT: A MAJOR THREAT TO OLIVE CULTIVATION

Biology and pathogenicity of *V. dahliae* Kleb.

The *V. dahliae* Kleb. is a soil fungus which attacks the vascular system of the plants. It is a highly polyphagous fungus which can survive in soil for very long time periods, thus posing serious threats to agriculture. This fungus, an Eukaryota organism, belongs to taxonomic classification groupings under Kingdom: Fungi; Phylum: Ascomycota; Subphylum: Pezizomycotina; Class: Sordariomycetes.

Of the 10 known species of *Verticillium*, *V. dahliae* is regarded as the most pathogenic and economically important one (Inderbitzin et al., 2011; Inderbitzin and Subbarao, 2014). The fungi affect more than 400 plants in different genera, such as cotton, potatoes, and tomatoes (Song et al., 2020; Klosterman et al., 2009; Njoroge et al., 2009; Wheeler and Johnson, 2016). *V. dahliae* occurs extensively throughout the temperate and warm zones, from 60°N to 50°S latitude (Harris, 1998; Pegg and Brady, 2002). It causes considerable damage to olive trees especially in the Mediterranean region, where it represents a major problem. Apart from olives, this pathogen is known to attack several other host species such as potato (*Solanum tuberosum*), pistachio (*Pistacia vera*), eggplant (*Solanum melongena*), almond (*Prunus dulcis*), cotton (*Gossypium hirsutum*), and tomatoes (*Solanum lycopersicum*) (Jiménez-Díaz et al., 2012; Klosterman et al., 2009; Kowalska, 2021).*V. dahliae* was considered an asexually reproducing organism without any knowledge about its sexual phase (Usami et al., 2009).

From the morphological perspective, the anamorph phase of *V. dahliae* is characterized by hyaline conidiophores with verticillate branching (Figure 2). The conidiophores are usually erect, sparsely branched, brown to dark brown, with usually thick and warty walls. Annellations develop due to percurrent growth of the conidiogenous cells (Schubert et al., 2003). Conidia are approximately 2.5 to 5 µm long and 1.25 to 2.5 µm wide. At 15 days of incubation at a temperature of 25 °C in darkness, most of the *V. dahliae* isolates form microsclerotia, which are compacted and melanized, allowing them to survive for long periods within the soil (Gharbi et al., 2016). On PDA medium, there are variations between the growth rates of the mycelium. At temperatures of 23-25 °C without light, the growth rate averages from 1.9 to 3.66 mm/day (Kaliterna et al., 2016; Varo et al., 2016). The characteristics of persistence within the soil environment, wide host range, adaptability within the genome, and ability to colonize plant vascular tissue make *V. dahliae* one of the most persistent plant pathogens that is difficult to manage.

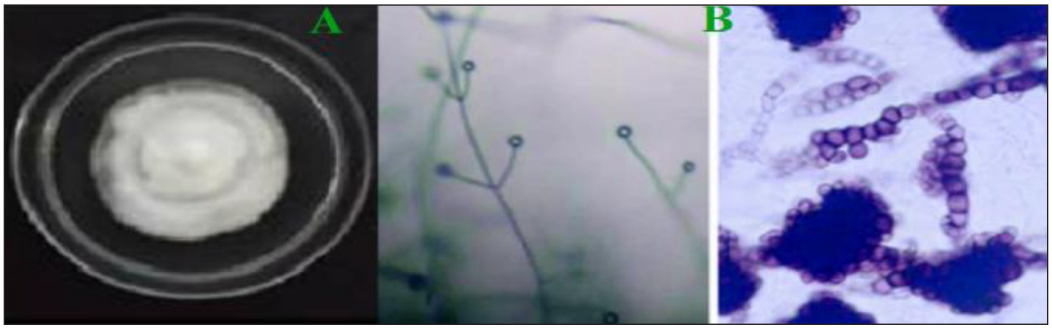


Figure 2. Morphological characteristics of *V. dahliae* strains isolated from symptomatic olive tissue (Keykhasaber et al., 2018; Jiménez-Díaz et al., 2012)

Symptoms in olive trees

Typical symptoms observed for *V. dahliae* infection in olives are a consequence of vascular impairment (Figure 3). This leads to chlorosis, early leaf senescence, stunted plant growth, necrosis, leaf fall, and eventually dieback and plant mortality (Montes-Osuna and Mercado-Blanco, 2020). An unequivocal symptom of infection involves darkened browning of the vascular system, visible when slicing stems of the olive plant (systemic infection of the fungus). With disease development, branches of the infected plants become desiccated with dead leaves persisting on their surface. The lower canopy is typically more affected since there is more soil inoculum at the root level. Olive plants infected by the fungus are weakened and exhibit canopy defoliation in severe cases (Rhouma et al., 2023). These effects highlight the considerable economic significance of the pathogen.



Figure 3. Characteristic disease symptoms of *Verticillium* wilt in *Olea europaea*: partial or complete tree wilting with defoliation (A, B), shoot and branch dieback (C), and vascular discoloration and necrosis (D) (Antón Domínguez, 2024)

Two types of the disease have been identified: one being apoplexy (acute) and the other slow decline (chronic). Apoplexy occurs in the Mediterranean region during late winter to early spring, where there is sudden wilt in primary and secondary shoots. The leaves become chlorotic, necrotic, and inwardly curled without falling off, resulting in drying up. This type of the disease affects young trees greatly, sometimes causing total tree death (Blanco-López et al., 1984; Jiménez-Díaz et al., 1998). *V. dahliae* annually results in significant losses to the economy globally.

The chronic variant appears more slowly. The symptoms manifest themselves starting from the spring period and intensify during summer by such signs as chlorosis, necrosis, shedding of leaves that retain their green color, and mortality of inflorescences. Defoliation may affect certain branches, while green leaves remain on the shoot tips (Jiménez-Díaz et al., 1998). It is possible for both types to occur in the same tree depending on external factors and inoculation. Mummification of the fruits can also be seen from the spring to the autumn periods. In addition, the disease changes the taste characteristics of olives and lowers oil quality (Landa et al., 2019).

Geographic distribution of *V. dahliae* in *Olea europaea*

Verticillium wilt, which is caused by the fungus *V. dahliae* that lives in the soil, is the most severe fungal disease to affect olive crops around the globe (Figure 4). In the last 20 years, *verticillium* wilt has killed many trees because of the cultivation of susceptible varieties, irrigation, and olives grown in former host crops (Montes-Osuna and Mercado-Blanco, 2020). The first report was done in Sicily on varieties including Bella di Spagna, Nocellara, and Ogliarola (Ruggeri, 1946). It then expanded into other Italian areas (Cirulli, 1975, 1981) before reaching other European nations, the Middle East, and USA (Jiménez-Díaz et al., 1998). The propagation and maintenance of *V. dahliae* infection in the orchards have been associated with current agricultural practices involving the use of self-rooted nursery stocks in compact plantations, irrigation using the drip system, zero tillage, and excessive fertilizer application on productive or recently established lands (Jiménez-Díaz et al., 2011).

V. dahliae has spread globally through major agricultural regions, according to the EPPO Global Database (EPPO, 2025). This fungal pathogen can be found in Spain, Italy, France, Germany, and the United Kingdom in Europe. In North America, it has been observed in several states of the United States and Canada. Also, it is prevalent in Brazil, Argentina, and Chile in South America. In Asia, it can be found throughout China, India, Turkey, and several other countries located in the Middle East and Central Asia. In Africa, it is present in Egypt, Tunisia, Kenya, and South Africa. The pathogen is present in New Zealand and Australia as well. Such extensive spread throughout various types of climate proves that *V. dahliae* is a highly adaptable organism that can settle in the soil of olive-growing areas for quite a long time.

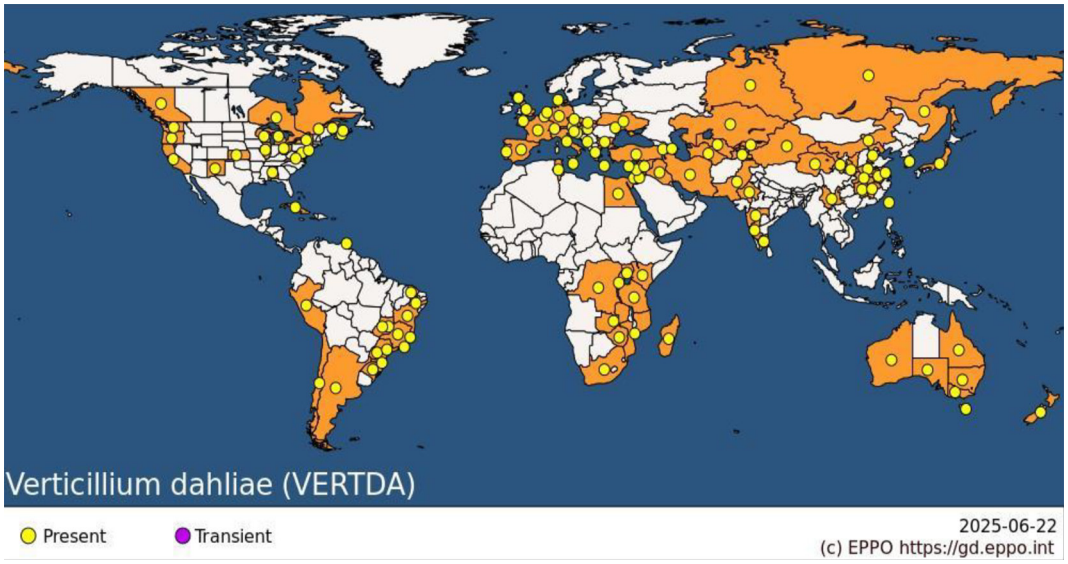


Figure 4. Worldwide distribution of *V. dahliae* (EPPO, 2025)

Life cycle and infection biology of *V. dahliae* in olive trees

Verticillium wilt of olive has two stages in which disease progression takes place, namely the saprophytic stage in the soil and the parasitic stage within the host (Figure 5). Microsclerotia are the chief means by which the fungus survives on soil, and they have been found to be able to live up to 15 years without the presence of a host as dark-colored resting structures in the soil (Wilhelm, 1955). Production of melanin is strongly linked to the development of microsclerotia in the fungus, therefore, any darkened region signifies MS development (Wang et al., 2018b). Microsclerotia develop within dead or decaying plant tissues to act as an important source of inoculum for further infection (Schreiber and Green, 1963).

Microsclerotia germination is induced by root exudates from host plants, which allow the fungus to emerge and invade the plant roots either via their apex or wounds created alongside roots (Bishop and Cooper, 1983).

Exudates released from susceptible plants promote germination of microsclerotia. Hyphae then enter the roots, either through the tips of the roots or by entering lateral roots at the sites of wounds (Bishop and Cooper, 1983). When the conidia have germinated on the roots' surface, there will be a development of the hypopodium, which produces a penetration peg for entry into the root cells (Zhao et al., 2016). The fungus is able to grow through the root system into the xylem vessels, affecting its functions of transporting nutrients and water (Jiménez-Díaz et al., 2012). The process of continuous conidial formation ensures germination, infection, and colonization cycles, which eventually lead to wilting of branches or plants (Häner and Diederichsen, 2016).

Symptoms of *Verticillium* wilt occur even at extremely low levels of inoculum, where infection may occur with microsclerotia concentrations as little as 0.1 MS/gm of soil, emphasizing the high infectious nature of this fungus (Hiemstra, 1998). Disturbance in water and nutrient balance leads to characteristic symptoms such as chlorosis and defoliation in *Verticillium* wilt occurrence. Symptoms are determined by the particular pathotype of *V. dahliae*, and development of the disease after planting is also affected by the type of soil (Dervis et al., 2010).

Current knowledge on *V. dahliae* and its interaction with *Olea europaea*

The specificity of the pathotypes, either moderately virulent non-defoliating (ND) or extremely virulent defoliating (D), in isolates of *V. dahliae* has been established from genotypic variation, where informative markers could be found within genes related to host-specific virulence control (Keykhasaber et al., 2018).These terms of pathotypes (D and ND) define the phenotype, and the two major ones which influence olive in some instances have been (Mercado-Blanco et al., 2003; López-Escudero and Mercado-Blanco, 2011).

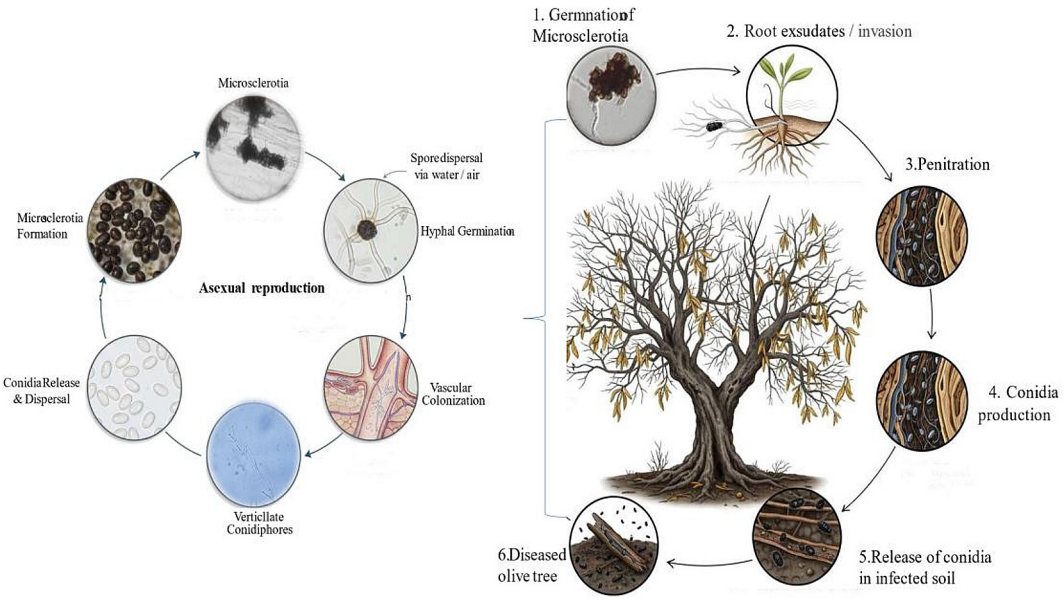


Figure 5. Schematic diagram depicting the infection cycle of *Verticillium* wilt in tree species

There are two races of *V. dahliae* termed Race 1 and Race 2 based on the existence and non-existence of the Ave1 effector protein gene (Popov et al., 1972; Maruthachalam et al., 2010; de Jonge et al., 2012). The Race 1 is characterized by fungi with Ave1 that is identifiable (makes the host organisms avirulent) in presence of Ve1 gene in plants, whereas the race 2 is without Ave1 that helps to evade the Ve1 resistance of the host plant for infection. Racial differentiation is critical for population genetics and host range studies of *V. dahliae* (Baroudy et al., 2019).

There is considerable genetic diversity in *V. dahliae* with respect to its pathogenicity and host spectrum. *V. dahliae* has genetic variation in terms of chromosomal rearrangement and horizontal gene transfer enabling evolutionary adaptability (de Jonge et al., 2013; Chen et al., 2018). Genetic analysis studies show variable degrees of diversity along with mixed reproductive behavior, such as genetic segregation into two distinct groups in Uruguay strains, which exhibited moderate genetic diversity and linkage disequilibrium (Bernaschina et al., 2020). Various markers like microsatellites have been used to analyze genetic diversity in single orchards and extensive geographic populations (Puri et al., 2017; Short et al., 2015).

Variation of virulence, host range, and environment adaptation within *V. dahliae* isolates due to its high level of genetic variability poses a challenge for disease management (Jeseničnik et al., 2023). The secretome of the fungus is made up of nearly 800 proteins, among which there are many effector proteins that assist in promoting host infection and pathogenic activity (Klosterman et al., 2011; Lo Presti et al., 2015). Nevertheless, even with such versatility, the population structure of *V. dahliae* is frequently highly clonal as a result of frequent asexual propagation (Fradin and Thomma, 2006; Milgroom et al., 2014). With such genetic flexibility, it is possible to develop coevolution with hosts as well as new pathotypes (Atallah et al., 2010; Song et al., 2020).

The genetic and phenotypic diversity of *V. dahlia* is expressed at distinct biological levels that must be clearly differentiated. Pathotypes are defined by disease phenotype and virulence: the defoliating (D) pathotype causes rapid defoliation and high mortality, whereas the non-defoliating (ND) pathotype induces milder vascular wilt and often allows plant recovery (Sánchez-Hernández et al., 1998; López-Escudero & Mercado-Blanco, 2011).

Vegetative compatibility groups (VCGs), in contrast, are genetic lineages based on the ability of asexually reproducing isolates to form stable heterokaryons (Puhalla, 1979; Leslie, 1993). At least eight VCGs have been described and largely correspond to distinct clonal lineages (Jiménez-Gasco et al., 2014; Milgroom et al., 2014). Importantly, pathotypes and VCGs are not equivalent. Although occasional associations between certain VCGs and virulence phenotypes exist, no consistent correlation allows VCG membership to predict pathogenicity. VCG classification informs population structure but cannot serve as a direct marker of virulence (Acharya et al., 2020).

Factors influencing the development and spread of *Verticillium* wilt in *Olea europaea*

The evolution of *Verticillium* wilt is highly dependent on host-pathogen-environmental dynamics where inoculum level and means of spread play crucial roles (Pegg and Brady, 2002; Katan, 2017). Although the physiological condition of the olive plant influences significantly the expression of the disease, environmental conditions and farm management practices are equally important.

The thermal condition in the soil has a major effect on the effectiveness of *V. dahliae*. The optimum temperature for growth of the fungi is 20-25°C, which is usually the temperature during spring season in the Mediterranean climate (Pegg and Brady, 2002). Temperatures that are lower than 20°C can allow fungal growth in the host but not in the soil (Fradin and Thomma, 2006; Thanassoulas et al., 2006).

High levels of soil moisture, high humidity levels, and over irrigation favor a higher density of inoculum and increased incidence of disease development (Tsror, 2011; López-Escudero and Blanco-López, 2005; Pérez-Rodríguez et al., 2016). Within Spain, the highest incidences occur from February to June, coinciding with optimum infection conditions for the pathogen (García-Ruiz et al., 2014).

V. dahliae affects olives regardless of the soil type, but disease development is determined by the climate and the soil. Lighter soils (sandy and loamy) in colder climatic conditions are favorable for rapid disease development, while heavier soils (clay and silt) in warmer climates worsen the disease symptoms (Goicoechea, 2006).

Dispersal by insect vectors has been observed. *Xylophagus* species such as *Scolytus intricatus*

and *Xyleborus dispar* can transport the pathogen (Riziero and Ragazzi, 1998; Riziero et al., 2002). Though there is uncertainty surrounding their ability to serve as *V. dahliae* vectors for olives, a few pieces of research indicate their involvement in pathogen spread in specific instances (Liu et al., 2021; El-Hamalawi, 2008).

Locally, the disease spreads via contaminated soil, contaminated irrigation water, diseased plant material, and wind-borne debris. Poor sanitation via the use of poorly disinfected equipment plays a crucial role in the spread from one tree to another. Diseased trees shed their microsclerotia into the surrounding soils, thus ensuring that the pathogen remains locally persistent and infectious (Liu et al., 2021; El-Hamalawi, 2008).

Long-distance dispersal occurs through human activities such as moving infected plant stocks, roots containing infected soil, or through contaminated tools. The introduction of infected plant materials into non-infested orchards is the principal method of spreading *V. dahliae*.

The current agricultural practices such as planting high density, regular irrigation, intensive mechanization, and application of fertilizers favor growth of *V. dahliae*. Such practices can affect the soil and cause damage to the roots hence allowing the pathogen easy access to host tissues (Montes-Osuna and Mercado-Blanco, 2020)

CLIMATE CHANGE AND THE OLIVE–*VERTICILLIUM DAHLIAE* PATHOSYSTEM

Climate change is expected to alter the environmental factors that control the olive-*V. dahliae* pathosystem. While there is not much direct evidence yet, three types of studies indicate the effect of climate on the disease: (i) the established thermophilic and hygrophylic requirements of the fungus, (ii) field observations correlating climatic factors with the presence of the pathogen, and (iii) ecological niche models predicting shifts in response to future climates (Table 1).

The manifestation of the disease in olive trees is highly dependent on temperatures. The optimal growing conditions for fungi are between 20–25 °C, while the degree of symptom manifestation decreases sharply above 30 °C during the summer season (Requena-Mullor et al., 2020). Under laboratory conditions, soil temperature has a different effect on the development of the two pathotypes in olive varieties: infection with the defoliated pathotype (D) is favoured between 16–24 °C in the susceptible grower 'Picual' and between 20–24 °C in the other less susceptible cultivator 'Arbequina', while infection with the non-defoliated pathotype (ND) occurs between 16–20 °C (Calderón et al., 2014).

In 779 olive orchards in Granada, *V. dahliae* exhibited a higher frequency with a low daily temperature range compared to the seasonal temperature range; irrigation decreased this effect, demonstrating that proper irrigation management could help prevent symptoms at the optimal thermal level of the pathogen (Requena-Mullor et al., 2020). At the landscape scale, these climatic conditions were integrated into ecological niche models and temperature, rainfall seasonality and isothermality became the main predictors of the distribution (Arias-Giraldo et al., 2025). In line with these data, climate change projections for southern Spain reveal a redistribution of adapted regions towards the south and southeast of Andalusia without an overall decrease in areas suitable for development (Arias-Giraldo et al., 2026).

Excessive water in the soil and over-irrigation increase inoculum levels and disease occurrence (López-Escudero & Blanco-López, 2007; Santos-Rufo et al., 2017). Indeed, the incidence and severity of disease are very much controlled by irrigation amount and frequency, especially in the case of susceptible cultivars; the effect also depends on the degree of susceptibility to the disease (Santos-Rufo et al., 2017, 2018; Santos-Rufo & Rodríguez-Jurado, 2021). Thus, with higher temperatures and lower precipitation, irrigation performed by growers might lead to the development of conditions favouring the disease pathogen. Furthermore, both infection by the pathogen and drought cause closure of stomata and decrease in transpiration (Calderón et al., 2014); nevertheless, the combined effect of these factors has not yet been measured for olives. Experiments performed on other pathosystems indicate that transpiration is a factor facilitating transportation of conidia in the xylem (Pennypacker et al., 1991); however, this has not yet been tested for olives.

Variability in climatic conditions impacts all the methods mentioned above. Resistance screening ought to be done using a range of temperatures. Biocontrol and biostimulant effects have been little studied under varying temperatures and humidity conditions. Indices of thermal and

Table 1. Climatic drivers, their expected effects on *Verticillium* wilt of olive and implications for management, with the level of evidence

Climatic driver	Expected effect	Implication for management	Evidence level
Temperature	Pathotypes favoured by temperatures of about 20–25 °C (air) and 16–24 °C (soil); ND favours 16–20 °C soil temperatures in 'Picual'. High summer temperatures (>28–30 °C) reduce symptom expression. Shift of infection window due to warming is primarily hypothetical.	Screen cultivars and rootstocks for their tolerance to soil temperatures; concentrate monitoring in spring and autumn periods; do not plant in places where the conditions may become favourable in the future.	Level 2 (Calderón et al., 2014); Level 1 (Requena-Mullor et al., 2020; Arias-Giraldo et al., 2025)
Temperature oscillation and isothermality	Higher occurrence is characteristic where diel differences are small compared to annual differences; isothermality negatively affects occurrence but is influenced by rainfall seasonality.	Risk assessment based on climate analysis; include isothermality in decision-making instruments for new plantings.	Level 1 (Requena-Mullor et al., 2020; Arias-Giraldo et al., 2025)
Precipitation seasonality	Seasonality weakens the negative impact of isothermality; occurrence is enhanced with seasonality and mild conditions.	Seasonality indices should be taken into account when creating risk maps; do not plant in favourable seasonal areas under future scenarios.	Level 1 (Requena-Mullor et al., 2020; Arias-Giraldo et al., 2025)
Soil moisture and irrigation	Excessive and frequent irrigation increases inoculum levels, disease incidence and severity, especially in susceptible varieties; irrigation diminishes the influence of isothermality. Increased irrigation need due to drought currently lacks direct evidence.	Irrigation scheduling is an important tool here; choose less irrigation or deficit irrigation in case of susceptible cultivars.	Level 1–2 (Santos-Rufo et al., 2017; Santos-Rufo et al., 2018)
Humidity, evapotranspiration and vapour pressure	Near-surface moisture, vapour pressure and potential evapotranspiration contain important niche indicators of pathogen presence.	Include layers for humidity and evapotranspiration in models of niches and risks; monitor microclimates in densely planted orchards.	Level 1, niche modelling (Arias-Giraldo et al., 2025)
Drought and heat stress	Both infection and drought cause stomata closure and increased canopy temperature; interactions between these variables in regard to host susceptibility remain unknown and thermal stress indicators lack specificity to disease.	Thermal indices can be used for early detection, but molecular or visual confirmation is needed for avoiding misinterpretation of drought for disease..	Level 2 physiological data (Calderón et al., 2014)
Combined climate projections	Suitable habitat moves towards southern/ southeastern Andalusia (without any decrease).	Choose pathogen-free planting material and places based on current and future risk maps.	Level 1, modelling (Arias-Giraldo et al., 2026)

Note: Level – 1 field trials or surveys in olive; Level 2 – controlled experiments in olive; Level 3 – in vitro/in silico; Level 4 – other hosts.

physiological stress from remote sensing that are used for assessment of water stress can be biased by drought conditions. Irrigation scheduling, fertilization, and diagnostics need to take into account climate variables. It is thus important to conduct climate-relevant evaluations of the methods.

INTERACTION BETWEEN *OLEA EUROPAEA* AND *V. DAHLIAE*

Interaction between olive and *V. dahliae* has been studied extensively at both cell and tissue levels (Garber and Houston, 1966; Perry and Evert, 1983; Gerik and Huisman, 1988; Rodríguez-Jurado et al., 1993; Zhou et al., 2006; Eynck et al., 2007). Nevertheless, the amount of the pathogen does not necessarily determine the intensity of disease symptoms (Mercado-Blanco et al., 2003; Markakis et al., 2009).

Colonization mechanisms of *V. dahliae* in *Olea europaea*

Colonization of the vascular system is one of the main characteristics that make *V. dahliae* pathogenic. The process uses an exoproteome with the role of helping in tissue penetration, growth inside the host and symptoms manifestation (Klosterman et al., 2009; Fradin and Thomma, 2006; Chen et al., 2016). Colonization of roots and xylem invasion are made easier through the action of pectinase and cellulase enzymes, which have the capacity to break down plant cell walls. On the other hand, olive trees have lignin

synthesis, which makes the plant cell wall harder to penetrate (Klosterman et al., 2011; Zhang et al., 2017; Gharbi et al., 2017).

Plant defense response

Trait characteristics of the root systems play a big role in determining whether it is susceptible or not. Dense, branching lateral roots can present a high risk of attack since their surface is more exposed to soil pathogens. According to work carried out by Cardoni et al. in 2022, at the initial stage after inoculation with *V. dahliae*, the roots of tolerant varieties are less branched and have a larger root diameter, which stimulates their lignin content and root membrane permeability after inoculation. Furthermore, this contributes to stimulating the expression of olive genes associated to the lignin biosynthetic pathway with defense mechanisms, including the induction of innate immunity: the brassinosteroid insensitive 1-associated receptor kinase gene (BAK1) and (WRKY5) and the production of hydrolytic enzymes capable of degrading the fungal cell wall (β-1,3-glucanase), as well as lignin biosynthetic processes in the cell wall (C4H and CO-MT).

In contrast to susceptible varieties, which induced increased expression of the salicylic acid signal transduction factor (WRKY5) and CO-MT, and a related decrease in C4H expression, Higher concentrations were observed of S-monolignols, along with a decrease in G-monolignols resulting a reduction in overall lignin content. Also, the decreased activity of enzymes that protect olive cells against ROS toxins, such as ascorbate peroxidase (APX), restricted ROS clearance, making the plant more susceptible to *V. dahliae* (Figure 6).

Lignin serves as a physical barrier against entry by pathogens (Ferreira et al., 2007; Vanholme et al., 2010; Lee et al., 2019). Lignin levels in roots are generally higher in tolerant varieties (Frantoio) than in susceptible ones (Bubici and Cirulli, 2012). Furthermore, reactive oxygen species (ROS) are involved, where, in case of susceptible varieties like Picual, there is ROS-related gene expression following infection. However, it is worth noting that this process comes later on, compared to the initial action of pathogens (Jiménez-Ruiz et al., 2017).

Molecularly, Tolerant varieties initiate a fast and synchronous transcriptional response upon infection, where genes involved in the synthesis of lignin (C4H, COMT), enzymes that modify

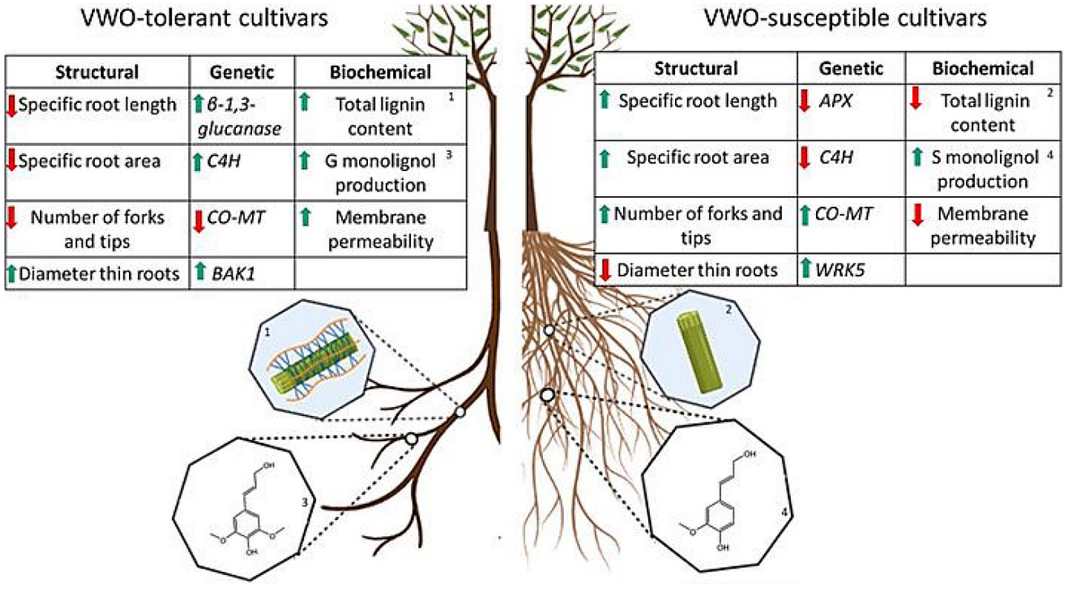


Figure 6. Schematic representation summarizing the main defense strategies against pathogens based on root system functioning in VWO-resistant (left) and VWO-sensitive (right) olive varieties infected by *V. dahliae.* The structural, genetic and biochemical differences between the roots of resistant and susceptible olive varieties following inoculation with *V. dahliae* are presented in the table. Increases and decreases in lignin are indicated by green and red arrows respectively; similarly, the blue lines and green rectangles represent the presence or absence of lignin in the cell structure respectively; lines indicate a higher concentration (¹), whilst the absence of lines represents lower concentrations (²). G- and S-type monolignols are indicated respectively by the structures of coniferyl alcohol and sinapyl alcohol (Cardoni et al., 2022)

plant cell walls (such as β 1,3 glucanase), as well as defense proteins like BAK1 and WRKY5 are activated. The early initiation of these pathways increases resistance through the strengthening of barriers against pathogen colonization (Cardoni et al., 2022).

Effector interactions and disruption of plant immunity

Effectors secreted by *V. dahliae* allow the fungus to overcome or avoid the immune response in the host plant, break down physical structures for colonization (Zhang et al., 2022; Sun et al., 2023). For instance, LysM effector VdPDA1 protects chitin in the fungus from the action of plant chitin receptors and inhibits chitin-triggered resistance (Gao et al., 2019). Additionally, *V. dahliae* synthesizes chemicals that can kill host cells such as protein-lipopolysaccharides and sulfacetamide (Luo et al., 2014; Zhang et al., 2016; Fradin and Thomma, 2006).

DIAGNOSIS AND MONITORING

VWO is difficult to manage partly because colonisation can remain symptomless and microsclerotia persist in soil. Diagnostic methods must therefore be specific. Conventional methods of detection of *V. dahliae* including virulence test and soil screening, later followed by cultivation have been employed conventionally. But these methods are laborious and time-consuming, taking up to six-eight weeks to provide any results (Ju et al., 2020). Delay in diagnosis can allow the spread of pathogens without getting noticed.

The use of such DNA based molecular methods has been inevitable in order to deal with some shortcomings of the classical techniques as a result of their increased speed, accuracy, and sensitivity. The traditional PCR technique has also been shown to be an efficient and economical approach for the detection of *V. dahliae* in both plant and soil specimens (Nazar et al., 1991; Pérez-Artés et al., 2000; Kuchta et al., 2008). Enabling much faster diagnostics than culture based approaches.

Another benefit of RT-qPCR is its ability to combine sensitivity and quantification in one step. This technique allows quantifying the presence of fungal DNA and estimating both the biomass and number of microsclerotia in the analyzed sample, providing valuable data about the dynamics of pathogens (Bilodeau et al., 2012; Kageyama et al., 2003; Wei et al., 2015). Importantly, qPCR makes it possible to detect the pathogen even prior to symptom development, which makes it an integral part of integrated management of olives infected by *V. dahliae* (Montes-Osuna and Mercado-Blanco, 2020).

Some improvements have also been made to PCR-based techniques. The nested PCR technique is able to detect organisms better by using two rounds of amplification (Mercado-Blanco et al., 2001; Pérez-Artés et al., 2005), whereas multiplex PCR makes it possible to simultaneously detect different organisms in a single test (Inderbitzin et al., 2013). These advances have helped shorten diagnosis times and increase confidence in detecting pathogens (Gramaje et al., 2013; Wang et al., 2013; Borza et al., 2018; Dan et al., 2001; Gayoso et al., 2007; Duressa et al., 2012).

Apart from traditional PCR-based assays, isothermal amplification methods were also employed as a consequence of their applicability under field conditions. Methods such as Recombinase polymerase amplification (RPA), Loop-mediated isothermal amplification (LAMP), and Rolling circle amplification (RCA) render any need for a thermocycler unnecessary, thus providing more rapid, portable, and convenient options for pathogen identification. Nevertheless, problems with these assays include difficulties like contamination, nonspecific amplification, and primer-dimer formation, all resulting in false-positive results. (Joung et al., 2020; Wang et al., 2018a).

Hybrid platforms that integrate nucleic acid amplification tests for speed and CRISPR-based detection systems for specificity offer an opportunity to address deficiencies inherent in using one diagnostic method alone. For instance, LAMP-CRISPR/Cas12a test combines the quick loop-mediated isothermal amplification technique with the CRISPR-Cas12a cleavage, thus making possible the specific detection of target DNA (Zhu et al., 2022; Yang et al., 2022; Mahas et al., 2021; Li et al., 2022; Fan et al., 2023). One of the quickest diagnostic approaches is the use of RPA-LFD, which is recombinase polymerase amplification combined with lateral-flow detection and that can provide a result in 25 minutes compared to more than 2.5 hours required for PCR or 1 hour for LAMP (Ju et al., 2020; Reid et al., 2018).

However, these techniques are not as highly validated for VWO (Table 2). The nested and duplex nested PCRs were developed and validated

in olive plants to test for D and ND pathotypes, with the latter removing ambiguous results due to heterologous amplification of the D pathotype marker gene in ND-infected plants (Mercado-Blanco et al., 2003). The LAMP test that was applied to soils of the olive orchard was able to detect 5 microsclerotia per gram of soil artificially inoculated with the fungus, and LAMP (26 of 32) and direct LAMP (24 of 32) gave more positive results than nested PCR (22 of 32) (Moradi et al., 2014). The colorimetric LAMP technique applied to crude extracts of naturally infected olive woods gave results within 35 min and detected lower infection rates than nested PCR and SYBR qPCR in un-purified extracts, at a 80% sensitivity rate through multisampling (Megariti et al., 2024). However, the RPA and CRISPR/Cas12a techniques mentioned above were mainly demonstrated on other pathogens/hosts, and there is no olive plant validation for *V. dahliae* in our research; hence, these techniques can only serve as proof of concept for VWO (Table 2).

Aside from the molecular approaches, Remote sensing also provides a non-destructive approach towards assessing crop growth and development through the detection of electromagnetic radiation that is either emitted, reflected or backscattered by plants. With respect to *Verticillium* wilt disease, remote sensing techniques such as multispectral, thermal, and hyperspectral imaging have proven successful in early detection of symptoms of infection in olives. When integrated into unmanned aerial vehicle (UAV) systems, remote sensing techniques allow rapid mapping and analysis of the occurrence of disease. Image processing and the computation of vegetations indices provide information regarding healthy trees, trees with moderate infection and severely infected trees. Remote sensing is used to make decisions and actions needed to prevent the further spreading of *Verticillium* Wilt (Calderón et al., 2013; Martinelli et al., 2015). Moreover, the use of UAV imagery-based vegetation indices assists in evaluating the plant stress caused by *V. dahliae* infection, thereby facilitating effective disease management.

However, the remote sensing signals correspond to the physiological effects of vascular disruption, primarily water stress, but not the pathogen per se. The physiological variables of canopy temperature, the Crop Water Stress Index, blue-band vegetation indices and chlorophyll fluorescence have been used successfully for the early diagnosis and categorization of different severities of natural infection (Calderón et al., 2013). In applying the technique to a commercial olive-producing area with 3,000 hectares, Calderón et al. (2015) obtained an average accuracy rate of 59.0% using the linear discriminant analysis technique but an accuracy rate of 79.2% using support vector machines. However, both techniques were highly divergent in their detection of early infection. In addition, other causes, such as drought, nutrition

Table 2. Validation status of detection methods for *V. dahliae* in olive

Method	Evidence in olive / *V. dahliae*	Stage for VWO	Main limitation
Isolation and virulence tests	results in 6–8 weeks (Ju et al., 2020).	Established	Slow; delays diagnosis and allows unnoticed spread.
Nested / duplex nested PCR	Validated in planta for D and ND pathotypes in olive (Mercado-Blanco et al., 2003).	Established (laboratory)	Laboratory equipment; uneven pathogen distribution in tissues complicates sampling.
qPCR	Protocols developed to quantify *V. dahliae* DNA in olive tissues (see Montes-Osuna and Mercado-Blanco, 2020).	Established (laboratory)	Needs purified DNA and thermocycler.
LAMP	Olive-orchard soils (Moradi et al., 2014); crude olive wood extracts from naturally infected trees (Megariti et al., 2024)	Validation in progress; field-oriented prototypes	Limited number of orchards/ cultivars; contamination and false positives need control.
RPA / RPA-LFD, RCA	Evidence mainly from other hosts or pathosystems; no olive-specific validation identified in our search.	Proof of concept for olive	Sensitivity and specificity in olive tissues unknown.
LAMP–CRISPR/ Cas12a	Demonstrated for other pathogens (Zhu et al., 2022; Yang et al., 2022).	Proof of concept; not validated for VWO	Requires olive-specific design and validation.
Remote sensing (thermal, hyperspectral, UAV)	Olive-specific studies in naturally infected orchards (Calderón et al., 2013, 2015); discrimination from *Xylella fastidiosa* (Poblete et al., 2022).	Validated at research scale	Detects physiological stress rather than the pathogen; separation from drought and nutrient stress not demonstrated; ground truthing needed.

problems, and other vascular or root diseases, can lead to a signal that may be misinterpreted. Therefore, ground-truth measurements and molecular diagnostics are still important in validating remote sensing maps and cannot replace the traditional diagnostic tests. However, research on olive trees is only available for few orchards and geographic locations. Thus, more validation under varying conditions, especially North African orchards, will be needed in order to test the validity of these techniques. Likewise, while Navrozidis et al. (2023) used machine-learning algorithms to classify olive diseases from hyperspectral data, the techniques were only validated on a few orchards. Thus, digital agriculture can be viewed as a complement to molecular diagnostics and not a replacement, hence the need for more validation.

INTEGRATED DISEASE MANAGEMENT STRATEGIES FOR *V. DAHLIAE*-INDUCED WILT IN OLIVE

V. dahliae is known to be a difficult phytopathogen due to lack of management strategies and its ability to infect plant tissues as well as form microsclerotia that can persist for many years (Calvo-Peña et al., 2025). Chemically, there are not enough methods to treat this pathogen and since the elimination of fumigation chemicals like methyl bromide according to the Montreal Protocol is inevitable, the situation gets worse (Panth et al., 2020).

The significance of *Verticillium* wilt of olive (VWO) can be justified by: (a) a very high degree of susceptibility for most olive varieties (López-Escudero and Mercado-Blanco, 2011; Trapero et al., 2013); (b) lack of chemical solutions for this disease (López-Escudero and Mercado-Blanco, 2011); and (c) a long life cycle in soil, up to 14 years (Tjamos and Jiménez-Díaz, 1998). Climate changes might make it more difficult for farmers to handle this issue (Kocmánková et al., 2009). Neither one method nor a combination can solve the problem completely due to the extensive host range and persistence of this pathogen in the environment (Schnathorst, 1981). Thus, efficient control measures should be aimed at minimizing microsclerotia in soil and inhibiting germination (Antonopoulos et al., 2008).

Considering the longevity of microsclerotia and the ineffectiveness of fungicides, control has been directed towards preventive and ecological means of disease management (López-Escudero and Mercado-Blanco, 2011; López-Moral et al., 2021). In view of the low efficiency of the individual measures, it is recommended that IDM be used, which entails the integration of cultural practices (Figure 7), resistant genotypes, selective chemicals, antagonistic microbes, plant defense elicitors, and phytochemicals (Milgroom et al., 2014).

An effective approach towards combating the *V. dahliae* infection demands an IDM system including both pre-planting and post-planting approaches (Tsror, 2011; Jiménez-Díaz et al., 2012). Since the number of fungicides that can act as preventers or treatments is limited, different practices must be undertaken before planting as well as after planting to minimize the chances of infection (López-Escudero and Mercado-Blanco, 2011; Mulero-Aparicio et al., 2020; Santos-Rufo and Rodríguez-Jurado, 2021).

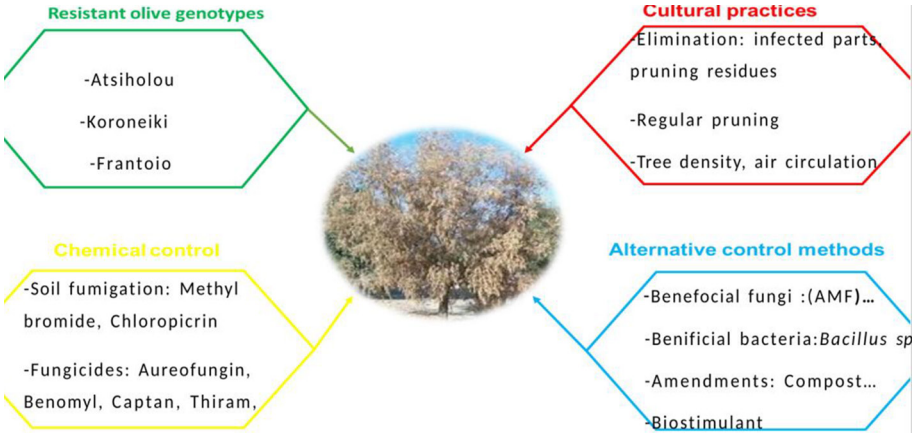


Figure 7. Control scheme for *Verticillium* wilt of *Olea europaea* due to *V. dahliae* infection (Milgroom et al., 2014)

Preventive measures and pre-planting strategies

The right agricultural practices are vital for olive pest and disease management, and even more so for minimizing *Verticillium* wilt. Prevention measures are very effective in decreasing disease occurrence and spreading. Decisions made before planting, including site selection, planting density, and orchard design, play an important role in disease prevention due to the conditions favoring disease development such as lack of aeration, poor light, and high humidity. Pathogen-free propagation material (Morello et al., 2016), optimal irrigation management (Baroudy et al., 2018), and monitoring should be applied. Pathogens can also be controlled using disinfection through chemigation (Gómez-Gálvez et al., 2019, 2020). Nutritional and irrigation management are crucial when using fertilization irrigation (fertigation) (Barranco et al., 2010).

Disinfection in irrigation systems is achieved through hypochlorites and chlorine gas. However, chlorine gas must be handled with care since it has corrosive tendencies and must be controlled in terms of pH and concentration (Newman, 2004). Alternation of crops with non-host plants or using resistant varieties decreases the inoculum in the soil (Fan et al., 2020). Activated peroxide and quaternary ammonium compounds have been used in Spain to avoid biofilms in irrigation systems (de Liñán-Vicente and de Liñán-Carral, 2019). It should be noted that certain cultural methods like spreading manure containing infected plant debris can actually disseminate the pathogen (López-Escudero and Blanco-López, 1999).

Quantification of *V. dahliae* microsclerotia before crop planting is a critical step in the management of the disease. PCR-based tests provide a rapid means of detecting and quantifying *V. dahliae* in plant samples (Dan et al., 2001; Hu et al., 1993; Li et al., 1999) and soil samples (Mahuku and Platt, 2002). Competitive PCR with an internal standard will enable relative quantification of *V. dahliae,* providing greater comparability among test results. Knowledge about the specific pathotypes associated with a particular field is also crucial since, in general, olive cultivars have higher susceptibility to the defoliating (D) pathotype than to the non-defoliating (ND) pathotype and, hence, growing olive plants that are prone to D infection in D-infected soils is not a good practice. The information regarding soil inoculum levels may be useful in a risk prediction model for the development of *Verticillium* wilt of olive (VWO), and hence pre planting soil tests are valuable tools in VWO prevention (López-Escudero and Blanco-López, 2007; Pérez-Artés et al., 2005).

New development areas for olives are usually sites where the previous crops were hosts to *V. dahliae* (cotton, potato, and sunflower), raising the chance of having this pathogen infect the crop. In terrains with hills, the site selected should have slopes that are well exposed to sunlight (south, southwest, southeast, west, or east); low lying sites with poor air circulation, impermeable soil, and proximity to water sources such as rivers should be avoided (Agosteo and Schena, 2011). Ensuring good soil drainage and adopting practices that reduce soil moisture also help lower disease incidence.

Historically, Mediterranean olive tree density was set at 100 to 300 trees per hectare. In recent times, there have been increased plant densities ranging from 300 to 400 trees per hectare up to very high densities, such as more than 1,500 trees per hectare (Hall, 2011; López-Escudero and Mercado-Blanco, 2011; Connor et al., 2014).

For such optimization, a combined strategy involving orchard design, pruning, controlled deficit irrigation, and fertilization is necessary. All this is needed for reducing canopy humidity and better penetration of fungicides, thus decreasing the incidence of infection (Connor et al., 2014). According to Requena-Mullor et al. (2020), correct irrigation at crucial times of pathogen presence (spring and fall) may prevent the manifestation of symptoms.

The approach focuses on the utilization of preventive and sustainable measures which minimize the reliance on artificial chemicals. One such measure is the use of natural alternatives which possess low persistence, high bioactivity, low mammalian toxicity, and environmental safety and therefore can be used effectively as components in the management of VWO as substitutes for chemical fungicides (Varo et al., 2017; Gea et al., 2019). In their study assessing the effectiveness of twenty EOs against *V. dahliae*, Varo et al. (2017) established that EOs of Thymus spp. are most effective in inhibiting both the growth of the fungus and microsclerotia germination.

Soil solarization is another validated, sustainable pre planting control for *V. dahliae* (López-Escudero and Blanco-López, 2001). By covering soil with transparent plastic to trap solar heat,

solarization reduces populations of soilborne pathogens, nematodes, and weeds. It is particularly useful soon after pathogen introduction and has documented benefits for disease reduction and soil health, so broader adoption is recommended (Gamliel and Katan, 2012; Panth et al., 2020; Simmons et al., 2014).

Organic amendments and biostimulants

Beyond classical biological control agents, several soil amendments and biostimulants show promise against *V. dahliae* in olive cultivation. One such promising approach is the use of biochar as a soil amendment.

Biochar improves soil structure, boost microbial diversity, and suppress some soilborne pathogens, including *V. dahliae* (Poveda et al., 2021). Furthermore, the deployment of biostimulants and biological fertilizers gained popularity, not only for enhancing plant nutrition but also for contributing to disease suppression and increasing stress tolerance in plants (Compant et al., 2016; Hassani et al., 2018; López-Moral et al., 2021). Their use is increasing as part of sustainable crop management.

Marine algal extracts (alginate, laminarin, carrageenan, ulvan) act as elicitors in olive, upregulating defense enzymes such as phenylalanine ammonia lyase (PAL) and promoting lignin deposition, which reduces the extent of vascular discoloration in infected shoots (Salah et al., 2018).

Arbuscular mycorrhizal fungi (AMF) are particularly beneficial for increasing nutrient uptake, reducing plant stress, and limiting pathogen establishment at root infection sites (Bagyaraj, 2018; Pozo et al., 2010; Singh et al., 2019).

Overall, combining these measures, Biostimulants which include microbial, botanical, and chemically derived formulations are now a key component of sustainable crop management because they reliably improve plant growth and health (Corsi et al., 2022). In the case of olive plants, biostimulants have been reported to enhance vigor and confer some resistance to *verticillium* wilt disease (Almadi et al., 2020; Regni et al., 2021; López-Moral et al., 2021).

Research indicates that entomopathogenic fungi such as *M. brunneum* and *B. bassiana* may decrease susceptibility to *verticillium* wilt and reduce the soil inoculum level of *V. dahliae* in sensitive olive genotypes (Lozano-Tovar et al., 2017). Agricultural by-products abundant in polyphenols including grape and olive pomace have been found to have antifungal and phytotoxic properties. Olive mill wastewater (OMW) in particular has notable in vitro antifungal activity and can inhibit the growth of the fungus beyond the microsclerotial region of *V. dahliae* (Soultatos et al., 2025). These properties may be attributed to the presence of nitrogen compounds such as nitrate, which has the capacity to disintegrate microsclerotia (Tenuta and Lazarovits, 2002). Unfortunately, the increased cost and preference of local cultivars limit their use.

Bioprotection at present means two things: utilization of living organisms that are biocontrol agents, and use of naturally occurring bioactive compounds (such as extracts from plants and crustaceans) (Collinge et al., 2022; Stenberg et al., 2021). In the past couple of decades, there have been various kinds of biological/ecological techniques that have been investigated for their effectiveness against VWO: organic fertilizers, essential oils, seaweed extracts, plant biostimulants, natural fertilizers, and microorganisms. Mycorrhizal fungi are special since not only do they suppress the growth and virulence of *V. dahliae* but they also prime the plant defense response (Montes-Osuna and Mercado-Blanco, 2020; López-Moral et al., 2021; Poveda and Baptista, 2021).

Biocontrol has often been advocated as a sustainable solution to decrease the use of pesticides, with reduced chances of developing resistance when compared to single site fungicides; yet, the sustainability of biocontrol for olive trees has hardly ever been evaluated(Pandit et al., 2022; Shang et al., 2024). However, in controlled experiments, there were several materials from nature that decreased the incidence of *V. dahliae,* and microorganisms serve as "mini chemical factories" capable of producing different bioactive compounds (Berdy, 2005). Rhizobacteria such as *Pseudomonas* (Mercado-Blanco et al., 2004; Gómez-Lama Cabanás et al., 2018b) and *Paenibacillus* (for example *P. polymyxa PIC73)* have shown promising activity against VWO in planta, mainly under controlled conditions (Gómez-Lama Cabanás et al., 2018a). *Streptomyces* species are also promising BCAs (Calvo-Peña et al., 2023; Díaz-Díaz et al., 2024).

BCAs work through multiple mechanisms: enhancing soil suppressiveness, establishing as endophytes, direct antagonism of the pathogen, and eliciting host defenses (Tjamos et al., 2004, 2005; Ruano-Rosa et al., 2017; Varo et al., 2018;

Mulero-Aparicio et al., 2019a,b; Azabou et al., 2020; Montes-Osuna and Mercado-Blanco, 2020; López-Moral et al., 2021; Poveda and Baptista, 2021). For example, *Paenibacillus alvei K165* suppresses microsclerotial germination and controls the defoliating pathotype in 'Kalamon' olives (Markakis et al., 2016). Co-inoculation with *Lactobacillus plantarum* and *Streptomyces* spp., combined with olive-mill waste compost, reduced disease incidence by about 80% in one study (Varo-Suárez et al., 2018).

Biocontrol tends to be most effective in controlled settings such as nurseries and greenhouses, whereas evidence from commercial orchards remains limited; However, the use of biological control agents (BCAs) in the propagation process has proven to be a viable method, especially for its potential to prevent infections at an early stage, despite the lack of empirical data to support this claim. (Angelopoulou et al., 2014).

Recently, research has focused on the role of olive microbiome in developing novel strategies for biocontrol. Epiphytic and endophytic microbial associations in olive trees play an important role in maintaining plant wellbeing. Utilization of Synthetic microbial communities (SynComs), Agosteo SynComs are a promising but still exploratory approach; whether they provide more robust or durable protection than single strains has not been demonstrated against *V. dahliae*.

The majority of literature on the topic of biostimulant and biocontrol use in olives was conducted under controlled conditions. The screening of 32 compounds found that Aureobasidium pullulans and Phoma sp. were among the most efficient treatments applied to the foliage (López-Moral et al., 2021). However, further research admitted that the efficiency of the majority of these substances has not yet been proved in natural olive plantations (López-Moral et al., 2022). This means that the efficiency of those treatments cannot be compared between themselves and with field experiments, due to differences in methods of inoculation, density of the inoculum, pathotype, cultivar, age of the plant and timing of application. That is why literature recommends conducting screening under field-like conditions.

Further evidence, published since 2023, provides additional support for this precaution, but is still limited to controlled environments. In a two-year programme, 25 candidates were tested in vitro, in planta and in the field; of these, only a few (e.g. *A. pullulans*, *F. proliferatum*, *T. asperellum* and *B. velezensis* strains) were able to reduce disease in 'Picual', while an even fewer number was validated in the field (Muhammed-Ahmed et al., 2026). Such reduction in the number of candidates indicates that in vitro antagonism is not a good predictor of the field performance. The greenhouse experiments support this trend: *R. irregularis* decreased disease severity, incidence and defoliation in 'Picholine Marocaine', as well as increased lignin and phenolic accumulation (Boutaj et al., 2025), while a consortium of *P. yamanorum* and *T. longibrachiatum* with olive-mill-waste compost reduced symptoms up to 80% on detached leaves, however, depending on the variety (Hajji-Hedfi et al., 2026a,b). There have been screened *Trichoderma* strains as native candidates (Carrasco et al., 2024).

With the unreliable results obtained by using inoculants of single strains, researchers have started looking at SynComs as an improved solution. However, for the olive tree, most of the information about its rhizospheric microbiome is largely descriptive.

An integrative management strategy can be adopted whereby resistant/tolerant genotypes (or grafting the susceptible genotype onto resistant genotypes) and proper irrigation/cultivation techniques are used to reduce inoculum spread (Jiménez-Díaz et al., 2011; Bubici and Cirulli, 2012; Jiménez-Fernández et al., 2016). The genotype-to-phenotype approach has been useful in identifying some of the candidate genes for disease resistance using transcriptome analysis on a small set of cultivars (Jiménez-Ruiz et al., 2019; Leyva Pérez et al., 2018). Resistance mechanisms involve the action of pattern-recognition receptors (PRRs) that identify PAMPs to elicit PTI responses, and specific resistance proteins that recognize effectors to induce ETI (Jones and Dangl, 2006; Bacete et al., 2018).

Resistance rootstock has a role in reducing susceptibility, delaying disease development and the progression rate (Porras-Soriano et al., 2003; Bubici and Cirulli, 2012; Yildiz et al., 2020). Using resistant varieties is the most practical approach to managing VWO, but the prevalence of defoliating type pathogens can limit its effectiveness (Jiménez-Díaz et al., 2011, 2012). There are no varieties that have full immunity to the infection (Bubici and Cirulli, 2012; Trapero et al., 2013, 2015; García-Ruiz et al., 2014; Montes-Osuna and Mercado-Blanco, 2020), but 'Empeltre', 'Frantoio', 'Oblonga' and 'Changlot Real'

varieties have demonstrated high resistance levels by slowing down disease symptoms, recovery and low death rates (López-Escudero et al., 2004; López-Escudero and Mercado-Blanco, 2011).

Several wild genotypes also show strong resistance to the defoliating race, which makes them interesting for rootstock development (Jiménez-Fernández et al., 2016). Their asymptomatic nature is correlated with reduced growth of the pathogen and limited acrosetal colonization, an essential criterion for rootstock selection (Jiménez-Fernández et al., 2016; Beckman and Talboys, 1981).

Current screening has increased the sample size of genotypes but has also revealed the limitations of the evidence. Of 77 genotypes tested for resistance against defoliating isolates, only 7.8% have been found to be highly resistant (six genotypes, including Frantoio and Ghiacciolo), 24.7% were found to be resistant, while 67.6% were found to be moderately to highly susceptible, some even more susceptible than Picual (Vizzarri et al., 2026). Resistance is thus not common; however, the above findings are based on five plants per genotype, one isolate, ten weeks of study, and one temperature regime.

Resistance has been associated with vascular structure (Santos-Rufo et al., 2023) and plant reactions in a wide range of cultivars (Serrano et al., 2023); however, these studies have been largely descriptive and have not led to selection markers that have been verified. Breeding programs for disease resistance also tend to be time-consuming (Valverde et al., 2023) and resistant rootstock can be ineffective in soil environments with high inoculum concentration (Valverde et al., 2021).

Alternative control methods

Numerous research articles propose different methods to overcome *V. dahliae*. The suggested means of dealing with this problem include organic substances extracted from olive mill waste (OMW), such as composts, extracts, as well as microorganisms that live in this waste. These materials have shown positive results in laboratory experiments and, in some cases, in field studies, although results should be interpreted with caution given the heterogeneity of protocols and the limited number of olive-orchard trials. As OMW exhibits antifungal properties, it presents an ecologically safe alternative in combating plant diseases.

Allium species (onions, garlic, Welsh onions) produce organosulfur compounds that have been extensively investigated for their antibacterial nature. The antifungal properties observed against *V. dahliae* suggest their suitability as biological control agents for *V. dahliae* (Sarfraz et al., 2020; Deberdt et al., 2012; Sorlozano-Puerto et al., 2018, 2020; Borlinghaus et al., 2014). Considering the prevalence of the crops and the natural antibacterial properties possessed by the chemical compounds produced, they can be considered as one feasible eco-friendly method of controlling *V. dahliae* in olive groves.

Plant extract alternatives are becoming increasingly important. The effect of pomegranate peel and carob leaf extracts was first characterised against *V. dahliae*, slowing down disease development in olives (Antón-Domínguez et al., 2024a); thereafter, these extracts were suggested as being potential inducers of host resistance (Antón-Domínguez et al., 2025a). Likewise, natural-based commercially available products were studied as bioprotectors (Antón-Domínguez et al., 2024b), and one particular product based on onion extract had a biostimulant effect and protected against *Verticillium* wilt (Falcón-Piñeiro et al., 2024). The majority of those results have been obtained in controlled conditions; field experiments are scarce, but nonetheless, a set of 19 natural products and microorganisms were evaluated in field conditions (Agustí-Brisach et al., 2025), building on previous works (Mulero-Aparicio et al., 2020). Plant nutrition was also investigated since nitrogen and potassium unbalance was studied as a possible factor affecting susceptibility to *Verticillium* wilt (López-Moral et al., 2022). However, for all those treatments, standardisation of the extract content, doses, timing and costs, together with commercial validation, need to be established.

Post-planting control measures

Biofumigation consists of incorporating plant tissues rich in glucosinolates (GSLs) into the soil to suppress soilborne pathogens (Wei et al., 2016). In the presence of disruption of the GSL-containing tissues, myrosinase enzyme catalyzes the conversion of GSLs to isothiocyanates (ITC) that have a biocidal action on soil pathogens (Kirkegaard et al., 1993; Kirkegaard and Matthiessen, 2004). GSLs are found in several families of plants belonging to the Capparales order, especially the Brassicaceae family (Fenwick et al., 1983; Brown and Morra, 1997; Van Dam et al., 2009).

Of these, *brassica* species with high levels of glucosinolates have especially been found to be successful in reducing the population of *V. dahliae* in the soil, and their early use as biofumigants has been shown to reduce VWO infection rates and increase yields, validating their use as a post-establishment measure in olive cultivation.

Control of *V. dahliae* is challenging due to its long period of survival in the soil in the form of microsclerotia for up to 14 years and also its capacity to survive as an endophyte in xylem tissue of the host plants (Pegg and Brady, 2002; Alström, 2001). Chemical control measures are still limited (Trapero et al., 2015; Mulero-Aparicio et al., 2020). Chemigation using disinfectants via drip irrigation has been considered as a promising component of integrated VWO management.

Various chemicals have been reported to inhibit growth of *V. dahliae*, such as aureofungin, benomyl, captan, thiram, fosetyl-Al, azoxystrobin, trifloxystrobin and acibenzolar-S-methyl (López-Escudero and Mercado-Blanco, 2011). Additionally, Conn et al. (2005) also reported that ammonium chloride can induce microsclerotial degradation under certain conditions, suggesting targeted chemical interventions may offer additional control options when integrated with other strategies.

RECENT ADVANCES – OMICS AND DIGITAL AGRICULTURE

Most recently, omics-based investigations into the plant species-specific response have refocused on the constitutive, rather than induced defences (Leyva-Pérez et al., 2018; Jiménez-Ruiz et al., 2019). Expanding upon that, the transcriptome analysis of wild olive clones revealed the association of the resistance to the D pathotype with the lignification and phenylpropanoid metabolism as well as the development of systemic acquired resistance. Despite the similar levels of total lignin between resistant and susceptible clones, there was a difference in the monolignols (Mascuñano et al., 2025). Similarly, in the study using the LC-MS technique to profile the roots, stems and leaves from ten different cultivars, certain metabolites were identified, whose presence or absence was associated with the resistance or susceptibility, respectively, which allowed for the identification of potential biomarkers (Serrano-García et al., 2023). While such data can be used for marker-assisted selection, the problem is that it is still correlative, involves only a small set of genotypes grown in controlled conditions, and, as far as the authors know, was never validated as a predictor of field resistance.

However, digital technologies are developing in parallel with the mentioned molecular techniques. The UAV-based imaging with RGB camera and subsequent analysis with YOLOv5 model was already used to identify the olive trees and classify them according to their health status (Mamalis et al., 2023). Further in this direction, the three-stage machine learning model based on thermal and hyperspectral features has shown success in the differentiation of *V. dahliae and X. fastidiosa* infections in 27 olive orchards in Italy and Spain, producing the false-positive rate of 4%, overall accuracy of 92% and kappa coefficient of 0.8 for *X. fastidiosa* identification (Poblete et al., 2021). In effect, it means that one source of the confounding factors, another vascular disease, was solved. However, whether the distinction between the disease and drought or nutrient stress can be made under varying irrigation regime remains unknown.

Comparative synthesis of control strategies and level of evidence

Control approaches based on the experimental system, evidence level, effect observed, shortcomings and field application potential have been summarized in Table 3. Any quantifiable reduction of effects is presented only when such data have been mentioned in the reviewed sources; the effect sizes can be incomparable among the experiments. For the olives, the most convincing evidence exists regarding resistant cultivar utilization and clean planting material, while biological and biostimulant approaches have promising potential but are mainly supported by controlled environment experiments.

Three aspects that need to be known to conduct a practical comparison are scarcely known in olives. First, studies of host resistance and orchard management are usually performed in several seasons, while information on biologicals and biostimulants is based on studies conducted in one season or in laboratory conditions. Second, the effect of cultivar and pathotype on the performance of resistance is known; however, reaction of the cultivar depends on the pathotype and temperature (Calderón et al., 2014). Performance of BCAs is well studied as strain-dependent, and

Table 3. Comparative summary of control strategies for *Verticillium* wilt of olive

Strategy	Host and experimental system	Evidence level	Reported effect	Main limitations	Field readiness
Resistant cultivars	Olive; field and controlled inoculation; breeding programme (Valverde et al., 2023)	1–2	'Frantoio', 'Empeltre' and 'Changlot Real' show high resistance; no cultivar is fully immune	Few resistant cultivars; agronomic and commercial traits; pressure of the D pathotype	High (available)
Resistant or tolerant rootstocks, including wild olive	Olive; controlled conditions (Jiménez-Fernández et al., 2016; Díaz-Rueda et al., 2021)	2	Several wild genotypes strongly resistant to the D pathotype; 15 of 68 genotypes (22%) resistant in one screening	Scion compatibility and field performance need validation	Moderate (selection stage)
Biostimulants and defence inducers	Olive; controlled conditions (López-Moral et al., 2021; López-Moral et al., 2022)	2	*Aureobasidium pullulans*, *Phoma* sp. and copper phosphite among the most effective in planta	Efficacy not shown in natural olive groves; dependence on dose, timing and cultivar	Low to moderate
Biocontrol agents (*Pseudomonas*, Bacillales, *Fusarium*, *Streptomyces*)	Olive; in vitro, nursery, greenhouse and soil experiments (Gómez-Lama Cabanás et al., 2018a; Mulero-Aparicio et al., 2020b)	2–3	Strain-dependent suppression; a non-pathogenic *F. oxysporum* strain prevented symptoms in naturally infested soil	Inconsistent field performance; formulation and scale-up (Deketelaere et al., 2017); few field studies	Low to moderate (nurseries)
Synthetic microbial communities	Mainly other hosts (cotton; Wu et al., 2024); olive microbiome characterisation	3–4	Disease reduction in cotton; no olive field validation identified	Host transferability; strain compatibility	Low (exploratory)
Organic amendments, olive mill waste, essential oils, *Allium* compounds, biofumigation, solarisation	Olive and other hosts; laboratory to field (Varo-Suárez et al., 2018; López-Escudero and Blanco-López, 2001)	2–4	Variable; in a bioassay, grape marc compost reduced severity by 100% and other amendments by 63–73%	Heterogeneous protocols; limited olive-orchard validation; mostly pre-planting or site-specific	Variable
Chemical control	Olive; limited efficacy (López-Escudero and Mercado-Blanco, 2011)	1–3	No fully effective option; chemigation under evaluation (Gómez-Gálvez et al., 2020)	Environmental and regulatory constraints; methyl bromide phase-out (Panth et al., 2020)	Low

Note: Evidence levels: 1 – field studies in olive, 2 – controlled-condition studies in olive, 3 – in vitro/in silico studies, 4 – studies on other hosts.

their effect on cultivars is poorly studied (Gómez-Lama Cabanás et al., 2018a). Third, economic efficiency has not been quantified and is scarcely known, and there is no cost-benefit analysis of most approaches.

An integrative framework linking biology, diagnostics and management

Verticillium wilt of olive can be organized into the following four complementary pillars based on their ability to address different stages of the disease cycle : prevention (site history and pathogens free materials), host resistance (cultivars and rootstock), inoculum reduction (biologicals, amendments, and soil solarization), and adaptive management (irrigation, scouting, mapping, and sampling) (Figure 8 and Figure 9).

Biological and epidemiological knowledge of the pathosystem is essential for developing diagnostic methods and management strategies. Since there is no single approach that would be completely efficient (López-Escudero & Mercado-Blanco, 2011; Montes-Osuna & Mercado-Blanco, 2020), the combination approach should be used. The preventive pillar includes pathogen-free planting material and proper site and pre-planting selection. The host resistance pillar, which has the most olive-specific evidence base, includes planting only the resistant varieties/rootstocks. The inoculum suppression pillar involves using biocontrol agents, biostimulants, and organic amendments, despite the lack of many studies in the field. Adaptive management combines irrigation practices, climate-based risk

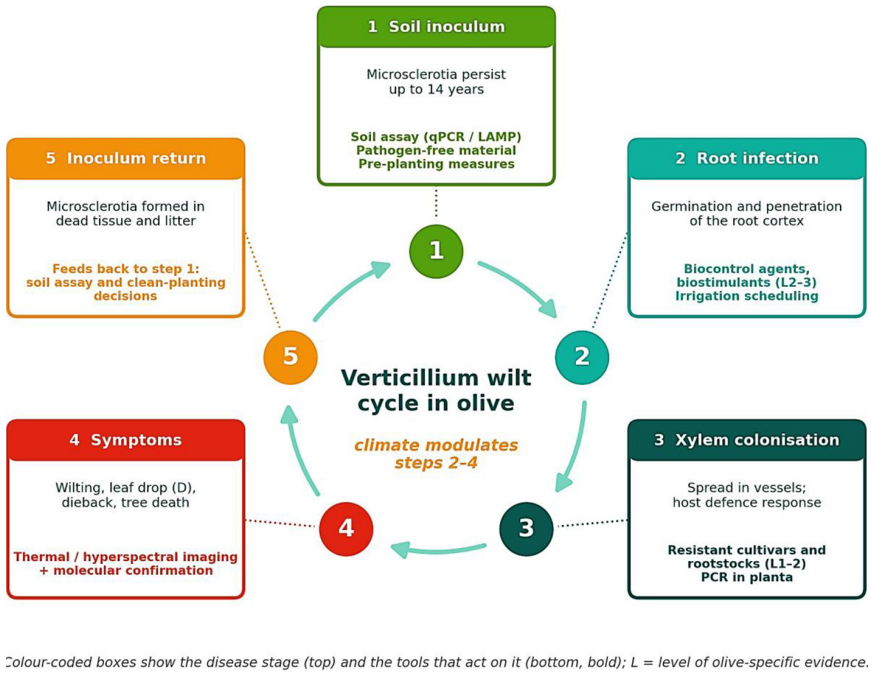


Figure 8. Disease cycle of *Verticillium* wilt in olive and the stages at which diagnostic and control tools act. L, level of olive-specific evidence; D, defoliating pathotype

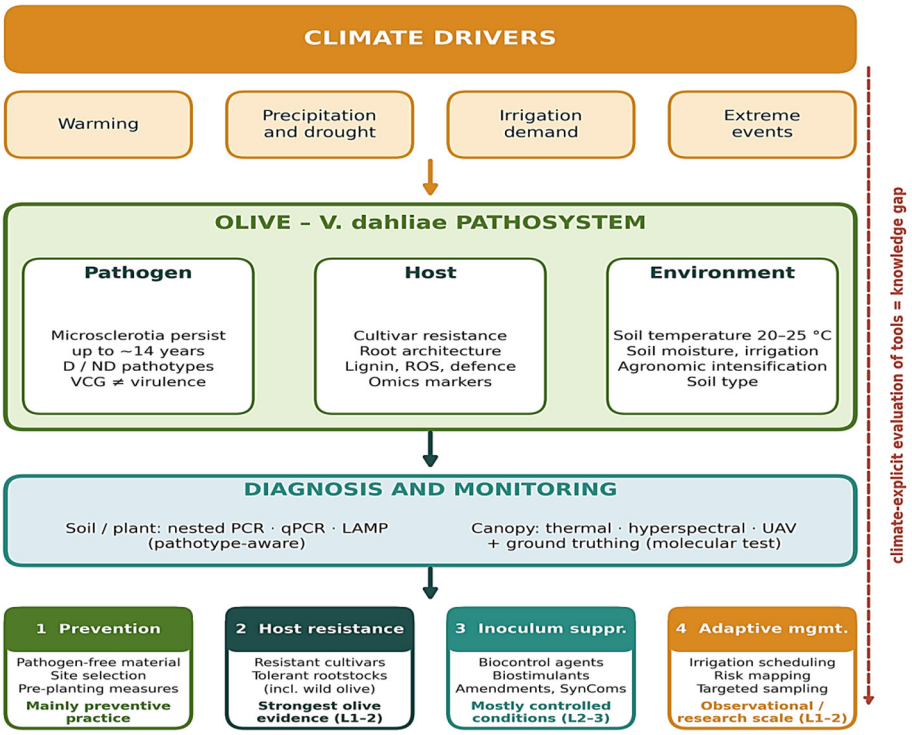


Figure 9. Conceptual framework linking climate drivers, the olive–*V. dahliae* pathosystem, diagnosis and the four management pillars, graded by level of olive-specific evidence (L1–L3 as defined in the note to Table 3)

assessment and sampling. Overall, these four pillars, ranked according to the olive-specific evidence base, create a comprehensive decision making framework linking the life cycle of the pathogen and management practices.

CONCLUSIONS

Olive cultivation is a cornerstone of Mediterranean agriculture, but it is increasingly threatened by *Verticillium* wilt, a severe disease caused

by the soil-borne fungus *V. dahliae*. The pathogen survives for long periods in soil, infects many plant species, and is difficult to control, causing significant economic losses in olive orchards. Current management strategies are limited and rely mainly on preventive measures, resistant cultivars, and biological control. Sustainable approaches, including beneficial microorganisms, organic amendments, and natural plant-based products, also show promise. An integrated strategy combining advanced diagnostics, biological control, resistant cultivars, and digital agriculture tools emerges from the reviewed literature as the most promising way to protect olive production and the long-term sustainability of Mediterranean orchards.

The best supported components of olive are resistant varieties, clean planting material, knowledge of pathotype and molecular diagnosis, and irrigation and agronomy, which are based on field observations and experiments. Biological control and biostimulants are based primarily on laboratory experiments, while SynComs, CRISPR-based diagnostics and specificity of remote sensing indicators are still under research. An integrated approach involving diagnostics, host resistance, biological control and digital technologies looks like the most efficient way of protecting olive from diseases. This approach is not validated by experiments as an integrated system but is based on the fact that none of these measures is efficient enough by itself and works at a certain step of the disease cycle. Climate change makes this system more complicated since temperature and moisture conditions can affect the disease development, reaction of varieties and efficiency of protective measures.

Acknowledgments

The authors are grateful to the CNRST for providing financial support through the 'PhD-ASSOCIATE Scholarship – PASS' Program, and also to the Faculty of Sciences, Mohammed V University in Rabat.

REFERENCES

1. Abdelfattah, A., Li Destri Nicosia, M. G., Cacciola, S. O., Droby, S., & Schena, L. (2015). Metabarcoding analysis of fungal diversity in the phyllosphere and carposphere of olive (*Olea europaea*). PLoS ONE, 10(7), e0131069. https://doi.org/10.1371/journal.pone.0131069
2. Acharya, B., Ingram, T.W., Oh, Y., Adhikari, T.B., Dean, R.A., & Louws, F.J. (2020). Opportunities and challenges in studies of host-pathogen interactions and management of *Verticillium dahliae* in tomatoes. Plants, 9(11), 1622. https://doi.org/10.3390/plants9111622
3. Al-Jaleely, E.T., Alalaf, A.H., & Kako, S.M. (2025). Impact of brassinolide, nano-silicon, and mycorrhizae on the nutrient composition and productivity of olive trees (Bashika cv.). Mesopotamia Journal of Agriculture, 53(2), 174–188. https://doi.org/10.33899/mja.2025.161230.1619
4. Almadi, L., Paoletti, A., Cinosi, N., Daher, E., Rosati, A., Di Vaio, C., & Famiani, F. (2020). A biostimulant based on protein hydrolysates promotes the growth of young olive trees. Agriculture, 10(12), 618. https://doi.org/10.3390/agriculture10120618
5. Alström, S. (2001). Characteristics of bacteria from oilseed rape in relation to their biocontrol activity against *Verticillium dahliae*. Journal of Phytopathology, 149, 57–64. https://doi.org/10.1046/j.1439-0434.2001.00585.x
6. Angelopoulou, D.J., Naska, E.J., Paplomatas, E.J., & Tjamos, S.E. (2014). Biological control agents (BCAs) of *verticillium* wilt: Influence of application rates and delivery method on plant protection, triggering of host defence mechanisms and rhizosphere populations of BCAs. Plant Pathology, 63, 1062–1069. https://doi.org/10.1111/ppa.12198
7. Antonopoulos, D.F., Tjamos, S.E., Antoniou, P.P., Rafeletos, P., & Tjamos, E.C. (2008). Effect of *Paenibacillus alvei*, strain K165, on the germination of *Verticillium dahliae* microsclerotia in planta. Biological Control, 46, 166–170. https://doi.org/10.1016/j.biocontrol.2008.05.003
8. Antón Domínguez, B.I. (2024). Bioprotection and genetic resistance against *Verticillium* wilt of olive and pistachio [Doctoral dissertation, University of Córdoba] (in Spanish).
9. Antón-Domínguez, B.I., Díaz-Díaz, M., Acedo-Antequera, F.A., Trapero, C., & Agustí-Brisach, C. (2024b). Use of natural-based commercial products as an alternative for providing bioprotection against *Verticillium* wilt of olive. Journal of the Science of Food and Agriculture. https://doi.org/10.1002/jsfa.13461
10. Antón-Domínguez, B.I., et al. (2025b). Severity assessment of isolates of defoliating and nondefoliating *Verticillium dahliae* pathotypes on woody and herbaceous hosts. Journal of Plant Pathology. https://doi.org/10.1007/s42161-025-02092-w
11. Antón-Domínguez, B.I., López-Moral, A., Romero-Salguero, F.J., Trapero, A., Trapero, C., & Agustí-Brisach, C. (2024a). Bioprotection of olive trees against *Verticillium* wilt by pomegranate and carob extracts. Plant Disease, 108, 1073–1082.
12. Antón-Domínguez, B.I., Mascuñano, B., Muñoz-Blanco, J., Molina-Hidalgo, F.J., & Agustí-Brisach,

C. (2025a). Evaluation of carob and pomegranate extracts as inducers of resistance against *Verticillium* wilt in olive tree. Plant Disease. https://doi.org/10.1094/PDIS-05-25-1032-RE

13. Arias-Giraldo, L.F., Cobos, M.E., Peterson, A.T., Landa, B.B., & Navas-Cortés, J.A. (2025). Unraveling the ecological niche signals of *Verticillium dahliae*: Insights from Mediterranean landscapes. Plant Disease, 109(1), 123–131. https://doi.org/10.1094/PDIS-02-24-0443-RE
14. Arias-Giraldo, L.F., Cobos, M.E., Peterson, A.T., Landa, B.B., & Navas-Cortés, J.A. (2026). Modeling the ecological niche of *Verticillium dahliae* in southern Spain: Current patterns and projected shifts under climate change. Plant Disease. https://doi.org/10.1094/PDIS-06-25-1163-RE
15. Atallah, Z.K., Maruthachalam, K., du Toit, L., Koike, S.T., Davis, R.M., Klosterman, S.J., Hayes, R.J., & Subbarao, K.V. (2010). Population analyses of the vascular plant pathogen *Verticillium dahliae* detect recombination and transcontinental gene flow. Fungal Genetics and Biology, 47, 416–422. https://doi.org/10.1016/j.fgb.2010.02.003
16. Azabou, M. C., Gharbi, Y., Medhioub, I., Ennouri, K., Barham, H., Tounsi, S., & Triki, M. A. (2020). The endophytic strain *Bacillus velezensis* OEE1: An efficient biocontrol agent against *Verticillium* wilt of olive and a potential plant growth promoting bacteria. Biological Control, 142, 104168. https://doi.org/10.1016/j.biocontrol.2019.104168
17. Bacete, L., Mélida, H., Miedes, E., & Molina, A. (2018). Plant cell wall-mediated immunity: Cell wall changes trigger disease resistance responses. The Plant Journal, 93, 614–636. https://doi.org/10.1111/tpj.13807
18. Bagyaraj, D.J. (2018). Arbuscular mycorrhizal fungi and biological control of soil-borne plant pathogens. Kavaka, 51(1), 1–6. https://www.fungiindia.co.in/images/kavaka/51/1.pdf
19. Baroudy, F., Habib, W., Tanos, G., Gerges, E., Saab, C., Choueiri, E., et al. (2018). Long-distance spread of *Verticillium dahliae* through rivers and irrigation systems. Plant Disease, 102, 1559–1565. https://doi.org/10.1094/PDIS-08-17-1189-RE
20. Baroudy, F., Putman, A.I., Habib, W., Puri, K.D., Subbarao, K.V., & Nigro, F. (2019). Genetic diversity of *Verticillium dahliae* populations from olive and potato in Lebanon. Plant Disease, 103(4), 656–667. https://doi.org/10.1094/PDIS-03-18-0420-RE
21. Barranco, D. (2008). Variedades y patrones [Cultivars and rootstocks]. In D. Barranco, R. Fernández-Escobar, & L. Rallo (Eds.), El cultivo del olivo (6th ed., pp. 63–92). Mundi-Prensa and Junta de Andalucía (in Spanish). https://www.researchgate.net/publication/271847614_Variedades_y_Patrones
22. Barranco, D., Fernández-Escobar, R., & Rallo, L. (Eds.). (2010). Olive growing. Junta de Andalucía/Mundi-Prensa/RIRDC/AOA.
23. Barranco, D., Fernández-Escobar, R., & Rallo, L. (Eds.). (2017). El cultivo del olivo [Olive growing] (7th ed.). Mundi-Prensa (in Spanish).
24. Beckman, C.H., & Talboys, P.W. (1981). Anatomy of resistance. In M.E. Mace, A.A. Bell, & C.H. Beckman (Eds.), Fungal wilt diseases of plants (pp. 487–521). Elsevier.
25. Berdy, J. (2005). Bioactive microbial metabolites: A personal view. The Journal of Antibiotics, 58, 1–26. https://doi.org/10.1038/ja.2005.1
26. Bilodeau, G.J., Koike, S.T., Uribe, P., & Martin, F.N. (2012). Development of an assay for rapid detection and quantification of *Verticillium dahliae* in soil. Phytopathology, 102, 331–343. https://doi.org/10.1094/PHYTO-05-11-0130
27. Bishop, C.D., & Cooper, R.M. (1983). An ultrastructural study of root invasion in three vascular wilt diseases. Physiological Plant Pathology, 22, 15–27. https://doi.org/10.1016/S0048-4059(83)81034-0
28. Blanco-López, M.A., Jiménez-Díaz, R.M., & Caballero, J.M. (1984). Symptomatology, incidence and distribution of *Verticillium* wilt of olive trees in Andalucía. Phytopathologia Mediterranea, 23(1), 1–8. https://www.jstor.org/stable/42684673
29. Borlinghaus, J., Albrecht, F., Gruhlke, M.C.H., Nwachukwu, I., & Slusarenko, A.J. (2014). Allicin: Chemistry and biological properties. Molecules, 19, 12591–12618. https://doi.org/10.3390/molecules190812591
30. Borza, T., Beaton, B., Govindarajan, A., Gao, X.X., Liu, Y.H., Ganga, Z., & Wang-Pruski, G. (2018). Incidence and abundance of *Verticillium dahliae* in soil from various agricultural fields in Prince Edward Island, Canada. European Journal of Plant Pathology, 150, 825–830. https://doi.org/10.1007/s10658-017-1408-1
31. Boutaj, H., Chakhchar, A., Meddich, A., Wahbi, S., El Alaoui-Talibi, Z., Douira, A., Filali-Maltouf, A., & El Modafar, C. (2020a). Bioprotection of olive tree from *Verticillium* wilt by autochthonous mycorrhizal fungi. Journal of Plant Diseases and Protection, 127, 349–357. https://doi.org/10.1007/s41348-020-00323-z
32. Boutaj, H., Meddich, A., Chakhchar, A., Wahbi, S., El Alaoui-Talibi, Z., Douira, A., & El Modafar, C. (2020b). Arbuscular mycorrhizal fungi improve mineral nutrition and tolerance of olive tree to *Verticillium* wilt. Archives of Phytopathology and Plant Protection, 53(13–14), 673–689. https://doi.org/10.1080/03235408.2020.1792603
33. Boutaj, H., Meddich, A., Wahbi, S., El Alaoui-Talibi, Z., Douira, A., Filali-Maltouf, A., & El Modafar, C. (2025). Biocontrol of *Verticillium* wilt of olive using *Rhizophagus irregularis*: Insights into oxidative stress and phenolic pathways. International Journal of Plant Biology, 16(1), 21. https://doi.org/10.3390/ijpb16010021

34. Bouymajane, A., Oulad El Majdoub, Y., Cacciola, F., Russo, M., Salafia, F., Trozzi, A., Rhazi Filali, F., Dugo, P., & Mondello, L. (2020). Characterization of phenolic compounds, vitamin E and fatty acids from monovarietal virgin olive oils of "Picholine marocaine" cultivar. Molecules, 25(22), 5428. https://doi.org/10.3390/molecules25225428
35. Brown, P.D., & Morra, M.J. (1997). Control of soil-borne plant pests using glucosinolate-containing plants. Advances in Agronomy, 61, 167–231. https://doi.org/10.1016/S0065-2113(08)60664-1
36. Bubici, G., & Cirulli, M. (2012). Control of *Verticillium* wilt of olive by resistant rootstocks. Plant and Soil, 352, 363–376. https://doi.org/10.1007/s11104-011-1002-9
37. Calderón, R., Lucena, C., Trapero-Casas, J.L., Zarco-Tejada, P.J., & Navas-Cortés, J.A. (2014). Soil temperature determines the reaction of olive cultivars to *Verticillium dahliae* pathotypes. PLoS ONE, 9(10), e110664. https://doi.org/10.1371/journal.pone.0110664
38. Calderón, R., Navas-Cortés, J.A., & Zarco-Tejada, P.J. (2015). Early detection and quantification of *Verticillium* wilt in olive using hyperspectral and thermal imagery over large areas. Remote Sensing, 7(5), 5584–5610. https://doi.org/10.3390/rs70505584
39. Calderón, R., Navas-Cortés, J.A., Lucena, C., & Zarco-Tejada, P.J. (2013). High-resolution airborne hyperspectral and thermal imagery for early detection of *Verticillium* wilt of olive using fluorescence, temperature and narrow-band spectral indices. Remote Sensing of Environment, 139, 231–245. https://doi.org/10.1016/j.rse.2013.07.031
40. Calvo-Peña, C., Cobos, R., Sánchez-López, J.M., Ibáñez, A., & Coque, J.J.R. (2023). Albocycline is the main bioactive antifungal compound produced by *Streptomyces* sp. OR6 against *Verticillium dahliae*. Plants, 12(20), 3612. https://doi.org/10.3390/plants12203612
41. Calvo-Peña, C., Ruiz-Muñoz, M., Nouioui, I., Kirstein, S., Neumann-Schaal, M., Sánchez-López, J.M., Ghoreshizadeh, S., Cobos, R., & Coque, J.J.R. (2025). Rapamycin plays a pivotal role in the potent antifungal activity exhibited against *Verticillium dahliae* by *Streptomyces iranensis* OE54 and *Streptomyces lacaronensis* sp. nov. isolated from olive roots. Microorganisms, 13(7), 1622. https://doi.org/10.3390/microorganisms13071622
42. Cardoni, M., Gómez-Lama Cabanás, C., Valverde-Corredor, A., Villar, R., & Mercado-Blanco, J. (2022). Unveiling differences in root defense mechanisms between tolerant and susceptible olive cultivars to *Verticillium dahliae*. Frontiers in Plant Science, 13, 863055. https://doi.org/10.3389/fpls.2022.863055
43. Carrasco, F., Miranda, V., Sede, S.M., Bustos, S., González, V., Otero, L., et al. (2024). Screening for native *Trichoderma* strains as potential biocontrollers of the olive pathogen *Verticillium dahliae*. Arid Land Research and Management, 38, 122–143. https://doi.org/10.1080/15324982.2023.2233933
44. Chen, J.Y., Liu, C., Gui, Y.J., Si, K.W., Zhang, D.D., Wang, J., Short, D.P.G., Huang, J.Q., et al. (2018). Comparative genomics reveals cotton-specific virulence factors in flexible genomic regions in *Verticillium dahliae* and evidence of horizontal gene transfer from *Fusarium*. New Phytologist, 217, 756–770. https://doi.org/10.1111/nph.14861
45. Cirulli, M. (1975). Il deperimento dell'olivo da *Verticillium dahliae* Kléb. [The decline of olive caused by *Verticillium dahliae* Kléb.]. L'Italia Agricola, 112, 120–124 (in Italian).
46. Cirulli, M. (1981). Attuali cognizioni sulla verticilliosi dell'olivo [Current knowledge on *Verticillium* wilt of olive]. Informatore Fitopatologico, 1–2, 101–105 (in Italian).
47. Collinge, D.B., Jensen, D.F., Rabiey, M., Sarrocco, S., Shaw, M.W., & Shaw, R.H. (2022). Biological control of plant diseases – What has been achieved and what is the direction? Plant Pathology, 71, 1024–1047. https://doi.org/10.1111/ppa.13555
48. Compant, S., Saikkonen, K., Mitter, B., Campisano, A., & Mercado-Blanco, J. (2016). Editorial special issue: Soil, plants and endophytes. Plant and Soil, 405, 1–11. https://doi.org/10.1007/s11104-016-2927-9
49. Connor, D.J. (2005). Adaptation of olive (*Olea europaea* L.) to water-limited environments. Australian Journal of Agricultural Research, 56, 1181–1189. https://doi.org/10.1071/AR05169
50. Connor, D.J., Gómez-del-Campo, M., Rousseaux, M.C., & Searles, P.S. (2014). Structure, management and productivity of hedgerow olive orchards: A review. Scientia Horticulturae, 169, 71–93. https://doi.org/10.1016/j.scienta.2014.02.010
51. Dan, H., Ali-Khan, S.T., & Robb, J. (2001). Use of quantitative PCR diagnostics to identify tolerance and resistance to *Verticillium dahliae* in potato. Plant Disease, 85(7), 700–705. https://doi.org/10.1094/pdis.2001.85.7.700
52. de Jonge, R., Bolton, M.D., Kombrink, A., van den Berg, G.C., Yadeta, K.A., & Thomma, B.P. (2013). Extensive chromosomal reshuffling drives evolution of virulence in an asexual pathogen. Genome Research, 23, 1271–1282. https://doi.org/10.1101/gr.152660.112
53. de Jonge, R., van Esse, H.P., Maruthachalam, K., Bolton, M.D., Santhanam, P., Saber, M.K., Zhang, Z., Usami, T., Lievens, B., Subbarao, K.V., & Thomma, B.P. (2012). Tomato immune receptor Ve1 recognizes effector of multiple fungal pathogens uncovered by genome and RNA sequencing. Proceedings of the National Academy of Sciences

USA, 109, 5110–5115. https://doi.org/10.1073/pnas.1119623109

54. Deberdt, P., Perrin, B., Coranson-Beaudu, R., Duyck, P.-F., & Wicker, E. (2012). Effect of *Allium fistulosum* extract on *Ralstonia solanacearum* populations and tomato bacterial wilt. Plant Disease, 96, 687–692. https://doi.org/10.1094/PDIS-07-11-0601
55. Deketelaere, S., Tyvaert, L., França, S.C., & Höfte, M. (2017). Desirable traits of a good biocontrol agent against *Verticillium* wilt. Frontiers in Microbiology, 8, 1186. https://doi.org/10.3389/fmicb.2017.01186
56. Dervis, S., Mercado-Blanco, J., Erten, L., Valverde-Corredor, A., & Pérez-Artés, E. (2010). *Verticillium* wilt of olive in Turkey: A survey on disease importance, pathogen diversity and susceptibility of relevant olive cultivars. European Journal of Plant Pathology, 127, 287–301. https://doi.org/10.1007/s10658-010-9595-z
57. Duressa, D., Rauscher, G., Koike, S.T., Mou, B., Hayes, R.J., Maruthachalam, K., et al. (2012). A real-time PCR assay for detection and quantification of *Verticillium dahliae* in spinach seed. Phytopathology, 102(4), 443–451. https://doi.org/10.1094/PHYTO-10-11-0280
58. Díaz-Díaz, M., Antón-Domínguez, B.I., Raya, M.C., Bernal-Cabrera, A., Medina-Marrero, R., Trapero, A., & Agustí-Brisach, C. (2024). *Streptomyces* spp. strains as potential biological control agents against *Verticillium* wilt of olive. Journal of Fungi, 10, 138. https://doi.org/10.3390/jof10020138
59. Díaz-Rueda, P., Aguado, A., Romero-Cuadrado, L., Capote, N., et al. (2021). Wild olive genotypes as a valuable source of resistance to defoliating *Verticillium dahliae*. Frontiers in Plant Science, 12, 662060. https://doi.org/10.3389/fpls.2021.662060
60. EPPO. (2025). EPPO Global Database: *Verticillium dahliae* (VERTDA), distribution. Retrieved June 22, 2025, from https://gd.eppo.int/taxon/VERTDA/distribution
61. Eynck, C., Koopmann, B., Grunewaldt-Stoecker, G., Karlovsky, P., & von Tiedemann, A. (2007). Differential interactions of *Verticillium longisporum* and *V. dahliae* with *Brassica napus* detected with molecular and histological techniques. European Journal of Plant Pathology, 118(3), 259–274. https://doi.org/10.1007/s10658-007-9144-6
62. Falcón-Piñeiro, A., Zaguirre-Martínez, J., Ibáñez-Hernández, A.C., Guillamón, E., Santander, K., Barrero-Domínguez, B., López-Feria, S., Garrido, D., & Baños, A. (2024). Evaluation of the biostimulant activity and *Verticillium* wilt protection of an onion extract in olive crops (*Olea europaea*). Plants, 13, 2499. https://doi.org/10.3390/plants13172499
63. Fan, R., Gong, X., Gao, L., et al. (2020). Temporal dynamics of the survival of *Verticillium dahliae* microsclerotia with or without melanin in soils amended with biocontrol agents. European Journal of Plant Pathology, 157, 521–531. https://doi.org/10.1007/s10658-020-02014-9
64. Fan, Z., Mei, Y., Xing, J., Chen, T., Hu, D., Liu, H., Li, Y., Liu, D., Liu, Z., & Liang, Y. (2023). Loop-mediated isothermal amplification (LAMP)/Cas12a assay for detection of *Ralstonia solanacearum* in tomato. Frontiers in Bioengineering and Biotechnology, 11, 1188176. https://doi.org/10.3389/fbioe.2023.1188176
65. FAO. (2020). FAOSTAT: Production statistics. Retrieved September 8, 2022, from http://www.fao.org/faostat/es/#data
66. FAOSTAT. (2021). Crops and livestock products: Oil, olive. https://www.fao.org/faostat/es
67. FAOSTAT. (2025). Crops and livestock products. Retrieved July 3, 2025, from https://www.fao.org/faostat/en/#data/QCL/visualize
68. Fenwick, G.R., Heaney, R.K., Mullin, W.J., & VanEtten, C.H. (1983). Glucosinolates and their breakdown products in food and food plants. CRC Critical Reviews in Food Science and Nutrition, 18(2), 123–201. https://doi.org/10.1080/10408398209527361
69. Ferreira, R.B., Monteiro, S., Freitas, R., Santos, C.N., Chen, Z., Batista, L.M., et al. (2007). The role of plant defence proteins in fungal pathogenesis. Molecular Plant Pathology, 8, 677–700. https://doi.org/10.1111/j.1364-3703.2007.00419.x
70. Fradin, E. F., & Thomma, B. P. H. J. (2006). Physiology and molecular aspects of *Verticillium* wilt diseases caused by *V. dahliae* and *V. albo-atrum*. Molecular Plant Pathology, 7(2), 71–86. https://doi.org/10.1111/j.1364-3703.2006.00323.x
71. Gamliel, A., & Katan, J. (Eds.). (2012). Soil solarization: Theory and practice. APS Press. https://doi.org/10.1094/9780890544198
72. Gao, F., Zhang, B.-S., Zhao, J.-H., Huang, J.-F., Jia, P.-S., Wang, S., et al. (2019). Deacetylation of chitin oligomers increases virulence in soil-borne fungal pathogens. Nature Plants, 5, 1167–1176. https://doi.org/10.1038/s41477-019-0527-4
73. Garber, R. H., & Houston, B. R. (1966). Penetration and development of *Verticillium albo-atrum* in the cotton plant. Phytopathology, 56, 1121–1126.
74. García-Ruiz, G.M., Trapero, C., Del Rio, C., & López-Escudero, F.J. (2014). Evaluation of resistance of Spanish olive cultivars to *Verticillium dahliae* in inoculations conducted in greenhouse. Phytoparasitica, 42, 205–212. https://doi.org/10.1007/s12600-013-0353-6
75. Gayoso, C., de la Ilarduya, O.M., Pomar, F., & de Caceres, F.M. (2007). Assessment of real-time PCR as a method for determining the presence of *Verticillium dahliae* in different Solanaceae cultivars. European Journal of Plant Pathology, 118(3), 199–209. https://doi.org/10.1007/s10658-007-9134-8

76. Gea, F.J., Navarro, M.J., Santos, M., Diánez, F., & Herraiz-Peñalver, D. (2019). Screening and evaluation of essential oils from Mediterranean aromatic plants against the mushroom cobweb disease, *Cladobotryum mycophilum*. Agronomy, 9(10), 656. https://doi.org/10.3390/agronomy9100656
77. Gerik, J. S., & Huisman, O. C. (1988). Study of field-grown cotton roots infected with *Verticillium dahliae* using an immunoenzymatic staining technique. Phytopathology, 78(9), 1174–1178.
78. Gharbi, Y., Barkallah, M., Bouazizi, E., Hibar, K., Gdoura, R., & Triki, M. (2017). Lignification, phenols accumulation, induction of PR proteins and antioxidant-related enzymes are key factors in the resistance of *Olea europaea* to *Verticillium* wilt of olive. Acta Physiologiae Plantarum, 39(2), 43. https://doi.org/10.1007/s11738-016-2343-z
79. Gharbi, Y., Bouazizi, E., Triki, M., & Gdoura, R. (2016). Phenotypic and molecular characterization of *Verticillium dahliae*, the causal agent of *Verticillium* wilt of olive in Tunisia. Journal of Applied Life Sciences International, 8(4). https://doi.org/10.9734/JALSI/2016/23696
80. Gramaje, D., Pérez-Serrano, V., Montes-Borrego, M., Navas-Cortés, J.A., Jiménez-Díaz, R.M., & Landa, B.B. (2013). A comparison of real-time PCR protocols for the quantitative monitoring of asymptomatic olive infections by *Verticillium dahliae* pathotypes. Phytopathology, 103(10), 1058–1068. https://doi.org/10.1094/PHYTO-11-12-0312-R
81. Green, P.S. (2002). A revision of *Olea* L. (Oleaceae). Kew Bulletin, 57, 91–140. https://doi.org/10.2307/4110824
82. Green, P.S. (2004). Oleaceae. In K. Kubitzki & J.W. Kadereit (Eds.), The families and genera of vascular plants: Vol. VII. Flowering plants – Dicotyledons (pp. 296–306). Springer. https://doi.org/10.1007/978-3-642-18617-2_16
83. Gómez-Gálvez, F.J., Hidalgo-Moya, J.C., Vega-Macías, V., Hidalgo-Moya, J.J., & Rodríguez-Jurado, D. (2019). Reduced introduction of *Verticillium dahliae* through irrigation systems and accumulation in soil by injection of peroxygen-based disinfectants. Plant Pathology, 68, 116–126. https://doi.org/10.1111/ppa.12917
84. Gómez-Gálvez, F.J., Vega-Macías, V., Hidalgo-Moya, J.C., Hidalgo-Moya, J.J., & Rodríguez-Jurado, D. (2020). Application to soil of disinfectants through irrigation reduces *Verticillium dahliae* in the soil and *Verticillium* wilt of olive. Plant Pathology, 69, 272–283. https://doi.org/10.1111/ppa.13114
85. Gómez-Lama Cabanás, C., Legarda, G., Ruano-Rosa, D., Pizarro-Tobías, P., Valverde-Corredor, A., Niqui, J.L., Triviño, J.C., Roca, A., & Mercado-Blanco, J. (2018a). Indigenous *Pseudomonas* spp. strains from the olive (*Olea europaea* L.) rhizosphere as effective biocontrol agents against *Verticillium dahliae*: From the host roots to the bacterial genomes. Frontiers in Microbiology, 9, 277. https://doi.org/10.3389/fmicb.2018.00277
86. Gómez-Lama Cabanás, C., Ruano-Rosa, D., Legarda, G., Pizarro-Tobías, P., Valverde-Corredor, A., Triviño, J.C., et al. (2018b). Bacillales members from the olive rhizosphere are effective biological control agents against the defoliating pathotype of *Verticillium dahliae*. Agriculture, 8(7), 90. https://doi.org/10.3390/agriculture8070090
87. Hadiddou, A., Oukabli, A., Moudaffar, M., Mamouni, A., Laaboun, M., Mekaoui, A., Ssaini, L., & El Fechtali, M. (2013). Évaluation des performances de production de 4 variétés d'olivier (*Olea europaea* L.) nationales et méditerranéennes dans deux systèmes contrastés de culture (pluvial et irrigué) au Maroc [Evaluation of the production performance of 4 national and Mediterranean olive varieties under two contrasting cropping systems in Morocco]. Al Awamia, 127, 22–43 (in French).
88. Hajji-Hedfi, L., Bargougui, O., Al-Ani, L.K.T., Oueslati, S., Sukmawati, D., Wannassi, T., et al. (2026b). Sustainable integrated management of olive *Verticillium* wilt (*Verticillium dahliae*) using a microbial consortium of *Pseudomonas yamanorum–Trichoderma longibrachiatum* and compost mill waste. Journal of Soil Science and Plant Nutrition. https://doi.org/10.1007/s42729-026-03297-3
89. Hajji-Hedfi, L., Dali, S., Wannassi, T., et al. (2026a). Harnessing a microbial consortium and organic soil amendments to control *Verticillium* wilt (*Verticillium dahliae*) in olive plants (*Olea europaea*). Journal of Plant Diseases and Protection, 133, 14. https://doi.org/10.1007/s41348-025-01206-x
90. Harris, D.C. (1998). Introduction to *Verticillium* wilts. In J.A. Hiemstra & D.C. Harris (Eds.), A compendium of *Verticillium* wilts in tree species (pp. 1–4). Ponsen & Looijen.
91. Hassani, M.A., Durán, P., & Hacquard, S. (2018). Microbial interactions within the plant holobiont. Microbiome, 6, 58. https://doi.org/10.1186/s40168-018-0445-0
92. Hiemstra, J.A. (1998). Some general features of *Verticillium* wilts in trees. In J.A. Hiemstra & D.C. Harris (Eds.), A compendium of *Verticillium* wilts in tree species (pp. 5–11). Ponsen & Looijen. https://edepot.wur.nl/211512
93. Hu, X., Nazar, R.N., & Robb, J. (1993). Quantification of *Verticillium* biomass in wilt disease development. Physiological and Molecular Plant Pathology, 42, 23–36. https://doi.org/10.1006/pmpp.1993.1003
94. Häner, E., & Diederichsen, E. (2016). Belowground defence strategies against *Verticillium* pathogens. In Belowground defence strategies in plants (pp. 119–150). Springer. https://doi.

org/10.1007/978-3-319-42319-7_6

95. Inderbitzin, P., & Subbarao, K.V. (2014). *Verticillium* systematics and evolution: How confusion impedes *Verticillium* wilt management and how to resolve it. Phytopathology, 104, 564–574. https://doi.org/10.1094/PHYTO-11-13-0315-IA
96. Inderbitzin, P., Bostock, R.M., Davis, R.M., Usami, T., Platt, H.W., & Subbarao, K.V. (2011). Phylogenetics and taxonomy of the fungal vascular wilt pathogen *Verticillium*, with the descriptions of five new species. PLoS ONE, 6(12), e28341. https://doi.org/10.1371/journal.pone.0028341
97. Inderbitzin, P., Davis, R.M., Bostock, R.M., & Subbarao, K.V. (2013). Identification and differentiation of *Verticillium* species and *V. longisporum* lineages by simplex and multiplex PCR assays. PLoS ONE, 8(6), e65990. https://doi.org/10.1371/journal.pone.0065990
98. International Olive Council. (2025). Sector statistics – January 2025. https://www.internationaloliveoil.org/sector-statistics-january-2025
99. Jeseničnik, T., Kaurin, A., et al. (2023). Novel identification of the collection of pathogenic fungal species *Verticillium* with the development of species-specific SSR markers. Pathogens, 12, 535. https://doi.org/10.3390/pathogens12040535
100. Jiménez-Díaz, R.M., Cirulli, M., Bubici, G., del Mar Jiménez-Gasco, M., Antoniou, P.P., & Tjamos, E.C. (2012). *Verticillium* wilt, a major threat to olive production: Current status and future prospects for its management. Plant Disease, 96, 304–329. https://doi.org/10.1094/PDIS-06-11-0496
101. Jiménez-Díaz, R.M., Olivares-García, C., Landa, B.B., del Mar Jiménez-Gasco, M., & Navas-Cortés, J.A. (2011). Region-wide analysis of genetic diversity in *Verticillium dahliae* populations infecting olive in southern Spain and agricultural factors influencing the distribution and prevalence of vegetative compatibility groups and pathotypes. Phytopathology, 101, 304–315. https://doi.org/10.1094/PHYTO-07-10-0176
102. Jiménez-Díaz, R.M., Tjamos, E.C., & Cirulli, M. (1998). *Verticillium* wilts of major tree hosts: Olive. In J.A. Hiemstra & D.C. Harris (Eds.), A compendium of *Verticillium* wilts in tree species (pp. 13–16). Ponsen & Looijen. https://edepot.wur.nl/211512
103. Jiménez-Fernández, D., Trapero-Casas, J.L., Landa, B.B., Navas-Cortés, J.A., Bubici, G., Cirulli, M., et al. (2016). Characterization of resistance against the olive-defoliating *Verticillium dahliae* pathotype in selected clones of wild olive. Plant Pathology, 65, 1279–1291. https://doi.org/10.1111/ppa.12516
104. Jiménez-Gasco, M.M., Malcolm, G.M., Berbegal, M., Armengol, J., & Jiménez-Díaz, R. (2014). Complex molecular relationship between vegetative compatibility groups (VCGs) in *Verticillium dahliae*: VCGs do not always align with clonal lineages. Phytopathology, 104, 650–659. https://doi.org/10.1094/PHYTO-07-13-0180-R
105. Jiménez-Ruiz, J., de la O Leyva-Pérez, M., Schilirò, E., Barroso, J.B., Bombarely, A., Mueller, L., Mercado-Blanco, J., & Luque, F. (2017). Transcriptomic analysis of the *Olea europaea* L. roots during the *Verticillium dahliae* early infection process. The Plant Genome, 10. https://doi.org/10.3835/plantgenome2016.07.0060
106. Jiménez-Ruiz, J., Leyva-Pérez, M.O., Gómez-Lama, C., Barroso, J.B., Luque, F., & Mercado-Blanco, J. (2019). The transcriptome of *Verticillium dahliae* responds differentially depending on the disease susceptibility level of the olive (*Olea europaea* L.) cultivar. Genes, 10, 251. https://doi.org/10.3390/genes10040251
107. Jones, J.D., & Dangl, J.L. (2006). The plant immune system. Nature, 444, 323–329. https://doi.org/10.1038/nature05286
108. Joung, J., Ladha, A., Saito, M., Segel, M., Bruneau, R., Huang, M.W., et al. (2020). Detection of SARS-CoV-2 with SHERLOCK one-pot testing. New England Journal of Medicine, 383(15), 1492–1494. https://doi.org/10.1056/NEJMc2026172
109. Ju, Y., Li, C., Shen, P., Wan, N., Han, W., & Pan, Y. (2020). Rapid and visual detection of *Verticillium dahliae* using recombinase polymerase amplification combined with lateral flow dipstick. Crop Protection, 132, 105226. https://doi.org/10.1016/j.cropro.2020.105226
110. Kageyama, K., Komatsu, T., & Suga, H. (2003). Refined PCR protocol for detection of plant pathogens in soil. Journal of General Plant Pathology, 69, 153–160. https://doi.org/10.1007/s10327-002-0037-4
111. Kaliterna, J., Miličević, T., Bencic, D., & Mesić, A. (2016). First report of *Verticillium* wilt caused by *Verticillium dahliae* on olive trees in Croatia. Plant Disease, 100, 2526. https://doi.org/10.1094/PDIS-04-16-0481-PDN
112. Katan, J. (2017). Diseases caused by soilborne pathogens: Biology, management and challenges. Journal of Plant Pathology, 99(2), 305–315. https://doi.org/10.4454/jpp.v99i2.3862
113. Keykhasaber, M., Thomma, B.P.H.J., & Hiemstra, J.A. (2018). *Verticillium* wilt caused by *Verticillium dahliae* in woody plants with emphasis on olive and shade trees. European Journal of Plant Pathology, 150, 21–37. https://doi.org/10.1007/s10658-017-1273-y
114. Kirkegaard, J.A., & Matthiessen, J.N. (2004). Developing and refining the biofumigation concept. Agroindustria, 3(3), 233–239.
115. Kirkegaard, J.A., Gardner, P.A., Desmarchelier, J.M., & Angus, J.F. (1993). Biofumigation: Using *Brassica* species to control pests and diseases

in horticulture and agriculture. In 9th Australian Research Assembly on Brassicas (p. 77). Wagga Wagga, Australia.

116. Klosterman, S.J., Atallah, Z.K., Vallad, G.E., & Subbarao, K.V. (2009). Diversity, pathogenicity, and management of *Verticillium* species. Annual Review of Phytopathology, 47(1), 39–62. https://doi.org/10.1146/annurev-phyto-080508-081748
117. Klosterman, S.J., Subbarao, K.V., Kang, S., Veronese, P., Gold, S.E., Thomma, B.P., et al. (2011). Comparative genomics yields insights into niche adaptation of plant vascular wilt pathogens. PLoS Pathogens, 7, e1002137. https://doi.org/10.1371/journal.ppat.1002137
118. Kocmánková, E., Trnka, M., Juroch, J., Dubrovský, M., Semerádová, D., Možný, M., et al. (2009). Impact of climate change on the occurrence and activity of harmful organisms. Plant Protection Science, 45, S48–S52.
119. Kowalska, B. (2021). Management of the soil-borne fungal pathogen – *Verticillium dahliae* Kleb. causing vascular wilt diseases. Journal of Plant Pathology, 103, 1185–1194. https://doi.org/10.1007/s42161-021-00937-8
120. Landa, B.B., Pérez, A.G., Luaces, P., Montes-Borrego, M., Navas-Cortés, J.A., & Sanz, C. (2019). Insights into the effect of *Verticillium dahliae* defoliating-pathotype infection on the content of phenolic and volatile compounds related to the sensory properties of virgin olive oil. Frontiers in Plant Science, 10, 232. https://doi.org/10.3389/fpls.2019.00232
121. Lee, M., Jeon, H.S., Kim, S.H., Chung, J.H., Roppolo, D., Lee, H., et al. (2019). Lignin-based barrier restricts pathogens to the infection site and confers resistance in plants. The EMBO Journal, 38, e101948. https://doi.org/10.15252/embj.2019101948
122. Leslie, J.F. (1993). Fungal vegetative compatibility. Annual Review of Phytopathology, 31, 127–150. https://doi.org/10.1146/annurev.py.31.090193.001015
123. Levin, A.G., Lavee, S., & Tsror, L. (2003). Epidemiology of *Verticillium dahliae* on olive (cv. Picual) and its effect on yield under saline conditions. Plant Pathology, 52(2), 212–218. https://doi.org/10.1046/j.1365-3059.2003.00809.x
124. Leyva-Pérez, M.O., Jiménez-Ruiz, J., Gómez-Lama Cabanás, C., Valverde-Corredor, A., Barroso, J.B., Luque, F., & Mercado-Blanco, J. (2018). Tolerance of olive (*Olea europaea*) cv Frantoio to *Verticillium dahliae* relies on both basal and pathogen-induced differential transcriptomic responses. New Phytologist, 217, 671–686. https://doi.org/10.1111/nph.14833
125. Li, C., Chen, X., Wen, R., Ma, P., Gu, K., Li, C., Zhou, C., Lei, C., Tang, Y., & Wang, H. (2022). Immunocapture magnetic beads enhanced the LAMP-CRISPR/Cas12a method for the sensitive, specific, and visual detection of *Campylobacter jejuni*. Biosensors, 12, 154. https://doi.org/10.3390/bios12030154
126. Li, K.N., Rouse, D.I., Eyestone, E.J., & German, T.L. (1999). The generation of specific DNA primers using randomly amplified polymorphic DNA and its application to *Verticillium dahliae*. Mycological Research, 103, 1361–1368. https://doi.org/10.1017/S0953756299008357
127. Lo Presti, L., Lanver, D., Schweizer, G., Tanaka, S., Liang, L., Tollot, M., Zuccaro, A., Reissmann, S., & Kahmann, R. (2015). Fungal effectors and plant susceptibility. Annual Review of Plant Biology, 66, 513–545. https://doi.org/10.1146/annurev-arplant-043014-114623
128. Lozano-Tovar, M.D., Garrido-Jurado, I., Quesada-Moraga, E., Raya-Ortega, M.C., & Trapero-Casas, A. (2017). *Metarhizium brunneum* and *Beauveria bassiana* release secondary metabolites with antagonistic activity against *Verticillium dahliae* and *Phytophthora megasperma* olive pathogens. Crop Protection, 100, 186–195. https://doi.org/10.1016/j.cropro.2017.06.026
129. Luo, X., Xie, C., Dong, J., Yang, X., & Sui, A. (2014). Interactions between *Verticillium dahliae* and its host: Vegetative growth, pathogenicity, plant immunity. Applied Microbiology and Biotechnology, 98, 6921–6932. https://doi.org/10.1007/s00253-014-5863-8
130. López-Escudero, F.J., & Blanco-López, M.A. (1999). First report of transmission of *Verticillium dahliae* by infested manure in olive orchards in Andalucía (southern Spain). Plant Disease, 83, 1178. https://doi.org/10.1094/PDIS.1999.83.12.1178B
131. López-Escudero, F.J., & Blanco-López, M.A. (2001). Effect of a single or double soil solarization to control *Verticillium* wilt in established olive orchards in Spain. Plant Disease, 85(5), 489–496. https://doi.org/10.1094/PDIS.2001.85.5.489
132. López-Escudero, F.J., & Blanco-López, M.A. (2007). Relationship between the inoculum density of *Verticillium dahliae* and the progress of *Verticillium* wilt of olive. Plant Disease, 91, 1372–1378. https://doi.org/10.1094/PDIS-91-11-1372
133. López-Escudero, F.J., & Mercado-Blanco, J. (2011). *Verticillium* wilt of olive: A case study to implement an integrated strategy to control a soil-borne pathogen. Plant and Soil, 344, 1–50. https://doi.org/10.1007/s11104-010-0629-2
134. López-Escudero, F.J., del Río, C., Caballero, J.M., & Blanco-López, M.A. (2004). Evaluation of olive cultivars for resistance to *Verticillium dahliae*. European Journal of Plant Pathology, 110, 79–85. https://doi.org/10.1023/B:EJPP.0000010150.08098.2d

135. López-Moral, A., Agustí-Brisach, C., & Trapero, A. (2021). Plant biostimulants: New insights into the biological control of *Verticillium* wilt of olive. Frontiers in Plant Science, 12, 662178. https://doi.org/10.3389/fpls.2021.662178

136. López-Moral, A., Llorens, E., Scalschi, L., García-Agustín, P., Trapero, A., & Agustí-Brisach, C. (2022). Resistance induction in olive tree (*Olea europaea*) against *Verticillium* wilt by two beneficial microorganisms and a copper phosphite fertilizer. Frontiers in Plant Science, 13, 831794. https://doi.org/10.3389/fpls.2022.831794

137. Mahas, A., Hassan, N., Aman, R., Marsic, T., Wang, Q., Ali, Z., & Mahfouz, M.M. (2021). LAMP-coupled CRISPR-Cas12a module for rapid and sensitive detection of plant DNA viruses. Viruses, 13, 466. https://doi.org/10.3390/v13030466

138. Mahuku, G.S., & Platt, H.W. (2002). Quantification of *Verticillium dahliae* in soils collected from potato fields using a competitive PCR assay. American Journal of Potato Research, 79, 107–117. https://doi.org/10.1007/bf02881519

139. Mallamaci, R., Budriesi, R., Clodoveo, M.L., Biotti, G., Micucci, M., Ragusa, A., et al. (2021). Olive tree in circular economy as a source of secondary metabolites active for human and animal health beyond oxidative stress and inflammation. Molecules, 26(4), 1072. https://doi.org/10.3390/molecules26041072

140. Mamalis, M., Kalampokis, E., Kalfas, I., & Tarabanis, K. (2023). Deep learning for detecting *Verticillium* fungus in olive trees: Using YOLO in UAV imagery. Algorithms, 16(7), 343. https://doi.org/10.3390/a16070343

141. Markakis, E.A., Tjamos, S.E., Antoniou, P.P., Paplomatas, E.J., & Tjamos, E.C. (2016). Biological control of *Verticillium* wilt of olive by *Paenibacillus alvei*, strain K165. BioControl, 61, 293–303. https://doi.org/10.1007/s10526-015-9669-0

142. Martinelli, F., Scalenghe, R., Davino, S., Panno, S., Scuderi, G., Ruisi, P., et al. (2015). Advanced methods of plant disease detection. A review. Agronomy for Sustainable Development, 35, 1–25. https://doi.org/10.1007/s13593-014-0246-1

143. Maruthachalam, K., Atallah, Z.K., Vallad, G.E., Klosterman, S.J., Hayes, R.J., Davis, R.M., & Subbarao, K.V. (2010). Molecular variation among isolates of *Verticillium dahliae* and polymerase chain reaction-based differentiation of races. Phytopathology, 100, 1222–1230. https://doi.org/10.1094/PHYTO-04-10-0122

144. Megariti, M., Panagou, A., Patsis, G. et al. Rapid real-time quantitative colorimetric LAMP methodology for field detection of *Verticillium dahliae* in crude olive-plant samples. Plant Methods 20, 139 (2024). https://doi.org/10.1186/s13007-024-01251-x

145. Mercado-Blanco, J., Collado-Romero, M., Parrilla-Araujo, S., Rodríguez-Jurado, D., & Jiménez-Díaz, R.M. (2003a). Quantitative monitoring of colonization of olive genotypes by *Verticillium dahliae* pathotypes with real-time polymerase chain reaction. Physiological and Molecular Plant Pathology, 63, 91–105. https://doi.org/10.1016/j.pmpp.2003.10.001

146. Mercado-Blanco, J., Rodríguez-Jurado, D., Hervás, A., & Jiménez-Díaz, R.M. (2004). Suppression of *Verticillium* wilt in olive planting stocks by root-associated fluorescent *Pseudomonas* spp. Biological Control, 30, 474–486. https://doi.org/10.1016/j.biocontrol.2004.02.002

147. Mercado-Blanco, J., Rodríguez-Jurado, D., Parrilla-Araujo, S., & Jiménez-Díaz, R.M. (2003b). Simultaneous detection of the defoliating and nondefoliating *Verticillium dahliae* pathotypes in infected olive plants by duplex, nested polymerase chain reaction. Plant Disease, 87(12), 1487–1494. https://doi.org/10.1094/PDIS.2003.87.12.1487

148. Milgroom, M. G., Jiménez-Gasco, M. M., Olivares-García, C., Drott, M. T., & Jiménez-Díaz, R. M. (2014). Recombination between clonal lineages of the asexual fungus *Verticillium dahliae* detected by genotyping by sequencing. PLoS ONE, 9(9), e106740. https://doi.org/10.1371/journal.pone.0106740

149. Montes-Osuna, N., & Mercado-Blanco, J. (2020). *Verticillium* wilt of olive and its control: What did we learn during the last decade? Plants, 9(6), 735. https://doi.org/10.3390/plants9060735

150. Moradi, A., Almasi, M.A., Jafary, H., & Mercado-Blanco, J. (2014). A novel and rapid loop-mediated isothermal amplification assay for the specific detection of *Verticillium dahliae*. Journal of Applied Microbiology, 116(4), 942–954.

151. Morello, P., Diez, C.M., Codes, M., Rallo, L., Barranco, D., Trapero, A., et al. (2016). Sanitation of olive plants infected by *Verticillium dahliae* using heat treatments. Plant Pathology, 65, 412–421. https://doi.org/10.1111/ppa.12432

152. Muhammed-Ahmed, O., López-Moral, A., Saigner, M.C., Sánchez-Pereira, L., Luque-Cruz, C., Antón-Domínguez, B.I., & Agustí-Brisach, C. (2026). Selection of beneficial microorganisms as potential biological control agents against *Verticillium* wilt of olive, and their validation in the field. Plant Disease. https://doi.org/10.1094/PDIS-12-25-2592-RE

153. Mulero-Aparicio, A., Varo, A., Agustí-Brisach, C., López-Escudero, F.J., & Trapero, A. (2020). Biological control of *Verticillium* wilt of olive in the field. Crop Protection, 128, 104993. https://doi.org/10.1016/j.cropro.2019.104993

154. Navrozidis, I., Pantazi, X.E., Lagopodi, A., Bochtis, D., & Alexandridis, T.K. (2023). Application of machine learning for disease detection

tasks in olive trees using hyperspectral data. Remote Sensing, 15, 5683. https://doi.org/10.3390/rs15245683

155. Nazar, R.N., Hu, X., Schmidt, J., Culham, D., & Robb, J. (1991). Potential use of PCR-amplified ribosomal intergenic sequences in the detection and differentiation of *verticillium* wilt pathogens. Physiological and Molecular Plant Pathology, 39(1), 1–11. https://doi.org/10.1016/0885-5765(91)90027-F
156. Newman, S.E. (2004). Disinfecting irrigation water for disease management. In 20th Annual Conference on Pest Management on Ornamentals. San Jose, California. https://kh.aquaenergyexpo.com/wp-content/uploads/2022/11/Disinfecting-Irrigation-Water-for-Disease-Management.pdf
157. Njoroge, S.M.C., Kabir, Z., Martin, F.N., Koike, S.T., & Subbarao, K.V. (2009). Comparison of crop rotation for *Verticillium* wilt management and effect on *Pythium* species in conventional and organic strawberry production. Plant Disease, 93, 519–527. https://doi.org/10.1094/PDIS-93-5-0519
158. Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., ... & Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. PLoS Medicine, 18(3), e1003583. https://doi.org/10.1371/journal.pmed.1003583
159. Pandit, M.A., Kumar, J., Gulati, S., Bhandari, N., Mehta, P., Katyal, R., et al. (2022). Major biological control strategies for plant pathogens. Pathogens, 11, 273. https://doi.org/10.3390/pathogens11020273
160. Panth, M., Hassler, S.C., & Baysal-Gurel, F. (2020). Methods for management of soilborne diseases in crop protection. Agriculture, 10, 16. https://doi.org/10.3390/agriculture10010016
161. Pegg, G.F., & Brady, B.L. (2002). *Verticillium* wilts. CABI Publishing. https://doi.org/10.1079/9780851995298.0000
162. Pennypacker, B., Leath, K., & Hill, R.J. (1991). Impact of drought stress on the expression of resistance to *Verticillium albo-atrum* in alfalfa. Phytopathology, 81, 1014–1024. DOI: 10.1094/Phyto-81-1014.
163. Perry, J. W., & Evert, R. F. (1983). Histopathology of *Verticillium dahliae* within potato roots. Canadian Journal of Botany, 61(12), 3405–3421.
164. Poblete, T., Navas-Cortes, J.A., Camino, C., Calderon, R., Hornero, A., Gonzalez-Dugo, V., Landa, B.B., & Zarco-Tejada, P.J. (2021). Discriminating *Xylella fastidiosa* from *Verticillium dahliae* infections in olive trees using thermal- and hyperspectral-based plant traits. ISPRS Journal of Photogrammetry and Remote Sensing, 179,133-144 .https://doi.org/10.1016/j.isprsjprs.2021.07.014.
165. Popov, V.I., Tarunina, T.A., & Usmanov, Z.U. (1972). On the physiologic races of *Verticillium dahliae* Kleb., a causal agent of cotton wilt. Mikologiya i Fitopatologiya, 6, 500–502.
166. Porras-Soriano, A., Soriano-Martín, M.L., & Porras-Piedra, A. (2003). Grafting olive cv. Cornicabra on rootstocks tolerant to *Verticillium dahliae* reduces their susceptibility. Crop Protection, 22, 369–374. https://doi.org/10.1016/S0261-2194(02)00180-1
167. Poveda, J., & Baptista, P. (2021). Filamentous fungi as biocontrol agents in olive (*Olea europaea* L.) diseases: Mycorrhizal and endophytic fungi. Crop Protection, 146, 105672. https://doi.org/10.1016/j.cropro.2021.105672
168. Pozo, M.J., Jung, S.C., López-Ráez, J.A., & Azcón-Aguilar, C. (2010). Impact of arbuscular mycorrhizal symbiosis on plant response to biotic stress: The role of plant defence mechanisms. In H. Koltai & Y. Kapulnik (Eds.), Arbuscular mycorrhizas: Physiology and function (pp. 193–207). Springer. https://doi.org/10.1007/978-90-481-9489-6_9
169. Puhalla, J. E. (1979). Classification of isolates of *Verticillium dahliae* based on heterokaryon incompatibility. Phytopathology, 69, 1186–1189.
170. Puri, K.D., Gurung, S., Short, D.P.G., Atallah, Z.K., Sandoya, G., Davis, R.M., Hayes, R.J., & Subbarao, K.V. (2017). Short-term host selection pressure has little effect on the evolution of a monoclonal population of *Verticillium dahliae* race 1. Phytopathology, 107, 1417–1425. https://doi.org/10.1094/PHYTO-02-17-0071-R
171. Pérez-Artés, E., García-Pedrajas, M.D., Bejarano-Alcázar, J., & Jiménez-Díaz, R.M. (2000). Differentiation of cotton-defoliating and nondefoliating pathotypes of *Verticillium dahliae* by RAPD and specific PCR analyses. European Journal of Plant Pathology, 106, 507–517. https://doi.org/10.1023/A:1008756307969
172. Pérez-Artés, E., Mercado-Blanco, J., Ruz-Carrillo, A.R., Rodríguez-Jurado, D., & Jiménez-Díaz, R.M. (2005). Detection of the defoliating and nondefoliating pathotypes of *Verticillium dahliae* in artificial and natural soils by nested PCR. Plant and Soil, 268, 349–356. https://doi.org/10.1007/s11104-004-0378-1
173. Pérez-Rodríguez M, Alcántara E, Amaro M, Serrano N, Lorite IJ, Arquero O, Orgaz F, López-Escudero FJ. The Influence of Irrigation Frequency on the Onset and Development of *Verticillium* Wilt of Olive. Plant Dis. 2015 Apr;99(4):488-495. 10.1094/PDIS-06-14-0599-RE
174. Ramos, M.I., Cubillas, J.J., Cordoba, R.M., & Ortega, L.M. (2025). Improving early prediction of crop yield in Spanish olive groves using satellite imagery and machine learning. PLoS ONE, 20(1), e0311530.

https://doi.org/10.1371/journal.pone.0311530

175. Requena-Mullor, J.M., García-Garrido, J.M., García, P.A., & Rodríguez, E. (2020). Climatic drivers of *Verticillium dahliae* occurrence in Mediterranean olive-growing areas of southern Spain. PLoS ONE, 15(12), e0232648. https://doi.org/10.1371/journal.pone.0232648
176. Rhouma, A., Hajji-Hedfi, L., Kouadri, M.E.A., Atallaoui, K., Okon, O.G., & Khrieba, M.I. (2023). *Verticillium* wilt of olive and its control caused by the hemibiotrophic soil-borne fungus *Verticillium dahliae*. Microbial Biosystems, 8(2), 25–36. https://doi.org/10.21608/MB.2024.255400.1089
177. Rodríguez-Jurado, D., Blanco-López, M. A., Rapoport, H. F., & Jiménez-Díaz, R. M. (1993). Present status of *Verticillium* wilt of olive in Andalucía (southern Spain). EPPO Bulletin, 23(3), 513–516. https://doi.org/10.1111/j.1365-2338.1993.tb01360.x
178. Ruano-Rosa, D., Valverde-Corredor, A., Gómez-Lama Cabanás, C., Sesmero, R., & Mercado-Blanco, J. (2017). What lies beneath: Root-associated bacteria to improve the growth and health of olive trees. In M. Lukac, P. Grenni, & M. Gamboni (Eds.), Soil biological communities and ecosystem resilience (pp. 107–122). Springer. https://doi.org/10.1007/978-3-319-63336-7_7
179. Salah, I.B., Aghrouss, S., Douira, A., Aissam, S., Alaoui-Talibi, Z.E., Filali-Maltouf, A., et al. (2018). Seaweed polysaccharides as bio-elicitors of natural defenses in olive trees against *Verticillium* wilt of olive. Journal of Plant Interactions, 13, 248–255. https://doi.org/10.1080/17429145.2018.1471528
180. Santos-Rufo, A., & Rodríguez-Jurado, D. (2021). Unravelling the relationships among *Verticillium* wilt, irrigation, and susceptible and tolerant olive cultivars. Plant Pathology, 70, 2046–2061. https://doi.org/10.1111/ppa.13442
181. Santos-Rufo, A., Hidalgo, J.J., Hidalgo, J.C., Vega, V., & Rodríguez-Jurado, D. (2017). Assessment of the effect of surface drip irrigation on *Verticillium dahliae* propagules differing in persistence in soil and on *Verticillium* wilt of olive. Plant Pathology, 66(7), 1152–1163. https://doi.org/10.1111/ppa.12652
182. Santos-Rufo, A., Hidalgo, J.J., Hidalgo, J.C., Vega, V., & Rodríguez-Jurado, D. (2018). Morphophysiological response of young olive trees to *Verticillium* wilt under different surface drip irrigation regimes. Plant Pathology, 67(4), 848–859. https://doi.org/10.1111/ppa.12788
183. Santos-Rufo, A., Molina-Molina, M., Alcántara-Vara, E., Weiland-Ardáiz, C., & López-Escudero, F.J. (2023). Vessel anatomical features of 'Picual' and 'Frantoio', two olive cultivars different in resistance against *Verticillium* wilt of olive. Plants, 12, 2910. https://doi.org/10.3390/plants12162910
184. Sarfraz, M., Nasim, M.J., Jacob, C., & Gruhlke, M.C.H. (2020). Efficacy of allicin against plant pathogenic fungi and unveiling the underlying mode of action employing yeast based chemogenetic profiling approach. Applied Sciences, 10, 2563. https://doi.org/10.3390/app10072563
185. Schnathorst, W.C. (1981). Life cycle and epidemiology of *Verticillium*. In M.E. Mace, A.A. Bell, & C.H. Beckman (Eds.), Fungal wilt diseases of plants (pp. 81–111). Academic Press.
186. Schreiber, L. R., & Green, R. J. (1963). Effect of root exudates on germination of conidia and microsclerotia of *Verticillium albo-atrum* inhibited by soil fungistasis. Phytopathology, 53, 1446–1447.
187. Serrano, A., Rodríguez-Jurado, D., Ramírez-Tejero, J.A., Luque, F., López-Escudero, F.J., Belaj, A., et al. (2023). Response to *Verticillium dahliae* infection in a genetically diverse set of olive cultivars. Scientia Horticulturae, 316, 112008. https://doi.org/10.1016/j.scienta.2023.112008
188. Serrano-García, I., et al. (2023). Metabolomic profiling of olive cultivars differing in resistance to *Verticillium dahliae*. Antioxidants, 12(12), 2120. https://doi.org/10.3390/antiox12122120
189. Shang, H., He, D., Li, B., Chen, X., Luo, K., & Li, G. (2024). Environmentally friendly and effective alternative approaches to pest management: Recent advances and challenges. Agronomy, 14, 1807. https://doi.org/10.3390/agronomy14081807
190. Short, D.P.G., Gurung, S., Gladieux, P., Inderbitzin, P., Atallah, Z.K., Nigro, F., Li, G., Benlioglu, S., & Subbarao, K.V. (2015). Globally invading populations of the fungal plant pathogen *Verticillium dahliae* are dominated by multiple divergent lineages. Environmental Microbiology, 17, 2824–2840. https://doi.org/10.1111/1462-2920.12789
191. Simmons, C.W., Claypool, J.T., Marshall, M.N., Jabusch, L.K., Reddy, A.P., Simmons, B.A., Singer, S.W., Stapleton, J.J., & VanderGheynst, J.S. (2014). Characterization of bacterial communities in solarized soil amended with lignocellulosic organic matter. Applied Soil Ecology, 73, 97–104. https://doi.org/10.1016/j.apsoil.2013.08.014
192. Singh, A., Kumar, R., & Singh, D. (2019). Mycorrhizal fungi as biocontrol agent for soil borne pathogens: A review. Journal of Pharmacognosy and Phytochemistry, 8(1S), 281–284.
193. Song, R., Li, J., Xie, C., Jian, W., & Yang, X. (2020). An overview of the molecular genetics of plant resistance to the *Verticillium* wilt pathogen *Verticillium dahliae*. International Journal of Molecular Sciences, 21(3), 1120. https://doi.org/10.3390/ijms21031120
194. Sorlozano-Puerto, A., Albertuz-Crespo, M., Lopez-Machado, I., Ariza-Romero, J.J., Baños-Arjona, A., Exposito-Ruiz, M., & Gutierrez-Fernandez, J. (2018). In vitro antibacterial activity of

propyl-propane-thiosulfinate and propyl-propane-thiosulfonate derived from *Allium* spp. against Gram-negative and Gram-positive multidrug-resistant bacteria isolated from human samples. BioMed Research International, 2018, 7861207. https://doi.org/10.1155/2018/7861207

195. Sorlozano-Puerto, A., Albertuz-Crespo, M., Lopez-Machado, I., Gil-Martinez, L., Ariza-Romero, J.J., Maroto-Tello, A., Baños-Arjona, A., & Gutierrez-Fernandez, J. (2020). Antibacterial and antifungal activity of propyl-propane-thiosulfinate and propyl-propane-thiosulfonate, two organosulfur compounds from *Allium cepa*: In vitro antimicrobial effect via the gas phase. Pharmaceuticals, 14(1), 21. https://doi.org/10.3390/ph14010021
196. Soultatos, S.K., Chatzaki, A., Karas, P.A., Papadaki, A.A., Kalantzakis, G.S., Psarras, G., Goumas, D.E., Karpouzas, D.G., & Markakis, E.A. (2025). Biocontrol potential of raw olive mill wastes against *Verticillium dahliae* in vegetable crops. Plants, 14(6), 867. https://doi.org/10.3390/plants14060867
197. Stenberg, J.A., Sundh, I., Becher, P.G., et al. (2021). When is it biological control? A framework of definitions, mechanisms, and classifications. Journal of Pest Science, 94, 665–676. https://doi.org/10.1007/s10340-021-01354-7
198. Sun, L., Wu, X., Diao, J., & Zhang, J. (2023). Pathogenesis mechanisms of phytopathogen effectors. WIREs Mechanisms of Disease, 15, e1592. https://doi.org/10.1002/wsbm.1592
199. Sánchez-Hernández, M.E., Ruiz-Dávila, A., Pérez de Algaba, A., Blanco-López, M.A., & Trapero-Casas, A. (1998). Occurrence and etiology of death of young olive trees in southern Spain. European Journal of Plant Pathology, 104, 347–357. https://doi.org/10.1023/A:1008624929989
200. Tenuta, M., & Lazarovits, G. (2002). Ammonia and nitrous acid from nitrogenous amendments kill the microsclerotia of *Verticillium dahliae*. Phytopathology, 92, 255–264. https://doi.org/10.1094/PHYTO.2002.92.3.255
201. Tjamos, E.C., & Jiménez-Díaz, R.M. (1998). A compendium of *Verticillium* wilts in tree species. Ponsen & Looijen. https://www.researchgate.net/publication/254834373_A_Compendium_of_Verticillium_Wilts_in_Tree_Species
202. Tjamos, E.C., Tsitsigiannis, D.I., Tjamos, S.E., Antoniou, P.P., & Katinakis, P. (2004). Selection and screening of endorhizosphere bacteria from solarized soils as biocontrol agents against *Verticillium dahliae* of solanaceous hosts. European Journal of Plant Pathology, 110, 35–44. https://doi.org/10.1023/B:EJPP.0000010132.91241.cb
203. Tjamos, S.E., Flemetakis, E., Paplomatas, E.J., & Katinakis, P. (2005). Induction of resistance to *Verticillium dahliae* in *Arabidopsis thaliana* by the biocontrol agent K-165 and pathogenesis-related proteins gene expression. Molecular Plant-Microbe Interactions, 18, 555–561. https://doi.org/10.1094/MPMI-18-0555
204. Trapero, C., Rallo, L., López-Escudero, F.J., Barranco, D., & Díez, C.M. (2015). Variability and selection of *Verticillium* wilt resistant genotypes in cultivated olive and in the *Olea* genus. Plant Pathology, 64, 890–900. https://doi.org/10.1111/ppa.12330
205. Trapero, C., Serrano, N., Arquero, O., Del Río, C., Trapero, A., & López-Escudero, F.J. (2013). Field resistance to *Verticillium* wilt in selected olive cultivars grown in two naturally infested soils. Plant Disease, 97, 668–674. https://doi.org/10.1094/PDIS-07-12-0654-RE
206. Tsror, L. (2011). Epidemiology and control of *Verticillium* wilt on olive. Israel Journal of Plant Sciences, 59(1), 59–69. https://doi.org/10.1560/IJPS.59.1.59
207. Usami, T., Itoh, M., & Amemiya, Y. (2009). Asexual fungus *Verticillium dahliae* is potentially heterothallic. Journal of General Plant Pathology, 75, 422–427. https://doi.org/10.1007/s10327-009-0197-6
208. Valverde, P., Barranco, D., López-Escudero, F.J., Díez, C.M., & Trapero, C. (2023). Efficiency of breeding olives for resistance to *Verticillium* wilt. Frontiers in Plant Science, 14, 1149570. https://doi.org/10.3389/fpls.2023.1149570
209. Valverde, P., Trapero, C., Arquero, O., Serrano, N., Barranco, D., Muñoz Díez, C., & López-Escudero, F.J. (2021). Highly infested soils undermine the use of resistant olive rootstocks as a control method of *Verticillium* wilt. Plant Pathology, 70, 144–153. https://doi.org/10.1111/ppa.13264
210. Van Dam, N.M., Tytgat, T.O., & Kirkegaard, J.A. (2009). Root and shoot glucosinolates: A comparison of their diversity, function and interactions in natural and managed ecosystems. Phytochemistry Reviews, 8(1), 171–186. https://doi.org/10.1007/s11101-008-9101-9
211. Vanholme, R., Demedts, B., Morreel, K., Ralph, J., & Boerjan, W. (2010). Lignin biosynthesis and structure. Plant Physiology, 153, 895–905. https://doi.org/10.1104/pp.110.155119
212. Varo, A., Mulero-Aparicio, A., Adem, M., Roca, L.F., Raya-Ortega, M.C., López-Escudero, F.J., & Trapero, A. (2017). Screening water extracts and essential oils from Mediterranean plants against *Verticillium dahliae* in olive. Crop Protection, 92, 168–175. https://doi.org/10.1016/j.cropro.2016.10.018
213. Varo, A., Raya-Ortega, M.C., & Trapero, A. (2016). Enhanced production of microsclerotia in recalcitrant *Verticillium dahliae* isolates and its use for inoculation of olive plants. Journal of Applied

Microbiology. https://doi.org/10.1111/jam.13167

214. Varo, A., Raya-Ortega, M.C., Agustí-Brisach, C., García-Ortiz-Civantos, C., Fernández-Hernández, A., Mulero-Aparicio, A., et al. (2018). Evaluation of organic amendments from agro-industry waste for the control of *Verticillium* wilt of olive. Plant Pathology, 67, 860–870. https://doi.org/10.1111/ppa.12798
215. Varo-Suárez, A., Raya-Ortega, M. C., Agustí-Brisach, C., García-García, M. C., & Trapero, A. (2018). Evaluation of organic amendments from agro-industry waste for the control of *Verticillium* wilt of olive. Plant Pathology, 67(4), 860–870. https://doi.org/10.1111/ppa.12798
216. Villar, J., & Pereira, J. (2018). International olive growing: Historical diffusion, strategic analysis and descriptive overview. Fundación Caja Rural de Jaén (in Spanish).
217. Vizzarri, V., Ienco, A., De Rose, I., Lombardo, L., Godino, G., Perri, E., & Polizzo, F. (2026). Comparative assessment of *Verticillium dahliae* tolerance in 77 olive cultivars. Crops, 6(1), 9. https://doi.org/10.3390/crops6010009
218. Vossen, P. (2007). Olive oil: History, production, and characteristics of the world's classic oils. HortScience, 42, 1093–1100.
219. Wang, Y., Hu, X., Fang, Y., Anchieta, A., Goldman, P.H., Hernandez, G., et al. (2018a). Transcription factor VdCmr1 is required for pigment production, protection from UV irradiation, and regulates expression of melanin biosynthetic genes in *Verticillium dahliae*. Microbiology, 164, 685–696.
220. Wang, Y., Wang, Y., Li, D., Xu, J., & Ye, C. (2018b). Detection of nucleic acids and elimination of carryover contamination by using loop-mediated isothermal amplification and antarctic thermal sensitive uracil-DNA-glycosylase in a lateral flow biosensor: Application to the detection of *Streptococcus pneumoniae*. Microchimica Acta, 185, 212.
221. Wang, Y.L., Wang, Y., & Tian, C.M. (2013). Quantitative detection of pathogen DNA of *Verticillium* wilt on smoke tree *Cotinus coggygria*. Plant Disease, 97(12), 1645–1651.
222. Wei, F., Fan, R., Dong, H.T., Shang, W.J., Xu, X.X., Zhu, H.Q., Yang, J.R., & Hu, X.P. (2015). Threshold microsclerotial inoculum for cotton *Verticillium* wilt determined through wet-sieving and real-time quantitative PCR. Phytopathology, 105(2), 220–229.
223. Wei, F., Passey, T., & Xu, X. (2016). Effects of individual and combined use of bio-fumigation-derived products on the viability of *Verticillium dahliae* microsclerotia in soil. Crop Protection, 79, 170–176.
224. Wheeler, D.L., & Johnson, D.A.(2016). *Verticillium dahliae* infects, alters plant biomass, and produces inoculum on rotation crops. Phytopathology, 106, 602–613.
225. Wilhelm, S. (1955). Longevity of the *Verticillium* wilt fungus in the laboratory and field. Phytopathology, 45, 180–181.
226. Wu, CD., Fan, YB., Chen, X. et al. (2024). Analysis of endophytic bacterial diversity in seeds of different genotypes of cotton and the suppression of *Verticillium* wilt pathogen infection by a synthetic microbial community. BMC Plant Biol 24, 263.
227. Yang, B., Shi, Z., Ma, Y., Wang, L., Cao, L., Luo, J., Wan, Y., Song, R., Yan, Y., Yuan, K., et al. (2022). LAMP assay coupled with CRISPR/Cas12a system for portable detection of African swine fever virus. Transboundary and Emerging Diseases, 69, e216–e223.
228. Yildiz, M., Yildiz, F., & Erten, L. (2020). Research on control of *Verticillium* wilt of olive by grafting susceptible cultivars onto resistant rootstocks and varieties. Journal of Turkish Phytopathology, 49, 19–24.
229. Zhang, D.D., Wang, X.Y., Chen, J.Y., Kong, Z.Q., Gui, Y.J., Li, N.Y., Bao, Y.M., & Dai, X.F. (2016). Identification and characterization of a pathogenicity-related gene VdCYP1 from *Verticillium dahliae*. Scientific Reports, 6, 27979.
230. Zhang, L., Ni, H., Du, X., Wang, S., Ma, X.W., Nürnberger, T., Guo, H.S., & Hua, C. (2017). The *Verticillium*-specific protein VdSCP7 localizes to the plant nucleus and modulates immunity to fungal infections. New Phytologist, 215(1), 368–381.
231. Zhang, S., Li, C., Si, J., Han, Z., & Chen, D. (2022). Action mechanisms of effectors in plant-pathogen interaction. International Journal of Molecular Sciences, 23(12), 6758.
232. Zhao, Y.L., Zhou, T.T., & Guo, H.S. (2016). Hyphopodium-specific VdNoxB/VdPls1-dependent ROS-Ca^{2+} signaling is required for plant infection by *Verticillium dahliae*. PLoS Pathogens, 12, e1005793.
233. Zhou, L., Hu, Q., Johansson, A., & Dixelius, C. (2006). *Verticillium longisporum* and *V. dahliae*: Infection and disease in *Brassica napus*. Plant Pathology, 55(1), 137–144.
234. Zhu, Z., Li, R., Zhang, H., Wang, J., Lu, Y., Zhang, D., & Yang, L. (2022). PAM-free loop-mediated isothermal amplification coupled with CRISPR/Cas12a cleavage (Cas-PfLAMP) for rapid detection of rice pathogens. Biosensors and Bioelectronics, 204, 114076. https://doi.org/10.1016/j.bios.2022.114076