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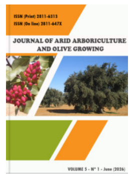

Verticillium Wilt of Olive in Tunisia: An Integrated Review of Pathogen, Disease Dynamics and Sustainable Management Strategies

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Abstract
Verticillium wilt, caused by the soil-borne fungus *Verticillium dahliae*, represents a major threat to olive cultivation (*Olea europaea* L.) in Tunisia, a leading global producer of olive oil. Since its initial detection in 2006 in the south, the disease has spread to key olive-growing areas, causing significant economic losses through tree mortality, yield reduction, and diminished oil quality. Tunisian research has been pivotal in characterizing the local pathogen, revealing significant genetic diversity and the presence of highly virulent defoliating (D) pathotypes (Triki et al., 2011). This review synthesizes recent advances (2006-2024) in understanding the pathogen's biology, genetic diversity, and interaction with the host and environment, with a specific emphasis on the Tunisian context. It provides a critical evaluation of integrated disease management (IDM) strategies developed and tested within the country, from pre-planting diagnostics using advanced molecular tools to the identification of promising local biocontrol agents and the evaluation of resistant cultivars. This review also highlights emerging insights from worldwide studies, including the exploration of the olive holobiont and the potential of RNA interference (RNAi) and phage therapy as next-generation control methods (Tuberosa, 2012). Finally, we outline future research priorities based on local findings, emphasizing the need for climate-resilient solutions and a holistic "holobiont" approach to safeguard the sustainability of Tunisia's vital olive sector.

1. Introduction

Olive cultivation is a cornerstone of Tunisian agriculture and economy. However, this vital industry faces a severe biotic constraint in Verticillium wilt, first reported in the country in 2006 and now widespread (Triki et al., 2011). The resilience of *V. dahliae* stems from its production of melanized microsclerotia, which can persist in soil for decades, and its adaptability to modern agricultural practices (López-Escudero and Mercado-Blanco, 2011). In Tunisia, the shift towards intensive farming, including high-density orchards and irrigation, has been linked to increased disease severity, a phenomenon actively investigated by national researchers. This review aims to consolidate findings from Tunisian and international research, integrating molecular, epidemiological, and agronomic perspectives to present a comprehensive picture of the pathosystem in Tunisia. We also explore cutting-edge concepts being adopted in Tunisia, such as the application of omics technologies for predictive disease modeling (Montes-Osuna and Mercado-Blanco, 2020). The integration of these novel approaches, informed by local data, is crucial for developing next-generation, sustainable management strategies tailored to Tunisian conditions.

2. The Pathogen: *Verticillium dahliae* Biology and Genetic Diversity in Tunisia

2.1. Symptoms and Biological Cycle of *Verticillium dahliae* on Olive Trees

Verticillium wilt manifests through progressive vascular dysfunction in olive trees, beginning with subtle foliar symptoms that intensify over time. Initial signs include wilting and yellowing of leaves, often unilateral, affecting specific branches before spreading to the entire canopy. As the disease advances, infected branches exhibit characteristic brown discoloration of the vascular tissues and progressive desiccation, eventually leading to branch dieback and canopy defoliation. In severe cases, asymmetric canopy mortality occurs, where portions of the tree remain green while others collapse, reflecting the pathogen's localized vascular colonization. Cross-sections of infected stems reveal distinctive brown streaking within the xylem, a hallmark of *V. dahliae* infection (Figure 1).

The biological cycle of *V. dahliae* begins with microsclerotia—small, darkly pigmented resting structures—persisting in soil for extended periods, sometimes remaining viable for over a decade. Upon favorable conditions, microsclerotia germinate and produce hyphae that penetrate olive root systems, establishing infection at the root cortex. The fungus subsequently colonizes the xylem vessels, producing toxins and blocking water transport, which causes the characteristic wilt symptoms. Once established in the plant, *V. dahliae* produces abundant new microsclerotia, particularly in senescent tissues and woody debris. These microsclerotia are released into soil as infected plants decompose, creating a persistent inoculum source that perpetuates the disease cycle in subsequent growing seasons. The long survival of microsclerotia in soil, combined with the pathogen's ability to infect a wide range of plant hosts, makes Verticillium wilt one of the most challenging diseases to manage in olive cultivation.

Figure 1. Symptoms of Verticillium wilt (*V. dahliae*) on olive trees. (top left) wilting and defoliation of an infected tree in the field; (top right) unilateral browning and desiccation of branches characteristic of vascular collapse; (bottom left) brown vascular discoloration within the woody stem indicating pathogen colonization of the xylem; (bottom right) partial tree mortality with asymmetric canopy dieback and retention of green foliage on unaffected branches, illustrating the progressive nature of the disease

2.2. Genetic Diversity and Pathotype Distribution of *V. dahliae* in Tunisian Olive Groves

Verticillium dahliae exhibits significant genetic plasticity, facilitated by asexual reproduction and horizontal gene transfer. In Tunisia, molecular epidemiological studies have been extensive, characterizing the population structure of *V. dahliae* from olive trees (Gharbi et al., 2015). Research has confirmed the dominance of the defoliating (D) and non-defoliating (ND) pathotypes, with molecular analyses using AFLP (Amplified Fragment Length Polymorphism) markers and VCG (Vegetative Compatibility Group) typing revealing significant genetic structuring between regions (Gharbi et al., 2015). For instance, a study of 42 isolates from diseased olive trees showed that most belonged to VCG2A and VCG4B, associated with the ND pathotype, though the presence of the highly virulent D pathotype has also been confirmed (Table 1). This research demonstrated clear genetic differentiation between populations in central versus coastal olive-growing regions, linking genetic diversity to geographic origin.

Table 1. Genetic characteristics of Tunisian *V. dahliae* isolates by PCR-VCG and PCR-pathotype (Gharbi et al., 2015). All isolates were recovered from naturally infected olive trees of the cultivar 'Chemlali'

Geographical origin	Isolates	Pathotype	VCG group
Kairouan	VD3, VD7, VD8	ND	VCG2A/4B
Kasserine	VD4, VD9, VD33, VD34, VD37, VD39, VD40	ND	VCG2A/4B
Mahdia	VD5	ND	VCG2A/4B
Monastir	VD29	D	VCG2A/4B
Monastir	VD26, VD27, VD25, VD30, VD21	ND	VCG2A/4B
Monastir	VD1	ND	$VCG2B^{824}$
Sfax	VD10, VD17, VD22, VD23, VD31, VD35, VD2, VD11, VD18, VD28, VD32, VD36, VD38, VD41, VD42	ND	VCG2A/4B
Sousse	VD12	D	$VCG2B^{334}$
Sidi Bouzid	VD6	ND	$VCG2B^{824}$
Sidi Bouzid	VD13, VD14, VD19, VD20, VD16	ND	VCG2A/4B
Zaghouane	VD15, VD24	ND	VCG2A/4B

Genomic studies internationally have identified lineage-specific regions enriched in effector genes. Recent research has uncovered that *V. dahliae* secretes extracellular vesicles (EVs) containing small RNAs (sRNAs) that can silence host defense genes, a mechanism known as cross-kingdom RNAi (Cai et al., 2018). This represents a novel virulence strategy beyond traditional effectors. The horizontal acquisition of effectors like *Ave1* from plants further complicates breeding for durable resistance (Alexander et al., 2016). Recent phylogenomic studies suggest the potential for hybridization between VCGs, which could rapidly generate new virulence combinations, underscoring the need for continuous genomic surveillance already initiated in Tunisia (Wheeler et al., 2019). Population genomic analyses have further elucidated the molecular basis of the defoliation phenotype, revealing that specific deletions within genomic regions, particularly the G-LSR2 locus containing VdDf genes, are responsible for the highly virulent defoliating characteristics observed in aggressive Tunisian isolates (Zhang et al., 2019). Additionally, epigenetic mechanisms, including DNA methylation patterns have been shown to regulate the differential virulence expression in *V. dahliae* isolates, suggesting that plastic virulence phenotypes may be controlled at multiple regulatory levels (Ramírez-Tejero et al., 2020).

3. Disease Epidemiology and Host-Pathogen-Environment Interactions in the Tunisian Context

3.1. Symptomatology and Spread

Disease dissemination in Tunisia is accelerated by agricultural intensification. High-density planting creates microclimates favoring microsclerotia germination, and intercropping with solanaceous hosts like tomato and potato, a common practice, has been identified as a key factor significantly amplifying soil inoculum and contributing to the disease's spread in young orchards across southern and central Tunisia (Markakis et al., 2016).

3.2. The Role of Abiotic Factors

Irrigation & Climate Change: Excessive irrigation greatly facilitates root infection. In Tunisia, the conversion of olive groves from dryland to irrigated systems has been experimentally linked to disease outbreaks (Montes-Osuna and Mercado-Blanco, 2020). Climate change introduces compounded stresses; warming may accelerate pathogen growth, while drought impairs host defenses (Figure 2). New climate models project that increased frequency of heatwaves and erratic rainfall will exacerbate these effects, potentially expanding the disease's geographical range. Furthermore, elevated CO_2 can alter root exudate profiles, indirectly influencing the rhizosphere microbiome and its suppressive capacity (Chakraborty et al., 2000). Tunisian research has begun to investigate the influence of temperature on both mycelial growth of local isolates and subsequent disease development.

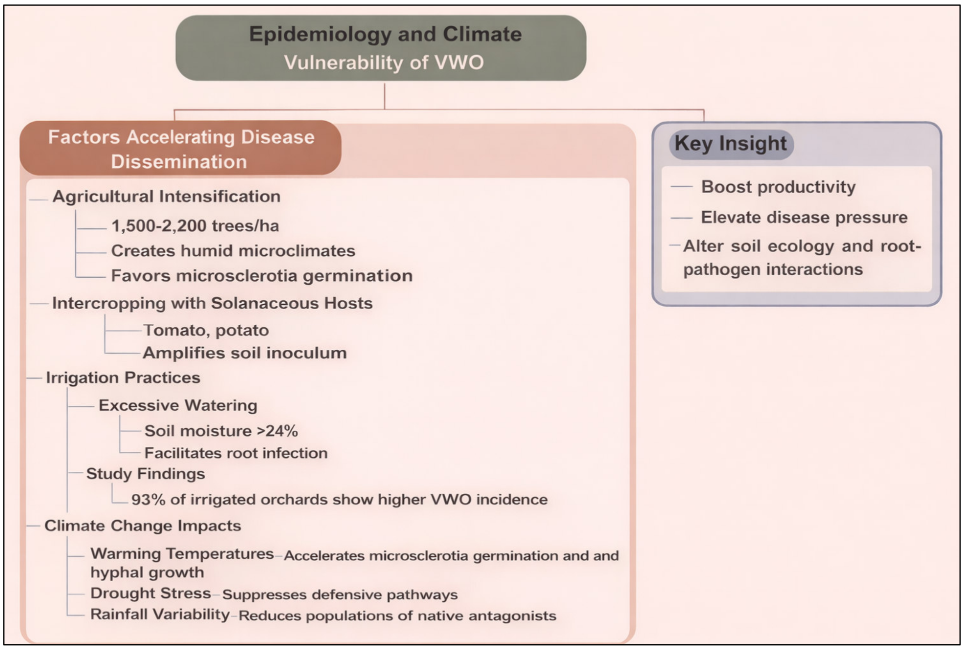

Figure 2. Conceptual diagram illustrating the epidemiology and climate vulnerability of Verticillium Wilt of Olive (VWO)

3.3. Host Adaptation and Virulence

V. dahliae demonstrates a capacity to adapt to the host's cell wall composition and defense mechanisms. Tunisian research has contributed to this field by characterizing the differential expression of genes controlling cell wall-degrading enzymes (CWDEs) in *V. dahliae* isolates from different hosts, suggesting a mechanism for host-specific adaptation (Zhao et al., 2013). Emerging research on effector-triggered susceptibility (ETS) and immunity (ETI) is revealing specific molecular dialogues (Dodds and Rathjen, 2010). For instance, the recognition of the *V. dahliae* effect or VdSCP41 by an olive immune receptor has been characterized, providing a direct target for marker-assisted breeding (Jiménez-Ruiz et al., 2019). Comparative transcriptomic analyses further demonstrate that the pathogen's gene expression pattern is significantly altered depending on the susceptibility level of the host cultivar being infected, with differential upregulation of virulence-related genes in susceptible varieties (Jiménez-Ruiz et al., 2019 ; Gómez-Lama Cabanás et al., 2019). This evolutionary potential underscores the importance of crop rotation to disrupt the accumulation of host-specific virulence factors (Figure 3).

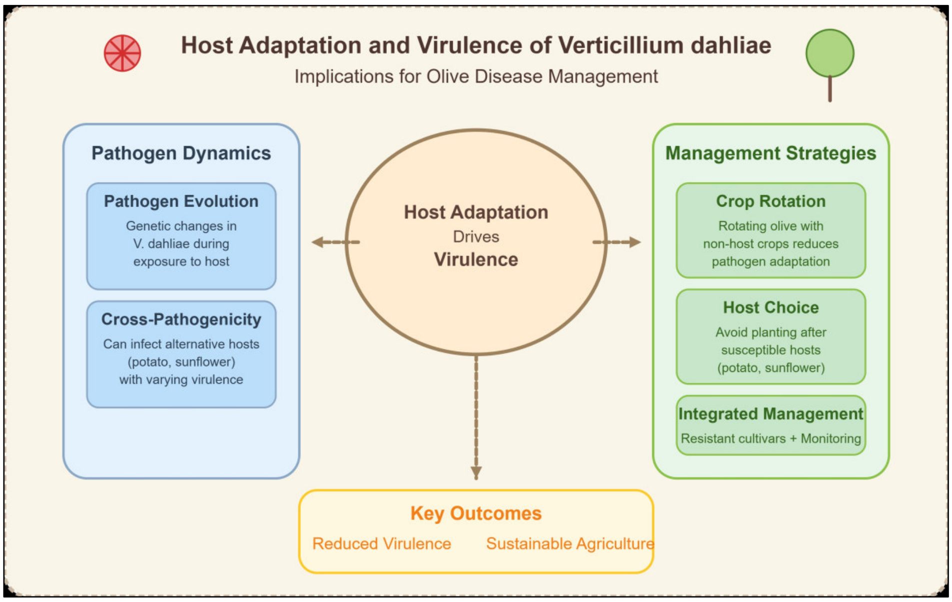

Figure 3. Conceptual framework illustrating how host adaptation drives the virulence of *V. dahliae* and its implications for olive disease management

4. Integrated Management of Verticillium Wilt in Tunisia: A Multi-Tiered Approach

4.1. Pre-Planting Strategies: The First Line of Defense

Effective disease management begins before planting, through comprehensive soil assessment and risk evaluation. Understanding the disease status of soil is fundamental to preventing Verticillium wilt establishment in new plantings (Figure 4).

Soil Diagnosis: Real-time PCR allows for sensitive quantification of microsclerotia. The integration of isothermal amplification techniques (e.g., LAMP) offers potential for rapid, in-field pathogen detection, a tool of great value for Tunisian nurseries and farmers (Fang et al., 2024). Furthermore, metagenomic analysis of soil DNA can now profile the entire soil microbiome, providing a "health index" that predicts disease suppressiveness beyond just pathogen load (Wei et al., 2019).

Accurate pathogen detection is critical for pre-planting risk assessment. Traditional soil plating methods, which rely on culturing microsclerotia, are being replaced by molecular techniques (Gharbi et al., 2016). A newly validated assay detects *V. dahliae* DNA at concentrations as low as 1 microsclerotia/g of soil, offering 98% sensitivity (Gharbi et al., 2016). This method enables rapid, large-scale soil testing, helping farmers avoid infested sites.

Cultural Control: Crop rotation combined with the judicious application of organic and mineral fertilizers helps suppress pathogen populations naturally. Rotating to non-susceptible crops interrupts the disease cycle and allows soil microbiota to gradually suppress *V. dahliae*. Balanced fertilization improves plant vigor and helps plants withstand any residual pathogen pressure.

Soil Disinfection: Chemical and physical treatments offer more rapid pathogen reduction. Solarization harnesses solar energy to elevate soil temperatures and kill microsclerotia, while chemical control methods provide alternative approaches for large-scale land preparation. These methods significantly reduce initial inoculum levels before susceptible crops are planted.

Uninfected Soil Management: When pre-planting soil testing confirms the absence of *V. dahliae*, preventive measures focus on maintaining soil health and using only pathogen-free plant material. The use of healthy, certified planting material is paramount—beginning cultivation with disease-free nursery stock ensures that the soil remains uninfected and the risk of new pathogen introduction is minimized.

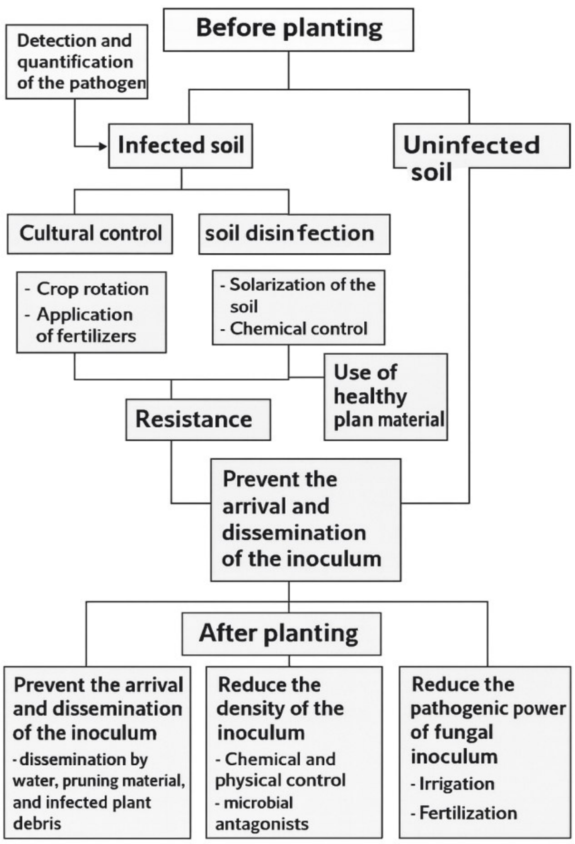

Figure 4. Summary diagram of a management model based on control measures before and after planting

4.2. Cultural and Physical Control Tactics

Tactics like soil solarization, organic amendments, and regulated deficit irrigation remain foundational (Gargouri et al., 2013). Recent advances include the combination of soil solarization with the application of biofumigant crops (e.g., *Brassica juncea*), which releases volatile glucosinolates that synergistically enhance microsclerotia degradation (Tsror et al., 2007). In Tunisia, research into organic amendments has shown promise, with olive oil waste compost and compost teas demonstrating inhibition of *V. dahliae* mycelial growth and reduced disease incidence in olive plants (Gargouri et al., 2013).

4.3. Biological Control: A Sustainable Alternative Developed in Tunisia

Tunisian researchers have been highly productive in identifying promising local biocontrol agents (BCAs). Several effective BCAs have been isolated and characterized, most notably *Bacillus velezensis* OEE1, an endophytic strain isolated from olive roots, producing lipopeptides that inhibit *V. dahliae* growth (Azabou et al., 2020). In field trials, soil application reduced microsclerotia density by 85% and disease severity by 92%. The genome of this strain has been sequenced, and its efficacy has been documented in multiple studies. Other isolates, including indigenous *Pseudomonas* spp. and *Trichoderma* strains from the olive rhizosphere, have also shown potent antagonism against Tunisian *V. dahliae* isolates, with several characterized for their mechanisms of action and root colonization abilities (Figure 5).

Beyond single-agent applications, the concept of constructing synthetic microbial communities tailored to the olive rhizosphere presents a promising frontier for achieving more consistent and resilient biocontrol (Pascale et al., 2019). The initial soil microbiome composition has been shown to significantly influence subsequent disease suppressiveness, suggesting that microbial community structure itself can be a critical determinant of disease outcome (Wei et al., 2019). Additionally, the exploration of bacteriophages (phages) specific to *V. dahliae* is an emerging, highly specific biocontrol strategy (Tuberosa, 2012). Lytic phages capable of lysing microsclerotia have been isolated, showing promise in pot experiments.

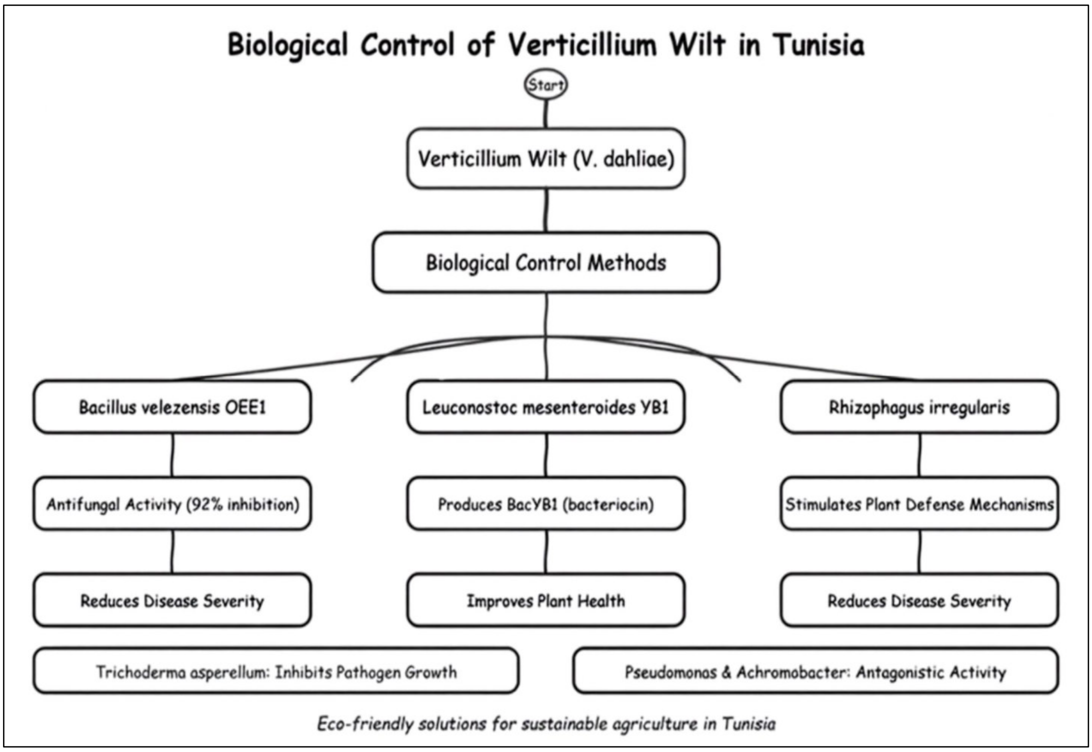

Figure 5. Biological control strategies used to manage Verticillium wilt (*V. dahliae*) in Tunisia

4.4. Host Resistance: Mechanisms and Utilization in Tunisian Cultivars

In Tunisia, researchers have actively evaluated the susceptibility of local and international cultivars (Gharbi et al., 2017). Evaluation of local germplasm revealed a critical vulnerability in the economically dominant 'Chemlali' and 'Chetoui' cultivars, which were classified as extremely susceptible to the pathogen with high disease severity scores. Conversely, the study identified promising sources of resistance in indigenous varieties such as 'Sayali' and 'Meski', positioning them as valuable candidates for breeding programs and sustainable management strategies (Table 2).

Studies have focused on contrasting cultivars like 'Chemlali' and 'Sayali', revealing differential biochemical and physiological defense responses, including variations in antioxidant systems, PR proteins, and hormone signaling pathways (SA, JA, ET) (Gharbi et al., 2017). This work is crucial for identifying resistant or tolerant varieties that can withstand the pathogen's attack and minimize yield losses. Wild olive genotypes represent a particularly valuable source of genetic diversity for resistance, with recent studies identifying several wild accessions showing immunity or high tolerance to defoliating *V. dahliae* isolates through multiple defense mechanisms, including avoidance and enhanced biochemical resistance (Díaz-Rueda et al., 2021). The application of speed breeding and genomic selection can significantly accelerate the development of next-generation, climate-resilient cultivars (López-Moral et al., 2022). Furthermore, the potential of Host-Induced Gene Silencing (HIGS), where olive plants are engineered to produce RNAi molecules that target essential pathogen genes, offers a highly specific and durable resistance mechanism (Song and Thomma, 2018).

Table 2. Classification of tested olive cultivars inoculated with a non-defoliating *V. dahliae* isolate based on the AUDPC, PDP, and FMS parameters (S: Susceptible, MS: Moderately Susceptible, R: Resistant, E : Extremely Susceptible, AUDPC : Area Under Disease Progress Curve, FMS : Final Mean Severity, PDP : Percentage of Dead Plants)

Cultivars	AUDPC mean ± SD	FMS	PDP (%)	Classification
Picholine	51.86 ± 1.95	3	44.40	S
Coratina	32.01 ± 1.47	2	13.00	MS
Manzanille	52.30 ± 2.02	3	33.33	S
Koroneiki	34.66 ± 1.44	1.5	16.66	MS
Frangivento	27.10 ± 0.88	1	00.00	R
Arbequina	53.48 ± 1.56	2.5	41.60	S
Zalmati	67.59 ± 1.37	3	44.40	S
Jarboui	67.65 ± 1.23	3	55.55	S
Oueslati	62.00 ± 1.35	2.5	55.55	S
Rkhami	62.11 ± 1.09	2.5	66.66	S
Meski	27.12 ± 2.11	1	00.00	R
Sayali	26.13 ± 1.89	1	00.00	R
Chetoui	71.26 ± 1.82	3.5	33.33	E
Chemlali	73.51 ± 1.96	4	88.00	E

4.5. Novel and Emerging Control Strategies

Nanotechnology represents a promising frontier in disease management, with engineered nanoparticles being explored as fungicide carriers or direct antimicrobial agents due to their remarkable ability to penetrate xylem tissues and target vascular pathogens with high efficiency. This approach leverages the unique properties of nanoparticles to deliver therapeutic compound directly to the site of infection, potentially reducing the amount of fungicide needed while maximizing efficacy.

Induced Systemic Resistance (ISR) primers offer another innovative strategy for disease prevention, with new chemical primers such as hexanoic acid demonstrating effective protection against Verticillium wilt by pre-activating the plant's defense system (Swaminathan et al., 2022). This preventive approach empowers plants to mount a faster and more robust response to pathogenic threats before infection occurs, offering a more sustainable alternative to traditional chemical treatments.

Water treatment utilizing hydrogen peroxide-based disinfectants, exemplified by OX-VIRIN®, has demonstrated significant promise in experimental settings by reducing the viability of *V. dahliae* in irrigation water and soil, thereby lowering disease incidence without compromising olive tree growth. This method addresses a critical transmission pathway for the pathogen and highlights the importance of integrated approaches that target the pathogen across multiple environments.

Plant extracts derived from sources such as thyme, clove, and garlic have also shown considerable potential in preliminary investigations, with essential oils displaying significant inhibition of mycelial growth in Tunisian *V. dahliae* isolates (Krid et al., 2025). Although research in this area remains limited, these natural compounds may offer environmentally friendly alternatives or complementary strategies to conventional fungicides.

An emerging and particularly innovative approach centers on understanding and modifying the xylem microbiome, as research has revealed that microbiota composition can significantly influence host resistance to *V. dahliae* (Anguita-Maeso et al., 2021). Evidence indicates that deliberate modification of xylem microbiota can alter disease susceptibility, offering a holobiont perspective that opens new pathways for engineering resistant olive germplasm and fundamentally shifting how researchers conceptualize plant-pathogen interactions from individual organisms to integrated biological systems.

5. Conclusion and Future Directions

Verticillium wilt represents a critical challenge to Tunisia's olive cultivation, demanding a comprehensive response grounded in local scientific expertise. An Integrated Disease Management (IDM) approach, informed by robust local research, provides the most effective strategy for addressing this threat. Tunisian scientists have demonstrated substantial progress in characterizing the pathogen, elucidating epidemiological drivers, and developing both biological and cultural control measures. To safeguard the future of olive production in Tunisia, research priorities must encompass several interconnected areas.

Genomic surveillance forms a foundational element of future work, building on existing research to continuously track pathotype expansion and VCG hybridization patterns across the region. Durable resistance development represents another critical frontier, utilizing cutting-edge molecular tools such as CRISPR for targeted gene editing and incorporating genetic material from wild olive species. This approach builds directly on foundational work already conducted through cultivar screening programs and identification of wild germplasm resources suited to Tunisian conditions. Microbiome engineering offers promising avenues for sustainable disease suppression, with researchers developing synthetic communities based on locally-identified effective biocontrol agents, including *Bacillus velezensis* OEE1 and indigenous *Pseudomonas* species that have demonstrated efficacy in the Tunisian context (Cheffi et al., 2019).

Beyond single-organism approaches,holobiont approaches incorporating investigation of tripartite interactions through single-cell RNA sequencing promise deeper understanding of how belowground and xylem microbiota communities contribute to Verticillium wilt tolerance in olive plants. Advanced delivery systems utilizing nanocarriers for biocontrol agents and RNAi-based fungicides represent emerging technologies with significant potential for improved field efficacy and reduced environmental impact.

Successfully translating these scientific advances into practical field-scale applications requires strong, sustained collaboration among researchers, farming communities, and policymakers. Equally important, future research initiatives must prioritize socio-economic investigations to identify adoption barriers and develop extension services capable of guiding farmers through the transition to these sophisticated IDM strategies, ultimately ensuring the long-term resilience of Tunisia's economically vital olive sector.

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