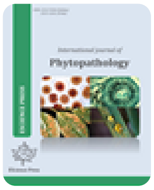
OPEN ACCESS Int. J. Phytopathol. 14 (03) 2025. 233-245 DOI: 10.33687/phytopath.014.03.5787

Check for updates



Available Online at EScience Press

International Journal of Phytopathology

ISSN: 2312-9344 (Online), 2313-1241 (Print)

https://esciencepress.net/journals/phytopath

APPLE SCAB IN MOROCCO: RESISTANCE TO CHEMICAL FUNGICIDES AND PERSPECTIVES OF CONTROL: A REVIEW

[a]Hicham Zitoun*, [a]Adil Laaziz, [b]Rajae Belkhou, [a,c]Abdelouahed Hajjaji

[a] *Laboratory of Biotechnology ,Environment, Agri-Food and Health (LBEAS), Faculty of Sciences Dhar El Mahraz, Sidi Mohamed Ben Abdellah University, Fez, Morocco.*

[b] *Biotechnology, Environment, Agro-Food and Health Laboratory (LBEAS), Higher School of Technology, Sidi Mohamed Ben Abdellah University, Route d'Imouzzer, 30000 Fez, Morocco.*

[c] *Biotechnology and Sustainable Development of Natural Resources Unit, Polydisciplinary Faculty of Béni Mellal, Sultan Moulay Slimane University, Beni Mellal, Morocco.*

ARTICLE INFO

Article History
Received: July 15, 2025
Revised: December 13, 2025
Accepted: December 30, 2025

Keywords
Apple scab
Biocontrol
Fungicides
Morocco
Resistance mechanisms

ABSTRACT

Apple scab, caused by the ascomycete fungus *Venturia inaequalis* (Cooke) G. Winter (1875), is one of the most devastating diseases of apple (*Malus × domestica*) worldwide, including in Morocco, where apple cultivation plays an important role in the arboriculture sector. This disease can spread widely under favorable environmental conditions and in the absence of effective preventive and curative measures, leading to severe economic losses due to fruit damage, reduced yields, and increased costs associated with fungicide applications. Moreover, the intensive and repeated use of chemical fungicides has contributed to the emergence of *V. inaequalis* strains that are resistant to several active substances. In Morocco, thirteen active fungicidal compounds are currently used to control this disease. This review presents all the active ingredients authorized for use in Morocco against apple scab and evaluates their efficacy. It also discusses the development of resistance to systemic fungicides by *Venturia inaequalis* at both the national and global levels and assesses their future prospects. Finally, this article highlights alternative approaches to chemical control, including biological and genetic interventions in the management of apple scab, with an emphasis on the potential of these strategies to guide and support future research efforts.

Corresponding Author: Hicham Zitoun
Email: hicham.zitoun@usmba.ac.ma

INTRODUCTION

Apple (*Malus domestica*) is an economically important Rosaceae that occupies approximately a quarter of the cultivated area dedicated to rosaceous fruit in Morocco. Nevertheless, its production is severely affected by scab disease caused by the fungus *Venturia inaequalis*, which is a major disease that affects apple orchards. It can lead to significant yield losses while reducing fruit quality and tree growth. In Moroccan orchards, popular cultivars such as Golden Delicious, Starking Delicious and Gala are used (Lahlali *et al*., 2019). Owing to the polycyclic nature of *Venturia inaequalis* and the susceptibility of most commercial apple cultivars to this disease (Rekanović *et al*., 2012; Demiwal *et al*., 2024), the high genetic variability, induced by the mixing and random distribution of genes (Padder *et al*., 2021), makes the control of this disease particularly complex. Indeed, in Morocco, the management of apple scab involves multiple fungicide applications per season. Various fungicides, including difenoconazole, trifloxystrobin, and thiophanate-methyl, have been employed.

Among these fungicides, trifloxystrobin has shown high efficacy in curative applications (96.38%), outperforming other fungicides such as thiophanate-methyl and difenoconazole (Lahlali *et al*., 2019). However, another study in the same region indicated that trifloxystrobin had higher EC50 values than difenoconazole did, suggesting some level of resistance (Gouit, Chiadmi, *et al*., 2025). However, intensive use of fungicides can lead to the emergence of resistant strains (Stewart *et al*., 2023). Thus, fungicides can in turn become ineffective and even useless, causing serious problems for farmers, manufacturers, retailers and the community in general (Carmona *et al*., 2018). Several studies have highlighted the existence of different physiological races of *Venturia inaequalis* that can overcome the major resistance genes of apple trees (Masny, 2017). These breeds have high genetic diversity and significant gene flow without a marked geographical structure. This pathogenic variability has been observed in various regions, such as Kashmir (Padder *et al*., 2013), Poland (Masny, 2017), central Russia (Pikunova & Sedov, 2019), and Latvia (Sokolova & Moroèko-Bièevska, 2022), highlighting the need for regular virulence monitoring to adapt resistance management strategies. Despite the economic importance of apple cultivation in these regions, few detailed studies have been conducted on the local epidemiology of apple scab and on integrated management strategies adapted to Moroccan agroclimatic conditions. The aim of this review is to present information on all the active ingredients of systemic fungicides used in Morocco against apple scab. This study will also provide the current status of resistance development in *V. inaequalis* to various chemical classes of systemic fungicides, both globally and in Morocco, and assess the prospects for their future use.

DATA COLLECTION

The present literature review is based on a systematic documentary approach, in accordance with the principles of systematic reviews. The objective was to collect and analyze available data on fungicides registered against *Venturia inaequalis* in Morocco, the resistance of this pathogen to systemic fungicides, and alternatives to chemical control. The first phase consisted of collecting official data on fungicides registered for the control of *Venturia inaequalis* in Morocco in 2025. This information was obtained from the main regulatory source, namely the official website of the National Office of Food Safety (ONSSA). The second phase involved a bibliographic review aimed at gathering scientific information on the resistance of *Venturia inaequalis* to systemic fungicides used in Morocco, as well as on possible alternatives to conventional chemical control. The main sources consulted included recognized scientific databases and journals such as Scopus, ScienceDirect, Web of Science, PubMed, Google Scholar, FRAC, as well as other reliable publications. The literature search was conducted using relevant keywords, including: *Venturia inaequalis*, apple scab, Morocco, chemical control, resistance to chemical fungicides, cultural control, biological control, and resistant varieties. Regarding inclusion criteria, original research articles, systematic reviews, and meta-analyses published between 2000 and 2025 were selected. The selected studies had to specifically address resistance of *Venturia inaequalis* to fungicides or explore alternative control methods, with particular emphasis on studies relevant to the agricultural and climatic context of Morocco.

MECHANISM OF INFECTION CAUSED BY *VENTURIA INAEQUALIS*

The conidia/ascospores of *V. inaequalis* adhere to wet hydrophobic surfaces immediately after contact, even before germination begins. This adhesion is facilitated by a droplet of adhesive material called spore tip glue at the spore apex, which contains proteins and carbohydrates (Schumacher *et al*., 2008). Once adhered, the spores germinate by producing germ tubes, which are generally from the apical end of conidia or any of the two cells of the ascospore (Jha *et al*., 2009). The germ tubes differentiate into appressoria, which secrete enzymes such as cutinases that degrade the plant cuticle, facilitating penetration of the leaf or fruit surface (Kolattukudy, 1985; Köller, 1991). Additionally, at their base, these appressoria form a melanized appressorial ring structure (MARS), which acts as a sealing ring and is essential for breaching the cuticle (Kucheryava *et al*., 2008). Moreover, MARS contributes to the stability and function of the fungal cell wall, enhancing pathogen tolerance to environmental stressors and fungicides (Steiner & Oerke, 2023). After penetration, *V. inaequalis* colonizes the subcuticular space of the host, forming specialized structures called runner hyphae and stromata. These structures appear to play a role in the acquisition of nutrients and the release of effectors (virulence factors), but they also give rise to conidia that propagate through the infection cycle (Rocafort *et al*., 2023).

CHEMICAL CONTROL OF APPLE SCAB IN MOROCCO

In Morocco, the main commercial apple cultivars are susceptible to scab, and fungicides are frequently used to protect them (Lahlali *et al*., 2019). In addition, fruit growers have at their disposal 13 active ingredients registered by the National Office for Food Safety as fungicides in 2025, with different modes of action and application periods (Table 1). These fungicides include multisite protective fungicides, which affect primarily spore germination, such as captan and dithianon (Quinone class), copper and sulfur (inorganic mineral class), and systemic fungicides, which are absorbed by the plant and affect fungal growth; these fungicides include succinate dehydrogenase inhibitors (SDHIs), demethylation inhibitors (DMIs), guanidines (diodines), external quinone inhibitors (QoIs), anilopyrimidines (APs) and quinones (anthraquinones) (ONSSA, 2025).

Table 1. Chemical control of apple scab in Morocco: mechanisms of action and risk of resistance.

Class Chemical/ Active ingredient	Target site	Resistance Mechanisms	*Risk of resistance
Inorganic minerals			
Copper (different salts)	Multisite inhibitors acting against thiol groups in proteins and peptides (FRAC, 2025).	Unknown	Low
Sulphur			
Phthalimides			
Captan	Multisite contact activity	Unknown	Low Risk
Anilinopyrimidines (APs)			
Cyprodinil	inhibition of methionine biosynthesis (Gisi *et al*, 2019)	Activation of ATP-binding Cassette (ABC) transporters or the modification of the target sites (Leroux *et al*., 2002).	Medium Risk
Pyrimethanil			
Demethylation inhibitors (DMIs)			
Difenoconazole	Inhibit enzyme sterol 14α-demethylase (cyp51). (Leroux & Walker, 2011)	Multiple point mutations in the Cyp51 gene, Notable mutations include Y133F and M141T(Hoffmeister *et al*., 2021).	Medium Risk
Succinate- dehydrogenase inhibitors (SDHI)			
Boscalid	Block the ubiquinone-binding sites in the mitochondrial complex II, disrupting fungal respiration (Avenot & Michailides, 2010)	Mutations in the SDH subunits B, C, or D, such as B-T258I, C-N85S, and C-H151R (Hoffmeister *et al*., 2024; Nasonov *et al*., 2024)	Medium to High Risk
Fluxapyroxad			
Quinone outside Inhibitors (QoI)			
Pyraclostrobin	Inhibit the cytochrome bc_1 complex of mitochondrial respiration (Torriani *et al*., 2009)	Mutations in the cytochrome b (cyt b) gene, specifically the G143A mutation (De Artur Teixeira *et al*., 2015)	High Risk
Trifloxystrobin			
Kresoxim-methyl			
Dithianon	Multisite contact activity	without any signs of resistance developing (FRAC, 2025)	Low Risk
Guanidines			
dodine	Cell membrane disruption (Herce *et al*, 2014)	The exact mechanism of resistance to the guanidine class is not yet understood (FRAC, 2025)	Low to Medium Risk

* FRAC resistance risk classification (FRAC, 2025).

In Morocco, apple growers commonly use multisite fungicides instead of systemic fungicides (Moinina *et al*., 2018), likely because of their lower cost, wider availability, and broad-spectrum mode of action. Consequently, multisite protective fungicides such as captan, dithianon, copper, and wettable sulphur, as well as succinate dehydrogenase inhibitors (SDHIs), are primarily used as preventive treatments.

These compounds act as broad-spectrum enzyme inhibitors that mainly target spore germination and are associated with a low risk of resistance development (Brent & Hollomon, 2007; Chatzidimopoulos *et al*., 2022). Although these fungicides offer demonstrable benefits for disease and fungicide resistance management, the sustainability movement in agriculture aims to reduce reliance on such fungicides owing to their broader environmental impacts (Ayer *et al*., 2021).

However, the main disadvantage of multisite fungicides is that they easily wash off the surfaces of leaves and fruits via rain (Xu *et al*., 2008), which is why they are generally applied either early in the season, when there are only a few leaves on the trees, or in anticipation of rain-free periods (Chatzidimopoulos *et al*., 2020). Furthermore, concerns about the phytotoxicity of natural copper- or sulfur-based chemicals limit their use in scab control strategies (Guérin & Cam, 2004; Padder *et al*., 2021).

While systemic fungicides are mainly used after periods of rain, when protectant fungicides become insufficient to effectively protect the crop and when the risk of primary infection is high, they can also be used to protect initial plant growth in spring (Jobin & Carisse, 2007; Chatzidimopoulos *et al*., 2020). These fungicides are absorbed by the plant, move differently through its tissues, and then target specific sites at the level of the pathogenic fungus (Bartlett *et al*., 2002; Chapman *et al*., 2011). However, the repeated use of these fungicides can promote the emergence of resistant strains of *V. inaequalis*, thus reducing their long-term effectiveness. These risks are due to the systematic use of fungicides with active substances having a similar mechanism of action, which leads to rapid selection of resistant forms of the fungus (Villani & Cox, 2014; Nasonov *et al*., 2022).

In several apple-producing countries, *Venturia inaequalis* has rapidly developed resistance to almost all systemic fungicides, including dodine (Köller *et al*., 1999; Carbone *et al*., 2021), benzimidazoles (benomyl) (Quello *et al*., 2010), thiophanate-methyl (Polat & Bayraktar, 2021), myclobutanil (Nabi *et al*., 2023), sterol demethylation inhibitors (DMIs) such as difenoconazole and myclobutanil (Köller & Wilcox, 2001; Hoffmeister *et al*., 2021), kresoxim-methyl and trifloxystrobin (Lesniak *et al*., 2011), and carbendazim (Nasonov *et al*., 2022). However, trifloxystrobin has been reported to be effective against *V. inaequalis* in the Saïs region of Morocco (Lahlali *et al*., 2019). In contrast, a more recent study conducted in the Fès–Meknès region reported higher EC_{50} values for trifloxystrobin than for difenoconazole, indicating reduced sensitivity and suggesting the emergence of resistance (Gouit *et al*., 2025). The development of resistance to single-site fungicides (systemic fungicides) is explained by their narrowly selective mode of action, unlike multisite fungicides. Indeed, a single genetic mutation can be enough to inhibit the efficacy of a fungicide against *Venturia inaequalis*. The probability of such mutations occurring is relatively high in this fungus, which favors the rapid emergence of resistant strains (Nasonov *et al*., 2022).

RELEVANCE AND IMPLICATIONS FOR MOROCCAN RESISTANCE MANAGEMENT

The ability of *Venturia inaequalis* to rapidly adapt to fungicide pressure has led to the emergence of multifungicide resistance, complicating management and threatening sustainable apple production. Globally, resistance has been reported across all major fungicide classes used for scab control, including benzimidazoles, QoIs, DMIs, and anilinopyrimidines (APs), with increasing reports of isolates resistant to multiple classes simultaneously. This trend is mirrored in Morocco, where an average of 20 treatments per season is common, generating a complex resistance landscape that reflects global patterns while maintaining local specificity (Moinina *et al*., 2018; Nasonov *et al*., 2022; Gouit *et al*., 2025).

Table 2 summarizes the resistance status of *V. inaequalis* across major chemical classes, comparing Moroccan apple-growing regions with global patterns.

Phthalimides

Since the 1930s, organic compounds such as phthalimides have become important tools for disease control (Hermann & Stenzel, 2019; Megadi *et al*., 2010). Phthalimides are primarily used as protective fungicides and including them in spray programs helps reduce selection pressure on single-site fungicides. For example, the integration of multisite fungicides such as mancozeb and captan has been shown to be effective in managing resistance and maintaining disease control (Ayer *et al*., 2021).

Table 2. Comparison of Fungicide Classes, Active Ingredients, and Resistance Status of *Venturia inaequalis* in Morocco and worldwide.

Fungicide Class	Active Ingredient(s)	Status Worldwide	Status in Morocco	References
Anilinopyrimidines	Cyprodinil, Pyrimethanil	Moderate resistance to cyprodinil reported in Greece	No resistance data currently available	Köller *et al*., 2005; Larsen *et al*., 2013; Chatzidimopoulos *et al*., 2022
Demethylation Inhibitors (DMIs)	Difenoconazole	Resistance reported in some regions such as Russia and China	Preventive applications reduce disease severity up to 85.8%; curative efficacy may decline to 24.6%	Lahlali *et al*., 2019; Li *et al*., 2021; Nasonov *et al*., 2022; Gouit *et al*., 2025
Quinone Outside Inhibitors (QoIs)	Pyraclostrobin	Low efficacy in resistant populations; improved performance when applied in mixtures	No documented resistance to QoIs in Morocco	Lesniak *et al*., 2011
	Trifloxystrobin	Up to 92% of isolates resistant in some areas of Greece; effective in Saïs region, reduced sensitivity in Fès–Meknès	Reduced sensitivity reported in Fez-Meknes; effective in Saïs	Gouit *et al*., 2025
	Kresoxim-methy	Up to 92–97% control in Greece and Turkey	No resistance data currently available	Frederick *et al*., 2014; Turan *et al*., 2016; Matsuzaki *et al*., 2025
	Dithianon	High field efficacy: mixtures provide 85–97% disease control in Serbia; ~6% of isolates show reduced sensitivity in Greece	No resistance data currently available	Rekanović *et al*., 2012; Chatzidimopoulos *et al*., 2022
Succinate Dehydrogenase Inhibitors (SDHIs)	Boscalid	Complete resistance to boscalid reported in Turkey; low shift in sensitivity observed in other populations; resistance remains rare and generally unstable globally	No resistance data currently available	Özkılınç *et al*., 2025; Hoffmeister *et al*., 2021; Weber *et al*., 2025
Guanidines	Dodine	Localized but persistent resistance reported in Uruguay, Poland, northeastern USA, Canada, and New Zealand	No resistance data currently available	Weber *et al*., 2025; FRAC, 2022; Carbone *et al*., 2021

Phthalimides have a low risk of resistance development because they target multiple sites within fungal cells, making it difficult for the pathogen to develop resistance (Shaik *et al*., 2024). In Morocco, commonly used multisite and protectant fungicides include Captan (a phthalimide). Captan is a broad-spectrum protectant that has been widely applied since 1951 to control various fungal diseases, including apple scab (*Venturia inaequalis*). This fungicide remains integral to apple scab management programs in Morocco due to its effectiveness and relatively low risk of resistance (Song, 2014; Adeli *et al*., 2023), but its use should be carefully integrated with site-specific fungicides to optimize efficacy and delay resistance evolution.

Anilinopyrimidines (APs)

Globally, resistance to anilinopyrimidines has emerged in several European regions, particularly in Greece, where moderate resistance levels to cyprodinil are now widespread (Chatzidimopoulos *et al*., 2022). Resistance to AP fungicides in *V. inaequalis* is complex and involves multiple genes. Several studies have reported that reduced sensitivity to APs, such as pyrimethanil and cyprodinil, is correlated with resistance to demethylation inhibitors (DMIs). These findings suggest that some genes conferring DMI resistance also reduce sensitivity to APs (Köller *et al*., 2005). Interestingly, resistance to anilinopyrimidines (cyprodinil, pyrimethanil) was reported to have disappeared approximately 15 years after its widespread occurrence in northern Germany, suggesting that sensitivity can be restored over time if these fungicides are not used (Weber *et al*., 2025).

In Morocco, anilinopyrimidines are used exclusively as monocomponent formulations containing either cyprodinil or pyrimethanil for the control of apple scab. Cyprodinil is particularly valuable for its curative activity against *V. inaequalis*, making it a useful option during the early stages of infection (Hirayama, 2022). However, field trials have shown that although cyprodinil can effectively control apple scab, its performance is sometimes inferior to that of nonspecific protectants such as mancozeb or captan. This variability may be attributed to environmental conditions, application timing, or the presence of *V. inaequalis* populations displaying reduced sensitivity (Köller *et al*., 2005). Pyrimethanil has also demonstrated high efficacy in other countries; for example, in Serbia, control rates of apple scab ranged from 85.6% to 97.2% when it was applied alone or in combination with other fungicides (Rekanović *et al*., 2012).

Demethylase Inhibitors (DMIs)

DMIs (demethylase inhibitors) are a major group of systemic fungicides used extensively in agriculture and medicine due to their broad-spectrum antifungal activity (Hassold & Backhaus, 2009). However, the continuous application of DMIs has led to the emergence of DMI-resistant populations of the fungal pathogen *Venturia inaequalis*. This resistance has been documented in various regions, including New York, New England, and Turkey (Frederick *et al*, 2015; Villani *et al*., 2015; Polat and Bayraktar, 2021). Resistance to DMI fungicides in various pathogens, including *Venturia inaequalis*, is often associated with mutations in the CYP51 gene, which encodes the target enzyme 14α-demethylase for these fungicides (Hoffmeister *et al*., 2021). North African apple orchards, especially in Morocco, have reported declining DMI efficacy, raising concerns about underlying resistance mechanisms and the need for targeted surveillance (Gouit *et al*., 2025).

Difenoconazole is one of the most important triazole active ingredients (DMI family) approved in Morocco for the control of apple scab (ONSSA, 2025). Recent studies conducted in the Fès–Meknès region of Morocco have documented a shift in sensitivity to difenoconazole, with EC_{50} values ranging from 0.05 to 1.46 µg/mL, which are often close to the practical resistance threshold established by the FRAC (Gouit *et al*., 2025). In the Saïs region, under the agricultural conditions evaluated, difenoconazole displayed reduced curative efficacy, with effectiveness values as low as 24.62% (Lahlali *et al*., 2019). This difference highlights the variable sensitivity of *Venturia inaequalis* isolates and emphasizes the importance of prioritizing preventive interventions to optimize product efficacy. In other regions, such as Russia and China, resistance to difenoconazole has been reported (Li *et al*., 2021; Nasonov *et al*., 2022).

Quinone Outside Inhibitors (QoIs)

The most common mechanism of fungicide resistance in *Venturia inaequalis* is mutation of the mitochondrial cytochrome b (Cytb) protein. Specifically, the G143A point mutation in the Cytb gene is well known to confer resistance to quinone outside inhibitor (QoI) fungicides (Fontaine *et al*., 2009; Viljanen-Rollinson *et al*., 2013). This mutation has been widely studied and detected in various regions, including France, New Zealand, Brazil, and the United States (Fontaine *et al*., 2009; Viljanen-Rollinson *et al*., 2013; Frederick *et al*., 2014; De Artur Teixeira *et al*., 2015).

In Morocco, three active ingredients from this fungicide group are currently registered for the control of apple scab. They include single-component formulations containing trifloxystrobin or kresoxim-methyl, as well as mixed formulations combining pyraclostrobin with boscalid and kresoxim-methyl with difenoconazole (ONSSA, 2025). High EC_{50} values for trifloxystrobin (2.94–29.62 µg/mL) have been reported in the Fez-Meknes region, indicating widespread resistance among *Venturia inaequalis* isolates (Gouit, *et al*., 2025). In contrast, in vivo tests conducted in the Saïs plain at a concentration of 10 µg/mL showed high efficacy of trifloxystrobin (96.38%) in controlling *V. inaequalis*, further supporting its effectiveness in this region (Lahlali *et al*., 2019). In contrast, studies from other apple-growing regions worldwide have demonstrated substantial regional variation in fungicide resistance levels. For example, in Greece, monitoring efforts revealed that up to 92% of isolates in certain areas exhibited strong resistance to trifloxystrobin, illustrating the global challenge of QoI fungicide resistance (Chatzidimopoulos *et al*., 2022). However, recent studies in China reported EC_{50} values for difenoconazole ranging from 0.143 to 6.735 µg/mL among 90 isolates, with 19 isolates exhibiting resistance (Li *et al*., 2021). Although direct data on kresoxim-methyl resistance in Moroccan populations of *Venturia inaequalis* are currently lacking, high levels of resistance have been reported elsewhere; for example, up to 97 % of isolates examined in Turkey were found to be resistant. (Polat & Bayraktar, 2021). In contrast, in India, kresoxim-methyl applied at 0.05% was highly effective, providing 97.25% control of leaves and 98.48% control of fruits (Bhat *et al*., 2021). This contrast highlights the significant geographical variability in fungicide performance and resistance development.

Dithianon remains a key tool for apple scab management in Morocco and is frequently used in combination with other fungicides to increase its efficacy. For example, mixtures such as pyraclostrobin + dithianon and kresoxim-methyl + dithianon have demonstrated high control levels, with disease reduction rates ranging from 85.6% to 97.2% in field trials conducted in Serbia (Rekanović *et al*., 2012). However, isolated cases of reduced sensitivity have been reported. For example, in Greece, 6% of isolates were less sensitive to dithianon (Chatzidimopoulos *et al*., 2022).

Succinate Dehydrogenase Inhibitors (SDHIs)

Resistance to SDHIs in *Venturia inaequalis* primarily arises from mutations in the SDH subunits B, C, or D. Specific mutations, including B-T258I, C-N85S, and C-H151R, have been identified and are known to alter the fungicide target site, thereby reducing efficacy. However, these mutations do not significantly increase in frequency over time (Hoffmeister *et al*., 2024).

In Morocco, two active ingredients from the succinate dehydrogenase inhibitor (SDHI) class are registered for the control of apple scab. They are typically formulated in combination products: boscalid coformulated with pyraclostrobin and fluxapyroxad coformulated with difenoconazole (ONSSA, 2025). This combination works by combining two different biochemical modes of action, reducing the risk of resistance development (Hauke *et al*., 2004). The combination of boscalid and pyraclostrobin has been effective in managing apple scab, although its efficacy is slightly lower than that of other fungicide mixtures in Serbia (Rekanović *et al*., 2012). However, resistance to pyraclostrobin can develop, as observed with other fungicides do, necessitating careful management and rotation with other fungicides to prevent resistance buildup (Rekanović *et al*., 2012). Studies have shown that the use of boscalid combined with pyraclostrobin at reduced doses, when integrated with resistance-inducing agents, can achieve a level of pathogen control comparable to that of full-dose applications (Percival & Graham, 2021). However, a study conducted in Turkey revealed that the examined *Venturia inaequalis* population had developed complete resistance to boscalid (Özkılınç *et al*., 2025). Long-term field studies have shown that repeated applications of fluxapyroxad can lead to a reduction in the sensitivity of *V. inaequalis* to fungicides. Over four years, apple orchards treated with fluxapyroxad tended toward decreased sensitivity, particularly with low-dose applications, suggesting that higher doses may be more effective in managing resistance (Ayer *et al*., 2020). Another study revealed that fluxapyroxad had greater activity against *V. inaequalis* than did boscalid, with a relatively small shift in sensitivity observed in the studied populations (Nasonov *et al*., 2024).

Guanidines

Dodine, the only active ingredient from the guanidine family introduced in 1960, was one of the first scab fungicides with pronounced postinfection activities, in addition to good protectant activity. However, in the early 1970s, the first resistance to *Venturia inaequalis* was observed in New York orchards after more than a decade of exclusive use (Köller *et al*, 2009). Although specific data on dodine resistance in Moroccan *V. inaequalis* populations are not available, studies from other regions indicate significant resistance issues. For example, in Uruguay, dodine resistance was observed in all assessed *V. inaequalis* populations, with highly resistant isolates (mycelial relative growth ≥ 95%) present in all orchards (Carbone *et al*., 2021). Similarly, in Poland, high resistance to dodine was found in 7 out of 64 monitored orchards, with resistance levels above 50% (Beata *et al*., 2008). Similar resistance then appeared in other northeastern U.S. states, Canada, Poland, and New Zealand (FRAC, 2022). However, the exact mechanisms of guanidine resistance in *V. inaequalis* are not known (FRAC, 2025).

Management of Fungicide Resistance

The control of fungal plant pathogens has increasingly been characterized by resistance to many fungicides, which is now one of the most critical challenges in managing *Venturia inaequalis*. The development of fungicide resistance in plant pathogens is a complex process influenced by the pathogen's biology and intrinsic variability, the fungicide's mode of action, and the application strategies employed (Carmona *et al*., 2018). Several strategies have been proposed to prevent, or at least delay, resistance problems. These include alternating between different fungicides on the basis of their mode of action; reducing the number of treatments per season by adjusting the sowing date, dosage, and number of fungicide applications; using fungicide mixtures; alternating between different fungicides; and alternative methods, such as the use of biological control agents and the combination of several treatments (Jørgensen *et al*., 2017; Bhaik *et al*., 2022). These are promising alternatives for reducing the economic damage caused by these fungal diseases.

Cultural and Alternative Approaches for Scab Control in Morocco

Apple scab, caused by *Venturia inaequalis*, is the most significant disease affecting apple production in Morocco, particularly in regions such as Fez-Meknes and Saïs. This disease leads to substantial yield losses and quality degradation, prompting growers to rely heavily on chemical fungicides, most notably difenoconazole, trifloxystrobin, and thiophanate-methyl, for control. This reliance frequently leads to up to 20 fungicide applications per growing season, rendering fungicide inputs a major contributor to total production costs and raising significant concerns regarding environmental contamination and potential risks to human health associated with repeated chemical exposure (Moinina *et al*., 2018; Gouit *et al*., 2025). In response, Morocco has progressively reformed its regulatory framework, withdrawn hazardous pesticides, promoted integrated pest management, and encouraged the adoption of biological and cultural alternatives. These reforms are aligned with broader sustainability goals, such as those articulated in the Green Morocco Plan, which seeks to modernize and green the agricultural sector (Bahouq *et al*., 2021; Gouit *et al*., 2025).

Surveys conducted among apple growers in the main agricultural production areas show that cultural control practices are systematically integrated but often in combination with chemical treatments rather than standalone strategies. In the Fez-Meknes region, all surveyed producers apply phytosanitary treatments during the growing season, and approximately 60% use visual monitoring of pests before intervention; however, most tend to systematically revert to the use of chemical products even after cultural observations (Moinina *et al*., 2018).

In addition to cultural control, several biological and ecological approaches are currently being evaluated or implemented on an experimental scale in Morocco for the management of apple scab. The use of antagonistic microorganisms, particularly Trichoderma spp., has shown promising potential for reducing *Venturia inaequalis* inoculum, with mycelial growth inhibition rates ranging from 50% to 81% in vitro. However, their efficacy generally remains lower than that of synthetic fungicides such as difenoconazole (Gouit *et al*., 2024), which limits their adoption in commercial practice without the use of chemical additives. Furthermore, the use of antagonistic bacteria (*Bacillus* spp.) has demonstrated even greater efficacy, with inhibition reaching up to 92% in vitro, suggesting a promising avenue for future biofungicides (Gouit, *et al*., 2025). However, this approach remains largely exploratory and has not yet been fully integrated into orchard scab management programs.

Although the integration of certain cultural practices and plant health monitoring systems is relatively common in production systems, the adoption of alternative approaches, particularly organic farming and biological control methods, remains marginal. This low adoption is attributed mainly to a lack of technical training, as well as economic uncertainty related to market opportunities for products from production systems that are less dependent on chemical inputs (Lahlali *et al*., 2021). Furthermore, agricultural extension services remain underdeveloped, which limits the dissemination and adoption of integrated pest management principles. In this context, training and capacity building for farmers appear essential for promoting the effective adoption of integrated and sustainable disease management strategies (Karkach *et al*., 2025).

CONCLUSIONS

Apple scab remains one of the most significant diseases affecting apple production. Although conventional fungicide treatments offer short-term effectiveness, their long-term use carries risks, including the emergence of resistance to this pathogen. In Morocco, various classes of systemic and multisite fungicides are used to treat apple scab. However, resistance to several of these fungicide classes has been reported in most apple-growing regions worldwide. The risk of fungicide resistance varies geographically and depends on the specific chemical class used. Notably, resistance to anilinopyrimidines, demethylation inhibitors (DMIs), and succinate dehydrogenase inhibitors (SDHIs) has been documented in field populations of *Venturia inaequalis*. The risk of resistance development is generally considered low to moderate for guanidines and low for phthalimides. Early diagnosis can maximize the effectiveness of fungicide applications by alternating modes of action, reducing treatment frequency, and minimizing the risk of resistance development. Furthermore, the integration of biocontrol strategies and resistant cultivars can help limit apple scab development and rationalize the use of phytosanitary treatments.

REFERENCES

Adeli, I., H. MohammadSadeghi and B. Bameri. 2023. Captan, In: Encyclopedia of toxicology, 4th ed. Elsevier. https://doi.org/10.1016/B978-0-12-824315-2.00331-6

Avenot, H. F. and T. J. Michailides. 2010. Progress in understanding molecular mechanisms and evolution of resistance to succinate dehydrogenase inhibiting (SDHI) fungicides in phytopathogenic fungi. Crop Protection, 29: 643–651. https://doi.org/10.1016/j.cropro.2010.02.019

Ayer, K. M., D. A. Strickland, M. Choi and K. D. Cox. 2021. Optimizing the integration of a biopesticide (*Bacillus subtilis* QST 713) with a single-site fungicide (benzovindiflupyr) to reduce reliance on synthetic multisite fungicides (captan and mancozeb) for management of apple scab. Plant Disease, 105: 3545–3553. https://doi.org/10.1094/PDIS-02-21-0426-RE

Ayer, K. M., M. W. Choi, S. T. Smart, K. D. Cox and A. E. Moffett. 2020. The effects of succinate dehydrogenase inhibitor fungicide dose and mixture on development of resistance in *Venturia inaequalis*. Applied and Environmental Microbiology, 86. https://doi.org/10.1128/AEM.01196-20

Bahouq, M., H. Bahouq and A. Soulaymani. 2021. Bibliographic review of phytopharmacovigilance actions and measures on plant protection products in Morocco. E3S Web of Conferences, 319. https://doi.org/10.1051/e3sconf/202131901034

Bartlett, D. W., J. M. Clough, J. R. Godwin, A. A. Hall, M. Hamer and B. Parr-Dobrzanski. 2002. The strobilurin fungicides. Pest Management Science, 58: 649–662. https://doi.org/10.1002/ps.520

Beata, M., A. Broniarek-Niemiec and A. Bielenin. 2008. Resistance of *Venturia inaequalis* to strobilurin and dodine fungicides in Polish apple orchards. Phytopathologica Polonica, 57–61.

Bhaik, A., M. K. Mboup and J. L. Genet. 2022. Fungicide resistance: threats and management approaches, In: Sustainable management of potato pests and diseases. Springer, Singapore, pp. 59–81. https://doi.org/10.1007/978-981-16-7695-6_3

Bhat, M. A., Z. A. Bhat, G. H. Mir, S. Banday and T. Ahmad. 2021. Kresoxim methyl SC-a quinone outside inhibitor against major fungal foliar diseases of apple. Pesticide Research Journal, 33: 65–74. https://doi.org/10.5958/2249-524X.2021.00040.6

Brent, K. J. and D. W. Hollomon. 2007. Fungicide resistance in crop pathogens: how can it be managed? FRAC Monograph No. 1. Fungicide Resistance Action Committee.

Carbone, M. J., S. Alaniz, O. Bentancur and P. Mondino. 2021. Sensitivity of *Venturia inaequalis* to dodine in Uruguay. Tropical Plant Pathology, 46: 643–650. https://doi.org/10.1007/s40858-021-00467-9

Carmona, M., M. R. E. and S. Francisco. 2018. Fungal resistance to fungicides in field crops: a growing problem worldwide, In: Fungicides: perspectives, resistance management and risk assessment, pp. 149–192.

Chapman, K. S., G. W. Sundin and J. L. Beckerman. 2011. Identification of resistance to multiple fungicides in field populations of *Venturia inaequalis*. Plant

Disease, 95: 921–926. https://doi.org/10.1094/PDIS-12-10-0899

Chatzidimopoulos, M., F. Lioliopoulou, E. Vellios and A. Zambounis. 2022. Detection of *Venturia inaequalis* isolates with multiple resistance in Greece. Microorganisms, 10. https://doi.org/10.3390/microorganisms10122354

Chatzidimopoulos, M., F. Lioliopoulou, T. Sotiropoulos and E. Vellios. 2020. Efficient control of apple scab with targeted spray applications. Agronomy, 10. https://doi.org/10.3390/agronomy10020217

De Artur Teixeira, A., P. Longhi, P. Ritschel, R. Gava, R. M. V. Sanhueza and K. Cox. 2015. Use of RFLP-PCR method to detect kresoxim methyl-resistant *Venturia inaequalis* isolates from the south of Brazil. Summa Phytopathologica, 41: 224–226. https://doi.org/10.1590/0100-5405/2085

Fontaine, S., F. Remuson, L. Fraissinet-Tachet, A. Micoud, R. Marmeisse and D. Melayah. 2009. Monitoring of *Venturia inaequalis* harbouring the QoI resistance G143A mutation in French orchards as revealed by PCR assays. Pest Management Science, 65: 74–81. https://doi.org/10.1002/ps.1649

FRAC. 2022. Group U12 (guanidines) dodine recommendations. Fungicide Resistance Action Committee. https://www.frac.info/media/525fag4z/group-u12-guanidines-dodine-recommendations-20th-october-2022.pdf

FRAC. 2025. FRAC code list 2025: fungal control agents sorted by cross-resistance pattern and mode of action (including coding for FRAC groups on product labels). Fungicide Resistance Action Committee. https://www.frac.info/media/ljsi3qrv/frac-code-list2025.pdf

Frederick, Z. A., S. M. Villani and K. D. Cox. 2015. The effect of delayed-dormant chemical treatments on demethylation inhibitor (DMI) sensitivity in a DMI-resistant population of *Venturia inaequalis*. Plant Disease, 99: 1751–1756. https://doi.org/10.1094/PDIS-12-14-1253-RE

Frederick, Z. A., S. M. Villani, D. R. Cooley, A. R. Biggs, J. J. Raes and K. D. Cox. 2014. Prevalence and stability of qualitative QoI resistance in populations of *Venturia inaequalis* in the northeastern United States. Plant Disease, 98: 1122–1130. https://doi.org/10.1094/PDIS-10-13-1042-RE

Gisi, U., U. Müller and S. Hall. 2019. Fungicides acting on amino acids and protein synthesis, In: Modern crop protection compounds. Wiley, pp. (chapter reference). https://doi.org/10.1002/9783527699261.ch16

Gouit, S., I. Chair, Z. Belabess, I. Legrifi, K. Goura, A. Tahiri, A. Lazraq and R. Lahlali. 2024. Harnessing *Trichoderma* spp.: a promising approach to control apple scab disease. Pathogens, 13. https://doi.org/10.3390/pathogens13090752

Gouit, S., M. Radi, I. Chair, Z. Belabess, A. Farhaoui, A. Tahiri, A. Lazraq and R. Lahlali. 2025. Potential of bacterial isolates for the biological control of apple scab (*Venturia inaequalis*). Journal of Natural Pesticide Research, 14: 100165. https://doi.org/10.1016/j.napere.2025.100165

Gouit, S., S. Chiadmi, K. Goura, I. Legrifi, M. El Jarroudi, Z. Belabess, A. Tahiri, A. Lazraq, M. Baala and R. Lahlali. 2025. Assessing *Venturia inaequalis* response to common fungicides in Morocco. Journal of Fungi, 11: 493. https://doi.org/10.3390/jof11070493

Guérin, F. and B. Le Cam. 2004. Breakdown of the scab resistance gene Vf in apple leads to a founder effect in populations of the fungal pathogen *Venturia inaequalis*. Phytopathology, 94: 364–369. https://doi.org/10.1094/PHYTO.2004.94.4.364

Hassold, E. and T. Backhaus. 2009. Chronic toxicity of five structurally diverse demethylase-inhibiting fungicides to the crustacean *Daphnia magna*: a comparative assessment. Environmental Toxicology and Chemistry, 28: 1218–1226. https://doi.org/10.1897/08-339.1

Hauke, K., P. Creemers, W. Brugmans and S. Van Laer. 2004. Signum, a new fungicide with interesting properties in resistance management of fungal diseases in strawberries. Communications in Agricultural and Applied Biological Sciences, 69: 743–755.

Herce, H. D., A. E. Garcia and M. C. Cardoso. 2014. Fundamental molecular mechanism for the cellular uptake of guanidinium-rich molecules. Journal of the American Chemical Society, 136: 17459–17467. https://doi.org/10.1021/ja507790z

Hermann, D. and K. Stenzel. 2019. FRAC mode-of-action classification and resistance risk of fungicides, In: Modern crop protection compounds. Wiley, pp. (chapter reference). https://doi.org/10.1002/9783527699261.ch14

Hirayama, K. 2022. Curative effects of fungicides against *Venturia inaequalis* causing apple scab. Journal of General Plant Pathology, 88: 264–269. https://doi.org/10.1007/s10327-022-01071-8

Hoffmeister, M., P. Scheu, A. Glaab, R. Zito and G. Stammler. 2024. Sensitivity evolution in *Venturia inaequalis* towards SDHIs in comparison to other modes of action. European Journal of Plant Pathology, 168: 763–773. https://doi.org/10.1007/s10658-023-02798-6

Hoffmeister, M., R. Zito, J. Böhm and G. Stammler. 2021. Mutations in Cyp51 of *Venturia inaequalis* and their effects on DMI sensitivity. Journal of Plant Diseases and Protection, 128: 1467–1478. https://doi.org/10.1007/s41348-021-00516-0

Jha, G., K. Thakur and P. Thakur. 2009. The *Venturia* apple pathosystem: pathogenicity mechanisms and plant defense responses. Journal of Biomedicine and Biotechnology, 2009. https://doi.org/10.1155/2009/680160

Jobin, T. and O. Carisse. 2007. Incidence of myclobutanil- and kresoxim-methyl-insensitive isolates of *Venturia inaequalis* in Quebec orchards. Plant Disease, 91: 1351–1358. https://doi.org/10.1094/PDIS-91-10-1351

Jørgensen, L. N., F. van den Bosch, R. P. Oliver, T. M. Heick and N. D. Paveley. 2017. Targeting fungicide inputs according to need. Annual Review of Phytopathology, 55: 181–203. https://doi.org/10.1146/annurev-phyto-080516-035357

Karkach, I., N. Eloutassi, H. El Yacoubi and A. Rochdi. 2025. Perceptions and practices of peach producers in Fez-Meknes region and evaluation of environmental impacts using an environmental indicator of pesticide pressure. Environment, Development and Sustainability. https://doi.org/10.1007/s10668-025-06065-y

Kolattukudy, P. E. 1985. Enzymatic penetration of the plant cuticle by fungal pathogens. Annual Review of Phytopathology, 23: 223–250. https://doi.org/10.1146/annurev.py.23.090185.001255

Köller, W. 1991. Role of cutinase in the penetration of apple leaves by *Venturia inaequalis*. Phytopathology, 81: 1375. https://doi.org/10.1094/Phyto-81-1375

Köller, W. and W. F. Wilcox. 2001. Evidence for the predisposition of fungicide-resistant isolates of *Venturia inaequalis* to a preferential selection for resistance to other fungicides. Phytopathology, 91: 776–781. https://doi.org/10.1094/PHYTO.2001.91.8.776

Köller, W., D. Parker, W. Turechek, D. Rosenberger, W. Wilcox, J. Carroll, A. Agnello and H. Reissig. 2005. Fungicide resistance of apple scab: status quo and management options. New York Fruit Quarterly, 13: 9–17.

Köller, W., W. F. Wilcox and A. L. Jones. 1999. Quantification, persistence and status of dodine resistance in New York and Michigan orchard populations of *Venturia inaequalis*. Plant Disease, 83: 66–70. https://doi.org/10.1094/PDIS.1999.83.1.66

Köller, W., W. F. Wilcox and D. M. Parker. 2005. Sensitivity of *Venturia inaequalis* populations to anilinopyrimidine fungicides and their contribution to scab management in New York. Plant Disease, 89: 357–365. https://doi.org/10.1094/PD-89-0357

Kucheryava, N., J. K. Bowen, P. W. Sutherland, J. J. Conolly, C. H. Mesarich, E. H. A. Rikkerink, E. Kemen, M. Plummer, K. M. Hahn and M. D. Templeton. 2008. Two novel *Venturia inaequalis* genes induced upon morphogenetic differentiation during infection and in vitro growth on cellophane. Fungal Genetics and Biology, 45: 1329–1339. https://doi.org/10.1016/j.fgb.2008.07.010

Lahlali, R., A. Moinina, S. Ezrari, D. Maclean and M. Boulif. 2019. Apple scab disease severity in the Sais region of Morocco and its sensitivity to three commercial fungicides. Notulae Scientia Biologicae, 11: 249–257. https://doi.org/10.15835/nsb11210434

Lahlali, R., M. Boulif and A. Moinina. 2021. Pratiques phytosanitaires des pomiculteurs: cas de la région Fès-Meknès. Revue Marocaine des Sciences Agronomiques et Vétérinaires, 9: 151–157.

Leroux, P. and A. S. Walker. 2011. Multiple mechanisms account for resistance to sterol 14α-demethylation inhibitors in field isolates of *Mycosphaerella graminicola*. Pest Management Science, 67: 44–59. https://doi.org/10.1002/ps.2028

Leroux, P., R. Fritz, D. Debieu, C. Albertini, C. Lanen, J. Bach, M. Gredt and F. Chapeland. 2002. Mechanisms of resistance to fungicides in field strains of *Botrytis cinerea*. Pest Management Science, 58: 876–888. https://doi.org/10.1002/ps.566

Lesniak, K. E., T. J. Proffer, J. L. Beckerman and G. W. Sundin. 2011. Occurrence of QoI resistance and detection of the G143A mutation in Michigan populations of *Venturia inaequalis*. Plant Disease, 95: 927–934. https://doi.org/10.1094/PDIS-12-10-0898

Li, X., H. Li, Z. Yu, L. Gao and J. Yang. 2021. Investigating the sensitivity of *Venturia inaequalis* isolates to difenoconazole and pyraclostrobin in apple orchards in China. European Journal of Plant Pathology, 161: 207–217. https://doi.org/10.1007/s10658-021-02316-6

Masny, S. 2017. Occurrence of *Venturia inaequalis* races in Poland able to overcome specific apple scab resistance genes. European Journal of Plant Pathology, 147: 313–323. https://doi.org/10.1007/s10658-016-1003-x

Megadi, V. B., P. N. Tallur, S. I. Mulla and H. Z. Ninnekar. 2010. Bacterial degradation of fungicide captan. Journal of Agricultural and Food Chemistry, 58: 12863–12868. https://doi.org/10.1021/jf1030339

Moinina, A., R. Lahlali, D. Maclean and M. Boulif. 2018. Farmers' knowledge, perception and practices in apple pest management and climate change in the Fès-Meknès region, Morocco. Horticulturae, 4. https://doi.org/10.3390/horticulturae4040042

Morais, C. 2014. Advances in drug resistance research, In: Advances in drug resistance research.

Nabi, A., M. Ahmad, M. D. Shah, B. A. Padder, M. S. Dar and S. Banday. 2023. First report of myclobutanil resistance and shift in sensitivity to difenoconazole and flusilazole in north-western Himalayan *Venturia inaequalis* populations. Australasian Plant Pathology, 52: 13–22. https://doi.org/10.1007/s13313-022-00894-5

Nasonov, A. I., G. V. Yakuba and E. V. Lobodina. 2022. The long-term resistance to carbendazim in *Venturia inaequalis* in the Krasnodar region (Russia). Mikologiya i Fitopatologiya, 56: 374–378. https://doi.org/10.31857/S0026364822050087

Nasonov, A. I., G. V. Yakuba, I. L. Astapchuk and N. A. Marchenko. 2024. Sensitivity baseline and orchard populations of *Venturia inaequalis* to the succinate dehydrogenase inhibitor fungicides (SDHI). Siberian Journal of Life Sciences and Agriculture, 16: 189–210. https://doi.org/10.12731/2658-6649-2024-16-1-707

Nasonov, A., G. Yakuba, N. Marchenko, E. Lobodina and I. Astapchuk. 2022. Evaluation of sensitivity of apple scab pathogen to difenoconazole using the discriminatory dose technique. BIO Web of Conferences, 47. https://doi.org/10.1051/bioconf/20224710002

ONSSA. 2025. Office national de sécurité sanitaire des produits alimentaires. https://eservice.onssa.gov.ma/IndPesticide.aspx

Özkılınç, H., B. T. Fidanoğlu, S. Öncel, E. Kurtuluş and İ. E. Kadıoğlu. 2025. Resistance evolution and local adaptation of *Venturia inaequalis* to old and new generation SDHI fungicides. Fungal Biology, 129: 101543. https://doi.org/10.1016/j.funbio.2025.101543

Padder, B. A., T. A. Sofi, M. Ahmad, M. U. D. Shah, A. Hamid, S. Saleem and F. A. Ahanger. 2013. Virulence and molecular diversity of *Venturia inaequalis* in commercial apple growing regions in Kashmir. Journal of Phytopathology, 161: 271–279. https://doi.org/10.1111/jph.12061

Padder, S. A., S. Mansoor, S. A. Bhat, T. R. Baba, R. A. Rather, S. M. Wani, S. M. Popescu, S. Sofi, M. A. Aziz, D. I. Hefft, O. M. Alzahrani, A. Noureldeen and H. Darwish. 2021. Bacterial endophyte community dynamics in apple (*Malus domestica* Borkh.) germplasm and their evaluation for scab management strategies. Journal of Fungi, 7: 923. https://doi.org/10.3390/jof7110923

Percival, G. C. and S. Graham. 2021. Evaluation of inducing agents and synthetic fungicide combinations for management of foliar pathogens of urban trees. Arboriculture and Urban Forestry, 47: 85–95. https://doi.org/10.48044/jauf.2021.008

Pikunova, A. V. and E. N. Sedov. 2019. The racial composition of *Venturia inaequalis* in environments of the Oryol region. Mikologiya i Fitopatologiya, 53: 293–300. https://doi.org/10.1134/S0026364819050040

Polat, Z. and H. Bayraktar. 2021. Resistance of *Venturia inaequalis* to multiple fungicides in Turkish apple orchards. Journal of Phytopathology, 169: 360–368. https://doi.org/10.1111/jph.12990

Quello, K. L., K. S. Chapman and J. L. Beckerman. 2010. In situ detection of benzimidazole resistance in field isolates of *Venturia inaequalis* in Indiana. Plant Disease, 94: 744–750. https://doi.org/10.1094/PDIS-94-6-0744

Rekanović, E., M. Stepanović, I. Potočnik, S. Milijašević-Marčić, B. Todorović and M. Stević. 2012. Some experiences in control of apple scab in Serbia. Acta Horticulturae.

Rocafort, M., V. Srivastava, J. K. Bowen, S. M. Díaz-Moreno, Y. Guo, V. Bulone, K. M. Plummer, P. W. Sutherland, M. A. Anderson, R. E. Bradshaw and C. H. Mesarich. 2023. Cell wall carbohydrate dynamics during the differentiation of infection structures by the apple scab fungus *Venturia inaequalis*. Microbiology Spectrum, 11. https://doi.org/10.1128/spectrum.04219-22

Schumacher, C. F. A., U. Steiner, H. W. Dehne and E. C. Oerke. 2008. Localized adhesion of nongerminated *Venturia inaequalis* conidia to leaves and artificial surfaces. Phytopathology, 98: 760–768. https://doi.org/10.1094/PHYTO-98-7-0760

Shaik, S., J. H. Lee, Y. G. Kim and J. Lee. 2024. Antifungal, anti-biofilm and anti-hyphal properties of N-substituted phthalimide derivatives against *Candida* species. Frontiers in Cellular and Infection Microbiology, 14. https://doi.org/10.3389/fcimb.2024.1414618

Sokolova, O. and I. Moročko-Bičevska. 2022. Evaluation of apple scab and occurrence of *Venturia inaequalis* races on differential *Malus* genotypes in Latvia. Proceedings of the Latvian Academy of Sciences, Section B: Natural, Exact and Applied Sciences, 76: 488–494. https://doi.org/10.2478/prolas-2022-0075

Song, X. 2014. Captan, In: Encyclopedia of toxicology, 3rd ed. Elsevier. https://doi.org/10.1016/B978-0-12-386454-3.00105-6

Steiner, U. and E. C. Oerke. 2023. A melanin-deficient isolate of *Venturia inaequalis* reveals various roles of melanin in pathogen life cycle and fitness. Journal of Fungi, 9. https://doi.org/10.3390/jof9010035

Stewart, K., T. Passey, C. Verheecke-Vaessen, Z. Kevei and X. Xu. 2023. Is it feasible to use mixed orchards to manage apple scab? Fruit Research, 3. https://doi.org/10.48130/FruRes-2023-0028

Torriani, S. F. F., P. C. Brunner, B. A. McDonald and H. Sierotzki. 2009. QoI resistance emerged independently at least four times in European populations of *Mycosphaerella graminicola*. Pest Management Science, 65: 155–162. https://doi.org/10.1002/ps.1662

Viljanen-Rollinson, S. L. H., S. M. Thompson, S. Keenan, S. R. Bulman, P. J. Wright, P. N. Wood, N. M. Park and R. M. Beresford. 2013. Resistance of *Venturia inaequalis* to quinone outside inhibitor (QoI) fungicides in New Zealand apple orchards. New Zealand Plant Protection, 66: 284–292. https://doi.org/10.30843/nzpp.2013.66.5659

Villani, S. M. and K. D. Cox. 2014. Heteroplasmy of the cytochrome b gene in *Venturia inaequalis* and its involvement in quantitative and practical resistance to trifloxystrobin. Phytopathology, 104: 945–953. https://doi.org/10.1094/PHYTO-06-13-0158-R

Villani, S. M., A. R. Biggs, D. R. Cooley, J. J. Raes and K. D. Cox. 2015. Prevalence of myclobutanil resistance and difenoconazole insensitivity in populations of *Venturia inaequalis*. Plant Disease, 99: 1526–1536. https://doi.org/10.1094/PDIS-01-15-0002-RE

Weber, R. W. S., R. Busch and J. Wesche. 2025. Spatial and temporal aspects of fungicide resistance in *Venturia inaequalis* (apple scab) populations in northern Germany. BioTech, 14: 44. https://doi.org/10.3390/biotech14020044

Xu, X., J. Yang, V. Thakur, A. Roberts and D. J. Barbara. 2008. Population variation of apple scab (*Venturia inaequalis*) isolates from Asia and Europe. Plant Disease, 92: 247–252. https://doi.org/10.1094/PDIS-92-2-0247