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Apple Scab (Venturia inaequalis): Advances in Pathogen Biology, Fungicide Resistance, and Integrated Control

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Abstract

Apple scab, caused by the hemibiotrophic ascomycete *Venturia inaequalis*, remains the most economically destructive disease of apple worldwide, despite more than a century of intensive research and management efforts. The pathogen's polycyclic life cycle, combined with strong selection pressure from frequent fungicide applications and genetically uniform host cultivars, has driven rapid evolutionary adaptation, resulting in widespread fungicide resistance and repeated breakdowns of host resistance. This review synthesizes recent advances in *V. inaequalis* biology, fungicide resistance mechanisms, and integrated disease management strategies. Genomic and transcriptomic studies reveal a "two-speed" genome architecture enriched in transposable elements, which accelerates effector diversification and underpins the rapid erosion of monogenic resistance, exemplified by the global failure of the widely deployed Rvi6 (Vf) gene. Concurrently, extensive resistance to major fungicide classes including qualitative resistance to QoI fungicides via the cytb G143A mutation and quantitative resistance to DMIs mediated by *CYP51* mutations and overexpression has culminated in stable multi-fungicide resistant populations with minimal fitness penalties. These developments severely constrain chemical control options. The review highlights that sustainable apple scab management requires a paradigm shift toward integrated strategies that reduce selection pressure and enhance durability. Key approaches include rigorous cultural practices to suppress primary inoculum, precision fungicide use guided by decision support systems capable of reducing chemical inputs by up to 80%, and the deployment of durable host resistance through gene pyramiding supported by molecular breeding and cisgenic technologies. Ultimately, the long-term viability of apple production depends on the integration of pathogen genomics, resistance stewardship, precision epidemiology, and advanced breeding to outpace the adaptive capacity of *V. inaequalis*.

Keywords: *Venturia Inaequalis*; Apple Scab; Fungicide Resistance; QoI; DMI; *CYP51*; Rvi6 (Vf); Effector Biology; Two-Speed Genome; Integrated Pest Management; Decision Support Systems; Durable Resistance

I. Introduction

Apple scab, caused by the ascomycete fungus *Venturia inaequalis* Cooke (Wint.), is globally recognized as the most economically damaging disease affecting apple cultivation. The pathogen is classified as hemibiotrophic, characterized by an initial phase of asymptomatic host colonization followed by the destructive phase of lesion development. While *V. inaequalis* has been continuously researched for over 100 years, its ability to cause severe damage to fruit and leaves continues to challenge growers worldwide (Müller et al., 2019). The economic impact of apple scab is immense, resulting in greater losses than any other apple disease across major growing regions, including North and South America, Europe, and Asia. The disease is particularly problematic in climates characterized by cool, moist spring weather, which favors ascospore release and infection. Losses can approach 100 percent of the harvest if management is neglected, primarily due to the reduction in fruit size, quality, and storage life (Agha et al., 2024; Schilder et al., 2013). The high value of marketable fruit, coupled with consumer demand for unblemished appearance, creates intense pressure on growers to maintain immaculate cosmetic quality (Pons et al., 2024).

Figure1.1 Symptoms of Apple scab

The necessity of producing unblemished fruit underpins the traditional reliance on intense chemical control. On susceptible commercial varieties, conventional orchard farming typically requires between 10 to 20 fungicide applications per season this represents a high cost and environmental load, often accounting for over 70% of the total pesticide treatments in conventional apple orchards (Schilder et al., 2013).

The polycyclic nature of the *V. inaequalis* life cycle drives this intense management The disease cycle commences with the primary infection phase, initiated by sexual ascospores released from pseudothecia overwintering in fallen leaves These primary lesions subsequently produce asexual conidia, which are responsible for repeated, rapid secondary infections throughout the growing season (Müller et al., 2019) The destructive potential of this polycyclic reproduction system, combined with high economic pressure, necessitates extensive prophylactic spraying. This continuous, high intensity application of chemical agents has, by exerting relentless selection pressure, directly led to the evolution of widespread fungicide resistance, a central challenge discussed in this review (Schilder et al., 2013).

This paper provides an expert analysis of recent advances in the understanding and control of *V. inaequalis*. It focuses on three critical, interwoven areas: molecular pathogen biology illuminated by genomics, the mechanisms and extent of current fungicide resistance, and the application of integrated control strategies, including durable host resistance and precision Decision Support Systems (DSS). The findings underscore that a continuation of traditional management reliant on single site chemistry and monogenic host resistance is unsustainable, necessitating a transition to complex, knowledge-based disease management (Okoro et al., 2024).

2. Pathogen Biology and Genomic Insights

2.1. Next Generation Sequencing and Genome Architecture

Recent advancements in sequencing technologies have significantly accelerated the understanding of the *V. inaequalis* genome. The development of a high quality PacBio genome assembly for the reference strain EU B04, complemented by the re sequencing of 79 strains from various populations and related *Venturia* species (*V. pirina*, *V. aucupariae*, *V. asperata*), provides a robust foundation for genetic and population genomics studies (Villani et al., 2019).

Analysis of the reference genome reveals a key structural feature: a mosaic, "two speed" architecture. The genome is composed of two distinct compartments: GC equilibrated regions, which primarily contain core genes necessary for fundamental metabolism, and AT rich regions, which are densely populated by Transposable Elements (TEs). These TEs, largely belonging to the Gypsy and Copia LTR superfamilies, are thought to have substantially influenced the evolutionary trajectory of *Venturia* species (Oggenfuss et al., 2023).

This genomic organization is believed to be the fundamental mechanism driving the pathogen's rapid adaptation. The concentration of TEs in AT rich regions promotes localized genetic instability and higher mutation rates. If virulence genes, particularly those encoding effectors, are physically clustered within these unstable regions, they are more susceptible to rapid mutation or deletion events. This rapid genomic variability provides the pathogen with the capacity to quickly overcome host R gene recognition, confirming the genetic basis for the observed, quick failure of monogenic resistance in the field (Möller et al., 2017).

2.2. Secretome and Effector Biology: The Molecular Basis of Virulence

The secretome the collection of proteins secreted by the fungus during host interaction is crucial to the infection process. A significant finding is that the *V. inaequalis* secretome is dominated by small secreted proteins (SSPs), with an estimated 76.52\% of SSPs predicted to function as effectors. These effectors serve diverse roles, either acting as virulence factors that facilitate disease development or as avirulence factors that are recognized by host resistance genes, thereby triggering a defense response (Zhu et al., 2023).

Transcriptome sequencing and functional annotation have provided deeper comprehension of these effectors and their role in host pathogen interactions (Sharma et al., 2013). Notably, the pathogen's effector repertoire features expanded families that exhibit predicted structural similarity to known avirulence proteins in other plant pathogenic fungi, even in the absence of primary sequence homology (Caffier et al., 2015). This functional convergence suggests that the three-dimensional configuration required for suppressing conserved host immunity mechanisms may be maintained across different fungal species. This finding has strong implications for breeding, suggesting that research efforts should prioritize the identification of host R genes that target these conserved functional domains, which are potentially more immutable than highly variable protein sequences. Differences in gene complement, particularly the number of predicted SSPs, are also hypothesized to account for the observed host specialization across various *Venturia formae specialis* (Villani et al., 2019).

2.3. Host Pathogen Coevolution and Specialization

The relationship between *V. inaequalis* and its hosts provides a clear case study in coevolution. The evidence suggests that the pathogen acquired greater overall pathogenicity and increased virulence on cultivated apple (*Malus domestica*) through a process termed "host tracking," which accompanied the domestication of the host (Piron et al., 2012). Isolates originating from wild relatives, such as the European crabapple, generally exhibited reduced aggression and virulence on non-endemic hosts compared to populations adapted to commercial apples This historical context explains why the pathogen today poses such a threat in agricultural systems, where genetic monoculture provides an ideal environment for selection toward high virulence. (Oggenfuss et al., 2023).

3. The Crisis of Fungicide Resistance: Mechanisms and Global Monitoring

The cumulative effect of continuous reliance on site specific systemic fungicides in commercial orchards has generated a global crisis, marked by widespread resistance across multiple fungicide classes. Effective disease management today requires strict adherence to FRAC (Fungicide Resistance Action Committee) guidelines, which mandate rotation of Fungicide Mode of Action (MOA) groups, limiting the total applications of single site fungicides per season, and utilizing multi-site contact products (Schilder et al., 2013).

3.1. Quinone outside Inhibitors (QoIs, FRAC 11)

QoI fungicides (e.g., trifloxystrobin, kresoxim methyl) have faced swift and substantial efficacy failure. Resistance to this class is qualitative and highly established globally. In major apple growing areas of Greece, resistance frequencies reached an alarming range of 89% to 92% (Hadjimitsou et al., 2022). Similarly, QoI resistance became practically relevant in Chile after only 5 to 6 years of commercial application, leading to dramatic declines in disease control efficacy (López Martínez et al., 2005).

The molecular mechanism responsible for this high-level resistance is the G143A point mutation in the mitochondrial *cytochrome b* (cytb) gene (Hadjimitsou et al., 2022). The qualitative nature of this single point mutation means that its presence confers a high degree of resistance and is rapidly selected for under field conditions. Consequently, molecular diagnostic tools, such as the CAPS assay and allele specific PCR, have been developed to efficiently detect this G143A mutation, enabling growers to monitor resistance prevalence proactively and adjust spray strategies (Caffier et al., 2008).

3.2. Demethylation Inhibitors (DMIs, FRAC 3)

Demethylation Inhibitors (DMIs, triazoles like difenoconazole and myclobutanil) are a cornerstone of conventional apple scab control, inhibiting sterol synthesis in the pathogen while reduced sensitivity to DMIs is widely confirmed the mechanisms are generally quantitative and more complex than QoI resistance. (Schilder et al., 2013).

The identified resistance mechanisms include point mutations in the CYP51A1 gene (Jurick et al., 2023) and, importantly, the overexpression of the CYP51 gene This overexpression, measured at 9-to-13-fold increases, is associated with a 169 bp repeatable element located upstream of the CYP51 coding region (Jurick et al., 2023).

A critical finding reveals that the overexpression mechanism can exhibit fungicide specificity. This mechanism was clearly linked to resistance against difenoconazole but showed no consistent association with myclobutanil resistance this variability within the DMI class means that a simple rotation between two different DMI molecules (both FRAC 3) may fail to conserve the MOA, as both compounds might select for similar mechanisms of reduced sensitivity. Therefore, resistance stewardship requires compound specific monitoring and tailored rotation strategies, moving beyond the assumption that all members of a single FRAC group present an identical resistance risk. (López Martínez et al., 2005).

3.3. Prevalence of Multi Fungicide Resistance and Fitness

Multi fungicide resistance is now a common feature of *V. inaequalis* populations globally. Extremely high resistance levels have been reported for older chemical classes, such as Benzimidazoles (FRAC 1), with thiophanate methyl resistance reaching 92.6% in US isolates (Schilder et al., 2013).

DMI resistance to myclobutanil was also found in 57.0% of isolates tested in the US Multi resistance to chemicals like thiophanate methyl and trifloxystrobin is widespread, notably confirmed in regions such as Morocco (Lahlali et al., 2025).

The most severe implication for long term management is the empirical observation that isolates exhibiting resistance to multiple fungicides maintain high biological fitness. Statistical analysis confirmed that multi resistant isolates showed no fitness penalty regarding mycelial growth or conidial production compared to sensitive isolates (Schilder et al., 2013). The permanent retention of the resistant genotype, even when selection pressure is removed, renders chemical rotation ineffective as a means of population reversion. This fact compels growers to adopt aggressive,

Table 3.1 Molecular Mechanisms and Global Status of Resistance to Key Fungicide Classes in *Venturia inaequalis*

Fungicide Class (FRAC Group)	Representative Examples	Primary Resistance Mechanism(s)	Molecular Target/Gene	Observed Resistance Frequency (Selected Regions)
QoI (11)	Trifloxystrobin, Kresoxim methyl	Target site modification (Qualitative resistance)	Cytochrome *b* (cytb) G43A mutation	High (e.g., 89–92% in Greece; widespread in Chile after 5 6 years) (Caffier et al., 2008; Hadjimitsou et al., 2022; López Martínez et al., 2005)
DMI (3)	Difenoconazole, Myclobutanil	Gene overexpression (9–13x increase); Point mutations	51 gene; Upstream repeatable element	Variable; High incidence of reduced sensitivity 57% myclobutanil resistance in US) (Jurick et al., 2023; Schilder et al., 2013)
Benzimidazole (1)	Thiophanate methyl	Target site modification	Beta tubulin	Extremely High (92.6% in US isolates) (Lahlali et al., 2025; Schilder et al., 2013)

permanent Integrated Pest Management (IPM) measures, with a strong focus on sanitation and inoculum reduction, as the chemical resource pool cannot be regenerated through rotation alone. (Jurick et al., 2023). Table 3. 1 provides a summary of the known molecular resistance mechanisms in *V. inaequalis*:

4. Development of Durable Host Resistance

4.1. The Erosion of Vf (Rvi6) Resistance

The development of disease resistant cultivars is a highly desirable long-term strategy, offering environmental and economic benefits. Since the 1970s, the apple breeding community has relied heavily on the Rvi6 gene (historically Vf), derived from *Malus floribunda* 821. This gene forms the basis of resistance in approximately 80% of all scab resistant cultivars released globally, including popular varieties like 'Liberty' and 'Enterprise' (Agha et al., 2024).

However, the pathogen's rapid adaptation, driven by its molecular architecture, has compromised this monogenic reliance. Rvi6 virulent isolates have been reported in Europe, and critically, a complete resistance breakdown in the original source, M. floribunda 821, has recently been documented in North America (Geneva, NY, U.S.A.). The emergence of these new virulent isolates from indigenous North American populations, rather than European introductions, confirms the immediate evolutionary capability of the pathogen to overcome this major resistance gene (Lahlali et al., 2025).

The failure of the Rvi6 gene demonstrates that the pathogen's evolutionary timeline is accelerating beyond the 15-to-20-year timeframe required for traditional perennial crop breeding. While the progenitor source lost resistance completely, many derived cultivars maintained some degree of field resistance, suggesting they benefit from a more intricate, multi component defense system. The Rvi6 gene itself is expressed highly in both leaves and fruits, particularly during late developmental stages (August–September) when both tissues are susceptible to infection (Geng et al., 2024).

4.2. Strategies for Durable Resistance: Gene Pyramiding

To ensure the long-term viability of resistant cultivars, breeders must transition from monogenic resistance toward **gene pyramiding** the simultaneous incorporation of multiple, distinct Rvi loci into a single cultivar. Genes such as Rvi6 and Rvi5 (Vm) have been confirmed to be inherited independently, making their combination genetically feasible (Brouwer et al., 2018).

Pyramiding is theoretically the most durable strategy for resistance deployment, as the probability of resistance breakdown is determined by the multiplicative probability of the pathogen acquiring simultaneous virulence against all combined genes (Sainsbury et al., 2017).

However, the application of classical breeding for gene stacking in long generation crops like apples is exceedingly slow and risks the loss of desirable elite cultivar traits. Therefore, advanced technologies are required (Zhong et al., 2024)

1. **Marker Assisted Selection (MAS):** The identification and use of gene specific markers (SSRs) are vital for rapidly tracking and selecting for multiple resistance alleles (Va, Vh2, Vh4, Vbj, Vr2, Vd, Vg) in breeding progeny (Sainsbury et al., 2017)
2. **Cisgenesis/Intragenesis:** This approach, which utilizes genetic modification only with genes derived from the apple genus, offers the most rapid and effective means to stack multiple R genes while precisely conserving the commercial properties of the original cultivar. The timely adoption of cisgenesis is necessary to develop new resistant cultivars at a pace that can match the pathogen's ability to evolve virulence. (Chibage et al., 2022)

Ultimately, achieving durable resistance requires a holistic approach that integrates major Rvi genes that recognize specific effectors with complementary genes that contribute to broad, effective downstream defense mechanisms (Zhong et al., 2024).

Table 4.1 Durable Resistance Strategies for *V. inaequalis* based on Rvi Gene Deployment

Strategy	Primary Mechanism of Durability	Hypothesized Durability Ranking	Limiting Factor in Apple
Pyramiding	Virulence requires simultaneous, multiple mutations	Highest durability (Sainsbury et al., 2017)	Extremely long breeding cycle (classical); regulatory hurdles (cisgenesis) (Wageningen University & Research, n.d.)
Rotation/Alternation	Spatial/temporal variation limits continuous selection pressure on one gene	Moderate durability (Sainsbury et al., 2017)	Requires complex regional coordination and cultivar turnover (Sainsbury et al., 2017)
Sequential Release	Minimal effort, constant selection for virulence	Lowest durability (Plug Plant Pray) (Sainsbury et al., 2017)	Guaranteed failure due to pathogen adaptation speed (Sainsbury et al., 2017)

5. Integrated Pest Management (IPM) and Decision Support Systems (DSS)

An Integrated Pest Management strategy, which optimally combines cultural tactics, resistant varieties, and targeted fungicides, is the only sustainable pathway for long term control of *V. inaequalis* (Marinko et al., 2024

5.1. Cultural Practices and Inoculum Reduction

The foundation of sustainable IPM is cultural control aimed at reducing the primary ascospore inoculum in the overwintering leaf litter. By reducing this initial source, the overall disease pressure for the subsequent season is significantly lowered, which in turn raises the threshold required to trigger chemical interventions. (Singh et al., 2023)

Applying a 5\% urea spray to the trees after harvest or to the fallen leaf litter in the spring accelerates leaf decomposition and directly interferes with the fungus's capacity to form its sexual pseudothecial stage, thereby reducing inoculum (tSaoir et al., 2010)

Mechanical shredding or mowing of fallen leaves with a flail mower significantly increases the decomposition rate, achieving an inoculum reduction of 50 60\%. Pruning practices are essential for improving air circulation and promoting the rapid drying of leaves and fruit, creating a microclimate that is unfavorable for infection (Bień et al., 2025)

Biological control agents (BCAs) are integral to developing innovative, sustainable management solutions. Research confirms the preventative biocontrol potential of agents such as *Trichoderma* isolates in detached leaf assays *in vivo*. However, the current efficacy of BCAs remains comparatively lower than that of highly effective chemical standards, such as difenoconazole (Marino et al., 2024).

In organic production, a systems based approach is necessary, focusing on conservation of natural enemies and rigorous cultural practices. Accepted organic materials, such as elemental sulfur and liquid lime sulfur (calcium polysulfide), are effective preventive measures. However, their reliance on being applied pre infection and their poor rain fastness necessitate much more frequent renewal than conventional synthetic fungicides (Schilder et al., 2013).

5.3. Precision Application via Decision Support Systems (DSS)

Decision Support Systems (DSS) are the most important technological development for fungicide conservation. These systems evolved from basic predictive schemes based on the Mills infection criteria (temperature and leaf wetness) to complex software platforms like ADEM and RIMpro. These tools track ascospore discharge and use weather forecasting to assess the daily and cumulative risk of infection (Tratwal et al., 2025)

RIMpro, a widely adopted model, synthesizes environmental variables (rain, temperature, light, spore inventory) to generate quantitative metrics, such as "RIM values," which represent the relative severity of contamination risk. The system monitors spore germination and tracks the history of infection for different leaf levels (cluster versus shoot leaves). Crucially, it informs the timing for curative treatments by identifying the period during which germinating spores are still sensitive to post infection contact fungicides (Juroszek et al., 2022)

The implementation of optimized DSS strategies enables growers to precisely align spray programs with actual infection events, moving away from routine calendar based prophylaxis (Pons et al., 2024) In optimized European trials, the use of DSS resulted in a documented fungicide reduction of up to 79% against apple scab during the primary season. This drastic reduction in chemical input is critical, as it functions as a primary resistance stewardship tool, minimizing the selection pressure on the limited pool of effective single site fungicides and extending their useful lifespan. (Schilder et al., 2013).

Table 5.1 Impact and Functionality of Decision Support Systems (DSS) in Apple Scab Management

DSS Model/Platform	Input Criteria	Key Output/Decision Support	Targeted Application Window	Quantified Impact (Fungicide Reduction)
Mills/MacHardy Model	Temperature, Hours of Leaf Wetness (NIAB, n.d.)	Baseline prediction of primary infection events	Preventive or short window curative sprays	Foundation of predictive epidemiology (NIAB, n.d.)
RIMpro	Weather forecast, Ascospore stock, Temperature, Light, Leaf growth stage (RIMpro, n.d.)	Real time infection risk (RIM values); Forecasted symptom visibility	Precision Preventive; Curative (within post infection window) (Pons et al., 2024; RIMpro, n.d.)	Up to \text{79}\% reduction in primary season fungicide applications achieved in optimized systems (Danish EPA, 2012)

6. Future Directions and Conclusion

6.1. Prioritizing Research

The successful long term management of apple scab requires continued molecular research focused on the pathogen's adaptive capabilities. Functional genomic studies must intensify efforts to elucidate the precise roles of effector molecules, particularly those encoded within the highly unstable, AT rich regions of the genome A functional understanding of effector manipulation of host defense systems is essential for identifying conserved targets for durable host resistance. (Zhu et al., 2023).

In breeding, the focus must shift entirely to gene stacking. Following the breakdown of the major gene, programs must accelerate the identification, isolation, and pyramiding of complementary quantitative resistance loci (QRLs) alongside new major resistance genes. These QRLs are necessary to ensure the robust, multi component defense systems required for long term field durability (Agha et al., 2024)

6.2. Policy and Implementation Challenges

Policy frameworks must be aligned with scientific necessity. To maintain the efficacy of existing chemical tools, regulatory bodies should mandate sophisticated, high throughput molecular diagnostics for resistance monitoring detection and overexpression assays) to provide compound specific resistance data and guide chemical rotation (Caffier et al., 2008). Furthermore, to outpace the pathogen's high evolutionary rate, regulatory frameworks must be adapted to support the rapid deployment of gene stacked cultivars developed through advanced techniques like cisgenesis/intragenesis (Jurick et al., 2023)

6.3. Concluding Remarks

The management of *Venturia inaequalis* has reached a critical juncture. The pathogen’s genomic architecture provides the necessary machinery for rapid adaptation, evidenced by the global failure of the monogenic resistance and the prevalence of multi fungicide resistance that retains high biological fitness. (Bień et al., 2025)

Sustainable viability rests upon a sophisticated, integrated strategy: first, by drastically reducing the selection pressure through rigorous cultural sanitation and the mandatory use of Decision Support Systems, which can reduce chemical input by nearly 80\% during the critical primary infection phase. Second, by implementing durable host resistance strategies via molecular assisted gene pyramiding, which is necessary to overcome the pathogen’s capacity for rapid evolution. The future of global apple cultivation requires the successful convergence of advanced genomics, precision epidemiology, and adaptive breeding programs. (Sainsbury et al., 2017)

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