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FUNGICIDE RESISTANCE IN VEGETABLES - MECHANISMS, IMPACTS, AND MANAGEMENT STRATEGIES: A REVIEW

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ABSTRACT

Vegetable crops are vital to global food and nutritional security but suffer substantial yield losses due to fungal diseases. Although fungicides remain central to disease management in vegetable production systems, their intensive and repeated use has accelerated the development of fungicide resistance, threatening the sustainability of chemical control. This review synthesizes current knowledge on fungicide resistance in vegetables, with emphasis on resistance mechanisms, impacts on disease control and crop productivity, and emerging management approaches. Major resistance mechanisms, including target-site mutations, efflux pump–mediated resistance, metabolic detoxification, and cross-resistance, are discussed in relation to their role in reducing fungicide efficacy. The consequences of resistance-such as increased disease incidence and severity, yield losses, economic impacts, and ecological shifts in pathogen populations-are highlighted. Recent advances in molecular diagnostics, including digital PCR, next-generation sequencing, long-read sequencing, and CRISPR-based detection, are examined for their contribution to early resistance monitoring and surveillance. The review underscores the importance of integrated resistance management strategies that combine judicious fungicide use, resistance monitoring, and effective farmer engagement to preserve fungicide efficacy and ensure sustainable vegetable production.

Key words : Fungicide resistance; Vegetable crops; Disease management; Resistance mechanisms; Molecular diagnostics

Introduction

Vegetables are central to global food and nutritional security, yet their consumption remains insufficient worldwide. Average intake is estimated at 186 g per person per day, well below the recommended 240 g per day in about 88% of countries (Kalmpourtzidou *et al.*, 2020). With the global population projected to reach 9.1 billion by 2050, vegetables will be increasingly critical for meeting future nutritional demands (Peter *et al.*, 2021).

Compared with cereals, vegetables offer higher productivity per unit area and are richer in essential micronutrients, making them vital tools for combating malnutrition and improving diet quality, particularly in developing regions (Ojiewo *et al.*, 2015).

Vegetable crops experience considerable yield losses due to diseases, with total annual losses estimated at 40–60% and attributed to a diverse range of pathogens. Numerous studies consistently report high susceptibility of vegetables to fungal, bacterial, viral, and nematode diseases (Tripathi *et al.*, 2024). These losses occur across the production chain, accounting for approximately 15–20% in the field, 15–20% during harvesting and storage,

and up to 30–40% during transportation (Tripathi *et al.*, 2022).

Loss severity varies among crops and production systems; for instance, reported losses include 18.38% in tomato, 13.82% in potato, and 10.13% in pepper (Tomm *et al.*, 2018). In some cases, individual pests or diseases can cause extreme damage, with yield losses reaching 70–75% in brinjal (Hasan *et al.*, 2025). Collectively, these losses pose serious threats to food security and farm profitability, highlighting the urgent need for effective and sustainable disease management strategies.

Synthetic fungicides remain a cornerstone of disease management in vegetable crops, effectively reducing postharvest losses by approximately 20–30% and providing reliable control of economically important fungal pathogens such as *Aspergillus*, *Alternaria*, and *Botrytis* (Singh *et al.*, 2021; Taþkýn *et al.*, 2016). However, the intensive and repeated application of fungicides, particularly those with site-specific modes of action, has exerted strong selection pressure on pathogen populations, accelerating the development of fungicide resistance. This growing resistance threatens the long-term sustainability of chemical disease control and necessitates a critical reassessment of fungicide use strategies in vegetable production systems.

Fungicide resistance represents an adaptive evolutionary process through which fungal pathogens survive chemical control measures, posing a serious challenge to crop protection and agricultural productivity. It has been defined as the evolutionary response of fungi to fungicide-induced selection pressure, particularly in the case of single-site mode-of-action fungicides (Valarmathi *et al.*, 2018). The emergence of resistance undermines the sustainability and economic viability of agricultural systems, especially given the limited number of available fungicide classes (Dorigan *et al.*, 2023).

Persistent use of fungicides sharing the same modes of action further accelerates resistance development in plant pathogens, significantly reducing control efficacy and threatening effective disease management (Yin *et al.*, 2023). These resistance phenotypes arise from complex target-site and non–target-site mechanisms that collectively compromise fungicide performance.

Studying fungicide resistance in vegetable crops is essential for sustaining effective disease management in intensively cultivated systems. Frequent fungicide applications and short pathogen life cycles accelerate resistance development, leading to reduced efficacy, higher production costs, and increased environmental burden. Understanding resistance mechanisms and trends supports targeted monitoring, informed fungicide use, and the design of integrated disease management strategies, thereby preserving available chemistries and strengthening long-term food and nutritional security**.** (Thind, 2022; Islam *et al.*, 2024)

Major Fungicide Classes Used in Vegetable Crops

Vegetable production employs multiple fungicide classes grouped by mode of action (MoA) to manage diverse fungal and oomycete diseases. Classification by the Fungicide Resistance Action Committee (FRAC) facilitates informed rotation and resistance management planning (FRAC, 2024). These classes differ in target specificity, systemic properties, and risk of resistance evolution.

Multi-site Protectants (Low Resistance Risk)

Multi-site protectants include chloronitriles (e.g., chlorothalonil), dithiocarbamates (e.g., mancozeb), and copper compounds. These fungicides interact with numerous cellular components, yielding broad-spectrum contact activity and low risk of resistance development. They are widely used as pre-infection protectants and in rotation with systemic chemistries to reduce selection pressure (EPA, 2024).

Demethylation Inhibitors (DMIs; Moderate Resistance Risk)

DMIs, including propiconazole, tebuconazole, and difenoconazole, inhibit lanosterol 14 α-demethylase (CYP51), a key enzyme in ergosterol biosynthesis required for fungal cell membranes. Their systemic and curative properties make them valuable against powdery mildews and leaf spots. Resistance arises through point mutations, promoter alterations, and increased gene expression, leading to gradual shifts in sensitivity rather than discrete resistant/non-resistant phenotypes (Cools & Fraaije, 2013; Lucas *et al*., 2015).

Quinone-outside Inhibitors (QoIs; High Resistance Risk)

QoI fungicides (e.g., azoxystrobin, pyraclostrobin) block electron transport at the Qo site of cytochrome b, disrupting fungal respiration. Due to their single binding site, mutations such as G143A rapidly confer high-level resistance in pathogens like *Alternaria* spp. and *Botrytiscinerea*. This has necessitated avoidance of repeated solo QoI applications in vegetable disease programs (FRAC, 2024; Ishii & Hollomon, 2015).

Succinate Dehydrogenase Inhibitors (SDHIs; Moderate to High Resistance Risk)

SDHIs (e.g., boscalid, fluopyram) target succinate

dehydrogenase subunits (sdhB, sdhC, sdhD) within the mitochondrial electron transport chain. Resistance has emerged via point mutations in these subunits, resulting in reduced fungicide affinity. Management relies on prudent use in rotation and mixtures with unrelated MoA fungicides to delay resistance selection (FRAC, 2024)

Benzimidazoles (High Resistance Risk)

Benzimidazoles such as carbendazim disrupt microtubule assembly by binding β-tubulin. Widespread resistance, due to single substitutions (e.g., E198A/G, F200Y), has diminished their efficacy in many vegetable pathogen populations, leading to regulatory restrictions and decreased use (Hahn, 2014).

Phenylamides (Very High Resistance Risk in Oomycetes)

Phenylamide fungicides, including metalaxyl and mefenoxam, act primarily against oomycete pathogens by interfering with RNA synthesis. Resistance appears rapidly through simple genetic changes, particularly in *Pseudoperonospora cubensis* (cucurbit downy mildew), limiting their long-term standalone utility (Parra & Ristaino, 2001; FRAC, 2024).

Anilinopyrimidines and Other Miscellaneous Classes

Anilinopyrimidines (e.g., cyprodinil) and other single-site chemistries provide targeted control against fruit rots and necrotrophs but may exhibit variable resistance development depending on pathogen biology and spray program design. Their use is most effective in rotation with multi-site protectants to reduce selection pressure (Mikaberidze *et al.,* 2017).

Biocontrol Agents and Botanical Fungicides

Biological fungicides and botanicals (FRAC BM groups) function through multiple modes, such as competition, antibiosis, and induced host resistance. Although typically less potent than synthetic single-site fungicides, they carry minimal resistance risk and integrate well into resistance management strategies, particularly under organic or residue-sensitive production systems (Lamichhane *et al.,* 2018).

Mechanisms of Fungicide Resistance

Target site mutations and alterations in fungicide binding.

Target-site mutations represent a major mechanism underlying fungicide resistance, arising from specific molecular changes that impair fungicide binding and reduce control efficacy. Extensive research has documented such mutations across multiple fungicide classes. Structural analyses have shown that single amino acid substitutions in lanosterol 14 α-demethylase can disrupt triazole binding by modifying key hydrogen-bond interactions (Sagatova *et al.,* 2016). Comparative studies further indicate that the predictability of target-site mutations varies among fungicide targets, with cytochrome b mutations occurring most consistently across species, whereas mutations in CYP51, the azole target, are more diverse and less repeatable (Hawkins *et al.,* 2021).These resistance-conferring changes typically involve point mutations, amino acid substitutions, or conformational alterations in target proteins that hinder effective fungicide interaction, ultimately compromising disease control (Dorigan *et al.,* 2023).

Efflux pumps and reduced intracellular fungicide accumulation

A widespread mechanism of fungicide resistance involves the activation of membrane-associated efflux pumps that can recognize and expel a broad range of chemical compounds, thereby conferring multidrug resistance (MDR) (Cowen *et al.,* 2015). Efflux pump–mediated resistance is a major non-target-site mechanism in fungi, allowing pathogens to actively lower intracellular fungicide concentrations and thereby develop multidrug resistance. Enhanced activity of membrane-associated efflux transporters has been widely reported as a key contributor to fungicide resistance, as these pumps expel fungicides and maintain intracellular levels below toxic thresholds (Hu *et al.,* 2021). This mechanism is particularly problematic because it can confer cross-resistance to multiple fungicide classes, leading to multidrug-resistant fungal populations (Kadariswantiningsih *et al.,* 2025).

Evidence for efflux-based resistance spans numerous plant pathogenic and clinical fungal species, underscoring its broad relevance and significance. Consequently, the use of efflux pump inhibitors is being investigated as a promising approach to restore fungicide sensitivity and enhance disease control.

Metabolic detoxification and degradation of fungicides

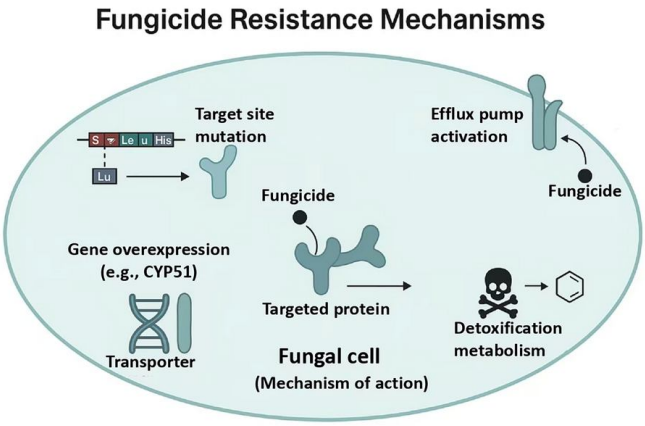
Fungal pathogens can acquire metabolic detoxification capabilities that enable them to evade fungicide toxicity through complex non-target-site resistance mechanisms. These strategies include enhanced activity of detoxifying enzymes, metabolic bypass of inhibited pathways, and modulation of stress response systems, allowing fungi to inactivate or transform fungicides before cellular damage occurs (Hu *et al.,* 2021; Islam *et al.,* 2024). Such mechanisms are frequently reported in plant pathogenic

fungi, including Fusarium species, where metabolic resistance can emerge rapidly and extend across multiple fungicide classes (Naqvi *et al.*, 2025). Although the molecular basis differs among species, resistance commonly arises from enzymatic modifications that substantially reduce fungicide efficacy.

Cross-resistance and multiple resistance mechanisms

Fungicide resistance arises from a combination of target-site and non–target-site mechanisms that enable fungal pathogens to develop cross-resistance and multiple resistance phenotypes against different fungicide classes. Documented mechanisms include target-site alterations, such as mutations in genes encoding fungicide targets, and non–target-site processes, including enhanced efflux pump activity, metabolic detoxification, and regulation of stress response pathways (Deising *et al.*, 2008; Hu *et al.*, 2021).

Studies across diverse fungal pathogens show that resistance can involve changes in target structure or expression levels, resulting in varying degrees of reduced fungicide sensitivity (Dorigan *et al.*, 2023). Continued reliance on fungicides with identical modes of action further accelerates resistance evolution, posing a serious and ongoing threat to effective crop protection (Yin *et al.*, 2023).



Comparative Overview of Major Fungicide Classes and Resistance Mechanisms

Understanding the relationship between fungicide mode of action (MoA), molecular mutation patterns, and resistance risk is central to resistance management. Single-site fungicides are particularly vulnerable to rapid resistance evolution due to their reliance on highly specific binding targets (FRAC, 2024; Lucas *et al.*, 2015).

QoI and benzimidazole resistance typically arises through single, high-impact mutations that can spread rapidly in clonal populations (Hahn, 2014; Ishii & Hollomon, 2015). In contrast, DMI resistance is often quantitative and polygenic (Cools & Fraaije, 2013).

Impact of Fungicide Resistance on Vegetables

Reduced efficacy of fungicides in disease control

Fungicide resistance has emerged as a major constraint to effective disease management in vegetable crops, posing a serious threat to sustainable agricultural productivity. Numerous investigations have reported widespread resistance among key vegetable pathogens (McGrath *et al.*, 2012). The primary mechanisms driving this phenomenon include alterations at fungicide target sites and the activation of efflux transport systems, both of which can rapidly diminish fungicide efficacy (Islam *et al.*, 2024).

Documented cases of resistance include the development of multiple fungicide resistance in *Botrytis cinerea* populations in strawberry production systems (Hahn *et al.*, 2014), rapid resistance evolution to metalaxyl in *Pseudoperonospora cubensis* (Malathrakis *et al.*, 1986), and the high adaptive potential of powdery mildew pathogens to overcome fungicidal control (McGrath *et al.*, 2001). The implications are substantial, as ineffective fungicide programs can render commercial vegetable cultivation economically unsustainable in several production regions (Wyenandt *et al.*, 2011). Consequently, there is an urgent consensus among researchers on the need to implement integrated fungicide resistance

Table 1: Major Fungicide Classes Used in Vegetables: Target Site, Common Mutations, and Resistance Risk.

Fungicide Class	FRAC Group	Molecular Target	Common Resistance Mutations	Resistance Risk
Multi-site protectants	M groups	Multiple cellular targets	Rare; non-specific	Low
DMIs (Azoles)	3	CYP51 (lanosterol 14 α-demethylase)	Y136F, I381V, promoter insertions, gene overexpression	Moderate
QoIs (Strobilurins)	11	Cytochrome b (Qo site)	G143A, F129L	High
SDHIs	7	Succinate dehydrogenase (sdhB, sdhC, sdhD)	B-H277Y, C-N75S, D-D123E	Moderate–High
Benzimidazoles	1	β-tubulin	E198A/G, F200Y	High
Phenylamides	4	RNA polymerase (oomycetes)	Multiple single-gene variants	Very High (oomycetes)

management strategies to safeguard long-term crop protection.

Increased disease incidence and severity

Fungicide resistance has directly contributed to increased disease incidence and severity in vegetable crops by allowing plant pathogenic fungi to survive and proliferate despite chemical control measures. As resistant populations expand, fungicide applications that were previously effective fail to suppress pathogen growth, resulting in more frequent and intense disease outbreaks (Islam *et al.,* 2024; Dorigan *et al.,* 2023).

The problem is particularly pronounced with fungicides having single-site modes of action, where resistance can develop rapidly due to strong selection pressure on pathogen populations (Valarmathi *et al.,* 2018). This rapid evolution of resistant strains leads to diminished fungicide performance over time, ultimately translating into increased disease spread, greater infection intensity, and heightened crop losses in vegetable production systems.

Economic losses and decreased crop yields

Recent bio-economic analyses demonstrate that fungicide resistance contributes to substantial crop yield losses by sustaining elevated disease incidence even under fungicide treatment. As resistant pathogen populations expand, fungicide efficacy declines, resulting in a higher proportion of infected fields at endemic equilibrium. Because diseased fields produce significantly lower yields than healthy fields, this persistence of infection translates directly into reduced overall crop productivity (Mikaberidze *et al.,* 2025).

Van den Bosch *et al*. (2020) demonstrate that fungicide resistance leads to crop yield losses primarily by reducing the ability of fungicide applications to suppress disease severity. Using long-term field data, the study shows that as the frequency of resistant strains increases, the dose–response relationship between fungicide application and disease control progressively flattens, resulting in higher residual disease levels even at increased doses. Because yield loss is directly related to disease severity, this erosion of fungicide efficacy translates into greater disease-induced yield penalties over time.

Ecological consequences, including shifts in pathogen populations

Fungicide resistance leads to profound ecological disturbances by reshaping pathogen population dynamics and undermining the long-term sustainability of agricultural systems. Several studies have documented these complex ecological effects. Kozhar *et al*. (2020) reported that fungicide application can exert a stronger influence on pathogen population structure than host-driven selection, resulting in increasingly localized and fragmented pathogen populations. Similarly, Yang *et al*. (2021) showed that greater host diversity reduces pathogen genetic variability and lowers the potential for fungicide resistance development, indicating that ecological diversification strategies can moderate resistance evolution.

Detection and Monitoring of Fungicide Resistance

The detection of fungicide resistance has advanced substantially in recent years, driven by the adoption of molecular approaches that enable sensitive and high-throughput identification of resistance-associated mutations in plant pathogens. A range of modern technologies is now being applied for resistance surveillance. Digital PCR, for example, allows the detection of resistance alleles present at extremely low frequencies, reportedly as low as 0.2% within mixed pathogen populations (Zulak *et al.,* 2018). Long-read sequencing platforms such as PacBio enable full-length sequencing of resistance-relate genes, facilitating detailed characterization of target-site mutations and structural variants (Samils *et al.,* 2021). In parallel, next-generation sequencing approaches are generating large-scale datasets on fungicide target genes, providing comprehensive insights into resistance diversity and evolution (Cherrad *et al.,* 2024).

In addition to sequencing-based methods, researchers have developed a variety of diagnostic tools, including quantitative PCR assays, third-generation sequencing technologies, and emerging CRISPR/Cas12a-based systems that enable rapid and visually interpretable detection of resistance mutations (Yin *et al.,* 2023). Collectively, these advances offer increasingly precise, rapid, and scalable tools for monitoring fungicide resistance dynamics in agricultural pathogen populations.

Crop-Specific Case Studies of Fungicide Resistance

Tomato: *Alternaria solani* (Early Blight)

Tomato early blight, caused by *Alternaria solani*, represents a classic example of resistance evolution under intensive fungicide programs. QoI resistance linked to the G143A mutation in cytochrome b has been documented globally (FRAC, 2024). Additionally, SDHI resistance mutations in sdhB and sdhC subunits have emerged in several production regions, reducing efficacy of carboxamide fungicides (Scalliet *et al.,* 2012). The high reproductive rate and repeated foliar sprays in tomato systems accelerate allele fixation, particularly in warm and humid conditions.

Cucurbits: *Pseudoperonospora cubensis* (Downy

Mildew)

Cucurbit downy mildew provides one of the earliest and most well-documented examples of phenylamide resistance. Field populations of *Pseudoperonospora cubensis* developed resistance to metalaxyl and mefenoxam shortly after their introduction (Parra & Ristaino, 2001). Resistance is typically governed by simple genetic mechanisms and can become widespread within a few growing seasons under continuous use. This case underscores the vulnerability of oomycete-targeted fungicides to rapid selection pressure.

Management Strategies for Fungicide Resistance

Effective management of fungicide resistance relies on an integrated framework that combines judicious fungicide use, continuous monitoring of pathogen populations, and active engagement with growers. Evidence from multiple studies supports several core management principles, including rotation among fungicides with different modes of action, restricting repeated use of single-site fungicides, and deploying fungicides in mixtures or alternation to reduce selection pressure (Corkley *et al.*, 2021).

Importantly, resistance management extends beyond technical recommendations to their on-farm adoption. Corkley *et al.* (2021) highlight that resistance mitigation strategies are only successful when growers implement them consistently, underscoring the need for effective communication and an appreciation of the trade-offs between short-term disease suppression and long-term preservation of fungicide efficacy.

Recent advances in molecular diagnostics further enhance resistance management by enabling early detection and large-scale surveillance of emerging resistance alleles, thereby allowing timely adjustment of control strategies (Yin *et al.*, 2023).

Conclusion

Fungicide resistance has emerged as a serious challenge to effective disease management in vegetable crops, largely due to intensive fungicide use and dependence on single-site modes of action. Resistance reduces fungicide efficacy, resulting in increased disease incidence and severity, yield losses, and economic constraints. Multiple target-site and non-target-site mechanisms contribute to cross- and multidrug resistance, further limiting available control options.

Recent advances in molecular diagnostics have improved resistance detection and monitoring; however, sustainable management depends on the adoption of integrated strategies, including fungicide rotation, use of mixtures, resistance surveillance, and informed on-farm implementation. Coordinated resistance management is essential to preserve fungicide effectiveness and ensure sustainable vegetable production systems.

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