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Review Article

The downy mildews of Iran: Unaddressed, hidden enemies

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ABSTRACT

Downy mildews, a group of obligate biotrophic oomycetes, are significant pathogens causing substantial agricultural losses globally. In Iran, these pathogens pose unaddressed challenges, impacting a wide range of economically important crops. This review consolidates current knowledge on downy mildews' taxonomy, biology, and phylogeny, focusing on their distribution and impact in Iran. We detail the various species affecting Iranian agriculture, such as *Plasmopara viticola* on grapevines and *Pseudoperonospora cubensis* on cucurbits, and highlight the economic implications and management difficulties posed by these pathogens. The review also examines historical outbreaks and their consequences, provides an overview of current diagnostic techniques, and discusses the limitations of existing management strategies in the Iranian context. Despite advances in molecular biology and genomics, the identification and control of downy mildews in Iran still need to be improved due to environmental and host diversity, limited research infrastructure, and evolving pathogen resistance. To address these issues effectively, we propose a comprehensive approach that includes: combining morphological data and the results of advanced molecular analyses; focusing on extensive sampling with the aim of identifying more than one species of some pathogenic genera on a single host species; applying enhanced molecular diagnostics; improving research collaboration; and implementing integrated pest management practices. Our findings underscore the importance of this comprehensive approach in mitigating the impact of downy mildews on Iranian agriculture.

KEYWORDS

Downy mildews, Host range, Molecular approaches, Morphology, Taxonomy.

INTRODUCTION

Downy mildews are a group of obligate biotrophic pathogens belonging to the order *Peronosporales* within the class *Oomycetes*. These pathogens are characterized by sporangia production on branched sporangiophores, which emerge from the stomata of infected host plants. Downy mildews primarily infect a wide range of economically significant crops, including grapevines, cucurbits, and brassicas, causing extensive foliar damage and compromising photosynthetic efficiency, leading to substantial agricultural losses globally (Thines and Kamoun 2010; Göker et al. 2007). The economic impact of downy mildews is substantial, as they can lead to significant yield losses, and necessitate increased fungicide applications, which result in higher production costs. Furthermore, these pathogens often display rapid adaptation and resistance to chemical compounds, complicating management strategies (Bourret et al. 2018). The oomycetes responsible for downy mildews are phylogenetically distinct from true fungi despite their similar morphological characteristics and ecological niches, which often confuses their identification and management (Bourret et al. 2018). Their phylogenetic distinction from true fungi, despite morphological similarities, emphasizes the necessity for

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precise taxonomic identification and tailored management approaches, which are crucial in mitigating the economic and agricultural impact of these diseases (Göker et al. 2007).

Recent molecular phylogenetic studies have provided profound insights into the taxonomy and evolution of these pathogens, emphasizing the need for precise identification to implement effective disease management strategies (Choi et al. 2015).

The global impact of downy mildews underscores the importance of continuous surveillance and the development of integrated pest management strategies. This includes the use of resistant cultivars, optimized chemical control, and cultural practices to mitigate the spread and severity of these diseases (Salcedo et al. 2021). In the context of climate change, understanding the epidemiology and adaptive potential of downy mildews becomes even more crucial, as environmental fluctuations can significantly influence their lifecycle and infection dynamics (Thines et al. 2023a). Therefore, the need for continuous surveillance and the development of integrated pest management strategies for downy mildews is more important than ever.

The economic impact of downy mildews in Iran is profound, with significant losses reported in crops such as grapevines and cucurbits. In Iran, downy mildews pose a significant threat to viticulture, as highlighted by research focusing on *Plasmopara viticola* (Berk. and M.A. Curtis) Berl. and De Toni, the causative agent of grapevine downy mildew, which has been responsible for severe yield reductions (Namvar-hamzanlue et al. 2020; Nasehi et al. 2023; Nityagovsky et al. 2024). Furthermore, the downy mildew affecting cucurbits, caused by *Pseudoperonospora cubensis* (Berk. and M.A. Curtis) Rostovzev, has been extensively studied in the region, revealing the pathogen's adaptive mechanisms and resistance to conventional fungicides (Pouzeshimiyab and Fani 2020). These pathogens not only reduce yield but also affect the quality of the harvest, leading to substantial financial losses for farmers (Pouzeshimiyab and Fani 2020; Nasehi et al. 2023; Nityagovsky et al. 2024). Effective management of downy mildews in Iran is hindered by the lack of experts for precise identification of these microorganisms, advanced tools, and the rapid evolution of pathogen resistance to fungicides (Zakeri et al. 2022; Nasehi et al. 2023).

Historical outbreaks of downy mildews worldwide and their consequences on agriculture

Historically, downy mildew outbreaks have had profound implications for global agriculture, often leading to devastating economic consequences. One of the most notorious outbreaks was the late 19th-century grapevine (*Vitis vinifera* L.) downy mildew epidemic caused by *P. viticola* in Europe, which decimated vineyards and necessitated the development of the Bordeaux mixture. The discovery of Bordeaux mixture revolutionized plant disease management (Fani et al. 2018; Fontaine et al. 2021). More recent outbreaks, such as those caused by *Ps. cubensis* on cucurbits in the United States, have highlighted the pathogen's ability to rapidly evolve and overcome resistance mechanisms, leading to significant crop losses and prompting ongoing research into sustainable control measures (Salcedo et al. 2021). These historical events affirm the importance of continuous monitoring, research, and innovation in combating downy mildews to mitigate their impact on agriculture.

Overview of downy mildews presence and possible impacts in Iran

In Iran, downy mildews pose a serious threat to several key agricultural sectors, particularly viticulture and horticulture. The presence of *P. viticola* has been documented in Iranian vineyards, causing considerable yield reductions and necessitating rigorous management practices (Namvar-hamzanlue et al. 2020; Nasehi et al. 2023). Similarly, *Ps. cubensis* poses a significant risk to cucurbit crops extensively cultivated nationwide. Research indicates that these pathogens can rapidly adapt to local environmental conditions and develop resistance to fungicides, making control efforts challenging (Pouzeshimiyab and Fani 2020). However, by implementing comprehensive strategies integrating resistant cultivars, effective chemical controls, and cultural practices, there is potential for success in sustainable disease management (Azadvar and Etebarian 2014).

Biology and lifecycle of downy mildews

Downy mildews, with their complex lifecycle involving both asexual and sexual reproduction, demonstrate remarkable adaptability and resilience. The asexual phase, where they produce sporangia on sporangiophores that emerge from the stomata of infected plants, allows for their rapid spread by wind or water to new hosts (Thines and Kamoun 2010). Sexual reproduction plays a crucial role in their survival and spread through the formation of oospores from the fusion of antheridia and oogonia. These oospores, capable of surviving in soil or plant debris, contribute significantly to overwintering and initiating new infection cycles (Göker et al. 2007; Bourret et al. 2018).

Host range and species diversity of downy mildews in Iran

Downy mildews in Iran, with their diverse host range, pose a significant threat to local agriculture by affecting multiple crops and wild plants. This adaptability not only challenges local management efforts but also has potential implications for global food security, as the spread of these pathogens can disrupt international agricultural trade and food supply chains. They affect numerous economically important crops across various regions (Table 1), with grapevines, cucurbits (*Cucurbitaceae*), and brassicas (*Brassicaceae*) being among the most impacted crops

(Pouzeshimiyab and Fani 2020; Nasehi et al. 2023). The diversity of downy mildew species in Iran, reflecting the country's varied climatic conditions, further exacerbates the problem by facilitating the proliferation of different pathogens. Species like *P. viticola* and *Ps. cubensis*, known for their significant agricultural impact, are a major concern (Namvar-hamzanlue et al. 2020). Comparative studies with global data reveal that downy mildews in Iran share many characteristics with those found worldwide, yet local adaptations present unique challenges for management (Salcedo et al. 2021).

Peronospora arborescens (Berk.) Casp., with its wide host range among the downy mildew species identified in Iran, infects 14 different hosts (Table 1), demonstrating its high adaptability and the complexity of the management of this pathogen. This adaptability can complicate management and control efforts, as this pathogen can survive and propagate across multiple crops and wild plants. Its extensive host range points to the necessity for comprehensive monitoring and integrated disease management strategies to mitigate its impact on agriculture. The second most versatile species is *Hyaloperonospora brassicae* (Gäum.) Göker, Voglmayr, Riethm., Weiss and Oberw., infecting six different hosts, followed by *Hyaloperonospora parasitica* (Pers.) Constant. and *Plasmopara halstedii* (Farl.) Berl. and De Toni, each infecting five hosts. While these species are less broadly adaptable than *P. arborescens*, they still exhibit robustness due to their ability to infect multiple host plants. The presence of multiple species with broad host ranges underlines the complexity of managing downy mildews especially in Iran. Each species' unique host interactions necessitate tailored approaches to disease prevention and treatment, highlighting the importance of more research in this field.

Major crops affected by downy mildews in Iran

In Iran, downy mildews primarily affect major crops such as grapevines, cucurbits, and various brassicas, leading to significant yield losses and economic strain on farmers (Fig. 1). Grapevine downy mildew, caused by *P. viticola*, is particularly destructive in the northern and northeast regions, where humid conditions favor the pathogen's lifecycle (Namvar-hamzanlue et al. 2020). Cucurbits, including cucumbers (*Cucumis sativus* L.) and melons (*C. melo* L. and *Cucumis* spp.), suffer from infections by *Ps. cubensis*, which can decimate entire fields if not managed effectively (Pouzeshimiyab and Fani 2020; Tör et al. 2023). Brassicas like white cabbage (*Brassica oleracea* var. '*capitata* f. *alba'* L.) and cauliflower (*Brassica oleracea* var. '*botrytis'* L.) are also vulnerable, with downy mildew pathogens causing severe foliar damage that reduces marketability and productivity. The widespread impact on these essential crops underscores the need for integrated disease management strategies, combining resistant cultivars, chemical treatments, and cultural practices to mitigate losses (Azadvar and Etebarian 2014).

Potential economic losses due to the effects of downy mildews in Iran

The economic implications of downy mildew infections in Iran are significant, potentially resulting in annual losses of millions of dollars worldwide and thousands of dollars in Iran. Beyond the well-documented impact on grapevines (*Plasmopara viticola*), which has jeopardized the viticulture sector with reduced yields and escalating fungicide costs (Namvar-Hamzanlue et al. 2020), other industries face similarly severe challenges.

In the cucurbit sector of Iran, *Pseudoperonospora cubensis* has led to notable reductions in cucumber and melon productivity. This pathogen thrives in the warm, humid conditions prevalent in certain agricultural zones, causing extensive foliage damage and necessitating frequent fungicide applications to mitigate losses (Pouzeshimiyab and Fani 2020). Likewise, the brassica industry struggles with *Hyaloperonospora brassicae*, which infects crops such as cabbage, cauliflower, and broccoli, resulting in stunted growth and diminished marketable yields. These pathogens exacerbate the financial strain on farmers, particularly smallholders, who often lack the resources for effective disease management (Sharifnabi and Nekoei 1995a).

The onion and garlic sectors are also affected by downy mildew caused by *Peronospora destructor* (Berk.) Casp. ex Berk., which leads to significant losses in bulb quality and storage longevity. In provinces such as Fars and Isfahan, outbreaks have been reported to devastate both local and export-oriented production, further undermining the profitability of these crops (Nasehi et al. 2023). Similarly, *Peronospora farinosa* on spinach presents challenges for leafy vegetable producers, where infection results in unsightly lesions and reduced consumer appeal, ultimately lowering market value (Banihashemi 2002).

Additionally, the legume industry has encountered issues with *Peronospora viciae* D.B. Jones, a pathogen impacting faba beans and lentils, leading to defoliation and poor seed set in key production areas like Khuzestan and Golestan provinces (Ahmed et al. 2000).

The economic toll of these pathogens extends beyond immediate crop losses, requiring ongoing investments in fungicides, resistant cultivars, and research into integrated management strategies. As observed globally, downy mildews in Iran exhibit a capacity for rapid adaptation, including resistance to chemical controls, further complicating management efforts (Salcedo et al. 2021; Tör et al. 2023).

List and description of known downy mildews of Iran

Iran is home to diverse downy mildew species, each with specific host preferences and ecological niches. Currently, there are eight genera of downy mildews in

Table 1. List of downy mildews reported from Iran.

Species	Matrix	Location	Reference
Bremia lactucae Regel			
	Lactuca sativa	Azarbaijan, Caspian sea area, Fars, Khuzestan	Ershad 1964; Scharif and Ershad 1966; Viennot-Bourgin et al. 1969; Ebrahimi and Minassian 1973; Vaziri 1973
	L. scariola	Khuzestan (Dezful)	Vaziri 1973
	Sonchus oleraceus	Khuzestan (Dezful), Hormozgan (Minab)	Vaziri 1973; Petreak 1956
	Willemetia tuberosus	Golestan (Kordkuy), Gilan (Lahijan), Mazanderan	Ershad 1964; Viennot-Bourgin et al. 1969
B. lactucae Regel **f. *carthami*** Milovtz			
	Carthamus tinctorius	Kermanshah, Khuzestan	Scharif and Ershad 1966; Viennot-Bourgin et al. 1969; Minassian 1971; Altman et al. 1972; Ebrahimi and Minassian 1973; Vaziri 1973; Alipour 2008
B. milovtzovae M. Mehrabi-Koushki, Z. Borjizad & R. Farokhinejad			
	Carthamus tinctorius	Khuzestan (Ahwaz)	Borjizad et al. 2024
B. sonchi Sawada			
	Sonchus asper	Hamedan	Viennot-Bourgin 1958
	S. oleraceus	Khuzestan (Dezful), Hormozgan (Minab)	Vaziri 1973; Petrak 1956
Hyaloperonospora brassicae (Gäum.) Göker, Voglmayr, Riethm., M. Weiss. and Oberw. [Syn. *Peronospora brassicae* Gaeum.]			
	Brassica caulorapa	Esfahan	Sharifnabi and Nekoei 1995
	B. deflexa	Karaj, Mazanderan	Sharifnabi and Nekoei 1995; Barari et al. 2004; Dehghani et al. 2008
	B. napus	Karaj, Khuzestan, Mazanderan	Scharif and Ershad 1965, 1966; Sharifnabi and Nekoei 1995; Barari et al. 2004
	B. oleracea	Esfahan	Sharifnabi and Nekoei 1995
	B. rapa		Sharifnabi and Nekoei 1995
	Sinapis arvensis	Hamedan, Tabriz, Tehran	Scharif and Ershad 1966; Viennot–Bourgin 1958
H. cheiranthi (Gäum.) Göker, Voglmayr, Riethm., M. Weiss. and Oberw. [Syn. *Peronospora cheiranthi* Gaeum]			
	Cheiranthus cheiri	Sari	Viennot-Bourgin et al. 1970
H. parasitica (Pers.) Constant. [Syn. *Peronospora parasitica*]			
	Eruca sativa	Tehran (Ramin)	Ebrahimi and Minassian 1973
	Euclidium syriacum	East Azerbaijan (Mardabad)	Hedjaroude and Abbasi 2000
	Lepidium campestre	Gilan (Fuman)	Ale-Agha 1978
	L. sativum	Khuzestan (Ahvaz), Golestan (Gorgan), Tehran (Ramin)	Scharif and Ershad 1965, 1966; Ebrahimi and Minassian 1973
	Malcolmia africana	Ghazvin, Razavi Khorasan (Gonabad)	Viennot-Bourgin et al. 1970; Ershad 1995
	Raphanus sativus	Khuzestan (Ahvaz), Tehran (Shahre Ray)	Ershad 1977; Etebarian 1989
	Sisymbrium irio	Khuzestan (Dezful)	Vaziri 1973
	Sisymbrium sp.	Khuzestan (Behbahan) Tehran (Ramin)	Viennot-Bourgin et al. 1969; Ebrahimi and Minassian 1973
H. thlaspeos–perfoliati (Cäum.) Göker; Voglmayr, Riethm, M. Weiss. and Oberw.			
	Thlaspi perfoliatum	Gilan (Lahigan)	Ale-Agha 1978
Peronospora aestivalis Syd.			
	Medicago minima	Golestan (Gorgan)	Ershad 1995
	M. lupulina	Tehran (Evin)	Hedjaroude and Abbasi 2000
	M. sativa	Widespread	Magnus 1899; Viennot-Bourgin 1958; Manuchehri 1964; Scharif and Ershad 1966; Viennot-Bourgin et al. 1970; Ebrahimi and Minassian 1973
P. alkannae Vienn.–Bourg.			
	Alkanna lutea	Tahran (Tonekabon)	Viennot-Bourgin 1968; Viennot-Bourgin et al. 1969
P. alta Fuckel			
	Plantago major	Uromieh	Viennot-Bourgin et al. 1970

Table 1. Continued.

Species	Matrix	Location	Reference
P. arborescens (Berk.) de Bary			
	Papaver somniferum	Khuzestan (Dezful), Esfahan, Fars, Semnan (Garmsar), Isfahan (Golpaygan), Hamedan, Sistan and Baluchestan (Iranshahr), Kermanshah, Kordestan, Lorestan, Hormozgan (Moghan), Hamedan (Nahavand), Tehran (Saveh), Semnan (Shahrud), Markazi (Tafresh), Yazd	Petrak and Esfasndiari 1941; Scharif and Ershad 1966; Scharif 1970; Vaziri 1973; Alavi 1974
	Papaver sp.	-	Golato 1960
P. destructor (Berk.) Casp. ex Berk.			
	Allium cepa	Azarbaijan, Gilan	Eskandari 1964; Scharif and Ershad 1966; Assadi and Izadyar 1973
P. effusa (Grev.) Rabenh., Klotzsc [Syn. *P. farinosa* (Fr.) Fr. f. sp. *spinaciae* Byford = *P. spinaciae* Laubert]			
	Spinacia oleracea	Laubert - Ahvaz, Dezful, Esfahan, Gorgan, Mazanderan, Varamin	Scharif and Ershad 1966; Daftari and Behdad 1968; Viennot-Bourgin et al. 1969; Ebrahimi and Minassian 1973; Vaziri 1973; Sadravi et al. 1995
P. erysimi **Gaeum.**			
	Erysimum cheiranthoides	Mazandaran **(**Sari)	Ale-Agha 1978
P. farinosa **(Fr.) Fr. f. sp.** ***betae*** Byford			
	Beta vulgaris	Ardebil, North Khorasan (Bojnord), Esfahan, Fars, Tehran (Ramin)	Anonymous 1969a; 1970; Shahidi 1970; Ebrahimi and Minassian 1973; Banihashemi 2002
P. farinosa **(Fr.) Fr. f. sp.** ***chenopodii*** Byford [Syn. *P. variabilis* Gaum]			
	Chenopodium album	Esfahan, Tehran (Evin), Mazandaran (Ghaemshahr), Golestan (Gorgan), Hamedan, Karaj, Mashhad, Tehran (Shemiran), Fars (Shiraz), Tehran (Varamin)	Petrak and Esfandiari 1941; Esfandiari 1946; Viennot-Bourgin 1958; Daftari and Behdad 1968
	C. murale	Khuzestan	Ebrahimi and Minassian 1973
	Chenopodium sp.	-	Daftari and Behdad 1968
P. iranica Petr. and Esfand			
	Conringia planisiliqua	Karaj	Petrak and Esfandiari 1941; Esfandiari 1946
P. lamii A. Braum			
	Satureja hortensis	Khuzestan (Ahzaz)	Ebrahimi and Minassian 1973
P. lepidii-sativi Gaeum.[*]			
	-	-	Ershad 1995
P. manshurica (Naumov) Syd.			
	Glycine max	Caspian sea area	Hedjaroude and Alé-Agha 1971; Zad 1979; Majidieh–Ghassemi 1986
P. maublancii Săvul. and Rayss.[*]			
	-	-	Ershad 1995
P. media Gacum.			
	Stellaria medias	Gilan (Anzali)	Viennot-Bourgin et al. 1970
P. meliloti Syd.			
	Melilotus alba	Karaj	Petrak and Esfandiari 1941
	M. ofivinalis	Karaj	Esfandiari 1946
P. minor (Casp.) Gaeum.			
	Chenopodium album		Esfandiari 1946
P. polygoni Halst.			
	Polygonum aviculare	Ahvaz, Gorgan	Ershad 1995
	Polygonum sp.		
P. rumicis Corda			
	Rumex chalepensis		Darvishnia et al. 2012
	Chenopodium murale	Ardebil	

Table 1. Continued.

Species	Matrix	Location	Reference
P. saturejae-hortensis			
	Satureja hortensis	Kermanshah	Khateri et al. 2021
P. sordida Berk.			
	Scrophularia alata	Kandevan	Petrak and Esfandiari 1941; Esfandiari 1946
P. sprasa Berk.			
	Rosa sp.	Ardebil	Esfandiari 1964
P. tabacina D.B. Adam.			
	Nicotiana tabacum	Azarbaijan, Caspian sea area, Kordestan	Niemann and Zalpoor 1963; Eskandari 1964; Zalpoor 1964, 1970; Ebrahim-Nesbat 1966; Niemann et al. 1966; Scharif and Ershad 1966; Ebrahim-Nesbat et al. 1969
P. trifoliorum de Bary			
	Trifolium sp.	Tehran (Ramin)	Ebrahimi and Minassian 1973
P. trigonellae Gaeum			
	Trigonella foenum-graecum	Golestan (Gorgan Kordkuy), Tehran (Ramin), Tehran	Khabiri 1958; Scharif and Ershad 1965; 1966; Ebrahimi and Minassian 1973
P. viciae (Berk.) Casp**. f. sp.** ***fabae*** Boerema, R. Pieters and Hamers			
	Vicia faba	-	Darvishnia et al. 2012
Peronosclerospora sorghi (W.Weston and Uppal) C.G. Shaw [Syn. *Sclerospora sorghi* W. Weston and Uppal.]			
	Sorghum sp.	Gilan (Rasht)	Ershad 1995
Plasmopara angustiterminalis Novot.			
	Xanthium strumarium	Gilan (Anzali), Esfahan	Ershad 1995
Pl. chaerophylli (Casp.) Trotter			
	Anthriscus sylvestris	Tehran (Damavand)	Viennot–Bourgin et al. 1970
Pl. halstedii (FarI.) Berl. and de Toni			
	Helianthus annus	Caspian sea area, Kermanshah, Kordestan, Lorestan, Markazi, Tehran	Minassian 1981; Viennot-Bourgin et al.1969; Scharif 1971; Anonymous 1973; Safaee 2004; Alizadeh and Rahmanpour 2005
Pl. skvortzovii Miura			
	Abutilon theophrasti	Gilan (Astara)	Ale–Agha 1987
Pl. viticola (Berk. and M.A. Curtis) Brel. and de Toni			
	Vitis vinifera	Azbarbaijan**,** Caspian sea area, Khorasan, Khuzestan	Esfandiari 1947, 1964; Viennot-Bourgin 1958; Eskandari 1964; Scharif and Ershad 1966; Altman et al. 1972; Anonymous 1973; Ebrahimi and Minassian 1973; Vazirri 1973
	Vitis sp.	Mazandaran (Ghaemshahr)	Kabiri 1952
Pseudoperonospora cubensis (Berk. and M.A. Curtis) Rostovzev			
	Citrullus vulgaris	Gilan, Kerman (Jiroft), Mazandaran	Scharif and Ershad 1966; Aazami-Sardouie et al. 1998
	Cucumis melo	Gilan, Kerman (Jiroft), Mazandaran	Ershad 1964a; Scharif and Ershad 1966
	C. sativus	Bandar Abbas, Gilan, Hajiabad, Kerman (Jiroft), Khuzestan, Mazandaran, Hormozgan (Moghan), Semnan	Eskandari 1946; Scharif and Ershad 1965, 1966; Anonymous 1969c; Mansoori 1991; Zakeri and Ommati 1991; Anonymous 2000
	Cucurbita pepo	Gilan, Mazandaran	Scharif and Ershad 1956, 1966
Ps. humuli (Miyabe and Takah.) G.W. Wilson			
	Humulus lupulus	Gilan (Astara)	Ale-Agha 1978
Sclerophthora macrospora (Sacc.) Thirum., C.G. Shaw and Naras.			
	Hordeum vulgare	Esfahan	Damad zadeh and Hasn–pour 1991
	Lolium sp.	Fars, Kohgiluyeh va Boierahmad	Izadpanah 1986

Table 1. Continued.

Species	Matrix	Location	Reference
	Sorghum sp.	Mashad	Izadpanah and Afsharifar 1990
	Triticum aestivum	Fars, Khorramabad, Kohgiluyeh va Boierahmad, Tehran (Varamin)	Minassian 1981; Izadpanah 1986
Sclerospora graminicola (Sacc.) J. Schröt			
	Pennisetum glaucum	Ardebil, Mazandaran (Ramsar), Tabriz	Viennot-Bourgin 1958
	S. italica	Fars (Shiraz)	Izadpanah and Ershad 1993
	Zea mays	Mazandaran (Ghaemshahr)	Viennot-Bourgin et al. 1970

* According to Ershad (1995), it is a synonym of *Peronospora parasitica*.

Iran, with 45 species infecting 20 different plant families (Table 1). These provinces of Iran, especially Khuzestan and Gilan Provinces, and they mostly infected the *Brassicaceae*, *Fabaceae*, and *Asteraceae* families. The genus *Peronospora,* with 26 species, is the most abundant and diverse genus in Iran, and *P. arborescens,* with a distribution among 15 different Provinces, is the most abundant species (Table 1). Key species include *P. viticola*, which mainly affects grapevines, causing characteristic oily spots on leaves and white downy growth on the undersides (Namvar-hamzanlue et al. 2020). *Pseudoperonospora cubensis*, responsible for cucurbit downy mildew, appears as angular yellow lesions on leaves, eventually leading to necrosis (Pouzeshimiyab and Fani 2020). Other notable species include *H. brassicae*, which targets brassicas, and *Pe. farinosa*, affecting sugar beet (*Beta vulgaris* L.; now *Peronospora farinose* f. sp. *betae*), spinach (*Spinacia oleracea* L.; now *P. effusa* (Grev.) Rabenh.), *Chenopodium album* L. (now *Peronospora variabilis* Gäum.), and other leafy greens (Nasehi et al. 2023).

Newly discovered species and their unique characteristics

Recent research has led to the identification of new downy mildew species in Iran, revealing unique characteristics that differentiate them from well-known pathogens (Borjizad et al. 2024). For instance, *P. halstedii*, discovered on sunflower (*Helianthus annuus* L.) crops, displays distinct morphological traits and pathogenicity profiles compared to its relatives (Alizadeh and Rahmanpour 2005). Similarly, some variants of *Ps. cubensis* have been identified, exhibiting resistance to commonly used fungicides and posing new challenges for cucurbit cultivation (Babadoost 2016; Pouzeshimiyab and Fani, 2020). Furthermore, species like *Peronospora saturejae-hortensis* Osipian and *Bremia milovtzovae* M. Mehrabi-Koushki, Z. Borjizad & R. Farokhinejad have recently been described from *Satureja hortensis* L. and *Carthamus tinctorius* L., respectively. *Bremia milvotzovae* was differentiated from other known species based on the phylogenetic analysis of cytochrome oxidase subunit II (*cox*2) gene (Borjizad et al. 2024). Advanced molecular techniques, such as DNA sequencing and phylogenetic analyses, have been instrumental in identifying and characterizing these new species, providing insights into their evolution and epidemiology (Bourret et al. 2018).

Current systematics of downy mildews

The systematics of downy mildews, belonging to the order *Peronosporales* within the class *Oomycetes*, has been significantly refined in recent decades due to advancements in molecular phylogenetics. While traditionally classified based on morphological characteristics, downy mildews are now better understood through the informative role of DNA sequencing techniques such as utilizing ribosomal DNA (rDNA), mitochondrial DNA (mtDNA), and other genomic markers, which have revealed extensive genetic diversity and complex evolutionary relationships among species (Thines and Choi 2016; Crouch et al. 2022). Molecular markers such as internal transcribed spacer (ITS), cytochrome oxidase subunit I (*cox*1), cytochrome oxidase subunit II (*cox*2), Large Subunit rRNA (LSU), Nicotinamide Adenine Dinucleotide (*NAD*) Dehydrogenase 1 (*NAD1*), and Ribosomal Protein S10 (*RPS10*) genes are commonly used in phylogenetic studies, providing robust frameworks for distinguishing between closely related species and understanding their evolutionary history (Göker et al. 2003; Mu et al. 2024a; Mu et al. 2024b). This genetic approach has also facilitated the identification of cryptic species and the reassessment of previously established taxonomic groups, leading to more accurate and comprehensive classifications (Bourret et al. 2018; Crouch et al. 2022; Mu et al. 2024b). Additionally, it was found that multiple species identified as the causal agents of downy mildew can infect the same plant species (Mu et al. 2024b).

Multi-locus phylogenetic analyses have led to the redefinition of genera like *Peronospora*, revealing polyphyletic groupings and prompting the reallocation of species to other genera, including *Hyaloperonospora* and *Plasmopara* (Göker et al. 2003; Voglmayr et al. 2006; Thines et al. 2023a). Redefining the boundaries of species has been supported by comprehensive multi-locus phylogenetic analyses, confirming the monophyly of downy mildews and highlighting their divergence from the *Pythiales* (Bourret et al. 2018; Khateri et al. 2021; Crouch et al. 2022; Thines et al. 2023a). Molecular phylogenetics has revolutionized the taxonomy of downy mildews by uncovering relationships previously obscured by similar morphological traits.

The application of molecular phylogenetics has been particularly impactful in the taxonomy of downy mildews in regions like Iran, where diverse climatic conditions foster the emergence of various downy mildew species. Through the use of multi-locus sequence analysis (MLSA), researchers have been able to construct detailed phylogenetic trees, elucidating the genetic relationships among species such as *P. viticola*, *Ps. cubensis*, and *H. brassicae* (Choi et al. 2015). In Iran, these techniques have unveiled unique genetic variants adapted to local conditions, underscoring the importance of region-specific studies in global taxonomic endeavors (Pouzeshimiyab and Fani 2020; Crouch et al. 2022; Nasehi et al. 2023). Integrating molecular data with traditional morphological and ecological information continues to improve the resolution and accuracy of downy mildew systematics (Thines et al. 2008; Crouch et al. 2022).

The whole-genome sequencing (WGS) of downy mildew, such as *P. viticola, Peronospora effusa* [Syn. *P. farinosa* (Fr.) Fr. f. sp. *spinaciae* Byford = *P. spinaciae* Laubert], and *Hyaloperonospora arabidopsidis*, has provided deeper insights into their evolution and host interactions. Comparative genomics of these pathogens has revealed a significant reduction in gene content, particularly in genes involved in primary metabolism, underscoring their reliance on host-derived nutrients (Baxter et al. 2010; Derevnina et al. 2015; Nasehi et al. 2023). Furthermore, identifying their effector proteins has also advanced our understanding of pathogenicity mechanisms, highlighting the role of RxLR effectors in host manipulation and immunity suppression, while elucidating evolutionary divergence and species differentiation (Win et al. 2008; Nasehi et al. 2023).

Phylogenetic and population genetic studies have elucidated the co-evolutionary dynamics between downy mildews and their hosts. The concept of host jumps, where downy mildews transition between different host species, has been substantiated by molecular data, suggesting a complex evolutionary history driven by host-specific adaptation (Thines 2014; Thines et al. 2023b). Host-specific adaptation is exemplified by *P. halstedii*, which infects sunflowers and exhibits significant genetic differentiation correlating with host plant diversity (Viranyi et al. 2015; Crouch et al. 2022).

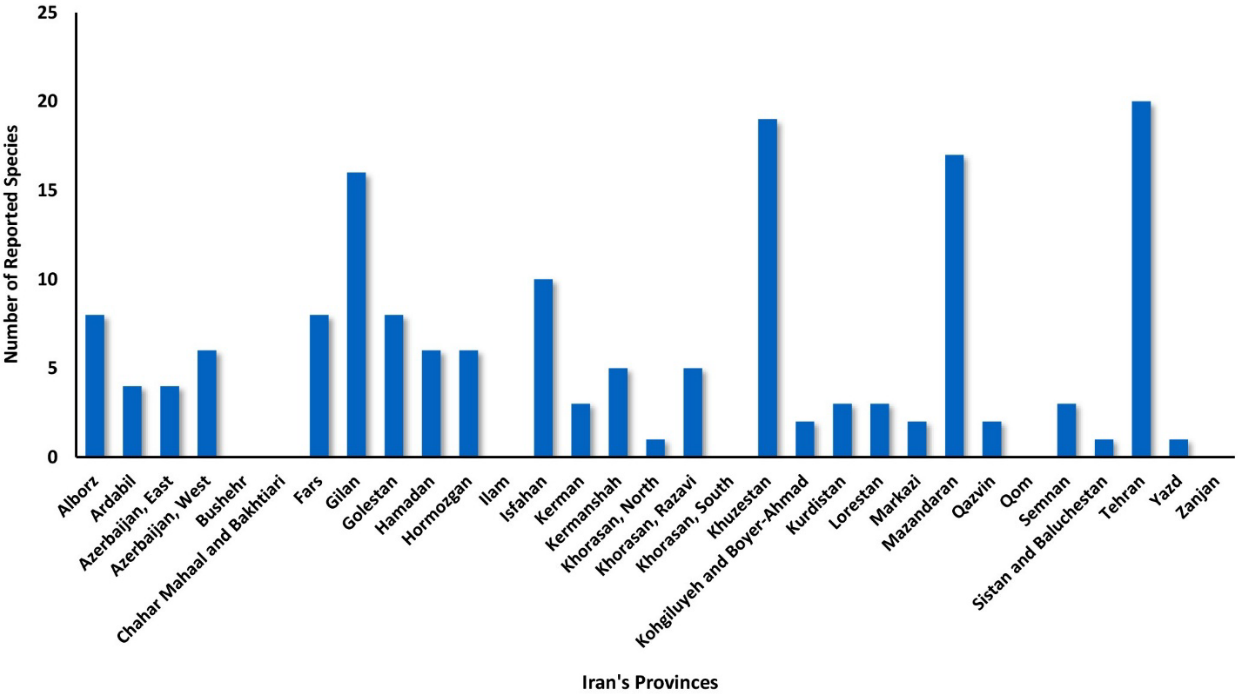

Fig. 1. A comparison of the number of reported downy mildew species from each province of Iran.

Impact of accurate identification on disease management

The refined systematics of downy mildews has profound implications for disease management and agricultural practices. Accurate species identification is crucial for developing effective control strategies, as different downy mildew species exhibit varying pathogenicity, host range, and treatment resistance (Fontaine et al. 2021). In Iran, precise taxonomic information aids in the deployment of targeted fungicides and resistant cultivars (Namvar-hamzanlue et al. 2020; Nasehi et al. 2023). Furthermore, understanding the evolutionary relationships and genetic diversity among downy mildews can inform breeding programs and develop integrated pest management (IPM) strategies tailored to local pathogen populations (Bourret et al. 2018; Salgado-Salazar et al. 2023). The ongoing research in molecular phylogenetics and systematics is a dynamic and exciting field, constantly revealing new insights and potential solutions for advancing scientific understanding and practical management of downy mildews worldwide (Thines 2014). The ecological significance of downy mildews extends beyond their direct impact on individual plant species. They influence plant community dynamics and biodiversity, acting as agents of natural selection. In agriculture, downy mildews seriously threaten crops such as grapes, lettuce, and cucurbits, necessitating ongoing surveillance and the development of resistant cultivars (Gobbin et al. 2003; Thines et al. 2008; Nasehi et al. 2023).

Detection and identification approaches of downy mildews

Traditional methods of identification of downy mildews and their taxonomic characterization

The identification and detection of downy mildews traditionally relied on morphological and histological methods. These classical approaches, once the cornerstone of our field, are now proven inadequate. They include the examination of symptoms in host plants, such as chlorotic lesions, wilting, premature leaf drop, crazy top, leaf curling, yellowing, stunt growth, reduced yield, and downy growth on the undersides of leaves, followed by microscopic analysis of the pathogen's sporangia and sporangiophores (Nasehi et al. 2023). Morphological characteristics, such as the shape, size, and structure of sporangia and oospores, as well as form of haustoria have been pivotal in differentiating downy mildew species (Hansen et al. 2012; Thines 2014; Mu et al. 2024a).

Downy mildews, exhibit specialized morphological and physiological features, many of which play a central role in their taxonomy (Göker et al. 2007; Thines and Kamoun 2010; Bourret et al. 2018). Among these, haustoria-specialized feeding structures formed within host cells, are particularly valuable for species differentiation (Thines 2014; Ah-Fong et al. 2019). Haustorial morphology is highly diverse across downy mildew species and provides a critical diagnostic tool for taxonomy, often correlating with host specificity and pathogenic strategy (Constantinescu and Fatehi 2002; Riethmüller et al. 2002; Voglmayr et al. 2004; Thines 2014). For instance, *Plasmopara halstedii*, a pathogen of sunflowers, produces digitate (finger-like) haustoria (Choi et al. 2009), while *Peronospora sparsa* Berk., which infects roses, forms globose or spherical haustoria (Thines and Choi 2016). These distinct morphologies not only reflect adaptations to different hosts but also serve as reliable taxonomic markers when examined microscopically (Thines 2014).

The shape, size, and branching patterns of haustoria are key in distinguishing morphologically similar species. For example, *Bremia lactucae* Regel, a pathogen of lettuce, forms complex, highly branched haustoria (Volgmayr et al. 2004), differing significantly from the simpler, knob-like haustoria of *Peronospora farinosa* (Fr.) Fr., (now known as *P. effuse* (Grev.) Rabenh., Klotzsc), which infects spinach (Feng et al. 2014). Similarly, *Hyaloperonospora arabidopsidis* (Gäum.) Göker, Riethm., Voglmayr, Weiss and Oberw., infecting *Arabidopsis thaliana* L., forms slender, elongated haustoria (Constantinescu and Fatehi 2002), contrasting with the stout and slightly branched haustoria of *Plasmopara viticola*, a pathogen of grapevines (Thines 2014). These differences, though subtle, are crucial in resolving taxonomic ambiguities in closely related species.

Further examples highlight the importance of haustoria in taxonomy. *Peronospora tabacina* D. B. Adam, the tobacco downy mildew, develops haustoria with distinctive wall thickenings near the base, a feature absent in other *Peronospora* species (Thines and Choi 2016). *Plasmopara geranii* (Peck) Berl. and De Toni, infecting geraniums, forms intricately branched haustoria that extend deeply into host cells (Volgmyr et al. 2006), contrasting with the sparsely branched haustoria of *Plasmopara obducens* (J. Schröt.) J. Schröt., which was previously known as *Impatiens* species (Choi et al. 2020). Additionally, *Peronospora manshurica* (Naumov) Syd., a pathogen of soybean, produces haustoria with unique globoid swellings at their tips, further distinguishing it from other species in the genus (Thines and Choi 2016).

The taxonomic significance of haustoria extends beyond morphology; their development and interaction with host tissues can reflect evolutionary relationships. For example, species with highly specialized haustoria, such as *Plasmopara halstedii*, often exhibit narrow host ranges, while those with simpler structures, like *Peronospora destructor*, may infect a broader array of plants. This relationship between haustorial complexity and host specificity provides valuable context for understanding pathogen diversity and evolution (Thines 2014; Ryley et al. 2022).

In addition to the importance of haustoria in morphological identification, conidiophore shapes, branch orders, and branch lengths have recently been used as key characteristics separating newly described species such as *P. psylliicola* M. Mu, J. Kruse and Thines which indicates that the morphological characteristics of *Peronospora* species may exhibit greater conservation compared to their host range, aligning with the numerous instances of host-switching reported within the genus (Telle and Thines 2012; Ploch et al. 2022; Mu et al. 2024b). By integrating haustorial morphology with other diagnostic features, such as sporangial shape, sporangiophore branching, and molecular data, taxonomists can achieve a more nuanced classification of downy mildews. In a field where cryptic species and morphological plasticity pose significant challenges, haustoria offer a stable, host-linked trait that enhances the accuracy and robustness of species identification. Traditional methods of identification often require extensive expertise and may not always provide definitive identification due to the phenotypic plasticity of the pathogens (Thines and Choi 2016; Mu et al. 2024b). Furthermore, traditional methods are time-consuming and may be inadequate for detecting early infections or distinguishing between closely related species (Hall 1996). In Iran, these conventional techniques have been fundamental in initial species cataloging, but their limitations necessitate the incorporation of more advanced methodologies for accurate and timely identification.

Advanced methods of identification of downy mildews worldwide

Molecular techniques have dramatically altered the methods of detection and identification of downy mildews, offering greater precision and reliability. Polymerase Chain Reaction (PCR)-based methods, including species-specific primers and real-time PCR, have become standard tools for identifying downy mildew pathogens at the genetic level (Ristaino et al. 1998; Thines and Choi 2016; Nasehi et al. 2023; Mu et al. 2024b). These techniques allow for the rapid and sensitive detection of downy mildews, even at early infection stages or from asymptomatic plant tissues. DNA barcoding, using loci such as the ITS and *cox*2, has facilitated the differentiation of closely related species and the identification of cryptic species (Göker et al. 2007; Mu et al. 2024a).

Researchers have also emphasized the significance of integrating traditional barcoding methods with advanced detection techniques to improve species identification in downy mildew pathogens (Salcedo et al. 2021). Secondary barcodes offer the resolution required to distinguish closely related species while increasing diagnostic accuracy. Thus, using a combination of primary (ITS) and secondary barcodes (CAM (calmodulin), *GAPDH* (glyceraldehyde-3-phosphate dehydrogenase), *GS* (glutamine synthetase), *NAD1*, *RpB2* (RNA polymerase II second largest subunit), and RPS10) allows for a more robust systematic framework that facilitates the detection of cryptic species and refines phylogenetic classifications (Bradshaw et al. 2022; Mu et al. 2024a). These advances significantly enhance the understanding of evolutionary relationships within downy mildews.

In addition, high-throughput sequencing technologies and metagenomics provide comprehensive insights into the pathogen community structure and genetic diversity (Thines et al. 2008; Nasehi et al. 2023). In Iran, integrating these advanced molecular tools with traditional methods enhances the accuracy of pathogen identification, and supports effective disease management strategies (Pouzeshimiyab and Fani 2020; Nasehi et al. 2023).

Challenges in identifying downy mildews

Despite significant advancements in detection and identification technologies, there is a pressing need for improved identification methods. The persistent challenges in accurately identifying downy mildews, due to their complex life cycles, morphological plasticity, and close genetic relationships with other plant pathogens, underscore the need for improvement. Specific environmental, agricultural, and infrastructural factors in Iran exacerbate these challenges. Recent advances in molecular biology and genomics have provided insights into these issues, yet several hurdles remain (Thines 2014; Nasehi et al. 2023).

Morphological characteristics of downy mildews can be highly plastic and influenced by environmental conditions, leading to misidentification. For example, species within the genus *Peronospora* exhibit significant morphological overlap, complicating accurate diagnosis (Thines 2014; Choi et al. 2015; Nasehi et al. 2023). Moreover, the potential presence of several species of downy mildews on a single host complicates the identification of species according to their host preferences (Mu et al. 2024b).

Molecular identification techniques such as ribosomal DNA (rDNA) sequencing, mitochondrial DNA (mtDNA) markers, and whole-genome sequencing have provided more reliable identification tools. However, the lack of comprehensive genomic databases for local downy mildew species hinders the effectiveness of these methods and complicates precise identification (Thines et al. 2008). Such limitations not only hamper accurate identification but also restrict the development of effective management strategies.

One major issue is the genetic variability within and between species, which can complicate the development of reliable molecular markers (Thines 2014). The horizontal gene transfer and hybridization events among downy mildew species further obscure phylogenetic relationships and complicate taxonomic classification (Choi et al. 2015).

Iran's diverse climatic regions, ranging from arid and semi-arid to temperate zones, create various ecological niches for downy mildews. This diversity complicates the establishment of a unified identification framework, as exemplified by *Plasmopara viticola*, the causal agent of grapevine downy mildew. Variations in pathogenicity and adaptation of *P. viticola* across Iran's climatic zones suggest the presence of regionally distinct pathotypes or genetic variants. While still classified as a single species, these variants differ in host specificity, aggressiveness, and environmental tolerance, underscoring the need for region-specific diagnostic tools and population-level studies (Thines and Choi 2016; Nasehi et al., 2023).

Similar complexities are observed in *Peronospora farinosa* populations infecting spinach in Iran's humid Caspian region, where isolates exhibit virulence profiles shaped by local host genotypes and environmental conditions (Lebeda et al. 2011; Feng et al. 2014). In Brassica crops, *Hyaloperonospora brassicae* populations from the semi-arid western regions display significant genetic differentiation from those in temperate zones, reflecting adaptation to regional climatic pressures and necessitating tailored fungicide application strategies (Constantinescu and Fatehi 2002; Pouzeshimiyab and Fani 2020). Likewise, *Pseudoperonospora cubensis*, infecting cucurbits, demonstrates notable genetic variation between arid and humid areas, complicating disease management and emphasizing the importance of localized diagnostic frameworks (Lebeda et al. 2011).

The pathogenic diversity of *Peronospora manshurica*, a downy mildew pathogen of soybean, further illustrates the taxonomic challenges in distinguishing closely related pathotypes. Populations in the western highlands of Iran have shown resistance to commonly used fungicides (Nasehi et al. 2023), which highlights the need for advanced molecular tools to screen for resistance genes and track population dynamics (Thines and Kamoun 2010; Thines 2014). Similarly, *Peronosclerospora sorghi* Mundkur, affecting maize and sugarcane in southern Iran as well as Caspian regions, exhibits genetic variability linked to fungicide resistance and local environmental adaptation, posing additional difficulties for taxonomic and diagnostic clarity (Crouch et al. 2022).

The integration of DNA-based tools, such as next-generation sequencing, phylogenetic analysis, and molecular markers, into population studies, is essential for resolving taxonomic ambiguities and understanding the pathogenicity mechanisms of downy mildews. These tools can identify cryptic diversity, detect fungicide resistance genes, and uncover region-specific adaptations, providing critical insights into population dynamics. For instance, DNA barcoding has been successfully applied to distinguish cryptic species within the *Plasmopara* genus, revealing variations that correlate with host and environmental conditions (Göker et al. 2007; Ascunce et al. 2017; Elameen et al. 2022). Such molecular approaches not only enhance taxonomic precision but also guide region-specific management strategies, offering a comprehensive solution to the challenges posed by pathogenic diversity.

This observation aligns with a broader understanding of oomycete systematics, which suggests that ecological factors frequently drive intraspecific genetic diversity, leading to the creation of distinct variants or populations within the same species.

Additionally, Iran's agricultural practices, including cultivating a wide range of susceptible crops such as grapevines, cucurbits, and legumes, provide ample opportunities for downy mildew outbreaks. The lack of standardized monitoring and reporting systems for downy mildew infections further challenges early detection and accurate identification (Babadoost 2016).

Environmental factors, such as temperature and humidity, play a significant role in the expression of morphological traits, which adds complexity to the identification process (Thines 2014; Nasehi et al. 2023). In regions like Iran, with diverse climatic conditions and host plants, these challenges are magnified, necessitating continuous monitoring and adaptation of identification protocols (Nasehi et al. 2023). Additionally, the need for specialized equipment and expertise for advanced molecular techniques can hinder their widespread adoption, particularly in resource-limited settings. Addressing these challenges requires ongoing research and global collaboration among scientists to develop robust, accessible, and accurate identification methods.

Research on downy mildews in Iran has historically been traditional host-based diagnosis and underfunded, resulting in limited local expertise and outdated diagnostic facilities. The need for more trained mycologists and plant pathologists is crucial, as their expertise is essential for conducting comprehensive identification and phylogenetic studies. However, the current lack of funding for advanced molecular research restricts the capacity to train and retain such experts. Moreover, collaboration between academic institutions and agricultural stakeholders is needed to ensure the translation of research findings into practical diagnostic tools. Establishing a centralized database and a network of diagnostic laboratories equipped with molecular identification capabilities is essential for overcoming these limitations.

Downy mildews exhibit rapid evolution and adaptability, often developing resistance to fungicides. This adaptive potential complicates identification as new, previously unrecorded strains emerge and poses a significant threat to agricultural productivity (Thines 2014). For example, the emergence of fungicide-resistant strains of *P. halstedii*, has been reported in several regions of Iran, making conventional identification and control measures less effective (Nasehi et al. 2023). This example underscores the urgent need for more effective diagnostic framework and the importance of ongoing research to stay ahead of these evolving pathogens.

The differentiation of host genera and their associated pathogens, particularly in *Hyaloperonospora* and *Peronospora*, is critical in resolving the complexities of downy mildew taxonomy. For example, the pathogen infecting *Cardaria draba* L., initially classified as *Peronospora lepidii-sativi* Gaeum, has been redefined as a distinct *Hyaloperonospora* species through ITS and LSU sequencing (Constantinescu and Fatehi 2002). Similarly, the pathogen on *Lepidium sativum* L. (*i.e. Hyaloperonospora parasitica*), often confused with the one infecting *Coronopus* sp. (*i.e. Perofascia lepidii* (McAlpine) Constant.), was identified as a separate species within *Hyaloperonospora* using molecular tools, underscoring the importance of host specificity (Göker et al. 2009). Initially, *Hyaloperonospora parasitica* was presumed to be the causal agent of *Lepidium* spp. and *Cornopus* sp.; however, subsequent studies revealed that these pathogens belong to distinct genera, *i.e. Hylaoperonospora* and *Perofascia* (Constantinescu and Fatehi 2002). In another case, the pathogen infecting *Brassica oleracea* (*Hyaloperonospora brassicae*) was historically grouped with similar pathogens on other *Brassicaceae* hosts, but molecular analyses clarified its unique host range and evolutionary history (Göker et al. 2009).

The model system of *Arabidopsis thaliana* and its pathogen *Hyaloperonospora arabidopsidis* further demonstrates the power of host-pathogen studies, with the complete genome sequence of *H. arabidopsidis* revealing its distinct taxonomic position (Ried et al. 2019). Population studies on pathogens, such as *Hyaloperonospora arabidopsidis* reveal insights into adaptive strategies, including fungicide resistance, which have significant implications for taxonomy and disease management. Similarly, the downy mildew pathogen associated with *Capsella bursa-pastoris* L. appeared morphologically similar to other *Brassicaceae* pathogens but was genetically distinct, illustrating the divergence driven by host specificity. On *Raphanus sativus* L., the pathogen *Hyaloperonospora raphani* was identified as separate from other species within the genus due to its unique host association, despite overlapping morphological features (Shainidze et al. 2023).

These examples emphasize the critical role of molecular tools in identifying subtle genetic differences that cannot be discerned through morphology alone. Moreover, by integrating host specificity and molecular phylogenies, these cases highlight the necessity of robust taxonomic frameworks to unravel host-pathogen co-evolution and inform agricultural practices effectively (Constantinescu and Fatehi 2002).

The identification of downy mildews in Iran is notably complex due to the country's diverse climatic zones and varied agricultural practices. These pathogens demonstrate significant morphological variability, making traditional identification methods insufficient and underscoring the need for molecular techniques such as DNA sequencing and phylogenetic analysis (Tör et al. 2023). However, the application of these advanced methods is hindered by limited access to diagnostic technologies and the absence of localized genomic databases for Iran's downy mildew species.

CONCLUSION

The identification and management of downy mildews have been substantially advanced by integrating traditional morphological methods with modern molecular techniques. While traditional identification methods, based on phenotypic traits and histological examination, provide foundational knowledge, their limitations in both accuracy and efficiency (Hansen et al. 2012; Nasehi et al. 2023) underscore the need for modern techniques. The advent of molecular phylogenetics has dramatically enhanced our understanding, offering precise and rapid identification through DNA sequencing and PCR-based methods (Ristaino et al. 1998; Göker et al. 2003). These approaches have revealed significant genetic diversity and evolutionary relationships, facilitating more effective disease management strategies (Thines and Choi 2016). However, challenges remain, particularly in regions with high biodiversity and environmental variability, such as Iran, where downy mildew species exhibit unique adaptations and genetic variations (Pouzeshimiyab and Fani 2020).

The downy mildews of Iran, often neglected and under-researched, continue to pose a significant threat to the country's agriculture. The integration of high-throughput sequencing technologies, combined with advanced bioinformatics, offers a promising avenue to identify these "hidden enemies" by refining their systematics and uncovering previously unknown species or genetic variants. This advanced molecular approach is critical for understanding the full diversity of downy mildews in Iran's varied ecological regions, thereby enabling a more accurate identification framework (Bradshaw et al. 2022; Nasehi et al. 2023).

Future research should focus not only on mapping this diversity but also on deciphering the genetic basis of host specificity. By exploring how downy mildews interact with their host plants, researchers can better predict disease outbreaks and design targeted control measures that are tailored to the region's agricultural needs. Furthermore, the potential application of CRISPR-Cas9 technology to edit the genomes of downy mildews represents an unprecedented opportunity, offering novel insights into their biology and pathogenicity. This advancement could enhance our ability to combat these pathogens, which have long remained unaddressed and hidden in Iran (Belhaj et al. 2017).

This shift toward genetic-level interventions marks a significant advancement in both the systematics and control of downy mildews in Iran, addressing the urgent need for sustainable, science-driven solutions to manage these pervasive pathogens.

Identifying research gaps

Despite the advancements of using several tools to identify the species assigned to the downy mildews and their genetic diversity determination, several research gaps still warrant further investigation. One critical area is the need for a comprehensive genetic database of downy mildew species, especially in understudied regions such as Iran. A comprehensive genetic database would enhance species identification and support the development of region-specific management strategies (Thines 2014). Additionally, it is crucial to understand the resistance mechanisms of pathogens to current control measures, such as fungicides, to develop sustainable management practices. Research into the evolutionary dynamics of downy mildews, including events such as horizontal gene transfer and hybridization, can provide valuable insights into their adaptability and resilience (Choi et al. 2015). Finally, focusing on the impact of climate change on the distribution and virulence of downy mildews is of great importance, as changing environmental conditions can alter pathogen behavior and host interactions (Fontaine et al. 2021).

A critical barrier to effective management is the lack of standardized monitoring systems and reporting frameworks for downy mildew infections. This deficiency delays early detection and undermines efforts to track outbreaks systematically. Compounding the issue is the pathogens' rapid evolution, which frequently results in resistance to fungicides, rendering many chemical control measures ineffective over time. This dynamic adaptability highlights the need for a robust, region-specific approach that combines advanced molecular diagnostics with proactive management strategies to mitigate the threats posed by downy mildews (Babadoost 2016; Salcedo et al. 2021).

Suggest areas for further investigation

Addressing the aforementioned challenges requires a multifaceted approach. Future research should prioritize the integration of advanced molecular techniques with traditional methods to enhance the resolution and accuracy of downy mildew identification. Enhancing molecular diagnostic facilities and training local experts in advanced identification techniques is crucial. Establishing regional diagnostic centers equipped with next-generation sequencing technologies can improve identification accuracy (Salcedo et al. 2021). Furthermore, developing high-throughput sequencing technologies and metagenomic approaches can provide comprehensive insights into pathogen community structure, enabling the identification of novel species and a deeper understanding of disease dynamics (Thines et al. 2008). Promoting collaborative research between Iranian and international institutions can facilitate knowledge transfer and the development of comprehensive genomic databases. Joint projects focusing on the phylogenetics and genomics of local downy mildew species will provide valuable insights for accurate identification. However, it is important to stress the urgency and significance of early detection and accurate identification. Implementing standardized monitoring protocols and creating a national repository of downy mildew samples will support this, and is a key part of our strategy. Expanding data collection and field assessments in Iran can help track the spread and evolution of downy mildew pathogens, particularly the emergence and spread of new strains, thereby informing effective control measures (Namvar-hamzanlue et al. 2020). Developing and promoting integrated pest management strategies that incorporate resistant cultivars, biological control agents, and sustainable agricultural practices can reduce the prevalence of downy mildew infections and minimize the selection pressure for resistant strains.

Future research on downy mildew management should adopt integrative approaches that bridge molecular insights with ecological and agronomic applications. Building on recent advances in effector biology, such as the identification of *Peronospora manshurica* effector targets in soybean (*Glycine max* L.) jasmonic acid pathways (Dong et al. 2018) and *Plasmopara halstedii'*s disruption of ROS signaling in sunflowers, priorities include developing multi-mechanism resistance strategies (Gouveia et al. 2024). For instance, stacking effector-neutralizing genes (e.g., those in resistant soybean cultivars) with systemic defense amplifiers (e.g., enhanced jasmonic acid signaling) could create durable resistance while mitigating pathogen adaptation. Concurrently, precision tools like CRISPR/Cas9 and RNAi should be optimized to silence pathogen effectors, as successfully applied in *Pseudoperonospora cubensis* in cucurbits (Tör et al. 2023), or edit host susceptibility factors as achieved in spinach transcription factors targeted by *Peronospora farinose* (Feng et al. 2014; Clark et al. 2024). Tracking effector evolution through pathogen population genomics will facilitate proactive breeding for climate-resilient crops, particularly as environmental stressors increasingly influence host-pathogen interactions (e.g., temperature effects on ROS-mediated defenses). Integrating multi-omics data to map effector-targeted networks, such as stomatal manipulation in cucumbers, could uncover novel engineering targets. Additionally, mining wild cultivars may reveal cross-applicable resistance traits. By synergizing these strategies, researchers can transition from reactive chemical treatments to predictive, systems-based frameworks that enhance global food security under evolving biotic and abiotic pressures.

In *Arabidopsis thaliana*, *Hyaloperonospora arabidopsidis* RXLR effectors interfere with immune signaling pathways by targeting intracellular hubs critical for defense activation. Insights from this model system are being applied to develop diagnostic tools for other crops with economic importance (McDowell 2014). These examples underscore the relevance of understanding effector biology in diverse host-pathogen systems, offering pathways to inform breeding, diagnostics, and advanced molecular strategies for sustainable disease management.

The distribution of reported downy mildew species in Iran, as illustrated in Fig. 1, reveals significant disparities among provinces. Khuzestan and Tehran show the highest numbers of reports, suggesting a stronger focus on research and identification efforts in these areas. Conversely, several provinces, with notably fewer or no reports, reflect gaps in systematic studies or underrepresentation of data. This emphasizes the need for broader investigations to better understand the actual diversity and distribution of downy mildews across the country.

Furthermore, interdisciplinary research that combines plant pathology, molecular biology, and climate science holds the potential for groundbreaking discoveries. This approach is crucial for addressing the complex interactions between downy mildews and their environments. It underscores the vital role of collaboration among international research communities in sharing knowledge, resources, and strategies. This collaboration is essential for enhancing global food security by mitigating the impact of downy mildews on agriculture (Bourret et al. 2018). Developing and promoting IPM strategies that incorporate resistant cultivars, biological control agents such as *Trichoderma* spp., *Bacillus* spp., and *Fusarium verticillioides* (Sacc.) Nirenberg (Djaenuddin et al. 2024), along with sustainable agricultural practices can significantly reduce the prevalence of downy mildew infections and minimize the selection pressure for resistant strains. Due to Iran's particular climatic conditions, where downy mildews pose a significant threat, increased research on the specific downy mildew pathogens affecting Iranian agriculture, combined with tailored IPM strategies, could greatly enhance crop resilience and ensure food security in the context of changing climate conditions.

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AUTHOR CONTRIBUTION

Fatemeh Salmaninezhad: Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. Zeinab Bolboli: Formal analysis, Investigation, Validation, Visualization, Writing – review & editing. Hossein Masigol: Validation, Writing – review & editing. Reza Mostowfizadeh-Ghalamfarsa: Conceptualization, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

DATA AVAILABILITY

The datasets generated during and analyzed during the current study are in supplementary tables or available from the corresponding author on reasonable request.

DECLERATION

The authors have no conflict of interest to declare.

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ETHICS APPROVAL

Not applicable.

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چکیده

سفیدک‌های کرکی، گروهی از اُآمیست‌های زیواپرور اجباری، بیمارگرهای مهمی هستند که به طور قابل توجهی به محصولات کشاورزی در سراسر جهان خسارت وارد می‌کنند. در ایران، این بیمارگرها چالش‌های حل‌نشده‌ای را ایجاد کرده، طیف وسیعی از محصولات کشاورزی مهم اقتصادی را تحت تأثیر قرار می‌دهند. این نوشتار، مروری بر دانش کنونی در مورد رده‌بندی، زیست‌شناسی و فیلوژنی سفیدک‌های کرکی با تمرکز بر پراکندگی و تأثیر آن‌ها بر محصولات زراعی و باغبانی در ایران است. گونه‌های مختلفی که بر کشاورزی ایران تاثیر می‌گذارند، از جمله *Plasmopara viticola* روی تاک انگور و *Pseudoperonospora cubensis* روی کدوییان، تشریح و پیامدهای اقتصادی و مشکلات مدیریتی ناشی از این بیمارگرها در این مطالعه برجسته شده‌اند. همچنین به تاریخچه‌ی طغیان این بیمارگرها و پیامدهای آن، ارائه مروری بر راه‌بردهای تشخیصی فعلی و بحث در مورد محدودیت‌های راه‌بردهای مدیریتی موجود در زمینه ایران پرداخته شده است. با وجود پیشرفت‌های صورت گرفته در زیست‌شناسی مولکولی و ژنومیک، شناسایی و مهار سفیدک‌های کرکی در ایران هنوز به دلیل تنوع محیطی، میزبانی، زیرساخت‌های تحقیقاتی محدود و تکامل مقاومت بیمارگرها نیازمند بهبود است. برای حل مؤثر این مشکلات، رویکردی جامع پیشنهاد شده که شامل تلفیق داده‌های ریخت‌شناختی و نتایج واکاوی‌های مولکولی پیشرفته، تمرکز بر نمونه‌برداری‌های گسترده با رویکرد شناسایی بیش از یک گونه از برخی جنس‌های بیمارگر روی یک گونه‌ی میزبان، ارتقای همکاری‌های پژوهشی و شیوه‌های مدیریت تلفیقی بیمارگرها می‌شود. یافته‌های ما بر اهمیت این رویکرد جامع در کاهش اثرات سفیدک‌های کرکی بر کشاورزی ایران تأکید دارد.

کلمات کلیدی

تاکسونومی، دامنه‌ی میزبانی، روش‌های مولکولی، ریخت‌شناسی، سفیدک‌های کرکی.

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