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REVIEW ARTICLE

Downy mildew of millets - An overview

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Abstract

Amidst global food insecurity, malnutrition, agricultural challenges, and climate change, millet farming is emerging as a viable alternative due to its high nutritional value, resilience to extreme weather conditions and adaptability to marginal soils. Often referred to as "super-crops", millets gained international recognition in March 2021 during the 75th session of the United Nations General Assembly. Millets rank among the most important crops globally, following rice, wheat, maize and sorghum. However, they are susceptible to more than fifty diseases, with the most destructive being 'Downy Mildew'. This disease is caused by oomycete pathogens such as *Sclerospora graminicola, Peronosclerospora sorghi* and *Sclerophthora macrospora*, posing a significant threat to millet production, with yield losses ranging from 50% to 100%. This review emphasizes the importance of millet and the devastating effects of downy mildew on its yields. It explores the physiological and histological changes induced by the disease, the characterization of effector protein and the genetic variability in millet populations. Additionally, various management techniques for combating downy mildew are examined, including chemical treatments, induced resistance, organic-based approaches, cultural practices, resistant genotypes and advancements in nanotechnology. By compiling current knowledge on millet disease and effective management strategies, this review aims to serve as a comprehensive resource for researchers and farmers, supporting sustainable millet farming and improving global food security.

Keywords

Downy mildew; millets; *Sclerospora graminicola; Peronosclerospora sorghi; Sclerophthora macrospora*

Introduction

Millets, belonging to the Poaceae family, are a diverse group of small-seeded grasses cultivated as cereal grains in periodic meadows. Known for their nutritional value, millets serve as a vital food source for economically disadvantaged populations, offering benefits such as resilience to pests, low nutrient application and drought resistance (NAAS, 2013). Currently, one-third of the world's population consumes millet, which is rich in minerals like iron, potassium, phosphorous and magnesium. Millets also contain anti-oxidants that help prevent hypertension and cardiovascular disorders, reduce the risk of cancer and regulate diabetes (1). Once referred to as the "coarse grains" of the past, millets are now celebrated as the modern "Nutri-cereals". In India, millet production is categorized into two types: minor and major millet. Economically important varieties include

sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*), finger millet (*Eleusine coracana*), and small millets like Kodo millet (*Paspalum scrobiculatum*), little millet (*Panicum sumatrense*), foxtail millet (*Setariaitalica*), barnyard millet (*Echinochloa esculenta*) and proso millet (*Panicum miliaceum*) (2).

In recognition of millets global significance, the 75th session of the United Nations General Assembly declared 2023 as the 'International Year of Millets'. India is among the top five global exporters of millet, with exports growing from 400 M USD in 2020 to 470 M USD in 2021. During the fiscal year 2022–2023, India's millet exports reached 75.46 M USD, up from 62.95 M USD in the previous fiscal year 2021-2022. Pearl millet production alone covers approximately 11,431 M ha in India (Indiastat, 2023). Despite India's long tradition of millet consumption, between 1972-73 and 2004-05, pearl millet or bajra consumption declined by 67% in urban areas and 59% in rural areas. The industrial potential of pearl millet, particularly in starch production, remains largely untapped (3). However, it is increasingly recognized for its intensive agriculture due to its adaptability to various management inputs (4). Sorghum, another important millet, demonstrated resilience to high temperatures and, to some extent, waterlogging (5). Globally, sorghum cultivation spans 47 M ha, producing 69 Mt of grain annually, with Africa contributing 20 Mt. Sorghum is critical for food security in Africa due to its genetic adaptation to drought, offering a level of resilience that primary crops like maize (*Zea mays*), rice (*Oryza sativa*), and wheat (*Triticum*) struggle to achieve under similar conditions(6).

Foxtail millet ranks second in global millet production and serves as a crucial staple in Southern Europe and Asia. It is extensively cultivated in arid and semi-arid regions across Asia, Africa and America (7). In India, it covers an area of 0.98 lakh hectares (L ha), with a production of 0.56 Lakh tonn (L t) and a productivity rate of 565 kg per ha. The primary cultivation area includes Karnataka, the coastal area of Andhra Pradesh, Tamil Nadu, Uttarakhand and selected northeast states (8, 9). Finger millet is grown in over 25 countries across Asia and Africa, accounting for 12% of the global millet cultivation area. Key producers include Uganda, Sri Lanka, India, Nepal, China, various regions in Africa, Madagascar, Malaysia and Japan. The crop demonstrates significant yield potential (10). In India, notable states for finger millet cultivation include Tamil Nadu, which contributes 9.94% of the cultivated area and 18.27% of total production; Uttarakhand, with 9.40% of the area and 7.76% of production; and Maharashtra, covering 10.56% of the area and producing 7.16% of the total output (10). Kodo millet is widely cultivated in Indian states such as Tamil Nadu, Maharashtra, Madhya Pradesh, Karnataka, Jharkhand, and Chhattisgarh. It is valued for its grains, which are rich in minerals, antioxidants and dietary fiber (11). Little millet *(P. sumatrense*), an annual herbaceous plant native to India, is extensively grown in India, Nepal and western Myanmar. It thrives in diverse agroecosystems and is recognized for its nutritional richness and low glycemic index (12).

Millets are predominantly cultivated in marginal and degraded lands with poor soil fertility and are highly susceptible to erratic rainfall patterns. Millet production in India, including varieties such as pearl millet, small millet, finger millet (ragi) and sorghum, measured in metric tons from 2000 to 2024, is illustrated in Fig. 1. The global production rate of millets in 2021 is illustrated in Fig. 2. Nutritionally, millets surpass major cereals such as maize, wheat and rice, offering higher levels of carbohydrates, protein, fiber, antioxidants, polyphenols, minerals and vitamins (13).

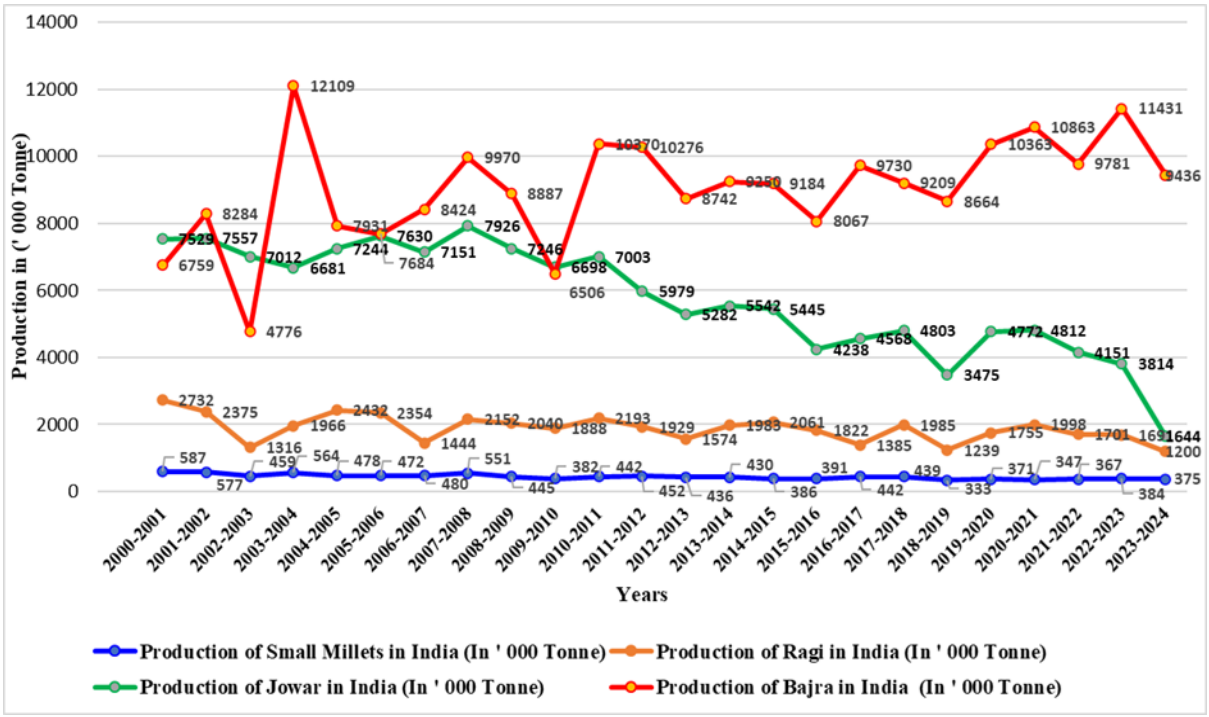

Fig. 1. Production rate of small millets, ragi, sorghum (jowar) and pearl millet (bajra)in tonnes from the year 2000 -2024.Source: Indiastat, 2023)

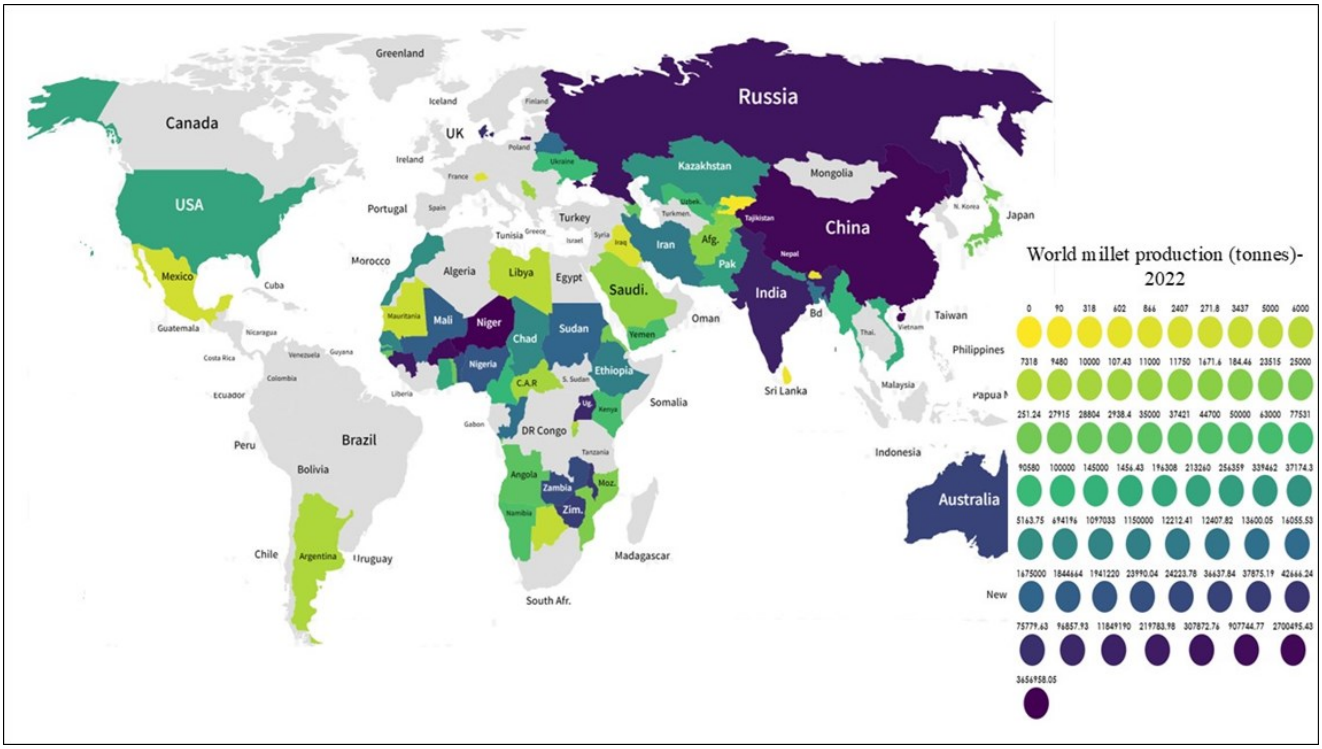

Fig. 2. Production rate of millet globally in the year 2022. (Source: World Population review -millet production by country 2022)

Millets are cultivated across diverse regions in India, including the hilly terrains of the Himalayas (14), Rajasthan, Maharashtra, Karnataka and Uttar Pradesh, where farmers have significantly increased overall production. However, several factors, both biotic and abiotic, contribute to declines in millet production. Biotic factors, particularly diseases, have a significant impact on intentionally cultivated millet crops, causing substantial economic losses. Some diseases occur sporadically under specific rainfall conditions and pose less severe threats to the crop. Among these, fungal diseases pose a greater threat to millets crop than viral and bacterial infections.

Historically, millet have been affected by diseases such as downy mildew, blast, rust, anthracnose, ergot, grain mold, smut, charcoal rot and sheath rot. These diseases attack various parts of the plant, including the roots, stems, leaves and grains, leading to reduced grain and fodder production as well as compromised quality. The fungal pathogens responsible for downy mildew belong to the *Peronosporaceae* family, within the class Oomycetes. Several species from this group pose significant threats to key crops such as pearl millet, sorghum and maize, demonstrating high levels of destructiveness. The main genera responsible for downy mildew include *Sclerospora, Peronosclerospora* and *Sclerophthora*.

Yield loss due to downy mildew disease globally

Sclerospora graminicola, a pathogenic organism affecting pearl millet, caused an annual yield reduction of up to 40%, resulting in an economic loss of USD 270 M each year (15). In India, during 1970 and 1980, downy mildew caused significant and sustainable yield losses. Grain yield reductions due to this disease have ranged from 10% to 60%. This high yield-reducing potential was demonstrated in the case of HB 3, a widely adopted hybrid (16). In India, about 50% of the 9 M ha of pearl millet cultivation is comprised of over 70 different hybrids. The incidence of downy mildew in these hybrids varies significantly, with some showing more than 90% infection rates in farmers' fields. The disease becomes particularly problematic when a single type of pearl millet is extensively cultivated in a region, leading to yield losses of 30-40%. In the United States, a significant outbreak of downy mildew disease in grain sorghum in the coastal counties of Texas resulted in an estimated financial loss of USD 2.5 M in a single season. In sorghum, yield losses of up to 78% have been recorded in the cultivar DMS 652. Certain regions in India have reported annual yield reductions due to Sorghum Downy Mildew (SDM) of at least 100,000 metric tons. Downy mildew caused by *S. graminicola* has also been documented in foxtail millet in several countries, including India. The disease has substantially impacted yield outcomes, leading to approximately 50% crop losses in some years (17).

Symptoms of downy mildew in millets

Downy mildew is a common disease affecting various small millets, pearl millet, and sorghum. In finger millet, the causative agent is *Sclerophthora macrospora*, while in foxtail millet and pearl millet, it is caused by *S. graminicola* (18). In sorghum, downy mildew is caused by the pathogen *Peronosclerospora sorghi* (19). The disease presents characteristic symptoms, including pale, chlorotic streaks that run from the base to the tip of the leaves, generally 1-3 mm in width, this may vary depending on the susceptibility of variety. As the disease progresses, the streaks undergo color changes. They initially appear greenish-yellow, then turn a clearer yellow, followed by patchy reddish-brown areas, and eventually become solid dark red. In severe infection, downy fungal growth may be visible on both the upper and lower surfaces of the leaves. The streaks often merge, leading to discoloration across the entire top surface of the leaf, which is sometimes affected by secondary fungi,

mainly saprophytes. The rapid spread of the fungal pathogen is facilitated by moist and humid conditions, particularly during rainy periods. Affected plants frequently fail to develop ears, severely impacting crop yields.

Distinctive symptoms

The symptoms of downy mildew disease in pearl millet, sorghum and foxtail millet have distinct characteristics and notable similarities. In pearl millet, the disease progresses through two phases: the downy mildew stage, which primarily affects the leaves through sporangia, and the green ear stage, where the inflorescence or ear is impacted by oospores. This differs from sorghum, where two categories of symptoms are observed: localized lesions on leaf surfaces and systemic infection caused by oospores or conidia colonizing the meristematic tissue. Interestingly, both pearl millet and sorghum display systemic infection through chlorosis, followed by specific symptoms. Pearl millet exhibits the "half-leaf" symptom, while sorghum develops whitish streaks that later turn brown, often accompanied by "leaf-shredding" (20, 21). In contrast, foxtail millet presents with distinct symptoms, such as shortened internodes and a bushy or bunchy growth pattern, along with a characteristic green ear appearance (22). Despite these differences, all three crops exhibit inflorescence malformations, though in different forms. Pearl millet shows a variety of malformations, including green leafy masses or a bristled appearance. Sorghum is marked by "leaf-shredding" and shortened internodes, while foxtail millet displays abnormal spikelet. Understanding these variations is crucial for developing effective disease management strategies tailored to the unique susceptibility and symptoms of each crop.

Histopathological changes in host plant

Histopathological examinations of finger millet (ragi) infected by *S. macrospora* reveal the presence of fungal mycelium in various plant parts, including roots, stems, floral components, and seeds, resulting in significant morphological and anatomical changes. The mycelium rapidly proliferates in sub-stomatal spaces, eventually producing sporangiophores through stomatal openings. Infected leaf tissues exhibit a reduction or absence of chloroplasts and leucoplasts, along with distortion of mesophyll cells. As the mycelial strands expand, the bundle sheath cells and surrounding parenchyma cells collapse. In some cases, invaded tissues dissolve, allowing the mycelium or sexual organs to occupy the space. Mycelial growth primarily occurs in the intercellular spaces adjacent to vascular sheaths, while sexual organs are predominantly observed near the vascular bundles. Infected leaves show restricted growth of epidermal hairs. Morphological alterations also affect ovules, leading to irregular pollen grains. Intercellular hyphae are detected within the floral primordium, stem, inflorescence peduncle, hypertrophied glumes, stamens and pistils.

Physiological changes in host plant

Chloroplasts play a key role in the production of phytohormones like salicylic acid (SA) and jasmonic acid (JA), making them essential for plant immunity against pathogens(23). Increasing evidence suggests that phytopathogens manipulate chloroplast homeostasis as a strategy to enhance their pathogenicity (24). *S. graminicola* inhibits chlorophyll synthesis and causes loose mesophyll cell arrangement in infected plants. During mid-infection, *S. graminicola* infiltrates mesophyll cells using haustoria, leading to the destruction of chloroplast structure. This results in a significant buildup of osmiophilic particles (OPs) and the disintegration of chloroplast grana lamellae. In foxtail millet, infected leaves also undergo longitudinal splitting in the later stages of infection, with a marked reduction in chlorophyll and carotenoid contents. Furthermore, the net photosynthetic rate (Pn) and stomatal conductance decline, while intercellular carbon dioxide concentrations increase, all in correlation with the lowered chlorophyll content following *S. graminicola* infection (25).

The phenomenon of floral reversion has been documented as being induced by fungal pathogens, particularly *S. graminicola* in pearl millet (26). Floral reversion refers to the alteration or reversal of normal floral development, resulting in the transformation of floral structure back into leafy growth. In the case of downy mildew caused by *S. graminicola*, the fungus induces phyllody in pearl millet, leading to the formation of a distorted inflorescence. The fungus alters the gene expression of meristematic cells involved in floral development at the shoot apical meristem (SAM). This modulation affects the physiological and hormonal regulation of the host's meristem, ultimately resulting in phyllody. Infected, resistant pearl millet tissues exhibit an accumulation of total phenols and ortho-dihydroxy (OD) phenols, leading to hyperphenolicity, even though there is an increase in the activities of peroxidase (PPO) and polyphenol oxidase (POX). Significant changes in the activities of PPO, POX, catalase and indole-3-acetic acid (IAA) oxidase have also been observed in the affected plants (27).

Disease cycle and pathogen description

The nomenclature "*Sclerospora*" is derived from the distinct characteristics of its thick-walled oospore, featuring a dark-walled exosporium and an attached oogonial envelope. *S. graminicola*, an obligate parasite, primarily survives in seeds or soil through its oospores, which can remain viable for up to eight years. Primary infections occur mainly through soil-borne oospores, which germinate alongside seed germination and systematically infect seedlings. *S. graminicola* reproduces both asexually, by producing sporangia, and sexually, by generating oospores. Although it is predominantly heterothallic, a few instances of homothallism have been documented, indicating a low occurrence of homothallic isolates in India (28). Oospore germination is an indirect process, initially producing a large, lemon-shaped sporangium. The mycelium occupies the endosperm and embryo compartments of infected seeds. These lemon-shaped sporangia, measuring 60-100 x 43-64 µm, are characterized by a distinct papilla and pedicel. They are produced prolifically during nighttime under natural conditions, thriving at temperatures between 20 and 25ºC and in high relative humidity (95-100% RH).

Under favorable conditions, sporangia develop extensively, primarily on the undersurface of infected leaves, occasionally appearing on the upper surface. This results in the emergence of a striking white 'downy' growth. Upon germination, the sporangia release numerous unequally biflagellate zoospores. *S. graminicola* exhibits two distinct mating types, and the presence and frequency of these types contribute significantly to the pathogen's variability.

In the disease cycle of *P. sorghi*, sexually generated oospores typically contribute to one infection cycle per season. In contrast, conidia produced asexually from an infected plant can infect new hosts within the same growing season, thereby accelerating the onset of a sorghum downy mildew epidemic. The conidia of *P. sorghi* are produced abundantly, characterized by thin walls and a short lifespan, which facilitates the rapid onset of an epidemic. In contrast, oospores have durable walls and prolonged viability, serving as a persistent stage for the pathogen and enabling long-distance dissemination. The oogonia of *P. sorghi* typically possesses a smooth wall, often with attached fragments of the oogonial stalk or antheridial cell, averaging a size of 22.9 µm. Oospores are consistently spherical, either centrally or eccentrically located, and range in size from 15.3 to 22.6 µm. The oospore wall is 2-3.9 µm thick, containing homogeneous, finely granular content with abundant oil reserves. Oospore production occurs from the early stages of infection until the disintegration of leaf tissues, with both external and internal seed-borne infection (29). The germination process of oospores is indirect. The oospore develops into a large, lemon-shaped structure called a sporangium, which releases 24-48 zoospores. The mycelium is found within both the embryo and endosperm of infected seeds. The lemon-shaped sporangia, characterized by a distinct papilla and pedicel, typically measure 60-100 x 43-64 µm. After germination, the sporangia release a substantial number of unequally biflagellate zoospores. The optimal temperature range for this process falls between 22 and 25°C. The zoospores exhibit pyriform, spherical, or irregular shapes and initiate germination by forming a germ tube, which develops an appressorium at its apex. Night and early morning temperatures ranging from 20 to 25°C promote the rapid germination of spores, consequently facilitating disease progression (30).

Epidemiology

Mode of spread and survival

Soil-borne

The initial infection occurs through oospores residing in the soil, which can persist for a duration ranging from 8 months to 10 years or longer (31-33). These oospores are commonly found in fallen, diseased leaves on the ground. Upon introduction to germinating seedlings through the soil, they can trigger the onset of initial disease symptoms within 7 to 8 days. Approximately 30-40% of oospore viability is established through the application of vital stains, such as 2,3,5-triphenyl tetrazolium chloride (TTC). The secondary dissemination of the disease begins with sporangia, which exhibits heightened activity in moist environments.

Seed-born

The inoculum of the downy mildew pathogen can be carried by seeds, either adhering to the seed coat or as simultaneous contamination with plant debris. While mycelium may be observed in various seed tissues, only the mycelium within the embryonic tissue is considered pathogenic. Although there are indications suggesting the possible seed-borne nature of *S. graminicola*, experimental validation of the pathogen's viability is necessary. Nonetheless, treating seeds is recommended as a precautionary measure to reduce the risk of introducing downy mildew disease.

Favorable condition

Sporangial infection by the downy mildew pathogen in millets occurs exclusively during the initial one or two leaf developmental stages of the seedling. After this stage, seedling susceptibility declines significantly (34). Oospores play a crucial role in the pathogen's ability to endure prolonged periods of hot and dry conditions between crops, a phenomenon commonly observed in various regions where they thrive. During early-season cultivation under cool and wet conditions, susceptible varieties may be infected by conidia, leading to systemic infection and ultimately affecting yield potential. Ambient temperatures ranging from 15 to 25°C, combined with relative humidity exceeding 85%, create highly favorable conditions for infection. Additionally, gentle drizzling and cool temperatures further enhance this conducive environment (35). In susceptible hosts, when weather conditions and inoculum levels are favorable, the duration of infection-to-disease progression (from spore initiation to spore production) typically lasts about seven days. A brief description of the pathogenic characterization is provided in Table 1.

Genetic variability of the pathogen

Precise and easily measurable heritable traits or markers are essential for genetic studies in any organism. However, fungi present challenges due to their microscopic nature and limited phenotypic markers, which include mating types, vegetative compatibility, and distinct virulence. The emergence of versatile genetic markers that rely on disparities in DNA sequences has revolutionized fundamental research in population and evolutionary biology concerning fungi. These molecular methodologies encompass DNA hybridization techniques, including PCR-based DNA markers, endogenous genomic analysis, DNA fingerprinting and mitochondrial RFLP (Restriction Fragment Length Polymorphisms). These methods have been extensively utilized to evaluate genetic diversity across various fungal species belonging to Ascomycetes, Zygomycetes and Deuteromycetes. Differences between fungi and oomycetes signify alterations in their genetic structure, primarily attributed to factors such as somatic recombination, mutation, sexual recombination, hybridization and heterozygosity. The introduction of molecular markers, particularly those reliant on DNA sequences, has been embraced in the study of *S. graminicola*. Researchers have illustrated the utility of DNA profiling for discerning genetic variations within pathogen

Table 1. Pathogen characteristics of *Sclerospora graminicola, Peronosclerospora sorghi* and *Sclerophthora macrospora* in major millets, pearl millet, foxtail millet, sorghum, ragi and barnyard millet.

Host	Pathogen	Sporangia/ Conidia	Sporangiophore/ Conidiophore	Zoospores	Oospore	Epidemiology	Reference
Pearl millet, Foxtail millet	*Sclerospora graminicola*	Hyaline, thin-walled, ellipsoidal, papillate, 15-40 µm	Robust trunk, minimally tapered base, bifurcated apex with 3-4 short branches, each bearing a sporangium	Kidney-shaped with two flagella of unequal length	Thick-walled, brownish-yellow, spherical, 20-50 µm	Temperature: 20-25°C, RH: 95-100%	(26,57)
Sorghum	*Peronosclerospora sorghi*	Hyaline, thin-walled, suborbicular, 10-25 µm; germinates by hyphal germ tube	Basal cell with successive dichotomous branches at the apex, basal cell is 7-9 µm wide and 100-150 µm long	-	Thick-walled, spherical to oval, 20-40 µm	Temperature: 20-22°C, RH: 98%, high humidity with dew or rainfall	(92)
Ragi, Barnyard millet	*Sclerophthora macrospora*	Rapidly maturing, releases 50+ motile zoospores, 25-50 µm diameter	Emerges via stomata, produces numerous lemon-shaped sporangia with apical pores, >6 sporangia per sporangiophore	Oval to pear-shaped, translucent, with apical papillae, 60 -115 × 29-50 µm; germinates in water, releases reniform zoospores	Globular to nearly globular, thick-walled, translucent, 20-50 × 10-30 µm; gives rise to oospores filling the oogonia	Temperature: 25-30°C	(29, 30)

populations.

The effectiveness of straight forward iterative DNA sequences, including (GATA)4, (GACA)4 and (GAA)6, has been noted in distinguishing polymorphisms among different variants of *S. graminicola*. Typically, the short tandem repeat (STR) probes exhibited greater polymorphism in *S. graminicola* when employing restriction enzymes characterized by a four-base specificity compared to hexacutter-specific enzymes. The durability of STR (GATA) 4-based fingerprinting remained intact after ten consecutive asexual generations of *S. graminicola*, highlighting the effectiveness of this probe in DNA fingerprinting. These findings were consistent with similar outcomes using the (GATA)4 probe across six pathotypes of *S. graminicola* (36).

Table 2. *Sclerospora graminicola* isolates of pearl millet reported from various states of India (95-97).

Isolates	Host genotype/ cultivar	Year	Location
Sg 004	7042S & HB 3	1998	Rajasthan
Sg 115	Hybrid	1996	Tamil Nadu
Sg 153	7042S & NHB 3	1997	Andhra Pradesh
Sg 047	BK 560	1994	Karnataka
Sg 015	7042S	1992	Haryana
Sg 511	Hybrid	2008	Uttar Pradesh
Sg 554	7042 S	2010	Maharastra
Sg 560	7042 S	2010	Gujarat
Sg 561	ICMP	2010	New Delhi
Sg431	7042 S	2005	Telangana

The different isolates of *S. graminicola* found in pearl millet from various locations in India are listed in Table 2. Notably, 37 pairs of primers originally intended for *P. sorghi* showed cross-transferability to *S. graminicola* (37). Screening of these 37 microsatellite markers with 23 Indian isolates of *S. graminicola* revealed that only 54% of the primers consistently amplified fragments. Remarkably, none of these amplified fragments exhibited polymorphism (38).

Effector protein of *S. graminicola*

Effector proteins are released by fungal pathogens to modify the function of host plants and promote resistance against biotic stress. The investigation focused on the role of the effector protein 35983_g, derived from *S. graminicola*, in managing downy mildew in pearl millet (*Pennisetum glaucum*). This effector protein triggered a hypersensitivity response (HR) and increased the activity of phenylalanine ammonia-lyase (PAL) and peroxidase enzymes in both susceptible and resistant varieties of pearl millet (39). Histochemical analysis indicated that the resistant variety, upon treatment with the effector protein, exhibited enhanced cell wall size due to increased lignin deposition compared to the untreated control cultivar. Overall, the effector protein from oomycetes holds potential as a biomarker for identifying downy mildew-resistant pearl millet lines in global breeding initiatives (39). The researchers identified and validated 17 RxLR-dEER effector protein-encoding genes in *S. graminicola* (39). Among 845 anticipated secretory transmembrane proteins, these effectors, particularly those featuring the Leucine-any amino acid-Phenylalanine-Leucine-Alanine-Lysine (LxLFLAK) and RxLR motifs, were identified. Five of the genes were successfully validated, marking the first report on effector genes in *S. graminicola*. This elucidation of the molecular mechanisms governing plant-pathogen interactions provides valuable insights for devising effective

disease management strategies in agricultural environments.

Management

Millets are predominantly grown under minimal input conditions, making their cultivation inherently organic. Herbicides, pesticides, fungicides and chemical fertilizers are typically avoided or used sparingly. In this context, disease management focuses on prevention by reducing primary sources of inoculum, minimizing infections and judiciously employing bio control agents for protection and treatment as needed. Diseases that cause crop damage continue to pose significant challenges in improving millet production and productivity through intensive cultivation. While pesticides are now used, they present issues such as affecting unintended targets, harming the environment, and contributing to pathogen resistance. Therefore, a more reliable approach is to assess resistance through biogenetic traits that are less influenced by environmental factors. The current necessity lies in integrating biocontrol agents into the management protocol for downy mildew in millet, emphasizing the reduction of environmental contamination, residual toxicity, the emergence of pathogen resistance and the economic inefficiencies associated with ongoing chemical applications. The exploration of botanical treatments, bio-agents and non-chemical strategies offers an eco-conscious alternative for effectively managing the disease in the field (40).

Cultural management

The management of downy mildews primarily focuses on cultural methods that emphasize sanitation practices and environmental manipulation. These strategies aim to create conditions that promote host plant growth while impeding pathogen proliferation. Historical references highlight the importance of eliminating, destroying and incinerating infected plant debris and weeds, as these serve as reservoirs for pathogen survival in the form of oospores within host tissues. To mitigate infection risks, it is advisable to maintain cleanliness and ensure proper drainage in agricultural soils. Implementing a two-year crop rotation involving non-host crops is also recommended (41, 42). Avoiding monoculture and introducing crop diversity within specific fields help reduce inoculum accumulation and limit virulence selection in pathogen populations. Furthermore, cultivating highly susceptible cultivars as trap crops during intercropping intervals offers a promising strategy (43). Harvesting these trap crops promptly upon symptom manifestation prevents the generation and introduction of sexual spores into the soil. These measures, when complemented by crop sanitation, deep tillage, over-planting and the removal of diseased plants, as well as strategic adjustments in planting dates, host nutrition and crop rotation, contribute significantly to disease control. Additionally, intercropping and mixed cropping methods have been proposed as effective strategies. Notable success in reducing oospore density in the soil and lowering the incidence of sorghum downy mildew has been observed in the United States through practices such as deep tillage and the removal of infected plants (44, 45). However, it is acknowledged that resource-constrained farmers in India may face challenges in implementing such practices. Collectively, these strategies play a crucial role in managing downy mildew diseases in various millet crops.

Resistant genotype

In a comprehensive examination of sorghum genotypes for resistance to downy mildew disease in Uganda, two genotypes, PI 656061 and PI 533831, were identified as resistant, alongside four moderately resistant genotypes: E 40, MAKSO 8, PI 655990 and Epuripur (46). These findings suggest promising candidates for integration into sorghum breeding programs aimed at enhancing resistance to downy mildew. Additionally, a diverse array of germplasm sources within the sorghum mini-core collection demonstrated resilience to downy mildew disease (47). Notable accessions, including IS# 28747, 31714, 23992, 27697, 28449 and 30400, exhibited significant tolerance, along with various other potential contributors identified by their accession numbers. The study emphasizes the availability of ample germplasm resources suitable for improving downy mildew resistance in sorghum breeding programs. Furthermore, researchers evaluated 20 pearl millet genotypes for resistance to downy mildew, pinpointing promising candidates such as IP22315, IP2295, SOSAT-C88-Sadore and SOSAT-C88-Pantacheru, which displayed stable resistance across different locations in Senegal (48). Another study highlighted the robust resistance exhibited by SOSAT C 88 among other genotypes, indicating its significance for enhancing pearl millet's resistance to downy mildew and other agronomic traits (49). A list of resistant varieties and genotypes against downy mildew diseases in sorghum, pearl millet and foxtail millet is provided in Table 3. Finally, a thorough assessment of 62 pearl millet entries revealed a substantial proportion exhibiting highly resistant reactions to downy mildew, including notable entries like BIB-7, BIB-19, BIB-20 and others (50). Remarkably, none of the entries were highly susceptible, indicating promising resistance levels across the evaluated genotypes. Collectively, these findings underscore the potential for leveraging resistant genotypes in breeding programs to combat downy mildew in sorghum and pearl millet, thereby contributing to improved crop resilience and productivity.

Chemical management

Strobilurins represent a novel category of antifungal agents initially identified or extracted from Basidiomycete fungi

Table 3. List of resistant varieties/genotypes against downy mildew diseases of sorghum, pearl millet and foxtail millet.

S. No.	Crop	Resistant variety/genotype	Reference
1.	Sorghum	PI 656061, PI 533831, PI 655990, IS 3547, IS 8283, IS 22230	(46)
2.	Pearl millet	P 18292, IP 18293, IP 18294, IP 18295, IP 18298, ICMR 01007	(16)
3.	Foxtail millet	FVX 629, DHFT 109-3, SiA 3282, SiA 3156, FXV 620	(98)

found in decaying wood (51). These compounds function by disrupting mitochondrial respiration. Specifically, they bind to a particular component known as the ubihydroquinone oxidation center in the mitochondrial bc1 complex, thereby inhibiting the transfer of electrons, which is essential for energy production (52). Among them, azoxystrobin exhibited the highest level of efficacy, providing 66% protection against downy mildew disease in pearl millet.

Metalaxyl, developed in the 1970s, effectively controls downy mildew in pearl millet caused by *S. graminicola*. The formulation Metalaxyl (Ridomil) 25 WP can control downy mildew in sorghum when applied as a seed treatment at a rate of 1 g of active ingredient (a. i.) per kg of seed and sprayed once (1 g a.i. per L, 750 L/ha) 40 days after planting. This treatment regimen provides complete control of systemic infections and local lesions. However, there are concerns regarding potential resistance development, as observed in other Oomycetes.

To mitigate this risk, combinations of metalaxyl, oxadixyl and mancozeb are being assessed for their efficacy, aiming to provide alternative strategies against potential resistance development in downy mildew. Incorporating both seed treatments and foliar sprays, particularly with metalaxyl or mancozeb, yielded superior results compared to seed treatment alone. Notably, the combination of metalaxyl seed treatment followed by a joint foliar spray of metalaxyl and mancozeb demonstrated greater efficacy than a single foliar spray with either fungicide.

Metalaxyl formulations effectively control pearl millet downy mildew in seed treatments, with the best results observed in seed soaking, resulting in a 9.8% infection index compared to 94.8% in untreated plots (53). Wettable powder formulations exhibited dose-dependent control, with dusting seeds at 2 g a.i. per kg providing efficient control (12.6% infection index vs. 78.9% in untreated plots).

Phosphorus-based compounds, specifically phosphorus acid (PA), have proven effective against oomycete diseases in several studies. In India, various commercial PA formulations are available, making it essential to understand their effectiveness. Di-potassium hydrogen phosphate, 2,3,5-triiodobenzoic acid and phosphorus acid (PA), along with the commercial formulations Akomon-40 and Potphos, have demonstrated variable efficacy in reducing pearl millet downy mildew (PDM) disease, consistently showing effectiveness in both greenhouse and field conditions (54).

Cyazofamid has exhibited strong curative activity and stable residual rain fastness, highlighting its potential as an effective fungicide for pearl millet downy mildew. Research has illustrated the significant utility of Cyazofamid, demonstrating its inhibitory effect on pearl millet downy mildew in vitro at a concentration of 0.3 mg/mL (15). Enhanced disease control was evident with seed treatment followed by either a single foliar application or two foliar applications. Applying Ridomil MZ 72WP at a rate of 3 g/kg during seed treatment serves as a protective strategy, shielding the seeds from both seed-borne infections and soil-borne inoculum (30). Additionally, the foliar application of Mancozeb at a concentration of 0.2% proved to be the most effective strategy, resulting in a notable 2.28% reduction in downy mildew incidence in pearl millet and a substantial enhancement in grain yield.

Biological control

Researchers at the Main Pearl Millet Research Station in Jamnagar, Gujarat, conducted a study during the kharif

Fig. 3. Distribution of pearl millet - *Sclerospora graminicola* worldwide. (Source: https://doi.org/10.1079/pwkb.species.49159)

seasons of 2021 and 2022 to identify eco-friendly approaches for minimizing downy mildew disease in pearl millet. The findings suggested that *Trichoderma harzianum* and phosphorus-solubilizing bacteria (PSB) formulations could serve as effective alternatives to chemical treatments for managing downy mildew while maintaining robust crop and fodder yields. It was demonstrated that both *T. harzianum* and *T. viride* were effective in reducing the disease (56). The endophytic strain *T. hamatum* UoM 13, sourced from pearl millet roots, improved both seed germination and seedling vigor (57). Treatment with this strain resulted in long-lasting immunity against downy mildew, characterized by heightened lignification and callose deposition upon infection. Additionally, there was a notable increase in the activity of defense enzymes, along with the overexpression of pathogenesis-related (PR) proteins and hydroxyproline-rich glycoproteins (HRGPs). Elevated levels of salicylic acid were also observed, indicating the involvement of the salicylic acid biosynthetic pathway in establishing systemic immunity against downy mildew. The best results for reducing pearl millet downy mildew and increasing yield were achieved with the following combinations: *T. viride* at 6 g/kg seed plus *P. fluorescens* spray at a concentration of 1 x 10^8 cfu/mL, applied 21 days after sowing and *T. harzianum* at 6 g/kg seed plus *P. fluorescens* spray at the same concentration and timing. When *P. fluorescens* was applied as a seed treatment and as a talc-formulated foliar spray, it enhanced seedling vigor and suppressed downy mildew disease (58).

Plant growth-promoting rhizobacteria (PGPR) contribute to enhanced growth and disease resistance in bajra (pearl millet) through mechanisms such as hormone release, antibiosis and competition for nutrients. PGPR seed treatments offer an efficient disease management strategy, promote growth and are environmentally safe, providing reliable pathogen control and resilience to abiotic stress. Laboratory, greenhouse and field trials have demonstrated the efficacy of PGPR in enhancing germination, vigor and yield by up to 40%, effectively managing downy mildew in experimental plots (16). A fungus called *Penicillium oxalicum*, found in the soil around pearl millet, has been shown to improve plant growth and provide resistance against downy mildew, effectively controlling the disease. This plant growth-promoting fungus enhances growth and induces resistance in pearl millet against downy mildew (59). In an assessment of various biological agents on the moderately susceptible hybrid B 2301, the combination of chitosan and *Bacillus pumilus* emerged as the most effective treatment, resulting in the lowest disease incidence at 9.3% and the highest recorded germination percentage of 53.5%. The grain yield obtained was 1,091.7 kg/ha (60). Additionally, the metabolites from *Trichoderma asperellum* (DL-81) showed a significant impact on downy mildew resistance in pearl millet, demonstrating potent anti -mildew and zoosporangium-sporicidal activity in greenhouse trials. This indicates a novel bio control mechanism for suppressing downy mildew in pearl millet (61).

Botanical approach

Researchers advocate for eco-friendly plant-based products, emphasizing the induction of host resistance as a safer and more effective alternative to conventional synthetic pesticides. One such alternative represents a delightful shift from chemical fungicides, prioritizing human and environmental well-being in the management of sorghum downy mildew. *Duranta repens*, a charming organic fungicide, effectively combats sorghum downy mildew at a concentration of just 5%, with its active compound, Durantol, demonstrating efficacy at an impressive 0.1%. Microscopic analyses reveal its ability to inhibit pathogen growth, while molecular docking studies suggest interference with membrane receptors. Additionally, pearl millet exhibits systemic resistance to downy mildew through treatments such as *Datura metel* extract, PGPR and abiotic inducers like benzothiadiazole, $CaCl_2$ and H_2O_2, as well as cerebrosides elicitors (62-66). Six medicinally important plants, including *Viscum album*, have been assessed for their efficacy against downy mildew (66). Treatment with *V. album* proved to be the most effective, enhancing seed quality and inducing resistance. A 10% concentration of *V. album* provided maximum protection, increasing pearl millet grain yield by 44-70% under greenhouse and field conditions. The induced resistance was linked to increased enzyme activities and the presence of antimicrobial compounds in *V. album* extracts. Leaf extracts from *Reynoutria sachalinensis* and *Azadirachta indica* have been shown to enhance resistance to leaf stripe disease in barley and powdery mildew in cucumber, respectively (67). Additionally, ginger extract has been effective in safeguarding peas from powdery mildew in the field, while Aajoene from garlic has been successful in managing powdery mildew as well (68).

Nanotechnology in downy mildew disease management

Nanotechnology is emerging as a promising frontier in the agricultural sector, offering innovative solutions for managing plant diseases. This cutting-edge approach leverages the unique properties of nanomaterials to enhance the efficiency and precision of disease control measures. By transforming metallic, non-metallic and bio-compounds into nanoforms, nanotechnology provides diverse applications in drug delivery, antimicrobial agents, and disease diagnosis and treatment. Nanomaterials can be synthesized through physical, biological (green synthesis) and chemical methods and they possess distinctive properties that impede the growth of infectious pathogens, owing to their small size and substantial surface-to-volume ratio. Addressing global environmental concerns requires minimizing agrochemical usage and exploring advanced alternatives. In this context, nanotechnology represents a novel approach to plant disease management, offering innovative solutions. A multitude of patented products containing nanomaterials, such as nano pesticides, nano fertilizers and nanosensors, have emerged, showcasing the potential of nanotechnology to transform agricultural practices (69).

Zinc oxide

Zinc plays a pivotal role in enhancing crop productivity and bolstering disease resistance, among other micronutrients

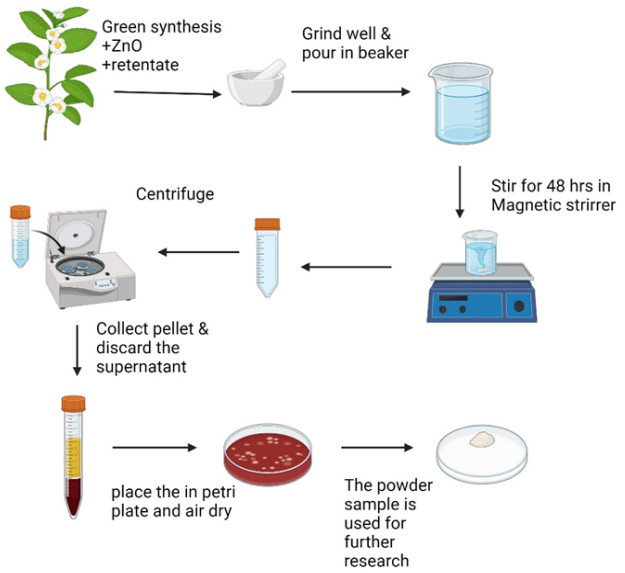

Fig. 4. Preparation of zinc-based nanoparticle with *Eclipta alba* extract. (Source: Created in BioRender.com)

(70). Green-synthesized zinc oxide nanoparticles, derived from a saponin-rich fraction of *Eclipta alba* (Fig. 4), effectively promoted the growth and seed germination of pearl millet while also increasing its resistance against downy mildew. This enhancement in resistance is associated with elevated plant defense enzyme activities and the induction of systemic resistance (71).

Chitosan nanoparticles

Chitosan, derived from chitin, enhances plant resistance against various pathogens. When applied before infection, it activates plant defense mechanisms, leading to increased production of protective substances, strengthened cell walls and heightened activity of defense enzymes (72). Nanochitosan has demonstrated the ability to induce resistance against a range of plant diseases across several host-pathogen interactions. Specifically, chitosan nanoparticles have been effective in suppressing rice and finger millet blast caused by the fungus *Pyricularia grisea* (73). In laboratory studies, the evaluation of chitosan nanoparticles (CNP), synthesized from low molecular weight chitosan, against pearl millet downy mildew (*Sclerospora graminicola*) revealed enhanced seed germination and vigor. When applied as a seed treatment, CNP induced systemic resistance, providing significant protection under greenhouse conditions. Gene expression analysis indicated the upregulation of defense-related genes. Moreover, nitric oxide modulation played a role in the protective effect of CNP, demonstrating significant efficacy at notably lower dosages for effective control of downy mildew (74).

Trichogenic

Selenium is a crucial micronutrient essential for the sustenance of both plant and animal life. Selenium nanoparticles (SeNPs) exhibit excellent bioavailability and unique physicochemical properties, characterized by a high surface-to-volume ratio. They demonstrate notable biological activities, including antimicrobial properties (75), antioxidant capabilities (76), anti-cancer effects and anti-inflammatory responses (77). *Trichoderma* species have been utilized to synthesize selenium nanoparticles for controlling downy mildew in pearl millet. Six *Trichoderma* species produced SeNPs using culture filtrate, cell lysate and crude cell wall, with culture filtrate showing the most significant results. The sizes of the SeNPs ranged from 49.5 to 312.5 nm, with zeta potentials varying from +3.3 mV to -200 mV. These nanoparticles effectively suppressed the growth, sporulation and zoospore viability of *S. graminicola*. In greenhouse applications, the combined use of SeNPs and *T. asperellum* synergistically enhanced early plant growth and reduced the incidence of downy mildew compared to individual treatments. This highlights the potential of Trichogenic-SeNPs in disease control (78).

Nanoemulsion

Nanoemulsions, known for their enhanced bioavailability and stability, are widely used formulations influenced by factors such as oil type and surfactant. In the nanoemulsion process, the properties of oils play a crucial role in determining the quality of the emulsion. The formulation of nanoemulsions from the membrane lipids of *Trichoderma* species aims to understand host-pathogen interactions and mechanisms involving pathogen-associated molecular patterns (PAMPs). It also seeks to evaluate the efficacy of the synthesized nanoemulsion in inducing disease resistance in pearl millet against downy mildew. A nanoemulsion was created from *Trichoderma* spp. membrane lipids using Tween 80 through ultrasonic emulsification, resulting in droplets with diameters ranging from 5 to 51 nm (79). The effects of this nanoemulsion on pearl millet seed growth and resistance to downy mildew were explored as part of an eco-friendly disease management approach. Priming seeds with the nanoemulsion provided significant protection and enhanced the expression of early defense genes. Lipid analysis identified oleic acid as a major component in *Trichoderma* spp. The purified lipid fraction from *T. brevicompactum* (UP-91) contained a potential molecule, (E) -N-(1,3-dihydroxyoctadec-4-en-2-yl) acetamide, which promotes systemic resistance against downy mildew. These findings suggest a promising strategy for long-lasting and widespread protection against biotrophic oomycetous pathogens.

Induced and triggers resistance against downy mildew

The induced resistance approach in plant disease management represents a proactive and sustainable strategy that leverages the innate capabilities of plants to defend themselves against pathogens. The use of low-dose elicitors, such as oligosaccharides with mannitol, N-acetyl chitooligosaccharides, β-aminobutyric acid and 3,5-dichloroanthranilic acid, has shown efficacy against pearl millet downy mildew (80, 81). While some bioagents have been identified, ongoing efforts are essential for developing a comprehensive set of effective inducers to achieve durable downy mildew resistance in pearl millet (82). Applying plant-resistance-inducing molecules at low doses is an effective and eco-friendly strategy for managing crop diseases, as highlighted in various studies (83, 84). This approach not only combats a wide range of pathogens in diverse plants but also enhances crop yield without exerting selective

pressures on pathogen populations, offering a promising avenue for sustainable disease management in agriculture. Plants rely on their innate immune systems, where salicylic acid (SA) plays a crucial role in defense. Low concentrations of salicylic acid (1 mM and 3 mM) enhance foxtail millet's resistance to downy mildew, while higher concentrations (6 mM and 9 mM) have minimal effects and may hinder plant growth. Optimal levels of SA promote the accumulation of chlorophyll, sugars, and proline, activate phenylalanine ammonia-lyase, and suppress malondialdehyde levels. These findings indicate the potential of exogenous SA to enhance resistance and guide improvements in downy mildew control (85).

Trehalose, a non-reducing disaccharide found in many organisms, including plants, has been identified as a metabolic osmoregulator and stress protectant. Seed treatment with commercially procured trehalose on the susceptible pearl millet cultivar "HB3" demonstrated significant protection against downy mildew, with a concentration of 200 mM trehalose applied for 9 h providing a 70.25% defense under greenhouse conditions (86). Field trials further confirmed its effectiveness, reducing disease severity to 32.75% compared to the untreated control. Consequently, the activity of defense-related enzymes is enhanced and resistance against downy mildew disease in pearl millet is induced through exogenous trehalose treatment. A comparative transcriptome analysis was conducted to explore the mechanisms of foxtail millet's resistance to *S .graminicola* in the resistant cultivar G1 and the susceptible cultivar JG21. This analysis revealed pathways such as glutathione metabolism, plant hormone signalling, and phenylalanine metabolism. Key regulators identified include leucine-rich protein kinases, Ser/Thr protein kinases, peroxidases and cell wall-degrading enzymes. Three crucial resistance genes, identified as Seita.8G131800, Seita.2G024900 and Seita.2G024800, share significance with their counterparts in rice and *Arabidopsis thaliana*, warranting further investigation in future studies on foxtail millet resistance to *S. graminicola* (87). Pearl millet seeds were primed with varying concentrations of chitosan (0.5, 1.5, 2.5 and 3 g/kg of seed). Notably, at the optimal concentration, chitosan showed no inhibitory effect on sporulation or the release of zoospores from sporangia (88). Following chitosan treatment, pearl millet seedlings exhibited increased levels of defense enzymes (chitosanase and peroxidase) compared to untreated seedlings when exposed to downy mildew. Chitosan proved effective in reducing downy mildew, achieving protection rates of 79.08% in greenhouse conditions and 75.8% in the field. Chitosan seed priming also promoted rapid nitric oxide (NO) accumulation in pearl millet seedlings, activating early defense responses within 2 h post-inoculation. Pre-treatment with the NO scavenger C-PTIO and the nitric oxide synthase inhibitor L-NAME diminished the disease-protective efficacy of chitosan, indicating that NO plays a significant role in chitosan-induced resistance (87). Cerebrosides represent a subclass of glycosphingolipids, which are complex molecules characterized by the linkage of a ceramide (a lipid) to a single sugar molecule. Specifically, cerebrosides consist of a ceramide molecule attached to one sugar residue (89). Cerebroside treatment induced significant systemic resistance against downy mildew in pearl millet caused by S. graminicola, with onset observed from 2 days post-treatment. Furthermore, cerebroside treatment not only suppressed the disease but also resulted in substantial yield enhancement, demonstrating promising outcomes in preliminary field trials.

In recent years, the importance of vitamins as both disease-fighting agents and essential nutrients has been emphasized (90). Vitamins such as menadione sodium bisulphite (MSB), riboflavin and roseoflavin have been shown to enhance plants defenses against various diseases. Given the information regarding the ability of vitamins to induce resistance, a range of vitamins was evaluated for their capacity to protect against downy mildew in millet. MSB, riboflavin and niacin provided significant protection against downy mildew, with MSB demonstrating the highest efficacy, resulting in a 73% reduction in disease incidence. However, combinations of these promising vitamins did not show any synergistic effects. Notably, applying seed treatment followed by a foliar spray containing MSB and niacin resulted in the highest level of protection, achieving a 74% reduction in disease incidence (91).

Future prospectives

Downy mildew remains a significant threat to pearl millet, with frequent epidemics raising major concerns. While host resistance to downy mildew (DM) has been widely utilized, the evolving virulence patterns of the pathogen, particularly in endemic regions, present ongoing challenges. Breeding for disease resistance continues to be the most effective strategy, with breeding programs leveraging resistant stocks to develop varieties that possess enhanced agronomic traits and improved resistance to DM. Research has highlighted global efforts in pearl millet, emphasizing advancements in genomics, breeding and production technologies, particularly regarding its nutritional value, climate resilience and role in ensuring food security under challenging ecological conditions (92).

In recent years, substantial progress has been made in exploring biological control agents, particularly focusing on host defense elicitors such as biochemical and natural compounds. Notable advancements include the use of raw cow milk and amino acids to stimulate resistance and activate defense-related enzymes against downy mildew in pearl millet. The effectiveness of biocontrol agents largely depends on the complex interactions among the pathogen, plant and soil ecosystems. A comprehensive understanding of these bio control mechanisms will facilitate the development of safer and more cost-effective strategies to protect pearl millet from downy mildew while enhancing yields. Millets, especially pearl millet, are vital crops in warm tropical drylands, with global demand increasing despite declining cultivation areas. Addressing biotic, abiotic and socio-economic challenges is essential for improving yields and maximizing their trade potential (93).

Moreover, identifying the biochemical components of resistance will be instrumental in guiding future breeding programs. However, pathogens tend to evolve and adapt to bypass the resistance mechanisms in crops. The ongoing selection pressures driven by agricultural practices and climate change could lead to the emergence of new strains of downy mildew with increased virulence or expanded host ranges, creating significant obstacles for disease management. Therefore, breeding programs may prioritize the development of millet cultivars with enhanced resilience to downy mildew. Recent reviews on *Cenchrus americanus* (bajra) highlight its cultivation across India, nutritional benefits and health-promoting properties, focusing on 80 released varieties suitable for different growing seasons (94). Advancements in biotechnology and genomics offer promising opportunities to expedite the identification and incorporation of resistance genes into commercial varieties, providing farmers with more effective control measures. Tissue culture techniques can also be employed to isolate somaclonal variants from elite varieties. The extraction and purification of the SG toxin from *Sclerospora graminicola* show potential for screening downy mildew-tolerant pearl millet lines. Molecular tagging of resistance genes will aid in developing resistant varieties through marker-assisted breeding, while transferring and pyramiding these genes into elite parental lines will help create hybrids with durable resistance to downy mildew.

Additionally, wild germplasm resistant to downy mildew should be identified and utilized in breeding programs. Notably, key downy mildew-resistant genes have been sourced from *Pennisetum polystachion*, a wild relative of pearl millet. The future management of downy mildew in millets will depend on a holistic approach that incorporates environmental, biological, technological and socio-economic factors. Proactive measures, sustained research funding and collaborative efforts will be essential to address emerging challenges and protect pearl millet cultivation from the adverse impacts of downy mildew.

Conclusion

Millets are recognized as a promising solution for addressing food scarcity in famine-prone regions due to their resilience in diverse climates and harsh environments, along with their low water requirements and positive environmental impact. However, to fully unlock their potential and ensure sustainable development, extensive research into disease-causing pathogens is crucial. This requires a comprehensive understanding of the pathogens' life cycles, virulence, interactions with host plants, and transmission methods. This review highlights the global significance of downy mildew, emphasizing the critical role millets play in this context. It provides an in-depth examination of the symptoms observed in various millet species, including pearl millet, sorghum, finger millet and foxtail millet, while discussing the physiological and histopathological changes induced by notable pathogens such as *Sclerospora graminicola, Peronosclerospora sorghi* and *Sclerophthora macrospora*. Additionally, the review addresses the management of millet downy mildew, focusing on the integration of innovative technological approaches to combat the disease. It also explores future research opportunities and management strategies, underscoring the importance of continued innovation and collaboration in overcoming the challenges posed by downy mildew in millet cultivation.

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Authors' contributions

YB collected information related to downy mildew disease in millet and assisted in compiling it. JI, KM, and AR reviewed the article and made corrections. All authors read and approved the final manuscript.

Compliance with ethical standards

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References

1. Sarita ES, Singh E. Potential of millets: nutrients composition and health benefits.JSIR.2016;5(2):46-50.https://doi.org/10.31254/jsir.2016.5204
2. Malathi B, Appaji C, Reddy GR, Dattatri K, Sudhakar N. Growth pattern of millets in India. Indian J Agric Res.2016;50(4):382-86. https://doi.org/10.18805/ijare.v50i4.11257
3. Ojediran J, Adamu M, Jim-George D. Some physical properties of Pearl millet (*Pennisetum glaucum*) seeds as a function of moisture content. Afr J Agric. 2010;6(1):39-46.
4. Izge A, Song I. Pearl millet breeding and production in Nigeria: problems and prospects. JEIADC. 2013;5(2):25.
5. Promkhambut A, Younger A, Polthanee A, Akkasaeng C. Morphological and physiological responses of sorghum (*Sorghum bicolor* L. Moench) to waterlogging. Asian J Plant Sci. 2010;9(4):183. https://doi.org/10.3923/ajps.2010.183.193
6. Patanè C, Saita A, Sortino O. Comparative effects of salt and water stress on seed germination and early embryo growth in two cultivars of sweet sorghum. J Agron Crop Sci. 2013;199 (1):30-37. https://doi.org/10.1111/j.1439-037X.2012.00531.x
7. Lata C, Gupta S, Prasad M. Foxtail millet: a model crop for genetic and genomic studies in bioenergy grasses. Crit Rev Biotechnol. 2013;33(3):328-43. https://doi.org/10.3109/07388551.2012.716809
8. Sharma R, Girish A, Upadhyaya HD, Humayun P, Babu T, et al. Identification of blast resistance in a core collection of foxtail millet germplasm. Plant Dis. 2014;98(4):519-24. https://doi.org/10.1094/PDIS-06-13-0593-RE
9. Hariprasanna K. Foxtail Millet, *Setaria italica* (L.) P. Beauv. In: Patil JV, editor. Millets and Sorghum: Biology and Genetic Improvement. Hyderabad: ICAR; 2017. p.112-49. https://doi.org/10.1002/9781119130765.ch4
10. Sakamma S, Umesh K, Girish M, Ravi S, Satishkumar M, Bellundagi V. Finger millet (*Eleusine coracana* L. Gaertn.)

production system: status, potential, constraints and implications for improving small farmer's welfare. J Agric Sci. 2017;10(1):162. https://doi.org/10.5539/jas.v10n1p162

11. Deshpande S, Mohapatra D, Tripathi M, Sadvatha R. Kodo millet -nutritional value and utilization in Indian foods. JGPS. 2015;2 (2):16-23.
12. Kumar A. Studies on grain smut of little millet (*Panicum sumatrense*Roth ex Roemer and Schultes) caused by *Macalpinomyces sharmae* K. Vanky. Doctoral Dissertation [thesis]. JNKVV; 2015.
13. Sendhil R, Joseph J, Akhilraj M, Devi TS, Swaminathan N. 04. Status of millets in India: Trends and prospects.In:Pouchepparadjou A, Krishnan V, Swaminathan N, Sendhil N, Umamaheswari L, Sivasakthi Devi T, Parthasarathi S, Vengadessan V, Umamageswari M, editors. Sensitizing the Millet Farming, Consumption and Nutritional security. India: Researchgate.net; 2023; 015-026.
14. Das I, Nagaraja A, Tonapi VA. Diseases of millets. Indian Farming. 2016;41-45.
15. Jogaiah S, Mitani S, Kestur Nagaraj A, Huntrike Shekar S. Activity of cyazofamid against *Sclerospora graminicola*, a downy mildew disease of pearl millet. Pest Manag Sci. 2007;63 (7):722-27. https://doi.org/10.1002/ps.1383
16. Shetty HS, Raj SN, Kini K, Bishnoi H, Sharma R, Rajpurohit B, et al. Downy mildew of pearl millet and its management. All India Coordinated Research Project on Pearl Millet (ICAR); 2016.
17. Pramitha L, Choudhary P, Rana S, Singh RK, Das P, Sharma S, et al. Foxtail millet (*Setaria italica* L.): a model for small millets. Neglected and Underutilized Crops: Elsevier. 2023;305-24. https://doi.org/10.1016/B978-0-323-90537-4.00020-X
18. Paul P, Sharma P. *Azadirachta indica* leaf extract induces resistance in barley against leaf stripe disease. Physiol Mol Plant Pathol. 2002;61(1):3-13. https://doi.org/10.1016/S0885-5765(02)90412-1
19. Das I. Millet diseases: current status and their management. In: Patil JV, editor. Millets and Sorghum: Biology and Genetic Improvement.Wiley Online Library; 2017;291-322. https://doi.org/10.1002/9781119130765.ch11
20. Singh Y, Sharma D, Kharayat BS. Major diseases of sorghum and their management. Diseases of Field Crops Diagnosis and Management: Volume 1: Cereals, Small Millets and Fiber Crops. 1st ed. New York: taylorfrancis.2020;153. https://doi.org/10.1201/9780429321849-7
21. Bock C. *Peronosclerospora sorghi* (sorghum downy mildew). Crop Protection Compendium. CABI.2013;44643.
22. Kumar B, Kumar J, Srinivas P. Occurrence of downy mildew or green ear disease of finger millet in mid hills of Uttarakhand. J Mycol Pl Pathol. 2007;37(3):532-33.
23. Nomura H, Komori T, Uemura S, Kanda Y, Shimotani K, Nakai K, et al. Chloroplast-mediated activation of plant immune signalling in *Arabidopsis*. Nat Commun. 2012;3(1):926. https://doi.org/10.1038/ncomms1926
24. Ishiga Y, Watanabe M, Ishiga T, Tohge T, Matsuura T, Ikeda Y, et al. The SAL-PAP chloroplast retrograde pathway contributes to plant immunity by regulating glucosinolate pathway and phytohormone signaling. MPMI. 2017;30(10):829-41. https://doi.org/10.1094/MPMI-03-17-0055-R
25. Zhang B, Liu X, Sun Y, Xu L, Ren Z, Zhao Y, et al. *Sclerospora graminicola*suppresses plant defense responses by disrupting chlorophyll biosynthesis and photosynthesis in foxtail millet. Front Plant Sci. 2022;13. https://doi.org/10.3389/fpls.2022.928040
26. Ghareeb H, Becker A, Iven T, Feussner I, Schirawski J. *Sporisorium reilianum* infection changes inflorescence and branching architectures of maize. Plant Physiol. 2011;156 (4):2037-52. https://doi.org/10.1104/pp.111.179499
27. Kumar A, Mali P, Manga V. Changes of some phenolic compounds and enzyme activities on infected pearl millet caused by *Sclerospora graminicola*. Int J Plant Physiol Biochem. 2010;2(1):6-10.
28. Pushpavathi B, Thakur RP, Rao KC. Inheritance of avirulence in *Sclerospora graminicola*, the pearl millet downy mildew pathogen. Plant Pathol J. 2006;5(1):54-59. https://doi.org/10.3923/ppj.2006.54.59
29. Raghavendra S, Safeeulla K. Histopathological studies on ragi (*Eleusine coracana* (L.) Gaertn.) infected by *Sclerophthora macrospora* (Sacc.) Thirum. Shaw and Naras. Proceedings of the Indian Academy of Sciences-Section B Part 2, Plant Sci. 1979;88:19-24.https://doi.org/10.1007/BF03046141
30. Kumar B, Srivastava JN. Finger millet or ragi (*Eleusine coracana* Gaertn.) diseases and their management strategies. Diseases of Field Crops: Diagnosis and Management; 2020. https://doi.org/10.1201/9780429321849-11
31. Jaiswal S, Sasode RS, Pandya R, Gupta PK. Bioagent and chemicals seed dressing for management of Pearl millet downy mildew incited by *Sclerospora graminicola*. Ann Plant Sci. 2021;29(2):110-13. https://doi.org/10.5958/0974-0163.2021.00023.9
32. Kumi F, Agbahoungba S, Badji A, Mwila N, Ibanda A, Anokye M, et al. Genetic diversity and population structure of *Peronosclerospora sorghi* isolates of Sorghum in Uganda; 2018.
33. Zhang B-j, Zhang Y-m, Sun Z-n, Fu Z-x, Xu L, Han Y-h. Impact of *Sclerospora graminicola* infection on spikelet differentiation and development of foxtail millet (*Setaria italica* L.). Acta Phytopathologica Sinica.2023;679-89.
34. Nagaraja A, Das IK. Disease resistance in pearl millet and small millets. Biotic Stress Resistance in Millets: Elsevier. 2016;p. 69-104. https://doi.org/10.1016/B978-0-12-804549-7.00003-2
35. Srivastava JN, Singh A. Diseases of field crops diagnosis and management, 2-volume set: volume 1: cereals, small millets and fiber crops volume 2: pulses, oil seeds, narcotics and sugar crops. CRC Press; 2022.
36. Thakur R, Rao V, Sastry J, Sivaramakrishnan S, Amruthesh K, Barbind L. Evidence for a new virulent pathotype of *Sclerospora graminicola* on pearl millet. J Mycol Pl Pathol. 1999;29(1):61-69.
37. Perumal R, Nimmakayala P, Erattaimuthu SR, No E-G, Reddy UK, Prom LK, et al. Simple sequence repeat markers are useful for sorghum downy mildew (*Peronosclerospora sorghi*) and related species. BMC Genetics. 2008;9(1):1-14. https://doi.org/10.1186/1471-2156-9-77
38. Sharma RK, Bhardwaj P, Negi R, Mohapatra T, Ahuja PS. Identification, characterization and utilization of unigene derived microsatellite markers in tea (*Camellia sinensis* L.). BMC Plant Biology. 2009;9:1-24. https://doi.org/10.1186/1471-2229-9-53
39. Hadimani S, Joshi SM, Geetha N, Shetty HS, Jogaiah S. Elucidating the role of effector protein as biomarker for enhanced resistance against pearl millet downy mildew disease. Physiol Mol Biol Plants. 2023. https://doi.org/10.1016/j.pmpp.2023.102076
40. Sasode RS, Pandya R, Fatehpuria PK. Management of pearl millet downy mildew by the application of bio-agents, chemicals and botanical. Int J Chem Stud. 2018;6(1):606-08.
41. Butler SEJ. Fungi and disease in plants. An introduction to the diseases of field and plantation crops, especially those of India and the East. Thacker, Spink and Company; 1918.
42. Vasudeva R. Diseases of rape and mustard. Rapeseed and Mustard. 1958;16:77-86.

43. Thakur D. Pearl millet downy mildew. In: Singh US, Mukhopadhyay AN, Kumar J, Chaube HS, editors. Plant Diseases of International Importance: Diseases of Pulses and Cereals. USA: CABI; 1992; 282-301.

44. Tuleen D, Frederiksen R, Vudhivanich P. Cultural practices and the incidence of sorghum downy mildew in grain sorghum. Phytopathol. 1980;70(9):905-08. https://doi.org/10.1094/Phyto-70-905

45. Janke G, Pratt R, Arnold J, Odvody G. Effects of deep tillage and roguing of diseased plants on oospore populations of *Peronosclerospora sorghi* in soil and on incidence of downy mildew in grain sorghum. Phytopathol. 1983;73(12):1674-78. https://doi.org/10.1094/Phyto-73-1674

46. Kumi F, Badji A, Mwila N, Odong T, Ochwo-Ssemakula M, Tusiime G, et al. New sources of sorghum resistant genotypes to downy mildew disease in Uganda. Biodiversitas. 2019. https://doi.org/10.13057/biodiv/d201136

47. Upadhyaya HD, Vetriventhan M, Asiri AM, CR Azevedo V, Sharma HC, Sharma R, et al. Multi-trait diverse germplasm sources from mini core collection for sorghum improvement. Agriculture. 2019;9(6):121. https://doi.org/10.3390/agriculture9060121

48. Zoclanclounon YAB, Kanfany G, Thiaw C, Fofana A, Mbaye N, Cisse N. Assessment of pearl millet genotypes for downy mildew resistance and agronomic performance under field conditions in senegal. Int J Agric Biol. 2018;20:493-98. https://doi.org/10.17957/IJAB/15.0504

49. Kanfany G, Fofana A, Tongoona P, Danquah A, Offei S, Danquah E, et al. Identification of new sources of resistance for pearl millet downy mildew disease under field conditions. Plant Genet Res. 2018;16(4):397-400. https://doi.org/10.1017/S1479262117000405

50. Saini K, Mathur A, Sharma R, Kumar V, Bagri R, Sharma YK, et al. Screening of pearl millet (*Pennisetum glaucum*) genotypes against downy mildew caused by *Sclerospora graminicola* (Sacc.) Schoret. J Pharm Innov.2022;11(2):1453-56.

51. Sauter H, Steglich W, Anke T. Strobilurins: evolution of a new class of active substances. Angew Chem Int Ed. 1999;38 (10):1328-49. https://doi.org/10.1002/(SICI)1521-3773(19990517)38:10<1328::AID-ANIE1328>3.0.CO;2-1

52. Bartlett DW, Clough JM, Godwin JR, Hall AA, et al. The strobilurin fungicides. Pest Manag Sci. 2002;58(7):649-62. https://doi.org/10.1002/ps.520

53. Williams R, editor. Downy mildews of tropical cereals. Advances in Plant Pathology; 1984.

54. Chaluvaraju G, Basavaraju P, Shetty N, Deepak S, et al. Effect of some phosphorous-based compounds on control of pearl millet downy mildew disease. Crop Prot. 2004;23(7):595-600. https://doi.org/10.1016/j.cropro.2003.11.008

55. Chaudhari R, Parmar G, Juneja R, Parmar S, Mungra K. Eco friendly management of pearl millet downy mildew (*Sclerospora graminicola*) by using organic compounds.J Pharm Innov. 2023;12(6):762-65.

56. Mane S, Chaudhari K, Patil B. Efficacy of biological control agents against downy mildew of bajara.Plant Dis. 2007;2(2):245-46.

57. Siddaiah CN, Satyanarayana NR, Mudili V, Kumar Gupta V, Gurunathan S, Rangappa S, et al. Elicitation of resistance and associated defense responses in *Trichoderma hamatum* induced protection against pearl millet downy mildew pathogen. Sci Rep. 2017;7(1). https://doi.org/10.1038/srep43991

58. Saini K, Mathur A, Sharma R, Kumar V, Bagri R, Gautum V. Biocontrol potential of three antagonists against downy mildew of pearl millet caused by *Sclerospora graminicol* (Sacc.) Schoret. JBC. 2020;180-84. https://doi.org/10.18311/jbc/2020/25991

59. Murali M, Amruthesh KN. Plant growth-promoting fungus *Penicillium oxalicum* enhances plant growth and induces resistance in pearl millet against downy mildew disease. Plant Pathol J. 2015;163(9):743-54. https://doi.org/10.1111/jph.12371

60. Sangwan P, Raj K. Evaluation of bioagents for management of downy mildew of pearl millet caused by *Sclerospora graminicola* (Sacc.) Schroet. Forage Res. 2016;42(1):44-47.

61. Nandini B, Geetha N, Prakash HS, Hariparsad P. Natural uptake of anti-oomycetes *Trichoderma* produced secondary metabolites from pearl millet seedlings-A new mechanism of biological control of downy mildew disease. JBC. 2021;156: https://doi.org/10.1016/j.biocontrol.2021.104550

62. Shivakumar P, Geetha H, Shetty H. Peroxidase activity and isozyme analysis of pearl millet seedlings and their implications in downy mildew disease resistance. Plant Sci. 2003;164(1):85-93. https://doi.org/10.1016/S0168-9452(02)00339-4

63. Raj SN, Deepak S, Basavaraju P, Shetty HS, Reddy M, Kloepper JW. Comparative performance of formulations of plant growth promoting rhizobacteria in growth promotion and suppression of downy mildew in pearl millet. Crop Prot. 2003;22(4):579-88. https://doi.org/10.1016/S0261-2194(02)00222-3

64. Geetha H, Shetty H. Induction of resistance in pearl millet against downy mildew disease caused by *Sclerospora graminicola* using benzothiadiazole, calcium chloride and hydrogen peroxide-a comparative evaluation. Crop Prot. 2002;21(8):601-10. https://doi.org/10.1016/S0261-2194(01)00150-8

65. Deepak S, Raj SN, Umemura K, Kono T, Shetty HS. Cerebroside as an elicitor for induced resistance against the downy mildew pathogen in pearl millet. Ann appl Biol. 2003;143(2):169-73. https://doi.org/10.1111/j.1744-7348.2003.tb00283.x

66. Chandrashekhara, Niranjan Raj S, Manjunath G, Deepak S, Shekar Shetty H. Seed treatment with aqueous extract of *Viscum album* induces resistance to pearl millet downy mildew pathogen. J Plant Interact. 2010;5(4):283-91. https://doi.org/10.1080/17429140903556539

67. Daayf F, Schmitt A, Belanger R. The effects of plant extracts of *Reynoutria sachalinensis* on powdery mildew development and leaf physiology of long English cucumber. Plant Dis. 1995;79 (6):577-80. https://doi.org/10.1094/PD-79-0577

68. Singh S, Shetty H. Efficacy of systemic fungicide metalaxyl for the control of downy mildew (*Sclerospora graminicola*) of pearl millet (*Pennisetum glaucum*). Indian J Agric Sci. 1990;60(9):575-81.

69. Prasad V, D'Souza C, Yadav D, Shaikh A, Vigneshwaran N. Spectroscopic characterization of zinc oxide nanorods synthesized by solid-state reaction. Spectrochim Acta A Mol Biomol Spectrosc. 2006;65(1):173-78. https://doi.org/10.1016/j.saa.2005.10.001

70. Cakmak I. Enrichment of cereal grains with zinc: agronomic or genetic biofortification? Plant and Soil. 2008;302:1-17. https://doi.org/10.1007/s11104-007-9466-3

71. Nandhini M, Rajini S, Udayashankar A, Niranjana S, Lund OS, Shetty H, et al. Biofabricated zinc oxide nanoparticles as an eco-friendly alternative for growth promotion and management of downy mildew of pearl millet. Crop Prot. 2019;121:103-12. https://doi.org/10.1016/j.cropro.2019.03.015

72. Xing K, Zhu X, Peng X, Qin S. Chitosan antimicrobial and eliciting properties for pest control in agriculture: a review. Agron Sustain Dev. 2015;35:569-88. https://doi.org/10.1007/s13593-014-0252-3

73. Sathiyabama M, Manikandan A. Chitosan nanoparticle induced defense responses in fingermillet plants against blast disease caused by *Pyricularia grisea* (Cke.) Sacc. Carbohydr Polym. 2016;154:241-46. https://doi.org/10.1016/j.carbpol.2016.06.089

74. Siddaiah CN, Prasanth KVH, Satyanarayana NR, Mudili V, Gupta VK, Kalagatur NK, et al. Chitosan nanoparticles having higher degree of acetylation induce resistance against pearl millet downy mildew through nitric oxide generation. Sci Rep. 2018;8 (1):2485. https://doi.org/10.1038/s41598-017-19016-z

75. Tran PA, Webster TJ. Selenium nanoparticles inhibit *Staphylococcus aureus* growth. Int J Nanomedicine. 2011;1553-58. https://doi.org/10.2147/IJN.S21729

76. Kong H, Yang J, Zhang Y, Fang Y, et al. Synthesis and antioxidant properties of gum arabic-stabilized selenium nanoparticles. Int J Biol Macromol. 2014;65:155-62. https://doi.org/10.1016/j.ijbiomac.2014.01.011

77. Wang X, Zhang W, Chen H, Liao N, Wang Z, Zhang X, et al. High selenium impairs hepatic insulin sensitivity through opposite regulation of ROS. Toxicol Lett. 2014;224(1):16-23. https://doi.org/10.1016/j.toxlet.2013.10.005

78. Nandini B, Hariprasad P, Prakash HS, Shetty HS, Geetha N. Trichogenic-selenium nanoparticles enhance disease suppressive ability of *Trichoderma* against downy mildew disease caused by *Sclerospora graminicola* in pearl millet. Sci Rep. 2017;7(1):2612. https://doi.org/10.1038/s41598-017-02737-6

79. Nandini B, Puttaswamy H, Prakash HS, Adhikari S, Jogaiah S, Nagaraja G. Elicitation of novel trichogenic-lipid nanoemulsion signaling resistance against pearl millet downy mildew disease. Biomo. 2019;10(1):25. https://doi.org/10.3390/biom10010025

80. Shailasree S, Melvin P. b-amino butyric acid–resistance inducing agent in pearl millet. J Plant Biochem Physiol. 2015;2 (144):2.

81. Lavanya S, Amruthesh K. 3, 5-dichloroanthranilic acid (DCA)-an elicitor induces systemic resistance against downy mildew in pearl millet. Int J Life Sci. 2016;4:97-106.

82. Murali M, Sudisha J, Amruthesh K, Ito SI, Shetty HS. Rhizosphere fungus *Penicillium chrysogenum* promotes growth and induces defence-related genes and downy mildew disease resistance in pearl millet. Plant Biology. 2013;15(1):111-18. https://doi.org/10.1111/j.1438-8677.2012.00617.x

83. García-Mier L, Guevara-González RG, Mondragón-Olguín VM, Verduzco-Cuellar BdR, Torres-Pacheco I. Agriculture and bioactives: achieving both crop yield and phytochemicals. Int J Mol Sci. 2013;14(2):4203-22. https://doi.org/10.3390/ijms14024203

84. Pushpalatha H, Sudisha J, Shetty HS. Cellulysin induces downy mildew disease resistance in pearl millet driven through defense response. Eur J Plant Pathol. 2013;137:707-17. https://doi.org/10.1007/s10658-013-0281-9

85. Hou S, Liu Z, Li Y, Yang M, Hou S, Han Y, et al. Exogenous salicylic acid enhanced resistance of Foxtail millet (*Setaria italica*) to *Sclerospora graminicola*. Plant Growth Regulation. 2023;99(1):35-44. https://doi.org/10.1007/s10725-022-00854-5

86. Govind SR, Jogaiah S, Abdelrahman M, Shetty HS, Tran L-SP. Exogenous trehalose treatment enhances the activities of defense-related enzymes and triggers resistance against downy mildew disease of pearl millet. Front Plant Sci. 2016;7:1593. https://doi.org/10.3389/fpls.2016.01593

87. Wang H, Han Y, Wu C, Zhang B, Zhao Y, Zhu J, et al. Comparative transcriptome profiling of resistant and susceptible foxtail millet responses to *Sclerospora graminicola* infection. BMC Plant Biol. 2022;22(1):567. https://doi.org/10.1186/s12870-022-03963-5

88. Girigowda Manjunatha GM, Sathyanaraya Niranjan-Raj SN-R, Prashanth G, Shantharaj Deepak SD, et al. Nitric oxide is involved in chitosan-induced systemic resistance in pearl millet against downy mildew disease. Pest Manag Sci. 2009;65(7):737-43. https://doi.org/10.1002/ps.1710

89. Aida K, Takakuwa N, Kinoshita M, Sugawara T, Imai H, Ono J, et al. editors. Properties and physiological effects of plant cerebroside species as functional lipids. Advanced Research on Plant Lipids: Proceedings of the 15th International Symposium on Plant Lipids. Springer.2003. https://doi.org/10.1007/978-94-017-0159-4_54

90. Beyer P, Al-Babili S, Ye X, Lucca P, Schaub P, Welsch R, et al. Golden rice: introducing the β-carotene biosynthesis pathway into rice endosperm by genetic engineering to defeat vitamin A deficiency. J Nutr. 2002;132(3):506S-10S. https://doi.org/10.1093/jn/132.3.506S

91. Pushpalatha H, Mythrashree S, Shetty R, Geetha N, Sharathchandra R, et al. Ability of vitamins to induce downy mildew disease resistance and growth promotion in pearl millet. Crop Prot. 2007;26(11):1674-81. https://doi.org/10.1016/j.cropro.2007.02.012

92. Tonapi VA, Thirunavukkarasu N, Gupta S, Gangashetty PI, Yadav O, editors. Pearl millet in the 21st century. Singapore: Springer Nature Singapore; 2024.https://doi.org/10.1007/978-981-99-5890-0

93. Deevi KC, Swamikannu N, Pingali PR, Gumma MK. Current trends and future prospects in global production, utilization and trade of pearl millet. In: Tonapi VA, editor. In: Pearl Millet in the 21st Century: Food-Nutrition-Climate resilience-Improved livelihoods. Singapore: Springer Nature Singapore; 2024. p. 1-33. https://doi.org/10.1007/978-981-99-5890-0_1

94. Acharya Balkrishna RS, Prajapati UB, Srivastava A, Joshi RA, Tripathi P. A review on Bajra/Pearl millet (*Cenchrus americanus* (L.) Morrone). JSIR . 2024;13:1-8. https://doi.org/10.31254/jsir.2024.13101.https://doi.org/10.31254/jsir.2024.13101

95. Raj C, Sharma R. Sexual compatibility types in F_1progenies of *Sclerospora graminicola*, the causal agent of pearl millet downy mildew. J Fungus. 2022;8(6):629. https://doi.org/10.3390/jof8060629

96. Sharma R, Rao V, Senthilvel S, Rajput S, Thakur R. Virulence diversity in north Indian isolates of *Sclerospora graminicola*, the pearl millet downy mildew pathogen. Plant Pathol J. 2011;93 (1):71-78.

97. Thakur R, Chandrashekara Rao K, Rao V, Pushpavathi B. Characterization of *Sclerospora graminicola* isolates from pearl millet for virulence and genetic diversity. Plant Pathol J. 2006;22 (1):28-35. https://doi.org/10.5423/PPJ.2006.22.1.028

98. Andersen EJ, Nepal MP. Genetic diversity of disease resistance genes in foxtail millet (*Setaria italica* L.). Plant Gene. 2017;10:8-16. https://doi.org/10.1016/j.plgene.2017.03.002