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Review

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Current insights on rice (*Oryza sativa* L.) bakanae disease and exploration of its management strategies

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Abstract: Bakanae is an emerging rice disease caused by the seed- and soil-borne pathogen *Fusarium fujikuroi*. It is becoming a more serious threat to sustainable rice production throughout rice-growing regions. Bakanae disease infection is responsible for high yield losses ranging from 3% to 95%, and disease incidence varies based on the region and cultivars. Hence, understanding the nature of the pathogen, its pathogenicity, disease epidemiology, symptoms, host–pathogen interaction, and the role of secondary metabolites in the disease cycle will be helpful in the development of effective and sustainable management strategies. However, very few comprehensive studies have described the details of rice bakanae disease. Thus, in this review we summarize and discuss in detail the information available from 1898 to 2023 on various critical facets of bakanae disease, and provide perspectives on future research.

Key words: Rice; Bakanae disease; *Fusarium fujikuroi*; Host–pathogen interaction; Pathogenicity; Gibberellic acid signaling; Disease management

1 Introduction

Rice (*Oryza sativa* L.) is the primary staple food crop, grown in many parts of the world, especially in Asia (about 90% of the total), Latin America, and Africa. China (29.21%) and India (24.64%) are the major contributors to total global rice production, followed by Bangladesh (7.09%), Indonesia (6.88%), and Vietnam (5.41%) (Childs and LeBeau, 2023). The global demand for rice has increased significantly due to population growth and consequent consumption. A recent International Food Policy Research Institute (IFPRI) survey indicates that rice production must increase to 38% by 2030 to feed the expanding population (Zhang et al., 2019). However, several constraints such as land degradation, scarcity of water and labor, and susceptibility to pests, diseases, and various environmental stresses hamper rice production (Gupta AK et al., 2015).

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Fungal diseases like false smut, blast, bakanae, brown spot, stem rot, and sheath blight are of major economic significance in rice production. Among them, "Bakanae disease" caused by *Fusarium fujikuroi* is an emerging and economically important disease that causes drastic yield losses of 3%–95% depending on the cultivar and geographic region (Jing and Suga, 2021). Since bakanae disease and *F. fujikuroi* have more than a hundred years of research history, several notable reviews and research works have studied the nature of the disease, its economic importance, management practices, and pathogenicity (Gupta AK et al., 2015; Bashyal et al., 2016; Sarwar et al., 2018; Singh et al., 2019). However, limited information is available on the infection cycle, host–pathogen interaction, and eco-friendly management strategies of the disease. Hence, in this review, we highlight the latest comprehensive information to understand the disease cycle, secondary metabolite (SM)-mediated disease induction through host–pathogen interaction, and progress made in the development of efficient disease-resistant, eco-friendly strategies to overcome the disease. We also review the influence of modern breeding techniques such as the identification of genes and

quantitative trait loci (QTL) for developing bakanae disease-resistant lines.

1.1 History of bakanae disease

Research on bakanae disease has a long history. The disease was first reported at the beginning of the 19th century in Japan. Literally translated, "Bakanae" means "foolish seedlings," "naughty seedlings," or "stupid rice crop," referring to the abnormal growth of the rice plant. The disease was identified in 1828 in Japan (Ito and Kimura, 1931), and the pathogen responsible was first identified by Hori (1898). At the beginning of the 20th century, plant pathologist Kenkichi Sawada reported that the pathogenic fungus produced the "stimulus" that induced the symptoms like excess growth in rice (Sawada, 1912). Later, his colleague Eiichi Kurosawa observed that culture filtrate-treated rice seedlings showed remarkable elongation, and in 1926 suggested that the pathogenic fungus produced an unknown "toxin" with the effect of inducing rice overgrowth (Kurosawa, 1926). This finding attracted many researchers to uncover the chemicals responsible for bakanae disease induction. In 1935, agricultural chemist Teijiro Yabuta named this unknown toxin gibberellin (Yabuta, 1935), and its two crystalline variants were named gibberellin A and gibberellin B (Yabuta and Sumiki, 1938). In the mid-1950s, a British research group led by John Grove extracted a pure crystalline compound from the pathogen and called it gibberellic acid (GA) (Curtis and Cross, 1954). Later, Japanese chemists Nobutaka Takahashi and Saburo Tamura elucidated the chemical nature of gibberellin A as a mixture of three compounds, namely gibberellin A1, gibberellin A2, and gibberellin A3 (Takahashi et al., 1955). In 1963, Jean A. Hartsuck and William N. Lipscomb published the X-ray crystal structure of GA as its di-*p*-bromobenzoate methyl ester (Hartsuck and Lipscomb, 1963). All these research findings provided a stable platform for GA-based research. In the mid-1990s, researchers made a notable contribution to the identification of the cluster of GA biosynthesis genes (Mende et al., 1997), which helped attempts to produce a large quantity of GA by increasing the expression of GA biosynthesis genes and/or the development of genetically modified strains for commercial purposes.

The search for natural remedies for bakanae disease began in the 1930s through traditional breeding methods (Ito and Kimura, 1931). These methods evolved over the years, and modern breeding techniques have been developed to screen resistant lines with less time and labor consumption. More recently, breeders have adopted various molecular tools such as genome-wide association study (GWAS), fine mapping, transcriptomic profiling, QTL, and allele-specific polymerase chain reaction (PCR) marker-assisted selection (Yang et al., 2006; Volante et al., 2017; Cheon et al., 2019; Lee et al., 2019) to screen efficient bakanae disease-resistant lines in a short time. In the mid-1980s, alternative plant-based and other biocontrol strategies were initiated (Rosales et al., 1986). Besides biological approaches, various chemical fungicides have been applied for bakanae disease management. Initially, organo-mercury compounds were used extensively to control the pathogen (Takeuchi, 1972), but these compounds are no longer in use due to their non-targeted toxicity. In the mid-1970s, various single and combined chemical fungicides were developed and commercialized for bakanae disease management (Gangopadhyay and Kapoor, 1977). Fig. 1 describes the complete timeline of bakanae disease research.

1.2 Geographical distribution and economic importance of bakanae disease

Bakanae disease occurs widely in all rice-growing regions of the world, specifically Asia, Africa, North and South America, and some parts of Europe (Desjardins et al., 2000; Yang et al., 2006; Matic et al., 2017; Volante et al., 2017; Bashyal, 2018; Chen et al., 2019; Cheon et al., 2019). However, the yield loss differs due to differences in rice cultivars, climatic conditions, infection time, and growth stage (Kanjanasoon, 1965; Gupta A et al., 2015; Gupta AK et al., 2015). *F. fujikuroi* infections were responsible for 20% to 50% of yield loss in Japan in the early days (Ito and Kimura, 1931), 15% to 25% in India (Gupta AK et al., 2015), 10% to 50% in Pakistan, and 40% to 70% in Iran (Ghazanfar et al., 2013). Similarly, bakanae disease induces up to 40% of the yield loss in Nepal (Desjardins et al., 2000), 2% to 25% in Bangladesh, 15% to 25% in various states of India (Pannu et al., 2012), and 3.7% to 14.7% in Thailand (Kanjanasoon, 1965). Apart from Asian countries, considerable yield losses have been observed in Spain (5% to 23%), Italy (5% to 15%) and Australia (up to 70%) (Singh and Sunder, 2012; Matic et al., 2017).

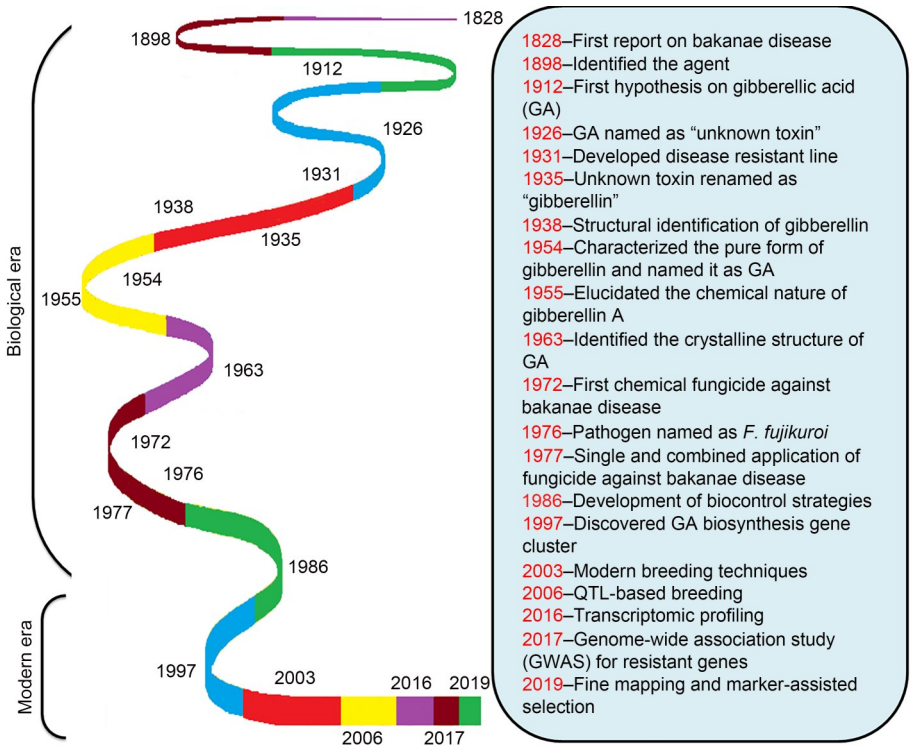

Fig. 1 Detailed history of bakanae disease research. *F. fujikuroi*: *Fusarium fujikuroi*; QTL: quantitative trait loci.

2 Pathogen

2.1 Nomenclature and mating population

F. fujikuroi is a filamentous fungus belonging to the phylum Ascomycota, class Sordariomycetes, order Hypocreales and family Nectriaceae, which is known to produce white mycelium on growth media. The causative agent of bakanae disease was first described by Hori (1898) and named *Fusarium heterosporum* Nees. Later, Sawada (1917) identified the perfect stage of the pathogen and described it as *Lisea fujikuroi* Saw, which was amended in 1931 to *Gibberella fujikuroi* by Ito and Kimura (1931), who also identified the asexual stage as *Fusarium moniliforme*. Initially, *F. moniliforme* was misidentified as the causative agent for bakanae disease (Sun and Snyder, 1981). Later it was re-identified as *F. fujikuroi* (Nirenberg, 1976), and the name *F. moniliforme* is no longer applied to the agent of rice bakanae disease (Singh and Sunder, 1997).

Initially, *G. fujikuroi* was considered a single species. Later, based on chemotaxonomic characterization, SM production, and mating population (MP) analysis, it was found to consist of several distinct species collectively known as the *G. fujikuroi* species complex (GFSC) (Kuhlman, 1982). However, Lima et al. (2012) described twelve MPs of the GFSC including: MP-A (*Fusarium verticillioides*), MP-B (*Fusarium sacchari*), MP-C (*F. fujikuroi*), MP-D (*Fusarium proliferatum*), MP-E (*Fusarium subglutinans*), MP-F (*Fusarium thapsinum*), MP-G (*Fusarium nygamai*), MP-H (*Fusarium circinatum*), MP-I (*Fusarium konzum*), MP-J (*Fusarium xylarioides*), MP-K (*Fusarium temperatum*), and MP-L (*Fusarium tupiense*). Accordingly, the name GFSC was changed to the *F. fujikuroi* species complex (FFSC), which consists of 50–100 distinct species. Compared to other FFSC members, *F. fujikuroi* has been widely identified from infected rice cultivars within different eco-climatic regions (Bashyal et al., 2016). Hence, here we have restricted our discussion to *F. fujikuroi* as it is the most predominant and virulent of all other species associated with bakanae disease induction.

2.2 Host range

F. fujikuroi infects a wide range of crops, including monocots, dicots, and gymnosperms. These host

plants are classified into primary hosts and alternative hosts. The pathogen completes its sexual cycle in its primary host; rice is the primary host of *F. fujikuroi* (Singh and Sunder, 2012). Besides rice, maize, barley, sorghum, sugarcane, wheat, pine, and rye are also known to be primary hosts for *F. fujikuroi* growth and sexual development (Gupta AK et al., 2015). During unfavorable conditions, pathogens spend their remaining lifetime with alternative host plants, such as tomato, cowpea, proso millet, and water grass (Puyam et al., 2019).

2.3 Symptoms

The symptoms of bakanae disease may differ based on the age and resistance of the rice cultivar and the virulence of the pathogen (Singh and Sunder, 2012). Both seedling and field-stage plants are susceptible to this disease. Infected seedlings are lanky and taller than healthier plants, and have pale yellowish leaves. Such infected seedlings die before or after transplantation to the field (Singh et al., 2019). Surviving seedlings often become significantly taller with a wider flag leaf angle in the field stage and die before grain formation (Figs. 2c–2f). Bashyal (2018) described the visible symptoms in aerial parts (elongated green plant, elongated and rotted plant, normal and rotted plant rotting in a few tillers, completely rotted plant, and an elongated plant bearing empty panicles and adventitious root formation) and in underground parts (rotting and blackening of roots and adventitious roots) of mature plants infected with bakanae disease. With these visible symptoms, infected plants and plant materials can be identified easily and eradicated before spreading the disease into another field. Recently, Kim et al. (2023) developed a drone imaging system to detect bakanae disease-infected bunches in large scale with 80.36% accuracy.

2.4 Identification of the pathogen

Conventionally, pathogens were categorized based on macroscopic and microscopic morphological traits. On potato dextrose agar media, *F. fujikuroi* forms a white, branched, hyaline, and septate mycelium, which becomes grey violet, magenta, or reddish brown with age (Ilija et al., 2009; Ahangar et al., 2014) (Figs. 2a and 2b). In microscopic observations, *F. fujikuroi* produces both sexual spores (ascospores) and asexual spores. The ascospores are piston-shaped with a cylindrical structure, and form within a sac (ascus) with a length of 90–120 μm and a width of 7–9 μm. Two types of asexual spores (i.e., macro- and microconidia) were observed from bakanae pathogens. Microconidia are cylindrical, with 0–1 septum, a length of 5–12 μm, and a width of 1.5–2.5 μm (Ahangar et al.,

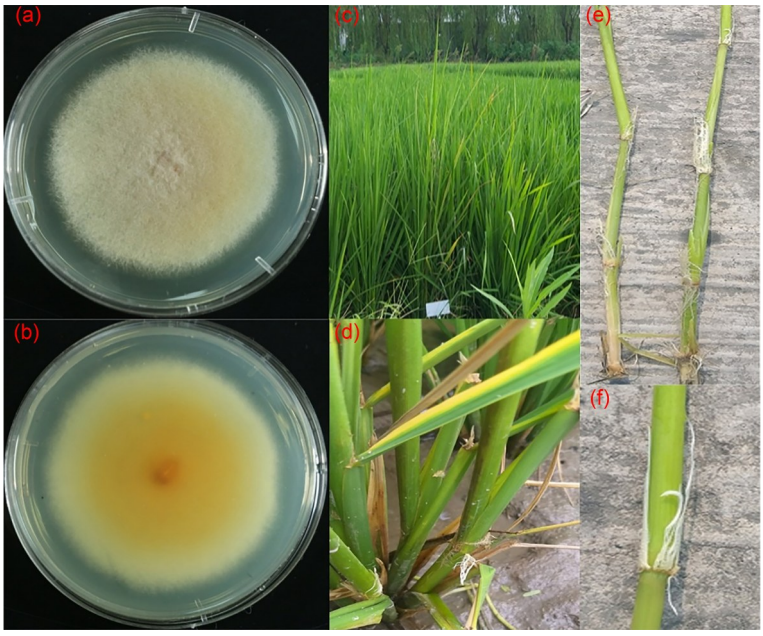

Fig. 2 Colony morphology of *Fusarium fujikuroi* strain and symptoms of bakanae disease. (a, b) Front (a) and back (b) views on potato dextrose agar media. (c) Rice plants infected by bakanae disease showing elongated pale yellow leaves in paddy fields. (d–f) Development of adventitious roots in infected plants.

2014). Macroconidia are delicate, medium-length, straight or sickle-shaped with 3–5 septa (Ilija et al., 2009).

2.4.1 Chemotaxonomic characterization

Chemotaxonomic characterization is another useful method to distinguish *Fusarium* spp. based on their biochemical behavior, and can serve as an additional tool to classify the closely associated species such as *F. fujikuroi*, *F. proliferatum*, and *F. verticillioides*. In general, members of the *Fusarium* genus produce a number of SMs such as GA, fusaric acid, fumonisin, moniliformin (MON), beauvericin, bikaverin, fusaproliferin, fusarins, and fusarubins, which contribute to variation in their virulence. Among the SMs, GA is directly associated with the virulence of the pathogens: with excessive GA secretion, *F. fujikuroi* is regarded as the most virulent species causing bakanae disease (Wang et al., 2021). Desjardins et al. (2000) validated the efficiency of GA production in different *Fusarium* spp. and observed that *F. fujikuroi* was a potential candidate to produce GA. Similarly, Malonek et al. (2005) studied the GA-producing ability of various *Fusarium* species isolated from infected rice plants and observed that none other than *F. fujikuroi* and *F. konzum* produced GA. These findings suggested that the detection of GA production could be a significant criterion for distinguishing *F. fujikuroi* from other associated species. However, Proctor et al. (2010) identified five *F. proliferatum* strains with the ability to produce GA and assumed that the GA biosynthesis gene might have been transferred to *F. proliferatum* through hybridization. These findings suggested that in addition to *F. fujikuroi*, closely related strains like *F. proliferatum* and *F. verticillioides* should also be considered to produce GA and be associated with bakanae disease.

Recently, Bashyal and Aggarwal (2013) identified that 90% of *F. fujikuroi* infections were responsible for the induction of tall, lanky plants with chlorotic leaves, whereas most *F. verticillioides* infections induced crown and stem rots. These research findings denote the importance of *F. fujikuroi* in bakanae disease induction. Although *F. fujikuroi* is the major causal agent of bakanae disease induction, other *Fusarium* spp. such as *F. proliferatum* and *F. verticillioides* were also identified in diseased plants at a lower incidence. Morphological and chemotaxonomic characterization results could be easily misinterpreted with these phylogenetically close species. Compared to morphological and chemotaxonomic characterization, molecular characterization techniques offer the most accurate and reliable methods for pathogen identification.

2.4.2 Nature of pathogenicity

The chemotaxonomic properties of the pathogen are directly associated with induction of the disease. Most virulent *F. fujikuroi* strains produce an excess quantity of GA, which significantly induces visible symptoms in rice seedlings. Based on their disease induction rates, pathogenic *F. fujikuroi* strains can be assigned to one of four categories: Scale 1, non-virulent (slightly infected pale-green seedlings without elongation); Scale 2, moderately virulent (moderately infected yellow-green seedlings, slightly elongated compared to the control); Scale 3, virulent (infected yellow-green seedlings, slightly elongated compared to Scale 2); and Scale 4, extremely virulent (severely infected yellowish seedlings, abnormally elongated compared to the control, and/or seedling death) (Fig. 3). Recently, Yan et al. (2022) optimized the mass production of the spores using supplements of different medium combinations and evaluated the influence of different *F. fujikuroi* spore concentrations and different time of exposure on the induction of bakanae disease.

2.4.3 Molecular characterization

Molecular sequencing and its phylogenetic interpretation help us elucidate the genetic, ecological, and evolutionary relationships of pathogens and categorize them into standard racial classes and groups. Various molecular techniques have evolved rapidly over the last two decades to identify closely related pathogens based on their sequence information. Initially, bakanae pathogens were categorized using molecule-based techniques such as restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), inter simple sequence repeat (ISSR), and electrophoretic karyotype analysis (Moretti et al., 2004; Petrovic et al., 2013). Recently, sequence-based sequencing techniques have been widely used to identify pathogens associated with bakanae disease at the sub-species level (Bashyal and Aggarwal, 2013). These techniques include sequencing of internal transcribed spacer (ITS) regions, translation elongation factor (TEF) and TEF-1α genes, intergenic spacer (IGS),

β-tubulin (tub2) region, mitochondrial small subunit (mtSSU), and simple sequence repeats (SSR). For a better understanding, multi-locus sequence typing (MLST) was also used by targeting non-functional DNA segments such as ITS and RNA polymerase II subunit (RPB2). Zhang et al. (2019) used the loop-mediated isothermal amplification (LAMP) approach for large-scale detection of *F. fujikuroi*. Recently, Bashyal et al. (2020) screened *F. fujikuroi* strains using universal rice primers (URPs) and validated their virulence-related genes such as acetylxylan (*FFAC*), exopolygalacturanase (*FFEX*), and pisatin demethylase (*FFPD*) through quantitative real-time PCR (qRT-PCR) analysis (Tadasanahaller et al., 2023).

Modern technologies provide a useful platform to understand the whole genomic composition of the bakanae pathogen. Moreover, these techniques make it relatively easy to elucidate the functional genes responsible for disease induction. So far, more than ten *F. fujikuroi* strains have been characterized through whole genome sequencing with significant differences in their geographic distribution, spore production, chromosome size, SM production, genes, and pathogenicity (Jeong et al., 2013; Wiemann et al., 2013; Chiara et al., 2015; Bashyal et al., 2017; Niehaus et al., 2017). Details of these strains are presented in Table 1.

3 Disease epidemiology

The induction of bakanae disease is associated with various environmental factors (temperature, soil moisture, humidity, rainfall, cropping season, soil

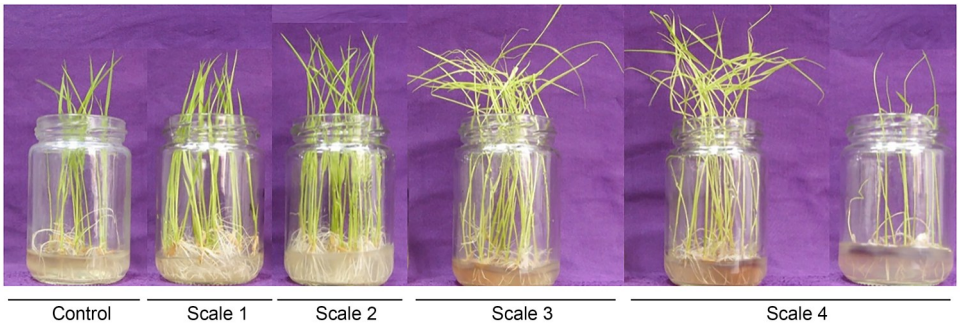

Fig. 3 Pathogenicity scales of *Fusarium fujikuroi*. Scale 1, non-virulent; Scale 2, moderately virulent; Scale 3, virulent; Scale 4, extremely virulent.

Table 1 *Fusarium fujikuroi* strains of which the genomes have been sequenced

Strain	Genome size (Mb)	Host type	Country	Reference
IMI58289	43.9	Rice	China	Wiemann et al., 2013
B14	43.8	Rice	Republic of Korea	Jeong et al., 2013
FGSC 8932	43.1	Rice	China	Chiara et al., 2015
KSU 3368	43.2	Rice	Thailand	
KSU X-10626	43.1	Little bluestem	USA	
F250	42.4	Rice	India	Bashyal et al., 2017
m567	44.0	Rice	Japan	Niehaus et al., 2017
MRC2276	45.0	Rice	Philippines	
C1995	45.8	Rice	China	
E282	46.1	Rice	Italy	
NCIM 1100	45.3	Rice	India	
B20	44.3	Rice	Republic of Korea	
FSU48	46.1	Maize	Germany	
COH1152	48.0	Clinical isolate	USA	Urbaniak et al., 2018
FUS01	49.0	Fuel environmental	USA	Radwan et al., 2018
SG4	46.5	Rice	Italy	Piombo et al., 2021
C2S	45.8	Rice		
I1.3	45.8	Rice		

fertilizer, wind, and water) and biological factors (rice cultivar genotype and virulence of the pathogen), which determine the disease incidence, pathogen survival, and infection cycle.

3.1 Environmental factors

Temperature is the key factor affecting disease induction. The optimum temperature for bakanae disease induction is 27–35 ℃. A moderate level of disease induction occurs at 25 ℃, while at a lower temperature (20 ℃) *F. fujikuroi* fails to induce the disease efficiently (Matic et al., 2017; Bashyal, 2018). Similarly, disease incidence is greater in dry nurseries and seedbeds than in wet conditions. The pathogen can survive up to 280 d in dry soil with 10% of the moisture holding capacity. In contrast, the survival rate is drastically reduced to 115 d with 45% and to 45–75 d with 100% of the moisture holding capacity (Yu and Sun, 1976). Moreover, a higher supplementation of nitrogenous fertilizers can also reduce the multiplication of the pathogen in soil (Mandal and Chaudhuri, 1988). Apart from temperature and soil nutrients, wind and water play a crucial role in spreading spores. Matic et al. (2017) conducted a field study to monitor the influence of the wind in spore migration using spore traps, which confirmed that wind and rain might play a vital role in the transmission of *F. fujikuroi* conidia from one field to another.

3.2 Biological factors

3.2.1 Genotypic variation

Genotypic variation among rice cultivars is the biological factor, which largely determines the infection rate. This kind of natural variation among rice lines in bakanae disease resistance has been studied in different parts of the world. Cultivars have been categorized as highly resistant (HR), resistant (R), moderately resistant (MR), moderately susceptible (MS), susceptible (S), or highly susceptible (HS). For instance, rice genotypes like ‘Samgwang,’ ‘Wonseadaesoo,’ ‘Nampyeong,’ ‘Athad,’ ‘Appunu,’ ‘BPT5204,’ ‘C101A51,’ ‘Chandana,’ ‘Himju,’ and ‘IR58025B’ were found to be more resistant to bakanae disease (Cheon et al., 2019; Kang et al., 2019; Lee et al., 2019). However, cultivars such as ‘Pusa Basmati 1121,’ 1176, 1401, 1509, 2511, ‘CSR30,’ ‘Junam,’ ‘Ilpum,’ ‘Pakistani,’ and ‘Dehradun Basmati,’ and ‘Taraori’ were all susceptible to bakanae disease. Among the susceptible rice cultivars, Basmati/scented rice cultivars were most susceptible (Hur et al., 2015; Kang et al., 2019). Details of the resistance and susceptibility patterns of the different rice germplasm lines are presented in Table 2.

The pathogenicity of *F. fujikuroi* strains is also determined by the production of SMs, including growth hormones, mycotoxins, and pigments (Janevska and Tudzynski, 2018). These SMs are not directly involved in the fundamental growth of *F. fujikuroi*. They are involved in the pathogen’s survival in the ecological growing zone. However, the biological significance of these SMs appears to vary among the *F. fujikuroi* strains. Sunder (1998) classified 28 pathogens into five groups based on their pathogenicity and GA production. Zainudin et al. (2008) compared the bakanae disease-associated *F. fujikuroi* and *F. verticillioides* strains for their SM production and disease induction. They found that *F. fujikuroi* induced bakanae disease efficiently by producing GA, fumonisin B1, and MON. Recently, Bashyal et al. (2016) also evaluated the effect of single and combined *F. fujikuroi*, *F. proliferatum*, and *F. verticillioides* strains on disease induction in the ‘Pusa Basmati 1121’ rice cultivar. A maximum disease severity of 70% was recorded in a single *F. fujikuroi* inoculation.

3.2.2 Pathogen survival

The viability of the pathogen is the primary phase leading to pathogenesis, which ensures the survival of the spore, thereby sustaining the disease cycle. Infected plant parts like seeds, dead culms, kernels, stubble, roots, and crowns serve as the carrier materials for the pathogen from one cropping season to another. The duration of survival varies among pathogens based on their virulence and host tissues. Dispersal of infected seeds is the predominant source of primary inoculum to induce the disease because the inoculum present in the field in contaminated plant debris is reduced quickly through natural decomposition processes. Even under unfavorable conditions, the pathogen survives on the seed coat. Rice hulls are the central component of the bakanae cycle; the pathogen has been recovered from hulled grains and caryopses. The maximum recovery of the pathogen was achieved from the lemma, followed by the palea, basal glumes, embryo, and endosperm. Kanjanasoon (1965) observed that pathogens remained viable in infected seeds for

Table 2 Genotypic variation among rice cultivars in resistance to bakanae disease

Degree of resistance	Genotypes	References
Highly resistant	Samgwang, Wonseadaesoo, Nampyeong, Athad, Appunu, Amulya, Sabita, Ereimaphou, Prasanna, Akutphou, Chandana, Himju, Karjat x 13-21, C101A51, BPT5204, IR58025B, IR58109-109-1-1-3, IR58109109-1-1-3, IR-6, DR-82, BR1067-84-1-32-1, BR4363-8-11-4-9, BR1257-31-1-1, BR4367-8-11-4-9, ADT-40, ADT-44, ADT-41, ASD-16, GR-4, IR-64, MTU-1010, and C4-64	Ghazanfar et al., 2013; Bashyal et al., 2014; Puyam et al., 2017; Cheon et al., 2019; Kang et al., 2019; Lee et al., 2019; Kwon et al., 2021; Tadasanahaller et al., 2023
Resistant	Nampyeongbyeo, Inwolbyeo, C4-63G, AS34011, BG936, CNA3886, HKR86-104, IR39464-54-1-3-2-1-3, PR106, C4-64, IR-8, DR-83, KS-282, DM-15-1-95, GS-88, Co18, Co22, Adt8, PTB7, GEB24, IR50, GS-79, GSL-302, GSL-19, SK-423, SI-6, IR-6, and KSK-133	Singh and Sunder, 1997; Manandhar, 1999; Iqbal et al., 2011; Lee et al., 2011; Bashyal et al., 2014; Lone et al., 2016; Puyam et al., 2017; Tadasanahaller et al., 2023
Moderately resistant	Hwadongbyeo, Seokjeongbyeo, Samgwangbyeo, Sampyeongbyeo, Nonghobyeo, Heukjinjubyeo, Joanbyeo, Mushkibudgi, China-972, Guinata, Hansraj, Kamod, Lua Nhe, Macunting, Milpal, Kanak-Jeer, IRG52, HKR91-417, BR802-118-4-2, BR827-35-2-1-HR, HKR42, HKR46, HKR126, HKR91-104, HKR91-108, HKR91-110, HKR91-112, HKR91-119, HKR91-120, IR51673-50-2-1, IR57301-195-3-3, Jaya, PR110, RP2235-113-85-20, RP2240-52-4-8, IRG52, GS-27, GSL-19, SK-421, SI-4, GSL-225, SI-6, Bas-kernel, and Bas-198	Manandhar, 1999; Iqbal et al., 2011; Lee et al., 2011; Kumar et al., 2016; Lone et al., 2016; Puyam et al., 2017; Tadasanahaller et al., 2023
Moderately susceptible	China-988, Pusa Basmati 1, ANP115-3-3-3-3, SK-404, GSL-20, GSL-29, GSL-311, SK-423, SI-V17, SK-292, GS-308, GS-20, GS-82, MR81, MRQ74, MR73, MR127, MR159, MR77, MR123, MR27, PAU-2K13-3275, BB Semi-dwarf Bas 386, Punjab Basmati 2, PAU-3237-15-1-B-B-19-4, Dewe Gowda, PAU-2K13-6307-2-ctk-1336, PAU-2K13-6294-ctk-1309, PAU-2K13-6288-ctk-1294, PAU-2K13-1-1374, PAU-2K13-6304-1-ctk-13264, Kamad, PAU-2K13-6318-3-ctk-1359, PAU-2K13-6321-2-ctk-136, Chenab, PAU-2K13-6322-ctk-1365, SK-408, SK-406, SK-407, PB-1, PAU-2K13-6338-1-ctk-1385, PAU-2K13-6401-2-ctk-1473, PAU-2K13-6389-1-ctk-1454, PAU-2K13-6459-1-ctk-1526, PAU-2K13-6461-2-ctk-1531, PAU-2K13-6525-2-1603, and PAU-2K13-6541-1-1622	Halim et al., 2015; Jain et al., 2016; Kumar et al., 2016; Lone et al., 2016; Puyam et al., 2017; Tadasanahaller et al., 2023
Susceptible	Junam, Pakistani, Dehradun Basmati, Dorell, Nipponbare, Dongjin AD, Taraori PB-5, Taraori PB-6, Taraori PB-385, Taraori PB-1176, Taraori PB-1401, Taraori PB-2511, CSR30, K-14, BPT-5204, PS-5, IR841, Bas-385, Bas-Super, MR211, Bas370, Bas386, Pusa Punjab Bas-1509, PAU-2K13-6291-1-ctk-1302, PAU-2K13-6387-ctk-1449, PAU-2K13-6533-2-1609, PB1509, PB6, BPT-5204, and PS-5	Manandhar, 1999; Iqbal et al., 2011; Halim et al., 2015; Kumar et al., 2016; Puyam et al., 2017; Ji et al., 2018; Kang et al., 2019; Tadasanahaller et al., 2023
Highly susceptible	Ilpum, Rasi, Basmati 385, Punjab Basmati 1121, Sharbati, Tilak Chandan, PAU-2K13-6306-1-ctk-1330, PAU-2K13-6329-ctk-1372, PAU-2K13-6552-2-ctk-1633, HKR03-408, HKR07-440, RP5900-28-11-5-3-2-2, and RP5900-89-5-3-2-1-1	Ghazanfar et al., 2013; Hur et al., 2015; Jain et al., 2016; Kumar et al., 2016; Puyam et al., 2017; Tadasanahaller et al., 2023

4–10 months at room temperature. In another study, Manandhar (1999) identified that the bakanae pathogen survived in rice seeds for 22–26 months at 10 °C. Apart from seed, *F. fujikuroi* conidia are viable for up to 4 months on infected stubble and 10–82 weeks on plant debris (Pannu et al., 2012).

4 Disease cycle

Rice bakanae disease is monocyclic in nature. The pathogen *F. fujikuroi* inducing bakanae disease is seed-borne. It is also known as soil-borne, but the seed-borne inoculum is a more significant source as

soil-borne inoculum is reduced rapidly with the passage of time (Gupta AK et al., 2015). Once pathogens receive chemical signals (root exudates, especially sugar and amino acids) from a germinated seedling, they start invading the plant through the root or crown/basal tissues. The critical time for disease development is 72 h after seed germination (Matic et al., 2017). Upon infection, the pathogen grows systemically in plants, using xylem gaps and large vessels for its growth. The mycelium then starts concentrating in leaf blades, sheaths, and adventitious roots, becoming established in the plant body and producing GA, which induces bakanae symptoms (Chen et al., 2020). From flowering to the late maturation phase of the crop, dead and infected plants produce excessive conidia in the basal region, which act as "seed" for the next season. Through wind and water, conidia/ascospores infect flowers, germinate, grow intercellularly in the stigma and anthers, and finally reach the embryo within 48 h under favorable conditions (Matic et al., 2017). The bakanae disease cycle is described in Fig. 4.

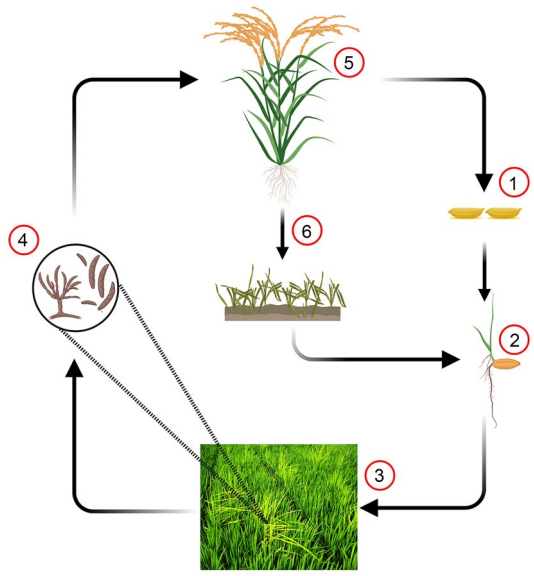

Fig. 4 Disease cycle of bakanae disease. Rice bakanae is a monocyclic disease, mainly transmitted through seeds which are infected from the previous season. However, the overwintering pathogen in the plant debris or soil may also act as primary inoculum in the next season. When infected seeds are sown, typical symptoms, including elongated growth, yellowing of leaves, and seedling rot, appear in rice nurseries. Conidia formed at the tillering stage are dispersed by rain splash or wind during the flowering stage, subsequently infecting floral organs of rice and ultimately leading to seed infection at later stages. (1–4) Infected seeds (1), infected seedlings (2), dead seedlings (3), and conidia (4) from plant debris and infected plants are dispersed through wind and rain, infecting mature rice plants at later stages; (5) Infection of mature plants; (6) Infected/dead plant debris in the field.

Upon infection and establishment inside the rice tissues, *F. fujikuroi* starts producing GA, the level of which determines the intensity of bakanae disease. In the first step of GA biosynthesis, acetyl-coenzyme A (CoA) is converted to mevalonate through the catalytic activity of hydroxymethylglutaryl CoA reductase (HmgR) (Mende et al., 1997). After a few subsequent conversions, the common GA biosynthesis precursor geranylgeranyl diphosphate (GGDP) is synthesized from farnesyl diphosphate (FDP) through GGDP synthase 2 (GGS2). After synthesis of GGDP, the first GA-specific intermediate *ent*-kaurene is formed via a two-step cyclization through *ent*-copalyl diphosphate (CDP) by the bifunctional terpene cyclase CDP synthase/*ent*-kaurene diphosphate synthase (Cps/Ks) (Mende et al., 1997; Tudzynski and Hölter, 1998). Further, *ent*-kaurene is converted to *ent*-kaurenoic acid through kaurene oxidase P450-4 (Tudzynski and Hölter, 1998). In GA biosynthesis, C20 oxidase P450-2 plays a key role, converting GA_{14} to the first biologically active gibberellin GA_4 by losing carbon C20. The subsequent desaturation of GA_4 through GA_4 1,2-desaturase (Des) results in the formation of GA_7. Finally, GA_7 is converted to GA_3 as a major end-product through C13 oxidase P450-3. The same enzyme is involved in the formation of the minor end-product GA_1 from GA_4 (Tudzynski et al., 2003) (Fig. 5b).

The GA metabolic pathway involved in the induction of bakanae disease was completed after the discovery of the GA-INSENSITIVE DWARF 1 (GID1) receptor in 2005. In the first step, once the GID1 receptor recognizes GA signal, it forms a GA-GID1 complex. The GA-GID1 complex enhances the interaction of GID1 and DELLA, which results in the rapid degradation of DELLAs via the ubiquitin-proteasome pathway with the help of a specific ubiquitin E3 ligase complex S-phase kinase-associated protein 1 (SKP1)-cullin 1-F-box ubiquitin ligase ($SCF^{SLY1/GID2}$) (Gao et al., 2011; Wallner et al., 2016). DELLA is a key component in GA-induced plant growth, repressing GA-signaling and restricting GA-mediated growth promotion through transcriptional reprogramming. Degradation of DELLA proteins results in considerable

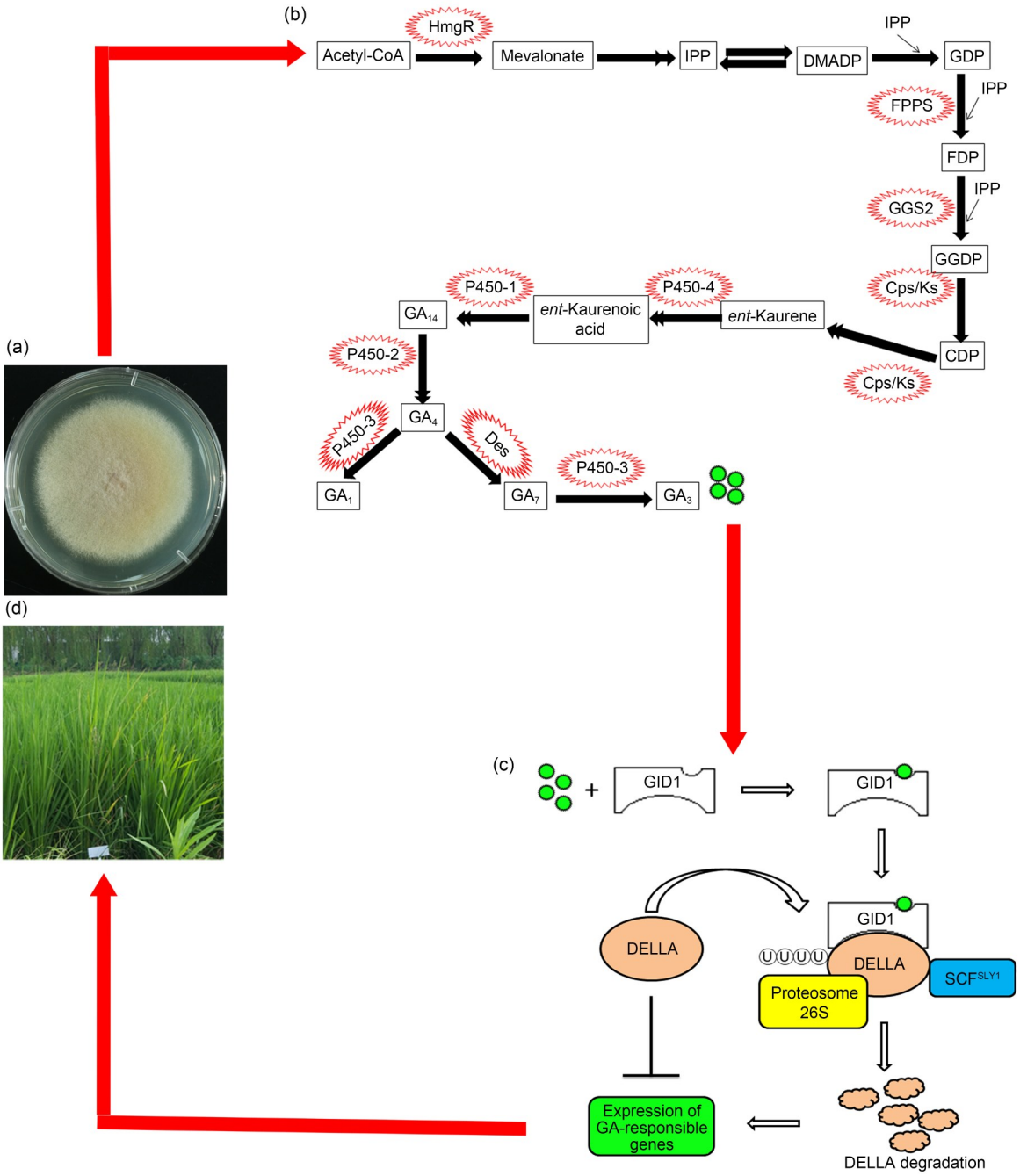

Fig. 5 Schematic representation of the bakanae disease cycle. (a) Pathogen *Fusarium fujikuroi*; (b) Gibberellin biosynthesis in *F. fujikuroi*; (c) GA metabolism in plants; (d) Bakanae disease-infected plant. Enzymes involved in gibberellin biosynthesis are highlighted by red stars, single arrows indicate the sequential biosynthesis steps, double arrows indicate the multiple reactions, and the remaining names are either the major intermediates or end-products. The bioactive GAs are marked as green circles. GA: gibberellic acid; CoA: coenzyme A; HmgR: hydroxymethylglutary CoA reductase; IPP: isopentenyl diphosphate; DMADP: dimethylallyl diphosphate; GDP: guanosine diphosphate; FDP: farnesyl diphosphate; GGDP: geranylgeranyl diphosphate; FPPS: farnesyl pyrophosphate synthase; GGS2: GGDP synthase 2; CDP: *ent*-copalyl diphosphate; Cps/Ks: CDP synthase/*ent*-kaurene diphosphate synthase; Des: 1,2-desaturase; GID1: GA-INSENSITIVE DWARF 1; SCF^{SLY1}: S-phase kinase-associated protein 1 (SKP1)-cullin 1-F-box ubiquitin ligase.

changes in the gene expression profile and promotes cell elongation and elasticity, consequently enhancing stem elongation (Pattanaik et al., 2014; Wallner et al., 2016) (Figs. 5c and 5d).

5 Disease management

Management of bakanae disease is essential for the sustainable production of quality rice grains. Since bakanae is a monocyclic seed-borne disease, treatment of infected seeds using various physical, chemical, or biological approaches is the most common and effective approach to eradicate *F. fujikuroi* (Matic et al., 2017; Ochi et al., 2017). However, the efficiency of these management strategies depends largely on the dosage of the controlling agent, age of the plant, and method of treatment. The practical application and environmental significance of various management strategies are discussed in detail in the following sections.

5.1 Physical treatments

Disinfection of seeds with hot water and steam, dry heat, and electrons are well-known physical treatments that help to kill or inactivate pathogens without affecting seed viability. Among these techniques, hot water treatment is a well-established and efficient technique that involves immersing infected seeds in agitated water with programmed timing and temperature (15 min at 60 ℃) (Miyasaka et al., 2000). Kusakari et al. (2004) also suggested the treatment of infected seeds with heated acidic electrolyzed water at 50 ℃ for about 10–20 min to reduce the *F. fujikuroi* infection rate by up to 90% in laboratory and field conditions. Use of natural solar energy is an alternative strategy to kill pathogens and weeds. Natural solar energy is harvested through translucent polythene sheets to raise the soil temperature (up to 10 to 15 ℃) (Katoch et al., 2019).

Apart from thermotherapy treatments, treating infected seeds with electrons is a modern physical disinfection method in seed-borne pathogen management. Infected seeds are exposed to electrons for milliseconds to destroy the DNA of the pathogen (Mancini and Romanazzi, 2014). Seed irradiation with atmospheric plasma containing electrons reduced the bakanae disease severity index by up to 18.1% and the percentage of infected plants by 7.8% (Ochi et al., 2017). In addition, seed dressing with soluble silicate clay zeolite (a mixture of 25% (mass fraction) silicic acid (acting as a binder) and the zeolite (acting as a coating powder)) can minimize the incidence of bakanae disease (Kang et al., 2016). However, to ensure the success of these physical treatment techniques, various small- and large-scale field studies are needed.

5.2 Chemical control

When the population of pathogens is too high, the treatment of seeds with chemical fungicides had been found more efficient and is used as a common management practice for disease control (Li et al., 2023; Xue et al., 2023). Worldwide, various chemical fungicides and their combinations such as benomyl, thiram, bavistin, carbendazim, carboxin, fludioxonil, mancozeb, iprodione, triticonazole, deconil, dithane-M, derosil, prochloraz, thiophanate-methyl, ipconazole, propiconazole, shibaoke, Jinzhongling, kasugamycin, triforine, ferimzone, tebuconazole, trifloxystrobin, ethynyl phenyl amide, amide compound, pyrazole-4-carboxamide, kresoxim methyl, and sodium hypochlorite have been used for bakanae disease management (Singh and Sunder, 2012; Gupta A et al., 2015; Singh et al., 2019; Li et al., 2023). Treatment of *F. fujikuroi* with fluazinam significantly reduced mycelial growth (with an average concentration for 50% of maximal effect (EC_{50}) of (0.2038±0.0099) μg/mL), conidium germination (with an average EC_{50} value of (0.3552± 0.0181) μg/mL), and conidial production. Moreover, fluazinam treatment can damage the cell membrane structure of *F. fujikuroi* by changing its permeability (Qu et al., 2018). Li et al. (2018) evaluated the individual and combined effects of phenamacril (0.1544 μg/mL) and ipconazole (0.0472 μg/mL) on *F. fujikuroi* growth. A 2:1 (volume ratio) combination of phenamacril and ipconazole showed 100% inhibition of mycelial growth. On the other hand, sporulation was most affected by ipconazole alone, then with a 2:1 combination, and least with phenamacril alone. Inhibition by phenamacril and ipconazole alone or by the 2:1 combination was considerably lower for spore germination than for mycelial growth or sporulation. In seedling treatment, exposure of infected roots to carbendazim 50% wettable powder/tebuconazole 50%+ trifloxystrobin 25% (mass fraction) (75% water dispersible granules) combinations significantly decreased the disease incidence with increased yield compared to other fungicides (Bashyal et al., 2022). However, with continuous exposure to these fungicides for consecutive years, pathogens tend to develop resistance through point mutations, i.e., the GAG→GTG mutation at codon 198, TTC→TAC mutation at codon

200, and GGC→GGT at mutation at codon 235 in the *β2TUB* gene (Chen et al., 2014). Recent research reports suggest that some *F. fujikuroi* strains exhibit strong resistance against prochloraz, phenamacril, benzimidazole, tebuconazole, and benomyl (Wu et al., 2020; Peng et al., 2022).

5.3 Biological control

Controlling bakanae disease using biological organic compounds from microbial (bacterial and fungal) or plant sources has gained interest worldwide due to the economic feasibility and eco-friendly nature of this approach (Kazempour and Elahinia, 2007; Kazempour et al., 2007). These biological agents efficiently suppress the spore formation, spore germination, and mycelial growth of *F. fujikuroi*.

5.3.1 Microbial biocontrol

Beneficial soil/plant-associated microorganisms can produce various metabolic substances like hydrolytic enzymes, antibiotics, siderophores, volatile compounds, and organic acids, which can be used for plant disease management. Even though microorganism-based biocontrol is an ancient technique in disease management, there is limited knowledge on bakanae disease management. Here, we highlight the efficiency of the microorganisms and their associated compounds in the management of bakanae disease.

5.3.1.1 Bacterial biocontrol

Both Gram-positive and Gram-negative bacterial strains like *Bacillus subtilis*, *Pseudomonas fluorescens*, *Bacillus cereus*, *Bacillus oryzicola*, *Bacillus thuringiensis*, *Bacillus megaterium*, and their derived SMs have been studied for bakanae disease management (Dehkaei et al., 2004; Kazempour and Elahinia, 2007; Kumar et al., 2007; Hossain et al., 2016) (Table 3). Sarwar et al. (2018) evaluated the biocontrol effect of surfactin-producing *Bacillus* strains (NH-100 and NH-217) and purified surfactin A against the bakanae pathogen using dual culture, hydroponic, and pot experiments. In a dual culture plate assay, purified surfactin A at 2000 ppm (part per million) showed maximum (84%) growth inhibition against the bakanae pathogen. In hydroponic and pot experiments, disease incidence was reduced up to 80% by purified surfactin A, which also improved plant growth and yield parameters such as height, tiller number, panicles, spikelet number, grain weight, and yield percentage. In another study, root drenching of *F. fujikuroi*-infected seedlings with *B. oryzicola* strain YC7007 reduced the bakanae disease severity by 46%–78% in pot and nursery box tests. Moreover, inoculation of *B. oryzicola* YC7007 improved plant health through induced systemic resistance (ISR) by primed induction of the jasmonic acid pathway and antibiotic production (Chung et al., 2015; Hossain et al., 2016). Kazempour and Anvary (2009) also suggested that volatile microbial compounds could inhibit the growth of *F. fujikuroi* under in vitro conditions.

5.3.1.2 Fungus-based biocontrol

Previous studies have identified *Trichoderma* spp. as the most promising fungal species for bakanae disease management (Kumakura et al., 2003; Watanabe et al., 2007; Bhramaramba and Nagamani, 2013; Halim et al., 2015; Ng et al., 2015) (Table 3). Pal et al. (2019) studied the combination of *Trichoderma* strains S1 and S7 and chemical fungicides on bakanae disease management under field conditions. Among the treatments, the minimum disease incidence (0%) was observed in the *Trichoderma* S1 treatment, followed by 0.1% disease incidence with the *Tricoderma* S1+saaf treatment. Moreover, the maximum yield (4×10^3 kg/ha) was recorded with the *Tricoderma* S1 treatment. Gupta A et al. (2015) also identified the efficiency of bavistin (0.2% (volume fraction)) combined with 0.4% (4 g/L) *Trichoderma viride* in bakanae disease control.

Apart from *Trichoderma* species, co-inoculation of *Piriformospora indica*, along with *F. proliferatum*, protected rice plants from pathogen attack by improving the ISR and consequent regulation of pathogenesis-related genes such as NONEXPRESSOR OF PATHOGENESIS-RELATED 1 (*NPR1*), PATHOGENESIS-RELATED 1 (*PR1*), *PR4*, and *PR5*, and transcriptional factor genes (*WRKY62* and *WRKY85*) (Hajipour et al., 2015). Treatment of infected rice seeds with *Pichia guilliermondii* R9 and *Metschnikowia pulcherrima* R23 reduced the infection rate of *F. fujikuroi* by up to 20.0% and the disease index by 28.5% (Matić et al., 2014). In slide culture, *Talaromyces* spp. KNB-422 inhibits the growth of *G. fujikuroi* by collapsing the hyphal cell wall, causing cytoplasmic leakage (Kato et al., 2012). Recently, Ramesh et al. (2020) also observed that inoculation of endophytic fungi (*Chaetomium globosum* NR-R688, *C. globosum* NR-SH321, and *Penicillium* spp. NR-L243) reduced the

Table 3 Management of bakanae disease with biological agents

Biological agents	References
Bacterial agents	
Bacillus subtilis NH-100 and *Bacillus* spp. NH-217	Sarwar et al., 2018
Pseudomonas fluorescens	Kazempour and Anvary, 2009
P. fluorescens and *Bacillus cereus*	Kazempour and Elahinia, 2007
Bacillus oryzicola YC7007	Chung et al., 2015; Hossain et al., 2016
P. fluorescens PF-9 and PF-13, and *Bacillus thuringiensis* B-44	Kumar et al., 2007
B. subtilis and *Bacillus* spp.	Dehkaei et al., 2004; Li et al., 2006
Antagonistic bacteria from paddy water, rhizosphere soils, sclerotia, and rice plants	Rosales and Mew, 1997
P. fluorescens and *B. cereus*	Kazempour et al., 2007
Fungal agents	
Metschnikowia pulcherrima R23 and R26, *Pichia guilliermondii*, and *Sporidiobolus pararoseus*	Matić et al., 2014
Trichoderma asperellum SKT-1	Watanabe et al., 2007
Trichoderma S1 and S7	Pal et al., 2019
Piriformospora indica	Hajipour et al., 2015
Talaromyces spp. KNB-422	Kato et al., 2012
Trichoderma harzianum	Halim et al., 2015
Water extract of *Pleurotus ostreatus*	Oh et al., 2016
Trichoderma spp.	Bhramaramba and Nagamani, 2013
T. harzianum and *Trichoderma virens*	Dehkaei et al., 2004
Trichoderma viride combination with chemical fungicides	Gupta A et al., 2015
Trichoderma spp.	Ng et al., 2015
Trichoderma spp.	Raghu et al., 2018
Bioactive compounds from *Cordyceps dipterigena*	Varughese et al., 2012
Chaetomium globosum NR-R688, etc.	Ramesh et al., 2020
Trichoderma spp. SKT-1	Kumakura et al., 2003
Talaromyces flavus (Tf1, Tf2, and Tf3), *Fusarium equiseti*, etc.	Rawat et al., 2022
Fusarium commune W5	Saito et al., 2021
Phomopsis liquidambaris B3	Zhu et al., 2022
Plant extracts	
Ginkgo biloba outer seed coat extract	Oh et al., 2017
Extract of *Azadirachta indica*	Pawar, 2011
Methanolic extract of *Decalepis hamiltonii*, etc.	Mohana et al., 2011
Oil of *Acorus calamus* and *Hedychium spicatum*	Mishra et al., 2003
Neem cake, press mud, and groundnut cake	Kumar et al., 2016
Bulbils and tubers extract of *Dioscorea bulbifera*	Adeleye and Ikotun, 1989
Compost tea	Manandhar and Yami, 2008
Leaf extract of *Andrographis paniculata*, etc.	Yasmin et al., 2008
Extract of *Ammi visnaga*, *Eucalyptus globulus*, etc.	Zeinab and Hassan, 2019
Natural organic compounds	
Citral, honokiol, osthole, carvacrol, cinnamaldehyde, resveratrol, and allicin	Chen et al., 2022
Natural polymer polysaccharides	Fang et al., 2023
Other sources	
COS and EDTA	Kim et al., 2016
Seed dressing with chitosan S-II	Jiang et al., 1999

COS: chitosan oligosaccharide; EDTA: ethylene diamine tetraacetic acid.

disease induction rate by up to 97.4%, and consequently enhanced the growth and yield parameters of rice plants under greenhouse conditions.

Solvent extracts of *Pleurotus ostreatus* and *Cordyceps dipterigena* showed considerable bakanae disease suppression under both in vitro and in vivo conditions

(Oh et al., 2016). Among the tested solvents, butanol extracts of *P. ostreatus* inhibit the growth of pathogen up to 80% under greenhouse conditions. In addition to solvent extracts, some fungal-derived compounds like cordycepsidone A and cordycepsidone B can significantly inhibit mycelial growth (Varughese et al., 2012). Saito et al. (2021) showed that nonpathogenic *Fusarium commune* inhibited hyphal extension of *F. fujikuroi* on/in rice flowers and seedlings, possibly by competing with the pathogen, and survived on/in rice seeds for at least six months. Recently, Zhu et al. (2022) suggested that pre-inoculation of the endophytic fungus *Phomopsis liquidambaris* B3 significantly reduced bakanae disease induction by triggering the salicylic acid-dependent defense pathway and improving plant growth parameters.

5.3.2 Plant extracts in bakanae disease management

Extracts from different plant parts like the bulbils and tubers of *Dioscorea bulbifera* L. (Adeley and Ikotun, 1989), leaves of *Azadirachta indica* (Pawar, 2011), roots of *Asparagus racemosus* (Yasmin et al., 2008), and outer seed coat of *Ginkgo biloba* (Oh et al., 2017) were successfully used to inhibit *F. fujikuroi* (Table 3). Zeinab and Hassan (2019) recently studied the effects of *Ammi visnaga*, *Eucalyptus globulus*, *Artemisia judaica*, and *Coriandrum sativum* ethanolic extracts on bakanae disease management under greenhouse and field conditions. They found that ethanolic extracts from *A. visnaga* and *E. globulus* significantly reduced the number of dead and infected seedlings and increased the germination percentage, antioxidant activity (peroxidase, polyphenol oxidase, and hydrogen peroxide), and yield parameters. Apart from plant extracts, soil treatment with agricultural by-products, like a combination of neem cake and groundnut cake, can also reduce pathogen proliferation (Panneerselvam and Saravanamuthu, 1996; Kumar et al., 2016).

5.3.3 Compost and organic compounds

Compost tea extract and organic decomposed materials have been used for centuries for their beneficial effects on plant growth and disease control (Table 3). Manandhar and Yami (2008) conducted a field trial with four types of tea compost, namely aerated vermicompost tea, non-aerated vermicompost tea, aerated compost tea, and non-aerated compost tea, for bakanae disease management. Among the four tested combinations, aerated vermicompost tea showed maximum disease control (25.6%), followed by aerated compost tea (22.4%) and non-aerated compost tea (13.6%). Interestingly, organic compounds have also been tested for the inhibition of *F. fujikuroi*. For example, chitosan oligosaccharides exhibited a rapid and efficient fungicidal effect on hyphal growth of *F. fujikuroi* (Kim et al., 2016). Chen et al. (2022) studied the inhibitory effect of natural organic compounds against *F. fujikuroi*. Honokiol, osthole, and cinnamaldehyde were found to be potential inhibitors of mycelial growth. Though these biocontrol strategies have advantages in bakanae disease management in vitro, there are still many issues to resolve before they can be adopted in large-scale field applications. In particular, more analysis is needed on the aspects of biosafety, compatibility with other beneficial organisms, regulatory issues for commercialization, stability, traceability, and the fate of biocontrol agents in the environment (Ptaszek et al., 2023).

5.4 Agronomic and genetic control

Agronomic practices such as the selection of seed and rice cultivars, transplanting methods, cropping season, time of plantation, irrigation management, and balanced fertilization are simple and ancient techniques to eliminate pathogens from the field (Gupta A et al., 2015; Gupta AK et al., 2015). In field conditions, removing all infected plants is a suitable way to restrict re-entry of the pathogen in the next cropping season. Seed selection and removal of lightweight unhealthy seeds could minimize the disease rate. In seedling transplantation, minimizing root damage caused by uprooting the seedlings has been found helpful in preventing the primary route of pathogen entry (Singh et al., 2019). Moreover, seedling age and transplantation time also influence the incidence of bakanae disease. Kumar et al. (2016) observed that when 20- and 30-d-old PB1121 seedlings were used for field transplantation, the disease incidence was 15.87% and 16.87%, respectively. However, the disease incidence increased to 23.25%, 26.62%, and 28.62% in 40-, 50-, and 60-d-old transplanted seedlings, respectively. Organic amendments and available soil nutrients also play a key role in pathogen survival and multiplication. Neem cake and press mud reduced the disease incidence by 40.82% and 15.54%, respectively. However, groundnut cake increased the disease incidence by

92.97% (Panneerselvam and Saravanamuthu, 1996; Kumar et al., 2016). Combined application of NPK, $ZnSO_4$, and $FeSO_4$ significantly reduced pathogen survival after eight months of incubation (Mandal and Chaudhuri, 1988).

5.5 Host resistance

5.5.1 Germplasm screening

Selection of a particular rice cultivar with bakanae disease resistance through germplasm screening is a simple and traditional technique used to manage the fungal disease. Ito and Kimura (1931) identified the first bakanae disease-resistant Japanese genotypes through germplasm screening. Later, Aktas and Tunali (1986) screened bakanae disease-resistant rice cultivars using a spore suspension for disease induction. In a similar field study, Ilyas and Iftikhar (1997) identified 20 highly resistant, 14 resistant, and 10 moderately resistant rice lines out of 203 germplasm lines. However, these traditional field-screening techniques are time- and labor-consuming, require large-scale cultivation areas, and are influenced by various biotic and abiotic factors, which may affect the accuracy of the results.

Modern greenhouse- and laboratory-based germplasm screening techniques are more rapid and less labor-intensive techniques with maximum accuracy. Kim et al. (2014) developed a new in vitro method of *F. fujikuroi* microconidia using a tissue-embedding cassette and seedling tray to screen resistant rice cultivars against bakanae disease. This technique was fast and reproducible for accurately evaluating bakanae disease resistance. Lee et al. (2011) adopted a short-term in vitro germplasm screening technique to identify two resistant cultivars ('Nampyeongbyeo' and 'Inwolbyeo') and seven moderately resistant cultivars ('Hwadongbyeo,' 'Seokjeongbyeo,' 'Samgwangbyeo,' 'Sampyeongbyeo,' 'Nonghobyeo,' 'Heukjinjubyeo,' and 'Joanbyeo') within 2–3 weeks. Recently, Yan et al. (2022) established an artificial inoculation system for the fast and efficient induction of bakanae disease, aiming to screen large populations to identify bakanae disease-resistant lines efficiently. Pathogen-free screening techniques have also been evolved to screen resistant rice cultivars in a risk-free way. Hossain et al. (2013) have screened resistant rice cultivars from huge germplasm collections using different concentrations of GA for disease induction instead of the pathogen. Conventional germplasm-assisted breeding practices have been successful in the past few decades and have sustained agricultural productivity to a large extent. On the other hand, they have several limitations in improving rice cultivars. They depend on the existence of sufficient genetic variation in the plant population, and are labor-intensive and time-consuming (Chincinska et al., 2023; Zhang et al., 2023).

5.5.2 Quantitative trait loci mapping and cultivar resistance

Rice genomes carrying various genetic variants that exhibit resistance towards bakanae disease can be used to develop disease-resistant rice cultivars. However, few studies have envisaged and identified bakanae disease-resistance/associated quantitative trait loci (QTL) from different rice cultivars (Table 4). Bakanae disease-resistant QTL mapping was first initiated by Yang et al. (2006) who identified two bakanae disease-resistant QTL, namely *qB1* and *qB10*, in a susceptible japonica/indica doubled haploid (DH) population. A Korean research group led by Hyeonso Ji identified various bakanae disease-resistant QTL including *qFfR1* (Ji et al., 2018), *qFfR9* (Kang et al., 2019), *qFfR1-1*, and a novel QTL *qFfR6* (Cheon et al., 2019). In addition, Kang et al. (2019) identified eight possible bakanae disease-resistant candidate genes (*Os09g0298332*, *Os09g0298400*, *Os09g0298500*, *Os09g0298700*, *Os09g0299200*, *Os09g0299400*, *Os09g0299500*, and *Os09g0301800*) from *qFfR9* and suggested that *qFfR9* could be a suitable resource to develop bakanae disease-resistant rice cultivars.

Similarly, another Korean research group led by Dong-Soo Park has contributed remarkably to the development of bakanae disease-resistant lines by identifying various bakanae disease-resistant QTL. Hur et al. (2015) identified the bakanae disease-resistant QTL *qBK1* from a backcross of the resistant indica cultivar 'Shingwang' with the susceptible japonica cultivar 'Ilpum.' Lee et al. (2018) identified the bakanae disease-resistant QTL $qBK1^{WD}$ in the 'Wonseadaesoo' cultivar. Further, they have studied the gene pyramiding effect of two QTL, qBK^{WD} and the previously developed *qBK1*, on bakanae disease resistance. They confirmed that the combination of qBK^{WD} and *qBK1* showed higher bakanae disease resistance (80.2%) than lines with the individual QTL. Lee et al. (2019) identified the bakanae disease-resistant QTL *qBK1* and disease-resistant candidate genes *LOC_Os01g41770*,

Table 4 Bakanae disease-resistant candidate QTL from previous reports

Rice population	QTL	QTL region (Mb)	Chromosomal location	Marker interval (cM)	LOD score	Phenotypic variation (%)	Reference
Japonica/indica-doubled haploid population, derived from 'Chunjiang 06' and 'TN1'	*qB1*		1	RM7180–RM486	2.32	13.4	Yang et al., 2006
	qB10		10	RM1108–RM304	2.50	13.3	
Cross between a resistant donor 'YR24982-9-1' and a susceptible parent 'Ilpum'	*qBK1*	23.21–23.72	1		33.21	65	Hur et al., 2015
RILs derived from the indica rice parents 'Pusa 1342' and 'Pusa Basmati 1121'	*qBK1.1*	21.43–21.78	1	*RM9–RM11282*	3.86	6.49	Fiyaz et al., 2016
	qBK1.2	3.10–3.36	1	RM10153–RM5336	12.07	24.74	
	qBK1.3	4.65–8.41	1	RM10271–RM35	2.73	4.76	
Japonica germplasm (138 cultivars: 41 tropical japonica and 97 temperate japonica)	*qBK1_628091*	0.62–1.04	1				Volante et al., 2017
	qBK4_31750955	31.16–31.75	4				
RILs derived from an 'IR64'×'Nipponbare' cross	*qBK1.4*	0.40–0.42	1			27	Chen et al., 2019
	qBK1.5	2.25–2.32	1			18	
	qBK1.6	22.08–22.24	1			28	
	qBK1.7	23.63–23.64	1			25	
	qBK3.2	27.48–27.63	3			19	
	qBK4.1	22.37–22.42	4			33	
	qBK6.1	3.27–3.63	6			22	
	qBK6.2	4.86–5.05	6			28	
	qBK6.3	25.29–25.63	6			20	
	qBK8.1	6.14–6.23	8			28	
	qBK10.1	5.67–6.02	10			25	
	qBK10.2	6.84–6.86	10			21	
	qBK10.3	9.09–9.33	10			26	
	qBK11.1	22.57–22.58	11			13	
RILs derived from a 'Wonseadaesoo'×'Junam' cross	$qBK1^{WD}$	13.54–15.13	1	chr01_10336087–chr01_26628298	8.29	20.2	Lee et al., 2018
RILs of 'Shingwang' (resistant) and 'Ilpum' (susceptible)	*qBK1*	23.63–23.67	1				Lee et al., 2019
Cross between the resistant cultivar 'Zenith' and the susceptible cultivar 'Ilpum'	$qBK1^{Z}$	1.43–2.16	1	RM1133–RM3530	13.43	30.9	Lee et al., 2021
'Nampyeong' (resistant) and mutant 'DongjinAD' (susceptible) line derived from the Korean japonica cultivar 'Dongjin6'	*qFfR1*	22.56–24.10	1	87.9–91.7	22.7		Ji et al., 2018
From crosses between three Korean japonica cultivars: 'Nampyeong' (resistant)×'Saenuri' (moderately resistant) and 'Nampyeong' (resistant)×'Junam' (moderately resistant)	*qFfR1-1*		1	95.8–100.7	21.4		Cheon et al., 2019
	qFfR6		6	57.1–62.7	5.99		
From a cross between Korean japonica rice cultivars 'Samgwang' (resistant) and 'Junamm' (susceptible)	*qFfR9*	7.24–7.56	9	29.9–31.2	60.3		Kang et al., 2019
From a cross between 'Shingwang' (resistant) and 'Ilpum' (susceptible)	*qBK1*, *qBK1.1*, and *qFfR1*						Kwon et al., 2021

QTL: quantitative trait loci; cM: centiMorgans; LOD: logarithm of odds; RILs: recombinant inbred lines.

LOC_Os01g41780, *LOC_Os01g41790*, and *LOC_Os01g41800* in the 'Shingwang' cultivar. The same research group recently identified the bakanae-resistant QTL $qBK1^{Z}$ in the 'Zenith' cultivar (Lee et al., 2021).

Other researchers have also made a significant contribution to QTL-based bakanae-resistant rice cultivar development. Fiyaz et al. (2016) identified major and minor QTL for bakanae disease resistance, e.g., *qBK1.1*, *qBK1.2*, and *qBK1.3*, in recombinant inbred lines (RILs), which accounted for 6.49%, 24.74%, and 4.76% of the phenotypic variation, respectively. An Italian research group identified two novel genomic regions, *qBK1_628091* (on the short arm of chromosome 1) and *qBK4_31750955* (on the long arm of chromosome 4), conferring high bakanae disease resistance in a japonica rice cultivar, using GWAS. Moreover, candidate genes with a putative role in bakanae disease resistance were identified in two genomic regions through differentially expressed gene (DEG) analysis (Volante et al., 2017). Recently, Chen et al. (2019) discovered two of the key genes responsible for bakanae disease (*Os01g0601625* and *Os01g0601675*) from 14 newly identified QTL using GWAS analysis. These disease-resistant QTL could be helpful in developing competent bakanae disease-resistant rice cultivars using marker-assisted breeding in a short time (Fiyaz et al., 2016). Despite these successes, QTL-assisted breeding suffers from two major limitations: (1) only the allelic diversity that segregates between the parents of each particular F2 cross or within each RIL population can be assayed, and (2) the amount of recombination that occurs during the creation of the RIL population places a limit on the mapping resolution. It is difficult to keep pace with increasing food demand, particularly during an era of global climate change. These challenges to our current agricultural practices suggest the need for new technologies.

6 New breeding techniques

Recent advancements in biotechnology offer an efficient and alternative strategy to tackle pathogen attack by inserting, deleting, or replacing DNA at a precise location within the genome through genome editing techniques, such as clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) (Shah et al., 2019; Li et al., 2021; Zhang et al., 2023). Recently, Távora et al. (2022) developed rice blast-resistant lines through CRISPR/Cas9-targeted knockout of the blast susceptibility genes (*OsDjA2* and *OsERF104*). The resistant lines had a decreased number of blast lesions and diseased leaf area compared with wild-type infected control plants. Previously, rice blast- and sheath blight-resistant rice lines had been developed using the CRISPR/Cas9 approach (Wang et al., 2016; Ma et al., 2018; Shah et al., 2019). Because no genes conferring resistance to bakanae disease have been cloned, no bakanae disease-resistant lines have yet been developed through CRISPR/Cas9-based gene editing. Therefore, it is essential to perform more studies to identify bakanae disease-resistant genes. To start with, physically overlapping QTL with a large logarithm of odds (LOD) score for bakanae disease resistance identified by different groups are of particular interest, e.g., *qBK1* (23.21–23.72 Mb, chromosome 1) (Hur et al., 2015). *qBK1* overlaps well with *qFfR1* (22.56–24.10 Mb) (Ji et al., 2018) and both have a high LOD score. On the other hand, the new breeding approaches need to pass various checkpoints such as ethical issues and public acceptance before they can be implemented at the field level.

7 Conclusions and future prospects

Bakanae is an economically significant rice disease that induces drastic yield losses worldwide in rice-cultivating countries. Various aspects of bakanae disease have been well studied by different researchers. However, to develop integrated and sustainable disease management strategies, the following aspects need to be further explored:

(1) Since *F. fujikuroi* is highly diverse, the identification of pathotypes/races and mapping of gene(s) for virulence, and studies of the pathogenicity mechanisms and genetics of resistance are of utmost importance.

(2) The role of GA in bakanae disease induction and its biosynthesis gene cluster is now well understood, but little is known about the association of other SMs (mycotoxins and pigments) with bakanae disease. Moreover, a better understanding of the exact molecular interaction behind the host–pathogen interactions is needed urgently, and could help identify new targets for developing disease-resistant rice cultivars.

(3) The biocontrol efficiency of some bacterial and fungal strains has been studied well. However,

molecular biocontrol mechanisms and other beneficial interactions between biocontrol agents and rice plants are relatively unknown. Moreover, various environmental, ecological, and social factors that affect the implementation of different management strategies, such as the availability of resources, access to technology, and cultural practices, need to be investigated before planning for large-scale commercial applications.

(4) The development of biodegradable fungicides, as an alternative to toxic fungicides, along with a decision support system, needs proper attention to devise practical disease management systems.

(5) Further research is necessary to identify the most promising bakanae disease-resistant/susceptible gene(s) for developing highly resistant rice lines by enhancing the expression of target gene(s) or knocking out susceptible gene(s) through new breeding techniques.

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Author contributions

Chinnannan KARTHIK and Qingyao SHU conceived and designed the review. Chinnannan KARTHIK prepared the manuscript including figures and tables. Qingyao SHU revised, edited, and checked the final version. Both authors have read and approved the final manuscript.

Compliance with ethical guidelines

Chinnannan KARTHIK and Qingyao SHU declare that they have no conflict of interest.

This article does not contain any studies with human or animal subjects performed by either of the authors.

References

Adeleye A, Ikotun T, 1989. Antifungal activity of dihydrodioscorine extracted from a wild variety of *Dioscorea bulbifera* L. *J Basic Microbiol*, 29(5):265-267. https://doi.org/10.1002/jobm.3620290504

Ahangar AM, Bhat ZA, Najeeb S, et al., 2014. Bakanae disease: a new threat to rice production under temperate ecology of Kashmir. *J Agric Life Sci*, 1(2):45-47.

Aktas H, Tunali B, 1986. Determination of the reactions of promising rice cultivars and lines to *Pyricularia oryzae* Bri. & Cav., *Drechslera oryzae* Subram. & Jain and *Fusarium moniliforme* Sheld. in Turkey. *Bitki Koruma Bull*, 26(1-2):41-58.

Bashyal BM, 2018. Etiology of an emerging disease: bakanae of rice. *Ind Phytopathol*, 71(4):485-494. https://doi.org/10.1007/s42360-018-0091-2

Bashyal BM, Aggarwal R, 2013. Molecular identification of *Fusarium* spp. associated with bakanae disease of rice in India. *Indian J Agric Sci*, 83(1):72-77.

Bashyal BM, Aggarwal R, Banerjee S, et al., 2014. Pathogenicity, ecology and genetic diversity of the *Fusarium* spp. associated with an emerging bakanae disease of rice (*Oryza sativa* L.) in India. *In*: Kharwar RN, Upadhyay RS, Dubey NK, et al. (Eds.), Microbial Diversity and Biotechnology in Food Security. Springer, New Delhi, p.307-314. https://doi.org/10.1007/978-81-322-1801-2_27

Bashyal BM, Aggarwal R, Sharma S, et al., 2016. Single and combined effects of three *Fusarium* species associated with rice seeds on the severity of bakanae disease of rice. *J Plant Pathol*, 98(2):405-412. https://doi.org/10.4454/JPP.V98I3.001

Bashyal BM, Rawat K, Sharma S, et al., 2017. Whole genome sequencing of *Fusarium fujikuroi* provides insight into the role of secretory proteins and cell wall degrading enzymes in causing bakanae disease of rice. *Front Plant Sci*, 8:2013. https://doi.org/10.3389/fpls.2017.02013

Bashyal BM, Aggarwal R, Rawat K, et al., 2020. Genetic diversity and population structure of *Fusarium fujikuroi* causing Bakanae, an emerging disease of rice in India. *Indian J Exp Biol*, 58(1):45-52.

Bashyal BM, Gupta AK, Parmar P, et al., 2022. Management of bakanae disease using fungicides and their effect on disease symptomatology. *Indian J Agric Sci*, 92(9):56-61. https://doi.org/10.56093/ijas.v92i8.112530

Bhramaramba S, Nagamani A, 2013. Antagonistic *Trichoderma* isolates to control bakanae pathogen of rice. *Agric Sci Digest*, 33(2):104-108.

Chen CY, Chen SY, Liu CW, et al., 2020. Invasion and colonization pattern of *Fusarium fujikuroi* in Rice. *Phytopathology*, 110(12):1934-1945. https://doi.org/10.1094/PHYTO-03-20-0068-R

Chen SY, Lai MH, Tung CW, et al., 2019. Genome-wide association mapping of gene loci affecting disease resistance in the rice-*Fusarium fujikuroi* pathosystem. *Rice*, 12:85. https://doi.org/10.1186/s12284-019-0337-3

Chen TT, Wu X, Dai YY, et al., 2022. Sensitivity testing of natural antifungal agents on *Fusarium fujikuroi* to investigate the potential for sustainable control of kiwifruit leaf spot disease. *J Fungi*, 8(3):239. https://doi.org/10.3390/jof8030239

Chen ZH, Gao T, Liang SP, et al., 2014. Molecular mechanism of resistance of *Fusarium fujikuroi* to benzimidazole fungicides. *FEMS Microbiol Lett*, 357(1):77-84. https://doi.org/10.1111/1574-6968.12504

Cheon KS, Jeong YM, Lee YU, et al., 2019. Kompetitive allele-specific PCR marker development and quantitative

trait locus mapping for bakanae disease resistance in Korean japonica rice varieties. *Plant Breed Biotech*, 7:208-219.
https://doi.org/10.9787/PBB.2019.7.3.208

Chiara M, Fanelli F, Mulè G, 2015. Genome sequencing of multiple isolates highlights subtelomeric genomic diversity within *Fusarium fujikuroi*. *Genome Biol Evol*, 7(11): 3062-3069.
https://doi.org/10.1093/gbe/evv198

Childs N, LeBeau B, 2023. USDA (The United States Department of Agriculture), Rice Outlook: August 2023. https://www.ers.usda.gov/publications/pub-details/?pubid=107163

Chincinska IA, Miklaszewska M, Sołtys-Kalina D, 2023. Recent advances and challenges in potato improvement using CRISPR/Cas genome editing. *Planta*, 257:25.
https://doi.org/10.1007/s00425-022-04054-3

Chung EJ, Hossain MT, Khan A, et al., 2015. *Bacillus oryzicola* sp. nov., an endophytic bacterium isolated from the roots of rice with antimicrobial, plant growth promoting, and systemic resistance inducing activities in rice. *Plant Pathol J*, 31(2):152-164.
https://doi.org/10.5423/PPJ.OA.12.2014.0136

Curtis PJ, Cross BE, 1954. Gibberellic acid. A new metabolite from the culture filtrates of *Gibberella fujikuroi*. *Chem Ind*, 35:1066.

Dehkaei FP, Jajaei SHM, Rouhani JH, 2004. Effects of paddy soil antagonistic microorganisms of Guilan on the causal agent of rice bakanae disease. *J Sci Technol Agric Nat Resources*, 8(1):213-222.

Desjardins AE, Manandhar HK, Plattner RD, et al., 2000. *Fusarium* species from Nepalese rice and production of mycotoxins and gibberellic acid by selected species. *Appl Environ Microbiol*, 66(3):1020-1025.
https://doi.org/10.1128/aem.66.3.1020-1025.2000

Fang JF, Zeng DF, Xu T, 2023. Preparation of an environmentally friendly rice seed coating agent and study of its mechanism of action in seedlings. *Sustainability*, 15(1):869.
https://doi.org/10.3390/su15010869

Fiyaz RA, Yadav AK, Krishnan SG, et al., 2016. Mapping quantitative trait loci responsible for resistance to Bakanae disease in rice. *Rice*, 9:45.
https://doi.org/10.1186/s12284-016-0117-2

Gangopadhyay S, Kapoor KS, 1977. Control of *Fusarium wilt* of okra with seed treatment. *Indian J Mycol Plant Pathol*, 7(2):147-149.

Gao XH, Xiao SL, Yao QF, et al., 2011. An updated GA signaling 'relief of repression' regulatory model. *Mol Plant*, 4(4):601-606.
https://doi.org/10.1093/mp/ssr046

Ghazanfar MU, Javed N, Wakil W, et al., 2013. Screening of some fine and coarse rice varieties against bakanae disease. *J Agric Res*, 51(1):41-49.

Gupta A, Kumar R, Maheshwar VK, 2015. Integration of seed treatments, seedling dip treatments and soil amendments for the management of bakanae disease in paddy variety Pusa Basmati 1121. *Plant Pathol J*, 14(4):207-211.
https://doi.org/10.3923/ppj.2015.207.211

Gupta AK, Solanki IS, Bashyal BM, et al., 2015. Bakanae of rice-an emerging disease in Asia. *J Anim Plant Sci*, 25(6): 1499-1514.

Hajipour A, Sohani MM, Babaeizad V, et al., 2015. The symbiotic effect of *Piriformospora indica* on induced resistance against bakanae disease in rice (*Oryza sativa* L.). *J Plant Mol Breed*, 3(2):11-19.
https://doi.org/10.22058/JPMB.2015.15370

Halim WNAWA, Razak AA, Ali J, et al., 2015. Susceptibility of Malaysian rice varieties to *Fusarium fujikuroi* and in vitro activity of *Trichoderma harzianum* as biocontrol agent. *Malaysian J Microbiol*, 11(1):20-26.
https://doi.org/10.21161/mjm.61714

Hartsuck JA, Lipscomb WN, 1963. Molecular and crystal structure of the di-*p*-bromobenzoate of the methyl ester of gibberellic acid. *J Am Chem Soc*, 85(21):3414-3419.

Hori S, 1898. Some observations on "Bakanae" disease of the rice plant. *Mem Agric Res Sta (Tokyo)*, 12:110-119.

Hossain KS, Mia MAT, Bashar MA, 2013. New method for screening rice varieties against bakanae disease. *Bangladesh J Bot*, 42(2):315-320.
https://doi.org/10.3329/bjb.v42i2.18036

Hossain MT, Khan A, Chung EJ, et al., 2016. Biological control of rice bakanae by an endophytic *Bacillus oryzicola* YC7007. *Plant Pathol J*, 32(3):228-241.
https://doi.org/10.5423/PPJ.OA.10.2015.0218

Hur YJ, Lee SB, Kim TH, et al., 2015. Mapping of *qBK1*, a major *QTL* for bakanae disease resistance in rice. *Mol Breed*, 35(2):78.
https://doi.org/10.1007/s11032-015-0281-x

Ilija KK, Mitrw SK, Kostadin ED, 2009. *Gibberella fujikuroi* (Sawada) Wollenweber, the new parasitical fungus on rice in the Republic of Macedonia. *Prot Nat Sci*, (116): 175-182.
https://doi.org/10.2298/ZMSPN0916175K

Ilyas MB, Iftikhar K, 1997. Screening of rice germplasm and fungi toxicants against bakanae disease of rice. *Pak J Phytopathol*, 9(1):67-73.

Iqbal M, Javed N, Sahi ST, et al., 2011. Genetic management of bakanae disease of rice and evaluation of various fungicides against/*Fusarium moniliforme* in vitro. *Pak J Phytopathol*, 23:103-107.

Ito S, Kimura J, 1931. Studies on the bakanae disease of the rice plant. *Rep Hokkaido Natl Agric Exp Stn*, 27:1-95.

Jain J, Sidhu N, Lore JS, et al., 2016. Evaluation of aromatic rice genotypes for resistance against foot rot disease. *Plant Dis Res*, 31(2):150-153.

Janevska S, Tudzynski B, 2018. Secondary metabolism in *Fusarium fujikuroi*: strategies to unravel the function of biosynthetic pathways. *Appl Microbiol Biotechnol*, 102(2): 615-630.
https://doi.org/10.1007/s00253-017-8679-5

Jeong H, Lee S, Choi GJ, et al., 2013. Draft genome sequence of *Fusarium fujikuroi* B14, the causal agent of the bakanae disease of rice. *Genome Announc*, 1(1):e00035-13. https://doi.org/10.1128/genomeA.00035-13

Ji H, Kim TH, Lee DS, et al., 2018. Mapping of a major quantitative trait locus for bakanae disease resistance in rice by genome resequencing. *Mol Genet Genomics*, 293(3): 579-586. https://doi.org/10.1007/s00438-017-1407-0

Jiang HP, Kan LB, Ding LL, et al., 1999. Seed dressing with Chitosan S-II can control bakanae disease of rice. *China Rice*, 5:29.

Jing LF, Suga H, 2021. Various methods for controlling the *bakanae* disease in rice. *Rev Agric Sci*, 9:195-205. https://doi.org/10.7831/ras.9.0_195

Kang DU, Cheon KS, Oh J, et al., 2019. Rice genome resequencing reveals a major quantitative trait locus for resistance to bakanae disease caused by *Fusarium fujikuroi*. *Int J Mol Sci*, 20(10):2598. https://doi.org/10.3390/ijms20102598

Kang YS, Kim WJ, Kim YJ, et al., 2016. Bakanae disease reduction effect by use of silicate coated seed in wet direct-seeded rice. *Korean J Crop Sci*, 61(1):9-16. https://doi.org/10.7740/kjcs.2016.61.1.009

Kanjanasoon P, 1965. Studies on the Bakanae Disease of Rice in Thailand. PhD Dissemination, Tokyo University, Tokyo, Japan.

Kato A, Miyake T, Nishigata K, et al., 2012. Use of fluorescent proteins to visualize interactions between the Bakanae disease pathogen *Gibberella fujikuroi* and the biocontrol agent *Talaromyces* sp. KNB-422. *J Gen Plant Pathol*, 78(1):54-61. https://doi.org/10.1007/s10327-011-0343-9

Katoch P, Katoch A, Paudel M, et al., 2019. Bakanae of rice: a serious disease in Punjab. *Int J Curr Microbiol Appl Sci*, 8(5):129-136. https://doi.org/10.20546/ijcmas.2019.805.017

Kazempour MN, Elahinia SA, 2007. Biological control of *Fusarium fujikuroi*, the causal agent of bakanae disease by rice associated antagonistic bacteria. *Bulg J Agri Sci*, 13: 393-408.

Kazempour MN, Anvary M, 2009. Isolation of *Fusarium fujikuroi* antagonistic bacteria and cloning of its phenazine carboxylic acid genes. *Afr J Biotechnol*, 8(23):6506-6510. https://doi.org/10.4314/ajb.v8i23.66175

Kazempour MN, Tabatabaei SM, Hassanzadeh N, 2007. Genetic diversity of antagonistic bacteria against sheath blight and bakanae rice disease by RAPD. *Int J Biol Biotechnol*, 4(4):329-333.

Kim D, Jeong S, Kim B, et al., 2023. Automated detection of rice bakanae disease via drone imagery. *Sensors*, 23(1):32. https://doi.org/10.3390/s23010032

Kim MH, Hur YJ, Lee SB, et al., 2014. Large-scale screening of rice accessions to evaluate resistance to bakanae disease. *J Gen Plant Pathol*, 80(5):408-414. https://doi.org/10.1007/s10327-014-0528-0

Kim SW, Park JK, Lee CH, et al., 2016. Comparison of the antimicrobial properties of chitosan oligosaccharides (COS) and EDTA against *Fusarium fujikuroi* causing rice bakanae disease. *Curr Microbiol*, 72(4):496-502. https://doi.org/10.1007/s00284-015-0973-9

Kuhlman EG, 1982. Varieties of *Gibberella fujikuroi* with anamorphs in *Fusarium* section *Liseola*. *Mycologia*, 74(5): 759-768. https://doi.org/10.1080/00275514.1982.12021583

Kumakura K, Watanabe S, Toyoshima J, 2003. Effect of *Trichoderma* sp. SKT-1 on suppression of six different seedborne diseases of rice. *Jpn J Phytopathol*, 69(4):393-402. https://doi.org/10.3186/jjphytopath.69.393

Kumar MN, Laha GS, Reddy CS, 2007. Role of antagonistic bacteria in suppression of bakanae disease of rice caused by *Fusarium moniliforme* Sheld. *J Biol Control*, 21(1): 97-104.

Kumar P, Sunder S, Singh R, et al., 2016. Management of foot rot and bakanae of rice through non-chemical methods. *Indian Phytopathol*, 69(1):16-20.

Kurosawa E, 1926. Experimental studies on the nature of the substance excreted by the 'bakanae' fungus. *Trans Nat Hist Soc Formos*, 16:213-227.

Kusakari S, Achiwa N, Abe K, 2004. Control of bakanae disease by soaking seed in heated electrolyzed acid water (EAW) under field conditions. *J Antibact Antifungal Agents*, 32(12):581-585.

Kwon SW, Kim NE, Jin SH, et al., 2021. Evaluation of the rsistant to bakanae disease in Korean rice landraces (*Oryza sativa* L.). *Plant Breed Biotech*, 9(4):355-359. https://doi.org/10.9787/PBB.2021.9.4.355

Lee SB, Hur YJ, Cho JH, et al., 2018. Molecular mapping of *qBK1*^{WD}, a major QTL for bakanae disease resistance in rice. *Rice*, 11:3. https://doi.org/10.1186/s12284-017-0197-7

Lee SB, Kim N, Hur YJ, et al., 2019. Fine mapping of *qBK1*, a major QTL for bakanae disease resistance in rice. *Rice*, 12:36. https://doi.org/10.1186/s12284-019-0295-9

Lee SB, Kim N, Jo S, et al., 2021. Mapping of a major QTL, *qBK1*^{Z}, for bakanae disease resistance in rice. *Plants*, 10(3): 434. https://doi.org/10.3390/plants10030434

Lee YH, Lee MJ, Choi HW, et al., 2011. Development of *in vitro* seedling screening method for selection of resistant rice against bakanae disease. *Res Plant Dis*, 17(3): 288-294. https://doi.org/10.5423/RPD.2011.17.3.288

Li B, Xie GL, Lü YL, et al., 2006. Community composition of Gram-positive bacteria associated with rice and their antagonists against the pathogens of sheath blight and bakanae disease of rice. *Chin J Rice Sci*, 20(1):84-88 (in Chinese).

https://doi.org/10.3321/j.issn:1001-7216.2006.01.015

Li C, Brant E, Budak H, et al., 2021. CRISPR/Cas: a Nobel Prize award-winning precise genome editing technology for gene therapy and crop improvement. *J Zhejiang Univ-Sci B (Biomed & Biotechnol)*, 22(4):253-284. https://doi.org/10.1631/jzus.B2100009

Li FJ, Ebihara A, Sakahara Y, et al., 2023. Synergistic effect of amino acid substitutions in CYP51B for prochloraz resistance in *Fusarium fujikuroi*. *Pestic Biochem Physiol*, 189:105291. https://doi.org/10.1016/j.pestbp.2022.105291

Li MX, Li T, Duan YB, et al., 2018. Evaluation of phenamacril and ipconazole for control of rice bakanae disease caused by *Fusarium fujikuroi*. *Plant Dis*, 102(7):1234-1239. https://doi.org/10.1094/PDIS-10-17-1521-RE

Lima CS, Pfenning LH, Costa SS, et al., 2012. *Fusarium tupiense* sp. nov., a member of the *Gibberella fujikuroi* complex that causes mango malformation in Brazil. *Mycologia*, 104(6):1408-1419. https://doi.org/10.3852/12-052

Lone ZA, Bhat ZA, Najeeb S, et al., 2016. Screening of rice genotypes against bakanae disease caused by *Fusarium fujikuroi* Nirenberg. *Oryza*, 53(1):91-97.

Ma J, Chen J, Wang M, et al., 2018. Disruption of *OsSEC3A* increases the content of salicylic acid and induces plant defense responses in rice. *J Exp Bot*, 69(5):1051-1064. https://doi.org/10.1093/jxb/erx458

Malonek S, Bömke C, Bornberg-Bauer E, 2005. Distribution of gibberellin biosynthetic genes and gibberellin production in the *Gibberella fujikuroi* species complex. *Phytochemistry*, 66(11):1296-1311. https://doi.org/10.1016/j.phytochem.2005.04.012

Manandhar J, 1999. *Fusarium moniliforme* in rice seeds: its infection, isolation, and longevity. *J Plant Dis Prot*, 106(6): 598-607.

Manandhar T, Yami KD, 2008. Biological control of foot rot disease of rice using fermented products of compost and vermicompost. *Sci World*, 6(6):52-57. https://doi.org/10.3126/sw.v6i6.2634

Mancini V, Romanazzi G, 2014. Seed treatments to control seedborne fungal pathogens of vegetable crops. *Pest Manag Sci*, 70(6):860-868. https://doi.org/10.1002/ps.3693

Mandal DN, Chaudhuri S, 1988. Survivality of *Fusarium moniliforme* Sheld. under different moisture regimes and soil conditions. *Int J Trop Plant Dis*, 6:201-206.

Matić S, Spadaro D, Garibaldi A, et al., 2014. Antagonistic yeasts and thermotherapy as seed treatments to control *Fusarium fujikuroi* on rice. *Biol Cont*, 73:59-67. https://doi.org/10.1016/j.biocontrol.2014.03.008

Matic S, Gullino ML, Spadaro D, 2017. The puzzle of bakanae disease through interactions between *Fusarium fujikuroi* and rice. *Front Biosci (Elite Ed)*, 9(2):333-344. https://doi.org/10.2741/e806

Mende K, Homann V, Tudzynski B, 1997. The geranylgeranyl diphosphate synthase gene of *Gibberella fujikuroi*: isolation and expression. *Mol Gen Genet*, 255(1):96-105. https://doi.org/10.1007/s004380050477

Mishra D, Samuel CO, Tripathi SC, 2003. Evaluation of some essential oils against seed-borne pathogens of rice. *Ind Phytopath*, 56:212-213.

Miyasaka A, Sonoda R, Iwano M, 2000. Control of the bakanae disease of rice by soaking seeds in hot water for the hydroponically raised seedling method in the long-mat type rice cultivation. *Annu Rep Kanto-Tosan Plant Prot Soc*, 2000(47):31-33. https://doi.org/10.11337/ktpps1999.2000.31

Mohana DC, Prasad P, Vijaykumar V, et al., 2011. Plant extract effect on seed-borne pathogenic fungi from seeds of paddy grown in Southern India. *J Plant Prot Res*, 51(2):101-106. https://doi.org/10.2478/v10045-011-0018-8

Moretti A, Mulè G, Susca A, et al., 2004. Toxin profile, fertility and AFLP analysis of *Fusarium verticillioides* from banana fruits. *Eur J Plant Pathol*, 110(5):601-609. https://doi.org/10.1023/B:EJPP.0000032399.83330.d7

Ng LC, Ngadin A, Azhari M, et al., 2015. Potential of *Trichoderma* spp. as biological control agents against bakanae pathogen (*Fusarium fujikuroi*) in rice. *Asian J Plant Pathol*, 9(2):46-58. https://doi.org/10.3923/ajppaj.2015.46.58

Niehaus EM, Kim KH, Münsterkötter M, et al., 2017. Comparative genomics of geographically distant *Fusarium fujikuroi* isolates revealed two distinct pathotypes correlating with secondary metabolite profiles. *PLoS Pathog*, 13(10):e1006670. https://doi.org/10.1371/journal.ppat.1006670

Nirenberg H, 1976. Untersuchungen über die morphologische und biologische Differenzierung in der *Fusarium*-Sektion *Liseola*. Kommissionsverlag Paul Parey, Berlin, Germany, p.1-117 (in German). https://doi.org/10.5073/20210624-085725

Ochi A, Konishi H, Ando S, et al., 2017. Management of bakanae and bacterial seedling blight diseases in nurseries by irradiating rice seeds with atmospheric plasma. *Plant Pathol*, 66(1):67-76. https://doi.org/10.1111/ppa.12555

Oh TS, Park YJ, Kim SM, et al., 2016. Seed disinfectant effect of *Pleurotus ostreatus* (Heuktari) extract on *Fusarium fujikuroi* Nirenberg. *Korean J Org Agric*, 24(1):61-71. https://doi.org/10.11625/KJOA.2016.24.1.61

Oh TS, Park YJ, Kim CH, et al., 2017. Effect of seed disinfection on bakanae disease in *Ginkgo biloba* outer seed coat extract. *Emir J Food Agric*, 28(9):671-675. https://doi.org/10.9755/ejfa.2016-04-357

Pal S, Khilari K, Jain SK, et al., 2019. Management of bakanae disease of rice through combination of *Trichoderma* spp. and fungicides. *Int J Curr Microbiol App Sci*, 8(11):494-501. https://doi.org/10.20546/ijcmas.2019.811.060

Panneerselvam A, Saravanamuthu R, 1996. Studies on the saprophytic survival of *Fusarium moniliforme* J. Sheld in soil under treatment of oil cakes. *Indian J Agric Res*, 30(1):12-16.

Pannu PPS, Kaur J, Singh G, et al., 2012. Survival of *Fusarium moniliforme* causing foot rot of rice and its virulence on different genotypes of rice and basmati rice. *Indian Phytopathol*, 65:149-209.

Pattanaik S, Patra B, Singh SK, et al., 2014. An overview of the gene regulatory network controlling trichome development in the model plant, *Arabidopsis*. *Front Plant Sci*, 5:259.
https://doi.org/10.3389/fpls.2014.00259

Pawar BT, 2011. Antifungal activity of some leaf extracts against seed-borne pathogenic fungi. *Int Multidiscipl Res J*, 1/4:11-13.

Peng Q, Younas MW, Yang JK, et al., 2022. Characterization of prochloraz resistance in *Fusarium fujikuroi* from Heilongjiang Province in China. *Plant Dis*, 106(2):418-424.
https://doi.org/10.1094/PDIS-02-21-0372-RE

Petrovic T, Burgess LW, Cowie I, et al., 2013. Diversity and fertility of *Fusarium sacchari* from wild rice (*Oryza australiensis*) in Northern Australia, and pathogenicity tests with wild rice, rice, sorghum and maize. *Eur J Plant Pathol*, 136(4):773-788.
https://doi.org/10.1007/s10658-013-0206-7

Piombo E, Rosati M, Sanna M, et al., 2021. Sequencing of non-virulent strains of *Fusarium fujikuroi* reveals genes putatively involved in bakanae disease of rice. *Fungal Genet Biol*, 156:103622.
https://doi.org/10.1016/j.fgb.2021.103622

Proctor RH, Desjardins AE, Moretti A, 2010. Biological and chemical complexity of *Fusarium proliferatum*. *In*: Strange RN, Gullino ML (Eds.), The Role of Plant Pathology in Food Safety and Food Security. Springer, Dordrecht, p.97-111.
https://doi.org/10.1007/978-1-4020-8932-9_9

Ptaszek M, Canfora L, Pugliese M, et al., 2023. Microbial-based products to control soil-borne pathogens: methods to improve efficacy and to assess impacts on microbiome. *Microorganisms*, 11(1):224.
https://doi.org/10.3390/microorganisms11010224

Puyam A, Pannu PPS, Sethi S, et al., 2017. Evaluation of resistance sources against foot rot and bakanae disease of basmati rice. *Agric Res J*, 54(4):594-596.
https://doi.org/10.5958/2395-146X.2017.00115.6

Puyam A, Pannu PPS, Kaur J, et al., 2019. Understanding bakanae: a major threat and an emerging disease of basmati rice. *Indian Phytopathol*, 72(4):599-605.
https://doi.org/10.1007/s42360-018-0069-0

Qu XP, Li JS, Wang JX, et al., 2018. Effects of the dinitroaniline fungicide fluazinam on *Fusarium fujikuroi* and rice. *Pestic Biochem Physiol*, 152:98-105.
https://doi.org/10.1016/j.pestbp.2018.09.010

Radwan O, Gunasekera TS, Ruiz ON, 2018. Draft genome sequence of *Fusarium fujikuroi*, a fungus adapted to the fuel environment. *Genome Announc*, 6(3):e01499-17.
https://doi.org/10.1128/genomeA.01499-17

Raghu S, Yadav MK, Prabhukarthikeyan SR, et al., 2018. Occurance, pathogenicity, characterization of *Fusarium fujikuroi* causing rice bakanae disease from Odisha and *in vitro* management. *Oryza*, 55(1):214-223.
https://doi.org/10.5958/2249-5266.2018.00025.5

Ramesh NK, Naeimi S, Rezaee S, et al., 2020. Biological control of rice bakanae disease caused by *Fusarium fujikuroi* using some endophytic fungi. *J Appl Entomol Phytopathol*, 87(2):281-296.
https://doi.org/10.22092/jaep.2020.128244.1309

Rawat K, Tripathi SB, Kaushik N, et al., 2022. Management of bakanae disease of rice using biocontrol agents and insights into their biocontrol mechanisms. *Arch Microbiol*, 204(7):401.
https://doi.org/10.1007/s00203-022-02999-3

Rosales AM, Nuque FL, Mew TW, 1986. Biological control of bakanae diseases of rice with antagonistic bacteria. *Phil Phytopathol*, 22:29-35.

Rosales AM, Mew TW, 1997. Suppression of *Fusarium moniliforme* in rice by rice-associated antagonistic bacteria. *Plant Dis*, 81(1):49-52.
https://doi.org/10.1094/PDIS.1997.81.1.49

Saito H, Sasaki M, Nonaka Y, et al., 2021. Spray application of nonpathogenic *Fusaria* onto rice flowers controls bakanae disease (caused by *Fusarium fujikuroi*) in the next plant generation. *Appl Environ Microbiol*, 87(2):e01959-20.
https://doi.org/10.1128/AEM.01959-20

Sarwar A, Hassan NM, Imran M, 2018. Biocontrol activity of surfactin A purified from *Bacillus* NH-100 and NH-217 against rice bakanae disease. *Microbiol Res*, 209:1-13.
https://doi.org/10.1016/j.micres.2018.01.006

Sawada K, 1912. Diseases of agricultural products in Japan. *Form Agric Rev*, 63:10-16.

Sawada K, 1917. Beitrage über formosas-pilze No. 14. *Trans Nat Hist Soc Formosa*, 31:31-133 (in German).

Shah PR, Varanavasiappan S, Kokiladevi E, et al., 2019. Genome editing of rice *PFT1* gene to study its role in rice sheath blight disease resistance. *Int J Curr Microbiol Appl Sci*, 8(6):2356-2364.
https://doi.org/10.20546/ijcmas.2019.806.281

Singh R, Sunder S, 1997. Foot rot and bakanae of rice: retrospects and prospects. *Intl J Trop Plant Dis*, 15:153-176.

Singh R, Sunder S, 2012. Foot rot and bakanae of rice: an overview. *Rev Plant Pathol*, 5:566-604.

Singh R, Kumar P, Laha GS, 2019. Present status of bakanae of rice caused by *Fusarium fujikuroi* Nirenberg. *Indian Phytopathol*, 72(4):587-597.
https://doi.org/10.1007/s42360-019-00125-w

Sunder S, 1998. Vegetative compatibility, biosynthesis of GA_3 and virulence of *Fusarium moniliforme* isolates from

bakanae disease of rice. *Plant Pathol*, 47(6):767-772. https://doi.org/10.1046/j.1365-3059.1998.00303.x

Sun SK, Snyder WC, 1981. The bakanae disease of the rice plant. *In*: Nelson PE, Toussoun TA, Cook RJ (Eds.), Fusarium: Diseases, Biology and Taxonomy. The Pennsylvania University Press, University Park, p.104-113.

Tadasanahaller PS, Bashyal BM, Yadav J, et al., 2023. Identification and characterization of *Fusarium fujikuroi* pathotypes responsible for an emerging bakanae disease of rice in India. *Plants*, 12(6):1303. https://doi.org/10.3390/plants12061303

Takahashi N, Kitamura H, Kawarada A, et al., 1955. Biochemical studies on "bakanae" fungus: part XXXIV. Isolation of gibberellins and their properties. Part XXXV. Relation between gibberellins, A_1, A_2 and gibberellic acid. *Bull Agric Chem Soc Japan*, 19(4):267-281. https://doi.org/10.1080/03758397.1955.10856832

Takeuchi S, 1972. Climatic effect on seed infection of rice plant with bakanae disease and disinfection with organic mercury compounds. *Annu Rep Kansai Plant Prot Soc*, 14:14-19 (in Japanese). https://doi.org/10.4165/kapps1958.14.0_14

Távora FTPK, Meunier AC, Vernet A, et al., 2022. CRISPR/Cas9-targeted knockout of rice susceptibility genes *OsDjA2* and *OsERF104* reveals alternative sources of resistance to *Pyricularia oryzae*. *Rice Sci*, 29(6):535-544. https://doi.org/10.1016/j.rsci.2022.04.001

Tudzynski B, Hölter K, 1998. Gibberellin biosynthetic pathway in *Gibberella fujikuroi*: evidence for a gene cluster. *Fungal Genet Biol*, 25(3):157-170. https://doi.org/10.1006/fgbi.1998.1095

Tudzynski B, Mihlan M, Rojas MC, et al., 2003. Characterization of the final two genes of the gibberellin biosynthesis gene cluster of *Gibberella fujikuroi*: *des* and *P450-3* encode GA_4 desaturase and the 13-hydroxylase, respectively. *J Biol Chem*, 278(31):28635-28643. https://doi.org/10.1074/jbc.M301927200

Urbaniak C, Dadwal S, Bagramyan K, et al., 2018. Draft genome sequence of a clinical isolate of *Fusarium fujikuroi* isolated from a male patient with acute myeloid leukemia. *Genome Announc*, 6(25):e00476-18. https://doi.org/10.1128/genomeA.00476-18

Varughese T, Rios N, Higginbotham S, et al., 2012. Antifungal depsidone metabolites from *Cordyceps dipterigena*, an endophytic fungus antagonistic to the phytopathogen *Gibberella fujikuroi*. *Tetrahedron Lett*, 53(13):1624-1626. https://doi.org/10.1016/j.tetlet.2012.01.076

Volante A, Tondelli A, Aragona M, et al., 2017. Identification of *bakanae* disease resistance loci in *japonica* rice through genome wide association study. *Rice*, 10:29. https://doi.org/10.1186/s12284-017-0168-z

Wallner ES, López-Salmerón V, Greb T, 2016. Strigolactone versus gibberellin signaling: reemerging concepts? *Planta*, 243(6):1339-1350. https://doi.org/10.1007/s00425-016-2478-6

Wang FJ, Wang CL, Liu PQ, et al., 2016. Enhanced rice blast resistance by CRISPR/Cas9-targeted mutagenesis of the ERF transcription factor gene *OsERF922*. *PLoS ONE*, 11(4):e0154027. https://doi.org/10.1371/journal.pone.0154027

Wang Y, Wang YT, Yang RF, et al., 2021. Effects of gibberellin priming on seedling emergence and transcripts involved in mesocotyl elongation in rice under deep direct-seeding conditions. *J Zhejiang Univ-Sci B (Biomed & Biotechnol)*, 22(12):1002-1021. https://doi.org/10.1631/jzus.B2100174

Watanabe S, Kumakura K, Izawa N, et al., 2007. Mode of action of *Trichoderma asperellum* SKT-1, a biocontrol agent against *Gibberella fujikuroi*. *J Pest Sci*, 32(3):222-228. https://doi.org/10.1584/jpestics.G06-35

Wiemann P, Sieber CMK, von Bargen KW, et al., 2013. Deciphering the cryptic genome: genome-wide analyses of the rice pathogen *Fusarium fujikuroi* reveal complex regulation of secondary metabolism and novel metabolites. *PLoS Pathog*, 9(6):e1003475. https://doi.org/10.1371/journal.ppat.1003475

Wu JY, Sun YN, Zhou XJ, et al., 2020. A new mutation genotype of K218T in myosin-5 confers resistance to phenamacril in rice bakanae disease in the field. *Plant Dis*, 104(4):1151-1157. https://doi.org/10.1094/PDIS-05-19-1031-RE

Xue ZL, Zhong S, Shen JH, et al., 2023. Multiple mutations in SDHB and $SDHC_2$ subunits confer resistance to the succinate dehydrogenase inhibitor cyclobutrifluram in *Fusarium fujikuroi*. *J Agric Food Chem*, 71(8):3694-3704. https://doi.org/10.1021/acs.jafc.2c08023

Yabuta T, 1935. Biochemistry of the "bakanae" fungus of rice. *Agric Hortic*, 10:17-22.

Yabuta T, Sumiki T, 1938. Communication to the editor. *J Agric Chem Soc Japan*, 14:1526.

Yan YX, Zhang XY, Tan YY, et al., 2022. Establishment of an artificial inoculation system for the efficient induction of rice bakanae disease. *Crop Des*, 1(2):100016. https://doi.org/10.1016/j.cropd.2022.100016

Yang CD, Guo LB, Li XM, et al., 2006. Analysis of QTLs for resistance to rice bakanae disease. *Chin J Rice Sci*, 20(6):657-659 (in Chinese). https://doi.org/10.3321/j.issn:1001-7216.2006.06.016

Yasmin M, Hossain KS, Bashar MA, 2008. Effects of some angiospermic plant extracts on in vitro vegetative growth of *Fusarium moniliforme*. *Bangladesh J Bot*, 37(1):85-88. https://doi.org/10.3329/bjb.v37i1.1569

Yu KS, Sun SK, 1976. Ascospore liberation of *Gibberella fujikuroi* and its contamination of rice grains. *Plant Prot Bull Taiwan*, 18(4):319-329.

Zainudin NAIM, Razak AA, Salleh B, 2008. Secondary metabolite profiles and mating populations of *Fusarium* species in section Liseola associated with bakanae disease of rice. *Malay J Microbiol*, 4(1):6-13. https://doi.org/10.21161/mjm.01708

Zeinab K, Hassan AA, 2019. Antifungal potential and characterization of plant extracts against *Fusarium fujikuroi* on rice. *J Plant Prot Pathol*, 10(7):369-376. https://dio.org/10.21608/jppp.2019.53671

Zhang SY, Dai DJ, Wang HD, et al., 2019. One-step loop-mediated isothermal amplification (LAMP) for the rapid and sensitive detection of *Fusarium fujikuroi* in bakanae disease through *NRPS31*, an important gene in the gibberellic acid bio-synthesis. *Sci Rep*, 9:3726. https://doi.org/10.1038/s41598-019-39874-z

Zhang YM, Zheng L, Xie KB, 2023. CRISPR/dCas9-mediated gene silencing in two plant fungal pathogens. *mSphere*, 8(1):e00594-22. https://doi.org/10.1128/msphere.00594-22

Zhu Q, Wu YB, Chen M, et al., 2022. Preinoculation with endophytic fungus *Phomopsis liquidambaris* reduced rice bakanae disease caused by *Fusarium proliferatum* via enhanced plant resistance. *J Appl Microbiol*, 133(3):1566-1580. https://doi.org/10.1111/jam.15656