

REVIEW

Unveiling the intricacies of the rice-*Rhizoctonia* pathosystem: a comprehensive review of host-pathogen interactions, molecular mechanisms, and strategies for sustainable management

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Abstract

Sheath blight disease in rice, induced by the necrotrophic basidiomycetes *Rhizoctonia solani*, has emerged as a significant menace to global rice cultivation, especially with the widespread adoption of high-yielding varieties. The pathogen's capacity to endure unfavorable conditions and its wide host range contribute to the increased challenge for management. The occurrence of sheath blight in rice is intensified when high-yielding semi-dwarf cultivars are employed, coupled with dense planting and the application of substantial amounts of nitrogenous fertilizers. Managing this pathogen is a formidable challenge due to its broad host range, substantial genetic variability, and the absence of satisfactory levels of natural resistance in the existing rice germplasm. Due to the absence of complete resistance sources, the predominant approach for managing sheath blight has been through chemical control methods. It is imperative to explore solutions to combat this pathogen, in order to reduce rice yield losses and safeguard global food security. Developing genetic resistance provides an alternative to the use of potentially harmful chemical fungicides. This review crucially delivers efforts to enhance the understanding of the host-pathogen relationship, which involves identification of gene loci/markers associated with resistance responses, modification of host genome through transgenic approaches, examining the wide host range, epidemiology and its managerial approaches. Recent advancements and current research on the *R. solani*-rice pathosystem, along with a gap analysis, are presented.

Keywords: genetic variability, pathosystem, resistance, *Rhizoctonia solani*, sheath blight

Introduction

From a global perspective sheath blight is considered to be the most devastating threat to rice growers. It is caused by the necrotrophic pathogen *Rhizoctonia solani* Kühn (Rao *et al.* 2020). The disease is synonymously well known as “rotten foot stalk”, “mosaic foot stalk” and “snake skin disease” due to its peculiar manifestations.

Rice sheath blight (RSB) in fields is mainly because of intensive planting of semi-dwarf, high yield cultivars where high nitrogen fertilizers have been applied

extensively over the last two decades (Yellareddygari *et al.* 2014). In 1910 RSB was first documented in Japan and later popularized in Asia, Africa, and America (Miyake 1910). In India sheath blight of rice was first reported in 1963 in Gurdaspur of Punjab by Paracer and Chahal. RSB appeared in China for the first time in 1934 as the second leading rice disease. It causes 30–50% yield losses annually in various geographical locations of South China and the Yangtze River valley rice growing areas (Yu *et al.* 2019; Zhu *et al.* 2019). Each year, over 15 million hectares are affected by sheath blight disease in China (Shu *et al.* 2019). Because no resistant germplasm is available, breeding for

RSB-resistant rice varieties is happening too slowly. The most effective forms of controlling and preventing the disease are currently chemical fungicides and cultivation practices (Yellareddygari *et al.* 2014; Singh *et al.* 2019). Recent reviews on integrated management strategies, genomics, proteomics, transcriptomic approaches, genetic variability and QTL mapping provides some astonishing information about genetic resistance against rice sheath blight (RSB) rots.

Etiology and distribution

Sheath blight pathogens are present in crop debris and survive by forming sclerotia which can survive from one cropping cycle to another. Pathogens survive in the collateral weed host in tropical climates. Sclerotia which arise in previous rice crops serve as the primary inoculum that causes primary infection in temperate regions. At the harvest and post harvest field operational stages, resting sclerotia survive in the infected plant debris and under soil micro biota throughout the cropping cycle which revives when there are favorable environmental conditions. Climate plays an important role in the aggravation of disease. An increased level of CO₂ concentration can boost sheath blight and blast disease severity under field conditions. The initial density of sheath blight pathogen was positively correlated with the disease's severity and spread. Furthermore, rice yields were severely decreased as the severity of the disease and the proportion of afflicted rice tillers increased. The average length of daylight in the first 5 days, followed by average relative humidity and temperature are the three key factors influencing the vertical growth of rice sheath blight. Under *in-vitro* laboratory conditions sheath blight lesions increase symptomatically (their length and breadth) under optimal environmental conditions (high temperatures and high relative humidity). Moreover the lesions progressed more rapidly in sheaths that were inoculated with sclerotia than in those that were already infected.

Sandy soil is favorable for the aggressiveness of sheath blight. Additionally, in moist soil the disease prevalence is highest when there is a water holding capacity of about 50–60%. In submerged soil having a water holding capacity of 100% the disease severity becomes low. The resistance level of a rice strain to the incidence of sheath blight depends on the average daily temperature and the amount of rain fall. However, there was no discernible relationship between the onset of disease and the degree of sheath blight devastation. Disease prevalence and growth were more noticeable in 20 to 30 days old seedlings than in

seedlings 30 to 40 days old in a pot culture study under artificially inoculated conditions. Numerous plants has been reported as a host of *R. solani* such as: *Cyprus rotundus*, *C. difformis*, *Cynodon dactylon*, *Echinochloa colonum*, *Setaria glauca* (*S. pumila*), *Panicum repens*, *Brachiaria* sp., *Commelina* sp., *Obliqua* sp. and *Amaranthus viridis*. The pathogens can overwinter in these hosts even in the absence of a rice crop. Sivalingam *et al.* (2006) conducted a study on the seed borne nature of *R. solani* for the occurrence of sheath blight in rice. They discovered that there was no connection between the incidence of pathogen isolation and the severity of seed discoloration. Also, they used *Trichoderma harzianum*, *T. viride*, *T. virens* (*Gliocladium virens*), *Pseudomonas fluorescens*, and Carbendazim for biocontrol study. Their experiment confirmed that *R. solani* is internally seed borne. *R. solani* was very poorly transmitted to rice plants in the field, despite being strongly present in seeds.

Pathogenic diversity and pathogenicity

In the intricate world of plant-pathogen interactions, the exploration of pathogenic diversity and pathogenicity within the context of *R. solani* has undergone a transformative evolution with the integration of cutting-edge DNA and genomic evidence. *R. solani*, a soil-borne fungal pathogen of multifaceted implications, serves as an illustrative model to dissect the intricate genetic and molecular underpinnings of its interactions with diverse host plants. Biology and pathogenicity study of *R. solani* depicted through Table 1. As researchers delve into the genomic tapestry of *R. solani* populations, insights into the intricacies of its pathogenicity dynamics emerge, casting light on the multifarious factors shaping its virulent potential. The advent of state-of-the-art DNA sequencing technologies, including next-generation sequencing (NGS), has unraveled the genomic mosaic that defines the pathogenic diversity within *R. solani* populations. Through comparative genomics, researchers can dissect the intricate landscape of genes, recombination events, and mobile genetic elements that engender the diversification of virulence factors and effector profiles. These findings give genomic insight, showing deviation in nucleotide orientation, and help to pave the way to discern the genetic markers that delineate pathogenic phenotypes, offering a broader understanding of the intricate host-pathogen interplay. At the heart of *R. solani*'s pathogenic repertoire lies the phenomenon of horizontal gene transfer (HGT), an evolutionary mechanism contributing to the swift assimilation of

Table 1. Insights into *Rhizoctonia solani* biology and pathogenicity

Aspect	Description and insights
Genetic diversity	<i>Rhizoctonia solani</i> exhibits diverse genetic profiles among strains, reflecting polymorphisms, recombination, and mobile genetic elements. This diversity underlies its capacity to infect a wide array of hosts
Host range variation	<i>Rhizoctonia solani</i> strains showcase varied host preferences, allowing the pathogen to target plants across diverse botanical families
Horizontal gene transfer (HGT)	horizontal gene transfer is evident in <i>Rhizoctonia solani</i> , contributing to the transfer of virulence-associated genes and facilitating the adaptation to different host environments
Effector profiles	the diversity of effector molecules in <i>Rhizoctonia solani</i> influences its interactions with hosts, affecting recognition, colonization, and disease progression
Virulence factor variation	variability in virulence factors among <i>Rhizoctonia solani</i> strains contributes to the varying degrees of pathogenicity observed across different hosts
Genetic markers for pathogenicity	genetic markers associated with pathogenicity in <i>Rhizoctonia solani</i> strains offer insights into the genetic basis of their virulence and potential host interactions
Epigenetic regulation	epigenetic mechanisms, including DNA methylation and histone modifications, play a role in regulating gene expression and pathogenicity in <i>Rhizoctonia solani</i>
Diagnostic tools	DNA-based diagnostic tools enable the accurate identification of <i>Rhizoctonia solani</i> strains, aiding in monitoring its presence and distribution
Functional genomics	functional genomics techniques, including gene editing, uncover the roles of virulence factors and effectors in <i>Rhizoctonia solani</i> pathogenicity
Interactions with host immunity	the interplay between <i>Rhizoctonia solani</i> effectors and host immunity influences disease outcomes, contributing to the diverse manifestations of pathogenicity
Adaptation and Evolution	<i>Rhizoctonia solani's</i> genetic and molecular adaptability contributes to its pathogenic diversity, enabling rapid evolution in response to changing environments.
Management Implications	Insights into pathogenic diversity and pathogenicity guide disease management strategies, influencing the development of targeted interventions and resistant crops.

virulence attributes. An analysis of genomic data shows instances of HGT engendering the acquisition of effector genes and other virulence determinants, underlining its pivotal role in forging pathogenic diversity. Furthermore, the canvas of epigenetic regulation comes into play, wherein DNA methylation, histone modifications, and small RNA orchestration contribute to the dynamic modulation of gene expression. Epigenetic insights into *R. solani's* arsenal of virulence attributes unveil its capacity to swiftly adapt to varying host environments and circumvent host defenses. Utilizing the tools of comparative genomics and secretome analyses, researchers prognosticated a tally of 985 secreted proteins alongside 103 minuscule effector candidates rich in cysteine, encapsulated within the genomic landscape of *R. solani* AG1 IA. Noteworthy are distinct effectors, such as AG1IA_09161, AG1IA_05310, and AG1IA_07795, which have been demarcated as catalysts of cell death in rice and maize plants. These effectors bear hallmark domains, including glycosyltransferase GT family 2, cytochrome C oxidase assembly protein CtaG/cox11, and peptidase inhibitor. Multiomic dimensions as gene expression, unveiled by transcriptome analysis. Numerous presumptive genes

encodes secreted proteins and effector candidates during the incursion of *R. solani* AG1 IA. Within this array, specific proteins such as AG1IA_02392, AG1IA_06487 and AG1IA_03906 experience preferential upregulation upon invading susceptible rice cultivars. The role played by AG1IA_02392, housing a distinctive Nudix domain, remains poised for thorough elucidation. Adding to the intrigue is the lipase effector AGLIP1, inciting cell death in both *Nicotiana benthamiana* and rice protoplasts. Notably, its expression exerts a dual effect – repressing basal defenses and fostering bacterial propagation within Arabidopsis. In summative reflection, the intricate molecular interplay governing the rice – *R. solani* co-evolution underscores its pivotal role in steering innovative strategies against the menace of rice sheath blight. Pathogens of the ilk of *R. solani* strategically marshal a gamut of molecules, including effectors, to adroitly recalibrate host immunity and amplify their virulent impact. Deciphering the nuanced roles played by specific effector proteins and their intricate interplay with the host landscape stands poised to catalyze the evolution of forward-looking methodologies in the domain of disease management.

Host range

Rhizoctonia solani, a soil-borne fungal pathogen of ubiquitous prevalence, exhibits an expansive and polymorphic host range (Table 2), attesting to its capacity to infect a diverse array of plant taxa spanning a wide botanical spectrum. This phytopathogen is renowned for instigating an array of plant diseases collectively referred to as “*Rhizoctonia* diseases”. Its dynamic host interaction underscores its profound impact on agricultural, horticultural, and ornamental sectors, influencing plant health, productivity, and aesthetic value.

Within its purview, an extensive range emerges:

Cereals: *Rhizoctonia solani* exerts its influence on cereal crops such as *Oryza sativa* (rice), *Triticum aestivum* (wheat), *Hordeum vulgare* (barley), and *Avena sativa* (oats). These pivotal food sources succumb

to symptoms of root rot, damping-off, and stunted growth, resulting in compromised yields and diminished establishment success.

Vegetables: A wide cohort of vegetable taxa, encompassing *Solanum tuberosum* (potato), *Beta vulgaris* (sugar beet), *Daucus carota* (carrot), *Phaseolus vulgaris* (common bean) and *Cucumis sativus* (cucumber), falls within the pathogenic grasp of *R. solani*. These vital crops endure the consequences of root rot, stem cankers, and collar rot, leading to economic losses and hampered agricultural productivity.

Ornamental Plants: The realm of ornamental flora, including *Rosa* sp. (roses), *Pelargonium* sp. (geraniums), and *Euphorbia pulcherrima* (poinsettias), suffer from *R. solani* (Debener and Byrne 2014). Showing stem cankers, root decay, and damping-off, these aesthetically valued species experience compromised

Table 2. *Rhizoctonia solani*, its impact on different host plants

Host range by scientific name	Host range by common name	Notable symptoms and effects
<i>Lactuca sativa</i>	lettuce	damping-off, root rot, reduced lettuce quality
<i>Prunus persica</i>	peach	root rot, stem cankers, diminished peach fruit quality
<i>Spinacia oleracea</i>	spinach	damping-off, root rot, stunted spinach growth
<i>Vitis vinifera</i>	grapevine	root rot, stem cankers, decreased grape yield
<i>Hordeum vulgare</i>	barley	stunted growth, root rot, damping-off in barley plants
<i>Musa spp.</i>	banana	root rot, leaf symptoms, decreased banana production
<i>Carica papaya</i>	papaya	stem cankers, root rot, reduced papaya fruit quality; <i>Cucumis sativus</i>
<i>Cucumis sativus</i>	cucumber	stem cankers, damping-off, growth reduction in cucumber plants
<i>Papaver somniferum</i>	opium poppy	root rot, damping-off, reduced opium poppy production
<i>Brassica oleracea</i> var. <i>capitata</i>	cabbage	damping-off, root rot, stunted growth in cabbage crops
<i>Beta vulgaris</i> subsp. <i>cycla</i>	swiss chard	leaf spot, root rot, reduced growth in swiss chard plants
<i>Gossypium hirsutum</i>	cotton	root rot, stunted growth, reduced cotton fiber yield
<i>Vitis vinifera</i>	grapevine	root rot, stem cankers, decreased grape yield
<i>Zea mays</i>	corn, maize	seedling damping-off, root rot, reduced corn yield
<i>Medicago sativa</i>	alfalfa	root rot, stunted growth, reduced alfalfa yield
<i>Helianthus annuus</i>	sunflower	stem cankers, root rot, compromised sunflower growth
<i>Citrus spp.</i>	citrus trees	root and stem damage, compromised fruit quality in citrus trees
<i>Spinacia oleracea</i>	spinach	damping-off, root rot, stunted spinach growth
<i>Lycopersicon esculentum</i>	tomato	damping-off, root rot, decreased tomato production
<i>Vigna unguiculata</i>	cowpea	root rot, stunted growth, diminished cowpea yield
<i>Cucurbita pepo</i>	zucchini	stem cankers, root rot, reduced zucchini yield
<i>Solanum tuberosum</i>	potato	root rot, stem cankers, yield reduction in potato crops
<i>Persea americana</i>	avocado	stem cankers, root rot, compromised avocado tree health
<i>Citrullus lanatus</i>	watermelon	stem cankers, root rot, diminished watermelon yield
<i>Fragaria ananassa</i>	strawberry	root rot, stunted growth, decreased strawberry yield

ornamental quality, affecting both market desirability and horticultural aesthetics.

Turfgrasses: Even the tranquil landscapes of turfgrasses are susceptible to *R. solani* which engenders afflictions such as brown patch, damping-off and blemishes the pristine appeal of lawns or green spaces. The ensuing visual blight underscores the necessity for stringent turfgrass management to abrogate its deleterious effects.

Fruit Crops: The influence of *R. solani* extends to fruit-bearing species like *Fragaria* × *ananas* (strawberry) and *Citrus* sp. (citrus trees), instigating damage to roots and stems that in turn curtails fruit yield and quality.

This pathogen's adaptability to varying environmental conditions and its penchant for colonizing plant parts – particularly subterranean root systems and basal stems – underscore its versatility in host interaction. Moreover, its capacity for survival in the form of sclerotia or mycelial aggregates within the soil milieu, coupled with its ability to propagate and colonize with alacrity, heightens its menace. Mitigation strategies entail multifaceted approaches encompassing strategic crop rotation, selection of resistant cultivars, optimized soil hydraulic conductivity, precision planting practices, and judicious fungicide application (Agyare *et al.* 2023). In a more comprehensive context, *R. solani* encompasses multiple strains with varying degrees of host affinity and pathogenicity. Different anastomosis groups (AGs), which are indicative of genetic relatedness, exhibit distinct preferences for hosts and geographic ranges. For instance, AG-1 affects sugar beet and AG-4 primarily affects turfgrasses. The AG-8 strain, a destructive agent in rice cultivation, underscores the pathogen's adaptability across diverse ecosystems. The complexity of host interactions and strain diversity reaffirm the exigency of continuous research to fathom the intricate biology of *R. solani*. Concomitant with the burgeoning agricultural challenges of our era, the mitigation of its impact remains a crucial domain of scientific inquiry, with ramifications extending to sustainable crop production, ecological balance, and the safeguarding of global food security.

Morphological and cultural variability

Rhizoctonia solani, a soil-borne fungal pathogen, stands as a testimony to the fascinating world of morphological and cultural variability. This organism, known for its broad host range (Table 2) and capacity

to induce a spectrum of diseases collectively termed “*Rhizoctonia* diseases”, shows remarkable adaptations in its appearance and behavior. By delving into the intricate details of its morphological characteristics and cultural preferences, we gain insights into the diverse manifestations of this pathogen, its interactions with host plants, and the challenges it poses in the realm of agriculture. Morphological diversity is a hallmark of *R. solani*, encapsulating a myriad of colony textures, hyphal characteristics, and specialized structures. The colony morphologies are displayed by various strains ranging from fluffy to cottony or powdery. The complex and adaptable nature of the pathogen makes it more vigorous and cosmopolitan globally. For instance, the AG-4 strain of *R. solani* exhibits cottony mycelium, a distinct feature that can aid in its identification. The hyphal characteristics, including diameter and branching patterns, vary among different species. *R. zeae*, for instance, produces thick-walled hyphae with frequent septation, contrasting with the finer hyphae of other strains. The production of sclerotia (Fig. 1), compact survival structures, further contributes to the morphological diversity. *R. solani* AG-1 IA forms large sclerotia, while AG-4 produces smaller, irregularly shaped ones, adding a layer of intricacy to its appearance. Cultural characteristics of *R. solani* encompass a range of preferences that influence its growth, behavior, and ultimately, its pathogenicity (Table 3). The optimal growth conditions, encompassing temperature and humidity preferences, reflect the pathogen's adaptation to different ecological niches. Some strains, such as *R. solani* AG-2-2, prefer cooler temperatures between 25°C and 30°C, aligning with their affinity for temperate climates. Media preferences further shed light on the diverse nature of *R. solani*. For instance, *R. oryzae* thrives on oatmeal agar, while *R. solani* AG-3 finds its favored habitat on potato dextrose agar. Pigmentation variations are also evident, with different strains displaying colors ranging from white to tan or even reddish hues. The distinct growth patterns, like concentric rings or radial expansion, contribute to the intricate tapestry of cultural diversity. In the context of pathogenicity, the morphological variability of *R. solani* takes on a deeper significance. Host-specific adaptations become apparent, where different strains display morphological traits tailored to specific host plants. This nuanced adaptation shapes the infection structures and colonization patterns, enhancing the pathogen's ability to exploit certain hosts. Furthermore, the formation of pathogenic structures – such as infection cushions, appressoria, and penetration pegs – reveals the pathogen's finely tuned mechanisms for invading host tissues. These structures provide an edge in host interactions, further underscoring the importance of

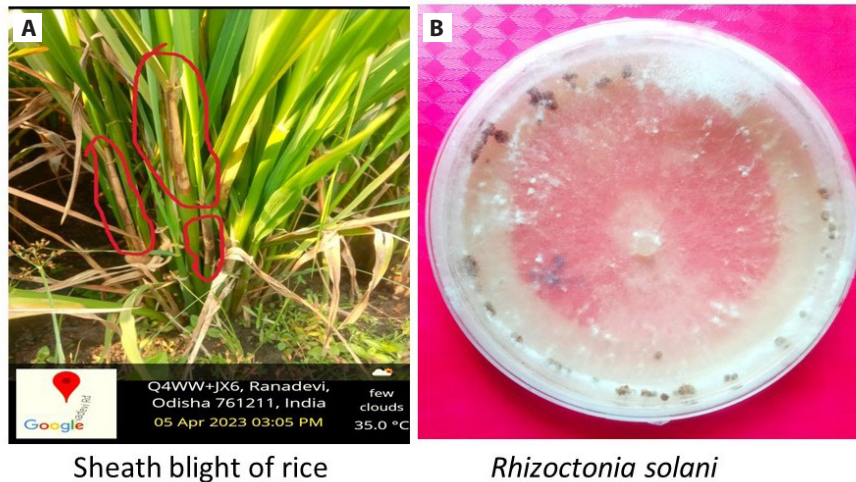


Fig. 1. Symptomatic characterization of sheath blight disease on rice – A and *Rhizoctonia solani* cultural growth on PDA culture media – B.

Table 3. Morphological and cultural characteristics of *Rhizoctonia solani*

Morphological characteristics	Description and examples
Colony morphology	<i>Rhizoctonia solani</i> exhibits varied colony morphologies, such as fluffy, cottony, or powdery textures. For instance, <i>R. solani</i> AG-4 produces cottony mycelium
Hyphal characteristics	the hyphal diameter and branching patterns vary among <i>Rhizoctonia</i> species. <i>R. zeae</i> produces thick-walled hyphae with frequent septation
Sclerotia formation	<i>R. solani</i> AG-1 IA produces large sclerotia, while <i>R. solani</i> AG-4 produces smaller, irregularly shaped sclerotia
Mycelial growth rate	<i>R. solani</i> AG-3 grows faster on potato dextrose agar compared to <i>R. solani</i> AG-2.
Cultural characteristics	
Optimal growth conditions	<i>R. solani</i> AG-2-2 prefers temperatures between 25°C and 30°C for optimal growth
Media preferences	<i>R. oryzae</i> grows well on oatmeal agar, while <i>R. solani</i> AG-3 prefers potato dextrose agar
Pigmentation	<i>R. zeae</i> produces white mycelium with pink pigmentation on media, while <i>R. solani</i> AG-1 IA shows tan mycelium
Growth patterns	<i>R. solani</i> AG-5 produces a characteristic “spoke and wheel” growth pattern on potato dextrose agar
Morphological variation in pathogens	
Host-specific adaptations	<i>R. solani</i> AG-4 HG-III has been associated with damping-off in beans, showing an affinity for this particular host
Pathogenic structures	<i>R. solani</i> AG-1 IA forms infection cushions on rice roots, aiding in the penetration of host tissues
Cultural variability and pathogenicity	
Virulence correlations	isolates of <i>R. solani</i> AG-3 with more rapid mycelial growth rates on media have been linked to increased aggressiveness on host plants
Host range influence	<i>R. oryzae</i> AG-1 IA is commonly associated with rice, while <i>R. solani</i> AG-4 is known for its broad host range across various plant species
Environmental adaptations	<i>R. solani</i> AG-2-2 exhibits a preference for cooler temperatures, allowing it to thrive in temperate climates and impact crops like potatoes
Taxonomic considerations	
Species identification	DNA sequencing revealed that <i>R. solani</i> AG-2 isolates with similar morphologies belong to distinct genetic groups
Taxonomic updates	recent taxonomic revisions have led to the differentiation of <i>R. zeae</i> from <i>R. solani</i> , emphasizing the importance of molecular methods in accurate classification

morphological adaptations in disease development. Cultural variability, often linked with pathogenicity, presents a compelling narrative. Virulence correlations have been observed, where isolates of *R. solani* AG-3 with rapid mycelial growth rates on media have been associated with heightened aggressiveness on host plants. The influence of cultural traits on host range is also evident. *R. oryzae* AG-1 IA, for instance, is closely tied to rice, while *R. solani* AG-4 has a wide host range, epitomizing its versatility. Moreover, environmental adaptations are mirrored in cultural traits. *R. solani* AG-2-2's preference for cooler temperatures is intertwined with its ability to impact crops in temperate climates, making it a significant player in potato cultivation. Taxonomic considerations add an intriguing layer to the exploration of morphological and cultural variability. Species identification, relying on morphological traits, intersects with DNA sequencing methods, refining our understanding of *R. solani*'s taxonomy. Recent taxonomic updates have unveiled distinctions between closely related species, such as *R. zea* from *R. solani*, emphasizing the pivotal role of molecular methods in accurate classification. In conclusion, the world of *R. solani*'s morphological and cultural variability is a captivating realm rich with diversity, adaptations, and interactions. The interplay between colony textures, hyphal structures, cultural preferences, and pathogenicity highlights the dynamic nature of this pathogen. Understanding its morphological intricacies and cultural behaviors provides a deeper comprehension of its ecological roles, disease potential, and the challenges it poses in agricultural landscapes. As we navigate the complex interplay of form and function within *R. solani*, we gain valuable insights into mitigating its impact and fostering sustainable crop management practices.

Geographical occurrence of *Rhizoctonia solani*

The pervasive presence of *R. solani*, an adaptable and soil-dwelling fungal pathogen, reflects its remarkable capacity to exploit shifting environmental dynamics. This adaptability is underscored by recent studies showing the fungal ability to respond to changing temperature regimes, altering soil conditions, and varying moisture levels (Abdel-lateif 2017). Emerging research indicates that these environmental shifts influence the pathogen's distribution patterns. Even though it thrives in regions previously considered less suitable the pathogen's versatile nature is further substantiated by reports of its successful infection in a wide range of host plants, from traditional cereal crops to emerging high-value horticultural species. The economic ramifications of *R. solani*'s impact on agriculture are well-documented. Empirical studies have quantified yield losses exceeding 30% in various crops, including wheat, potatoes, and soybeans, causing significant financial strain on farmers and agribusinesses. Furthermore, the intricate interplay between changing climate patterns (Table 4) and the pathogen's distribution is increasingly evident, with climatic models projecting a widening geographical range for the pathogen in the coming decades (Badaluddin *et al.* 2018). The global movement of *R. solani* has been substantiated by rigorous molecular analyses (de França *et al.* 2015). Genetic studies employing DNA fingerprinting techniques have elucidated distinct genetic lineages within the pathogen's anastomosis groups (AGs), showing the pathogen's adaptability on a genetic level (Naqvi *et al.* 2024). This genetic diversity, coupled with mounting

Table 4. Regional crop vulnerabilities and key findings

Region	Climate	Host crops	Key findings
North America	temperate	wheat, soybean, potato	<ul style="list-style-type: none"> – high incidence in wheat – emerging in soybean crops – frequent outbreaks in potato
Europe	varied	sugar beet, rapeseed	<ul style="list-style-type: none"> – sugar beet vulnerability – rapeseed damage on the rise – impact on crop rotations
Asia	diverse	rice, cotton, vegetables	<ul style="list-style-type: none"> – rice paddies as a hotspot – cotton yield reduction – vegetable crop susceptibility
South America	tropical	coffee, sugarcane	<ul style="list-style-type: none"> – coffee plantations hit – sugarcane disease outbreak – impact on tropical crops
Africa	varying	maize, cassava	<ul style="list-style-type: none"> – maize production challenges – cassava root rot epidemic – emerging threats in Africa

evidence of AG-specific host preferences, underscores the complexity of the host-pathogen interactions that shape its geographical occurrence (Tables 5, 6, 7, 8, 9, 10). In response to this dynamic threat, multidisciplinary strategies have gained momentum (Das *et al.* 2014). Research on biological controls, such as beneficial soil microorganisms, reveals promising avenues for sustainable management. Concurrently, studies on the genetics of host resistance have unearthed valuable genomic markers that hold a potential role for the development of resilient crops in sustainable agricultural practices. Furthermore, climate projections portend further challenges in combating *R. solani*'s global expansion. Research on pathogen evolution, transmission dynamics, and host-pathogen interactions will be pivotal in proactive strategies for agricultural sustainability. The narrative of *R. solani*'s journey through changing landscapes and its genetic adaptations serves as a cautionary tale and a beacon

of opportunity, guiding agricultural stakeholders toward science-based solutions in a rapidly transforming world.

Molecular foreplay between rice and *Rhizoctonia solani*

To defend against pathogen attacks plants have developed intricate and interconnected signaling pathways. Most of the pathogen-responsive signaling pathways rely heavily on salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). *Rhizoctonia solani* tends to be thought of as a necrotrophic fungal disease, although it is possible that it also exhibits hemibiotrophic behavior on a suitable host. Kouzai *et al.* (2018) proposed the hemibiotrophic nature of *R. solani*. Resistance to

Table 5. Occurrence of *Rhizoctonia solani* and notable diseases in Indian states

States of India	Reported occurrence of <i>R. solani</i>	Host crops	Notable diseases
Andhra Pradesh (Lat. 12.5°N–19.5°N, Long. 77.5°E–84.5°E)	yes	rice, groundnut	sheath blight, damping-off
Assam (Lat. 24.5°N–28.5°N, Long. 89.5°E–96.5°E)	yes	rice, potato	sheath blight, black scurf
Bihar (Lat. 24.0°N–27.5°N, Long. 82.0°E–88.0°E)	yes	potato, cereals	black scurf, seedling damping-off
Gujarat (Lat. 20.0°N–24.5°N, Long. 68.5°E–74.0°E)	yes	groundnut, cotton	damping-off, root rot
Haryana (Lat. 27.0°N–30.5°N, Long. 74.0°E–77.5°E)	yes	wheat, potato	damping-off, black scurf
Karnataka (Lat. 11.5°N–18.5°N, Long. 74.0°E–78.5°E)	yes	rice, potato	sheath blight, black scurf
Kerala (Lat. 8.5°N–12.5°N, Long. 74.0°E–77.5°E)	yes	rice, vegetables	sheath blight, damping-off
Madhya Pradesh (Lat. 21.0°N–26.5°N, Long. 74.0°E–82.0°E)	yes	soybean, wheat	damping-off, stem cankers
Maharashtra (Lat. 15.5°N–22.0°N, Long. 72.5°E–81.5°E)	yes	cotton, sugarcane	damping-off, stem rot
Odisha (Lat. 17.5°N–22.5°N, Long. 81.0°E–87.5°E)	yes	rice, vegetables	sheath blight, damping-off
Punjab (Lat. 29.0°N–32.5°N, Long. 73.5°E–76.5°E)	yes	wheat, rice	root rot, sheath blight
Rajasthan (Lat. 23.5°N–30.0°N, Long. 69.5°E–78.5°E)	yes	mustard, pulses	damping-off, collar rot
Tamil Nadu (Lat. 8.0°N–13.5°N, Long. 76.0°E–80.5°E)	yes	rice, cotton	sheath blight, damping-off
Uttar Pradesh (Lat. 23.5°N–31.5°N, Long. 77.0°E–84.0°E)	yes	potato, wheat	black scurf, seedling damping-off
West Bengal (Lat. 21.5°N–27.0°N, Long. 85.5°E–89.5°E)	yes	rice, potato	sheath blight, black scurf

Table 6. Occurrence of *Rhizoctonia solani* and notable diseases in Japanese regions

Regions of Japan	Reported occurrence of <i>R. solani</i>	Crops affected	Notable diseases
Hokkaido (Latitude: 41.5°N - 45.5°N Longitude: 141.0°E - 145.5°E)	yes	potatoes, soybeans	black scurf, damping-off
Tohoku Region (Latitude: 37.0°N - 40.5°N Longitude: 139.0°E - 142.5°E)	yes	rice, soybeans, vegetables	sheath blight, seedling damping-off
Kanto Region (Latitude: 35.0°N - 36.5°N Longitude: 138.5°E - 141.0°E)	yes	rice, vegetables, Ornamental plants	sheath blight, damping-off
Chubu Region (Latitude: 34.0°N - 36.5°N Longitude: 136.0°E - 139.5°E)	yes	rice, potatoes, soybeans	seedling damping-off
Kansai Region (Latitude: 34.0°N - 35.5°N Longitude: 134.0°E - 136.0°E)	yes	rice, vegetables	sheath blight, root rot
Chugoku (Latitude: 34.0°N - 35.5°N Longitude: 132.5°E - 135.5°E)	yes	rice, vegetables	damping-off, collar rot
Shikoku: Latitude: 32.5°N - 34.0°N Longitude: 132.0°E - 134.5°E	yes	rice, vegetables	damping-off, collar rot
Kyushu Region (Latitude: 30.5°N - 33.5°N Longitude: 128.5°E - 131.5°E)	yes	rice, vegetables	sheath blight, stem rot

Table 7. Occurrence of *Rhizoctonia solani* and notable diseases in Indonesian regions

Province of Indonesia	Reported occurrence of <i>R. solani</i>	Crops affected	Notable diseases
Jakarta (Latitude: -6.2088 Longitude: 106.8456)	yes	rice, vegetables	sheath blight, damping-off
West Java (Latitude: -7.0909 Longitude: 107.6689)	yes	rice, corn, vegetables	sheath blight, seedling damping-off
Central Java (Latitude: -7.1500 Longitude: 110.1403)	yes	rice, sugarcane, vegetables	sheath blight, root rot
East Java (Latitude: -7.5361 Longitude: 112.7126)	yes	rice, vegetables	sheath blight, damping-off
Bali (Latitude: -8.4095 Longitude: 115.1889)	yes	rice, vegetables	sheath blight, collar rot
West Nusa Tenggara (Latitude: -8.6526 Longitude: 117.3616)	yes	rice, corn	sheath blight, stem rot
West Nusa Tenggara (Latitude: -8.5922 Longitude: 116.1186)	yes	rice, vegetables	sheath blight, damping-off
South Sulawesi (Latitude: -3.3199 Longitude: 119.9526)	yes	rice, corn, vegetables	sheath blight, seedling damping-off
Top of Form			

Table 8. Occurrence of *Rhizoctonia solani* and notable diseases in Pakistani regions

Province of Pakistan	Reported occurrence of <i>R. solani</i>	Crops affected	Notable diseases
Punjab (Latitude: 30.3753 Longitude: 69.3451)	yes	rice, wheat, sugarcane	sheath blight, root rot
Sindh (Latitude: 25.8943 Longitude: 68.5247)	yes	rice, cotton, vegetables	sheath blight, damping-off
Khyber Pakhtunkhwa (Latitude: 35.3191 Longitude: 72.4258)	yes	wheat, vegetables	seedling damping-off, root rot
Balochistan (Latitude: 27.4320 Longitude: 65.9041)	yes	rice, vegetables	sheath blight, stem rot
Gilgit-Baltistan (Latitude: 35.3191 Longitude: 75.5454)	yes	cereals, vegetables	damping-off, collar rot
Azad Kashmir (Latitude: 33.7491 Longitude: 74.3919)	yes	rice, vegetables	sheath blight, seedling damping-off
Islamabad Capital Territory (Latitude: 33.6844 Longitude: 73.0479) Top of Form	yes	vegetables, ornamental plants	damping-off, collar rot

Table 9. Occurrence of *Rhizoctonia solani* and notable diseases in regions of Bangladesh

Division of Bangladesh	Reported occurrence of <i>R. solani</i>	Crops affected	Notable diseases
Dhaka (Latitude: 23.8103 Longitude: 90.4125)	yes	rice, vegetables	sheath blight, damping-off
Chattogram (Latitude: 22.3569 Longitude: 91.7832)	yes	rice, jute, vegetables	sheath blight, collar rot
Rajshahi (Latitude: 24.3636 Longitude: 88.6241)	yes	rice, wheat, vegetables	sheath blight, root rot
Khulna (Latitude: 22.8456 Longitude: 89.5403)	yes	rice, sugarcane, vegetables	sheath blight, damping-off
Barishal (Latitude: 22.7029 Longitude: 90.3466)	yes	rice, vegetables	sheath blight, stem rot
Sylhet (Latitude: 24.8949 Longitude: 91.8687)	yes	rice, tea	sheath blight, seedling damping-off
Rangpur (Latitude: 25.7425 Longitude: 89.2750)	yes	rice, vegetables	sheath blight, seedling diseases
Mymensingh (Latitude: 24.7566 Longitude: 90.4069)	yes	rice, vegetables	sheath blight, damping-off

Table 10. Occurrence of *Rhizoctonia solani* and notable diseases in regions of Myanmar

Division/State of Myanmar	Reported occurrence of <i>R. solani</i>	Crops affected	Notable diseases
Yangon (Latitude: 16.8661 Longitude: 96.1951)	yes	rice, vegetables	sheath blight, damping-off
Mandalay (Latitude: 21.9588 Longitude: 96.0891)	yes	rice, pulses, vegetables	sheath blight, seedling damping-off
Naypyidaw (Latitude: 19.7633 Longitude: 96.0785)	yes	rice, vegetables	sheath blight, root rot
Sagaing (Latitude: 21.8802 Longitude: 95.9794)	yes	rice, pulses, vegetables	sheath blight, collar rot
Tanintharyi (Latitude: 12.4371 Longitude: 98.5989)	yes	rice, oilseeds	sheath blight, stem rot
Bago (Latitude: 17.3350 Longitude: 96.4795)	yes	rice, vegetables	sheath blight, damping-off
Ayeyarwady (Latitude: 17.3118 Longitude: 95.2122)	yes	rice, sugarcane	sheath blight, damping-off
Magway (Latitude: 20.1604 Longitude: 94.9170)	yes	rice, pulses	sheath blight, seedling diseases
Top of Form			

biotrophic infections develops because of signaling mediated by salicylic acid (SA), whereas resistance to necrotrophic pathogens develops because of signaling mediated by jasmonic acid (JA). In order to successfully infiltrate and infect rice plants the pathogen *R. solani* uses a number of different tactics. In response rice plants switch on many signaling pathways and produce antimicrobial substances to fend off this infection. At a molecular level we can now explore the interaction from three distinct angles: the pathogen perspective, the host plant perspective and the pathogen and host chemical conflict.

Pathogen effector

While performing the host defense mechanism *R. solani* AG1-1A employs several tactics and effector molecules to improve its colonization of the host plant (Lo Presti *et al.* 2015). The cytochrome C oxidase assembly protein CtaG/Cox11 domain, the glycosyltransferase GT family 2 domain and the peptidase inhibitor 19 domain are a few examples of putative secreted effectors that have been found and validated by researchers. These effectors have been set to trigger crop

defense reactions that result in cell death in the host. Several potential candidate effectors were predicted in a recent genomic analysis of two highly pathogenic Indian strains of *R. solani* AG1-1A, including histone acetyltransferase, histone deacetylase inhibitor, MDR transporter, O antigen biosynthesis protein, O-methyl sterigmatocystin oxidoreductase, polygalacturonase, and pectin lyase. When infecting various hosts, including rice, they discovered a total of 44 potential effector transcripts that were elevated in *R. solani* AG1-1A (Xia *et al.* 2017). Notably, the pathogen was found to upregulate the expression of two putative effectors, AG1A_08303 (the peroxidase) and AG11A03245 (a protein kinase domain) in the pathogen when it infected rice (Xia *et al.* 2017). Oxalate is a virulence component secreted by the fungus *R. solani* AG1-1A. Isolates with higher levels of virulence secrete more oxalate. It has been demonstrated that oxalate and oxalate oxidase are involved in *R. solani* pathogenesis and rice plant defense, respectively. Transgenic rice plants overexpressing oxalate oxidase are beneficial in improving resistance against the pathogen *R. solani* genes that are stimulated in rice plants during infection and post penetration phases which have been discovered using RNA sequencing analysis (Ghosh *et al.* 2018). In the investigation a few potential effector genes were also

discovered to be up regulated. Two polygalacturonase genes (RsPG3 and RsPG4) were discovered to have been cloned from *R. solani* in the investigation. These genes have been demonstrated to cause rice sheath blight and release reducing sugar, demonstrating their significance as pathogen virulence factor1. Recent research has also revealed that the polygalacturonase gene (AG1IA_04727) is crucial for pathogenesis of *R. solani* (Rao *et al.* 2019). The genetic transformation of *R. solani* differs from that of many other fungal pathogens because it is polynucleate and non-transformable. Therefore, the discovery of virulence genes in *R. solani* remains evasive due to the difficulties in applying genetic approaches. Interestingly, *R. solani* exploits an elegant deception to circumvent the plant's built-in defenses. *R. solani* uses an α -1,3 glucan layer to camouflage the chitin in the cell wall so that they do not trigger PRR's in the host during infection. As such, the introduction of transgenic expression of α -1,3-glucanase in rice plants that would mask and expose the fungal chitin PAMP might be beneficial in activating the plant's innate immunity.

Secondary messenger

However, unlike most other fungi that are easily genetically mutated, *R. solani* has numerous nuclei and for this reason, it is difficult to alter its genes. It is thus hard to know which of these genes becomes dangerous at the same time. However, researchers have discovered something else. It has an underhand trick through which it can beat a plant's defenses. The plant utilizes a special substance known as α -1, 3-glucan to camouflage its chitin; usually this means danger for the plant. The fungus is not recognized by the plant's defense mechanism. Therefore, it would be smart to introduce α -1, 3-glucanase in rice. The enzyme can split the α -1, 3-glucan sheath unveiling fungal chitin that activates plant defense mechanisms.

Application of omics technologies to understand pathogenesis

There are different techniques such as genomics, transcriptomics, and proteomics. Such methods allow researchers to grasp how various molecules are able to act as they do while being involved in biological processes or diseases. With the development of sequencing technologies, there has been an upsurge in omics techniques like genomics, for example, and RNA sequencing which has made it easier to study these particular interactions.

For instance, the first draft of the *R. solani* AG1-1A genome contains many genes, such as those linked to the interaction between the fungus and its host which helps to identify potential effector genes. A similar study was carried out by Nadarajah *et al.* (2017) on a Malaysian isolate of *R. solani* found somewhat smaller genome. The study of gene expression and genetic regulation in *R. solani* spp. on different plants provided insight into the genes involved in pathogenicity. For instance, in the work carried out on rice sheath blight resistance, researchers studied genomes of various rice lines and discovered potential genes that might play a role in resisting the disease. In the same vein, Ghosh *et al.* (2018), using samples of *R. solani* taken from infected sheaths, identified potential pathogenesis related genes.

Furthermore, according to Xia *et al.* (2017), alternative splicing of *R. solani* genes is crucial in its invasiveness of rice, soybean, and corn plants. The researchers found that there were discrepancies among genes while interaction was happening between *R. solani* and other crops. These findings provide an explanation as to why *R. solani* is able to infest many crops. In addition, researchers found small RNA molecules in the hyphae of *R. solani* some of which might be related to their pathogenicity. Findings on how *R. solani* induces disease are important in their own right. For those interested in exploring these findings, there is a user-friendly database called RS1ADB developed for *R. solani* AG1-1A, which can be accessed here: <http://genedenovoweb.ticp.net:81/rsia/index.php> (Chen *et al.* 2016).

An angle from the host plant

Results of several studies suggest that there are different signaling pathways when rice plants resist sheath blight disease caused by *R. solani*. For instance, jasmonic acid (JA) signaling pathway, together with the activity of lipoxygenase (LOX), were seen to be the main enzymes involved in the production of JA. This observation was confirmed through an example of a JA-deficient rice mutant called 'Hebiba', whose susceptibility to sheath blight disease was found. Moreover, it has been reported that the expression of LOX genes, responsible for JA synthesis, was increased in rice plants infected with *R. solani* (Sayari *et al.* 2014). In addition, the above study found that, the over expression of WRKY30 and WRKY80 genes in transgenic rice plants led to increased sensitivity to sheath blight by activating gene pathways linked to jasmonate biosynthesis. Ghosh *et al.* (2017) as well as Zhang *et al.* (2017) emphasized the role of JA and phenylpropanoid metabolism in resistance against brown rust. In addition,

ethylene seems to be involved in resistance to *R. solani*. Transgenic rice plants overexpressing an ethylene biosynthetic gene demonstrated higher levels of expression for PR1b and PR5 genes, thus increasing resistance against *R. solani*. Some of the effects may also be ascribed to the poisonous waste product cyanide that is formed when ethylene is synthesized. In contrast, ethylene-insensitive mutants showed higher susceptibility to *R. solani*. Overexpression of ERFs in *Medicago* was associated with resistance to the pathogen. In contrast, high levels of PR1b and PBZ1 genes expressed in rice plants infected with sheath blight disease indicated the involvement of the SA-mediated pathway. The PR5 gene in rice plants was induced on infection with *R. solani*. Additionally, enhanced expression of multiple PR genes (PR-3, PR-5, PR-9, PR-10, PR-12, and PR-13) and the PAL gene at varying stages of *R. solani* infection in rice confirmed activation of system PR genes like RC24 and PAL which were over-expressed as a result of sheath blight infection of transgenic rice plants, and showed an engagement of the SAR pathway. Additionally, the momilactone "A" biosynthesis pathway is activated, and PR proteins like β -1, 3-glucanases and exochitinases are induced. In conclusion, these reports have demonstrated that several signaling cascades such as JA, LOX, ethylene, SA, and SAR are activated during the defense mechanism of rice against *R. solani* attack. This indicates the complexity of the plant's defense system against the aforesaid pathway. Karmakar *et al.* (2017, 2019) demonstrated that external application of salicylic acid (SA) enhances resistance against the sheath blight pathogen. Evidence suggests that there is an intrinsic pathway similar to the NPR1 pathway of *Arabidopsis* (Chern *et al.* 2014). For instance, Kouzai *et al.* (2018) found that pre-treating with SA could make wheat resistant to sheath blight. Moreover, NahG-transformed rice lines deficient in SA had sheath blight more frequently than the wild type, confirming the relevance of SA based defense mechanisms (Kouzai *et al.* 2018). Results indicate that SA-mediated host defense plays a crucial role in host-pathogen interaction in rice-*R. solani* pathosystem. In fact, Yuan *et al.* (2018) showed that several other gibberellin (GA) receptor kinases such as GA receptor GID1L2 (Os09g28690.1) were upregulated during resistance.

Secondary messenger

However, it remains unclear whether any of the known secondary messenger signaling molecules directly participate in the interaction between rice and *R. solani*. Recently, a study showed that RGB1, the rice Gb subunit (Swain *et al.* 2019) becomes induced when

rice suffers from sheath blight (ShB) but RGG1 remains unaffected. The authors of this study also found improved sheath blight tolerance in transgenic rice plants containing high levels of RGB1. For instance, some comparative transcriptome and proteomic studies revealed that secondary messengers are involved in rice's immunity against *R. solani* (Zhang *et al.* 2017; Karmakar *et al.* 2019). Specifically, some notable genes in the calcium/calmodulin signaling pathway, including OsCPK10, OsCML16, OsCML26, OsCML27, OsCML31, and OsCam1-1, showed that differential WAKs are involved in pathogen-responsive signaling associated with different types of pectin present on/in plant cells. They bind various forms of pectin, including that resulting from pathogen-induced cell wall degradation. Six different WAK proteins were found upregulated on resistance in a resistant rice cultivar (Yuan *et al.* 2018) in response to *R. solani* infection. According to Al-Bader *et al.* (2019), in a preliminary study, the full-length protein product of OsWAK91 turned out to be involved in resistance to sheath blight. Karmakar *et al.* (2019) showed through a proteomic analysis that there was an increase in the expression of the 14-3-3 GF14f protein in infected transgenic rice plants. The 14-3-3 proteins, however, are central players in many signaling pathways, serving as docking protein substrates that bind phosphoproteins. Moreover, another significant secondary messenger, MAP kinase 6 (MPK6), has been widely detected in transgenic rice plants upon ShB disease infection (Karmakar *et al.* 2019).

Metabolic alternation in the host

An important dimension of such an interaction study is to investigate the metabolic profiling of diverse rice genotypes and its allied changes under the rice – *R. solani* pathosystem. Several researchers have delved into the effects of metabolic changes in a rice plant's reaction to *R. solani* infection. Most studies have centered on carbohydrate metabolism. For example, it was shown in one research that enzymes of glycolytic and pentose phosphate paths are more active in resistant rice lines than in susceptible ones when they respond to *R. solani* infection. In response to rice plant infection by *R. solani* the glycolytic pathway, the oxidative pentose phosphate pathway (OPPP), secondary metabolism, and the tricarboxylic acid cycle are active. Follow-up studies by the same research team indicated how glycolytic regulation is involved in response to *R. solani* infection. The two key regulatory enzymes, including pyrophosphate-fructose-6-phosphate phosphotransferase and 6-phosphofructokinase in the

glycolytic pathway, have been reported to be activated by the pathogen. Furthermore, higher amounts of glycolytic metabolites, activities of glycolytic enzymes and those of transketolase (TK), phenylalanine ammonia-lyase (PAL) and peroxidase were found in resistance. The results demonstrated that *R. solani*-infected rice plants had an upregulated glycolysis, leading to an enhanced synthesis of glyceraldehyde-3-phosphate (GAP), which possibly can be converted to erythrose-4. This can lead to increased lignin formation as an initial defense mechanism against *R. solani*. Likewise, the metabolite profiling study resulted in an accumulation of glycolysis and TCA cycle intermediates (Ghosh *et al.* 2017). Suharti *et al.* (2017) provided evidence that canavanine, a non-protein amino acid might be involved as a defense compound response of rice plants towards *R. solani* infection. Moreover, rice plants infected by *R. solani* had increased levels of proteinogenic amino among others as reported by Ghosh *et al.* (2017) and Suharti *et al.* (2016). The glycolytic enzyme GAPDH was induced in resistant rice lines upon inoculation with *R. solani* in a proteomic approach. In a similar study, the induction of enzyme 3- β -hydroxysteroid dehydrogenase/isomerase (3- β -HSD) revealed a defense role of steroid.

Omics studies to understand host defense

Omics technologies are very appealing in providing a comprehensive draft on pathogenic response under host-pathogen interactions through exploring metabolic changes and transcriptome responses (Zhang *et al.* 2017). Comparative transcriptomic analysis conceptualizes and frames differentially expressed genes (DEGs) involving ShB-tolerance rice cultivars (Teqing). Susceptible cultivar (Lemont) revealed a total of 4806 DEGs (Ghosh *et al.* 2017). In their recent research, Karmakar *et al.* (2019) examined proteometabolic changes in AtNPRI-transgenic rice lines during ShB infection. Karmakar *et al.* (2019) identified a total of 38 differentially expressed proteins and 40 differentially accumulated metabolites by comparing the proteome and metabolome of rice lines before and after ShB infection. Using both proteomic and metabolomic profiles, during *R. solani* infestation, the plant mainly alters its response associated with energy and carbon-containing compound metabolism (Karmakar *et al.* 2019). The same was applied in a metabolomics study conducted by Suharti *et al.* (2016). Furthermore, there were 23 probable rice miRNA candidates which can participate in the resistance mechanisms versus *R. solani* invasion.

The chemical battle between rice and *Rhizoctonia solani*

The chemical battle between host and pathogen determines which one is dominant. In response to perceived infection, plants mount defense responses that lead to the synthesis of defense related compounds such as phytoalexin products of secondary metabolism. It was seen that certain molecular components, for instance, bZIP transcription factor TGAP1, signaling kinases viz. MKK4, MPK3 and MPK6 are activated upon attack of chitin oligosaccharide (Suharti *et al.* 2016). Chlorogenic acid secondary metabolites increase more in tolerant rice cultivars than in susceptible rice cultivars. Similarly, Sakuran-tatin, a flavonoid phytoalexin was found to be antifungal to *R. solani* as identified by Park *et al.* (2014). It can also be stressed that the fungus employs various ways of detoxifying phytoalexins. For instance, *R. solani* converts the cruciferous phytoalexin camalexin into a less dangerous compound. Furthermore, Katsumata *et al.* (2018) demonstrated the degradation of sakuranetin by *R. solani* to produce less toxic compounds like sakuranetin-4'-O- β -d-xylopy. Conversely, the pathogen *R. solani* deploys host-specific RS toxin as one of its weapons to counteract rice defense mechanisms. RS-toxin composed of glucose, mannose, N-acetylgalactosamine, and N-acetylglucosamine, is secreted in higher quantities by highly virulent isolates than by less virulent ones. The sensitivity of rice plants to this toxin has been linked to susceptibility to sheath blight disease. Interestingly, the enzyme α -glucosidase from *Trichoderma viride* could degrade the RS toxin, suggesting the possible existence of a α -glucosidase-mediated resistance mechanism in partially resistant rice varieties. Additionally, osmotin, a cysteine-rich cytotoxic PR-5 protein, exhibits significant antifungal activity (Hakim *et al.* 2018). In response to sheath blight infection, a resistant rice variety displays elevated expression of the rice osmotin gene, OSM1, indicating that the production of osmotin protein may be a component of rice's chemical defense arsenal against the pathogen (Xue *et al.* 2016).

Quantitative trait loci (QTL) based resistance

Similar to other traits, sheath blight resistance in rice is considered to be a quantitative trait that is governed by cumulative effects of numerous genes (Zuo *et al.* 2014). Therefore, this would increase the speed involved in identifying, mapping, validating and characterization

processes for Quantitative trait loci (QTLs), which are crucial for map-based or positional cloning of key resistance genes. It could subsequently come in handy and result in production of rice that is resistant to sheath blight. A QTL refers to combinations of allelic variances at a particular location in a chromosome that has a causal relationship with any quantitative trait found in a population having genetic variants. Several QTLs for sheath blight resistance have been observed in all 12 rice genomic chromosomes, using various map populations and molecular markers since 1995. Before this study, two other studies had examined the issue of identifying ShB QTLs. Major and minor QTLs have been physically mapped to different rice chromosomes along with putative candidate genes. This has involved multiple tests on various molecular markers such as RFLP and SSR in mapping ShB qtl. Such studies also employed STS, indels and CAPS markers. For instance, morphological markers were some of the tools in mapping studies with a RIL population originating from Teqing x Lemont. This review stresses the changes from segmenting of F2 derived mapping populations to other populations such as RIP and DHP. Nevertheless, it must be noted that inbred lines derived from indica subspecies are more resistant to sheath blight than to those from japonica subspecies. Indica cultivars served as donor parents in 81.5% of the 22 studies. The vast majority of these studies involved mapping populations from inter-subspecific crosses, such as 'Indica' x 'Japonica', for identification of QTLs conferring resistance on a wide variety of genotypes. On the other hand, relations can offer useful resistant genes of sheath blight. One study revealed identification of the QTLs for the sheath blight between two varieties of wheat, which are *O. triticum*.

Major quantitative trait locis and underlying candidate gene

A second QTL qShB9-2 also plays a crucial role in SB resistance. Most importantly, the major QTL qShB9-2 has defense related genes and participates in defense mechanisms. Similar findings were observed by Yadav *et al.* (2015) with the co-existence of β -1, 3-glucanase of the defense family in the qShB9-2 loci. There are ten candidate genes at the qShB9-2 locus in three resistant rice lines – Jasmine 85, Teqing and MCR010277. More recently, Al-Bader *et al.* (2019) found four candidate genes which showed differential expression at a region near qShB9-2 between susceptible and resistant genotype. The presence of this resistance phenomenon is associated with the alteration of the Owsaka

008 gene where the changes involved are caused by the substitution of the C \rightarrow T mutation in the OsWAK 91 sequence. Zuo *et al.* (2014) found that this physical region of qSB9-TQ was mapped to a 146-Kb interval demarcated by the markers, CY85 on one end, and Y86 on the other. For instance, if we have a good quality reference genome sequence (IRGS, 2005) and can precisely map out the QTLs, this would give us an idea of the genes behind those loci, where 12 candidates were identified for qSB9. Furthermore, another significant QTL called qSBR11-1 originated from the rice variety, Tetep, with an average level of resistance and was precisely mapped at 0.85 Mb in the long arm of chromosome 11 marked by K39.

Surprisingly for that same chromosome 11, another QTL known as qSB11-LE originated from the susceptible Lemont cultivar. A total of 12 putative defense related genes within the qSB11-LE region have been suggested. The 12 genes were thought to involve in an order of preference a lipase like gene and two precursors of receptor-like protein kinase 5 for qSB11-LE. A total 154 genes were expected to reside at this region referred to as qSBR11-1. Of these, 26 genes had been specifically disease responsive. Eleven members of the class III Chitinase family, well known as antifungal genes were found among the disease's responsive genes. In addition, a chitinase gene (LOC_Os11g47510), present in the qSBR11-1 territory was manifested in ShB susceptible variety Taipei 309 with varying degrees of tolerance as confirmed by Richa *et al.* (2017). Unfortunately, the sheath blight QTLs have not yet yielded any new candidate genes amenable for breeding or genetic engineering.

Minor quantitative trait locis are not less important

Most of the ShB QTLs discovered with low LOD values add little to the phenotypic variation. They vary among different environments, years, and mapping populations, and are often classified as minor or rare QTLs. However, these minor QTLs can also contribute to changes in characters at different levels (Chen *et al.* 2014) but should not be downplayed. For instance, some genes related to minor QTLs like heading date in rice have been isolated, identified and their characters described. Nevertheless, for minor ShB QTLs, studies are still limited, while currently there is no identification of any candidate genes. Hence, it is important not to neglect small QTLs in ShB since they might entail resistance genes (Zeng *et al.* 2014). Ignoring these low effect QTLs could impede the identification of genes with increased resistance potential.

Relationship of resistance trait with morphological trait

Several QTL studies established an association between PH and HD with sheath blight (ShB) resistance. However, in contrast to this observation, others have suggested that there is no correlation between ShB resistance and other phenotypic characters. As plant height increases, the results of the ShB rating system are highly dependent on the lesion height of symptoms related to the plant's height. Changes in the heading date (either early or late maturity) also may affect the micro-environment of the plant causing favorable or unfavorable conditions for pathogen growth. Perhaps, it was this association that made ShBresistant-PH and ShBresistant-HD.

Zeng *et al.* (2014) also revealed an overlap between PH-QTLs and several ShB QTLs. These authors advised against targeting these ShB QTLs for utilization due to the fact that a number of PH-QTLs are mistakenly considered as ShB QTLs and have pleiotropic effects. Besides, Hossain *et al.* (2016) reported that two more morphological traits - plant density and leaf inclination, were closely associated with resistance against stem rot. The impact of plant compactness on the microclimate within the canopy is important as it may cause alterations of relative humidity and temperature. Such changes are vital for the growth of pathogens and sheath blight incidents.

Quantitative trait loci introgression and varietal development

In addition, it would be necessary to assess the performance of ShB QTLs as well for their incorporation into improving sheath blight resistance in rice. This review summarizes relevant findings. Furthermore, transfer of the QTL-qSBR11-1 from the donor parent Tetep to 'Improved Pusa Basmati 1' using marker assisted selection resulted in increased resistance. The joint impact of two QTLs, qSB9-2 and qSB12-1 (Teqing variant), produces a greater outcome than the sum of their separate influences on the overall resistance levels.

Similarly, the pyramid-effect resulting from the synergistic action of three QTLs (qSB7Tq, qSB9Tq, and qSB11Le) has been found on the resistance against ShB disease. Surprisingly, QTL-qSB-9Tq (derived from Teqing) introduced into nine distinct japonica varieties of varied ecological regions decreased ShB scores to 0.5–1.3. Notably, three rice lines, TIL (Teqing-into-Lemont) backcross introgression lines.

Development of blast-resistant rice cultivars for small-holder farmers using molecular markers was implemented through this way. Four out of five year-location combinations showed significant improvement in ShB resistance of these TIL lines. Two-pyramid QTL analysis for *Pyricularia oryzae* resistance in japonica rice, showed an average of 14% yield reduction under high blast conditions using susceptible japonica varieties.

Association mapping

The resistant locations have been identified through an alternative method called association mapping which is faster and more accurate than the traditional method. ShB-resistant locus identification using association mapping is different from conventional breeding between various parents. One hundred fifty-five markers were spread across the whole rice genome in 217 sub core rice and 10 marker regions were found showing correlation with ShB resistance. Other research found a relation between ShB resistance, 17 marker locations and three marker locations. However, it is notable that in the area of association mapping for linkage with trait-associated regions, there has been limited research despite having high quality genome sequences, lowered high-throughput sequencing costs and a vast rice germplasm. This high-resolution method must be applied comprehensively and in an efficient manner if one wants to fully understand the genetic basis of such a trait as sheath blight.

Transgenic approach

One of the best strategies for sustainable agriculture is producing a resistant rice variety either by genetically modifying it or by traditional plant breeding beyond the practice of crop rotation and IPM. Independently, this is about a 7.9–8% increase in rice productivity when using Bt generated resistance in host plants against ShB. Transgenic plant technology is therefore emerging as a preferred mechanism for manifestation of certain desirable features. Conventional breeding for resistance to *Rhizoctonia solani* kuhn has failed due to the non-existence of naturally resistant rice germplasm. Recently, many candidate genes that confer resistance to fungal infections have been identified, isolated, and characterized from both rice and different crop plants. Using available genetical engineering techniques that can be applicable to most rice varieties it is possible to test the influence of the expression of key defensive genes such as pathogenetic related

genes that show antifungal ability. Transgenics plant by introducing ethylene production gene through genetic knock in (by CRISPR-Cas 9) helps to resist two severe phytopathogens- *Magnaporthe oryzae* and *Rhizoctonia solani* (Helliwell *et al.* 2013).

Some plant-origin antifungal genes, antimicrobial genes, defense response-related genes and pathogenesis inhibitory genes have been incorporated into newly created rice lines by means of transformation techniques, which include the types of genes involved, approaches adopted for gene overexpression, and the efficacy of these genes to combat SB.

Pathogenesis related gene

The pathogenesis-related (PR) genes found in rice are crucial components of its defense system against pathogens, playing a significant role in the interaction between rice and pathogen. (Sayari *et al.* 2014). A widely used approach for the development of new rice transgenic varieties is the utilization of the Glycoside hydrolase protein that may degrade or break the fungal cell wall and membrane (Table 11). Chitinase for β -1, 4-glycosidic linkages in chitin and β -1,3-glucanase for β -1,3-linkages in the glucan polymer have been obtained from different sources. The first report, concerning transgenic expression of the class I Chitinase gene (*chi11*), in rice plants with respect to enhancement of resistance against sheath blight, showed that such transgenic rice exhibited positive correlation between chitinase expression and the level of plant resistance. OsPGIP1 mediated gene transformation and resistance was analyzed against rice sheath blight (Wang *et al.* 2015). These studies showed that transgenic rice plants expressing more *chi11* demonstrated higher tolerance to sheath blight, as do rice plants transcribing RC7, plant-derived CHIT1 from *Momordica charanta*, and fungal *cht42* from *Trichoderma*. Although β -1,3-glucanase is not an isolated gene per se nevertheless it can be used in conjunction with defense genes discussed earlier. Proteins exist such as *pr-5*, *tlp*, or *osmotins* that damage the fungal membranes. Some of the rice PR-5 genes like TLP-D-34 (TLP-P sub family) and OSM1 from another sub family (TLP-PA) have been expressed in order to boost resistance towards sheath blight (Xue *et al.* 2016).

Anti-microbial peptides (AMP)

AMPs, composed of short peptides with a high concentration of either cysteine or glycine, support the

innate host defense system. They are present in both plants and animals. Thionine, defensin, and lipid transfer protein are among famous plant AMPs that create pores in membrane. Subsequently, they cause leakage of ions/metabolites and the death of cells. Expressing plant AMPs of different origins in rice plants significantly improved their resistance to *R. solani*. In rice, enhanced ShB resistance has already been reported due to the ectopic expression of the AMP1 gene from *Dahlia merckii*, the AFP2 gene from *Raphanus sativus*, and, for example, Snakin-1 as a member of an AMP group showed resistance against *R. solani* when expressed in potato mutants. Some AMPs such as stomoxyn ZH1, purothionin, cecropin B, D4E1, and *phor21* are capable of inhibiting *R. solani* AG-1A in vitro (Elhag *et al.* 2017). It would be interesting to follow up with a study involving transgenic expression of genes coding for snakin-1 and other AMPs that would boost ShB resistance.

Signaling genes

When a plant is attacked and senses the presence of a pathogen it activates signal molecules which induce the production of defense proteins. As a result, upstream master signaling genes and transcription factors are activated as part of preventive measures against pathogens appear. An important regulator of the SAR pathway in Arabidopsis, which is mediated by SA, is NPR1. The introduction of the *BjNPR1* gene from *Brassica juncea* into rice has resulted in increased levels of resistance towards sheath blight of rice. *AtNPR1* has been competent in hardening rice against the disease by acting upon a few downstream protective genes (Karmakar *et al.* 2017). Excessive expression of WRKY30 or WRKY80 transcription factors activated either JA or JA + ET pathways, thus conferring more tolerance to ShB. Similarly, a transgenic plant with the ACS2 (an enzyme involved in synthesis of ethylene's signaling molecule) demonstrated resistance to *R. solani*.

Genes which act against pathogen effectors

Fungi secrete virulence factors or effectors during their infection, whereas plants attempt to degrade them upon recognition. It has been demonstrated that over expression of oxalate oxidase 4 (Molla *et al.* 2013) and oxalate decarboxylase (Qi *et al.* 2017), which can degrade the virulence factor oxalate, improved toler-

Table 11. Genetically modified rice designed to resist the sheath blight pathogen *Rhizoctonia solani*

Rice cultivar	Transformation method	Promoter used	Gene origin	Comments	References
Chinsurah Boro II	protoplast	CaMV35S	chi11 Rice	a class 1 chitinase a PR3 protein	Lin <i>et al.</i> (1995)
Chinsurah Boro II, IR72' and IR51500	protoplast and biolistic	CaMV35S	Tlp-D34 Rice	rice thaumatin-like protein-a PR5 protein	Datta <i>et al.</i> (1999)
Basmati 122, Tulsi and Vaidehi	agrobacterium mediated	CaMV35S	chi11 Rice	a class 1 chitinase	Datta <i>et al.</i> (2000)
IR72, IR64, IR68899B, MH63 and Chinsurah Boro II	biolistic	CaMV35S	RC7 Rice	class 1 chitinase	Datta <i>et al.</i> (2001)
M202	biolistic	maize ubiquitin	pinA pinB Wheat Puroindoline-antimicrobial peptides		Krishnamurthy <i>et al.</i> (2001)
Swarna	biolistic to anther-derived calli and embryo	CaMV35S	chi11 Rice	chitinase	Baisakh <i>et al.</i> (2001)
IR72	pyramiding of transgenes using marker-assisted selection	CaMV35S for chi11	chi11, xa21 and cry gene Rice	rice chitinase, receptor kinase-like protein and BT toxin protein	Datta <i>et al.</i> (2002)
Kenfong	biolistic	rice rbcS promoter for MOD1 and act1 promoter for RCH10	MOD1 and RCH10 Maize and rice	maize ribosome-inactivating protein and basic rice chitinase	Kim <i>et al.</i> (2003)
Pusa Basmati 1	agrobacterium mediated	maize ubiquitin	chi11 Rice	chitinase	Kumar <i>et al.</i> (2003); Sridevi <i>et al.</i> (2003)
Ishikari-shiroge	agrobacterium mediated	Act1	ech42, nag70, and gluc78 Trichoderma atroviride	endochitinase, exochitinase, and exo-1,3-b-glucanase	Liu <i>et al.</i> (2004)
ADT38, ASD16, IR50, and Taipei 309	biolistic	maize ubiquitin	tlp and chi11 Rice	rice thaumatin-like protein and chitinase	Kalpana <i>et al.</i> (2006)
Pusa Basmati 1	agrobacterium mediated	PAL promoter and ubiquitin	Ace-AMP1 Allium cepa	a nonspecific lipid transfer protein with antimicrobial properties	Patkar and Chattoo (2006)
Pusa Basmati 1, Co43, white Ponni, and ADT38	agrobacterium mediated	maize ubiquitin	RC7 Rice	chitinase	Nandakumar <i>et al.</i> (2007)
ASD16, ADT38, IR72, IR64, and White Ponni	biolistic	maize ubiquitin for tlp and chi11. Native promoter for xa21	tlp, chi11, and xa21 Rice	rice thaumatin-like protein, chitinase, and serine-threonine kinase	Maruthasalam <i>et al.</i> (2007)
Pusa Basmati 1	agrobacterium mediated	maize ubiquitin for chi11 and CaMV35S for glucanase	chi11 and b-1,3-glucanase Rice and tobacco	rice chitinase and tobacco b-1,3-glucanase	Sridevi <i>et al.</i> (2008)
Pusa Basmati 1	agrobacterium mediated	maize ubiquitin	chi11 Rice	chitinase	Sripriya <i>et al.</i> (2008)
Pusa Basmati 2	agrobacterium mediated	maize ubiquitin	Dm-AMP1 Dahlia merckii	defensin protein	Jha <i>et al.</i> (2009)
JinHui 35	agrobacterium mediated	maize ubiquitin	1 McCHIT1 Momordica charantia	a class 1 secretory endochitinase	Li <i>et al.</i> (2009)
Pusa Basmati 1	agrobacterium mediated	CaMV35S	cht42 <i>Trichoderma virens</i>	endochitinase	Shah <i>et al.</i> (2009)

Table 11. Genetically modified rice designed to resist the sheath blight pathogen *Rhizoctonia solani* – continued

Rice cultivar	Transformation method	Promoter used	Gene origin	Comments	References
Pusa Basmati 1	agrobacterium mediated	maize ubiquitin	RS-AFP2	<i>Raphanus sativus</i> plant defense protein	Jha and Chattoo (2010)
Pusa Basmati 1	agrobacterium mediated	maize ubiquitin	chi11 and CaMV35S	rice and tobacco chitinase and osmotin	Shah <i>et al.</i> (2009)
Xiushui 11	agrobacterium mediated	maize ubiquitin	OsWRKY30	rice transcription factor gene	Peng <i>et al.</i> (2012)
Kitaake	agrobacterium mediated	–	PBZ1	rice 1-Amino cyclopropane-1-carboxylic acid synthase	Helliwell <i>et al.</i> (2013)
Pusa Sugandhi-2	biolistic	rice PD54O-544	Osoxo4	rice oxalate oxidase	Molla <i>et al.</i> (2013)
Chaitanya and Samba Mahsuri	agrobacterium mediated	CaMV35S	BjNPR1	<i>Brassica juncea</i> nonexpressor of pathogenesis-related gene 1	Sadumpati <i>et al.</i> (2013)
Taipei 309	agrobacterium mediated	CaMV35S	RCH10 and AGLU1	basic chitinase and b-1,3-glucanase	Mao <i>et al.</i> (2014)
Zhonghua 11	agrobacterium mediated	CaMV35S	OsPGIP1	rice polygalacturonase-inhibiting proteins	Wang <i>et al.</i> (2015)
Pusa Sugandhi-2	biolistic	rice PD54O-544	AtNPR1	<i>Arabidopsis thaliana</i> non expressor of pathogenesis-related gene 1	Molla <i>et al.</i> (2016)
Xiushui 11	agrobacterium mediated	maize ubiquitin	OsWRKY80	rice transcription factor	Peng <i>et al.</i> (2016)
BR-29	agrobacterium mediated	rice PD54O-544 and maize PEPC	OsOXO4 and OsCHI11	rice oxalate oxidase 4 and rice chitinase 11	Karmakar <i>et al.</i> (2016)
Xudao 3	agrobacterium mediated	maize ubiquitin	OsOSM1	rice osmotin	Xue <i>et al.</i> (2016)
Jaldi-13	agrobacterium mediated	rice PD54O-544 and maize PEPC	AtNPR1 and OsCHI11	<i>Arabidopsis thaliana</i> and rice nonexpressor of pathogenesis-related gene 1 and rice chitinase 11	Karmakar <i>et al.</i> (2017)
Taipei 309 (TP-309)	biolistic	CaMV35S	chitinase	rice chitinase	Richa <i>et al.</i> (2017)
Nipponbare	agrobacterium mediated	CaMV35S	bacisubin <i>Bacillus subtilis</i> strain BS-916	oxalate decarboxylase	Qi <i>et al.</i> (2017)
Zhonghua 11	agrobacterium mediated	maize ubiquitin 1 promoter	OsASR2	rice abscisic acid, stress and ripening 2 protein	Li <i>et al.</i> (2018)
Nipponbare	agrobacterium mediated	maize ubiquitin 1 promoter	OsBSR2	rice cytochrome P450 protein (CYP78A family)	Maeda <i>et al.</i> (2019)

ance to the ShB pathogen. Notably several research revealed that the oxalate oxidase-mediated degradation produced H₂O₂, which may subsequently activate the plant's defense system. Similarly, ShB tolerance resulted from the overexpression of OsPGIP (polygalacturonase-inhibiting protein), which is able to inhibit the pectin-degrading enzyme polygalacturonase. These studies highlight that the degradation or inhibition of fungal virulence factors or cell wall-degrading enzymes represents an effective strategy to hinder pathogen progression.

Pyramiding of genes

It should therefore be noted that focusing on a single defense-related protein expression for fortifying the resistance as the last resort could be inappropriate. However, a broad range of research studies have been done on defensive gene expressions. For instance, there are several combinations like maize ribosomes inactivating protein gene MOD1 with RCH10, and rice chitinase (chi11) and thaumatin-like protein.

Comparatively, the power of a twin gene block outperforms the single gene block against ShB (Karmakar *et al.* 2017). The study further involved the analysis of three other genes belonging to the glycosidic hydrolysis category, namely ech 42 (endochitinase), nac 70 (exochitinase) and glu 78 (exo-1,3 β glucanase) obtained from *Trichoderma*.

Host induced gene silencing

One such approach is known as the HIGS which targets specific effector genes of the targeted pathogen using a certain RNAi configuration. Such inhibition of virulence genes can be achieved by delivering dsRNA or siRNA molecules into the pathogen during their mutual encounter causing silencing of the target messenger RNA. However, most of HIGS effectiveness depends on having a functioning RNAi silencing process in the pathogen. The latest research on it shows that HIGS is effective for the treatment of the rice – *R. solani* pathosystem. Studies done by Rao *et al.* (2019) and Tiwari *et al.* (2017) showed that the shibboleth RNA interference system is present in the ShB pathogen. In studying ShB resistance, Tiwari *et al.* (2017) focused on the silent control of PMK genes, while Rao *et al.* (2019) focused on PG in *R. solani*. Remarkably, it has been demonstrated that rice transgenics with RNAi constructs have lower ShB due to the efficient repression of these pathogen genes.

Choice of promoter

In genetic engineering, it is essential to cautiously consider the choice of a promoter. Many ShB tolerant improvement works used CaMV35S, rice actin 1 or maize ubiquitin for constant expression of transgenes. At times, these key signaling genes have been continuously expressed, leading to increased metabolic burden which has had unwanted aftermaths. For instance, expressions such as AtNPR1 led to a problem such as LMP and stunting, while LMP specifically under certain growth conditions in OSH1 (OSH1 considered as rice homoeobox gene expressed at the time of organ differentiation) (Chern *et al.* 2014). Furthermore, crossbreeding genes such as RCH10 and AGLU1 into transgenic rice caused low germination rates and poor seedling vigor (Mao *et al.* 2014).

As *R. solani* infects mainly green tissues, it is preferable for the gene expression to be restricted to this part. Recently, Molla *et al.* (2016) demonstrated that limiting AtNPR1 expression to the green parts of rice

raised the ShB resistance ability and did not have disadvantages that commonly occur. Xu *et al.* (2017) proposed an alternative approach to reduce fitness costs of expressing AthNPR1. This strategy employed the uORFsTBF1 cassette, consisting of an immune inducer promoter and two bacterial-dependent pathogen open-reading frames. The approach was able to confer resistant disease into the plant with no impact on the fitness of the plant. Most studies make use of constitutive promoters while only a few researchers try to explore green tissue specific promoters like rice rbcS, rice D54O-544 (Molla *et al.* 2016). However, it needs mentioning that the power of tissue-specific promoters is supposed to match that of constitutive promoters. In an alternative scenario, the utilization of inducible promoters provides a means for transgenic expression after infection. However, genes such as AceAMP1 and OsACS2 have been successfully expressed in rice under the control of pathogen-induced PAL, as well as PBZ1 promoters.

Management

Chemical control

Defense through chemical control is an alternative approach of natural resistance to combat sheath blight disease. Fungicides commonly applied for combating *R. solani* include sprays to leaves and seeds. However, systemic fungicides are better suited for controlling this disease than both systemic and non-systemic fungicides (Naik *et al.* 2017). The use of various protective fungicides to be applied from panicle differentiation up till maturity help secure effective shielding against sheath blight. Sheath blight management in susceptible varieties includes monitoring rice fields frequently while applying fungicides especially at the booting stage (Singh *et al.* 2016; Uppala and Zhou 2018).

Skepticism can be raised with regard to multiple chemical preparations used against sheath blight of rice (Table 12). Developmental efforts have centered on finding new target sites for fungicides that operate through different mechanisms of action. Currently, the strobilurin group of systemic fungicides is favored over others especially when dealing with sheath blight diseases in rice (Yellareddygaru *et al.* 2014). However, fungicides like Strobilurins obtained from the forest grown wild mushroom *Strobilurus tenacellus* are more powerful. One of these compounds is azoxystrobin which both controls the disease and enhances yield. Sheath blight is often controlled by triazole fungicides. The other chemicals that offer good control for this disease include flutolanil, carbendazim, iprobenfos, mancozeb, thifluzamide, and validamycin. Fungi

Table 12. Fungicides and their characteristics

Chemical group	Active ingredient	Trade name	Target site	Doses [g · ha ⁻¹]	Reference
Nano particle – fungicide	halogen substituted azomethines	–	effectively manages sheath blight	–	Siddhartha <i>et al.</i> (2020)
	silver and gold nanoparticle	–	reduces pathogen radial growth	–	Das and Dutta (2021)
Phenylureas	pencycuron	Monceren 22.9% SC	targets cytoskeleton in cell division	187.5	Kumar <i>et al.</i> (2013)
Glucopyranosyl antibiotic	validamycin	Sheathmar	inhibits trehalose	60	Miyagi (1990)
Carboxamide	thiﬂuzamide	Spencer 24% SC	targets respiration via NADH oxidoreductase	375	Sunder <i>et al.</i> (2003)
	ﬂuxapyroxad	–	targets pathogen mycelial growth inhibition	100	Chen <i>et al.</i> (2014)
Dithiocarbamate	mancozeb	Dithane M–45	multisite contact activity	875	Prasad <i>et al.</i> (2006); FRAC (2021)
Benzimidazoles	carbendazim	Bavistin 50% WP	targets cytoskeleton by assembling β-tubulin during mitosis	250	Prasad <i>et al.</i> (2006); Kandhari (2007)
Organophosphates	iprobenfos	Kitazin 48%EC	targets lipid synthesis via methyltransferase	240	Kumar <i>et al.</i> (2013)
Phenyl–benzamides	ﬂutolanil	Prostar	targets respiration by inhibiting succinate dehydrogenase	560	Kumar <i>et al.</i> (2013)
Triazole	difenoconazole	Score 25% EC	targets sterol biosynthesis in the cell membrane	62.5–125	Kumar <i>et al.</i> (2013); Naik <i>et al.</i> (2017); FRAC (2021)
	hexaconazole	Contaf 5% EC	–	50	–
	ﬂusilazole	Cursor 40% EC	–	120	–
	tebuconazole	Folicure 25.9% EC	–	187.5	–
Strobilurin	azoxystrobin	Amistar 23% EC	targets respiration by inhibiting the cytochrome bc1 at the quinone out site	125	Bag <i>et al.</i> (2016); FRAC (2021)
	Kresoxim-methyl	Sovran 250	–	250	–
	trifloxystrobin	Flint 150	–	150	–
	pyraclostrobin	Insignia	–	75–100	–
	ﬂuoxastrobin	Aftershock	–	–	–

are subjected to selection pressure as a result of using the same means of action repeatedly without change. Hence, it is prudent to apply chemicals such as Azoxystrobin 18.2%, Difenoconazole 11.4% (Kumar *et al.* 2018) among others so that the disease gets controlled properly. It is broad field control that is spread across all other fields but, with many shortcomings because of its nature. For example, natural disasters such as flooding, land-living, seepage of contaminated groundwater, among others, may cause damage to soil quality. The residues may be ingested by humans as well as animals, thus having further adverse impacts on the health of those who consume them. A new chemical molecule that attains the right equilibrium between disease-control and environmental safety does not fit in easily. Therefore, bio culture or culture resistance,

biology, and breeding of crop with sheath blight resistance are appropriate suppression mechanisms for pathogen development for sheath blight.

Biological control

Biological control appears to be a potential technique that can be considered in controlling necrotrophic fungus. Surprisingly, plant extracts, or botanical solutions have had significant success in the management of such diseases. Garlic, ginger, neem leaf, and clove extracts reduced over 80% of *R. solani* mycelium development (Chakrapani *et al.* 2020; Rajeswari *et al.* 2020). Competitive relations between microorganisms, particularly those in the soil, often lead to a significant decline of disease formation. Actinomycetes,

fungi, and bacteria are examples of different BCAs that have great possibilities. For example, actinomycetes that often colonize tomato roots have been reported to decrease tomato diseases caused by *R. solani* up to 63% (Singh *et al.* 2017). There is also an example of *Streptomyces* spp., which is another actinomycet that has been shown to reduce *R. solani* growth by 50% and *R. solani*-mediated suppression, can be reduced to 53.3%. Furthermore, ethyl acetate derived from *Streptomyces diastatochromogenes* KX852460 has potential activity against mycelium, sclerotium production, and hyphal growth on *R. solani* AG3 (Ahsan *et al.* 2019).

Various BCAs worked as potential antagonist against *Rhizoctonia*. Such as *Trichoderma*, *Corticium*, *Aspergillus*, and *Gliocladium* in order to manage sheath blight disease. The most popular kinds of BCAs are applied as foliar sprays, soil treatments, and root dips for seedlings. For instance, some specific strains of *Trichoderma* can suppress *Rhizoctonia* growth by 71% and reduce sheath blight infestation levels by around 59%. However, the *Trichoderma* has proven to be effective together with other BCAs such as Vesicular arbuscular mycorrhiza, *Pseudomonas*, and yeast (Mohammed *et al.* 2020). PGPR bacteria (BCA group) is one of the most common types of BCAs that is effective against a variety of plant pathogens. It helps to reduce diseases and support root growth by dissolving the phosphates from the soil, up taking nitrogen, chelating the ferrous through PGP bacteria like *Pseudomonas* and *Bacillus* which provides systemic resistance against sheath blight. For example, *P. fluorescense*-treated rice seedlings developed higher chitinase activity that induced sheath blight disease suppression. Similarly, some species of *Bacillus*, which are well known for their broad spectrum of antibacterial characteristics, have played an important role in reducing the development of *Rhizoctonia* (Abbas *et al.* 2019). Mixing *Bacillus subtilis* strain MBI600 and Azoxystrobin reduces diseases and increases yields by more than 14% (Zhou *et al.* 2021).

Other recent studies that focused on three types of nitrogen fixing cyanobacteria have reported a highly inhibitory impact on the growth of *R. solani* (Zhou *et al.* 2020). Nevertheless, the performance of BCAs in suppressing sheath blight may be attributed to their survivability, ability to spread rapidly, competence, and provision of additional supplements that enhance the growth of rice. Gold and silver nanoparticles have antifungal activities against *R. solani* (Das and Dutta 2021). Additionally, silver nano particles from rice leaves displayed high efficiency to fight against *R. solani* infestation on rice.

Application timing of some biocontrol agents in greenhouses against sheath blight using these bio fungicides prior to pathogen inoculation has shown outstanding effectiveness against the disease. An example

of such material is eugenol extracted from clove (*Syzygium aromaticum* L), which controls this pathogen by causing hydration of the cell and increases its permeability (Bai *et al.* 2023).

Phytochemicals

Steroids, tannins, flavonoids, and alkaloid phytochemicals have demonstrated antimicrobial properties against a few plant diseases (Persaud *et al.* 2019). These phytochemicals showed varying degrees of fungicidal activity. Their efficacy ranged from 33 to 100% depending on the different pathogens tested. The use of neem formulation has been popular in treating RSB disease and also improving crop production. A 4.5 ml · l⁻¹ concentration of neem formulation decreased the incidence of RSB and increased yield. There was a decrease in the disease incidence and infected tillers during greenhouse experiments with stabilized and saturated fractions of neem oil. Plants like *O. woder*, *P. glabra*, *L. alba*, and *O. sanctum* have been shown to limit by over 70% the mycelial development and sporulation caused by RSB disease pathogens in lab tests. The use of extracts from *O. woder* and *O. sanctum* recorded higher success rates in lessening RSB severities than did control plants. Additionally, there is another product known as Biotos, derived from *Gaultheria* spp., which reduces disease intensity and improves yield of grain. The performance of Biotos was higher than that of Achook (Azadirachtin 0.15% WW) with Tracer (Spinosad 44.03% SC) against RSB. The disease was also found to be vulnerable to extracts of various plants like *A. sativum*, *P. juliflora*, *G. pentaphylla*, *L. aspera*, and *V. negundo*. Moreover, palmarosa oil at a 0.1% level significantly affected mycelial growth and sclerotial germination in fungal pathogens. Recently extracts of lemongrass, thistle, thyme, marigold, and clove applied at 15% concentration prevented RSB's mycelium formation. Sheath blight has been effectively suppressed in both controlled trials and field experiments carried out with rice seedlings that were treated with leaf *C. odorata* extracts.

Conclusions

Sheath blight is one of several severe illnesses that influences rice plants. Genetic resistance is considered the least expensive and best for preservation of environmental health as well as efficient management of crop-related diseases. However, there is no known RSB resistance gene thus far. Understanding of the molecular interactions between *R. solani* and host plants reveals many pathogenicity factors and host resistance

genes. These strategies include pyramiding some RSB resistance QTLs, controlling or suppressing the expression of certain genes linked to plant defense, and utilizing host-derived RNAi and transgenic technology to disarm some important pathogenicity factors in *R. solani*. This review is a concise draft about genomic interaction, host-pathogen interaction, pathogenic variability, elicitor's based pathogenic immune response and disease management under the rice-*Rhizoctonia* patho-system.

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