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REVIEW

Sheath blight of rice: a review and identification of priorities for future research

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Abstract

Main conclusion **Rice sheath blight research should prioritise optimising biological control approaches, identification of resistance gene mechanisms and application in genetic improvement and smart farming for early disease detection.**

Abstract Rice sheath blight, caused by *Rhizoctonia solani* AG1-1A, is one of the most devasting diseases of the crop. To move forward with effective crop protection against sheath blight, it is important to review the published information related to pathogenicity and disease management and to determine areas of research that require deeper study. While progress has been made in the identification of pathogenesis-related genes both in rice and in the pathogen, the mechanisms remain unclear. Research related to disease management practices has addressed the use of agronomic practices, chemical control, biological control and genetic improvement: Optimising nitrogen fertiliser use in conjunction with plant spacing can reduce spread of infection while smart agriculture technologies such as crop monitoring with Unmanned Aerial Systems assist in early detection and management of sheath blight disease. Replacing older fungicides with natural fungicides and use of biological agents can provide effective sheath blight control, also minimising environmental impact. Genetic approaches that show promise for the control of sheath blight include treatment with exogenous dsRNA to silence pathogen gene expression, genome editing to develop rice lines with lower susceptibility to sheath blight and development of transgenic rice lines overexpressing or silencing pathogenesis related genes. The main challenges that were identified for effective crop protection against sheath blight are the adaptive flexibility of the pathogen, lack of resistant rice varieties, abscence of single resistance genes for use in breeding and low access of farmers to awareness programmes for optimal management practices.

Keywords Biological control · Fungicide · Genome editing · Integrated disease management · Smart farming · Transcription factor

Introduction

As the world population is expected to reach over 9 billion by 2050, it has been predicted that total food production will only be sufficient for 60% of the population (FAO 2018). Rice (*Oryza sativa* L.), the world's most widely consumed cereal crop, is especially important to the rapidly growing populations in South Asian countries (Pareja et al. 2011) and provides 20% of the dietary protein in the developing countries where rice is the staple to the diet (FAO 2004). Around 40,000 different varieties of rice (*Oryza sativa* L.) exist in the world (http://www.riceassociation.org.uk/content/1/18/types-of-rice.html). China produces largest amount of rice (142.3 million tonnes) followed by India (110.4 million tonnes) (According to FAO: Rice Market Monitor 2018). Rice productivity is affected by several pathogens that often place major constraints on production,. among which, *Rhizoctonia solani*, the causative agent of sheath blight (ShB), is responsible for yield loss up to 45% (Margani and Widadi 2018). The pathogen *Rhizoctonia solani* Kunh AG1-IA (*anamorph*), *Thanatephorus cucumeris* (Frank) Donk (teleomorph) is a soil-dwelling saprotroph and facultative

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parasite. The pathogen causes lesions on the sheath affecting grain filling and yield in rice (Wu et al. 2012).

ShB in rice was first reported in Japan in 1910. ShB in rice subsequently spread across the region, particularly where rice was grown under intense cultivation (Srinivasachary Willocquet and Savary 2011). As the disease spread to other Asian countries it was referred to by different names such as 'Oriental leaf and sheath blight', 'Sheath blight', '*Pellicularia* sheath blight', 'Sclerotial blight' and 'Banded blight of rice' (Srinivasachary Willocquet and Savary 2011). The ShB pathogen, *R. solani* Kühn, survives in the soil and water as sclerotia that remain viable for up to 3 years and form mycelia when coming into contact with plants (Kumar et al. 2009). The disease emerges around the late tillering to joint elongation stages in rice and achieves an aggressive state at the time of panicle differentiation. The early disease symptoms are the formation of lesions on the sheath leading to softness and lodging of the sheath and inhibition of grain filling (Wu et al. 2012). The fungus spreads rapidly via contact between plant parts such as tillers and leaves, and also via sclerotia (densely packed hyphal masses) present in surface water (Tsiboe et al. 2017). The severity of the disease depends upon cultivation practices, growth stages of the plant at the time of infection, usage of nitrogen fertilisers (Norman et al. 2003) and rice variety susceptibility (Tang et al. 2007).

ShB in rice is difficult to control because of the wide host range of the pathogen and persistence of sclerotia on exposure to adverse environmental conditions. Most insidiously, the pathogen evolves with time, allowing the sclerotia to overcome the resistance that may have been the hard-won achievement of the farmers and breeders. In order to combat the spread of ShB, it is necessary to use information compiled from studies of the biology of the pathogen, of the infection process and to determine how this information can be applied and supported with ShB management practices. Here we provide a review of the current information on identification criteria, modes of infection, hosts range and molecular basis of pathogenicity along with current management practices.

Biology of the sheath blight pathogen

Taxonomy and host range of the pathogen

Rhizoctonia solani Kunh is a collective species belonging to the order basidiomycetes but rarely producing basidiospores (Parmeter and Whitney 1970). Julius Kuhn first observed this fungus on diseased potato tubers in 1858 and named it *R. solani* (Almasia et al. 2008). *Rhizoctonia solani* infects over 27 families of plants, causing root, crown, hypocotyl, pod and belly rot, sheath and leaf blight, banded leaf, brown patch and canker (Sneh and Ichielevich-Auster 1998; Fenille et al. 2002) (Table 1). The species is subdivided into anastomosis groups (AG) based on their compatibility for hyphal fusion with known tester isolates. Anastomosis between genetically similar isolates that are compatible, form a fused hyphal network involving fusion of cell wall, cytoplasm and nuclei, whereas genetically distant isolates may form anastamoses but show no changes in the hyphal organisation (Kuninaga et al. 2002). A total of 14 different anastomosis groups (AG1 to AG13 and AGBI), which exhibit high variation in colony morphology, host range, aggressiveness and nutritional requirement, have been reported in *R. solani* (Guillemaut et al. 2003; Ahvenniemi et al. 2009; Ajayi-Oyetunde and Bradley 2018). Based on sequence homology and on size and shape of sclerotia, *R. solani* AG1 isolates are subdivided into three subgroups, IA, IB and IC (Sneh et al. 1991), all of which cause ShB, with the AG1-IA most commonly reported as the causal agent (Bernardes-De-Assis et al. 2009; Gonzalez-Vera et al. 2010).

Rice sheath blight infection and disease cycle

Typical *R. solani* infections result from sclerotia from a previous cropping season (Kumar et al. 2009). Initially, hyphae from sclerotia in the soil form a network and roots of newly planted seedling are penetrated at or near the water line (Ou 1985). Infection is favoured by warm temperatures (~28–32 °C), high humidity (~95%) and high levels of nitrogen fertiliser (Savary et al. 1995). The disease progresses in classical phases of early to late necrosis, with the cycle completed by the infection of soil by sclerotia from the infected rice plants (Fig. 1). After entering plant tissues, *R. solani* produces RS toxin, a mixture that includes *N*-acetyl glucosamine, *N*-acetyl galactosamine, glucose and mannose (Vidhyasekaran et al. 1997) along with pathogen effectors (such as glycosyltransferase, cytochrome C oxidase CtaG/cox11 and peptidase inhibitor I9), which co-relate with the virulence of the pathogen (Zheng et al. 2013). The fungus spreads in infected plant with the hyphae penetrating the stomata, producing lobate appressoria or infection cushions (Groth and Nowick 1992; Singh and Subramanian 2017). The formation of appressoria triggers enzymatic degradation, causing necrosis of the host plant and assisting colonisation by the fungal pathogen (Groth and Nowick 1992). The green or grey ellipsoid lesions (0.5–3 cm) formed on the sheath of leaves in acropetal succession (reviewed in Srinivas et al. 2013) give the classical sheath blight symptoms. As plant colonisation by the pathogen extends from leaf sheath to leaf blades, panicles and tillers, the necrotic lesions enlarge to 2–3 cm length and 1 cm width, with beached centres and borders turning purple-brown (reviewed in Srinivas et al. 2013). Finally, lesions on the upper part of leaves coalesce, covering entire stem and sheath of the

Table 1 Summary of hosts and the diseases caused by different anastomosis groups of *Rhizoctonia solani*

Family	Plant	Disease	Part of the plant infected	Disease symptoms	Anastomosis group/Subset	References
Poaceae	Rice	Sheath blight	Leaf sheath	Immergence of lesions on sheaths of lower leaves near the water line	AG1-IA	Miyake (1910)
	Barley	Barley stunt disorder	Roots	Patches of chlorosis on leaves stunted plants	AG3	Roberts and Sivasithamparam (1986)
	Maize	Sheath blight	Leaves, sheaths, stalks and ears	Stalk lesions (rind spotting), stalk breakage, clumping and caking of styles (silk fibres)	AG2-2	Ahuja and Payak (1982)
	Wheat	Root rot	Stem	Lesions with dark brown borders and pale, straw-coloured - centrrs on the lower portions of wheat stems (culm) near the base of the plant	AG8	Paulitz et al. (2002), Barnett et al. (2017)
	Sorghum	Sheath blight	Stem (ground side of sheath)	Lesions which are cloud-shaped, ash brown to ash white with reddish brown border on stem	AG-1 IA	Pascual and Raymundo (1988), Kasuga and Inoue (2000)
Solanaceae	Potato	Black scurf	Tubers	Raised black patches	AG3	Beagle-Ristaino and Papavizas (1985)
		Stem canker	Stem and colon	Sunken, brown lesions on the sprouts before they emerge from the soil		
	Tobacco	Leaf spot and root rot	Stem	Damping off and stem rot in young transplants, sore shin in older field plants and a foliar disease named ‘target spot’	AG-2-2 and AG-3	Lucas (1975), Gonzalez et al. (2011)
Amaranthaceae	Sugar beet	Root and crown rot	Root	Wilting of the leaves, scattered brown to black lesions on the root surface, blackening of petioles at the crown position	AG 2-2 IV and AG 2-2 IIIB	Pannecoucque et al. (2008)

Table 1 (continued)

Family	Plant	Disease	Part of the plant infected	Disease symptoms	Anastomosis group/Subset	References
Cucurbitaceae	Cucumber	Belly rot	Fruit	Lesions which grow as sunken, cratered, irregular in shape on fruits	AG4	Flentje et al. (1963), Lewis and Papavizas (1980), Hassan et al. (2015)
	Peanut	Pod rot	Seedlings	Seed decay, dark, sunken lesions just below the soil line on stem	AG4	Thiessen and Woodward (2012)
	Soya bean	Seedling blight, root and hypocotyl rot	Seedlings	Red-brown sunken lesions on hypocotyl, shrunken, reddish brown lesion or canker developing at or near the soil line	AG2-2IIIB, AG4 and AG5	Yang (2015), Ajayi-Oyetunde and Bradley (2018)
	Chickpea	Root rot/wet rot	Root	Root rotting, yellowing and wilting of leaves, rotted and discoloured tissues become wet	AG2 and AG3	Harveson (2011)
Rubiaceae	Coffee	Necrotic leaf spot	Leaves	Small and large necrotic spots on leaves	AG1-ID	Priyatmojo et al. (2001)
Brassicaceae	Oilseed rape and canola	Seedling damping-off, seedling root rot and basal stem or foot rot (brown girdling root rot) of adult plants.	Seedling hypocotyls and roots	Light brown lesions on the roots which becomes sunken, dark, enlarge enough to girdle the taproot	AG2-1 and AG4	Kataria and Verma (1992)
	Cauliflower	Damping off	Seedlings	Damping-off kills seedlings, rot beneath soil, Lesion near the tender stem causing the seedling to collapse or the seedling may continue to grow even though the lesion girdles the stem. The lesion is quite sunken, and the stem resembles a wire, hence the name wirestem. The girdled seedling eventually dies	AG2-1	Pscheidt and Ocamb (2008)
Malvaceae	Cotton	Root rot	Root	Damping–off, which included seed rot, lesions on the hypocotyls and root rot	AG4 and AG7	Rani et al. (2013)

Table 1 (continued)

Family	Plant	Disease	Part of the plant infected	Disease symptoms	Anastomosis group/Subset	References
Asteraceae	Lettuce	Bottom rot disease	Leaf midribs and leaf parts in contact with soil	Small rust-coloured necrotic spots on leaf midribs and leaf parts, lesions expand into a rot	AG 1-IB AG 1-IC and AG 2-1	Grosch et al. (2004)

plant leading to stem lodging. Stem lodging blocks the water transport, which disturbs canopy architecture and reduces photosynthetic capacity. As a result, grain filling is reduced and ultimately the infection leads to plant death (Bahuguna et al. 2012).

After rice harvest, *R. solani* sclerotia from infected plants persist in the soil for periods of up to 3 years and act as a source of infection for subsequent crop cycles (Savary et al. 1995). Individual sclerotia typically range from 5 mm in diameter to much bigger masses formed by fusion of multiple sclerotia (Keijer et al. 1996). Sclerotia are white initially and gradually turn brown after maturation as a result of melanin formation in the cell walls. The resilience of sclerotia can be related to the mature form, which has impermeable cell walls and high nutrient content: Melanin is an oxidised phenolic with hydrophobic properties (Willetts and Bullock 1992) reducing cell wall permeability and protecting cells from biological degradation (Sneh et al. 1991). Sclerotia have a rich nutrient reserve of proteins, polyphosphate, glycogen and lipids in the cytoplasm (Willetts and Bullock 1992), which serves as an energy source during extreme environmental conditions and also supports reinfection process (Keijer et al. 1996). The sclerotia are generally transported to the surrounding field from infected crops via irrigation of infested soil. At the time of re-infection, sclerotia undergo myceliogenic germination (Webster 1980) and hyphae spread horizontally (average is recorded to be 20 cm/day) on the plants hence making the disease to spread very fast (Savary et al. 1995). ShB development is also accelerated by high seedling rate, dense canopy of plants in the fields and growing of high-yielding improved varieties (which requires nitrogen fertilisers) (Savary et al. 1995).

Molecular basis of pathogenicity

The publication of whole genome sequence assemblies of *R. solani* AG1-1A (Zheng et al. 2013; Nadarajah et al. 2017), as well as genome sequences for rice (Eckardt 2000), provide useful resources for determining key mechanisms underlying *R. solani* infection and disease. Initial stages of ShB infection involve recognition between the rice host and the fungal pathogen. While rice roots produce exudates, comprised of carbohydrates and protein molecules that act as a chemoattractant for soil-borne bacteria (Bacilio-Jiménez et al. 2003) and influence fungal diversity (Van Der Wal et al. 2013; Hugoni et al. 2018), there are no reports of any specific fungal pathogen attracting molecules and a molecular mechanism explaining the role of root exudates in attracting *R. solani* is unknown. Genome sequence studies predict an array of secreted proteins, enzymes of primary and secondary metabolism, carbohydrate-active enzymes and transporters (such as ATP binding cassette) associated with

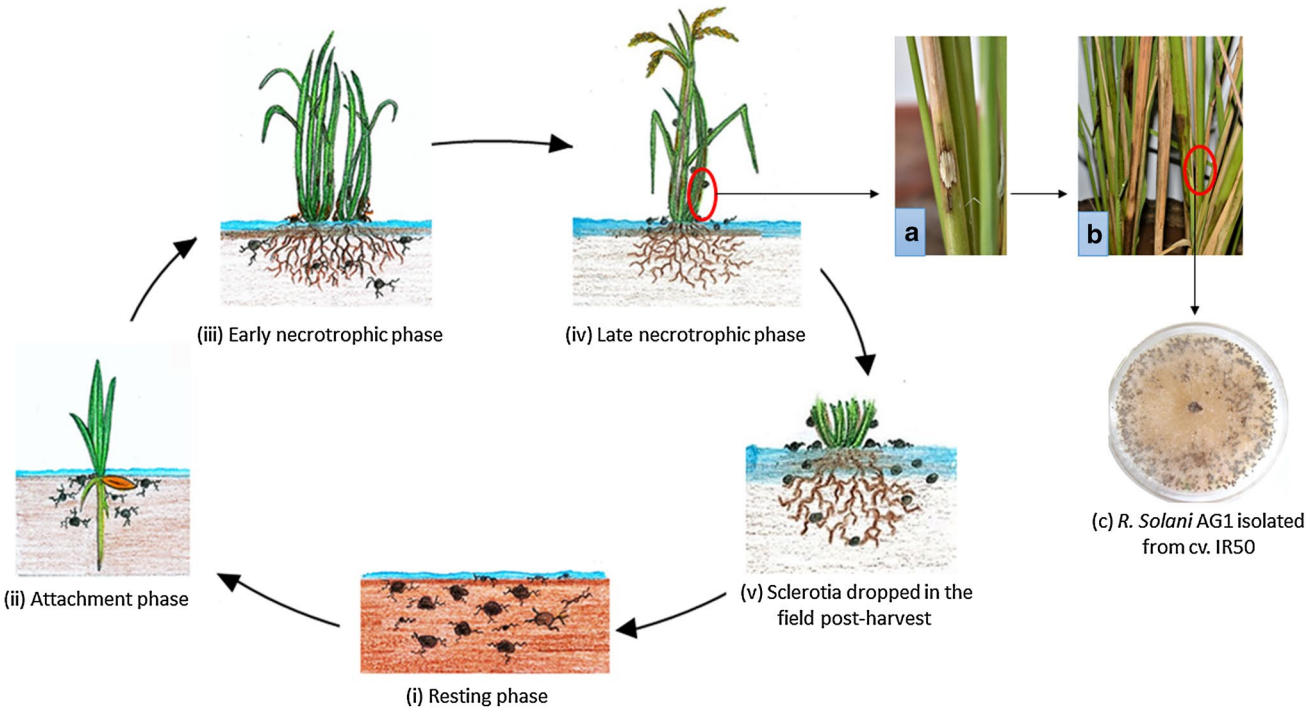

Fig. 1 Disease cycle of *Rhizoctonia solani* showing different phases of sclerotia development and disease symptom on rice

the necrotic phase of infection (Zheng et al. 2013). Following that, transcriptome analysis of *R. solani*=infected rice sheath also showed involvement of various plant genes such as extracellular protease, ABC transporter and transcription factors during establishment and sugar transporters, cellular metabolism and protein degradation-related genes during the necrotrophic phase of infection (Ghosh et al. 2018). Following attachment of the fungal hyphae to rice roots, enzymic degradation of the plant primary and secondary cell walls occurs. The breakdown of complex macromolecules of cell walls such as cellulose, hemicellulose and pectin into simple sugars via cell wall degrading enzymes (pectinase, laccase and xylanase) secreted by *R. solani* facilitates host cell penetration (Talbot 2010; King et al. 2011). In the later stages of the disease, the pathogen activates sugar membrane transporters to enable the transport of simple sugar molecules to the fungal cells (Zheng et al. 2013; Quistgaard et al. 2016; Ghosh et al. 2018).

Signal transduction mechanism in *R. solani* infection is not yet well understood, though it likely involves G protein-mediated signalling through second messengers including cAMP and a number of downstream pathogenesis effector molecules: The G protein (*Rga1*) homologue to Ga subunits reported in other fungi was identified in *R. solani* (Charoensopharat et al. 2008). The disruption of *Rga1* resulted in slow growth and reduction in pathogenicity, changes in colony structure and inability to form sclerotia. G proteins are the largest group of cell wall receptors in fungi, well-known for their function in promoting survival, propagation and virulence (Brown et al. 2018). A loss in pathogenicity because of disruption in G protein function has been reported for other pathogenic fungi including *Magnaporthe grisea* (Fang and Dean 2000) and *Fusarium oxysporum* (Jain et al. 2002). Changes in cAMP levels upon disruption of G proteins during infection have been reported for other pathogenic fungi but are yet to be explored in *R. solani.* A few studies have identified *R. solani* secreted proteins that are upregulated during infection and may be downstream effector molecules involved in enhancing plant infection and/or suppressing plant defense responses (Zheng et al. 2013; Ghosh et al. 2018). Studies of effector molecules identified in different *R. solani* strains show high diversity in gene sequences which indicates its adaptative flexibility (via gene duplication, deletion and point mutation) to escape host recognition and optimise virulence function (Oliver and Solomon 2010; De Wit et al. 2012; Ghosh et al. 2018). This could be one of the possible factors underlying the broad host range of *R. solani* strains.

Management of sheath blight disease in rice

Field disease history, weather conditions and prior information on cultivar susceptibility are major checkpoints to minimise disease occurrence. Current management practices and research to improve crop protection are discussed below

and can be considered as related to agronomic practices, to chemical and biological control and crop improvement (Fig. 2).

Agronomic practices

Rice cultivars have considerable variation in terms of morphological traits including plant height, days to heading (date of sowing to panicle emergence), plant compactness, tiller angle, flag leaf length and width and stem thickness, which each have been reported to be associated with susceptibility to sheath blight (Zou et al. 2000; Pinson et al. 2005; Willocquet et al. 2012; Dey et al. 2016). To increase the grain yield, rice varieties with short height and abundant tillers are generally used in the field. Such varieties are also commonly cultivated with a high use of nitrogen fertilisers (Norman et al. 2001), which together create a denser canopy than taller varieties and provides a microclimate that enhances *R. solani* infection (Tang et al. 2007). Hence a systematic study on variety selection and correlation of nitrogen fertiliser with the seedling stage as well as the frequency of ShB infection may provide better information for optimising the use of nitrogen fertiliser while minimizing infection.

Regular monitoring, early detection of inocula and removal of weed-hosts are important points to be considered for ShB management. ShB infection in rice is also associated with the spacing in the plantation: Field studies in China showed a wider space plantation method such as square (Yang et al. 2008) and sparse plantation (Sugiyama et al. 2007) to improve the canopy architecture, produce a higher leaf area index, increase the grain yield and reduce disease occurrence. Clearance of plant debris and tubers from rice fields and postharvest drying was found to be effective in minimising sclerotia movement (Ritchie et al. 2009). Following drainage, complete sanitation using fungicides and destroying host-weeds from field boundaries (Anand et al. 2014) and crop rotation with the non-host plant (Wright et al. 2017) should be practiced to reduce inoculum density for next cropping season.

Rice farmers are on the front line in responding to crop diseases in the field. It is, therefore, important for the farmer to understand the available options to mitigate crop damage and the possible control methods that can be applied in the field (Nelson et al. 2001). Farmers in many developing countries rely only on fungicides because of lack of information on alternative disease management techniques. Hence awareness programmes are needed for implementing more effective disease management systems (Khoury and Makkouk 2010). In the early 90s, a farmer field schools (FFS) programme was conducted by the FAO's Intercountry Programme on Rice Integrated Pest Management in South and Southeast Asia (Van de Fliert 1993; Matteson 1996) and farmers were trained with integrated disease management systems. In the programme, farmers were involved in observing and performing experiments such as rice genotype mixing to produce disease resistant cultivars; optimum use of nitrogen fertiliser for increasing yield and avoiding disease development; optimal plant density to avoid fungal infections and suitable concentrations of fungicides to grow susceptible varieties (Nelson et al. 2001). Likewise, more

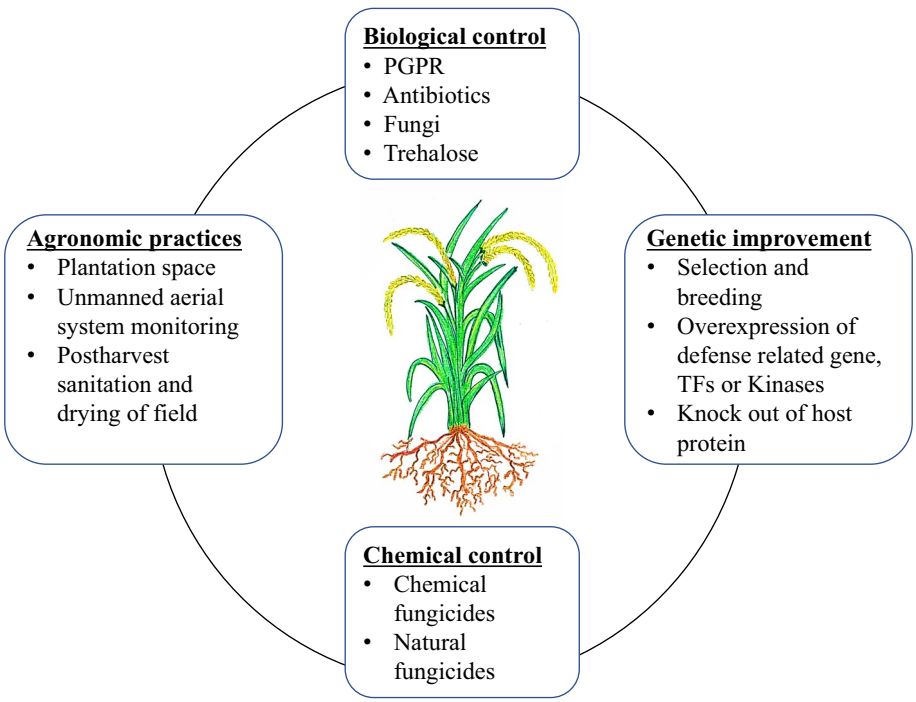

Fig. 2 Disease management approaches for sheath blight of rice

training programmes should be conducted to educate the farmers on good agricultural practices, marketing strategies and financial management, modern technologies such as remote sensing with Unmanned Aerial Systems (UAS, commonly known as drones) for early detection of ShB in the field. UAS provides high-spatial resolution to perform plant phenotyping and disease diagnosis (Mulla 2013). UAS equipped with multiple types of sensors are used to measure plant phenotypic traits, physiological status and water stress (reviewed in Yang et al. 2017). During ShB infection, the infected leaf tissue usually changes its colour from green (healthy tissue) to brown-to-yellow (diseased tissue) with the development of the disease. UAS equipped with digital and multispectral camera and green Seeker handheld crop sensor showed efficient detection of the colour changes during ShB infection in rice compared to manual disease scoring (Zhang et al. 2018). UAS can be further used to quantify the phenotypic parameter such as plant height, leaf texture and canopy architecture and physiological parameters such as chlorophyll content, photosynthetic activity and biomass and pigment content associated with ShB symptoms. By providing quick and accurate data on disease development, at a low cost, deployment of UAS can alert farmers to effectively take necessary measures on time and minimise the risk of spread and re-occurrence. Compared to manual methods for disease detection, the application of Unmanned Aerial Vehicle technology has helped to reduce the use of chemical fungicide as well as reduce soil and water pollution (Mulla 2013). The adoption of this technology can contribute to cost-effective and eco-friendly rice farm management by facilitating site-specific fungicide and/or fertiliser application, soil health scanning, planning irrigation schedules and yield rate estimation. A strong effective networking system connecting scientific research, management practices and farmer awareness programmes are highly recommended (Shaw and Pautasso 2014). Such improvements will enhance the livelihoods of vulnerable farmers and contribute to food security (FAO 2018) (Table 2).

Chemical control

The most widely applied method for control of ShB is through the application of fungicides (Kandhari et al. 2003). Fungicides are toxic substances, often chemical compounds (natural or synthetic) with unique modes of action, used to kill or inhibit fungi (reviewed in Gullino et al. 2000). Selection of fungicide depends upon the intensity of the disease and also the tolerance level of the rice cultivar (Biswas 2004). The most popular fungicide application methods practiced for ShB control are foliar spray (McGrath 2004) and seed treatment (Kabir et al. 2006). Fungicides restrict the disease development on rice sheaths, acting on *R. solani* and its sclerotia by various means such as damaging the fungal cell membrane (Roberts et al. 1998), acting as enzyme inhibitors (Kumar et al. 2018), interfering in key processes including respiration or energy production (Ichiba et al. 2000; Lal et al. 2017) or by interfering with metabolic pathways associated with sterol and chitin biosynthesis for cell wall formation (Morton and Staub 2008). The best time to apply fungicides in a field is from 7 days after panicle differentiation until heading reaches 50–75% (Uppala and Zhou 2018). For susceptible rice varieties, application of fungicide is needed early in the crop cycle, at the booting stage of rice, when the leaf stem bulges to initiate panicle emergence (Yeshi et al. 2013). Some of the commercially available fungicides that are used against ShB in rice, their active ingredients and their modes of action are shown in Table 3. Apart from chemical fungicides, a few natural fungicides such as strobilurins (also known as β-methoxyacrylates) or QoI (Quinone outside Inhibitors) derived from the wild mushroom *Strobilurus tenacellus* have been tested for ShB management (Bag et al. 2016). Among analogues of strobilurins, Azoxystrobin (Methyl(E)-2-2-[6-(2-cyanophenoxy) yrimidin-4 yloxy] phenyl-3- methoxyacrylate) (commercial name Quadris 2.08 SC, Syngenta, Raleigh, NC, USA) was reported to be effective in reducing ShB and increasing grain yield (Bag et al. 2016). The above-mentioned fungicides arrest fungal growth via disrupting the electron transport chain, preventing ATP synthesis and restricting respiration in fungi (Ichiba et al. 2000). A recent comparison of the effect of Azoxystrobin and of the chemical fungicides thifluzamide, pencycuron, validamycin and hexaconazole showed the chemical fungicides to completely inhibit sclerotia formation while the natural fungicide, Azoxystrobin, also reduced sclerotia formation and resulted in better grain yield (Kumar et al. 2018).

The use of fungicides has been highly effective for controlling fungal diseases of crops. However, this is not without important considerations over the choice of fungicide and application practices: The prolonged use of a single fungicide increases the risk of fungicide resistance (Uppala and Zhou 2018). Fungal genomes may mutate resulting in altered target sites of fungicide binding, increased production of the target protein, or reduced uptake or increased metabolic breakdown of the fungicide (reviewed in Gullino et al. 2000). The above processes result in varying levels of resistance described as quantitative fungicide resistance (Deising et al. 2008). Therefore, the composition of fungicides is frequently modified to enhance the specificity to recognise and attack target fungus (reviewed in Gullino et al. 2000). However, the process of screening and selection for more specific and durable fungicides creates a cost burden to developers that may end up being passed on to the farmers in terms of higher prices who may then continue to use less effective but lower-cost earlier generation fungicides. Another concern over fungicide use is associated

Table 2 Resistant rice cultivars generated using overexpression of defense-related genes

Gene	Type	Function	Method	Transformation system	References
OsCHI11	*Chitinase* gene	Antifungal activity by hydrolysis of internal β-1,4-linkages of chitin (a fungal cell wall component)	Overexpression	Polyethylene Glycol-mediated protoplast transformation of calli derived from mature rice seeds	Lin et al. (1995)
OsCHI11	*Chitinase* gene		Overexpression	*Agrobacterium*-mediated transformation of embryogenic derived rice calli	Datta et al. (2000)
OsRC7	*Chitinase* gene		Overexpression	1. Biolistic method for transformation of rice immature embryos 2. Polyethylene Glycol-mediated protoplast transformation of rice	Datta et al. (2001)
OsCHI11	*Chitinase* gene			*Agrobacterium*-mediated transformation of mature rice seeds	
Os11g47510	*Chitinase* gene		Overexpression	Biolistic method for transformation of mature seed	Richa et al. (2017)
PR-5	Thaumatin-like protein	Antifungal activity by hydrolysis of β-1,3-glucan (a fungal cell wall component)	Overexpression	Biolistic method for transformation of immature rice embryo	Datta et al. (1999)
RCH10 and *AGLU1*	*Chitinase* and *Alfalfa β-1,3-glucanase* gene	Hydrolysis of fungal cell wall components chitin and β-1,3-glucan	Overexpression	*Agrobacterium*-mediated transformation of mature embryos callus	Mao et al. (2014)
chi11, *tlp* and *Xa21*	*Rice chitinase*, thaumatin-like protein and serine-threonine kinase	Cell surface recognition of a pathogen ligand and hydrolysis of fungal cell wall components chitin and β-1,3-glucan	Overexpression	Biolistic method for transformation of immature rice embryos	Maruthasalam et al. (2007)
Dm-AMP1	*Antifungal plant defensin*	Antimicrobial peptides which damage cell wall and increase membrane permeability	Overexpression	*Agrobacterium*-mediated transformation of scutellum derived rice calli	Jha et al. (2009)
OsACS2	*Ethylene biosynthetic* gene	Ethylene regulate the defense-related pathways during fungal pathogenesis	Overexpression	*Agrobacterium*-mediated transformation of mature rice seeds	Helliwell et al. (2013)
OsOXO4	*Oxalate oxidase 4*	Oxalate oxidase breakdowns to produce H_2O_2 (antioxidant) which triggers plant's defense response	Overexpression	Biolistic method for embryo transformation	Molla et al. (2013)
OsOXO4 and *OsCHI11*	*oxalate oxidase 4* and *chitinase* gene	Oxalate oxidase breakdowns to produce H_2O_2 (antioxidant) which triggers plant's defense response and chitinase hydrolyzes the fungal cell wall component chitin	Overexpression	*Agrobacterium*-mediated transformation of embryo raised callus	Karmakar et al. (2016)
BjNPR1	*Brassica juncea Non-expressor of pathogenesis-related genes 1*	*NPR1* regulate salicylic acid mediated systemic acquired resistance for defense response	Overexpression	*Agrobacterium*-mediated transformation of rice calli	Sadumpati et al. (2013)
AtNPR1	*Arabidopsis thaliana Non-expressor of pathogenesis-related genes 1*		Overexpression	Biolistic method for mature rice embryo transformation	Molla et al. (2016)

Table 2 (continued)

Gene	Type	Function	Method	Transformation system	References
OsPGIP1	Polygalacturonase inhibiting proteins	PGIP inhibit polygalacturonase secreted by pathogen to degrade the plant cell wall	Overexpression	*Agrobacterium*-mediated transformation of the following: 1. Shoot apices, roots and calli derived from roots 2. Scutella, calli derived from scutella, and suspension cultures 3. Immature embryos	Wang et al. (2015b)
OsPGIP1			Overexpression	*Agrobacterium*-mediated transformation of rice callus	Chen et al. (2016)
chi11 and *ap24*	*Rice chitinase* and *Tobacco osmotin*	Chitinase hydrolyses fungal cell wall components chitin and osmotin diffuses across the fungal cell wall causing leakage of the cellular contents	Overexpression	*Agrobacterium*-mediated transformation of scutellum derived rice calli	Sripriya et al. (2017)
RPMK1-1 and *RPMK1-2*	Pathogenicity Map Kinases	*PMK* helps formation of appressorium for infection and overall viability inside host plant	Silencing	Biolistic method for mature seed derived calli transformation	Tiwari et al. (2017)

with hazard to human health (reviewed in Kim et al. 2017) and to natural ecosystems (Mahmood et al. 2016) requiring appropriate risk management strategies for their safe use. Many fungicides are persistent in soil and in above and below ground water bodies, ultimately entering and affecting the food chain (Rodrigues et al. 2018). Application of fungicides in agriculture also has a negative impact on aquatic organisms since the active ingredients of the fungicide often become concentrated in lakes and ponds through spray drift or agricultural runoff during heavy rainfall (Schulz 2004). The lethal effect of fungicides on detrivores also slows down leaf decomposition and thus impacts nutrient recycling (Hanazato 2001; Chang et al. 2005). The detrimental effect derived from fungicide treatment prompted policy actions that impose stringent regulation in several countries (Neha et al. 2017). Beside policy development, research and development efforts have been deployed to explore alternatives to the use of chemical fungicides such as use of biological agents to control ShB.

Biological control

Biocontrol is the use of parasites, predators or microorganisms (biocontrol agents) to reduce the population of a pest or pathogenic organism and is often considered to be a safe and reliable option for plant disease management (reviewed in Etesami and Maheshwari 2018). Microorganisms such as plant growth-promoting rhizobacteria (PGPR) can provide protection to rice cultivation via reducing *R. solani* infection (reviewed in Prasad et al. 2019). PGPR are free-living bacteria from the rhizosphere, which have been reported to actively participate in the biosynthesis of phytohormones (indole acetic acid, gibberellic acid, abscisic acid), increase N uptake, cause phosphate solubilization and interfere with pathogen toxin production (reviewed in Prasad et al. 2019). PGPR strains that are effective at controlling ShB infection in rice include *Pseudomonas fluorescens* and various *Bacillus* spp. (reviewed in Kumar et al. 2009; Karnwal and Mannan 2018). *Pseudomonas fluorescens* has been reported to inhibit *R. solani* by producing the antimicrobial compound hydrogen cyanide; the extracellular lytic enzymes β 1,3-glucanase and chitinase (Radjacommare et al. 2004) and by inducing systemic resistance in plants (Bakker et al. 2007). *Bacillus* spp. secrete phenylalanine ammonia lyase, peroxidase and other pathogenicity-related proteins to inhibit *R. solani* growth (He et al. 2002). Foliar spray of *B. subtilis* and *B. megaterium* was found to be highly effective in inhibiting the formation of sclerotia (40–60%) and mycelial growth (Li et al. 2003; Chen and Kang 2006). *Pseudomonas fluorescens* was also reported to be highly effective in preventing mycelial growth and sclerotia development (45%) when applied as a foliar spray or soil amendment (Kazempour 2004). Application of another strain of *Pseudomonas*, GRP3, as a

Table 3 Chemical control of sheath blight of rice

Trade name	Active ingredient	Formulation	Mode of action	Gram active ingredient/ hectare	References
Azoxystrobin	Strobilurin 23% SC	Suspension concentrate	Targets cytochrome bc1 (ubiquinol oxidase) at Qo-site which blocks the electron transport chain in fungi and prevent ATP formation	125	FRAC (2017), Bag et al. (2016)
Bavistin	Carbendazim 50% WP	Wettable powder	Disrupts β-tubulin assembly in mitosis of fungi and inhibits development of the germ tubes, formation of appressoria, and the growth of mycelia	250	Xiuguo et al. (2009)
Contaf	Hexaconazole 5% EC	Emulsifiable concentrate	Targets C14-demethylase in sterol biosynthesis (erg11/ cyp51) and inhibits spore germination, mycelium development, and sporulation in fungi	50	FRAC (2017), Kumar et al. (2013)
Cursor 40 EC	Flusilazole 40% EC	Emulsifiable concentrate		120	FRAC (2017)
Kitazin 48 EC	Eprobenfos 48%EC	Emulsifiable concentrate	Prevents phospholipid biosynthesis and methyltransferase activity disrupting chitin layer of the fungi, inhibits spore germination and their penetration	240	Kumar et al. (2013)
Score 25EC	Difenconazole 25% EC	Emulsifiable concentrate (EC)	Inhibits sterol demethylation, prevents the development of the fungus by inhibiting cell membrane ergosterol biosynthesis.	62.5–125	Kumar et al. (2018)
Eurofil-NT 35% SC	Mancozeb 35 SC	Suspension concentrate	Multisite contact activity, chelates metal cations, interferes with the vital thiol compounds in the fungal cell wall	875	Morton and Staub (2008)
Monceren 25 SC	Pencycuron 22.9% SC	Suspension concentrate	Inhibits fungal cell division and spindle microtubules assembly	187.5	Mian et al. (2004), Pal et al. (2005)
Tilt 25 EC	Propiconazole 25% EC	Emulsifiable concentrate	Prevents development of fungi by interfering with the biosynthesis of sterols in cell membranes	125	FRAC (2017), Kumar et al. (2013)
Folicure 25EC	Tebuconazole 25.9% EC	Emulsifiable concentrate	Demethylation inhibitor (DMI) of fungal sterol biosynthesis.	187.5	Roberts et al. (1998)
Spencer	Thifluzamide 24% SC	Suspension concentrate	Targets succinate dehydrogenase complex II in respiratory chain and affect the fungal respiration	375	FRAC (2017), Kumar et al. (2012)
Sheathmar 3L	Validamycin 3% L	–	Inhibits trehalase an important carbohydrate energy source in fungi	60	FRAC (2017), Kumar et al. (2012)

coating on rice seed, followed by root dipping of germinated seedlings showed inhibition of the *R. solani* sclerotia up to 46%. (Pathak et al. 2004).

Eukaryotic microbes, mainly fungi from the genera *Trichoderma* and *Gliocladium,* have also been used as antagonists for ShB management. *Trichoderma* spp. and *Gliocladium* spp. inhibit *R. solani* by competition for nutrients and by mycoparasitism involving antifungal secondary metabolites (Qualhato et al. 2013). The major antifungal secondary metabolites reported are volatile antibiotics (e.g. 6-pentyl-α-pyrone and isocyanide derivates), hydrophilic compounds (e.g. heptelidic acid or koningic acid) and amphipathic polypeptides (e.g. peptaibiotics and peptaibols) (reviewed in Lorito et al. 2010, Bailey and Lumsden 2014). Fungal antagonists in the form of conidial biomass are used in the preparation of talc formulations for application as fungicides (Singh and Nautiyal 2012). The formulations applied to soil, seeds, root dip and foliar spray have shown inhibition of sclerotia formation up to 59% (Nagaraju et al. 2002; reviewed in Kumar et al. 2009).

Integrated, or combination approaches have also shown effectiveness for ShB control. As an example, applying a combination of a PGPR with an antibiotic was found to be very effective in suppression of ShB infection in rice: *B. subtilis* NJ-18 strain with jinggangmycin (a glucosaminidase glycoside antibiotic produced by *Streptomyces* var. jinggangensis) showed suppression of *R. solani* infection in rice under greenhouse conditions (Peng et al. 2014). A combined application of PGPR and fungus also showed promising results in controlling *R. solani* infection. *T. viride* and *P. fluorescens* reduced the disease by 47.3% (measured based on percentage disease scoring) compared with the individual application of either *P. fluorescens* (42%) or *T. viride* (45.7%) (Mathivanan et al. 2005). Combined application of *T. viride* and *P. fluorescens* demonstrated escalation in phytoalexin production, callose deposition, lignification of the plant cell wall, antimicrobial secondary metabolite production and upregulation of pathogenesis-related (PR) proteins (Nanda et al. 2010; Singh et al. 2016). Despite the promising results with biocontrol agents, the introduction of new biocontrol agents involves various considerations such as the tedious work of selection and screening, optimization of mode of application to achieve best results (reviewed in Tabassum et al. 2017), shelf life of the organism, efficacy in the field trials, environmental safety, and registration to be used as a PGPR (reviewed in Etesami and Maheshwari 2018).

Molecular biocontrol agents, such as antibiotics and the cell derivative trehalose have also been used against ShB. Trehalose (α-D-glucopyranosyl-(1 → 1)-α-D-glucopyranoside) is a carbohydrate energy source (Jin et al. 2015) present in all organisms except mammals (Benaroudj et al. 2001). In fungi, it is reported to be an important component of energy conservation and is also used as a scavenger of ROS (reactive oxygen species) under stress conditions (Perfect et al. 2017). Although generation of ROS is related with stress, ROS production has been reported to be crucial for the formation of *R. solani* sclerotia (Wang et al. 2018). ROS production is accelerated at the hyphal branches during the initial stage of sclerotia formation (Georgiou et al. 2000). During the mycelial growth, fungal cells remain stable and the amount of intracellular oxygen remains low, but in the transition period between mycelial growth to differentiation, fungal cells produce free radicals [ROS: hydroxyl radicals ($^{\cdot}OH$), superoxide anion ($O_2^{\cdot-}$), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2), etc.], which stabilise the antioxidant level in the cells (Georgiou et al. 2006). The whole process leads to excessive accumulation of intracellular ROS, initiating the formation of sclerotia (Wang et al. 2018). The application of exogenous trehalose showed a prominent increase in the ROS-related enzyme activities and induced oxidative burst as well as the decline in *R. solani* sclerotial dry weight (Wang et al. 2018). In addition, application of other antioxidants such as β-carotene (Zervoudakis et al. 2003) and ascorbic acid (Georgiou et al. 2003) also showed inhibition of sclerotial biogenesis. Hence, application of antioxidant or mimetics (chemicals which can act as antioxidant) can be utilised to restrict the sclerotia biogenesis (Papapostolou and Georgiou 2010) (Table 4).

Genetic improvement of rice for sheath blight resistance

A long history of human selection, then traditional breeding in rice, are now supported by molecular information that can be used, often together with biotechnological approaches, to develop improved varieties, including ShB resistant cultivars. Below we discuss the different strategies which have been implemented in genetic improvement of rice against ShB infection:

Selection and breeding

ShB resistance is a quantitative trait which is controlled by multiple genes (Li et al. 1995; Zeng et al. 2011). Mapping of QTLs (quantitative trait loci) has revealed associations between gene loci and traits which have been used for marker-assisted selection in breeding (Mulualem and Bekeko 2016). Li et al. (1995) identified six QTLs associated with ShB resistance using restricted fragment length polymorphism (RFLP) analysis. Following this, more than 50 QTLs were identified for ShB resistance (Lavale et al. 2018), using mapping of various populations such as double-haploid populations (Zeng et al. 2015), a backcross population (Li et al. 2009), recombinant inbred lines (Channamallikarjuna et al. 2010), an F2 population (Sharma et al.

Table 4 Summary of putative genes/proteins involved in *Rhizoctonia solani*-rice interaction

Phase of infection	Genes/proteins	Role in infection[a]
Establishment phase	Polygalacturonase	Polygalacturonase secreted by *R. solani* degrades enzyme pectin which is a major plant cell wall component
	Extracellular metalloprotease, *Mpr*1	Fungalysins (zinc metalloproteases) which protect the pathogen from the action of host chitinases
	ABC3 (ATP-binding cassette) transporter	ABC3 helps to efflux of cytotoxic compounds such as phytoalexins produced by the host
	CRaZy (calcineurin-responsive zinc finger) transcription factor	Transcription factors helps in regulating expression of pathogenicity-associated genes during host colonisation
	*GAS*1	*GAS*1, encodes β-1,3-glucanosyltransferase which helps in formation of infection cushions
Necrotrophic phase	*AOX*1	*AOX*1 is involved in alternative oxidative pathway and provides resistance against oxidative stress during pathogenesis
	SidH	*SidH* (Enoyl-CoA hydratase protein family) is involved in siderophore production, which in turn assists the pathogen to survive under iron starved oxidative stress conditions
	DHOD	DHOD (dihydroorotate dehydrogenase) is involved in maintaining cellular redox homeostasis to survive in anaerobic host conditions
	MoCDIP4	*MoCDIP4* encodes effector proteins and cell wall degrading enzymes that induce cell death

[a]Source: Rao et al. 2019; Ghosh et al. 2019 and Ghosh et al. 2018

2009), chromosomal segment substitution lines (Zuo et al. 2014) and near-isogenic introgression lines (Loan et al. 2004). Association mapping of simple sequence repeats in rice genomes including landraces, further identified several markers significantly associated with ShB resistance (Jia et al. 2012; Lavale et al. 2018). However, the reliability of those QTLs is variable, as most of the QTLs remain undetected in multiple environments and/or mapping populations (Zuo et al. 2014; Eizenga et al. 2015). A recent genome-wide association study predicted two reliable QTL in rice based on significant correlation of the identified loci with ShB resistance in 299 cultivars (Chen et al. 2019). However, to date no QTL for ShB resistance has been well characterised: Identification of ShB resistance genes in QTL loci, functional characterization and application in marker associated breeding will be useful for generating resistant cultivars.

Genetic modification through biotechnology: Defense-related proteins and peptides

Genetic modification to develop resistant lines is a potentially powerful strategy to combat ShB infection in rice. The first tissue culture regeneration of rice (*Oryza sativa* cv. 'Nipponbare') was reported in 1985, using protoplasts derived from rice seed scutellum (Fujimura et al. 1985). The first genetically modified rice, (*Oryza sativa* L.v Taipei 309), containing an antibiotic resistance gene *neomycin phosphotransferase II* (*NPTII*), was reported in 1988 (Zhang et al. 1988). Following this, several genetically modified lines were developed expressing biotic and abiotic stress-resistant genes (reviewed in Ansari et al. 2015). More recently, the use of RNA interference (Tiwari et al. 2017) and gene editing (Gao et al. 2018) has demonstrated the possibilities to precisely manipulate expression of target genes to generate resistance rice varieties. Plant defense mechanisms are induced upon perception of a pathogen attack and include a hypersensitive response, generation of reactive oxygen species (ROS), accumulation of secondary metabolites such as phytoalexins, phenolics and tannins, and production and accumulation of pathogenesis-related (PR) proteins (Helliwell et al. 2013; Jain and Khurana 2018). Among the defense-related metabolites, expression of PR proteins has demonstrated potential to reduce ShB infection in rice (Table 2). Examples include rice plants overexpressing *PR* genes, such as *Oryza sativa chitinase 11* (PR3 family) to inhibit *R. solani* via hydrolysis of β-1,4 linkages of the *N*-acetylglucosamine polymer of fungal chitin and degradation of the cell wall (Datta et al. 2001). The use of multiple disease resistance genes is likely to provide more enduring resistance than use of single resistance genes. Plants expressing three *PR* genes; *chitinase-11* (PR3 family), *thaumatin-like protein* (PR5 family) and *Xa21* (receptor like kinase) together showed fewer lesions compared to plants expressing each individual gene (Maruthasalam et al. 2007), while Karmakar et al. (2017) showed plants expressing *OsCHI11* and *AtNPR1* together displayed fewer sheath blight symptoms than plants expressing either single gene.

Expression of small antimicrobial peptides (AMPs) (45–54 amino acids), such as defensins in rice, have also been demonstrated to inhibit *R. solani* infection (Jha et al.

2009). Plant defensins bind to the fungal hyphae damaging the cell wall and plasma membrane thereby inhibiting fungal growth (Van Der Weerden et al. 2008). Expressing *Dahlia merckii* derived defensin, *Dm-AMP1* in the apoplast of rice, suppressed the growth of *R. solani* by destabilising the plasma membrane. *Dm-AMP1* also reduced the hyphal proliferation inside the plant tissue creating a disease resistance cascade (Jha et al. 2009). Although the role of AMPs has been widely studied and well characterised against biotic stresses there is a concern on the stability and innate toxicity of AMP. Much research is needed to develop less toxic and more stable AMPs for plant protection against ShB (Tang et al. 2018).

The recent addition of gene editing technology to plant biotechnology has expanded the possibilities for gene targets for the inhibition of pathogenesis. CRISPR/Cas9 editing has been used to restrict the growth of the *R. solani* in rice (Gao et al. 2018): *R. solani* activates the *OsSWEET11* sugar transporter in infected plant cells, to efflux the sugar molecules for nutrition. Pathogen infection experiments showed that CRISPR-Cas9-based *OsSWEET11* knock-out mutants were less susceptible to ShB, compared to *OsSWEET11* overexpressing and wild-type plants (Gao et al. 2018). The precision of gene editing methods makes them attractive for crop improvement, particularly for loss of function mutations.

Genetic modification through biotechnology: Transcriptional and post-transcriptional regulation of gene expression

Strategies for manipulating gene expression at the transcriptional and post-transcriptional level have shown promise for improving rice ShB resistance. The rice genome encodes around 63 families of transcription factors (Gao et al. 2006), proteins that are master regulators of gene expression. Overexpression of members of the WRKY family of transcription factors, including OsWRKY30 (Peng et al. 2012), OsWRKY4 (Wang et al. 2015a) and OsWRKY80-OsWRKY4 (Peng et al. 2016) in rice each showed a reduction in the level of infection by *R. solani*. The reduction in the level of infection was found to be associated with WRKY-mediated elevated expression of defense-related PR genes of jasmonic acid and ethylene-responsive pathways (Peng et al. 2012; Wang et al. 2015a). Other than WRKY, transient expression of a rice transcription factor from the MYB family, *Osmyb4* in rice leaf also demonstrated to elevate the expression of disease-resistant genes (*aminotransferase*, *ankyrin* and *WRKY 12*) (Singh et al. 2015) associated with the *R. solani* resistance (Zhang et al. 2010).

Other than the manipulation of gene expression via transcription factors, post-transcriptional regulation via RNA silencing is an effective biotechnological approach that has been applied in various crop. RNA silencing exploits the innate mechanism of double-stranded RNA-mediated suppression of gene expression via targeted destruction of mRNAs (Guo et al. 2016). With recent advancements in dsRNA delivery methods such as topical application of crude bacterial extract of exogenous dsRNA (Tenllado et al. 2003; Lau et al. 2014) and clay nanosheets loaded with dsRNA (Mitter et al. 2017) RNA silencing has already shown effect in disease management, especially for crop viruses. Information for the application of RNA silencing-based control to manage fungal pathogens is expanding, and this method offers an additional tool against fungi for which existing fungicides have been ineffective (Mcloughlin et al. 2018). An RNA silencing approach was able to reduce infection and delay symptoms of ShB by expressing a hairpin construct designed from the coding sequence of the PATHOGENICITY MAP KINASE (PMK), *PMK1* and *PMK2* genes of *R. solani* in rice (Tiwari et al. 2017). *PMK* is required in the fungal developmental pathway including the formation of appressorium infection structures, penetration of plant cuticle and overall viability inside host plant (Mey et al. 2002; Jenczmionka et al. 2003).

Conclusion and future prospects

ShB in rice is favoured by warm climatic conditions and high humidity. The key factors behind ShB outbreaks are broad host range and absence of single resistance gene and lack of awareness and access to best management practices among farmers. The most common practice in the field is still the application of fungicide, which if not used with care and good management, has negative environmental consequences and harmful effects on human health. The persistent use of fungicides leads to accumulation in agricultural soil and to ground-water contamination. The prolonged use of a fungicide also induces pathogen resistance. A more sustainable approach for ShB management in rice, with less reliance on synthetic fungicides, is to make greater use of natural fungicides such as strobilurins and biological agents such as *P. fluorescens*, *Bacillus* spp., *Trichoderma* spp., *Gliocladium* spp. and trehalose to restrict ShB occurrence. Further, testing of combinations of natural fungicides with biological agents and/or antibiotics to inhibit *R. solani* infection will likely lead to improved strategies for ShB management and can be used to determine more cost-effective approaches for farmers in various different settings. As ShB spreads more quickly with a poor spacing between plants and with over use of nitrogen fertilisers, adopting a square method of spacing and sparse plantation to avoid plant to plant contact and a combination of management practices such as postharvest drying and clearing of the field, crop rotation with the non-host plant will aid in restricting the fresh infection

or re-occurrence. Furthermore, early disease detection of phenotypic and physiological parameters using Unmanned Aerial Systems can minimise the disease spread.

Use of tolerant and ideally resistant varieties is another sustainable approach. While QTL analysis has identified some potential ShB resistance loci and transcriptomic studies have identified candidate resistance genes, the underlying mechanisms for pathogenicity and resistance are not well understood and should be a priority for further studies. Also, genes associated with different phases of *R. solani* pathogenesis have been identified and further validation of such genes will serve as a reference for developing ShB tolerant varieties. Biotechnological approaches have shown promise: Transgenic lines overexpressing pathogenesis-related genes PR3, PR5, *OsCHI11* and *AtNPR1* (Table 2) and TF family WRKY (Peng et al. 2012; Wang et al. 2015a; Peng et al. 2016) showed inhibition against *R. solani* infection. It will be important to demonstrate protection against disease in field testing of the transgenic lines including underwarm and humid climates (optimal condition for *R. solani* infection) to further screen and select elite resistant varieties. Also, it will be interesting to study the productivity of transgenic lines in a field setting, especially at ShB hotspot locations. Host-derived dsRNA mediated silencing of pathogen-related kinase (*PATHOGENICITY MAP KINASE 1*) also demonstrated promising inhibition of *R. solani* infection. Exploration of pathogen- related genes through the exploitation of recent alternative approaches such as topical application of dsRNA as crude bacterial extract (Tenllado et al. 2003; Lau et al. 2014) or RNA clay (Mitter et al. 2017) and CRISPR mediated knock-out are additional approaches that should be included to achieve efficient and cost-effective disease management.

With climate change, ShB, along with other important crop diseases will require strong and concerted efforts in many areas of research from fundamentals though to applications. Strengthening linkages between researchers, media, non-governmental and community-based organisations in publicising information on ShB disease and its management will further aid in raising awareness to improve adoption of current available technologies to minimise ShB infection.

Author contribution statement PS and PM designed the outline of the article, composed the manuscript and figure. JAH and SB provided scientific feedback and critical comments to revise the content. All the authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest in the publication.

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