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Brown Spot of Rice: Worldwide Disease Impact, Phenotypic and Genetic Diversity of the Causal Pathogen *Bipolaris oryzae*, and Management of the Disease

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ABSTRACT

Rice brown spot caused by *Bipolaris oryzae* (syn. *Cochliobolus miyabeanus*) is a re-emerging disease worldwide. Under natural conditions, the disease causes approximately 4% in grain yield losses, ranging from 1% to 34% in countries of Africa and Asia. Rice seeds can be infected from relatively low (0.5%) to high (76%) rates. *B. oryzae* also infects wild rice (*Oryza australiensis*, *Oryza latifolia* and *Oryza rufipogon*) and other plant species, some of which are found in rice fields as alternative hosts. Characterisations of the pathogen's morphology, pathology and genetic diversity have been performed in several studies. *B. oryzae* colonies showed a wide range of colours varying from black to white and olive when grown on standard culture media. Strains isolated from rice are generally virulent with diverse aggressiveness, even within populations of the same geographic area. Clonal reproduction is predominant during epidemics. However, a low clonal fraction and balanced mating types suggest that sexual reproduction could take place in some areas. Most field studies reported high levels of pathogen genetic diversity and low population structure, suggesting that gene flow occurs between and among populations. Of the different methods used to control brown spot of rice, integrated management based on the use of healthy seed, resistant/tolerant varieties, balanced nitrogen fertilisation and water supply is preferred. This review reveals that a more precise estimation of the losses that this disease inflicts on rice production is needed. It also points out that knowledge of the population biology of the pathogen and epidemiological studies are required.

1 | Introduction

Many species of the genus *Bipolaris* infect a wide range of crops around the world (Manamgoda et al. 2014; Sun et al. 2020). *Bipolaris* fungi causing brown lesions, such as spot blotch of wheat (caused by *Bipolaris sorokiniana*), southern corn leaf blight of maize (caused by *B. maydis*) and brown spot (BS) of rice (caused by *B. oryzae*) have strong socio-economic impacts due to the importance of these crops in human and animal food chains (Bengyella et al. 2018). BS of rice can occur at any plant phenological stage. It can reduce grain germination, increase seedling mortality and limit the photosynthetic leaf area due to the occurrence of lesions leading to poor plant development and grain filling (Kumar et al. 2017).

Currently, the disease is found in most countries of Africa, Asia, the Americas, Oceania and Europe where rice is cultivated (CABI 2020; Farr and Rossman 2020), and it is of concern in Burkina Faso (Barro et al. 2021; Ouédraogo 2008), United States (Castell-Miller and Samac 2019), Bangladesh (Hossain et al. 2014), Ivory Coast (Bouet et al. 2015), Malaysia (Mahmad Toher et al. 2016) and India (Nayak and Hiremath 2019;

Valarmathi and Ladhalakshmi 2018). Worldwide losses in rice can reach 4% and the disease is listed in the top five most damaging pests and diseases of the crop (Savary et al. 2019). It is known as 'the poor farmers' rice disease' (Zadoks 1974), where mineral deficiencies in the soil have long been considered to be a major contributing factor to its occurrence (Barnwal et al. 2013; Kumar et al. 2017; Moletti et al. 1997; Ou 1985; Pantha and Yadav 2016). However, BS disease re-emergence (sensu Milgroom 2015) in several rice-cultivation areas in the last decade has led to other factors being identified, such as high temperature (e.g., global warming) and poor water supply (Kumar et al. 2017; Pantha and Yadav 2016; Savary et al. 2005, 2011) that not only cause plant stress but also can accelerate fungal growth and reproduction (Bregaglio et al. 2013; Mizobuchi et al. 2016).

Among the different species of *Bipolaris* that were isolated from lesions attributed to BS of rice (El Shafey et al. 2011; Gnancadja-André et al. 2005; Motlagh and Kaviani 2008; Nazari et al. 2015), *Bipolaris oryzae* (syn. *Helminthosporium oryzae*, teleomorph, *Cochliobolus miyabeanus*) is considered the most important. It is frequently encountered in rice seed lots (Mew and Gonzáles 2002). In addition, artificial inoculation tests showed that *B. oryzae* is the most pathogenic among *Bipolaris* species (El Shafey et al. 2011; Motlagh and Kaviani 2008).

Early reports of BS symptoms in rice date back to 1892 in Japan (Ohata 1989 cited by Mizobuchi et al. 2016). However, it was not until 1900 that Helminthosporium oryzae (*Bipolaris oryzae*) was identified as the causative agent (Breda de Haan 1900). This was followed by reports of the disease in the Philippines in 1918, the United States in 1920 (Louisiana; Ocfemia 1924), India in 1922 (Chakrabarti 2001), Australia in 1952 (Shivas 1989), Madagascar in 1957 (Dadant et al. 1960) and most recently in 2017 in Paraguay (Quintana et al. 2017). Nowadays, BS is present in almost all rice-producing countries (CABI 2020; Farr and Rossman 2020).

Bipolaris oryzae isolates are morphologically, pathologically and molecularly diverse. They exhibit a large range of variation in colour, mycelial growth rate and spore size (Chang 1978; Jaiganesh and Kannan 2019; Nayak and Hiremath 2019; Ocfemia 1924; Sivanesan 1987), as well as in genetic diversity (Ahmadpour et al. 2018; Archana et al. 2014a, 2014b; Burgos et al. 2013; Chaijuckam et al. 2019; El Shafey et al. 2011; Kamal and Mia 2009; Kandan et al. 2013; Motlagh and Anvari 2010). Understanding diversity and the mechanisms that influence genotypic changes in the pathogen population is a fundamental step in disease management strategies (Sunder et al. 2014). The aim of this report was to provide a state-of-the-art review of the disease impact on yield, the management of BS disease caused by *B. oryzae* on rice, and its morphological, pathologic and genetic diversities.

2 | Brown Spot Symptoms on Rice

Bipolaris oryzae is a necrotrophic fungus that infects coleoptiles, leaf blades, sheath, stems, glumes and seeds (Ou 1985; Sunder et al. 2014). Nodes and internodes are rarely infected (Ou 1985), although it can occasionally occur at the junction of the last leaf and the panicle stalk, resulting in partially filled to chaffy grains and panicles hanging over due to wet rot of the stalk (Sunder et al. 2014).

The most visible lesions appear on the leaves and glumes. In leaves, infections start as small circular or oval brown spots with near uniform distribution (Figure 1a); then lesions enlarge and have grey or whitish centres (Figure 1b; Burgos et al. 2013). In susceptible varieties, the lesion sizes can reach more than 1 cm in diameter (Ou 1985). Lesions are often surrounded by a yellow halo thought to be caused by toxins produced by the fungus (De Bruyne et al. 2016; Vidhyasekaran et al. 1986).

Infected rice seeds are spotted, and the fungus may be present only at the sterile lemmas or cover the entire surface of the grain (Mew and Gonzáles 2002). The embryo and endosperm are sometimes infected (Van Ba and Sangchote 2006).

3 | Other Host Plants of *B. oryzae*

In addition to Asian (*Oryza sativa*) and African (*Oryza glaberrima*) cultivated rice, *B. oryzae* has not only been described on many wild species of the genus *Oryza*, such as *Oryza australiensis*, *Oryza latifolia* and *Oryza rufipogon*, but also on species of the genus *Zizania*, including *Zizania aquatica*, *Zizania caduciflora*, *Zizania latifolia* and *Zizania palustris* (Farr and Rossman 2020; Liu et al. 2021; Manamgoda et al. 2014; Nyvall and Percich 1999). The symptoms described on *Oryza* wild rice and on *Zizania* leaves are similar to those described on cultivated rice.

Bipolaris oryzae was also reported on *Alopecurus aequalis*, *Alopecurus geniculatus*, *Arachis hypogaea*, *Chikusichloa aquatica*, *Cordia trichotoma*, *Cosmos bipinnatus*, *Cunninghamia lanceolata*, *Brachypodium distachyon*, *Echinochloa crus-galli*, *Eleusine indica*, *Leersia hexandra*, *Ischaemum rugosum*, *Panicum colonum*, *Panicum maximum*, *Panicum virgatum*, *Setaria italica*, *Strelitzia nicolai*, *Triticum aestivum*, *Typha orientalis* and *Zea mays* (Farr and Rossman 2020; Huang et al. 2018; Kaspary et al. 2018, 2019; Krupinsky et al. 2004; Sunder et al. 2014; Wang et al. 2019). Some of these plant species are found in rice fields and may act as alternative hosts (Chakrabarti 2001; Kumar et al. 2017).

4 | Brown Spot Disease Assessment and Worldwide Impact on Yield

Epidemiological studies have estimated the impact of BS on rice (Table 1), which largely depends on the type of varieties of the host, plant age at the time of infection, environmental conditions and crop management (Choudhury et al. 2019; Hossain et al. 2014). During the 1942 epidemic in Bengal, grain field losses were estimated to be between 40% and 90% and to have contributed to the 1943 great famine with approximately 2 million human deaths (Ghose et al. 1960; Padmanabhan 1973).

In the United States, the severity of BS in *Zizania* grain production can reach 52% of leaf area covered by lesions, and estimations indicated that BS could cause the State of Minnesota annual losses of $2.5 million (Nyvall et al. 1995). In Nepal, depending on the cultivars, average leaf severity is estimated to

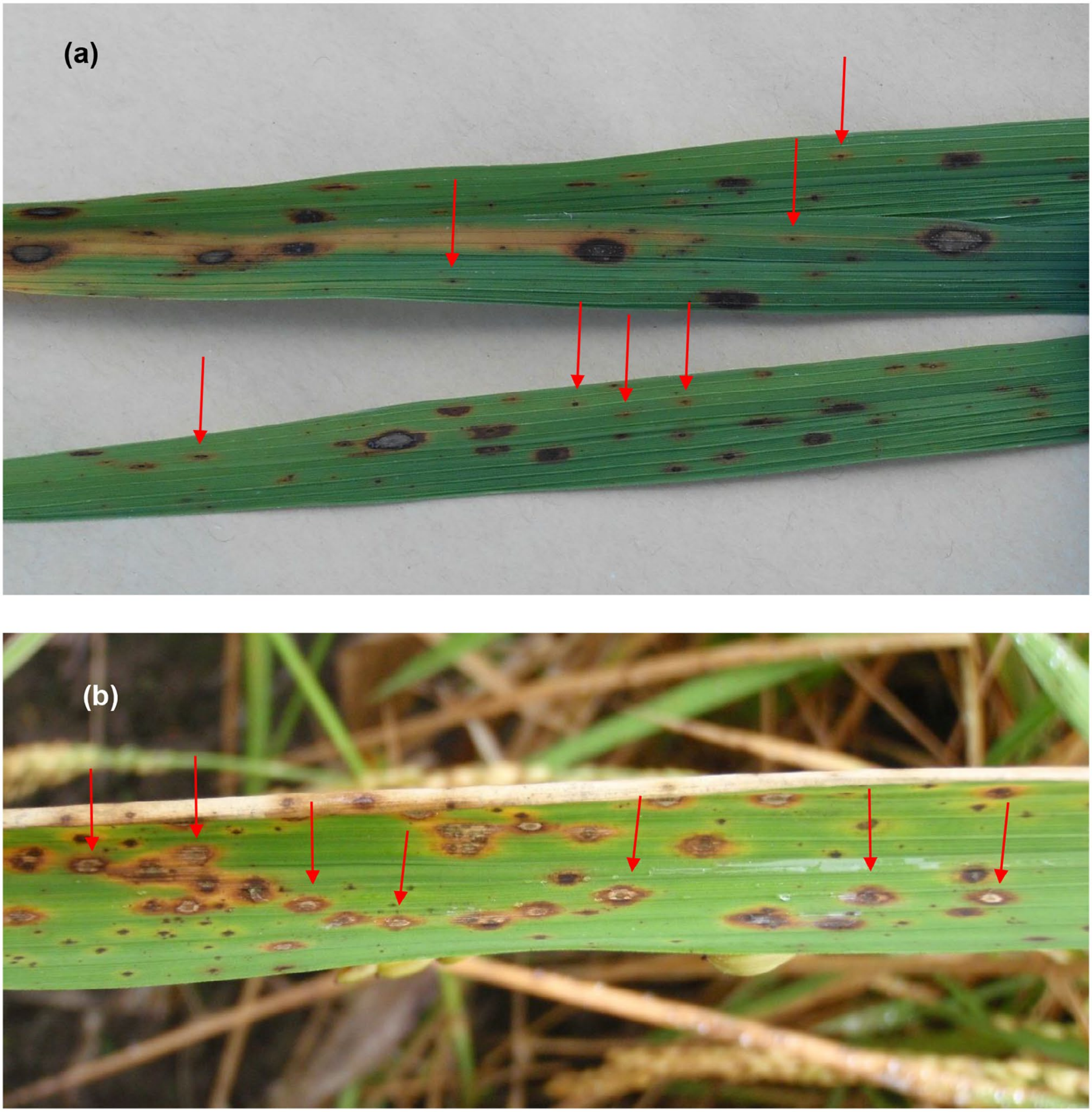

FIGURE 1 | Symptoms of brown spot on rice. (a) Small brown spots (red arrows) caused by *Bipolaris oryzae* at early stages of infection on leaves of rice variety KBR4 in Sourou, Burkina Faso. (b) Brown lesions with grey centre and yellow margin (red arrows) caused by *B. oryzae* on rice leaves in Yunnan, China.

range from 20% to over 50% (Magar 2015; Pantha et al. 2017), and from 45% to 77% in Bangladesh with incidence values of 40%–80% (Rashed et al. 2002). In Africa, average grain yield losses of 12%–24% (Awoderu 1974), 8%–23% (Fomba and Singh 1990) and 10%–16% (Ouédraogo 2008) were recorded in Nigeria, Sierra Leone and Burkina Faso, respectively. In food-insecure regions such as sub-Saharan Africa and the Indo-Gangetic Plain, crop losses due to BS are high, representing 3% and 5%, respectively, of total rice production in these regions (Savary et al. 2019).

Direct evaluation of losses caused by BS on rice grain yields is scarce. An accurate assessment of such losses requires a dedicated experimental approach conducted under natural field epidemics. Losses are then measured by comparing yields of a treatment with total protection (using fungicides) to obtain a disease level close to zero with yields from plots without any disease control. The majority of studies reporting loss estimates assessed the reaction of varieties with respect to the disease by referring to the incidence and/or severity of the disease using standardised methods such as the Standard Evaluation System for Rice of the International Rice Research Institute (Table 1) (IRRI 2013). For the few grain yield loss assessment studies carried out around the world, some of the data are old and may not reflect current reality. In addition, the results of grain yield loss assessments carried out in

TABLE 1 | Summary of the incidence, severity and loss of rice grain yield caused by brown spot disease over the last three decades.

Country or geographical area	Incidence[a] (%)	Severity[b] (%)	Grain yield loss (%)	Method and evaluation period	Sample size and geographic coverage	Reference
Asia	ND[c]	ND	> 0.4 t/ha	Modelling and natural infection	Surveys carried out in farmers' fields over 24 years (1987–2011)	Savary et al. (2021)
Bangladesh	ND	21–45	ND	IRRI[d], natural infection, doughy grain stage	Five varieties on experimental plots of BSMRAU Gazipur	Hossain et al. (2014)
Bangladesh	ND	26–48	ND	IRRI, natural infection	Eight varieties of aromatic rice on experimental plots in Dinajpur district	Kakoly et al. (2014)
Bangladesh	40.5–80	45–77	ND	IRRI, natural infection, 50–70 days after transplanting	Sixteen varieties on experimental plots from Bangladesh Agricultural University, Mymensingh	Rashed et al. (2002)
Bangladesh	15.5–25.8	0.6–4	ND	IRRI, natural infection, maturation	Fifteen varieties on experimental plots from Sher-e-Bangla Agricultural University, Dhaka	Faruq et al. (2015)
Bangladesh	ND	ND	18–22	IRRI, artificial inoculation	BR24 variety in greenhouse	Kamal and Mia (2009)
Burkina Faso	ND	1–38	1–16	IRRI, natural infection	Forty rice genotypes produced in vallée du Kou and Karfiguela	Ouédraogo (2008)
China	ND	ND	3.2	Survey by crop health experts	Experts surveyed between November 2016 and January 2017	Savary et al. (2019)
India	15–39	ND	ND	IRRI, natural infection	One hundred and sixty rice fields in four regions (Kollidam, Vaitheeswarankoil, Parangipettai and Bhuvanagiri)	Sumathra and Jaiganesh (2020)
India	ND	1–16	0.8–34	IRRI, natural infection	Nine varieties on farmers' fields in 15 districts of Punjab	Pannu et al. (2006)
Indo-Gangetic Plain	ND	ND	5.8	Survey by crop health experts	Two experts surveyed between November 2016 and January 2017	Savary et al. (2019)
Indonesia	ND	11–40	10–56	IRRI, artificial inoculation	Twenty-four varieties on farmers' fields, Lasiana, Kupang District	Mau et al. (2020)
Ivory Coast	ND	ND	20–56	IRRI[d], natural infection	Ten rice genotypes produced in Gbombelo	Bouet et al. (2022)

(Continues)

TABLE 1 | (Continued)

Country or geographical area	Incidence[a] (%)	Severity[b] (%)	Grain yield loss (%)	Method and evaluation period	Sample size and geographic coverage	Reference
Nepal	ND	21–69	ND	IRRI, natural infection, 66 days after transplanting	Twenty varieties on experimental plots of NRRP, Hardinath, Dhanusha	Pantha et al. (2017)
Nepal	ND	24–51	ND	IRRI[d], natural infection	Twelve varieties on experimental plots of IAAS, Paklihawa Campus, Bhairahawa	Aryal et al. (2016)
Nepal	ND	21–58	ND	IRRI, natural infection, 80 days after transplanting	Fourteen varieties on experimental plots of KRDC, Jyotinagar, Chitwan	Magar (2015)
Pakistan	1–14	6–51	ND	IRRI, natural infection	Four varieties on farmers' fields in 18 districts of Punjab	Choudhury et al. (2019)
Sierra Leone	ND	ND	8.2–23	IRRI, natural infection	Six varieties produced in the mangroves of Rokupr, Kibanka and Moribaia	Fomba and Singh (1990)
South-East Asia	ND	ND	2.9	Survey by crop health experts	Thirteen experts surveyed between November 2016 and January 2017	Savary et al. (2019)
Sub-Saharan Africa	ND	ND	3	Survey by crop health expert	One expert surveyed between November 2016 and January 2017	Savary et al. (2019)
Tanzania	35–99	5–25	ND	IRRI, natural infection	Twenty-seven farmers' fields in four districts in the Morogoro region	Mwakasege (2015)
Tropical Asia	ND	ND	5	Modelling and natural infection	Six sites in tropical Asian (456 farmers' fields)	Savary et al. (2000)
USA	ND	1–52	ND	Rating, natural infection	Two Minnesota fields	Nyvall et al. (1995)

[a]Incidence is the number of diseased plants divided by the total number of plants observed × 100.
[b]Severity is the leaf or panicle area covered by disease divided by the total leaf or panicle area × 100.
[c]ND, not reported in the study.
[d]IRRI, International Rice Research Institute. Assessment made using the Standard Evaluation System for Rice (IRRI 2013).

controlled environments should be treated with caution, as they could underestimate the interaction of the disease with its environment. As a result, losses may be under- or overestimated. Although highly valuable, the evaluation of crop losses in Savary et al. (2019) is based on a survey of experts' opinions and is probably limited by the low number of responses received from certain geographical areas.

Prevalence (percentage of infected seed lots) and rates of rice seed infection by *B. oryzae* (percentage of infected seed) are summarised in Table 2. Seed health assessments have shown that, depending on the rice-growing area, prevalence may vary from 77% to 97% in Burkina Faso (Ouédraogo et al. 2016), 38% to 100% in Ghana (Sadia 2012) and 37% to 90% in Brazil (Meneses et al. 2014). The percentage of infected seeds is high to moderate, reaching 76% in Burkina Faso, 72% in Nepal, 45% in Pakistan and 41% in Bangladesh. The average rate of rice seeds infected by *B. oryzae* in some regions of Brazil is higher than the 5% rate tolerated in seed regulations (Meneses et al. 2014). Depending on the level of infection, *B. oryzae* can reduce rice grain germination by 20%–84% (Kamal and Mia 2009). Infected rice grains mostly develop rotten coleoptiles and young roots (Nghiep and Gaur 2004). This leads to seedling damping-off, which can be very detrimental, especially to the success of the annual crop establishment in rainfed rice paddies. Grains infected with *B. oryzae* have direct consequences for their postharvest processing and, in addition, grains heavily infected have a sour taste after cooking, making them unfit for human consumption or even animal feed (Chakrabarti 2001). Based on BS disease assessment and general impact, BS is a serious disease of rice that negatively affects the productivity of various rice-growing systems, threatening food supply.

5 | Morphological Diversity of *B. oryzae*

This part of the review discusses the morphological descriptions of *B. oryzae*. We have retained only publications where the strains characterised had been previously assigned to *B. oryzae* using molecular tools. *B. oryzae* is a fungal species with morphological variability. A wide range of colony colours has been observed on samples collected within and from different countries. Isolates from India grown on potato dextrose agar (PDA) medium were black, grey, white, olive and variations of those colours (Kumar et al. 2011, 2016; Nayak and Hiremath 2019). Isolates from Thailand ranged from pale to dark grey and to olive (Chaijuckam et al. 2019; Marin-Felix et al. 2017), while isolates from Egypt were olive and olive-white (El Shafey et al. 2011).

Conidia are slightly curved with a bulge in the middle and tapering towards the extremities (Ou 1985). Conidia vary in size depending on the strain and geographical location where they were collected. Lengths of 63–99 μm long were reported in north-central Thailand (Chaijuckam et al. 2019), and of 112–116 μm in India (Kumar et al. 2016). Conidia of Indian isolates were 50–155 μm in length and 10–22 μm in width, with the majority of populations between 68 and 108 × 14–20 μm in length and width, respectively, and were 6–12 distoseptate (Manamgoda et al. 2014). Conidiophore dimensions vary from 150 to 625 × 6–8 μm.

When *B. oryzae* conidia are placed on culture medium, germ tubes may be formed from each of the terminal cells (polar germination), from intermediate cells (intercalary germination) or from a single polar cell (monopolar germination). Bipolar germination is predominant, irrespective of the nutrient medium and the geographical origin of the strains (Dela Paz et al. 2006).

Sexual structures of *B. oryzae* can be induced on Sach agar containing sterilised rice stem pieces (Ahmadpour et al. 2018; Ueyama and Tsuda 1975). The globose, black ascomata have diameters between 360 and 780 μm (Manamgoda et al. 2014; Sivanesan 1987). Clavate or broadly fusoid asci vary from 140–235 μm in length to 21–26 μm in width, and often contain 4 or 8 spores. The ascospores are filiform or flagelliform, with sizes of 235–470 μm in length to 4–9 μm in width and 8–12 septa (Manamgoda et al. 2014; Sivanesan 1987).

Molecularly identified isolates of *B. oryzae* species indicate that both asexual and sexual structures have diverse morphologies when grown in PDA or Sach agar, respectively.

6 | Reproduction of *B. oryzae* in the Field and Disease Cycle

The sexual and asexual cycles of the fungus can be induced under controlled environmental conditions. In the field, the fungus reproduces predominantly asexually. Asexual spores (conidia) are produced from specialised hyphae (conidiophores) developed from fungal infected tissue. Conidia emit germ tubes that adhere to the leaf surface via mucilaginous substances (Ou 1985). In most cases, the fungus forms an appressorium that allows direct penetration of leaf cells (Hau and Rush 1982; Ou 1985). In some rare cases, germ tubes penetrate through stomata (Horino & Akai 1966 cited by Ou 1985). The infecting hyphae invade the mesophyll and lesions appear between 18 and 36 h post-infection (Dallagnol et al. 2009; Johnson and Percich 1992; Tullis 1935). It is thought that 10–14 days is sufficient for *B. oryzae* in wild rice (*Zizania palustris*) to complete a cycle and produce conidia (Johnson and Percich 1992), while in cultivated rice, the peak of production of new conidia from lesions is about 6 days after infection (Barnwal et al. 2013; Ou 1985).

Bipolaris oryzae is a heterothallic fungus, that is, its sexual reproduction requires strains of opposite mating types idiomorphs (MAT1-1 and MAT1-2) (Ueyama and Tsuda 1976). Structurally and functionally, the mating type idiomorph sequences are dissimilar (Turgeon et al. 1995). Recombination within idiomorphs is not observed and each idiomorph is inherited from a single parent (Turgeon 1998). Molecular characterisation of isolates from the same rice fields indicates the coexistence of MAT1-1 and MAT1-2 isolates in nearly equal proportions and a small group of isolates was capable of sexual reproduction in vitro (Ahmadpour et al. 2018; Castell-Miller and Samac 2012; Kaboré et al. 2022; Shamsi et al. 2010). The coexistence of MAT1-1 and MAT1-2 is necessary but not sufficient for sexual reproduction to take place. In addition to the presence of both mating types, sexual reproduction requires a complex process from the production of gametes to the production of sexual spores (Leslie and Klein 1996). In fungi, fertility determinants are sometimes lost, making sexual reproduction impossible (Leslie and Klein 1996).

TABLE 2 | Summary of the prevalence and level of infection of rice seed by *Bipolaris oryzae*.

Country or geographical area	Prevalence[a] (%)	Seed infection rates[b] (%)	Method of evaluation	Sample size and geographic coverage	Reference
Bangladesh	ND[c]	18–41	ISTA[d], on filter paper	Five cultivars from experimental plots of BSMRAU, Gazipur	Hossain et al. (2014)
Brazil	37–90	0.6–8	ISTA, on filter paper	Seven hundred and twenty-two seed lots from six rice regions of Rio Grando	Meneses et al. (2014)
Burkina Faso	77–97	2–76	ISTA, on filter paper	One hundred and fifty-one grain lots from 28 sites in four provinces (Comoé, Houet, Mouhoun and Sourou)	Ouédraogo et al. (2016)
Ghana	38–100	0.5–29	ISTA, on filter paper	Thirty-three grain lots from four agro-ecological zones (Sudan Savannah, Savannah, Forest Zone and Coastal Savannah)	Sadia (2012)
India	62	6–15	ISTA, on paper and culture	Thirty seed lots of seven rice varieties from Tamil Nadu (South India)	Naveenkumar et al. (2016)
Nepal	ND	8–72	ISTA, on filter paper	Twenty rice genotypes collected by Nepal Agricultural Research Council, Hardinath, Dhanusha	Pantha and Yadav (2016)
Pakistan	ND	22–45	ISTA, on culture	Samples from Rice Research Institute, Kala Shah Kaku	Habib et al. (2012)
Sierra Leone	ND	4–25	ISTA, on filter paper	Seven varieties from the stock of the Rokupr Agricultural Research Centre, Kambia District	Taylor and Ngaujah (2016)
USA	ND	11–35	ISTA, on filter paper	Grains collected from two fields in Minnesota	Nyvall et al. (1995)

[a]Prevalence is obtained by dividing the lots infected with *B. oryzae* by the total number of lots collected × 100.
[b]Seed infection rate is obtained by dividing the number of *B. oryzae*-bearing grains by the total number of grains observed × 100.
[c]ND, not reported in the study.
[d]ISTA, International Rules for Seed Testing.

In wild rice fields in the United States and some Asian countries, *B. oryzae* isolates were found to have balanced mating types, but linkage disequilibrium (LD) tests (i.e., index of association) rejected the hypothesis of random mating (Ahmadpour et al. 2018; Castell-Miller and Samac 2012). High genotypic diversity and low LD can alternatively be explained by a high frequency of migration (Milgroom 1996) and sampling in several differentiated populations (De Meeûs and Balloux 2004). Failure to detect random mating may be due to a lack of power of the test, undetected substructures or migrations. In contrast to previous results, genomic studies of *B. oryzae* populations from Burkina Faso showed clear evidence of genome-wide recombination (Kaboré et al. 2022). These recent results, combined with balanced mating types in local populations, support the existence of sexual reproduction.

Mating-type frequencies, crossing tests and high genotypic diversity are consistent with the existence of sexual reproduction in some populations of *B. oryzae* (Ahmadpour et al. 2018; Castell-Miller and Samac 2012). However, the failure to demonstrate random mating and to observe pseudothecia in the field do not support this hypothesis. Asexual reproduction is thought to be the dominant mode of reproduction of *B. oryzae* populations in rice fields. Additional research is needed to fully understand the observed results and to define new strategies (when? where? and how?) to search for evidence of sexual reproduction (i.e., pseudothecia) in the field. Such strategies could be based on results from epidemiological studies and on population genetics. Epidemiological information is needed to make hypotheses on when and where to look for sexual reproduction. In some species, perithecia are resting structures allowing overwintering or survival between cropping seasons. Does this apply to *B. oryzae*? Can sexual reproduction take place on debris? Are there alternative hosts? Population structure can inform on where to search. In heterothallic fungi, both mating types are maintained in balanced frequency when species reproduce sexually. So, evidence of sexual reproduction must be searched for in places where both mating types are balanced. Molecular markers for the mating types could help to perform such surveys at the field scale.

7 | Pathological Diversity of *B. oryzae*

Pathogenicity tests of *B. oryzae* strains are usually carried out on rice varieties with different levels of BS resistance. The pathogenicity of isolates combines the range of varieties they infect (virulence spectrum) and their aggressiveness (quantity of symptoms on a given variety). Inoculation of 20 varieties of rice with 24 *B. oryzae* isolates collected in Egypt found eight strains capable of infecting all varieties (El Shafey et al. 2011). Based on the level of aggressiveness and the range of infected varieties, *B. oryzae* isolates from Ivory Coast, Burkina Faso, and Togo were divided into three groups independently of their geographical origin (Boka et al. 2018). Kamal and Mia (2009) found no agreement between strain pathogenicity and groups of isolates with different genetic variations. For example, the BO 423 strain belonging to the FPT1 genetic group induces a level of post-emergence damping-off similar to the BO 021 strain of the FPT12 genetic group. On the other hand, strains BO 617 and BO 019, both belonging to the genetic group FPT10, did not have the same level of aggressiveness. Pathogenicity tests on the rice variety IR72 with 15 strains belonging to the genetic haplotype CQ-E112 from the Philippines also showed pathogenic variability (Burgos et al. 2013). Geographical origin and genetic groups do not appear to explain the pathological variability of *B. oryzae* strains.

8 | Population Genetics of *B. oryzae*

Population structure is defined as the distribution in space and time of the genetic and genotypic diversity of populations (Carbone and Kohn 2004; Clark 2001). Estimates of genetic diversity are based on the number and frequencies of alleles at a single locus in a population, while genotypic diversity is calculated based on the number and frequency of multilocus genotypes (i.e., combinations of alleles at different loci [Carbone and Kohn 2004; Grünwald et al. 2003; Milgroom 1996]). In crop protection, the amount of genetic diversity and its distribution are used to characterise the biology (e.g., reproduction mode) and epidemiology (e.g., migration rate) of the pathogen and to improve control strategies (e.g., management of varietal resistances).

Studies on the genetic diversity of *B. oryzae* have been carried out using several molecular tools in different parts of the world. Most populations show high genotypic diversity with the exception of isolates from Thailand (Chaijuckam et al. 2019). Populations from Bangladesh (Kamal and Mia 2009), India (Archana et al. 2014a, 2014b; Kandan et al. 2015), Iran (Nazari et al. 2015), United States (Castell-Miller and Samac 2012) and Burkina Faso (Kaboré et al. 2022) were diverse with no or little geographical structure within the areas under study. A possibility is that sexual reproduction and long-distance dispersal of propagules could explain the genotypic diversity and population structures observed. Alternatively, seed exchange between producers in different regions of India was proposed as the potential cause of the dispersal of genotypes of *B. oryzae* over the entire territory (Archana et al. 2014a). Microsatellite (SSR) analysis of *B. oryzae* isolates from three Asian countries (Iran, Philippines and Japan) revealed a diversity between isolates within the same site and a population structure in three groups, partially explained by geography (Ahmadpour et al. 2018). In Iran, the absence of a significant correlation between cultivars of origin and fungal haplotypes seems to indicate that the pathogen structure is not determined by the host (Motlagh and Anvari 2010). By contrast, a study conducted with repeated tandem sequences (VNTR) by Burgos et al. (2013) showed that, in the Philippines, the diversity of the *B. oryzae* population at the field scale was very limited and that geography and varieties could explain the observed structure.

As stated previously, high genotypic diversity, low clonal fractions and alleles in linkage equilibrium are indications of sexual reproduction in heterothallic fungi (Milgroom 1996). High genotypic diversity and low clonal fraction were observed in several *B. oryzae* populations from Bangladesh, India, Iran, Japan, the United States and Burkina Faso (Ahmadpour et al. 2018; Castell-Miller and Samac 2012; Kaboré et al. 2022; Kamal and Mia 2009; Kumar et al. 2016; Kumar et al. 2011; Motlagh and Anvari 2010; Nazari et al. 2015). A collection of 168 *B. oryzae* isolates isolated from cultivated *Z. palustris* in the United States produced 102 haplotypes (Castell-Miller and Samac 2012). In *O. sativa*, Ahmadpour et al. (2018) observed 278 haplotypes within 288 isolates from three countries in Asia (Iran, Philippines and Japan).

From population genetics of *B. oryzae*, it can be concluded that the distribution of the genetic diversity of *B. oryzae* populations is generally neither associated with their geographical origin nor with the rice variety they were isolated from. Populations of *B. oryzae* are genetically variable, with often low population structure, suggesting important gene flow.

9 | Management of BS Disease

Management strategies used in rice for control of BS were reviewed recently (Barnwal et al. 2013; Imran et al. 2020; Sattari et al. 2015; Surendhar et al. 2021). The most usual approaches are cultural techniques, varietal resistance, biological control and synthetic fungicides (Imran et al. 2020; Pandey and Sharma 2019; Sattari et al. 2015; Surendhar et al. 2021).

9.1 | Cultural Management

Cultural practices to control BS are good soil moisture, destruction of alternate hosts and infected crop residues, use of healthy seed and a balance of certain micro- and macro-elements in the soil. The influence of soil mineral elements on BS has long been noted (Ou 1985; Zadoks 1974). This is an essential factor in the fight against BS. Much research on the impact of nitrogen (N), phosphorus (P), potassium (K) and silicon (Si) of various origins on BS has been conducted in different environments. Increasing N rates (0–180 kg/ha) in fields sown with different rice varieties in India led, on average, to a decrease (26%–10%) in leaf severity of BS (Sunder et al. 2005). A N supply of 100 mg/kg soil induced a 21% decrease in leaf severity (Carvalho et al. 2010). In Sri Lanka, inorganic inputs of 103.5 kg/ha of N (urea 46%), 3.9 kg/ha of P ($P_2 0_5$ 43.7%) and 30 kg/ha of K (K_2O 60%) were optimal for effective control of BS (Priyadashani et al. 2022). Silicon, in different forms, decreases BS impact, sometimes very significantly, leading to doubled grain production and reduction of up to 78% and 88% of disease incidence and severity, respectively (Dallagnol et al. 2014; Malav and Ramani 2015; Ning et al. 2014; Prabhu et al. 2012). Foliar application of zinc sulphate ($ZnSO_4$) at 3% also reduces the incidence of BS (22%) compared to untreated plants (64%) (Jaiganesh 2019). Thus, from the analysis of the impact of fertilisation on BS, it appears that mineral elements such as N, P, K and Si applied alone or in combination in a balanced manner protect the rice against BS and improve grain yields.

9.2 | Varietal Management

Varietal resistance is an effective and economical way for farmers to control BS (Sattari et al. 2015). It should reduce yield losses and fungicide use (Hossain et al. 2014). However, breeding efforts have not been as active as for other rice diseases such as leaf blast and bacterial blight (Savary et al. 2011). The first genetic analyses of resistance started in 2008, and three quantitative trait loci (QTLs) were identified on chromosomes 2, 9 and 11 of lines derived from crosses between cultivars Tadukan (resistant) and Hinohikari (susceptible) (Sato et al. 2008). On chromosomes 2, 7, 9 and 11 of lines derived from crosses between CH45 (resistant) and Koshihikari (susceptible), four QTLs were identified (Matsumoto et al. 2017; Mizobuchi et al. 2016). Four QTLs were also identified on chromosomes 3, 6, and 7 of lines derived from crosses between Dawn (resistant) and Koshihikari (susceptible) (Ota et al. 2021). Varietal screenings carried out in different countries have identified resistant or tolerant genotypes of cultivated rice that have been summarised in Table 3. Goel et al. (2006) identified four accessions of wild rice (*O. nivara*) resistant to BS. In many cases of the evaluation of cultivars/lines, no genotype with complete resistance to BS was identified. Therefore, resistance to BS appears to be quantitative and was shown to be subject to interactions with the environment (Sato et al. 2008, 2015). In addition to the influence of environmental conditions, the diversity of *B. oryzae* strains is also important. Varieties identified as resistant in BS screening need to be re-evaluated periodically because of the probable appearance of new, more virulent strains (Pantha et al. 2017). We conclude from this analysis that, although no complete resistance has been identified to date, breeding could exploit existing sources of quantitative resistance against BS.

9.3 | Biological Management

Biological management of BS is achieved through the use of plant extracts, antagonistic fungi and bacteria. Neem (*Azadirachta indica*) is one of the plants whose extract has shown efficacy against BS (Harish et al. 2008; Kumar and Simon 2016). When applied at the onset of symptoms and repeated 15 days later, it can reduce the incidence of BS by 75% and induce an increase in grain yield by 23% (Harish et al. 2008). Following the same protocol, *Nerium oleander* leaf extract reduced the incidence of BS by 53% with an 18% increase in grain yield (Harish et al. 2008). Essential oil of *Callistemon citrinus* as a seed treatment, combined with foliar treatments with ethanolic and aqueous extracts of the same plant or *Cymbopogon citratus*, significantly reduced BS of rice and increased grain yields by 25%–55% in irrigated rice and 54%–137% in rainfed rice (Nguefack et al. 2013).

Formulations of the fungus *Trichoderma harzianum* applied at 20 g/L at 60, 70 and 80 days after transplanting reduced disease levels by half and increased grain weight per panicle by more than 13% compared to untreated plots (Dey and Monjil 2016). Treatment of rice seed with *Trichoderma viride* combined with foliar treatments with *Pseudomonas fluorescens* reduced the severity of BS by 23% and resulted in a grain yield gain of 0.9 t/ha compared to untreated plots (Kumar et al. 2015).

9.4 | Chemical Management

BS is controlled by the application of synthetic fungicides either by seed and leaf treatments or by foliar treatments only. From various efficacy tests, propiconazole (triazole) was found to be the most effective product as a foliar treatment (Gupta et al. 2013; Kamei et al. 2020; Kumar et al. 2017; Poudel et al. 2019; Shrestha et al. 2017; Sunder et al. 2005). However, the dose and timing of application are important. According to Gupta et al. (2013), foliar

TABLE 3 | Rice cultivars and breeding lines resistant or tolerant to brown spot disease.

Country	Resistant or tolerant cultivars/breeding lines	References
India	NDR-359, CR-1, CR-2, N-18, PR-103, IR-36, Prasd, Narenda-2, IR-597, OC-1339, Cross-116, Rasi, JGL-1798, BR-2655, Raksha, KMP-201, BI-33, Sagbatta, Honnekattu, Klame, Kavekantak, Togarshi, Rajabhog, KMP-153, Akkalu, MTU-1010, Sagvad, Bilidodibudda, Sannamullu, CTH-1, IET-23403, IET-22876, IET-23392	Alam et al. (2016), Channakeshava and Pankaja (2018), Hosagoudar et al. (2019)
Iran	Gharib-Siyah-Reihani	Dariush et al. (2020)
Ivory Coast	Wita9, Bouaké-am, NIL130, WAS 63–22–5-1-7-7, JT2, CK801, ARCC3Fa3L10P1-1-B-1, WAB 891-SG12	Bouet et al. (2015, 2022)
Nepal	Kabeli Radha-4, Sabitri	Aryal et al. (2016), Pantha et al. (2017)
Nigeria	ITA 123, Suakoko	Nneke (2012)
Pakistan	HHZB, IR80416-B-32-3, IR84677-34-1-B, HHZ11-Y6-Y1-Y1, SACG 4, JH-15-1-1-1, RSP-4, IRRI-43, PARC-1, PARC-7, PARC-8, PARC-13	Arshad et al. (2013), Ashfaq et al. (2021), Yaqoob (2015), Yaqoob et al. (2011)
Uganda	NM-22-1, NM-22-2, NM-22-3, E22, NERICA 10, NERICA 4, E1, E11, P27H4, E186, E51, P8H13, E123, E3, E104, E99, E16, E135, E8, P26H6, P27H3, P3R1, P55H7	Lamo et al. (2021), Mwendo et al. (2017)

application of propiconazole at 0.1% at the onset of symptoms reduced the severity of BS by more than 60% and resulted in an increase in grain yields of more than 10% compared to untreated plots. When propiconazole applications are made until half of the panicles emerge, the reduction in foliar incidence reaches 86% with an improvement in grain yield of more than 14% (Sunder et al. 2005). The efficacy of propineb (dithiocarbamate) on BS is close to that of propiconazole (Kamei et al. 2020). Foliar treatments with propineb (70% at 2.5 kg/ha) from day 20 after sowing to the heading stage resulted in grain yield gains of 80% compared to plots without protection (Bouet et al. 2020). Seed treatment with carbendazim (benzimidazole) at a dose of 2 g/kg combined with foliar treatment with propiconazole at a dose of 1 mL/L reduces severity by 37%, inducing an increase in grain yields of 55% (Kumar et al. 2017). The mixtures azoxystrobin (strobilurin) + tebuconazole (triazole; Poudel et al. 2019), carbendazim + mancozeb (dithiocarbamate; Shrestha et al. 2017), azoxystrobin + difenoconazole (triazole; Barúa et al. 2019) and trifloxystrobin (strobilurin) + tebuconazole (Boka and Denezon 2020) significantly reduced the severity of BS and induced yield gains. Although many formulations are effective against BS, their use must be carefully considered in view of the potentially harmful consequences for humans and the environment and the possibility of the development of resistant strains.

9.5 | Integrated Management

The different control methods against BS applied individually have their limitations (e.g., resistance of *B. oryzae* isolates to fungicides, breakdown of varietal resistance). Effective control of BS requires an integrated approach that combines different control methods (Jaiganesh et al. 2019). Management strategies used in rice for the control of BS were reviewed recently (Barnwal et al. 2013; Imran et al. 2020; Sattari et al. 2015; Surendhar et al. 2021). These include the use of fertilisers such as organo-mineral fertilisation (farmyard manure, diammonium phosphate and muriate of potash and NPK) of the soil in addition to chemical treatments of the seed (e.g., carbendazim) combined with foliar treatments with fungicides such as tricyclazole, carbendazim and mancozeb at the grain-filling stage (Chelak et al. 2019). In an investigation of the fungicide difenoconazole (250 EC) on rice, it was found that it decreased the incidence of BS and gave the best revenue per hectare in combination with foliar fertilisation (NPK 20:20:20 at the rate of 500 g/ha) (Asghar et al. 2019). In Florida, the greatest reduction in BS development was obtained by integrating silicon fertilisation with propiconazole (Datnoff et al. 1997). In addition, the absence of water stress increases the tolerance of rice genotypes (Dariush et al. 2020).

Thus, a combination of soil fertility management, good water supply, use of resistant or tolerant varieties, seed disinfection and plant biological and chemical treatments can reduce the impact of BS of rice.

10 | Conclusion and Recommendations for Future Studies

BS of rice is a fungal disease that impacts rice productivity worldwide, and recent decades have witnessed a significant resurgence in several countries. Morphological characterisation studies carried out on *B. oryzae*, the main causal agent of BS of rice, have shown that its asexual and sexual structures are highly variable. Traditionally, asexual and/or sexual structures were the characters used for species identification. However, the advent of molecular tools has enabled the identification of other fungal species, in combination with *B. oryzae* or individually, to be isolated from typical BS symptoms (Barro et al. 2021; Kaboré et al. 2022). The role of these species in epidemics of rice BS needs to be elucidated in future studies.

In many rice-growing countries, the incidence and severity of BS have been measured by standardised methods such as the Standard Evaluation System for Rice of the International Rice Research Institute (IRRI 2013). The pathological diversity of *B. oryzae* isolates has also been demonstrated. However, more needs to be done to quantify rice grain yield losses and to calculate the financial impact for farmers and the effect on food security. Epidemiological approaches to BS of rice must be combined with socio-economic approaches.

Biology and genetics show that populations of *B. oryzae* can be clonal or recombinant. Recombination is most probably due to sexual reproduction, which is suspected to be frequent but has not been observed in rice fields. Therefore, it is necessary to develop methods to investigate the sexual reproduction structures of *B. oryzae* in rice fields, as has been carried out for *Mycosphaerella graminicola* on wheat (Eriksen and Munk 2003; Suffert et al. 2011). Most studies on the genetic diversity of *B. oryzae* have been conducted in Asia. However, as increasing occurrences of outbreaks have also been reported in Africa, South America and Europe, similar phenotypic and genetic diversity studies should be carried out in these continents. In addition, a better characterisation of the structure of *B. oryzae* populations, representative of rice cultivation areas on a continent-wide or even on a worldwide scale, is necessary to improve our knowledge of the biology of the pathogen. This step may prove invaluable in managing the disease through more efficient regulatory measures. Today, next-generation sequencing technologies, such as genotyping by sequencing, offer the possibility of processing thousands of isolates (Bhatia et al. 2013; Kaboré et al. 2022).

Varietal resistance is an important component of any integrated BS management system. Unfortunately, to date, research work remains focused on finding sources of resistance. We note the lack of use of modern and efficient breeding technologies for varieties against BS. Yet, genetic markers flanking QTLs offer an opportunity to create BS-resistant varieties using marker-assisted selection (Matsumoto et al. 2017).

To date, genomic studies of *B. oryzae* are limited. The reference genome of *B. oryzae* was obtained from the WK1C strain (ATCC 44560) isolated from rice in Taiwan and has a size of more than 31 Mb (Condon et al. 2013). The whole genome of the TG12bL2 strain isolated from wild rice (*Z. palustris*) was also sequenced (Castell-Miller et al. 2016). Deng et al. (2019) recently sequenced the mitochondrial genome of *B. oryzae*. Producing whole genome sequence data for more strains and for phylogenetically close species would be useful for conducting population genomics studies and developing diagnostic tools for species-specific detection of the fungus.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article, as no new data were created or analyzed in this study.

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