



The pathogen and control management of rice blast disease

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ABSTRACT

Outbreak of rice blast disease is a serious problem in all rice growing regions worldwide and is a threat to rice production. In Malaysia, the outbreak of rice blast is a recurrent problem where rice plant remain vulnerable to the disease. Nowadays, the generic name of rice blast pathogen is *Pyricularia oryzae* and *Magnaporthe oryzae* is the synonym. Rice pathogen infects mainly aerial parts of rice plant causing rotting and blast on the leaves, stems, peduncles, panicles and seeds leading to crop failure. Rice blast pathogen population is regarded as highly variable and consisted of multiple pathotypes which contribute to genetic diversity as well virulence diversity of the pathogen. The pathotypes can only be determined through pathogenicity test using a set of differential rice cultivars which generally differ by one or more resistance genes. Knowledge on the rice blast virulence and host resistant is important to manage the disease. Among the control methods, utilizing resistant cultivars is considered as the most effective approach to manage rice blast disease. Therefore, development of blast resistant cultivar becomes a priority.

Keywords: rice blast, *Pyricularia oryzae*, rice

INTRODUCTION

Rice blast is one of the most destructive diseases affecting rice (*Oryza sativa*) and is responsible for yield loss in epidemically favourable areas and crop seasons. The first known occurrence of rice blast was in China, where this disease was known as rice fever disease (Wang and Valent, 2009). The disease occurs in all regions where rice is cultivated and has been reported from more than 85 countries (Kato, 2001). Therefore, rice blast can seriously affect food security, especially in Asian countries where 55% of the world population lives and 92% of rice is grown and consumed (Wilson and Talbot, 2009). As population growth in these rice-cultivating areas is increasing rapidly, the demand for rice production has also increased per year by 3% (Barker *et al.*, 1985). Based on the analysis by International Food Policy Research Institute, a 38% increase in rice production by 2030 will be required to feed the increasing population sufficiently. Moreover, as more land that is arable being utilized for housing and establishment of industries, the amount of land area available for rice cultivation is decreasing progressively (Wilson and Talbot, 2009).

Rice blast is caused by *P. oryzae* (syn. *M. oryzae*) and this pathogen is highly adaptable to a wide arrange of environmental conditions. Rice blast disease has been observed in irrigated lowland, rain-fed upland, as well as

deepwater rice fields (Manibhushan Rao, 1994). Rice plants may get infected at any stage of growth by conidia of the fungi. Inoculum sources are mainly infested crop residue and seed (Bonman, 1992). Seed-borne inoculum is regarded as the primary cause of infection; however, weeds may also serve as the source of primary inoculum (Bonman, 1992). The symptoms of infection are lesions or spots on various parts of the plant including leaves, leaf collars, necks, panicles, pedicels, and seeds (TeBeest *et al.*, 2007). Leaf blast infection can kill seedlings or rice plants up to tillering stage. A severe infection at later stages of growth reduces leaf area for grain fill, thereby reducing yield (Rice Knowledge Bank <http://www.knowledgebank.irri.org>).

In Malaysia, the incidence of rice blast has been increasing from year to year and about 4033 ha area was affected during the outbreak in 2005 (Malaysian Quarantine Inspection Services, Department of Agriculture, unpublished data). Based on this data, although the affected area was less than 5% of the paddy planted area, the yield loss caused by the panicle blast was as high as 50-70%.

During the main rice-growing season of 2010/2011, a survey detected that several paddy fields in Kuala Muda, Yan, and Kota Setar in the state of Kedah were infected

with panicle blast. The infection occurred on a variety of rice, designated MR219, which was considered to be resistant to blast disease. The infection resulted in rotten panicles or broken grains or empty hulls, which in turn led to high yield losses (Informasi Pertanian, 2011).

Several new rice varieties were introduced by MARDI followed by the failure of MR219 to resist the infection, namely, MR253, MR263, and MR269, to reduce the infection and increase yield. The rice variety, MR284, introduced in 2015 was able to reduce the problems caused by leaves blast, panicle blast, as well as plant hopper infestation (Borneo Post Online, 2015). MARDI SIRAJ 297, another rice variety introduced in 2016, is resistant to leaves blast, panicle blast, and rice tungro disease, and also shows a lower resistance to brown planthopper infestation (MARDI Official Blog, 2016).

Muda Agricultural Development Authority (MADA) estimated that 10% of the 1006.85 km² paddy fields will be infected by the diseases, with 60,000 tons of rice being affected by neck and panicle blasts in the 2016/2017 second season of planting (Berita Harian, 2017). In such a case, the infection could incur huge losses and cut the paddy supply by 50%. The outbreak of rice blast is a recurrent problem in rice cultivating areas of Malaysia, where this is still an important and serious disease affecting rice as the plants remain vulnerable to the disease.

CLASSIFICATION AND NOMENCLATURE

The classification of the fungus is as follows: Division: Ascomycota, Subdivision: Pezizomycotina, Class: Sordariomycetes, Subclass: Sordariomycetidae, Order: Magnaporthales, Family: Pyriculariaceae, and Genus: *Pyricularia* (Mycobank, 2016).

Pyricularia is named after the pyriform shaped conidia of these fungi. The genus *Pyricularia* (Cooke) Sacc. was first described by Saccharo in 1880 based on isolation of *P. grisea* species from crabgrass (*Digitaria sanguinalis* L.). *Pyricularia* from rice, known as *P. oryzae* Cav., was identified by Cavara (1892) and this species has similar morphological characteristics to that of *P. grisea* (Bussaban *et al.*, 2005; Tosa and Chuma, 2014).

Pyricularia infects various other gramineous plants, including common millet, foxtail millet, finger millet, and wheat, in addition to rice plant (Kato *et al.*, 2000). Commonly, *P. oryzae* and *P. grisea* are studied in connection with blast disease. Although, *M. oryzae* and *M. grisea* are also studied extensively by researchers working on blast disease of rice and other crops.

Magnaporthe is the teleomorph stage of *Pyricularia*, which was first reported by Hebert (1971) by mating two *P. grisea* isolates from crabgrass, under the name *Ceratosphaeria grisea*. The teleomorph of *P. oryzae* was successfully produced by Japanese researchers by mating isolates from rice with isolates from finger millet (Ueyama and Tsuda, 1975; Kato *et al.*, 1976; Yaegashi and Nishihara, 1976). The name, *Magnaporthe grisea* was proposed by Barr (1977) and Yaegashi and Udagawa (1978). It was referred to the teleomorph stages

from the mating experiments conducted by Yaegashi and Udagawa (1978) among the blast isolates from rice, crabgrass, finger millet, and goosegrass. Pathogenicity tests demonstrated that cross-infectivity could occur between *M. grisea* isolates from crabgrass and those from rice (Choi *et al.*, 2013).

The teleomorph stage, *Magnaporthe*, is rarely encountered in nature and therefore, the fungus is generally referred by its anamorph stage name, *Pyricularia*. *P. oryzae*, the causative agent of rice blast was distinguished from *P. grisea* causing blast disease in grasses and other plants, based on their spore characteristics (Ellis, 1971). However, Rossman *et al.* (1990) do not agree with this differentiation as type specimens of both species are morphologically similar and the sexual stage can be produced when strains from rice and other hosts are crossed, suggesting that the two taxa are not genetically isolated as reported by Yaegashi and Udagawa (1978). According to Rossman *et al.* (1990), *P. oryzae* is synonymous with *P. grisea*, with the latter species name was preferred as rice blast pathogen.

With the advent of molecular methods applied in systematics and phylogenetic analysis of fungi, more information could be gathered to confirm the generic name of the blast pathogen as *Pyricularia* (syn. *Magnaporthe*) isolated from rice and other hosts. DNA fingerprinting has been used to identify and determine the genetic variation in blast isolates from rice and other grass hosts. A DNA repeat sequence present in the fungi, known as 'MGR' (*M. grisea* repeat) was reported to be able to distinguish rice blast pathogen from others and could be used as rice blast DNA fingerprinting for epidemiological studies (Hamer *et al.*, 1989). Several studies have also used the DNA fingerprinting to determine genetic variation in blast isolates from rice and other hosts (Levy *et al.*, 1991; Farman *et al.*, 1996; Dean *et al.*, 2005). Studies by Borromeo *et al.* (1993) and Kato *et al.* (2000) based on restriction analysis of mitochondrial DNA and Southern hybridisation using ribosomal, single-copy, and repetitive DNA probes, suggested that *Pyricularia* isolates from crabgrass and rice represent distinct species. Kato *et al.* (2000) also reported that interfertility occurs among isolates from rice, common millet, foxtail millet, and finger millet, and these isolates are biologically distinct from the isolates from crabgrass. The studies indicated that isolates from rice as well as other cereal grains were *P. oryzae* and *P. grisea* should be applied to blast isolates from crabgrass.

Phylogenetic species recognition approach based on concordance of multiple gene genealogies has become a well-known method to recognise and categorise fungal species (Taylor *et al.*, 2000). This approach has been applied in studies on the taxa of blast pathogen. Using multilocus phylogeny of three genes, actin, β -tubulin, and calmodulin, Couch and Kohn (2002) obtained similar results as Kato *et al.* (2000) and reported that these genes formed two clades. Of these, one clade consisted of isolates from rice and other cultivated grasses and the second clade comprised isolates from *Digitaria* spp. Couch and Kohn (2002) also reported that *M. oryzae* and

M. grisea are not interfertile, and concluded that the rice blast isolates were *M. oryzae*, whereas *M. grisea*, which was associated with *Digitaria* spp. warranted further nomenclature revision. These studies bring in an agreement between anamorphs and teleomorphs of blast isolates from rice and other hosts, wherein the teleomorph of *P. oryzae* is *M. oryzae* and that of *P. grisea* is *M. grisea*.

Hirata *et al.* (2007) used a multilocus phylogenetic analysis based on internal transcribed spacer (ITS), actin, β -tubulin, and calmodulin genes to examine *Pyricularia* isolates from various host plants. In their study, seven phylogenetic groups were obtained and among which *P. oryzae* formed a separate group. These phylogenetic analyses were then integrated with morphological and biological species identification criteria, and their results concluded that each of the seven phylogenetic groups is an evolutionary species and are monophyletic comprising *P. oryzae*, *P. grisea*, *P. zizaniaecola*, *P. zingiberi*, *P. higginsii* and two other cryptic species. These seven phylogenetic groups are regarded as a species complex, known as *P. grisea/P. oryzae* species complex or *M. grisea/M. oryzae* species complex.

Other phylogenetic studies have also shown that rice blast isolates formed a distinct group and suggested *Pyricularia* as generic name for the rice blast fungus. Zhang *et al.* (2011) reported that phylogenetic analysis based on six genes—*RPB1*, *TEF1*, *MCM7*, *ITS*, *SSU*, and *LSU*—showed that blast fungus (*P. oryzae/M. oryzae*), which has the capacity to infect both root and aerial parts of the plant, forms a separate clade. Similar results were reported by Luo and Zhang (2013) based on phylogenetic analysis of multiple genes, including *SSU*, *ITS*, *LSU*, *MCM7*, *RPB1*, and *TEF1*, among the plant pathogenic taxa in Magnaporthaceae. The analysis showed that the blast fungus was not congeneric with *M. salvinii*, the type species of genus *Magnaporthe*, and hence the blast fungus should be designated as *Pyricularia*. At the same time, *P. oryzae* and *P. grisea* formed a distinct clade in this study. Subsequently, Murata *et al.* (2014) also reported similar results as that of Zhang *et al.* (2011), and Luo and Zhang (2013), where phylogenetic analysis of the species of Magnaporthaceae based on rDNA-ITS and *RPB1* sequences resulted in two clusters with high bootstrap support, which grouped *Pyricularia* spp. separately from other species of Magnaporthaceae such as *Magnaporthe* spp. and *Gaeumannomyces* spp. They also concluded that blast fungi are a distinct phylogenetic group and was not congeneric with the type species of *Magnaporthe* and proposed that rice blast fungus should be designated as *Pyricularia*.

'One fungus one name' nomenclature emphasises on one fungus having only one correct name and considering its other names as synonyms (Hawksworth, 2011). Implementation of this nomenclature for rice blast pathogen arose questions on which name should be adopted, either *Pyricularia* or *Magnaporthe*. The *Pyricularia/Magnaporthe* Working Group, which was established under the advocacy of the International Commission on the Taxonomy of Fungi, has made some

recommendations including the rice blast fungus in the genera *Magnaporthales* (Zhang *et al.*, 2016). *Magnaporthe* was initially considered to be the taxon for rice blast fungus. However, this would require a change in the type species of this genus, since, as discussed earlier, the rice blast fungus is not congeneric with its type species, *M. salvinii*. Moreover, the placement of rice blast fungus in *Magnaporthe* was based on an incorrect morphological identification. Therefore, *Pyricularia* should be the correct name for the rice blast fungus, and *P. oryzae*, which corresponds well with the rice blast pathogen with respect to its pathogenicity, ecological, and evolutionary features, should be named for the rice blast fungus. Meanwhile, *M. oryzae* will be continued to be used as a synonym in publication as '*Pyricularia oryzae* (syn. *Magnaporthe oryzae*)' (Zhang *et al.*, 2016).

BIOLOGY OF RICE BLAST PATHOGEN

Conidia of *P. oryzae* are produced at the apex of the conidiophores, usually these are three-celled and found abundantly in the lesions (TeBeest *et al.*, 2007). The conidia are produced after exposure to high relative humidity for several hours and are released under windy conditions. The highest rate of conidia production is achieved in 3-8 d after the appearance of lesion and its daily production generally peaks between midnight and 0600 h (Bonman, 1992).

In the tropics, the conidia are present in the air throughout the year (Agrios, 2005). The conidia in the lesions of susceptible rice varieties sporulate under favourable conditions and a single leaf lesion carrying multiple conidiophores can discharge around 20,000 conidia per night for up to 20 d (Skamnioti and Gurr, 2009). The conidia are trapped during daytime showers and sporulation does not occur below 89% of relative humidity. The optimum temperature for sporulation ranged from 25-28 °C and it increases with increase in relative humidity beyond 93% (Bonman, 1992). At optimum temperatures, new blast lesions appear within 4 to 5 d (Agrios, 2005). Moisture on the leaf is required for infection. For conidia germination, the optimum temperatures ranged from 25-28 °C and for appressoria formation, from 16-25 °C (Bonman, 1992). Prolonged leaf wetness, exposure to night temperatures of around 20 °C, as well as high nitrogen fertilization favours the development of rice blast disease (Agrios, 2005).

Ascospores are produced in asci which are found within specialized structures, perithecia. The mycelium of *M. oryzae* is septate, nucleated and the ascospores are haploid (TeBeest *et al.*, 2007). The fungus is heterothallic with bipolar mating system, comprising two mating types (MAT1-1 and MAT1-2) and sexual reproduction can occur between the two opposite mating types (Valent *et al.*, 1991; Couch and Kohn, 2002; Talbot, 2003). Sexual reproduction has been absent or rarely been found in nature; however, existence of fertile strains were reported in some of the isolates from a few grass hosts (for instance, *Eleusine* spp.) (Zeigler 1998).

Nearly all rice blast isolates in the field are males and thus are unable to cross with one another, however many isolates from other grasses are hermaphrodites (Bonman, 1992), therefore it is a possibility that the isolates from rice and from other grasses can cross and produce fertile strains. These fertile strains can enhance the genotypic variability of *M. oryzae* populations where the progenies may have new capabilities to infect different rice cultivars (Samanta *et al.*, 2014).

DISEASE CYCLE

Rice blast is a polycyclic disease that attacks rice plants at all the stages of development and can infect leaves, stems, nodes, and panicles. When an airborne conidium lands on the rice plants, it adheres to the surface through the sticky mucilage released from an apical compartment in the tip of the conidium during hydration (Hamer *et al.*, 1989; Agrios, 2005; Wilson and Talbot, 2009). The conidia germinate when there is enough moisture on the plant surfaces. Germ tube emerge from the tapering end of the conidium and grow across the plant surface. After sometime, the germ tube become swollen and flattened to form appressorium. Formation of appressoria structure requires a hard surface (Talbot, 2003; Agrios, 2005; Wilson and Talbot, 2009). Appressoria contain chitin and melanin in the cell wall and the presence of glycerol increases the turgor pressure so that the penetration peg formed from the appressoria could penetrate the cuticle and the cell wall of the rice plant to gain an entry (Chumley *et al.*, 1990; de Jong *et al.*, 1997; Agrios, 2005). The appressoria can also enter the rice plant through stomata.

The fungal hyphae of the blast pathogen grow into the plant tissues and eventually produce lesions. Invasion and colonisation of plant tissues is mediated by invasive fungal hyphae that invaginate the plasma membrane and invade epidermal cells. During early tissue invasion, specialised feeding structures or feeding hyphae are formed to aid in colonising the tissues as well as in deriving nutrition from the living plant cells. Movement of the hyphae through the plant cells occur via plasmodesmata (Wilson and Talbot, 2009). The blast lesions become apparent between 72 and 96 h after infection (Agrios, 2005; Wilson and Talbot, 2009). Under high humidity, the fungus sporulate rapidly and release conidia. The conidia are spread to the nearby rice plants commonly by wind or rain splash starting a new disease cycle (Ou, 1985; Bonman, 1992; Wilson and Talbot, 2009).

PHYSIOLOGICAL RACES OF RICE BLAST PATHOGEN

The occurrence of rice blast pathogen physiological races was studied intensively in 1950s and 1960s by the Japanese and American researchers. The studies on pathogenic race was first initiated in Taiwan in the mid-1950s (Hung and Chien, 1961; Ou, 1980). The procedures used by the researchers were based on those

used for cereal rusts race determination. For this study, 10-12 differential rice varieties were inoculated with pure cultures of blast fungus and the observed for resistance and susceptibility to determine races or pathotypes (Ou, 1984). Differential varieties can distinguish races or pathotypes by their qualitative differential reactions to the pathogenic isolates (Telebanco-Yanoria *et al.*, 2008).

Based on studies by Goto *et al.* (1969), by 1962, Japanese researchers have identified 13 races and classified these races into three groups, namely, T, C, and N. These races were identified using 12 differential varieties comprising of two tropical, four Chinese, and six Japanese races. Subsequently, many other Asian countries including Malaysia, India, Thailand, and the Philippines began to identify rice blast races in their home country, however, each country used different rice cultivars as differential varieties (Ou, 1985).

Detailed reports on the race identification of rice blast pathogen were available from the comprehensive studies by Japanese researchers in 1950s and 1960s, but these reports were in Japanese and although an English summary was available, the information has not been easily available for non-Japanese researchers (Ou, 1980). Nevertheless, in 1960s to 1970s the number of identified rice blast races have increased, as more isolates of blast pathogens were tested for physiological races in many rice-growing countries. Japan identified 18 races (Hirano, 1967); Taiwan, 27 (Chien, 1967); USA, 20 (Marchetti *et al.*, 1976), India, 31 (Padmanabhan *et al.*, 1970), and the Philippines, more than 250 (International Rice Research Institute [IRRI], 1976).

During the earlier studies on pathogenic races of rice blast fungus, researchers encountered many challenges to establish a rice cultivar as resistant (R) or susceptible (S) to an isolate of the blast fungus. Inconsistent results were also observed where, the first inoculation produced one pattern of reactions on the tested cultivars, but a different pattern of reactions was observed during the second inoculation test. Moreover, different types of lesions, varying from resistant to susceptible, were observed on a single leaf. Sometimes, each differential cultivar may have numerous lesions, while other cultivars showed only a few lesions on a few seedlings. In many cases, the designation of a cultivar as resistant or susceptible from the above observations depended on the discretion of the researchers (Ou, 1980; Ou, 1984).

To overcome the issues in using different rice cultivars as differential varieties for rice blast race identification, the use of a uniform set of differential varieties was initiated by a collaboration between Japanese and American researchers. In this collaborative effort, several hundred isolates were tested and eventually, a set of eight differential varieties were chosen and 32 races in eight groups were characterised (Ou, 1980). The differential varieties were referred to as international differential varieties and designated as IA, IB, to IH on the basis of the susceptibility and the race numbers (Atkins *et al.*, 1967; Ou, 1980). The numbering of the international differential varieties was later standardised to avoid confusion (Ling and Ou, 1969). After the development of

international differential varieties, several countries have developed their own differential varieties based on the local blast rice pathogen populations (Yamada *et al.*, 1976; Kiyosawa, 1984; Mackill and Bonman, 1992).

In Malaysia, Malaysian Agriculture and Research Development Institute (MARDI) use eight differential varieties, namely, Mahsuri, MR1, Bahagia, Engkatek, Seribu Gantang, Tadukan, Pankhari 203, and Pongsu Seribu with varying degrees of blast resistance for identification of race or pathotype variability of rice blast isolates. However, the resistance genes harboured in these varieties are still unknown. In rice blast pathosystem, host resistance and fungal virulence can be explained by the gene-for-gene theory. Differential varieties are not only used to distinguish races or pathotypes by their qualitative differential reactions to pathogenic strains, but are also important in monitoring the blast population structure and predict the emergence of new pathotypes (Telebanco-Yanoria *et al.*, 2010).

The blast monogenic lines with Japonica-type genetic background were developed by IRRI-Japan Collaborative Research Project as differential varieties which consist of 24 resistance genes: *Pia*, *Pib*, *Pii*, *Pik*, *Pik-h*, *Pik-m*, *Pik-p*, *Pik-s*, *Pish*, *Pit*, *Pita*, *Pita-2*, *Piz*, *Piz-t*, *Piz-5*, *Pi1*, *Pi3*, *Pi5(t)*, *Pi7(t)*, *Pi9(t)*, *Pi11(t)*, *Pi12(t)*, *Pi19(t)*, and *Pi20(t)* (Telebanco-Yanoria *et al.*, 2008). Meanwhile, 27 of near-isogenic lines (NILs) with Indica-type genetic background, which included only 14 of the resistance genes, *Pib*, *Pik*, *Pik-h*, *Pik-m*, *Pik-p*, *Pik-s*, *Pish*, *Pita*, *Pita-2*, *Piz-t*, *Piz-5*, *Pi1*, *Pi5(t)*, and *Pi7(t)*, have been developed by the same research group (Telebanco-Yanoria *et al.*, 2011).

In rice blast research, 40 major resistance (R) genes have been identified, and among the genes are *Pia*, *Pib*, *Pid2*, *Pii*, *Pik*, *Pik-h*, *Pik-m*, *Pik-p*, *Pik-s*, *Pish*, *Pit*, *Pita*, *Pita-2*, *Piz*, *Piz-t*, *Piz-5*, *Pi1*, *Pi3*, *Pi5(t)*, *Pi7(t)*, *Pi9(t)*, *Pi11(t)*, *Pi12(t)*, *Pi19(t)*, *Pi20(t)*, and *Pi36*. Furthermore, some of these genes such as *Pib*, *Pita(t)*, *Pid2*, *Pi9(t)*, and *Pi36* have been characterised at molecular level (Jia and Martin, 2008). However, among the characterised R genes, the *Pi-ta* gene has been extremely valuable and useful in preventing the blast disease worldwide (Wang *et al.*, 2007).

These monogenic and near-isogenic lines need to be screened to identify the pathogenicity of local blast isolates, to characterise the pathogen population structure, and subsequently to estimate the blast resistance genes in rice varieties. Besides, the important genes to be incorporated in gene pyramiding to develop new or improved variety can be estimated using these lines. Therefore, these lines are also useful not only as a genetic tool for blast resistance study, but also as a source of genes for breeding purposes (Telebanco-Yanoria *et al.*, 2010).

MANAGEMENT OF RICE BLAST

Rice blast can be controlled by an integrated plant disease management by applying a variety of methods including cultivation practices, chemical application, biological control, resistant cultivars, and disease

forecasting systems. Cultivation practices including fertilizer management, water management, time of planting, and spacing have a positive effect on reducing rice blast disease (Pooja and Katoch, 2014).

Chemical control using fungicides

Some of the fungicides commonly applied against rice blast disease are benomyl, phthalide, edifenphos, iprobenfos, tricyclazole, isoprothiolane, probenazole, pyroquilon, felimzone (meferimzone), diclocymet, carpropamid, fenoxanil, and metominostrobin (Kato, 2001). Two antibiotics, blastocidin and kasugamycin have also been used against rice blast fungus (Kato, 2001). Efficiency of chemical control is mainly determined by the types of compound, the amount, timing and method of application, present disease levels, forecasting systems efficiency, and the emergence of fungicide resistant strains (Kato, 2001; Skamnioti and Gurr, 2009).

Rice blast resistance towards fungicides can be avoided by using chemicals with different modes of action (Kato, 2001). Certain fungicides are directed at specific stages of the rice blast pathogen life cycle. For instance, a plant defence activator, probenazole induces defence through systemic acquired resistance after the salicylic acid and pathogenesis-related protein accumulation is increased (Iwai *et al.*, 2007). Other chemicals such as, melanin biosynthetic inhibitors intervene in the formation of appressorium (Iwata, 2001; Kurahashi, 2001) and choline biosynthesis fungicides target the fungal membrane phosphatidylcholine synthesis (Uesugi, 2001).

Biological control

Biological control of rice blast pathogen using antagonistic bacteria and fungi has been reported in various studies. Induction of induced resistance is the major principle involved in use of fungal isolates used as biological control agent against blast pathogen for disease suppression (Gnanamanickam, 2009). By using weakly virulent or avirulent isolates of blast pathogen, some level of reduction of leaf blast was achieved (Fujita *et al.*, 1990; Ashizawa *et al.*, 2015). A study by Manandhar *et al.* (1998) have shown that inoculation of an avirulent isolate of blast pathogen and a non-rice pathogen, *Bipolaris sorokiniana* suppressed the development of rice blast. Other fungal isolates such as a phylloplane fungal isolate, designated as MKP5111B, and *Exserohilum monoceras*, which is a pathogen of *Echinochloa* sp., have also been reported to reduce rice leaf blast development (Tsukamoto *et al.*, 1999; Ohtaka *et al.*, 2008).

Several antagonistic bacteria including *Pseudomonas*, *Bacillus* and *Streptomyces* have been reported to be able to inhibit the growth of blast pathogen. Development of leaf and neck blast was found to be suppressed by *Pseudomonas fluorescens* Pf7-14, which produce an antibiotic identified as phenazine-1-carboxylic acid (Valasubramanian, 1994). *Bacillus licheniformis* BC98 isolated from soil has been reported to secrete lipopeptide that exhibited fungicidal activity towards rice blast

pathogen and further inhibit the growth of the pathogen (Tendulkar *et al.*, 2007). An antifungal aliphatic compound known as SPM5C-1, obtained from *Streptomyces* sp. PM5 was reported to decrease blast development and correspondingly increase the rice grain yield (Prabavathy *et al.*, 2006).

Resistant cultivars

Utilizing resistant cultivars is considered as the most effective approach to manage rice blast disease. Many resistance genes have been identified and documented. Some of the genes confer broad-spectrum resistance (Liu *et al.*, 2002; Hua *et al.*, 2012; Liu *et al.*, 2013) while some confer race-specific resistance (Hayashi *et al.*, 2010; Fukuoka *et al.*, 2014; Ma *et al.*, 2015). However, with the emergence of newer and stronger virulent strains or races of rice blast pathogen, resistance breakdown occurs within a few years of cultivation (Han *et al.*, 2001). To overcome the resistance breakdown, one of the methods proposed is pyramiding or stacking several resistance genes to reduce the selection pressure for resistant strains of blast pathogen (Bonman *et al.*, 1992; Hittalmani *et al.* 2000; Skamnioti and Gurr, 2009). Hittalmani *et al.* (2000) reported that rice plants carrying two- or three-gene combinations of resistance genes, when tested for resistance to leaf blast in the Philippines and India, indicated that having a combination of the resistance genes enhanced the resistance to infection.

Partial resistance or incomplete resistance is another form of blast disease resistance, which is inherited quantitatively and is mediated by multiple resistance genes. These genes are located on different chromosome loci, and these loci are referred to as quantitative trait loci (QTLs) (Parlevliet, 1979; Ballini *et al.*, 2008). Several QTLs have been identified to be effective against the rice blast strains tested. Ballini *et al.* (2008) reported that from over 350 partial blast resistance QTLs identified, 165 QTLs have major effects while the remaining have minor effects. Meanwhile, these minor QTLs still contribute to achieve broad and robust resistance to rice blast. This study also showed the usefulness of combining major resistance genes and QTLs to produce cultivars with broad and robust resistance against rice blast disease as well as of introgression with other desirable agronomic traits (Skamnioti and Gurr 2009).

Rice cultivar mixture

Using a rice cultivar mixture is another strategy to overcome the emergence of newer and stronger virulent strains or races of rice blast pathogen (Castilla *et al.*, 2003; Skamnioti and Gurr, 2009). The cultivar mixture involves mixtures of hybrid rice, blast resistant rice, and glutinous rice, as well as a mixture of blast-susceptible cultivars (Zhu *et al.* 2005). The use of rice cultivar mixtures have been implemented to control rice blast in irrigated rice fields in Yunnan Province, China (Zhu *et al.*, 2005), where highly susceptible glutinous rice plants planted with non-glutinous hybrid Indica rice reduced the

development of blast in glutinous rice. In another study, a rice cultivar mixture comprising a susceptible cultivar and a resistant cultivar in varying proportions, showed promising results in reducing the severity of leaf and panicle blast disease (Raboinab *et al.*, 2012). The use of cultivar mixtures are a promising strategy that could contribute to a more sustainable cultivation of rice even under upland conditions in Madagascar.

Rice blast forecasting system

Forecasting systems of rice blast have been developed in several countries and found to be effective in forecasting the incidence of the disease. Models developed for forecasting rice blast were based on incorporation of many variables or factors including meteorological variables such as air temperature, relative humidity, rainfall, and solar radiation (Calvero *et al.*, 1996), information related to pathogen infection and disease development (Ou, 1985; Teng, 1994), as well as planting date and number of air-borne spore trapped (Kim *et al.*, 2015). Examples of rice blast forecasting models include integration of rice growth simulation model, CERES-Rice, with a blast epidemic simulation model, BLASTSIM (Luo *et al.*, 1998); a generic epidemiological model, EPIRICE, to assess changes in disease probabilities under climate change scenarios to allow for a more robust planning for incidences of rice diseases including rice blast (Kim *et al.*, 2015); a simulation model, SiRBInt, for forecasting blast appearance in the field, which could be utilised for planning proper fungicide application (Biloni *et al.*, 2006); and a leaf blast simulation model, EPIBLAST, for quantitative forecasting of leaf blast incidence, which can also predict the peak time of leaf blast epidemic (Kim and Kim, 1993).

CONCLUSION

The issues pertaining to the nomenclature of the rice blast pathogen has been settled now as the fungus is referred as *P. oryzae* with *M. oryzae* being used as its synonym unanimously. Rice blast disease is still posing a serious threat in many rice growing regions including Malaysia. Although, currently other rice diseases particularly bacterial leaf blight has emerged as the most destructive rice disease in Malaysia, the threat from rice blast disease is persistent. The outbreak of rice blast in many rice-growing areas is recurrent and integrated disease management practices are being used to control the disease with some success. However, there is a need for continuous research and development in identifying new resistant rice cultivars using conventional breeding methods as well as using new biotechnology approaches such as genetic modification by incorporation of resistance genes since it is the most effective method to control the rice blast pathogen.

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