agronomy

Review

Rice Blast: A Disease with Implications for Global Food Security

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Received: 1 July 2019; Accepted: 6 August 2019; Published: 15 August 2019

Abstract: Rice blast is a serious fungal disease of rice (*Oryza sativa* L.) that is threatening global food security. It has been extensively studied due to the importance of rice production and consumption, and because of its vast distribution and destructiveness across the world. Rice blast, caused by *Pyricularia oryzae* Cavara 1892 (A), can infect aboveground tissues of rice plants at any growth stage and cause total crop failure. The pathogen produces lesions on leaves (leaf blast), leaf collars (collar blast), culms, culm nodes, panicle neck nodes (neck rot), and panicles (panicle blast), which vary in color and shape depending on varietal resistance, environmental conditions, and age. Understanding how rice blast is affected by environmental conditions at the cellular and genetic level will provide critical insight into incidence of the disease in future climates for effective decision-making and management. Integrative strategies are required for successful control of rice blast, including chemical use, biocontrol, selection of advanced breeding lines and cultivars with resistance genes, investigating genetic diversity and virulence of the pathogen, forecasting and mapping distribution of the disease and pathogen races, and examining the role of wild rice and weeds in rice blast epidemics. These tactics should be integrated with agronomic practices including the removal of crop residues to decrease pathogen survival, crop and land rotations, avoiding broadcast planting and double cropping, water management, and removal of yield-limiting factors for rice production. Such an approach, where chemical use is based on crop injury and estimated yield and economic losses, is fundamental for the sustainable control of rice blast to improve rice production for global food security.

Keywords: rice blast; rice; food security; fungal disease; climate change

1. Impact of Population Growth on Land and Water Resources

Climate change is increasing air temperature and the frequency and intensity of extreme weather events [1]. Meanwhile, the global human population is rapidly increasing and the availability of land and water resources for crop production continues to decline, escalating the challenge of global food security. The world's human population is anticipated to reach 9 billion by 2050 [2]. According to the Food and Agriculture Organization [3], food security is "when all people, at all times, have physical and economic access to sufficient, safe, and nutritious food to meet their dietary needs and food preferences for an active and healthy life". For food insecurity to recede, agricultural production on currently cultivated land will need to increase by 70% globally and 100% in the developing countries by 2050, relative to 2009 levels [4]. This is challenged by a shrinking amount of prime land for rice (*Oryza sativa* L.) production, which is expected to decline by 18% to 51% in the tropics during the next century due to global warming [5]. Water scarcity, salinization, and pollution of water bodies is also increasing [6], intensifying the challenge of global food security.

2. Rice Production in Food Security

Rice production is the main source of income and employment for more than 200 million households across the world [7,8]. Rice is the primary food for 2.5 to 3.5 billion people who are largely located in rapidly growing low-income countries [9–13]. In 2002, rice provided more than 500 calories person^{-1} d^{-1} for over three billion people, and a substantial amount of protein for 520 million people [13,14]. It is one of the most important cereals produced for food security and income by subsistence farmers [15–17]. In 2008, 480 to 685 million tons of rice were produced on 160 million ha [18]. At the present rate of human population growth, the requirement for global rice production in 2020 is estimated at 140 million tons, representing a 50% increase compared to 2009 [19,20].

Although rice production has improved substantially over time, it is inadequate to cope with the increasing global demand [21]. Since 2000, global rice production has been less than rice consumption and the deficit has been addressed by drawing on bumper stocks [18]. The annual shortage of rice is estimated to increase from 400,000 tons in 2016 to 800,000 tons by 2030 [22].

3. Impact of Climate Change on Rice Production

On 16 December 2002, the UN General Assembly declared the year 2004 as the International Year of Rice [23]. Decreasing hunger and poverty are key goals of the United Nations [18]; however, the rate of improvement in rice yield has diminished over time [24]. Rice yield growth has declined from 2.3% per year during the 1970s and 1980s to 1.5% during the 1990s, and to <1.0% during the first decade of the present century [24].

Rice is produced across a wide range of agro-climatic environments around the world and its productivity is affected by biotic stresses [25]. Biotic stresses resulting from climate change can impair varietal resistance to rice blast [26,27]. Climate change may change pathogen distribution and development rates, and alter the resistance, growth, and metabolism of rice [28]. Each stage of the rice blast disease cycle, from the germination of spores to the development of lesions, is significantly influenced by climatic factors such as temperature, precipitation, and dew, and are likely to affect pathogen distribution due to altered effectiveness of preventive approaches [28,29]. Consequently, management approaches that exploit host resistance will be greatly impacted by climate change [30]. Quantitative analyses of the effects of climate change on pathogens are lacking in field and laboratory research and in modeling-based assessments [31]. Therefore, mitigating the impact of biotic stresses on rice is key to increasing and stabilizing rice yield. Fungal diseases alone are estimated to reduce annual rice production by 14% globally [32]. Increased frequency and magnitude of extreme weather events combined with increased air temperature and atmospheric CO_2 concentration due to climate change are projected to spread rice diseases to new areas [33,34].

There has been limited research on rice diseases under field conditions that realistically mimic climate change, which has severely restricted the development of options for improved rice adaptation and disease control in future growing conditions [35]. There has also been limited success in identifying traits in rice for enhanced tolerance to drought and monsoon conditions [36].

A crucial challenge to rice production is rice blast, caused by the fungus *Pyricularia oryzae* Cavara 1892. Rice blast is one of the most serious and recurrent difficulties affecting lowland and upland rice production around the world [37–42]. Rice blast is responsible for yield losses of about 10% to 30% annually [43–45]. In favorable conditions, this disease can devastate entire rice plants within 15 to 20 d and cause yield losses of up to 100% [46].

Rice blast has become more difficult to control because of the pathogen's ability to survive and multiply in harsh environmental conditions and easily spread to new fields [47,48]. Varietal resistances have declined due to the appearance of new and more virulent strains of the pathogen, making management and control more challenging [49]. Additionally, fungicides and plant breeding have failed to provide long-lasting control of rice blast because they are too static to deal with the dynamic interactions between the pathogen and rice, which are influenced by the surrounding environment [50].

Understanding the effects of the rice blast pathogen, the efficacy of rice defense mechanisms, and the impact of climate change on rice blast are crucial for enhancing global food security [31].

Strategies to mitigate the negative effects of climate change are key to increasing rice production [51]. Understanding the effects of changing air temperature, rainfall, and sea level due to climate change would enable modifications in crop management for improved rice production [18]. Changes in duration, intensity, and frequency of rainfall would greatly impact the effectiveness of chemical control measures [30]. Rainfall following application of fungicide may increase its coverage on foliage [52], but a high amount or high intensity of rainfall can reduce fungicide coverage on foliage [53]. With long periods of rainy and cloudy conditions, both growth of rice and its resistance to rice blast are weakened [54]. Rice blast epidemics are favored by extended periods of rain, lack of sunshine, and dew, which induce the release of conidia [54]. The effect of rainfall on the dispersion of conidia is most prominent at the start of a rainy season and during heavy rains [55,56].

Sea level rise is an important concern for rice production since it could result in flooding of low-lying areas and intensify soil salinity [57,58]. Since rice blast can be spread by water, conidia in infected fields could spread to new fields with flooding [59]. Additionally, increased soil salinity due to flooding can restrict rice growth and grain formation [57,60], which could reduce resistance to rice blast [61].

The effects of atmospheric CO_2 concentration on rice blast are not well understood [28]. In a meta-analysis summarizing the response of rice yield to increased atmospheric CO_2 and O_3 concentrations, Ainsworth (2008) found that high CO_2 concentrations are anticipated to increase yield, while increased O_3 concentrations and elevated air temperature are anticipated to reduce yield. Other researchers have reported that elevated CO_2 concentrations are likely to increase the spread of rice blast [62–65]. Published results from simulation modeling research to predict the impact of climate change on rice blast are scarce; therefore, most assumptions are based on the epidemiology of the disease at specific temperature, humidity, and CO_2 levels [28].

In China, it has been predicted that climate change will reduce rice yield by up to 37% during the next 20 to 80 years [66]. Global warming may result in the need for greater resource investment to achieve equivalent or lesser rice production [67,68]. Increased salinity of water used in rice production resulting from a 0.3-m rise in sea level due to climate change is expected to reduce rice production by 0.5 million tons annually [69]. Since 40% of the world's total rice area is rainfed, changes in rainfall due to climate change will affect rice production [11]. Drought stress can severely damage or even kill rice plants when it occurs during the reproductive stages, and variation in the start of the rainy season leads to variation in the start of planting, which influences rice growth and development [18]. Global climate change, rising scarcity of water resources, and drought stress will severely influence future rice production [70].

4. Impact of Elevated Carbon Dioxide on Rice

Increased atmospheric CO_2 concentration enhances rice biomass production, but it can have a negative effect on grain yield if it is associated with increased air temperature, as projected with climate change [71–75]. Each 75-ppm increase in atmospheric CO_2 concentration is expected to increase rice yield by 0.5 tons ha^{-1}, while each 1 °C increase in average air temperature during the growing season is projected to decrease rice yield by 0.6 tons ha^{-1} [75]. This is because rice is a C_3 crop, thereby having reduced photosynthetic efficiency due to photorespiration in hot conditions [75]. Greater CO_2 levels can also reduce transpirational cooling and increase maintenance respiration when night air temperature exceeds 21 °C [73,76]. Responses of rice to elevated CO_2 concentrations depend on nitrogen supply; greater CO_2 levels with limited nitrogen and the absence of sinks for excess carbon can limit photosynthetic capacity and growth [72]. Increases in crop canopy and biomass with elevated CO_2 concentrations increases host size for a pathogen population [77–80]. A larger amount of crop residues can also increase pathogen survival and increase inoculum for subsequent crops and neighboring fields [29]. The impact of greater atmospheric CO_2 concentration on plant diseases is in part due to changes in host physiology and anatomy, such as reduced nutrient concentration and increased carbohydrate concentration in leaves, plant fiber content, leaf wax, layers of epidermal cells, and mesophyll cells [81–83]. Increased leaf blast and sheath blight severity has been associated with reduced silicon content in susceptible rice varieties under elevated CO_2 levels [64]. Additionally, increased leaf wax and epidermal thickness in rice can result in greater physical susceptibility to pathogens, along with enhanced pathogen fecundity and changes in pathogen virulence, activity, abundance, and distribution [29,82,83].

In high humidity environments, rice blast lesions produce spores in abundance, which are dispersed by wind and serve as inoculum for a new cycle of infection [84]. In comparison, a lack of humidity or rainfall can reduce disease severity [28]. Strong winds that blow soil particles can injure rice plants, creating wounds for easy penetration by pathogens [85]. Wind also stimulates transpiration of the host and promotes silicification of leaf tissue [86] and strengthens the resistance reaction of the host [54].

5. Impact of Warmer Air Temperature on Rice

According to the Intergovernmental Panel on Climate Change [87], the average annual global air temperature from 1990 to 2100 could increase by 1.8 to 5.8 °C, which would greatly threaten rice productivity and global food security. Optimal maximum daily air temperature during the growing season for rice grain yield is 23 to 26 °C [88]. Air temperature above 33 °C negatively affects anther dehiscence, pollen viability, spikelet fertility, and dry matter accumulation in grain [89–91]. A 2 °C increase in average air temperature during grain filling can decrease rice yield by 15% to 17% [92,93]. Increased air temperature due to climate change is also expected to enhance growth and sporulation of the rice blast pathogen [94].

The temperature under which rice is cultivated affects its susceptibility to the blast disease [95]. In cold subtropical zones, an increase in air temperature is expected to cause an increase in the severity of rice blast due to increased risk of infection [84,96]. Long periods of leaf dampness, high relative humidity, and temperatures of 17 to 28 °C favor rice blast growth [97]. Low humidity or dew favors the infection of rice blast [98]. When night air temperature rises above 20 °C there is less spore liberation and infection is absent, but rapid growth of lesions is favored by alternating daily minimum and maximum air temperatures of 25/32 °C to 20/32 °C [28,99]. Mild air temperature of 16 to 24 °C may sustain the sporulation capacity of lesions [28]. However, greater air temperatures that are predicted to occur as a result of climate change may reduce the incidence of rice blast in most rice growing zones [28]. More detailed modeling research and climate monitoring that take into consideration other factors affecting rice blast would be beneficial for disease management [28].

6. Disease Cycle of Rice Blast

Rice blast is caused by a filamentous ascomycete fungus and is a polycyclic disease spread by asexual spores (conidia) that infect aboveground tissues of rice plants [40,43,100–103]. The infection route requires an infection cell, called an appressorium, which uses a pressure-driven mechanism to break the tough cuticle of the rice plant and stick firmly by means of an adhesive carried in the spore apex, generating turgor pressure of up to 8.0 MPa that ruptures the cuticle of the affected rice [104–107]. Once inside the tissue, the fungus produces invasive hyphae that quickly colonize living host cells, secreting effector molecules to overpower host immunity and aid infection [108]. The effectors are transported into host cytoplasm by the aid of a biotrophic interfacial complex, a plant-derived membrane-rich structure in which effectors amass during transit to the host [108–111]. The pathogen can replicate quickly and successively by mitosis, nuclear migration, and death of conidia from which the infection originated, and produce appressoria capable of infecting aerial structures and hyphae capable of infecting roots of young and old rice plants [43,107,112,113]. Autophagic cell death of conidia is connected to cell cycle control and produces conidiophores that are dispersed to other tissues and plants by wind and water splash to reinitiate the infection cycle by attachment of a spore that germinates and forms an appressorium [32,34,43,106,114]. This allows the pathogen to infect epidermal cells with bulbous invasive hyphae that proliferate and grow from cell to cell, often through pit fields which invade neighboring cells through plasmodesmata that requires mitogen-activated protein kinase signaling and manipulation of jasmonate signaling [45,115–117]. Appressorium penetration is a septin-dependent process and is linked to a burst of reactive oxygen species in the infected cell [107,118]. Rice blast conidia can spread within 230 m from their source; dispersal is favored in darkness and with high relative humidity and winds greater than 3.5 m s^{-1} [119]. The primary source of inoculum is infected residue and seeds of rice, and in the tropics, airborne conidia are present throughout the year, enabling stable epidemics to occur year-round [100,120,121]. Initial symptoms of rice blast are oval-shaped lesions that are 0.3 to 0.5 cm wide and 1.0 to 1.5 cm long, ranging from white to gray and surrounded by darker borders, and older lesions are typically larger and may coalesce to kill entire leaves [122,123].

Environmental conditions favoring sporulation and lesion development include extended periods of leaf dampness, 92% to 96% relative humidity, and 25 to 28 °C air temperature [32,116,124]. Peak spore production occurs during the night when relative humidity is 100% and air temperature is near 22 °C [28,43]. Fungal growth within rice cells causes death of the infected tissues and necrotic lesions within 3 to 5 d [43]. The pathogen survives in the residue of host plants' tissues and the cycle repeats [100,119]. Under favorable conditions, there can be one cycle per week, with a single lesion producing hundreds of spores each night for more than 20 d [38]. Drought stress and excess nitrogen application increases susceptibility of rice to the rice blast pathogen. Though rice blast may tend to develop under dry conditions, its response is variable [125–127].

7. Strategies to Circumvent Rice Blast for Food Security

Crop diseases including rice blast are increasingly worrisome to rice farmers around the world and threaten global food security [128]. Since rice is an essential source of calories for much of the world's population, decreased rice yield due to rice blast is a serious threat to global food security. The basis for integrated management of rice blast is knowledge of the pathogen and monitoring for its appearance to implement control practices before yield loss exceeds control cost. A mechanistic understanding of the complex interactions among the pathogen, host, and environment will lead to accurate forecasts of pathogen distribution and greatly advance management of rice blast for global food security in the presence of climate change.

Food security is influenced by a complex set of sociopolitical and trade issues that are often more important than production and processing [38]. These challenges could be partially addressed by clearly communicated policies and research agendas, such as the 'New Rice for Africa' program by African Rice Center, which is focused on developing rice varieties with enhanced tolerance to harsh growing conditions with limited fertilizer and pesticide use [129].

Sustainable increases in rice production for global food security will require efforts to enhance the capacity of rice production systems to mitigate and adapt to climate change. Mitigation could involve strategies focused on increasing rice yield in the presence of rice blast and climate change [48,92], and reducing greenhouse gas emissions [18], while adaptation includes adjustments to decrease rice vulnerability to rice blast. Policies on rice research and development should include provisions for technology transfer to farmers and agricultural professionals to ensure that new varieties and production practices are adopted [18].

Crop simulation modeling is a useful tool for studying the impact of climate change on crop growth and yield in diverse agro-climatic conditions, with several models for rice available, including CERES-Rice [130] and ORYZA [131]. Models for estimating crop yield loss from rice blast should be integrated with crop growth models [132–135]. Disease tolerance, an area not commonly addressed in yield-loss assessment, should also be taken into account with projected climatic conditions [136].

Rice blast could be effectively managed through integrated use of cultural practices, chemicals, resistant varieties, and biocontrol agents. Segregation of affected grains reduces the spread of rice blast [137]. Additionally, broadcast sowing should be avoided because it can produce clusters of high plant densities due to non-uniform seed distribution, creating a favorable microclimate for the development of rice blast [119,138]. Transfer of agricultural technologies to farmers is more effective when the state, non-governmental, and private sectors work in partnership [139–141]. Local leaders, agricultural professionals, and government or non-profit educators will be key for technology transfer and adoption of best practices for controlling rice blast to improve food security [141,142]. Coordination among researchers from a variety of disciplines to map vulnerability and create early warning systems could enable the development of successful and sustainable adaptation strategies to reduce losses from rice blast [28].

Retrospective analysis of long-term data and herbarium specimens will add knowledge on the biology, distribution, and adaptive responses of plant pathogens and their vectors to climate change [135,143]. Increased collection of quantitative data on rice diseases and their pathogens will increase the ability to counteract new risks posed by climate change for endemic pathogens and circumvent new introductions [144]. A challenge will be linking this data to host–pathogen interactions on a spatial scale to determine future management options and comprehensive knowledge of the hosts, pathogen, and disease epidemiology in a cropping system, since parasitic and saprotrophic fitness should be considered [50].

Natural products for controlling rice blast that are safe for the environment, humans, and other organisms, such as microbial antagonists [145], are gaining interest as alternatives to chemical fungicides [146,147]. Examples include *Streptomyces* bacteria [148] and the biocontrol agent *P. fluorescens* Pf7-14, which produces antifungal phenazine-1-carboxylic acid [149]. Fungicides are an option for controlling rice blast, but care should be taken to avoid overuse of similar active ingredients and the development of pathogen resistance [137,150–152].

Crop breeding is a critical component of global food security, especially for rice [153,154]. Long-lasting and durable resistance to rice blast from a single gene is feasible but not often available, since the pathogen can rapidly mutate and attack resistant cultivars [47]. Many genes resistant to rice blast have been identified and are widely used as resistant donors in breeding programs including *Piz*, *Piz-t*, *Pit*, *Pik*, *Pik-m*, *Pik-p*, *Pita*, *Pita-2*, and *Pib* [155]. Pi_{21} appears to slow the plant's defense responses, which may support optimization of defense mechanisms [156]. *Ptr* is a new class broad-spectrum resistant gene that is also required for classical nucleotide-binding leucine-rich repeat against rice blast [157]. The *Pigm* locus contains a cluster of genes encoding nucleotide-binding leucine-rich repeat receptors that confer durable resistance to the fungus [128]. Gumei 4 (GM4)-derived varieties or near-isogenic lines with the *Pigm* resistance locus (NIL-*Pigm*) display high resistance and durability to rice blast and could be used to improve resistance against the blast disease [128,158]. The durability of resistance can be improved by crossing rice varieties with complementary genes to achieve multigenic resistance against a wide spectrum of pathogen races, thereby reducing selection pressure on a single blast isolate [159]. It is also important to consider pathogen evolution and the effectiveness of resistant plant varieties for accurate assessment of rice blast in the future [31]. Transgenic solutions should receive serious consideration in integrated disease management strategies to improve food security [25]. Transgenic rice lines harboring rice blast resistance gene *Pi-d2* transformed from vectors of *pCB6.3kb*, *pCB5.3kb*, and *pZH01-2.72kb*, displayed various levels of resistance (up to 92%) against 39 strains of rice blast [155].

Empirical investigations assessing the impacts of climate change on physical, chemical, and biological control of rice blast are critical to develop new tools and tactics for disease control; however, climate is only one driver of change when assessing future impacts of plant diseases [31]. Research to improve the adaptive capacity of rice by increasing its resilience to rice blast may not involve a completely new approach, although managing this disease may have an added advantage of mitigating rising CO_2 concentrations [160]. All crop protection practices for future research should be part of an integrated approach and should focus on developing adaptation and mitigation strategies for the control of rice blast in future climate conditions. Integrated solutions and international coordination in their implementation will be essential for effective control of this devastating disease to improve global food security [35].

Author Contributions: Conceptualization, A.E.A.; methodology, A.E.A.; software formatting/writing style, J.A.C.; validation, Q.C. and J.A.C.; formal analysis, J.A.C.; investigation, A.E.A.; resources, Q.C.; data curation/information, A.E.A.; writing, A.E.A.; editing, J.A.C.; supervision, Q.C. and J.A.C.; project administration, Q.C. and J.A.C.; All the above people have contributed immensely to the work reported.

Funding: This research received no external funding.

Conflicts of Interest: The authors declare no conflict of interest.

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