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Consequences and Mitigation Strategies of Biotic and Abiotic Stress in Rice (*Oryza sativa* L.)

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Abstract

Rice (*Oryza sativa*) is the staple food for more than 3.5 billion people worldwide. Yield levels in Asia have tripled and are expected to increase by 70% over the next 30 years due to population growth. In the US, Arkansas accounts for more than 50% of rice production. Over the last 68 years, rice production has continued to grow in Mississippi, placing it in fourth place after Arkansas, Louisiana, and California. Due to increasing rice acreage, regionally and worldwide, the need to develop abiotic stress tolerant rice has increased. Unfortunately, current rice breeding programs lack genetic diversity, and many traits have been lost through the domestication of cultivated rice. Currently, stressors stemming from the continued effects of climate change continue to impact rice. This chapter highlights current research that strives to discover abiotic and biotic stress tolerant rice. This chapter calls for directed research in genetics and genomics to address the need to discover biotic and abiotic stress tolerant traits. While many genes have been uncovered to arm rice against these stresses, decreased genetic variability in current rice traits presents a small gene pool for discovery.

Keywords: rice, *Oryza sativa*, abiotic, biotic, stress tolerance

1. Introduction

Rice, *Oryza sativa*, is a cultivated, food staple feeding more than one-half of the world's population [1]. Rice is regarded as one of the world's most important crops and is grown in more than one hundred countries producing more than 700 million tons annually [2, 3]. Asia currently accounts for more than 90% of rice that is grown and consumed [4]. In southern China alone, rice consumption is almost 50% higher than the global average due to a diet heavily rooted in rice [5]. It is predicted that rice yield must increase by 1% annually to continue to feed the growing population [6]. To meet this expectation, the development of high-yielding, stress-tolerant rice cultivars is necessary [7].

Rice is a tropical and sub-tropical plant that requires temperatures ranging from 20 to 40°C with flooded conditions, and is highly influenced by solar radiation [8]. It is an annual grass with a life cycle ranging from 105 to 145 days from germination to maturity contingent on various types of environmental contributions [9]. Rice domestication is estimated to have started more than 9000 years ago

via wild rice from China [10]. There are two species of cultivated rice (*O. sativa* and *O. glaberrima*) originating from Asia and Africa, respectively [11].

Globally, the Asian cultivar is grown on a large scale while the African cultivar is confined to West Africa [11]. It is a diploid species with an AA genome that can be subjected to traditional hybridization and selection [12]. In addition to two distinct species of rice, the crop can further be divided into two different varieties, *indica* and *japonica* [13]. In this review, knowledge of major abiotic and biotic associated with rice are presented to highlight a need for genomic-focused studies. As climate change continues to be a major contributor to stress in rice production fields, understanding current research strategies in rice stress is necessary.

2. Consequences and mitigation strategies of biotic stresses with specific focus on disease

2.1 Rice blast disease

Rice blast disease is caused by the fungal pathogen *Magnaporthe oryzae* (*M. oryzae*) formerly named *M. grisea*, which is a hemibiotrophic filamentous ascomycete that infects rice and causes yield losses worldwide [14, 15]. This is one of the most economically damaging grass fungi causing annual losses of up to 10% in global rice production [16]. Specific areas that reported devastating losses to blast include India, Japan, South Korea, and Indonesia ranging from 20 to 70% yield losses [17]. This fungal pathogen is so damaging because it can infect the crop at any growth stage and in any tissue above or below ground [18]. Symptoms of rice blast in leaf tissue include diamond-shaped tan lesions with a dark brown edge appearing 5–7 days after infection [19]. Economic losses are caused when the panicle of the plant, where the desired seed is exhibits symptoms of infection and lack of filling [14]. The infection can be located on the collar of the plant causing the tissue to rot leading to the entire panicle collapsing from lack of adequate structure [14].

Similar to most fungal pathogens, the conidia of *M. oryzae* are an essential part of the pathogens cycle [15]. The fungi attach to the plant tissue where they form structures called appressoria, a primary hypha, after germination. Bulbous invasive hypha structures at the end of the germ tubes of the conidia cause a buildup of turgor pressure allowing the pathogen to invade the outer plant tissue and settle in its host [15, 18]. After penetration, infected hypha migrates through the rice leaf cells. Molecules called effectors are released by the pathogen that competes for binding to the plant proteins, thereby disrupting natural processes [20]. These effectors are sometimes translocated to the cytosol of the host cell, where they alter the host's natural immunity responses [15]. Symptoms of blast infection manifest as streaks of dead leaf tissue on which the conidia are produced by the thousand and released for the spread of further infections [21]. *M. oryzae* favors the same humid growing conditions as rice and is spread through the air making it very hard to control when it has been introduced to a field. The pathogen can circulate through multiple lifecycles in one growing season making it dangerous to the crop at any stage [14].

In recent years, research efforts have focused on understanding the process of conidiation, appressoria formation, and responses in the host, rice, to the infection [20]. The effectors that are secreted by the pathogen into the intercellular spaces of the host interrupt natural plant processes and prey on a variety of host proteins, such as important parts during pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI), vesicle trafficking, effector-triggered immunity (ETI), autophagy, sugar transport, chloroplast and mitochondrial functions phytoalexin production, and more [20]. Pathogen response in plants often imitate normal

development processes for instance response to fungal gibberellic acid is very similar to the plants' natural response to its own produced gibberellin and auxins [22]. Gene expression regulates plant development and stress response and therefore, it can be stated that the proteins involved in these processes are regulated by a specific set of genes [22]. Study's find similar genes respond to environmental cues and stresses [22].

Understanding innate plant immunity is crucial for the advancing knowledge of plant stress response and the mechanisms it encompasses. Resistant rice cultivars are grown and developed to help control disease outbreaks and infections that can wipe out entire fields [23]. Natural immunity in plants stems from the recognition of PAMPS by the host sensors on the cell surface or pattern recognition receptors [23]. Pathogen-associated triggered immunity is the first kind of plant immunity [23]. Plant receptor protein kinases (RPKs) recognize microbial molecules like lipopolysaccharides (LPS), chitin, peptides, double-stranded RNA, as well as microbial DNA which then activate a mitogen-activated protein kinase (MAPK) element. This process is one of the earliest signaling actions post-plant sensing of the invading pathogen [23, 24]. The signaling channels of MAPKs regulate the production and function of a multitude of enzymes, transcription factors (TFs), hormones, antimicrobial chemicals and peptides, that all play critical roles in resistance to bacterial and fungal pathogens [24]. This first responder component of immunity is vital if a host is to survive an infection. Immune responses in rice have been found to be triggered by sulfated peptide Ax21, chitin, flagellin peptides and LPS [23]. Another level of plant immunity is effector-triggered immunity (ETI) which is a response to a wide variety of microbial molecules known as effectors, which are secreted from the fungus into the host during infection. Lastly, systemic acquired resistance (SAR) is another defense mechanism in plants [23].

Sensors in the rice membrane, as well as Nucleotide binding site/Leucine repeat (NBS-LRR) proteins, are needed for immune response. These NBS-LRRs job is to recognize the effectors secreted by the fungi. Four small protein effectors produced by the rice blast fungus *M. oryzae* have been characterized as *AvrPita*, *AvrPiz-t*, *AvrPik/km/kp*, and *AvrPia*, all having distinct structures. Recognition by these NBS-LRR proteins in rice depends on direct, decoy or bait models [23]. Thirteen NBS-LRR proteins that cause resistance to *M. oryzae* have been characterized in rice. *Pita* is the most studied rice NBS-LRR protein and interestingly has only one amino acid difference between susceptible and resistant alleles [23]. This protein triggers programmed cell death after it binds to a specific effector protein, *AvrPita*, which is hypothesized to keep the fungus from migrating to adjacent cells. This binding is an example of a recognition model of effector identification [23].

Chitin is a well-known product of PAMP that signals defense responses in plants, both monocots, and dicots [25]. This polymer of N-acetyl-D-glucosamine, is part of the fungal cell wall but is not found in plants although they do possess chitin degrading enzymes. The enzymes in plants can degrade the fungal cell wall, are also able to recognize when the fungal cell wall is releasing these chitin particles, and respond during infection [26]. Recognition of chitin by these enzymes activates the plants' defense pathway [26]. How chitin and its fragments, chitin oligosaccharides or N-acetylchitooligosaccharides, are able to notice a harmful pathogen and trigger defense is a topic of research [25]. Proteins in collaboration with receptor-like kinases, which serve as chitin elicitor binding proteins, subsequently bind chitin and play a critical role in chitin signaling in rice, thus activating intracellular events. Rice contains a large number of genes regulated by chitin. Many of these regulated genes are defense-related genes, such as those encoding pathogenesis-related proteins, TFs, and disease resistance proteins [26]. Studies found that in cultured rice cells in the lab, the recognition of chitin elicitor induces a series of defense

responses including the activation of MAPKs, ROS production, defense gene expression, phytoalexin production and the accumulation of an important signal molecule in plant response to stress, phosphatidic acid (PA) [23].

The ability to uptake nutrients can affect plant and immunity in response to pathogen introduction. Some of the genes that respond to mycorrhiza colonization may be involved in the uptake of phosphate in rice [27]. *M. oryzae* possessed mechanisms by which it can suppress rice host immunity by regulating the K⁺ channel 7. Potassium is important in many plant function including enzyme activation, cellular homeostasis, membrane transport, osmoregulation and immunoreaction [20]. Transporters and channels are responsible for the uptake and translocation of K. Often K fertilizers are applied in production systems and have been noted to reduce the occurrence of disease but it was unclear how. It is thought that high K concentrations in rice support immune response and inhibit the growth of the fungus [20]. Excess nitrogen applied as a fertilizer drastically increases rice susceptibility to *M. oryzae* [19].

After effector recognition and signal initiation, plant defense is activated causing responses such as cell wall reinforcement, accumulation of antimicrobial secondary metabolites, and expression of PR proteins [19, 23]. Several classes of antifungal metabolites are known and are non-essential for basic plant metabolism. Large numbers of terpenoid compounds are present in rice and serve in reducing pathogen toxicity [28]. Terpenoids have a plethora of key jobs including plant hormone functions, electron carriers, vitamins, pigments and membrane components, and importantly plant-pathogen interaction. Rice leaves produce momilactones A and B upon the introduction of *M. oryzae* infection and are widely studied for their anti-fungal activity during attack [28]. Also present in the rice leaves is oryzalexin A–D, which is classified as phytoalexin. Furthermore, Flavonoids belong to a large class of phytoanticipin and phytoalexin phenolic metabolites that are synthesized from phenylalanine in the shikimate pathway play part in plant resistance and defense. These flavonoids are known to directly inhibit the growth and germination of *M. oryzae* [28].

The cell wall in plant cells is armor against many pathogens that not only acts as a barrier, but it also produced chemicals to fight off pathogens that enter the cell. These chemicals include reactive oxygen species (ROS) and phenolics [29]. ROS production serves many functions in eukaryotic cells, including those in cellular defense. The generation of ROS is regarded as one of the first responses to fungal invasion [21]. In *M. oryzae*, intracellular ROS is critical to its pathogenicity in rice at the seedling stage. Interruption of the ROS production in the fungus causes it to lose toxicity in the host [21]. *M. oryzae* hyphae seem to initiate quick production of H₂O₂ in the host rice cells at the penetration sites. Small GTPase Rac complexes regulate accumulation of ROS generated through NADPH oxidases. Highly lethal strains of *M. oryzae* have been noted to repress the production of ROS thus suppressing immune responses. Plants that have high ROS accumulation tend to also have crosslinking of cell wall proteins that develop thick cell walls [30].

Plant proteins that are explicitly stimulated during pathogen invasion are referred to as Pathogenesis-related proteins (PRs) [23]. The accumulation of these proteins plays an essential role in active plant defense response [23]. Rice has several groups of PR genes that have been found to be triggered after species-specific infections [23]. Ubiquitin-proteasome system is used by plants to regulate protein production and usage for growth as well as abiotic and biotic stress response. E3s are a class of ligases that are common among the main types of ubiquitin-proteasome enzymes that play a role in pathogen response and interaction. About 1500 E3s are encoded in the rice genome, some of which are key to immunity in rice against fungal pathogens [29]. Some E3s are thought to play a vital role in cell wall

reinforcement, specifically after fungal infection. Pathogens try to interfere with the PTI pathway by producing proteins and sending them into the cell. Hyphae infected with *M. oryzae* release proteins that can direct the natural response process of the host cell defense in its favor [21]. Recently it has been found that the MoAP1 protein in the conidia of the fungus is highly expressed during the invasive stage of its lifespan [21]. Some of these proteins inhibit PTI by interfering with the E3 ligase activity, which normally acts as a positive regulator in immune response, or degrading them altogether. In immune plants, some of the defense E3 ligases in rice have the ability to degrade the proteins produced by the fungus [29].

Pathogens can create and mimic plant auxins that interrupt the plant pathways and repressed defense. Rice is often treated with a growth hormone called brassinolide (BL) to confer resistance to *M. oryzae* by reinforcing its natural hormone defenses [23]. Pathogenesis-related proteins and their corresponding receptor kinases in this case BAK1 induce the signal to initiate PTI. Hormones like abscisic acid (ABA), jasmonic acid (JA) have been used as well to trigger gene defense expression against *M. oryzae* [23].

About 60 genes for rice blast resistance have been found but this number includes allelic resistance; therefore, only five genes have been extensively used by breeders and shown to be reliable over the past few decades [17]. Molecular markers have made it possible to tag resistance genes [17]. Fungal pathogens have to break through physical surface barriers that serve as the plant's line of defense as well as the antimicrobial chemicals supplied by the host to survive [15]. Once it has penetrated the host immunity is stimulated, and defenses are up. Sensors in the host recognize the pathogenic microbes and the NBS-LRR proteins read the effectors that are projected into the cell. *M. oryzae* secretes about 740 different proteins during an invasion; therefore, in rice, its primary means of recognition are the NBS-LRR proteins [15, 23]. The signals these initial receptors trigger initiate MAPK activity and transcription factors, which then activate PR expression. Defense responses in the host attempt to reinforce the cell wall and produce secondary metabolites to combat that microbial invasion [23]. In-Depth knowledge of the mechanisms of resistance and host response to fungal pathogen invasion will help further agricultural development of blast resistant crops. Enhanced management practices for rice blast can also be achieved with an understanding of pathogen interactions and stress responses.

2.2 Rice sheath blight disease

Regarded as one of the most critical diseases in cultivated rice, rice sheath blight (*Rhizoctonia solani* Kuhn) is a widely distributed soil-borne disease prevalent in most rice-growing areas [31]. Within the U.S., rice sheath blight has increased due to increased crop rotation of rice with soybean (*Glycine max*) as aerial blight in soybean is caused by *R. solani* [32]. Globally, the widespread cultivation of semi-dwarf, high-yielding rice cultivars acclimated to high rates of nitrogen fertilizer has contributed to 50% yield reduction in susceptible cultivars [31]. The primary source of rice sheath blight inoculum is attributed to the formation of lesions near the waterline due to germinating sclerotia [33]. While effective fungicides are available to manage rice sheath blight, they are not considered a long-term solution due to health and environmental concerns [34].

Rice sheath blight (RSB) has the proven ability to survive from one crop season to another via sclerotia, plant debris, and weed hosts that may have dropped in the field during harvest [35]. Infection can occur at any growth stage from seedling to flowering due to different inoculum sources making it more prominent and common than other rice diseases [35]. Rice inoculation by the RSB pathogen results in

the production of enzymes that lead to callus breaking, degradation of sheath cells and organelles, cell wall cracking, and mitochondrial damage [36]. In addition to the production of degrading enzymes, toxin production can lead to visual symptoms on rice leaves, seedling wilting, reduced radical growth [35].

To decrease chemical control usage of fungicides against *R. solani*, researchers have turned to nanoparticle treatments. In an in vivo and in vitro study to assess the impact of silver nanoparticles on *R. solani*, the research found that increased inhibition of sclerotia formation (92%) and mycelia growth (85%) was observed when particles were applied at a concentration of 50 ppm [37]. Similar results were seen under microscopic observations of hyphae exposed to silver nanoparticles resulting in decreased sclerotial germination of 12% with just 7 ppm of silver nanoparticle-containing medium [38]. In a study done to observe the impact of silver nanoparticles on detached rice leaves infected with varying inoculations of *R. solani*, lesion lengths were significantly lower when leaves were treated with a nutrient broth containing silver nanoparticles compared to those that directly applied the nanoparticles [39].

3. Consequences and mitigation strategies of abiotic stresses

3.1 Cold stress

Although rice originates from tropical and sub-tropical areas, erratic climate change has led to cold-sensitive rice cultivars. While cold damage can occur at any growth stage, chilling injury at the early seedling stage can lead to slow growth, delayed crop maturity, poor establishment, and decreased yield [40]. In a universal screening method developed by Shirasawa et al. [41], rice plants are maintained in a cold deep-water irrigated pool during the entire booting stage, and the completion, spikelet fertility is used to determine cold tolerance in the population [42]. To evaluate cold tolerance, the parameters of germination percent, germination index, root, shoot, and seedling length, and seedling vigor are usually observed [43].

When evaluating rice genotypes for cold stress tolerance at the seedling stage, Rahul et al. [44] identified three rice cultivars with a decreased reduction in seedling vigor to two cold environments, 8 and 13°C, after germinating for 28 days. Evaluation of cold temperatures at the reproductive stage has pointed to spikelet sterility (90%), reduced numbers of spikelets (41%), and a decrease in panicle number per tiller (43%) when the duration of cold is greater than a day [45].

3.2 Drought stress

Drought has been identified as a significant problem in rain-fed lowland and upland rice [46]. Drought stress severely impacts rice production and affects approximately 23 million hectares of rice annually [47]. To produce 1 kg of rice seeds, 3000–5000 L of water is required making rice one of the least water-efficient crops produced [48]. Drought stress has been tied to rice yield variability due to climate variability with approximately 32% of rice harvesting regions experiencing climate variability due to global climate change [49]. As a result of drought stress, yield reduction can be 100% dependent upon the growth stage of the crop [50].

Drought patterns can be unpredictable, and traits are complex to understand; response mechanisms make it difficult to identify components tied directly to drought stress tolerance [51]. At the onset of drought stress, rice plants can respond by slowing down or stopping their growth, which is perceived as a survival technique [52]. Physically, drought stress can result in poor root development,

reduced leaf traits such as shape and epicuticular wax formation that can lead to direct affects to the leaf canopy, and decreased stem nutrient reserves [53]. Morphologically, drought stress can cause a reduction in germination, plant height, biomass, number of tillers, and leaf number and size [51].

To decrease the impact of drought stress in cultivated rice fields, researchers have attempted to introgress drought tolerant traits into high yielding cultivars using recombinant inbred lines (RILs) to detect quantitative trait locus (QTL) associated with plant protection traits [54]. Researchers used locally adapted *indica* rice lines to uncover these QTLs, but none were located in relation to yield [54]. Additional studies using RILs to detect drought tolerant traits have seen little success with one study reporting a 50% reduction in biomass, 39% reduction in grain yield, and 28% reduction in straw yield [55]. Although research continues to evolve, there are currently no commercially available, high-yielding rice cultivars available generating a direct need for improved research.

3.3 Heat stress

Although rice originated from tropical and subtropical regions, extremely high temperatures (above 38°C) can cause significant yield loss during the grain-filling stage [56]. While acclimated to higher temperatures, rice is most sensitive to heat stress during anthesis [57]. Heat stressed rice grains are subjected to decreased grain plumpness, starch content, and protein accumulation that decrease yield and grain quality [58]. In a study from 1992 to 2003 to assess the impact of climate change on rice production, researchers used weather data for the International Rice Research Institute to find that rice yield declined by 10% for each 1°C increase in temperature during the dry season [59]. High temperatures during reproductive stages such as before or during anthesis have resulted in decreased grain filling represented by a negative screening index [60]. When evaluating day and night temperature fluctuations, daytime temperatures above 33°C have proven to disrupt pollen tube formation, while nighttime temperatures above 29°C have led to seed sterility and decreased grain yield [57]. High temperature stress at the flowering stage has also proven to be injurious to rice. Temperatures above 35°C have led to decreased yield (60–90%), low grain quality, increased pollen and spikelet sterility (100%), resulting in an overall low harvest index [61].

Although heat tolerance is a multivariate trait, one *aus indica* variety “Nagina22” or N22 has been characterized as a heat tolerant cultivar [62]. While this rice variety has some physically undesirable traits, it does contain some morphophysiological traits such as early maturity, increased regeneration and recovery processes, and variability in the accumulation and mobilization of carbohydrates [63]. Many studies have been conducted in the development of recombinant inbred lines for quantitative trait loci (QTL) mapping for candidate genes with one study uncovering 11 QTLs that control young seedling tolerance to heat stress [64].

3.4 Salinity stress

The rising global population has put pressure on agricultural production systems, and it is becoming more common for unsuitable land, such as saline soils, to be used for agricultural production [65]. When soil or land is said to be salt-affected, it means that the soil is characterized by a high accumulation or concentration of soluble salts, such as NaCl. For soil to be officially defined as salt-affected, the electrical conductivity of the saturated paste extract (ECe) is measured to be at least 4 dS/m. This is the lowest ECe value that has been observed to affect crop growth and yield [66]. It is expected for global warming and rising sea levels to

increase the number of arable hectares degraded by salt waters, and to increase the concentration of salt in already salt-affected areas [67]. Saline soils are a problem for agricultural crops around the world. In Pakistan, around 40,000 hectares/year of cultivable land are reduced in quality due to the effects of increased saline concentration [68, 69]. Additionally, it is globally estimated that 800 million hectares are degraded by salt. Out of the 1500 hectares used for agriculture without irrigation systems in place, it is estimated that approximately 32 million hectares are salt-affected. Out of the 230 million hectares used for agriculture with irrigation systems in place, it is estimated that approximately 45 million hectares have accumulated deleterious salt concentrations [66].

Soils can acquire salt ions through natural and anthropogenic means. Oceanic winds and rains are capable of depositing salt ions onto land [66]. The use of brackish watering systems and other unsuitable irrigation systems further contribute to saline soils [65]. Land clearing also contributes to the salinization of lands because it leads to the water table rising and salt concentrating in the rhizosphere's root zone [66]. The deleterious effects of salty environments are exacerbated by dry or arid climates. Saline environments are a huge stressor for plants, affecting their overall growth and fecundity [70].

Rice (*Oryza* spp.) is a crop grown around the world, and makes up the diet of 3.5 billion people, especially in developing and poverty-stricken regions [67, 71]. There are approximately 22 species of *Oryza*, but only two are cultivated: *Oryza glaberrima* and *Oryza sativa* [71]. Nearly 75% of cultivated rice is grown on 85–90 million irrigated hectares out of the 230 million hectares utilized for agricultural production worldwide. From 1995 to 2000, rice demand exceeded rice production, and prices skyrocketed globally [71]. As climate change progresses and seawater rises, many rice fields are increasingly threatened by salt stress [67, 69, 71].

Stress in a plant is understood to be when the plant's energy levels are decreased and when energy or resources within the plant are allocated towards defense rather than biomass accumulation, reproduction, or maintenance [65]. The most evident effects of saline stress are inhibited growth and reduced photosynthetic rates [70]. Many plants will exhibit no growth because the energy gained through photosynthesis and cellular respiration is equivalent to the energy required to tolerate the salt stress. When the energy required to tolerate the salt stress exceeds the energy gained through photosynthesis and cellular respiration, the plant may exhibit injury or death [65]. When rice (*Oryza sativa*) is grown in the presence of salt, cell wall elasticity is reduced due to changes in metabolic pathways. The altered osmotic gradients and the interruption of photosynthetic activities result in imbalanced nutrient levels. These processes ultimately reduce plant growth, chlorophyll concentration, and overall leaf area [69]. Sterile panicles and panicles with reduced seed have been observed in rice plants grown in environments with a high saline concentration [72]. Reactive oxygen species (ROS) have been observed to act as signaling agents in response to salt stress; however, ROS are also capable of damaging cellular structures, such as the lipid membrane or enzyme activity, if they are present in high enough concentrations [65]. Although all the mechanisms have not been identified or fully understood, it is clear that saline environments cause stress in rice plants that reduce overall growth and fecundity.

Plants that grow in saline environments exhibit marked differences, both physiologically and biochemically, from plants that grow in non-saline environments [72]. Salt inhibits plant growth and development through the alteration of osmotic gradients, the accumulation of ions leading to ion toxicity, and the interruption of pathways related to photosynthesis and nutrition [69]. Salt concentrations present outside of plant tissues, such as outside of roots, make it difficult for the plant to uptake water and other nutrients [66]. Salinity injures plants through inhibition of

osmotic properties [70]. It was originally thought that rice crops suffered injury in saline environments as a result of increased chloride uptake due to hypothesized osmotic adjustments. In a research review by Gregoria et al. [73] studies conducted by Clarkson and Hanson indicated that the damage is a result of increased Na^+ uptake, which reduces yield because of an imbalance in Na-K within the plant's tissues. Osmotic responses to salinity concentrations outside of the plant tissues are the most rapid salt stress response and are primarily exhibited through a reduction in new shoot growth. New shoot growth is one of the first noticeable inhibitions because a reduction in leaf tissue/root ratio allows for decreased water required for the plant. This allows the plant to better control soil moisture when salt concentrations are high [66].

While salt concentrations outside of the plant cause stress and osmotic imbalances, the accumulation of salt and ions within the plant tissues also causes major biochemical and physiological problems [66]. The accumulation of Na^+ and Cl^- ions in the plant tissues, a mechanism of osmotic adjustment, can confer toxicity [68]. This saline stress response is slower than the initial osmotic effect previously discussed and eventually is illustrated in the discoloration and injury observed in older leaves [66]. It can result in other reduced growth parameters including shoot dry weight, root dry weight, and tillering capacity [68]. This phenomenon is observed in more mature plant tissues because mature tissues do not filter or dilute nutrients or ions, as new growth tissues do [66]. Furthermore, when experiencing salt stress, plants will close their stomata due to decreased water potential [61]. Closed stomata limit the amount of carbon dioxide that can be assimilated. This ultimately interrupts photosynthetic pathways, reducing energy assimilation and growth rates. Photosynthetic machinery has also been observed to be damaged as a result of extended stomata closure. This phenomenon also changes source-to-sink carbohydrate allocation in the plant [70].

When experiencing drought stress, plants maintain diverse biochemical and physiological mechanisms for coping. First, a plant must perceive a stressful environment and induce stress-related defense mechanisms to protect itself [74]. Salinity tolerance can be achieved through different mechanisms, such as the accumulation of compensatory osmolytes, which help to maintain stable osmotic environments within the cell or the overexpression of stress defense genes [70, 74]. To tolerate salty situations, many plants will make osmotic adjustments, which serve to sustain turgor pressure [65]. The two mechanisms involved in plant osmotic adjustments are ion exclusion and tissue tolerance. Ion exclusion is when the plant removes Na^+ and Cl^- ions from leaves and rely on organic solutes, such as proline and glycine betaine (GB) as osmoprotectants [65, 70, 75]. The osmoprotectants serve to regulate osmotic gradients and processes to continue water uptake in the presence of soluble salt ions [75]. Parenchyma cells located in the root xylem act as 'gatekeepers' in the exclusion of Na^+ and Cl^- . Tissue tolerance is when the plant acquires Na^+ and Cl^- within compartmentalized plant tissues [65]. In both mechanisms of osmotic adjustments, the plant accumulates osmolytes within cells. This lowers the osmotic potential of the cell to mimic the low water potential of the substrate. This mechanism helps to maintain stable osmotic environments within the cells, conferring tolerance of environmental stressors, such as drought or salinity, to the plant. Plant species that are able to tolerate higher salt concentrations have been observed to maintain high concentrations of Na^+ and Cl^- ions within plant tissues at all times. Plant species that are more sensitive to saline environments have been observed to maintain lower Na^+ concentrations within plant leaves and are hypothesized to rely more heavily on the ion exclusion mechanism [65].

It is unclear if osmotic adjustments are the only mechanisms a plant has to tolerate stressful environments, and the overall tolerant effect is likely a result of

multiple mechanisms working synergistically within the plant [70]. For example, when plants experience stressful environmental conditions, such as high salt concentrations or drought, stress-related genes may be induced for defense purposes. Some of the proteins observed to function in this manner are chaperone proteins, ion channels, transporters, antioxidation proteins, detoxification proteins, and osmotic adjustment proteins. The gene family NAC is a highly conserved group that is only observed in plants [74], which over 100 NAC genes described in the rice (*Oryza sativa*) genome [76]. While this gene family codes for a large array of proteins with various functions, a few genes have been identified in environmental stress response pathways. In 2015, Hakim et al. [77] identified SNAC1 and determined that this gene is expressed in response to abiotic stressors, including salt stress. Further analysis revealed the role of SNAC1 in regulating stomatal guard cells on the upper and lower sides of leaves. In transgenic plants designed to overexpress the SNAC1 gene, increased closure of stomata was observed; however, photosynthetic rates were not reduced. It was further determined that when the SNAC1 gene is overexpressed, no fitness costs are incurred [74]. Additional studies have identified the expression of NAC genes, OsNAC6 and SNAC2, as enhancing abiotic stress tolerance, including cold, salt, and drought tolerance [76].

As populations and sea levels rise, salt-affected soils will continue to pose challenges in agricultural production around the world [65]. Rice is an important crop, feeding approximately 3.5 billion people around the world [71]. It is understood that high concentrations of saline reduce photosynthesis, growth, and yield in rice through the interruption of osmotic gradients [66, 70]. Some plants and varieties of rice have been observed to tolerate salt stress through two osmotic adjustments: ion exclusion and tissue tolerance. Ion exclusion involves the accumulation of organic solutes, such as proline and glycine betaine (GB), to maintain osmotic gradients and uptake water from substrates with high concentrations of soluble salts [65, 70, 75]. Ongoing research has identified several genes within the NAC gene family that regulate abiotic stress response factors. These genes are SNAC1, SNAC2, and OsNAC6 [74, 76]. Transgenic rice crops have been developed to overexpress SNAC1, SNAC2, and OsNAC6 to better understand their role in abiotic stress defense, and it was determined that the overexpression of these genes incurs no fitness cost to the transgenic plant [76].

3.5 Submergence stress

Due to the negative impact of climate change, a majority of rice-producing countries have witnessed a steady decline in the performance of culturally selected rice cultivars [78]. The largest difficulties are due to rice's inability to adapt to multiple abiotic stresses such as flooding, drought, and soil salinity [79, 80]. Flooding causes the most negative impact because of difficulties in water accumulation due to increased rainwater, increased river discharges, and unexpected tidal movements [80]. In rice, flash flooding caused by extremely heavy rainfall can lead to crops being completely submerged for 10–15 days or longer in some countries causing them a substantial reduction in yield [81].

To counteract yield reduction, researchers set out to characterize and discover rice cultivars that demonstrated tolerance to complete submergence. Research completed at the Huntra Rice Experiment Station in Thailand showed only 6% of 3156 screened rice cultivars having a level of tolerance after 10 days of complete submergence, while IRRI only found 2% of 18,115 screened rice cultivars having submergence tolerance [82]. Comparisons were made to rice cultivar FR13A that was released in 1940, and showed increased tolerance to submergence serving as the model standard for complete submergence tolerance in rice [78]. While FR13A

survives complete submergence, it is still characterized as a low-yielding cultivar [83]. After additional studies, researchers were able to discover and clone the gene associated with submergence tolerance in FR13A, SUB1. This gene was able to be introgressed into high-yielding cultivars through marker-assisted backcrossing creating mega-varieties such as Swarna and IR64 [78]. These mega-varieties have proven to be very useful in affected areas, but increased tolerance is necessary to provide relief in low-lying areas [78].

In a study conducted by Iftekharuddaula et al. [84], it was observed that a mega-variety, BR11, introgressed with the SUB1 QTL produced BR11-Sub1 that was 99.8% identical to BR11 in yield, yield-component parameters, and grain properties. This is important, as BR11 is grown on more than 40% of the rice acreage in rain-fed lowland rice (RLR) of Bangladesh [85]. BR11-Sub1 demonstrated submergence tolerance after complete submergence stress of 21 days. This was comparable to the tolerant donor, IR40931-33-1-3-2, and the tolerant check, FR13A [84]. In both studies, Iftekharuddaula et al. [84] and Gonzaga et al. [78], submergence levels varied from 0.7 to 1.7 m, respectively demonstrating submergence tolerance in RLR areas that receive an average of 0.3 m of water or more [86].

4. Conclusions

As the demand for rice yield continues to increase over the next 20 years, research must continue to develop abiotic and biotic stress-tolerant rice cultivars. The impacts of climate change can be seen as research focuses on cold, drought, heat, and submergence stress. Climate change can lead to decreases in rice yields up to 100% due to fluctuating temperatures, and unexpected instances of flash flooding. There is also a need to identify a more diverse slate of traits that can arm rice in overcoming stress due to climate change. In rice, research has shifted towards studies focused on screening weedy rice (*Oryza sativa*) for abiotic stress tolerance. Recent discoveries have uncovered cold, heat, drought, and submergence tolerant weedy rice that could lead to traits that can be introgressed into the cultivated rice germplasm. This chapter focused on strategies used to discover biotic and abiotic stress tolerant rice germplasms to protect rice against climate change and disease resistance.

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