

The trade-off between UVB sensitivity and tolerance against other stresses in African rice species

Gideon Sadikiel MMBANDO, Jun HIDEWA*

Graduate School of Life Sciences, Tohoku University, Sendai 980-8577, Japan

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Abstract: Climate change and ozone depletion have caused increased ultraviolet B (UVB; 280-315 nm) radiation levels on earth, which has been predicted to cause decreased growth and yield of various crops, including rice, the most important staple food worldwide. UVB radiation sensitivity varies extensively in Asian rice (*Oryza sativa* L.) and African rice (*Oryza glaberrima* Steud. and *Oryza barthii* A. Chev.) cultivars, and the activity of cyclobutane pyrimidine dimer (CPD) photolyase that repairs UVB-induced CPD is an essential factor underlying UVB sensitivity in rice. Unlike Asian varieties, African rice possesses different origins, and it is cultivated in the African continent under environmental stresses and unstable climatic conditions and is well-adapted to various biotic and abiotic stresses. However, information regarding UVB sensitivity in African rice remains lacking. In this review, we describe recent research examining the sensitivity of rice species to UVB radiation, and we focus on UVB sensitivity and CPD photolyase genotypes with emphasis on African rice species. Consequently, the novel CPD photolyase genotype found only in African rice species results in a more severe phenotype termed “Super-hypersensitive” in cultivars grown only in West Africa, particularly at *O. glaberrima* domestication centres. We also describe possible reasons for the high UVB sensitivity of African rice cultivars in relation to plant morphology and other environmental stresses such as floods and pathogens. Finally, using the available knowledge, we suggest possible ways to develop multiple stress-resistant plants that can cope well in tropical environments under numerous environmental stresses. This review provides more tools for increasing food production for feeding the outgrowing population, particularly in tropical areas such as Africa.

Key words: African Rice, CPD photolyase, environmental multiple stresses, trade-off, UVB radiation, resistance

1. Introduction

As sessile organisms, plants are exposed to various biotic and abiotic stress conditions that affect their growth, development, and reproduction. Abiotic stresses include drought, heat, cold, salinity, ultraviolet (UV) radiation, and others, while biotic stresses are typically caused by phytophagous insects, bacterial pathogens, nematodes, and fungi. To counter the effects of these stresses, plants have evolved multiple mechanisms that help them to sense and acclimate to these environmental stresses (Gupta et al., 2015), and these mechanisms include shedding of affected tissue, stress neutralisation, renewal of tissue growth, and damage repair.

Sunlight is crucial for supporting life on our planet, but it consists of UV radiation. Photosynthetic organisms require sunlight and are, therefore, exposed to UV radiation. The UV region of the spectrum is divided into three portions based on wavelength, and these include UVA (315–400 nm), UVB (280–315 nm), and UVC (less than 280 nm). The shortest UV waves are the most detrimental to living organisms. Although the ozone layer

completely absorbs UVC radiation, this type of radiation is the most hazardous. In contrast, UVA cannot be absorbed by the ozone layer and, thus, is transmitted to the surface of the earth; however, it is less harmful than the other wavelengths of UV radiation (Hollosy, 2002). Although it contributes only a minor proportion (1.5%) (Cockell and Horneck, 2001; Horneck et al., 2010) of the total radiation among the three types of UV radiation, UVB is of high importance due to its ability to severely damage DNA and, thus, affect plant growth and development. In the past, there has been worldwide concern regarding the impact of increased UVB radiation on the surface of the earth and the organisms living there due to the destruction of the stratospheric ozone layer. Although the Montreal Protocol has prevented a significant increase in UVB radiation, as of 2020, we are now observing an unprecedented increase in UVB levels (Neale et al., 2020) in the Arctic due to stratospheric ozone depletion.

As they depend on sunlight for photosynthesis throughout their entire lives, plants are constantly exposed to harmful sunlight UVB radiation that suppresses

* Correspondence: jun.hidema.e8@tohoku.ac.jp

photosynthesis and protein synthesis, ultimately leading to a decrease in growth and productivity (Teramura et al., 1990, 1991; Kumagai et al., 2001; Hidema et al., 2005). Rice is one of the most important staple grains worldwide and is cultivated globally, including Africa where the amount of UVB radiation from sunlight is high (Jablonski and Chaplin, 2010). Cultivated rice belongs to the genus *Oryza* (AA diploid genome group). In this genus, there are only two cultivated rice species with two taxonomically distinct species, including *Oryza glaberrima* (*O. glaberrima*) and *Oryza sativa* (*O. sativa*), that were separated independently approximately 640,000 years ago. *O. sativa* was originated in Asia, while *O. glaberrima* was in West Africa (Wang et al., 2014; Meyer et al., 2016). Although *O. glaberrima* is cultivated in wetland conditions in Africa in an unstable environment and under poor traditional farming system, it has developed a number of useful traits to resist various biotic and abiotic stresses (Second, 1985; Brar and Khush, 1997; Sanchez et al., 2013). Rice is an important food in Africa and is not only a staple food but also highly appreciated for its taste, culinary qualities, and ritual values. However, it is cultivated under multiple environmental stresses such as flooding, drought, harsh temperatures, pests, pathogens, and UVB radiation, all of which may affect its productivity. Thus, understanding the possible interaction mechanisms between one stress such as UVB radiation and other stresses such as floods and pathogens will be of great importance in providing methods to develop multiple resistance crop plants possessing high yields and productivity.

UVB radiation exerts deleterious effects on plants primarily by inhibiting photosynthesis through the reduction of the expression of key photosynthesis genes. In response to UVB irradiation, the D1 and D2 (water-plastoquinone oxidoreductase complex) proteins of photosystem II in the chloroplast thylakoid are quickly degraded, and chlorophyll and the activity and amount of Rubisco are decreased (Mackerness, 1997; Jansen et al., 1998; Mackerness et al., 1999). UVB irradiation of plants increases hydrogen peroxide (H_2O_2) levels, damages the thylakoid membranes, and destroys chlorophyll and carotenoids (Karpinski et al., 1997; Takeuchi et al., 2003). Additionally, DNA is sensitive to UVB radiation, and, thus, absorption of UVB causes severe DNA lesions. The two UVB-induced DNA lesions are cyclobutane pyrimidine dimers (CPDs) and pyrimidine (6-4) pyrimidone photoproducts ([6-4] photoproducts) (Britt, 1996) that interfere with both DNA replication and transcription. UVB can also affect plants through photooxidation or the formation of reactive oxygen species (ROS) and free radicals that are produced during photosensitization (Caldwell, 1993; Foyer et al., 1994). Among all of these mechanisms, CPDs result in the majority of the DNA damage (approximately 75%),

while the (6-4) photoproducts account for the remainder (Mitchell and Nairn, 1989). Therefore, CPDs are the main cause of growth inhibition in rice plants (Hidema et al., 2007), and such damage may be lethal to various organisms (Brash et al., 1987) and may even cause cancer in humans (Brash et al., 1991). These damages can interfere with transcription and replication, and this is believed to be the cause of the adverse effects observed in plants. To cope with such damage, plants use two main mechanisms for DNA repair of CPDs and (6-4) photoproducts that are termed “photorepair (photoreactivation)” and “nucleotide excision repair (dark repair)”. In photorepair, the enzyme photolyase binds to the CPDs or to 6-4 photoproducts, and using photon energy from UVA to blue light (350–550 nm), it monomerizes or reverses the dimers in a lesion-specific manner, ultimately releasing DNA to its native state (Sancar, 1994). Conversely, for dark repair the photoproducts are removed from DNA through nucleotide excision repair (NER) processes that involve multiple complex steps to facilitate damage recognition, chromatin remodelling, excision of the damaged oligonucleotide, gap-filling DNA synthesis, and strand ligation within the correct order. Thus, in higher plants, photorepair is believed to be the major and most effective pathway for repairing UV-induced DNA lesions (Pang and Hays, 1991; Quaitte et al., 1994; Hidema et al., 1997), and this is likely due to the slower nature of the dark repair process compared to that of photorepair (Britt, 1999) and the knowledge that this process is highly energy-consuming due to the involvement of numerous enzymes. Despite this, both photorepair and dark repair of DNA have been reported in various plant species (Hidema et al., 2000).

UVB sensitivity varies widely among Asian rice species, and this difference is primarily caused by the difference in CPD photolyase activity (Teranishi et al., 2004; Hidema et al., 2005, 2007; Iwamatsu et al., 2008). Therefore, CPD photolyase may act as an essential factor for plants to withstand UVB-induced DNA damage. *O. sativa* transgenic rice plants possessing CPD photolyase overexpression exhibited a significant increase in UVB resistance compared to that of wild-type plants, thus, suggesting the importance of this enzyme in UVB tolerance (Hidema et al., 2007; Teranishi et al., 2012). However, it remains unknown how African rice species survive the harmful effects of tropical UVB radiation. There is little knowledge regarding the UVB sensitivity and CPD photolyase genotypes of African cultivated rice species in relation to those of Asian rice. It is of interest to determine if there any possible relationship between African rice morphology and UVB sensitivity. Additionally, it is of interest to determine if UVB sensitivity result can form a trade-off with other environmental stresses in African rice species and the UVB-sensitive Asian rice Surjamkhi.

In this review, first, we describe the UVB sensitivity and CPD photolyase genotypes of African rice compared to those of Asian rice. We also explain the morphological and geographical adaptation differences between the two species that led to various UVB-sensitive African rice cultivars and possibly the crosstalk between UVB sensitivity and other environmental stresses. Next, we describe the potential applications of the available resources of Asian rice cultivars to develop UV-resistant African rice cultivars that may exhibit a higher yield under tropical environmental conditions with high levels of UVB radiation. Finally, using the available knowledge, we suggest possible ways to develop multiple stress resistant plants that can cope well in tropical environments under numerous environmental stresses. This review provides more tools for increasing food production for feeding the outgrowing population, particularly in tropical areas such as Africa.

2. Historical background

2.1 Variation of UVB sensitivity in African cultivated rice

The activity of CPD photolyase is necessary for plants to survive harmful UVB irradiation stress (Britt et al., 1993). Our previous data demonstrated that UVB sensitivity varies widely among Asian rice cultivars. The evaluation of UVB sensitivity was divided into three groups according to the degree of UVB sensitivity: UVB-resistant, UVB-sensitive, and UVB-hypersensitive. The differences in UVB sensitivity among Asian rice cultivars were primarily caused by different CPD photorepair activities due to different CPD photolyase genotypes that were caused by spontaneous polymorphisms within the CPD photolyase gene that altered both the structure and activity of the enzyme (Teranishi et al., 2004; Hidema et al., 2005; Ueda et al., 2005; Iwamatsu et al., 2008): the CPD photolyase activity is higher in the UVB-resistant rice than in the UVB-sensitive rice, and the activity in UVB-hypersensitive rice is lower than that in the UV-sensitive rice. Interestingly, most of indica rice cultivated in Southeast Asia, which has a relatively high amount of UVB radiation, belongs to UVB-hypersensitive group (Sato and Kumagai, 1993; Hidema and Kumagai, 2006). This led us to investigate the UVB sensitivity of African rice cultivars.

Recently, Mmbando et al. (2020) examined the UVB sensitivity of 15 African rice cultivars belonging to *O. sativa*, *O. barthii*, and *O. glaberrima* that are cultivated in different geographical locations on the African continent in comparison to Asian rice UVB-resistant (*O. sativa* ssp. *japonica*, Sasanishiki), sensitive (*O. sativa* ssp. *japonica*, Norin 1), and hypersensitive (*O. sativa* ssp. *indica*, Surjamkhi) rice cultivars. Surprisingly, they observed that most of the African rice species examined in that study were highly sensitive to UVB radiation compared

to the sensitivity in Asian rice species, and certain cultivars exhibited even more severe damage phenotypes (UVB-super-hypersensitive) than did the hypersensitive Asian rice cultivar Surjamkhi (Figure 1A) (Hidema et al., 2005). Based on the UVB sensitivity index, they classified the UVB sensitivity of African rice into three groups that included UVB-sensitive that were similar to Asian rice (Norin 1), hypersensitive that were similar to the Asian rice Surjamkhi, and super-hypersensitive that was newly discovered in their study and was identified only in African rice species. There were no African rice cultivars with a higher UVB resistance index than that of Sasanishiki. Moreover, it was evident that the UVB-super-hypersensitivity of African rice cultivars was caused by low total CPD photolyase activity due to both the low amount and activity of CPD photolyase. The reduction in the activity of CPD photolyase was due to new specific amino acid changes in the CPD photolyase gene of these cultivars that affected the structure and activity of the enzyme (Mmbando et al., 2020). This study was surprising, as we know that UVB radiation is higher in tropical areas such as Africa (Jablonski and Chaplin, 2010); however, most of the African rice species exhibited increased sensitivity to UVB radiation stress, and there were no UVB-resistant African rice species. This study suggests that although the newly identified polymorphisms reduce the total CPD photolyase activity of African rice, they may also play a significant role in surviving and adapting African rice in West Africa.

2.2 Crucial factors for determining UVB sensitivity in African rice cultivars.

It is of interest to determine the crucial factors controlling UVB sensitivity in African rice cultivars. The UVB-super-hypersensitive African rice cultivars exhibited both a low amount and activity of CPD photolyase. The low CPD photolyase activity was due to the new polymorphisms that were conserved mainly in African rice species (Figure 1B). Additionally, the CPD photolyase content differed even among cultivars with the same genotype in both Asian and African rice (Mmbando et al., 2020). African rice is grown in a tropical environment with a higher amount of UVB radiation stress, and therefore, one should expect to possess a higher total CPD photolyase activity. Interestingly, the low total CPD photolyase activity was not only observed in UVB-super-hypersensitive African rice cultivars but also observed in the Asian rice Surjamkhi; thus, suggesting that the low total CPD photolyase activity among these cultivars contributed to a higher degree of sensitivity to UVB radiation (Mmbando et al., 2020).

There are a number of other UVB-sensitive Asian rice cultivars that belong to the *aus* ecotype from the Bengal region (Sato and Kumagai, 1993; Ueda et al., 2005; Hidema and Kumagai, 2006), and the major question is how these

genotypes can survive the high UVB radiation with such a low total CPD photolyase activity. Mmbando et al. (2020) proposed that the higher sensitivity among these cultivars may be beneficial for surviving other environmental stresses such as those caused by pathogens or herbivores (Kunz et al., 2006; Kunz et al., 2008; Qi et al., 2018). Alternatively, they suggested that, unlike Asian rice, the origin of African rice may be deep-sea rice (paddy rice), and, therefore, it became more resistant to African flood conditions by evolving distinct adaptive morphological structures with high growth rates and long stems (Jackson and Ram, 2003; Sakagami et al., 2009; Sakagami, 2012). However, in contrast, it may not possess an adaptation mechanism for UVB, as ultraviolet radiation does not easily pass through the water. This hypothesis will be explained in detail in the last section. However, it is of interest to determine the CPD photolyase genotypes possessed by African rice species and if they possess a genotype similar to that of Asian rice species.

2.3 Novel CPD photolyase polymorphisms cause UVB-super-hypersensitivity in African rice cultivars

We previously reported three CPD photolyase genotypes among cultivated and wild rice, and these genotypes were highly correlated with UVB sensitivity. One difference in the nucleotide adenine (A) at position 377 (exon 2) in Sasanishiki was changed to guanine (G) in Norin 1, and this causes amino acid changes at position 126 from glutamine (Q) to arginine (R). Moreover, the Sasanishiki and Surjamkhi CPD photolyase sequences differ by several positions (377, 888, 939, and 1248); however, it was the only alteration at positions 377 and 888 that led to a change. Specifically, the CAG codons at both positions 126 and 296 encoding Q in the Sasanishiki were changed to CGG and CAC codons in Surjamkhi that encode R and histidine (H), respectively (Teranishi et al., 2004; Ueda et al., 2005; Hidema et al., 2005). Thus, the UVB-resistant (Sasanishiki) at positions 126 and 296 were Q¹²⁶-Q²⁹⁶ ("Sasa-type"), while those in UVB-sensitive (Norin 1) were R¹²⁶-Q²⁹⁶ ("Nori-type") and UVB-hypersensitive (Surjamkhi) were R¹²⁶-H²⁹⁶ ("Sur-type") (Iwamatsu et al., 2008). Hidema et al. (2000) reported the mutation in Norin 1 compared to Sasanishiki caused by a decrease in the rate of binding to CPD through the use of photoflash analysis. Moreover, the QTL analysis test of the linkage between CPD photolyase and UVB sensitivity (Hidema et al., 2005) revealed that UVB sensitivity is a quantitative inherited trait. Furthermore, Ueda *et al.* reported that *qUVR-10* exhibits the largest genetic differences among QTLs associated with UVB resistance and encodes CPD photolyase (Ueda et al., 2005). These differences in genotypes primarily affected CPD photolyase activity. Therefore, the differences in UVB sensitivity among Asian and wild cultivars are determined

by the genotype of the CPD photolyase (Teranishi et al., 2004; Hidema et al., 2005; Iwamatsu et al., 2008). Based on this, it is of interest to further examine the CPD photolyase genotypes of African rice species.

The Sasa-type CPD photolyase genotype was not observed among all African rice cultivars examined in the study by Mmbando et al. (2020) and all cultivars possessed R¹²⁶ as in the Nori- and Sur-types. The Q²⁹⁶ genotype, similar to the Sasa- and Nori-types, was identified in UVB-super-hypersensitive African rice (TOB7307, Jiakawo Wodewo, MB3, C7251, TOG12380, TOG14928, and Maro Goudo), while the H²⁹⁶ genotype, as in the Sur-type, was observed in all African tropical *O. sativa* (TOS) and only one tropical *O. barthii* (TOB14466) that were examined in that study. They also observed new amino acid substitutions in African cultivars that possessed a Q²⁹⁶. The cytosine at position 232 in exon 1 (Sasanishiki) was changed to thymine in UVB-super-hypersensitive African rice cultivars, thus, leading to an amino acid change at position P⁷⁸ to S⁷⁸. Additionally, guanine at position 848 in exon 4 (Sasanishiki) was changed to cytosine in the same cultivars and also in TOG12380, thus, leading to an amino acid change at position G²⁸³ to A²⁸³. Of note, all African cultivars possessing the "S⁷⁸-R¹²⁶-A²⁸³-Q²⁹⁶" genotype with the exception of *O. glaberrima* (MB3), were classified as UVB-super-hypersensitive type. These results suggest that the "S⁷⁸-R¹²⁶-A²⁸³-Q²⁹⁶" genotype largely affects the UVB sensitivity of African rice species. Furthermore, the "S⁷⁸-R¹²⁶-A²⁸³-Q²⁹⁶" genotype was primarily found in UVB-super-hypersensitive African rice (*O. glaberrima* and *O. barthii*) and not in Ancestors or Asian rice species (Mmbando et al., 2020). These cultivars are also grown in the proposed domestication region of *O. glaberrima* in West Africa (Semon et al., 2005). Conversely, the countries of origin of all African *O. sativa* cultivars possessing genotypes identical to that of the Asian cultivar Surjamkhi (*O. sativa* ssp. *indica*) (P⁷⁸-R¹²⁶-G²⁸³-H²⁹⁶) were distributed widely throughout Africa and included countries proposed as the principal entry zone during the introduction of Asian *O. sativa* into West Africa. Asian *O. sativa* may have, thus, been introduced to various areas of Africa (including West Africa) by humans, perhaps during the period of the Atlantic slave trade (beginning ca. 1550) or earlier through trans-Saharan trade routes.

However, if these polymorphisms are advantageous for African rice species is yet to be determined, and it must be further explored if it is an adaptive response obtained during the domestication process. Nevertheless, this review raises the possibility of an interaction between UVB sensitivity and other environmental stresses, such as floods, pests and herbivores, among these species. These points require future clarification.

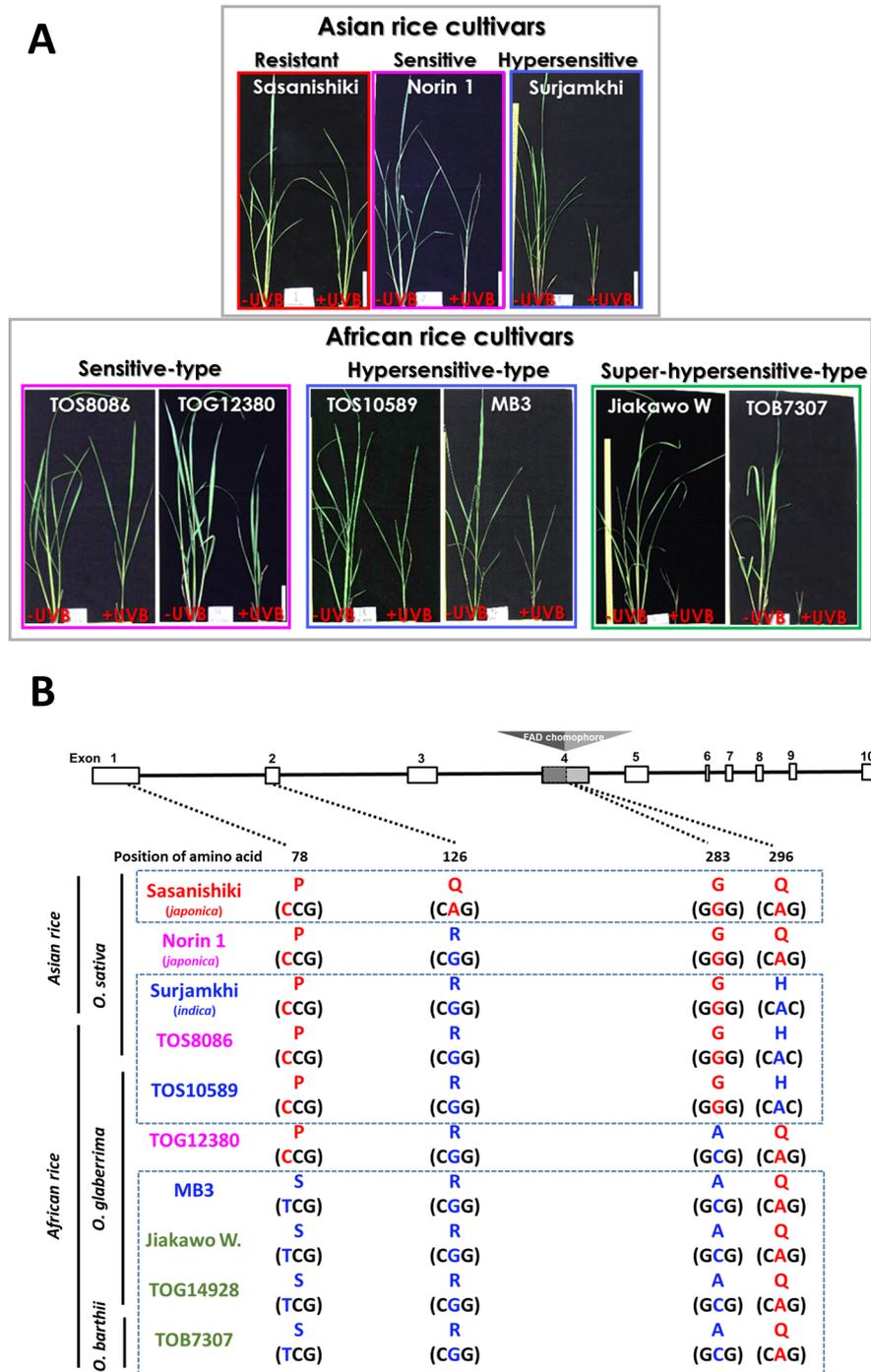


Figure 1. Variety of UVB sensitivity and CPD photolyase polymorphisms in African rice cultivars. (A) Asian (*Oryza sativa*; *japonica* rice Sasanishiki and Noron 1 and *indica* rice Surjamkhi) and African rice cultivars (Tropical *Oryza sativa*; TOS8086 and TOS10589, *O. barthii*; TOB7307, *O. glaberrima*; TOG12380, MB and Jiakawo W.) were grown in a growth cabinet for 21 days with (+UVB) or without (-UVB) UVB radiation. UVB sensitivity varied widely among Asian and African rice cultivars. Bars = 5 cm. (B) Cyclobutane pyrimidine dimers (CPD) photolyase genotype of African rice cultivars. The amino acid residues of CPD photolyase at the place where the mutation was identified, and its base sequence are shown. This figure is partially modified the figure published in Mmbando et al. (2020).

2.4 Growing conditions and morphological features that may influence the UVB sensitivity of African rice cultivars.

UVB radiation inhibits the growth and productivity of economically important crops such as rice by reducing cell division and elongation (Fina et al., 2017; Hopkins et al., 2002; Rajendiran and Ramanujam, 2003; Teramura, 1983). African rice cultivars are grown in the wetland of Africa in an unstable environment and under poor or traditional farming techniques with low human interference, and they are, therefore, prone to not only UVB radiation stress but also various stresses caused by climate fluctuations such as flooding (Sakagami and Kawano, 2011; Sakagami, 2012), drought, and temperature. As this rice has survived a harsh environment with low human interference, tolerance mechanisms have been developed to cope with various biotic and abiotic stresses (Second, 1985; Brar and Khush, 1997; Sanchez et al., 2013). Flooding has been demonstrated to be a significant abiotic stress affecting agricultural productivity of rice worldwide in areas with controlled irrigated conditions, deep-water rice, and rice in tidal wetlands, and these types of rice are well known to develop some morphological structures that enable them to survive such deep-water agriculture systems, including shoot and internodal elongation (Kende et al., 2002). African rice is known as a type of deep-water rice, and most of the African rice cultivars have developed submergence tolerance mechanisms (Sakagami and Kawano, 2011) and adapt well during flooding compared to these characteristics in Asian rice. Therefore, unlike Asian rice, the majority of African rice (*O. glaberrima*) cultivars have developed some structural and morphological adaptations as an escape strategy for surviving flooding conditions in West Africa (Jackson and Ram, 2003; Sakagami et al., 2009; Sakagami, 2012). Due to its taller structure and high potential for photosynthesis during flooding conditions (Sakagami et al., 2009), *O. glaberrima* is still preferred over *O. sativa* and is still cultivated today (Ndjiondjop et al., 2010) despite the knowledge that it possesses a lower productivity compared to that of Asian rice *O. sativa* (Oladele et al., 2016). However, during short-term submergence (flash flooding) caused by unstable climatic conditions, adaptation strategies for surviving flooding, including shoot and internode elongation, will make these species vulnerable to lodging and result in photoperiodic sensitivity (Sakagami and Kawano, 2011; Sakagami, 2012) and UVB sensitivity (Mmbando et al., 2020). Consequently, *O. glaberrima* differed in ligule shape, panicle branching, and tiller number formation (Portères, 1955; Besancon, 1993; Agnoun et al., 2012). Vigorous tillering, high leaf area index, and high specific leaf area of *O. glaberrima* contribute to its high competitiveness against weeds (WARDA, 1996; Rodenburg et al., 2009)

and flooding (Sakagami, 2012). However, rice plants possessing more tiller numbers and broader leaves may experience more UVB damage, as more tiller numbers and plant surface area will be exposed to UVB radiation. Therefore, it is reasonable to assume that the high tiller number, broad leaves, taller structure, longer shoot, and internode elongation will make *O. glaberrima* cultivars resistant to flooding but susceptible to UVB radiation. This could explain why most *O. glaberrima* cultivars exhibited super-hypersensitivity, while tropical *O. sativa*, an Asian rice that may have been introduced to Africa with low leaf area index, exhibited various UVB sensitivity phenotypes that were all less severe compared to that of *O. glaberrima* (Figure 1A) (Mmbando et al., 2020). Thus, it is possible that African rice species have evolved different plant shapes that expose them to different amounts of UVB radiation stress.

As African rice was cultivated under submergence conditions by individuals occupying the flood plains of the Niger River ~3,000 years ago (Portères, 1962; Portères and Harlan, 1976), *O. glaberrima* may not have perceived UVB radiation as the most serious stress from the environment due to the majority of its parts (shoot and leaves) typically growing underwater and thus experiencing less UVB damage. In this regard, UVB radiation may not penetrate deep water, and even if it penetrates, the intensity may be lower than the desubmergence growing condition. Consequently, *O. glaberrima* has grown mostly under the flooded environment in West Africa and has evolved predominantly unique plant features such as shoot elongation, taller plants, and large leaf area (Portères, 1955; Besancon, 1993; Sakagami, 2012) to better survive in weeds and flooded environments. However, these features make it vulnerable to other stresses such as UVB radiation (Mmbando et al., 2020). Furthermore, it remains to be clarified if the submergence growing conditions of *O. glaberrima* affect its metabolic rate in a manner that results in UVB-super-hypersensitivity. Moreover, it has yet to be determined if some African rice cultivars grown in the upland system under desubmergence conditions have developed a UVB tolerance mechanism similar to that of the Asian rice *O. sativa*. The relationship between UVB sensitivity and flood mechanisms of African rice cultivars and yield productivity under field conditions will be an exciting topic to explore in the future. Recently, Mmbando et al. (2020) developed UVB-tolerant African rice with transgenic technology that may perform well under the tropical conditions of Africa with high UVB radiation stress, and, thus, this rice holds a promising future for the African continent in regard to increasing rice yield production. However, if transgenic UVB-resistant African rice with high CPD photolyase activity will perform well under field conditions in Africa with multiple biotic and abiotic stresses has yet to be determined.

2.5 A possible reason for UVB-super-hypersensitivity in African rice species.

Due to their sessile nature, plants are exposed to various environmental stresses, including not only UVB radiation but also cold, heat, high light, drought, salinity, and others that may affect their growth and productivity. It has been demonstrated that exposure of plants to ambient UVB radiation can enhance the resistance to other stresses such as pathogens, and the capacity of the plant to repair DNA damage may be a crucial factor in determining the types of responses elicited by different fluence rates (Kalbin et al., 2001; Kunz et al., 2006; Kunz et al., 2008; Kobayashi et al., 2014; Piofczyk et al., 2015; Robson et al., 2015; Parada et al., 2015; Qi et al., 2018; Demkura and Ballaré, 2012). Kunz et al. (2008) reported that UV-induced DNA damage could activate the defence mechanism against *Hyaloperonospora parasitica*. African rice cultivars are grown in a tropical environment under multiple stresses and are well adapted to various biotic and abiotic stresses such as drought, soil acidity, iron, and, aluminium toxicity (Second, 1985; Brar and Khush, 1997; Sanchez et al., 2013). Mmbando et al. (2020) demonstrated that most *O. glaberrima* were UVB-super-hypersensitive compared to the sensitivity of the Asian rice *O. sativa*, and cultivars with this genotype were primarily identified in West Africa in locations that were believed to be domestication centres for *O. glaberrima*. In that study, they speculated that such a high sensitivity to UVB radiation could represent a positive adaptation response obtained by *O. glaberrima* during the domestication process in order to survive multiple stresses present on the African continent. Indeed, UV radiation has been proposed to act on downstream signalling pathways in elements that closely resemble pathogen defence, including pathways involving reactive oxygen species (Mackerness et al., 2001), calcium (Frohnmeier et al., 1999), mitogen-activated protein kinase (MAPK) (Ulm et al., 2001), ethylene, jasmonic acid, and salicylic acid (Brosché and Strid, 2003), thus suggesting its involvement in the defence signalling pathway. Therefore, it is possible that the high CPD levels in UVB-super-hypersensitive African rice cultivars with lower CPD photolyase activity induce high defence responses or systemic defence responses that enable them to survive tropical climates that are prone to pathogens. As plants encounter multiple environmental stresses under normal growing conditions, future studies should examine the yield of UVB-super-hypersensitive African rice cultivars grown under normal field conditions. Furthermore, it has been reported that even without UV irradiation, a triple *Arabidopsis* mutant that is defective in NER and also photoreactivation of CPDs with *tt5* mutation conferring chalcone isomerase deficiency (Li et al., 1993) exhibited resistance to infection by *H. parasitica* (Kunz et al., 2008). The *tt5* mutant

exhibited a deficiency in flavonoid production and was hypersensitive to UV radiation (Li et al., 1993), and thus, it was sensitive to reactive oxygen species, exhibited a high incidence of DNA strand breaks, and possessed a high increase in recombination frequency compared to that in wild-type plants (Filkowski et al., 2004). Therefore, it is intriguing to suggest that in addition to UV photoproducts, accumulation of other endogenous DNA damage caused by reactive oxygen species could also trigger resistance to pathogens (Kunz et al., 2006). These points will be an important topic for future research.

2.6 Development of a multiple resistance African rice plant

UVB radiation and pathogens may compromise the yield and productivity of rice plants. CPD photolyase has been overexpressed in transgenic rice plants, thus enhancing UVB resistance compared to that of wild-type plants (Hideema et al., 2007; Teranishi et al., 2012). This suggests the necessity of this enzyme to enhance productivity. However, under normal field conditions, particularly in tropical areas such as Africa, UVB radiation is not the only stress affecting rice productivity. Other stresses such as temperature, drought, and pathogens also reduce the yield. Such stresses reduce the productivity of various crops, including rice, and the same plant can be affected simultaneously by UVB radiation and other stresses. To date, environmental relevant UVB dose have been shown to enhance plants functions. For example, moderate doses of UVB were found to enhance the heat tolerance of cucumber (Teklemariam and Blake, 2003) and the cold tolerance of rhododendron (Chalker-Scott and Scott, 2004). Furthermore, several studies have shown the possible link between plant response to UVB and drought tolerance (Bandurska and Cieślak, 2013). Such effect of increase drought tolerance by UVB radiation was suggested to be through accumulation of foliar flavonoids and phenols (Ren et al., 2007), or via increasing proline synthesis and decreasing of stomata conductance (Poulson et al., 2006), or through photomorphogenic effects (Gitz and Liu-Gitz, 2003). Moreover, increase production of UVB-protective secondary metabolites has shown to affect plants colonization by herbivorous and arthropods (Mazza et al., 1999; Mewis et al., 2012). In addition, Hideg et al. (2013), demonstrated that a suitable UVB radiation can induce defensive mechanisms and reduce oxidative damage similar to (Fujibe et al., 2004) who indicated the production of active oxygen species (AOS)-scavenging enzymes by UVB and (Wang et al., 2007) on the reduction of efficacy of paraquat due to and important factors of the cross-resistance between oxidative stress and UVB. UVB radiation has been shown to inhibit the growth of plants through the downstream targeting of growth-regulating factors by miRNA396 (Casadevall et al., 2013;

Fina et al., 2017). In contrast, miRNA396 also modulates the innate immunity of fungi (Soto-Suárez et al., 2017). Therefore, fine-tuning miRNA369 may offer a possibility for generating both UVB- and pathogen-resistant plants. Alternatively, UVB photoproducts in UV photorepair mutants trigger resistance to certain pathogens, and there is a possible connection between CPD accumulation and increased pathogen resistance (Li et al., 1993; Kucera et al., 2003; Kunz et al., 2008). Thus, downstream control of UVB-induced growth inhibition that allows for a high accumulation of CPDs or other UV-induced DNA photoproducts without causing growth inhibition may also allow for priming of the defence process among these plants.

Breeding both UVB- and pathogen-resistant cultivars is challenging, and a high immune resistance level often results in yield penalties (Brown, 2002; Brown and Rant, 2013). To minimise the fitness cost, a UVB-resistant plant that can turn off its immune system in the absence of pathogens and then reactivate it in the presence of pathogens should be developed. Although plants lack a heat-shock factor-like transcription factor that specifically binds to the *cis*-element translocon 1 (TL1: GAAGAAGAA) needed for the activation of antimicrobial genes (Pajerowska-Mukhtar et al., 2012), engineering plants with TL1-binding factor, TBF1, may offer promising ways to develop multiple resistance plant with low fitness cost. Recently, transcription factor (TF), TBF1 has been demonstrated to reduce the fitness penalties associated with enhanced disease resistance in *Arabidopsis* and rice (Xu et al., 2017). TBF1 is well established to play an essential role in the growth-to-defence switch upon immune induction (Pajerowska-Mukhtar et al., 2012), and, therefore, TF TBF1 analysis in the context of CPD photolyase overexpressing plants may provide a promising means to develop a UVB- and disease-resistant primed plant. Future studies should explore the possibility of creating multiple resistance cultivars by targeting either miRNA 396, TF TBF1, or other factors and by regulating the amount of CPDs or the rate of oxidative damage. Climate change and ozone depletion will continue to affect most tropical areas, including Africa. The high amount of UVB radiation and virulence of pathogens will also evolve due to unstable weather conditions. Consequently, developing a UVB-tolerant and disease-resistant primed rice plant will be of enormous importance, particularly in Africa, as this is a tropical continent with a high level of UVB radiation in the sunlight and a location subject to pathogen infection and that possesses a rapidly growing population. UVB-resistant transgenic primed plants will not only minimise the use of chemicals for combating various pathogens that are detrimental to our health and

environment, but they will also increase the yield of this economically important crop that can eliminate hunger and poverty and feed the rapidly growing population of Africa.

3. Conclusion

African rice, *O. glaberrima*, is well adapted for cultivation in West Africa and is tolerant to biotic and abiotic stresses such as drought, soil acidity, and iron and aluminium toxicity. African rice, thus, has mechanisms to adapt to African climates and to protect itself against biotic and abiotic stresses. On the contrary, comparing the UVB sensitivity of rice cultivars with its cultivated region, very surprisingly, highly UVB sensitive cultivars (UVB-hypersensitive or -super-hypersensitive cultivars) with low CPD photolyase activity have been domesticated in tropical areas, such as South Asia or African continent, where the amount of UVB radiation is relatively high although UVB-resistant cultivars are expected to be cultivated in areas with high UVB radiation. Considering that highly UVB-sensitive rice cultivars with low CPD photolyase activity have been selected and cultivated during the long history of rice cultivation, a possible crosslink might exist between CPD photolyase activity and other tropical environmental stresses, and high UVB-sensitivity may be a beneficial trait for surviving in tropical areas. Indeed, UVB radiation can activate the pathways of defensive mechanisms and increase resistance to fungal disease, through induction of pathogenesis related proteins (PRs) in leaves of several species.

Sunlight is essential for photosynthetic plants, but, because they are constantly exposed to UVB, the plants are damaged by UVB. With such constant UVB damage, a strategy to acquire a mechanism of tolerance to various other unexpected stresses may be rational. Consequently, plants are always faced with multiple stresses at the same time. Therefore, the understanding of the network interactions, including crosstalk with multiple signals caused by stresses, should be helpful for development of improved rice cultivars. The knowledge provided here will help to develop multiple resistant African rice possessing a high yield that can be used for feeding the outgrowing population of the African continent, thereby, ultimately reducing hunger and poverty.

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