



Review article

The recent possible strategies for breeding ultraviolet-B-resistant crops

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ARTICLE INFO

Keywords:

UVB-Resistant
Transgenic plants
Antioxidant
Flavonoids
miRNA396
DNA methylation

ABSTRACT

The sensitivity of crops to ultraviolet B (UVB, 280–315 nm) radiation varies significantly. Plants' sensitivity to UVB is heavily influenced by the activity of the enzyme cyclobutane pyrimidine dimer (CPD) photolyase, which fixes UVB-induced CPDs. Crops grown in tropical areas with high level of UVB radiation, like *O. glaberrima* from Africa and *O. sativa* ssp. *indica* rice from Bengal, are more sensitive to UVB radiation and could suffer more as a result of rising UVB levels on the earth's surface. Therefore, creating crops that can withstand high UVB is crucial in tropical regions. There is, however, little information on current techniques for breeding UVB-resistant plants. The most recent techniques for producing UVB-resistant crops are presented in this review. The use of DNA methylation, boosting the antioxidant system, regulating the expression of micro-RNA396, and overexpressing CPD photolyase in transgenic plants are some of the methods that are discussed. CPD photolyase overexpression in transgenic plants is the most popular technique for producing UVB-resistant rice. The study also offers several strategies for creating UVB-resistant plants using gene editing techniques. To feed the world's rapidly expanding population, researchers can use the information from this study to improve food production.

1. Introduction

Ultraviolet (UV) rays from the sun are necessary for plant life and serve as a crucial environmental cue to regulate plant growth and survival. Being a sessile organism, plants are undoubtedly exposed to UVB from the sun. These UVB rays inhibits photosynthesis and protein synthesis and, as a result, reduce growth and productivity [1]. According to wavelength, solar UV radiation falls into three categories: UVA (315–400 nm), UVB (280–315 nm), as well as UVC (less than 280 nm) [2]. The most dangerous radiation is UVC, but the ozone layer completely absorbs it. Contrary to popular belief, UVA radiation is remitted to the earth's surface because the ozone layer is unable to absorb it, despite being less harmful than other UV radiation wavelengths [3]. Despite making up only 1.5% of the total radiation from the three types of UV radiation, UVB is still important because it has harmful effects on DNA that have an impact on the development and growth of plants [4]. Due to the anthropogenic release of methyl bromide (MeBr), hydrochlorofluorocarbons (HCFCs), and other halogen compounds from industries; there has recently been an increase in global concern over the increased amount of UVB radiation on the earth's surface [5].

The high reliance of plants on sunlight for photosynthesis results in increased vulnerability to UVB radiation stress. In addition to causing skin cancer in people [6], excessive UVB radiation also kills plant cells. This has been evidenced by physiological traits like leaf bleaching or yellowing, wilting, and decreases fresh weight and tiller numbers [1,7]. Photoreceptors, such as UV RESISTANCE LOCUS

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<https://doi.org/10.1016/j.heliyon.2024.e27806>

Received 18 October 2023; Received in revised form 22 February 2024; Accepted 6 March 2024

Available online 8 March 2024

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8 (UVR8), which allow acclimatization to UVB stress, regulate how UV light interacts with plants. UVR8 is associated with the chromatin of UVB-responsive genes, such as the promoter region of elongated hypocotyl 5 (HY5). Additionally, the E3 ubiquitin ligase, a constitutively photomorphogenic 1 (COP1), is associated with UVR8 activity. Numerous photomorphogenic responses are associated with UVR8-COP1 interaction [8]. Plants may experience stress either directly or indirectly from UVB radiation. The genome is less stable due to UVB because it produces pyrimidine dimers [9,10]. Cyclobutane pyrimidine dimers (CPDs) account for 75% of these lesions, with photoproducts making up the remaining (6-4) percentage [11,12]. These DNA alterations prevent transcription and DNA synthesis, which obstructs plant metabolism and growth. Reactive oxygen species (ROS), a class of molecules formed from molecular oxygen (O₂), are also increased by UVB radiation and cause oxidative stress to RNA, DNA, lipids, proteins, and other molecules in plant cells [13]. UVB radiation can directly affect the main photosynthetic machinery by reducing the photosystem II (PSII) proteins D1 and D2 [14]. UVB radiation can also alter how certain genes' DNA is methylated. These gene-specific variations in DNA methylation may be related to DNA repair, UVB stress response, and other biological UVB tolerance-related processes [15–17].

Plants have developed a variety of stress-response mechanisms to prevent UVB damage. Chloroplasts, for instance, can alter their positions to lessen the PSII damage and high-light absorption [18]. Moreover, plants are protected from the damaging effects of UVB radiation by UVB-absorbing sunscreen phenylpropanoids like polyphenols and flavonoids, which build up in epidermal cells [19]. UVB resistance is also significantly influenced by the anatomy and architecture of plants. Specialized hair-like structures called leaf trichomes can act as physical barriers by diffusing or reflecting UVB radiation away from vulnerable leaf tissues [20]. Furthermore, changes in leaf thickness and the existence of structural elements like lignin help to lower UVB radiation penetration, protecting important cellular components from possible harm [21]. Antioxidant enzymes such as superoxide dismutase (SOD), catalase, and peroxidase, in particular, are important for neutralizing ROS produced during UVB stress [22]. The plant uses these enzymes to control oxidative stress and shield cells from harm. Furthermore, hormones are important regulators that plants use to increase defenses against UVB rays. Jasmonic acid (JA) and abscisic acid (ABA) are essential for coordinating stress reactions [23]. According to Shi et al., ABA helps keep stomata closed, minimize water loss, and restrict UVB ray penetration [24]. JA controls the expression of genes linked to defense mechanisms, encouraging the production of secondary metabolites that have protective role [25]. Gibberellins (GAs) also have the ability to alter the size of leaves and stems, which may allow plants to alter their architecture in order to reduce UVB-induced damage or optimize UVB absorption [26]. Therefore, plant hormones play a crucial mediating role in allowing plants to adjust and endure the difficulties presented by high UVB radiation in their surroundings through the regulation of signaling pathways and gene expression. Moreover, plants are greatly shielded from UVB rays by mitogen-activated protein kinase (MAPK) cascades. The production of UV-absorbing chemicals, antioxidant enzymes, and defense genes are among the downstream reactions that are signaled by activated MAPKs [27,28]. Through this signaling pathway, the plant becomes more resilient overall to environmental challenges and is better able to withstand stress caused by UVB radiation. The photolyase can successfully repair DNA damage (CPDs and 6-4 PPs) during the photoreactivation process. Although replicative polymerases and the nucleotide excision repair (NER) system can bypass pyrimidine dimers and repair them; photoreactivation (photorepair) is thought to be a significant, effective, and the economical mechanism used by plants to repair UVB radiation damage [9,29]. After UV-induced DNA damage has occurred, it can be repaired through photoreactivation when exposed to blue light portion of the spectrum [12]. This process is carried out by the enzyme photolyases, which specifically bind to CPDs or 6-4 PPs after absorbing a photon with the right wavelength (350–450 nm); and use UVA/blue light to directly undo the damage in a perfectly manner [12].

Previous research on rice showed that transgenic plants with overexpressed CPD photolyase can produce UVB-resistant plants [30–33]. Another study on *Arabidopsis thaliana* (Landsberg erecta) found a modest growth in the production of biomass under conditions of increasing UVB radiation when CPD photolyase was overexpressed [34]. In addition, it has recently been shown that the receptor-like kinase OsRLCK160 and the phosphorylated bZIP transcription factor OsbZIP48 interact and positively control flavonoid accumulation, which is essential for rice's ability to tolerate UVB radiation [35]. Moreover, using non-targeted metabolomics, it was discovered that plants with mutations on the chloroplast-localized phosphate transporter OsPHT2; 1 (*osph2;1-2* mutants) have less UV tolerance and a decrease in various flavonoids [36]. Another study by Zeng et al. identified key pathways in regulating natural variations in phenylpropanoid content, including tyramine hydroxycinnamoyl acyltransferase, a MYB transcription factor, and flavone C-pentosyltransferase proteins, which are involved in UVB protection in Qingke (Tibetan hulless barley) [37]. Therefore, controlling transcription factors like MYB and HY5 may result in plants that are more tolerant to UVB rays and have higher flavonoid levels. Studies showed that overexpression of the bZIP transcription factor (Os bZIP48) [35] and UDP-dependent glycosyltransferases (UGTs) [38] improves the UVB tolerance in rice, in addition to CPD photolyase [30–32]. Moreover, a recent study by Zhang et al. found that overexpressing the UDP-dependent glycosyltransferase OsUGT706C2 in rice increases UVB resistance by improving ROS scavenging [39]. These findings point to the potential for using the glycosyltransferase OsUGT706C2 to improve crop UVB tolerance, particularly for crops grown in tropical regions.

Although the ozone layer has recently begun to recover, it is still essential to breed crops that are more resistant to UVB radiation. UVB radiation still hits the Earth's surface regardless of the ozone layer's recovery at various levels depending on elements like altitude, latitude, and atmospheric conditions [40]. UVB exposure continues to be an important environmental stressor for plants, especially in areas that have elevated UVB levels [1,7]. Global environmental conditions, including UVB radiation levels, are changing as a result of climate change. UVB penetration through the atmosphere can be affected by changes in atmospheric composition, changes in cloud cover, along with other climate-related factors [41,42]. Breeding UVB-resistant crops can aid in minimizing the potential drawbacks caused by elevated UVB exposure as a result of climate change, guaranteeing food security and agricultural sustainability. Further, although human-produced chlorofluorocarbons (CFCs) were the main contributor to ozone depletion, UVB sensitivity in crops is not only caused by ozone depletion. Other natural and human-caused sources of UVB radiation include solar radiation, volcanic eruptions, and some industrial processes [43–45]. Regardless of ozone depletion, breeding UVB-resistant crops

offers safeguard against UVB stress brought on by a variety of sources. This strategy encourages environmentally friendly agriculture and lessens the negative effects of crop protection on the environment. Future unknowns exist even though efforts are being made to protect and restore the ozone layer. Therefore, breeding UVB tolerance in crops allows us to increase their ability to withstand environmental stressors, guarantee food security, reduce risks associated with climate change, and support sustainable agriculture. Tropical plants that receive a lot of UVB radiation stress may have lower yields due to the harmful effects of UVB radiation because their repair mechanisms are unable to fully undo the UVB damage that has been caused. The development of UVB-resistant crops for tropical regions will be of utmost importance for increasing the productivity of many important agronomic crops, such as rice, which are sensitive to UVB radiation [1,7]. However, there is a shortage of information on alternative methods for creating UVB-tolerant crops, and new methods for creating UVB-resistant crops, however, are scarcely known. These could obstruct scientists' and molecular biologists' attempts to create tolerable varieties.

The most recent overview of various techniques for developing UVB-resistant crops was covered in this review. The discussion includes the use of transgenic plants with overexpressed CPD photolyase, the increase in flavonoids and other antioxidant systems, the regulation of miRNA396 and growth regulatory factors (GRFs), modification of DNA methylation, and other controlling mechanisms like ataxia telangiectasia mutated (ATM), ATM AND RAD3-RELATED (ATR), and MAP kinase (MAPK) kinase. The use of clustered regularly interspaced short palindromic repeats (CRISPR)-associated endonuclease Cas9 (CRISPR/Cas9), a gene editing tool, in those techniques to develop UVB-resistant crops is also discussed. The various strategies for creating UVB-resistant crops outlined here will be used to improve food security, particularly in tropical areas with high UVB exposure.

2. Potential strategies for breeding UVB-resistant plants

Plants can withstand low levels of UVB radiation by activating defense mechanisms like ROS scavengers and DNA repair mechanisms. The capacity for repair may not be able to keep up with the high rate of induction of UVB damage, and these repairing systems may not function in areas with high levels of UVB radiation, such as tropical areas. By inhibiting growth and lowering the number of tillers, UVB radiation lowers rice productivity in tropical regions of the African continent [7,46] and the Bengal region [47]. Therefore, increasing plants' capacity to fix UVB-induced DNA damage through molecular methods is crucial for raising crop productivity in tropical areas. Different approaches, such as removing, repairing, undoing, and tolerating UVB-induced damage, have been suggested to help plants adapt to high UVB exposure [48]. By enhancing these strategies' capacity using molecular methods, it may be possible to increase the capacity of crops to withstand high UVB stress. For instance, increasing the expression and copy number of the DNA repair enzyme photolyase in rice plants can result in UVB resistance [30–33]. Although the majority of UVB-sensitive plants, like African rice, are resistant to tissue culture, various suggested methods for promoting regeneration and transformation in those plants must be used to improve breeding [49]. For developing UVB resistance in crops, this study suggested the following various approaches (Table 1, Fig. 1).

2.1. Modifying DNA repairs enzymes like photolyase and nucleotide excision

One of the best techniques for treating UVB-induced DNA lesions in plants is photoreactivation, which is mediated by the enzyme photolyase [9,29]. Photoreactivation is a key determinant of UVB sensitivity in crops like rice [30]. UVB tolerance was affected by even small changes to the CPD photolyase gene, which changed the enzyme's activity [1,7,50]. Therefore, to increase UVB resistance in different plants, scientists have used genetic engineering tools to increase the copy number and expression level of CPD photolyase. For instance, by overexpressing the CPD photolyase gene, distantly related species like *Arabidopsis* had improved UVB resistance [34]. Additionally, Hidema et al. demonstrated an improved UVB resistance mechanism of (sense transgenic line [S–C]) with CPD overexpression in sense orientation compared to parental line (PL) plants, and (Antisense transgenic line) A-S in antisense orientation using Asian rice UVB resistance Sasanishi (*O. sativa* L. ssp. *japonica*) as PL plants [30]. Similar to this, using the sensitive Surjamkhi (*O. sativa* L. ssp. *indica*) and Asian rice Norin 1 (*O. sativa* L. ssp. *japonica*), overexpressing CPD photolyase improves their UVB resistance mechanisms [31]. Recently, Mmbando et al. generated the overexpressed Sasanishiki CPD photolyase gene in cultivar TOG12380 to create the UVB resistant African rice (*O. glaberrima*) [32]. These results suggest that the most efficient way to confer UVB resistance in crops is through CPD photolyase gene manipulation (Fig. 1A). DNA lesions caused by UVB can be repaired by photolyase as well as the NER system [9]. NER is currently thought to be the only UVB-induced DNA repair system in humans [51]. Therefore, genetic

Table 1
Various methods for breeding crops resistant to ultraviolet-B radiation stress.

Method	Description	References
Enhancing DNA repair enzymes	Overexpression of CPD photolyase gene from UVB resistance cultivars	[30–32]
Controlling microRNA396 and growth regulating factors	Regulate the endogenous expression level of miRNA396 or transcript levels and activity of some important growth regulating factors	[54,55]
Improving the antioxidant system	Improving ROS scavenging mechanisms in plants	[35,38,39]
Modification of UVR8 signaling pathway	Overexpression of UVR8 related to flavonoids and anthocyanin accumulations	[19,74,80,81]
Modifying DNA methylation changes	Modifying the DNA methylation status of particular genes or regulatory regions	[16,83,86]
Controlling MAPK phosphatase	Maintaining low levels of MKP3 and MKP6 expression using current gene editing methods	[27,28,63,92]

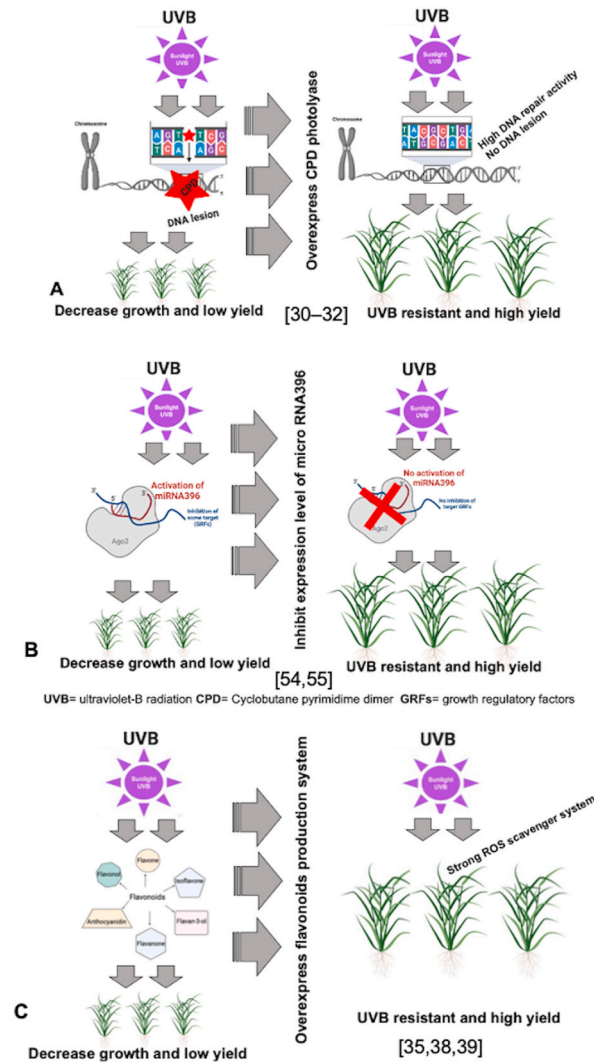


Fig. 1. The various techniques for producing UVB-resistant crops. (A) Crops can be bioengineered to have an overexpressed CPD photolyase gene, which will improve their UVB resistance mechanisms. (B) By regulating microRNA396 expression, which results in less inhibition of growth-regulating factors and cell proliferation, UVB resistant plants can be created. (C) The ROS scavenger system will become more effective by increasing the plant's flavonoid production, which will increase UVB resistance.

modification of the excision repair system can be used to create UVB resistance in human cells. For instance, Mazouzi et al. reported that MutY glycosylase homologue (MUTYH), a DNA glycosylase involved in the catalysis of excision of the adenine mispaired with 8-oxo-guanine of the base excision repair (BER) pathway, was lost in function by a double knockout (XPA-MUTYH) using CRISPR-Cas9; and this resulted in cells that were more resistant to UVB than wild-type cells [51], similar to prior finding [52]. Therefore, combining photolyase and NER to create UVB-resistant crops may be a promising strategy for producing UVB-tolerant plants.

2.2. Controlling miRNA396 and growth regulating factors

In maize leaves, it has been demonstrated that UVB radiation increases the expression of the miRNAs miR164, miR166, miR398, and miR165 while decreasing the expression of the miRNAs miR172, miR171, miR529, and miR396 [53]. One of them, miR396, was found to control cell growth by concentrating on GRF family members and was downregulated by UVB. It has been proposed that UVB radiation reduces plant growth by regulating miRNA396's downstream targeting of GRFs [54,55]. On the other hand, UVB stress inhibits plant growth by lowering the number of tillers, fresh weight, and dry weight [1,7,50,56]. Although more research is required to be sure, miRNA396's inhibition of some GRFs may be what causes plants exposed to UVB radiation to grow more slowly [54]. UVB radiation causes miRNA396 to be upregulated in developing Arabidopsis leaves, and this upregulation was associated with lower levels of its GRF targets [53]. miRNA396 activation inhibits cell proliferation without causing cell expansion [54]. There is less endogenous

microRNA activity in transgenic *Arabidopsis thaliana* plants that express MIM396 (an artificial target mimic targeted at miR396), which results in less inhibition of leaf growth [54]. These studies suggested that by using gene editing techniques to regulate the endogenous expression level of microRNA396, it may be possible to create plants that are less likely to experience UVB stress-induced growth inhibition. Because of this, controlling the upregulation of miRNA396 by gene knockout using CRISPR-Cas 9 techniques may allow for the creation of UVB-resistant plants. Increasing the transcript levels and activity of some important GRFs, such as GRF1, GRF2, and GRF3 in *Arabidopsis* and possibly GRF1, GRF2, GRF14, and GRF15 in maize [55], which are downregulated by miRNA396 in UVB stress, would be an alternative strategy to prevent the UVB-induced restriction on cell proliferation in proliferating cells [54] (Fig. 1B). In addition, it has been demonstrated that UVB inhibits pea shoot elongation and leaf expansion by altering the metabolism of GA in the shoot and signaling via DELLA proteins [57]. UVB radiation reduced the transcript levels of unidentified *GA20-oxidase* (*GA20ox*) and *GA3-oxidase* (*GA3ox*) family members involved in gibberellin biosynthesis [58]. Furthermore, gibberellin and brassinolide have been found to positively control the flag leaf angle under increased UVB radiation [59], possibly owing to an imbalance in cell division and growth on the adaxial and abaxial surfaces of the lamina [60,61]. The effects of UVB-induced growth inhibition may be controlled by regulating the gibberellin signaling pathway, which control cell division and elongation. Thus, modulating the level of gibberellins, which is also regulated by miRNA369 in the growth zone, could be another potential method for creating UVB resistance crops [23,26,55,62]. These methods provide a more effective method of creating UVB-tolerant crops in addition to modifying DNA repair enzymes. However, care should be taken when choosing which miRNAs to target because they might serve various purposes depending on the species.

2.3. Improving the antioxidant system

Different antioxidant mechanisms, including non-enzymatic antioxidants like ascorbic acid (AsA) and glutathione (GSH) and enzymatic ones like peroxidase (POD), SOD, and ascorbate peroxidase (APX), are involved in detoxifying ROS produced by UVB stress [48]. It has also been hypothesized that building up UV-absorbing substances like anthocyanins and flavonols on a plant's surface will shield its delicate cell components from UVB harm [63]. For instance, pollen grains have been demonstrated to accumulate flavonoids to protect against UVB damage and maintain viability after anthesis [64] in comparison to how flavonoids shield ovules by shielding ovaries from UV radiation [65]. The mutant *vtc1* (vitamin C-1) of *Arabidopsis* that lacks ascorbate is extremely sensitive to UVB radiation and other forms of oxidative stress [66,67]. The *uvt1* (UV tolerant 1) mutant and the AtMYB4 knockout mutant both had higher levels of UVB resistance and UV-absorbing compounds than wild-type plants [68,69], suggesting that molecular techniques may be used to enhance the UVB absorbing mechanism and other antioxidant systems to produce UVB resistant crops. Anthocyanin builds up and the chalcone synthase gene is activated in *Arabidopsis* when UVR8 is overexpressed under UVB light [33]. Additionally, the short-term UVB radiation-tolerant *Arabidopsis* mutant *rcd1-2* (radical-induced cell death 1–2), which confers improved activity of ROS-scavenging enzymes like stromal APX and plastidic Cu/ZnSOD, displayed a higher tolerance [70].

Moreover, by overexpressing OsUGT706C2, which improves ROS scavenging in rice due to an excess of flavonoids, UVB resistance plants can be created [39]. After being exposed to UVB light for 24 h, the OsUGT706C2 overexpressing lines in that study showed low levels of blue precipitate and H₂O₂ accumulation, which suggests that overexpressing OsUGT706C2 may enhance ROS scavenging by downregulating specific ROS-related genes [39]. Additionally, a recent study by Zhang et al. revealed that phosphomimicking OsBZIP48 and overexpression of OsRLCK160, OsBZIP48, significantly enhanced rice's flavonoid content and UVB resistance [35]. These studies suggested that a promising method for developing rice varieties that are resistant to UVB is to create transgenic plants that have the glycosyltransferase OsUGT706C2 and OsRLCK160 genes overexpressed. Flavone 7-O-glucosyltransferase (OsUGT706D1) and flavone 5-O-glucosyltransferase (OsUGT707A2) have also demonstrated a link in the adaptation to UV-B irradiance [38]. The biosynthesis of flavone O-glucosides was improved in transgenic plants with overexpressed UGT707A2 and OsUGT706D1, and UVB resistance was raised in rice. These studies suggest that increasing flavonoids contents through bioengineering could provide strategies for increasing crop yield under a variety of stresses, including UVB radiation, since flavonoids are involved in protection against other stresses like drought [38,71]. Furthermore, it has been demonstrated that *OsPHT2;1* mutations reduce grain yield and UVB tolerance while also preventing flavonoid accumulation [36]. Therefore, improving *OsPHT2;1* performance may increase UVB tolerance and yield, though additional research is required to support this idea. These studies suggested that bioengineering improvements to the antioxidant system, including flavonoids, anthocyanins, and the entire phenylpropanoid pathway for UVB protection [37], could be used to engineer plants to tolerate UVB radiation (Fig. 1C). However, because some of these studies were only carried out in laboratories, caution must be used when interpreting their findings. Field studies are therefore required for confirmation.

2.4. Modification of UVR8 signaling pathway

A complex series of plant responses to UVB were triggered by UVB photoreceptor UVR8, which detected UVB radiation and connected to a signaling pathway [72]. UV acclimation, which ultimately determines UVB tolerance, requires the UVR8-mediated pathway, and UVR8-COP1 interaction has been demonstrated to be a key, essential mechanism for UVB signaling [73]. Among the documented physiological reactions to UVB mediated by UVR8 are the accumulation of UVB-absorbing substances like flavonol glycosides and the inhibition of hypocotyl growth [8,74]. The activation of several genes by UVB is what causes this reaction. At higher UVB radiation levels, UVR8 can also regulate stomatal differentiation, endoreduplication, and leaf morphogenesis and enhance photosynthetic efficiency [75,76]. By rerouting metabolic energy, UVB-induced photomorphogenesis may serve as a survival tactic that reduces growth in favor of UVB tolerance [73]. The hypocotyl length of *uvr8* seedlings was the same under white light supplemented with UVB and white light alone, which is different from wild type, indicating that UVB-induced hypocotyl growth inhibition is

controlled by UVR8-mediated UVB perception [8]. Modulation of the UVR8 signaling pathway may enable the development of plants with high UVB acclimatization and improved UVB resistance because UVB perception regulates the inhibition of hypocotyl growth. According to Fasano et al., UVR8 may alter auxin homeostasis and change the accumulation of flavonoids, which are the primary mechanisms governing the observed growth phenotypes. As a result, UVR8 can be crucial in integrating stress signals and plant growth [77]. Targeting UVR8 may therefore enable the development of UVB resistance via increased flavonoid content or modulation of growth hormones.

Due to UVR8's crucial function in the UVB-mediated control of several genes, including those crucial for flavonoids activation [78], its constitutive presence enables an immediate response to preventing UVB damage [79]. In the liverwort *Merchantia polymorpha*, UVR8 plays physiological and molecular roles to regulate the transcription of several genes involved in UVB tolerance [80]. This indicated that UVR8 photoceptors, which regulate responses to photomorphogenesis, could be targeted in order to control the production of secondary metabolites, such as flavonoids and anthocyanins, that protect plants from UVB stress [19]. For instance, it has been demonstrated that gene silencing in tomato lines [*Solanum lycopersicum* (SI)] (SIUVR8Ri) increased UVB hypersensitivity while gene overexpression increased UVB tolerance. SIUVR8 may be essential for UVB response as evidenced by the significant reduction in anthocyanin accumulation and UVB response gene induction, including HY5 and CHS in SIUVR8Ri lines [81]. Similar to this, it has also been demonstrated that UVR8 overexpressed *Arabidopsis* mutants enhance UVB adaptation and tolerance [8,74]. Although *Arabidopsis* has been the subject of the majority of studies on UVR8, overexpressing the photoreceptor in other crops, such as rice, as demonstrated in tomato and *Arabidopsis*, may also result in the development of plants with enhanced UVB resistance mechanisms. Future research should, however, assess whether there is a connection between the number of copies of the UVR8 gene and the ability to tolerate UVB stress.

2.5. Modifying DNA methylation changes

Plants' DNA methylation patterns can be affected by UVB radiation as well [15,82,83]. DNA methylation is the process of adding a methyl group to the DNA molecule. This modification can affect how genes are expressed and control a number of biological functions [84,85]. One recently developed method for improving plant tolerance to UVB radiation is to breed UVB resistant plants by DNA methylating the DNA of the plants. While the field is still developing, the following are some potential strategies and factors to take into account when using DNA methylation in the breeding process. Finding people or populations with innate UVB tolerance can be aided by evaluating the natural variation in DNA methylation patterns among various plant genotypes. Breeders can choose potential candidates for additional breeding attempts by screening against particular DNA methylation patterns linked to UVB resistance [15, 16]. Additionally, recent developments in genome editing techniques, like CRISPR-based systems, have the capacity to change DNA methylation patterns in a precise way. Breeders may be able to improve UVB tolerance in crops by modifying the DNA methylation status of particular genes or regulatory regions [16,86]. However, it is crucial to take into account the legal and moral implications of using genome editing methods in crop breeding. Moreover, the creation of DNA methylation markers linked to UVB tolerance can help breeding programs use marker-assisted selection (MAS) [83,87]. Breeders can more effectively screen large populations of plants and choose individuals with wanted DNA methylation patterns to conduct additional breeding through the discovery of specific DNA methylation markers associated with UVB resistance [17,85]. Also, transgenerational epigenetic inheritance may be facilitated by DNA methylation patterns [88]. Breeding methods that take into account the evaluation of DNA methylation alterations in succeeding generations can shed light on the persistence and heritability of UVB-related DNA methylation modifications. This knowledge can direct breeding initiatives meant to improve UVB resistance over several generations. Further, QTL mapping and phenotypic selection are two examples of traditional breeding techniques that can be combined with DNA methylation-based breeding procedures [16, 89–91]. Breeders can employ more thorough and efficient methods for creating UVB-resistant crop varieties through the combination of DNA methylation data with other pertinent traits and genetic markers. It is important to note that more research is still being done on the intricate DNA methylation patterns and their functional significance to UVB tolerance. Research is still being done to better understand the epigenetic causes of UVB resistance and how to use that knowledge for breeding purposes. The use of DNA methylation as a tool for breeding UVB-resistant plants, however, shows promise and might offer a fresh method for enhancing crop resistance to UVB radiation.

2.6. Other approaches

Another UV response that is conserved among organisms is MAP kinase (MAPK), specifically MAPK PHOSPHATASE 1 (MKP1), which has been shown to contribute to UV resistance when UVR8-regulated UVB acclimation fails to withstand UVB stress [27,28]. Compared to the wild-type, the *Arabidopsis* MKP1 mutant *mkp1* is more sensitive to UVB [63]. MKP1's downstream targets MPK3 and MPK6 are activated by UVB stress. MKP1 has been discovered serving as a contra-regulator of MPK3 and MP6 activities in plant tolerance to UVB and salt stresses, as well as the bacterial pathogen *Pseudomonas syringae* [27,28,92]. The UVB-sensitive mutant *mkp1*, which imprecisely relies on MPK3 and MPK6, is not as resistant to UVB stress as the *mpk3* and *mpk6* mutants are [28]. According to these results, maintaining low levels of MKP3 and MKP6 expression may be another method for breeding UVB-resistant plants. Additionally, this can be accomplished using current gene editing methods like CRISPR-Cas9. This method can be used to disable MKP3 and MKP6 functions quickly, cheaply, and effectively [93]. ATR, a member of the family of phosphoinositide 3-kinase-like kinases, is involved in additional mechanisms and is crucial and activated in the DNA damage response [63]. Although ATR and ATM respond through multiple routes to UVB stress in roots [94], they are the primary regulators of the DNA damage response and are induced by replication stress and double-strand breaks, respectively [63]. We can therefore produce UVB-resistant crops by bioengineering the

ATR pathway. Engineering the ATR/or ATR and MAP pathways of UVB-resistant plants into UVB-sensitive ones could be an alternative strategy. Additionally, it has been demonstrated that DNA polymerase, such as Pol delta (δ), is crucial for preventing a variety of DNA damage, including that caused by chemical agents like benzo[*a*]pyrene and cisplatin [95] and 6-4 PPs brought on by UV radiation [95, 96]. UVB hyper-resistant varieties may be produced by breeding plants that can both avoid and repair DNA damage. Several recently proposed antibiotic-free marker-free techniques must be used in order to reduce public resistance to genetically modified UVB-resistant crops and biosafety worries [97]. To create super-hyper tolerant varieties, future research should investigate combining MAP kinase and ATR with DNA repair enzymes.

3. The legal, ethical, and biosafety concerns of using transgenic UVB-resistant crops

Although transgenic UVB-resistant crops have the potential to increase agricultural resilience and productivity, there are a number of ethical, legal, and biosafety issues that need to be carefully considered before using them [98]. For instance, from a legal standpoint, there are several international regulations governing the production and sale of transgenic crops. The legal frameworks concerning genetically modified organisms (GMOs) vary amongst nations [99]. Adherence to these regulations is imperative in order to avert legal complications and possible ecological damage [100]. Transgenic UVB-resistant crops must pass stringent testing and approval procedures before they can be released into the environment or consumed. Furthermore, concerns about transgenic UVB-resistant crops' effects on ecosystems, biodiversity, and conventional farming methods are ethical issues that need to be taken into account [98]. Concerns about the unexpected effects on the environment are brought up by the possible unintended consequences, which include the spread of genes to wild relatives or the emergence of pests that are resistant to treatment [101]. Furthermore, it is imperative to tackle concerns pertaining to informed consent, transparency, and the fair allocation of advantages and disadvantages among various stakeholders. In order to be ethically responsible, one must make sure that the introduction of these crops respects society values and does not adversely affect communities or jeopardize food security.

Furthermore, when working with transgenic organisms, biosafety considerations take precedence. Thorough risk assessments need to be carried out in order to assess potential threats to the environment and public health. This involves determining whether the modified crops are allergenic and whether there may be unforeseen side effects [102]. It is important to put strategies like monitoring and containment measures into practice to lessen these risks. Biosafety concerns are also raised by the potential for gene flow to wild relatives and the emergence of "superweeds" that are difficult to control [103]. These factors call for careful research and the adoption of preventive measures. In addition, one must take into account the long-term ecological impact of transgenic UVB-resistant crops. It is crucial to evaluate how these crops interact with regional ecosystems, taking into account their effects on biodiversity overall, soil health, and non-target organisms. Adaptive management techniques and surveillance need to be used to handle any unanticipated issues that may develop in the future [104]. Therefore, transgenic UVB-resistant crop adoption necessitates a thorough strategy to resolve ethical, legal, and biosafety issues. To successfully navigate the complicated world of biotechnology, cooperation between scientists, decision-makers, and the general public is essential. This cooperative strategy can assist in finding a middle ground between maximizing the potential advantages of UVB-resistant transgenic crops and making sure that this technology is used responsibly and sustainably to address global agricultural challenges.

4. Conclusion

This review concentrates on the most recent methods for producing UVB-resistant crops. Plants are protected from UVB stress by DNA repair enzymes like CPD photolyase in a UVR8-dependent manner, while ATM/ATR and MAPK have been implicated in a UVR8-independent manner. The discussion in this article includes methods for increasing the ability of these repair mechanisms using various molecular techniques. This article discusses several tactics, including creating transgenics plants that overexpress CPD photolyase, managing miRNA396 and GRFs, enhancing antioxidant and ROS scavenger systems, and modification of DNA methylation, MAPK, and ATR systems. The most widely used technique for creating crops with improved UVB resistance mechanisms was overexpressing CPD photolyase in transgenic plants [30–32]. To create UVB-resistant crops, future research should use cutting-edge gene editing techniques like CRISPR-Cas 9 that target downstream UVB-induced effects like GRFs, miRNA 396, MKP3, and MKP6, among others. Alternately, it should be investigated whether it is possible to combine these different methods to produce crops that are highly UVB resistant. Although careful observation should be made to determine whether the high UVB-resistant mechanism could affect other typical physiological mechanisms in these plants, as UVB is also advantageous for horticulture and disease resistance mechanisms in plants. Additionally, the majority of documented UVB-resistant transgenic plants or mutants have been developed primarily in controlled laboratory environments; further research is required to evaluate their performance in the field before commercialization. By using recently proposed antibiotic-free marker techniques, UVB-resistant crops can be produced without encountering public opposition or biosafety concerns [97].

With the help of the most recent techniques described in this study, biotechnologists can create crops with enhanced UVB resistance mechanisms. The UVB-resistant crops will improve food security, especially in tropical areas where UVB radiation is high and there is a high demand for food due to population growth.

Funding statement

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Data availability

No data was used for the research described in the article.

CRediT authorship contribution statement

Gideon Sadikiel Mmbando: Writing – review & editing, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The author will like to thank University of Dodoma for providing office space for research write-ups.

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