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CHAPTER SEVEN

INTERACTIONAL EFFECTS OF UV-B
RADIATION AND DROUGHT STRESS
ON PLANTS

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Due to their immobile nature, plants constantly face conditions of biotic and abiotic stress. These stresses have acute and adverse effects on plant growth and development. Plants are constantly exposed to a broad range of combined abiotic stresses. The majority of experimental work looks at abiotic stress under controlled conditions and the responses of plants to alteration in environmental conditions have generally focused on a single stressor. However, under natural conditions, combinations of two or more abiotic stresses can occur in the field at the same time. These may include conditions such as drought and salinity; drought and chilling; drought and UV; heat and ozone; UV and heavy metals; ozone and pathogens; and high CO_2 and drought. These are common to many agricultural areas around the world and can impact plant development, metabolism, and yield in novel ways that may be different to those caused by different stresses applied individually. To avoid this type of combined abiotic stress, plants have evolved many morphological, physiological, biochemical, and antioxidant mechanisms. Tolerant plants have evolved stomata closure, root growth stimulation, free proline accumulation, and osmolytic deposition in response to multiple stresses. Non-enzymatic and enzymatic antioxidant defense systems have also evolved for protection against drought stress and UV-B stress. Various non-enzymatic compounds, such as glycine betaine, ascorbate, and glutathione (low molecular antioxidants); and antioxidant enzymes, such as superoxide dismutase, catalase, and ascorbate peroxidase; as well as some secondary metabolites, such as polyamins, tochopherol, and cerotenoids, participate in the removal of ROS under increased UV-B and drought stress. The combined effect of drought stress and UV-B radiation induces responses that can be synergistic, additive, or antagonistic in comparison to responses to separate or individual

stresses. As such, drought stress may enhance tolerance to UV-B radiation and vice-versa. Hydrogen peroxide, nitric oxide, and some plant hormones participate in the activation of defense mechanisms against both these stress conditions. Here, we will address the combined impact of UV-B and drought stress on plant growth, and morphological, physiological, and biochemical responses and antioxidant defense mechanisms.

Introduction

Owing to their sessile lifestyle, plants are constantly exposed to a broad range of environmental stresses. These can have acute and adverse effects on plant growth and development (Rejeb et al., 2014). Ecological stress factors are divided into two groups: biotic and abiotic. Bacteria, fungi, insects, weeds, viruses, and human activities are all biotic stresses, while high UV radiation, drought, salinity, pesticides, low temperatures (chilling and freezing), O_3, decreased soil oxygen, mineral nutrient deficiency, metal toxicity, and pollutants are all abiotic stresses (Kanojia and Dijkwel, 2018). Among these stressors, abiotic factors are major hazards, particularly in terms of the negative affects on the growth and productivity of crop species. Abiotic stresses are responsible for more than 50 % of plant damage and reduced crop productivity across the world (Mittler et al., 2001). The majority of experimental work on abiotic stress in plants has focused on a single stress response to alteration in controlled environmental conditions (Cushman and Bohnert, 2000; Zhu, 2002). However, under natural conditions, combinations of two or more abiotic stresses can occur simultaneously. These combinations may include conditions such as drought and salinity; drought and chilling; drought and UV; heat and ozone; UV and heavy metals; ozone and pathogens; and high CO_2 and drought. Such combined stress conditions are common to many agricultural areas around the world and can impact plant development, metabolism, and yield in novel ways, which may be different to the results caused by each stress applied independently in the lab. In response to such abiotic stress conditions, plants build up several morphological, physiological, biochemical, metabolic strategies, and defense mechanisms. The majority of stress combinations studied have negative effects on crop yield and biomass production in the field.

Drought stress is the most common environmental constraint due to inadequate rainfall and reduced water availability. It is frequently accompanied by increased UV-B radiation (Ballaré et al., 2011; Bandurska et al., 2013). It has been revealed that the combined effect of high UV-B

radiation and drought stress results in the reduction and alteration of plant growth, as well as of morphological, physiological, and biochemical processes (Alexieva et al., 2001). Both these environmental factors act synergistically on the plant's secondary metabolism by increasing the production of flavonoids (Hofmann et al., 2003), which induce the production of cuticular waxes, thus facilitating the reflection of light and better water conservation. Enhanced and ambient UV-B radiation has a significant effect on the photosynthetic efficiency of crop plants due to a reduction in the efficiency of PS II and the activity of RUBISCO, PEP carboxylase, and carbonic anhydrase (Kataria et al., 2014). In contrast, drought stress restricts the productivity of crop plants by affecting photosynthetic processes either directly, or by feedback inhibition at the chloroplast level. The response pattern is regulated by the intensity, duration, and rate of progression of drought stress on plants (Pinheiro and Chaves, 2011). Stomatal characteristics are affected under mild to moderate conditions, reducing biomass, whereas non-stomatal factors can become dominant under severe conditions.

Morphological responses to UV-B and drought

During the co-occurrence of stresses, each stress factor may alleviate or increase the negative effects of the other stress (Mittler, 2006). However, the combined action of drought stress and UV-B stress can transform the response patterns. They can interact in a synergistic or additive manner, but can also interact to significantly increase resistance mechanisms. Plant reactions to combined stress depend on the sensitivity of the species, and the intensity, duration, exposure, and mode of action of the stress factors. In addition to the action of the stresses, sequential and simultaneous protective effects are observed, but the amplification of negative effects may occur simultaneously as well as sequentially with prolonged or severe stress. The responses of plants to abiotic stresses are shown in [**28**].
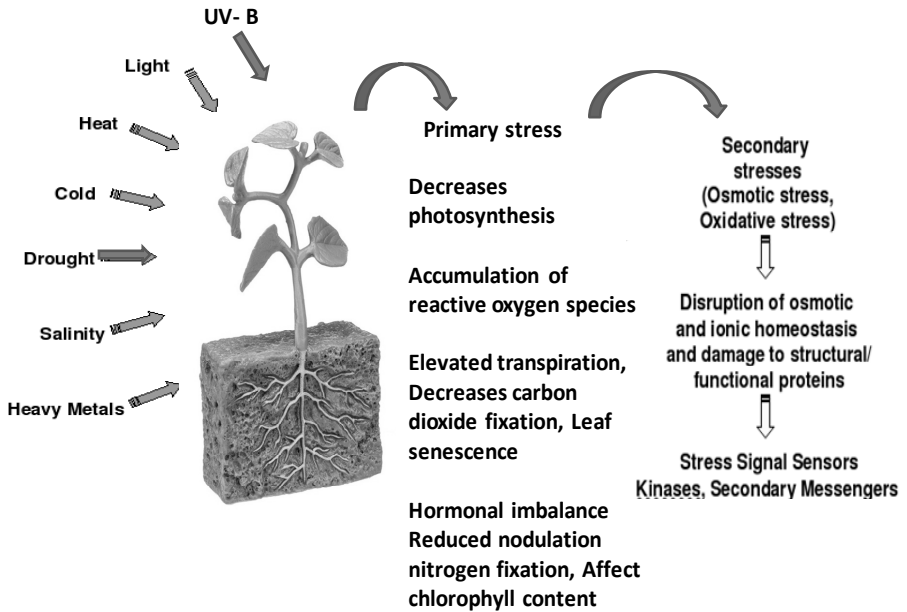
28. Responses of plants to various abiotic stresses.

Some investigations into combined UV-B and drought stress have shown it to reduce plant growth, photosynthetic capacity, pigment contents, biomass, and yield (Feng et al., 2007). In field-grown soybean, a decrease in productivity following UV-B exposure was shown to be moderated by soil water deficit (Sullivan and Teramura, 1990). It was found that radish seedlings were less sensitive to UV-B under water stress than cucumber seedlings. Radish showed higher leaf flavonoid contents, which possibly protected the seedlings by absorbing UV-B in the leaf epidermis. Nevertheless, the interaction between soil water deficit and UV-B stress in cowpeas resulted in benefits from the combined stresses in terms of greater growth and development compared to single stress exposure (Balakumar et al., 1993). Exposure to both UV-B and water stress was found to lead to decreased growth in cucumbers and radish, but protein content was increased. It was concluded that the UV-B irradiation could alleviate the negative effects of water stress on plants or exert an additional inhibitory effect on functional processes in soybeans (Tevini et al., 1983; Teramura et al., 1990). In contrast to Douglas fir seedlings grown in near-ambient UV-B radiation, decreased leaf area and increased

leaf thickness were reported in seedlings in response to high UV-B radiation (Nagel et al., 1998). Both UV-B and drought stress were shown to have negative effects on the growth of *Arabidopsis thaliana* (Rajabbeigi et al., 2013). Nikolopoulos et al. (1995) reported that enhanced UV-B radiation may be beneficial for Mediterranean pines, alleviating the adverse effects of summer drought through restriction of cuticular transpiration. The effectiveness of UV-B radiation may be reduced in the presence of drought, resulting in growth delay or a concurrent increase in UV-B protective mechanisms. Both UV-B and drought stress radiation treatments resulted in lower shoot dry matter per plant, but there was no significant interaction between the two treatments. Zhang et al. (2011) also found that conditions of moderate drought stress and enhanced UV-B radiation increased biomass accumulation in the root and stem. Under conditions of severe drought stress, enhanced UV-B radiation led to increased biomass accumulation in the root, as well as some increase in biomass accumulation in the stem. This verifies that enhanced UV-B radiation can reduce the influence of biomass accumulation of *Fagopyrum dibotrys* under drought. The interactive effect of UV-B and drought stress on growth during recovery also has important consequences for the maintenance of reproductive success. Furthermore, reduced final yields of siliques were observed in plants subjected to combined stress treatment. Sangtarash et al. (2009) found combined UV-B and drought stress to have an additive effect in terms of the reduction of leaf area and biomass production in *Stellaria longipes*. One currently under-researched aspect of plant responses to both UV-B and drought is their role as regulators of plant phenology and reproductive success. The maintenance of reproduction following stress is often accompanied by changes in phenology (Pigliucci and Schlichting 1995; Brun et al. 2003). Feng et al. (2007) found UV-B and drought to have opposite effects on phenological timings in *Triticum aestivum*; therefore, UV-B and drought stress may have interactive effects on plant phenology. Conversely, Alexieva et al. (2001) found that *Pisum sativum* and *Triticum aestivum* exposed to combined UV-B and drought stress achieved greater total biomass than plants exposed to UV-B stress alone.

Physiological and biochemical responses to UV-B and drought

Global attention has become focused on increasing UV-B intensity and drought (due to low rainfall), which can have negative impacts on ecological and biological systems (Caldwell et al., 2007; Ballare et al.,

2011). Most of the stress combinations studied, including combined UV-B and drought stress, have been shown to have harmful effects on crops (Bandurska et al., 2013). It has been found that the combined effect of UV-B radiation and drought stress leads to alterations and reductions in plant growth, physiology, and biochemical processes (Alexieva et al., 2001). Cechin et al. (2008) found that sunflowers subjected to UV-B and drought stresses saw lower shoot dry matter per plant, as well as reduced photosynthesis, stomatal conductance, transpiration, and chlorophyll-a pigment. On the contrary, in white clover seedlings both stresses were demonstrated as having no significant effect on photosynthesis and biomass accumulation (Hofmann et al., 2003). Drought stressed cucumber plants under increased UV-B radiation lost their stomatal closing capacity at midday, saw reduced stomatal conductance and transpiration, and experienced additional negative effects on net photosynthesis (Tevini et al., 1983; Teramura et al. 1984; Kyparissis et al., 2001; Feng et al., 2007).

At the physiological level, other factors potentially occur in response to restrictive UV-B effectiveness in drought stressed plants. For example, it has been found that exposure to high UV-B radiation alongside drought may reduce sensitivity and cause plant phosphorus deficiency. In addition, a reduction in growth, altered intercellular CO_2 concentration, and apparent limitations on the assimilation of photosynthetic capacity in soybean were found in response to both UV-B and drought stress. However, the amplitude of the effects of both stressors was dependent on their interactions. Water stress reduced photosynthetic pigments only under high UV-B radiation and the decrease was more accentuated for chlorophyll-a than for chlorophyll-b (Sullivan and Teramura, 1990; Feng et al., 2007). An adverse effect in response to UV-B radiation and drought stress in wheat was observed by Tian and Lei (2007). Hui et al. (2016) found that the combined application of UV-B and water-deficit produced significantly higher chlorophyll, carotenoid, and total flavonoid contents in *Bryum argenteum* plants. These results suggest that drought stress alleviates the negative effects caused by enhanced UV-B radiation.

The interactive effects of UV-B and drought stress on the production of secondary metabolites do not show a clear pattern. Prior treatment with a high ratio of UV-B to PAR treatment enhanced the production of flavonoids in pea plants that were subsequently subjected to drought conditions (Nogués et al., 1998). Conversely, simultaneous UV-B treatment and drought stress dramatically reduced the UV-B mediated induction of anthocyanins and flavonols in barley (Bandurska et al., 2012) and pea plants (Alexieva et al., 2001). When combined with drought, Alonso et al.

(2015) reported lower UV-B mediated induction of terpene compounds in grapevines (*Vitis vinifera*). Conversely, Llusia et al. (2012) showed that terpene emissions were altered by increased UV-B and drought stress in a species-specific manner in Mediterranean species of xerophytes (*Daphne gnidium* and *Pistacia lentiscus*) and mesophytes (*Ilex aquifolium* and *Laurus nobilis*). In one of these species, combined drought stress and UV-B conditions elicited a stronger response (Nguyen et al., 2016; Bravo et al., 2017). Hassan et al. (2013) observed the highest levels of anthocyanin and flavonoids after exposure to UV-B radiation, while the lowest content was found in drought induced *Vicia feba*. In addition, higher proline content in *Arabidopsis* plants under enhanced UV-B radiation may be responsible for its higher tolerance to drought stress (Poulson et al., 2006; Cechin et al., 2008).

Previous investigations of UV-B and drought stress have also indicated that accumulation of osmolytes is an important determinant of interaction between these factors. For example, in cases where UV-B has been shown to reduce the negative impact of concurrent drought stress, it is the accumulation of low molecular weight and soluble metabolites, such as sugars, which have been implicated (Schmidt et al., 2000; Alexieva et al., 2001). Drought has previously been shown to reduce the negative impact of UV-B on yield in *Glycine max* (Sullivan and Teramura, 1990). UV-B as well as drought is known to promote the activity of enzymes playing an important role in phenol metabolism, such as phenylalanine ammonia-lyase (PAL) (Dixon and Paiva, 1995; Treutter, 2010). Stress mediated PAL synthesis induced by UV-B has been documented in lettuce (Caldwell and Britz, 2006) and white asparagus spears (Eichholz et al., 2012). The amino acid proline is a prerequisite marker of drought stress (Alexieva et al., 2001) and may also act as a protective factor against UV stress (He et al., 2011). Furthermore, the impact of combined drought and UV-B radiation led to much higher total anthocyanin. It was found in a number of studies that PAL activity increased in response to stress impacts like UV and drought stress (Oh et al., 2010; Shehab et al., 2010; Rajabbeigi et al., 2013). Similarly, Tian and Lei (2007) found combined factors to have an additive negative effect on the growth of *Triticum aestivum* seedlings, possibly related to enhanced oxidative damage. Similarly, He et al. (2011) found that the pre-application of drought caused increased tolerance to UV-B and vice versa in *T. aestivum*, suggesting some cross-tolerance between these factors. Kilian et al. (2007) identified a substantial overlap in gene expression in *A. thaliana* in response to both UV-B and drought. Similarly, Schmidt et al. (2000) identified ameliorative effects of combined UV-B and drought stress on the maintenance of leaf

water content in *A. thaliana*. Nevertheless, whilst drought and UVB have been shown to interact, the responses found have not always been consistent between studies.

Effect of UV-B and drought on oxidative stress and the antioxidant system

The combined action of water deficit and UV-B radiation can modify plant response patterns. They can interact in an additive or synergistic manner increasing stress, but can also interact to greatly increase plant resistance. The amplification of negative effects may occur under the influence of simultaneous, as well as sequential action of prolonged or severe stress. However, there is only limited data in the literature relating to the interplay between drought and UV-B applied sequentially, as often occurs in nature. Many contradictory results about antioxidant enzyme responses to different stresses have emerged due to the fact that the levels of enzyme responses depend on the plant species, the plant's developmental stage, and the organs involved, as well as on the duration and severity of the stress (Rout and Shaw, 2001). In many plants, free proline accumulates in response to biotic and abiotic stresses, including UV-B irradiation (Carletti et al., 2003).

Tian and Lei (2007) concluded that drought stress and UV-B irradiation can both cause oxidative damage to plants through the generation of excessive reactive oxygen species (ROS). UV-B was shown to cause more severe stress than drought stress and the effect of UV-B and drought stress was seen to be additive in wheat seedlings. However, it is known that an excess of UV-B radiation and drought individually leads to accelerated production of ROS, such as singlet oxygen ($\cdot O_2$), superoxides (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH \cdot$). Free radicals are extremely reactive and directly oxidize many biomolecules, such as the phospholipids of plasma membrane, nucleic acids, and proteins. Moreover, they can lead to the modification and destruction of proteins and enzymes in polymers, such as ribulose-1,5-bisphosphate carboxylase (RUBISCO), ATPase violaxanthin de-epoxidase, and the protein subunit of photosystems I and II (Rai and Agrawal, 2017) leading to irreparable metabolic dysfunction and death of plant cells. On the other hand, some plants have well-developed resistance mechanisms for stress tolerance to UV-B radiation and drought stress in the form of an antioxidant system. Non-enzymatic antioxidants also play a role, including ascorbic acid, polyamines, tocopherol, carotenoids, alkaloids, and flavonoids (Rao et al., 1996);

antioxidant enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione S-transferase (GST), glutathione reductase (GR), glutathione peroxidase (GPX), and peroxidases (POX); and non-enzymatic compounds, such as ascorbate (ASA), glutathione (GSH) (Ueda and Nakamura, 2011; Siddiqui et al., 2011; Mackemess et al., 2001; Fedina et al. 2009; Broshe and Strid, 2003). Antioxidative responses of plants towards UV and drought stress are presented in [**29**].

Equally, UV-B and drought stress were seen to cause the formation of ROS; induce the synthesis of plant hormones, like absicic acid (ABA), ethylene, JA (Jasmonic acid), and SA (salicylic acid); activate defense mechanisms, including the accumulation of flavonoids (UV-B absorbing), polyamines, LEA proteins, and dehydrins; and improve the leaf water relationship through stomatal closure, osmolyte accumulation, and enzymatic and non-enzymatic antioxidant system upregulation (Siddiqui, 2011; Mackerness, 2001). On the contrary, prolonged action or high acute doses are potentially cytotoxic due to the generation of ROS, which can directly harm the normal function and components of cells (Sharma et al., 2012). Cellular damage and plant survival activity can be determined by the relation of pre-oxidants and antioxidant activity. The combined action of UV-B stress and drought stress is of great detriment to plants. UV-B radiation's combined action has an additive detrimental effect in wheat seedlings; when acting alone, it causes oxidative injuries and growth retardation (Tian et al., 2007).
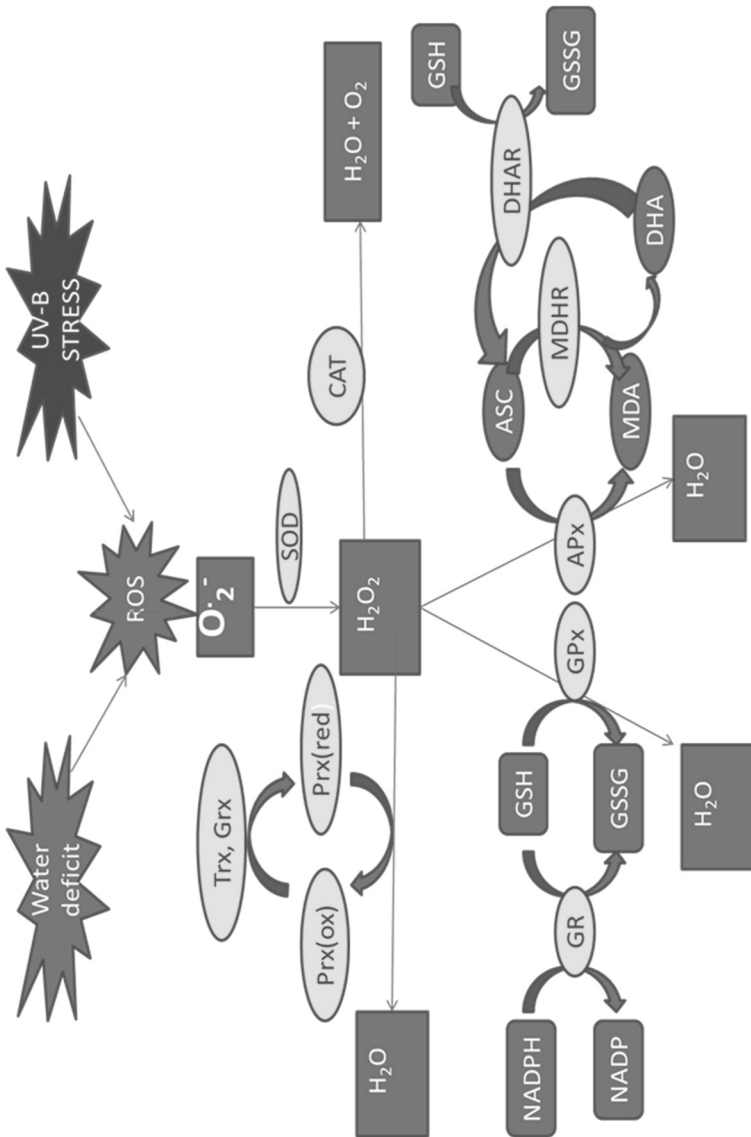
29. Antioxidative system in response to UV-B and drought stress.

Under natural field conditions, drought stress and high UV-B radiation operate separately; frequently, however, plants experience both stresses simultaneously. The co-occurrence of these stresses can alter the effect of individual stress responses. UV-B stress was shown to be alleviated by simultaneously applied moderate drought stress conditions, which led to an increase in catalase activity and flavonoid levels, thus reducing oxidative damage caused by UV-B in wheat and pea plants (Alexieva et al., 2001; Feng et al., 2007). Pre-treatment of plants with mild drought stress prior to UV-B radiation effectively reduced the level of H_2O_2, prevented lipid peroxidation, and reduced the rate of photosynthesis in tobacco (Hideg et al., 2003). Drought stress induced enhanced accumulation of UV-B absorbing compounds, caused a decrease in sensitivity to biologically effective UV-B radiation in *Trifolium repens*, and reversed the negative effect of UV-B radiation on growth in *Populus yunnanensis* (Hofmann et al., 2003; Daun et al. 2008). Tian and Lei (2007) found that the combined action of both stressors retarded seedling growth and increased the antioxidant activity of enzymes like superoxide dismutase, guaiacol peroxidase, and ascorbate peroxidase in wheat seedlings. Similar results have been noted in *Vigna unguiculata* L. (Balakumar et al., 1993), sunflowers (Cechin et al., 2008), *Picea asperata* (Lu et al., 2007), and barley seedlings (Bandurska et al., 2012).

Balouhci et al. (2009) found an increase in the proline contents of bean leaves in response to UV-B radiation and drought stress. The combined action of drought stress and UV-B radiation can modify response patterns in plants. For example, Siddiqui (2011) reported that simultaneous exposure to UV-B and drought stress causes the formation of ROS, H_2O_2, and NO; induces the synthesis of plant hormones like ABA, ethylene, jasmonic acid, and salicylic acid; and activates defense mechanisms, such as the accumulation of UV-B absorbing flavonoids, polyamines, and dehydrins etc.

When UV-B causes damage, the combined action of drought and UV-B usually becomes more detrimental. The combined action of moderate drought and ultra-high dose UV-B radiation had an additive detrimental effect in wheat seedlings (Tian and Lei, 2007). In barley seedlings the combined application of these stresses reduced the positive effect of UV-B on the synthesis of flavonoids, leading to higher membrane injury (Bandurska et al., 2012). Combined stress treatment also led to inhibition of the accumulation of soluble sugars, restricting the capacity for osmotic adjustment and having a negative additive effect on rosette growth (Comont et al., 2012). The negative effects of high ambient UV-B were

shown to be alleviated by the simultaneous application of moderate drought conditions, leading to an increase in catalase activity and flavonoid levels, reducing the oxidative damage caused by UV-B in wheat and pea plants (Alexieva et al., 2001; Fang et al., 2007). Pre-treatment of plants with mild drought prior to UV-B effectively reduced the level of H_2O_2, preventing lipid peroxidation, and a decrease in the photosynthetic rate of tobacco exposed to high-dose UVB. This improved tolerance to UV-B stress was primarily derived from the over expression of aldose/aldehyde reductase engages in the detoxification of lipid peroxidation products (Hideg et al., 2003).

It should be noted that drought induced accumulation of UV-B absorbing compounds in *P. yunnanensis* was accompanied by an increase in ABA concentration. Moreover, exogenous application of ABA was shown to significantly increase the accumulation of these compounds (Tossi et al., 2011, 2012a, 2012b). In some plants, a water deficit was shown to induce SA acid accumulation (Bandurska, 2013; Bandurska and clislak, 2012; Banduraska and stroinski, 2005). SA may play a role in water deficit induced mechanisms of cross-resistance to UV-B. Exogenous application of SA attenuated UV-B induced damage by increasing the level of superoxide dismutase and catalase activity, as well increasing the concentration of anthocyanins, leading to improved growth under UV-B stress (Pael et al., 2013). Taking into account the rapid increase in JA concentration in water stressed plants, it can be assumed that also this hormone regulates water deficit induced resistance to UV-B (Wastemack, 2007).

Supplemental UV-B radiation was observed to cause a two-fold increase in cuticule thickness, enabling the plant to avoid excessive water loss, improve water economy, and alleviate the adverse effects of summer drought on the efficiency of the photosynthetic apparatus (Manetas et al., 1997; Petropoulou et al., 1995). Similarly, seedlings of *Pseudotsuga menziesii* grown under high UV-B were more resistant to drought because they saw lower transpirational water losses and maintained better water status than seedlings grown without UV-B radiation (Paulson et al., 2002). Schmidt et al. (2000) found that UV-B induced improvment of leaf water status may be associated with the production of osmolytes and the accumulation of dehydrins, but not with stomatal closure. Moreover, reduced oxidative damage was observed in barley leaf cell membranes (Bandusrla and Clislak, 2012). The results of a number of experiments have revealed that the simultaneous application of UV-B radiation with water deficit compensated the negative effects of moderate drought on the

activity of antioxidant enzymes (superoxide dismutase, catalase) in *Vigna unguiculata* L. (Balakumar et al., 1993) and those of severe drought on lipid peroxidation in sunflowers (Cechin et al., 2008). The impact of UV-B radiation on alleviating drought induced cell membrane damage through a reduction in electrolyte leakage and a decrease in the level of lipid peroxidation was also found in *Picea asperata* populations (Lu et al., 2007).

Taking into account the increase in SA concentration in barley seedlings after pre-treatment with supra-physiological UV-B and the likely role of salicylate in plant responses to water deficits, we can assume that it is involved in UV-B induced cross resistance to drought (Bandurska and Clislak, 2012; Saruhan el al., 2012). The protective action of SA may include improvements in leaf water status through osmotic adjustment and stomatal closure, as well as the alleviation of water deficit induced injury by upregulation of the antioxidant system (Bandurska et al., 2013). Bearing in mind that UV-B causes an increase in ABA and NO concentrations, these regulators may have a role in mediating the UV-B induced alleviation of oxidative damage in water deficit stressed plants (Tossi et al., 2012). It has been postulated that ABA induced activation of antioxidant enzymes involve H_2O_2 dependent NO generation, which, in turn, activates mitogen-activated protein kinase cascades and gene expression (Zhang et al., 2007). However, ethylene and JA, whose concentrations increase on exposure to UV-B, may support ABA dependent defence mechanisms, or they may operate independently to increase water deficit resistance. It has been shown that ethylene and JA interact with ABA mediated stomatal closure via H_2O_2 generation and enhanced production of NO (Acharya and Assmann, 2009; He et al., 2011).

Conclusions and future prospects

The combined effect of UV-B and drought stress is of increasing interest in relation to the growth, development, physiology, biochemical changes, and antioxidant activity of plants. The elevation of both stresses at the same time has been found to cause changes in plant growth, physiology, biochemistry, and oxidative stress activity. Several components of the photosynthetic apparatus are affected by these stress factors at the molecular level. Alongside this, there have been significant advances in our understanding of the combined effects of these factors on terrestrial ecosystems, particularly in terms of plant response mechanisms.

Understanding the many underlying developmental and resistance mechanisms in plants has allowed us to observe their mediatiation of UV-B and drought stress. As a result, we can better understand common responses to these combined stress factors in plants, such as diminished growth, acclimation, and the stimulation and transmission of signals within the plants. The resulting modifications in gene expression may also alter common physiological, biochemical, and antioxidant responses in plants, or they may generate overlapping functions. However, the combined effect of UV-B and drought stress in plants is still not well understood and more research needs to be carried out under field conditions to provide definitive answers in this area.

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