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Interactive response of ultraviolet-B with other abiotic stress factors on plants

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Abstract

Depletion of stratospheric O_3 layer is leading to an increase in UV-B radiation on earth surface. Along with UV-B other abiotic stress factors are also changing simultaneously. Present review is summarizing the information available on the interactive effect of UV-B with other abiotic stress factors on various plant species. This article is an overview of literature of existing studies on the interactive effects of UV-B with water stress, nutrient stress, elevated carbon dioxide (CO_2), heavy metal and ozone (O_3). Experimental conditions along with doses of stress were also compared to make the clear view of difference in response of plants in natural and controlled conditions. Among all these studies only 25% studies were conducted in field conditions however rest of them were performed under controlled environment. Results of interactive effect at various levels as growth, anatomy, physiology, biochemical changes and yield were given in terms of increase and decrease. Mode of interaction was also discussed with other factors. Carbon dioxide and nutrient stress were found to alter the source and sink balance of carbon in plants which in turn provides protection against UV-B. Pathways for synthesis of UV-B and water stress induced secondary metabolites and signaling of defense gene expressions with heavy metals and UV-B were also compared in plants. Elevated carbon dioxide, nutrient stress were found to ameliorate the negative response of UV-B in most of the plant species however heavy metals, water stress and elevated level of O_3 were found to worsen the effect of UV-B in most of the studies. Interactive response of UV-B with other abiotic stresses is a broad area and results of few studies can't withdraw a definite conclusion. Field studies are also scanty and further needed to define the actual performance of plants in present and future environment.

Keywords: UV-B, CO_2, heavy metal, water stress, nutrient stress, O_3, growth, physiology, yield.

Introduction

Global climate is result of a complex system of various atmospheric processes and their products. Due to subsequent increase in industrialization, urbanization and agricultural practices

our atmosphere is undergoing a transition with the simultaneous increase in several abiotic factors such as UV-B, CO_2, O_3, temperature, heavy metals and excessive nutrients. With increasing trend of these abiotic factors the most important question to be answered is, whether these factors can counteract to nullify their negative effects or interaction may be antagonistic, synergistic or additive. During last few decades convincing evidences have been reported regarding the reduction in stratospheric O_3 layer due to emission of chlorine and bromine containing compounds. As these CFCs have a high half life ranging from 50 to 150 years and they can remain for the longer period in the upper atmosphere so it will take 2065 to return to the pre 1980 level if no further release will occur (UNEP, 2006). Since the discovery of ozone hole in 1979 by Farman and colleagues, consequential increase in solar UV-B is becoming a threat to all life forms on earth (Rozema et al., 2001). Goddard Institute of Space Studies (GISS) estimated that the maximum annual increase in Northern Hemispheric UV dose will be 14% in 2010-2020 (Taalas et al. 2000, 2002). Along with increase in UV-B other abiotic factors are also increasing simultaneously. Under natural field conditions it is common practice for a plant to encounter more than one environmental stress simultaneously. Depending on the mode of action of stress factors and plant species, net effect of two or more concomitant stresses can be antagonistic, additive or synergistic and it can also be possible that they can't influence each other's response. Present review is an attempt to summarize various studies pertaining with interaction of UV-B and other stress factors and emphasizing the possible mechanism behind their differential response.

Interaction of UV-B and CO_2

Increasing use of non-renewable natural resources especially fossil fuel is causing a steady increase of CO_2 concentration. Atmospheric CO_2 has increased from pre industrial value of 280 to the current level of 380 µmol mol^{-1} (IPCC, 2001) and according to predictions this may increase upto 700 µmol mol^{-1} by the end of this century (IPCC, 2007). Since CO_2 is a substrate of photosynthesis, its very important to assess how plants modify photosynthesis particularly Rubisco that catalyze CO_2 fixation. Various studies have been conducted to assess the impact of enhanced UV-B and CO_2 on plant. Lavola et al. (2000) have reported that 700 µmol mol^{-1} concentration of CO_2 is sufficient to ameliorate the harmful effect of UV-B (8.6 kJ m^{-2} day^{-1}) on birch seedlings however Tegelberg et al. (2008) have found similar level of CO_2 to be ineffective in ameliorating the harmful effect of UV-B (7.95 kJ m^{-2} day^{-1}) on birch plants. Under CO_2 enrichment the increased allocation of carbon is favored towards synthesis of condensed tannin than to other phenolic compounds. With the increases in carbon availiability under the enhanced UV-B more carbon allocation is reported for growth, lignifications, enhanced activity of enzymes and repairing processes (Lavola et al. 2000). Both UV-B and CO_2 are known to enhance flavonoid synthesis in plants but the quercetin glycosides were reported to be the most responsive flavonoid towards UV-B and CO_2 (Lavola et al. 1997, 2000). In a gymnospermic plant *Pinus taeda,* enhanced concentrations of CO_2 have modified the response of UV-B towards growth and biomass allocation of plant (Sullivan and Teramura, 1994). At CO_2 level of 350 µmol $mol^{-1,}$ biomass was preferentially allocated to shoot components while at elevated level of 650 µmol mol^{-1} it was preferred to root components at enhanced UV-B. Sullivan and Teramura, (1994) have

stated that increase in CO_2 favors carbon gain in plants by reducing diffusional limitation, lowering photorespiration and water use efficiency. Since UV-B also restricts growth of above ground part (leaf elongation, expansion etc.), both factors favor more allocation of biomass towards root and thus resulted a strong interactive effect of UV-B and CO_2 on biomass portioning.

Enhanced level of UV-B has reduced the stimulatory effect of CO_2 on biomass of *Vicia faba* plant but no interaction was noted with respect to photosynthetic parameters (Tosserams et al. 2001). The major responsive trait of plant towards elevated CO_2 is enhanced photosynthesis especially in C_3 plants. After a certain level of CO_2 plant shows acclimation response. Acclimation is nothing but down regulation of CO_2 fixation under elevated CO_2 due to the imbalance between supply and demand of assimilates. Increased accumulation of soluble carbohydrate and starch in leaves may down regulate the expression of nuclear photosynthetic genes including Rubisco (Pandurangam et al. 2006). Apart from direct end product feedback inhibition indirect decrease in photosynthesis also occurs through decrease in photosynthetic enzymes and reduced stomatal conductance (Sttit, 1991, Dijkstra et al. 1993). Acclimation can be recovered with demand of additional sinks for carbohydrate with the onset of flowering and fruiting. Tosserams et al. (2001) have also reported photosynthetic acclimation after 31 days of treatment and at that time total carbohydrate content was 11%. Similar response was noticed by Visser et al. (1997) in photosynthesis of *Vicia faba* but both of them changed the leaf optical properties of plant. Koti et al. (2005, 2007) have studied the growth, photosynthesis and floral attributes of another leguminous crop *Glycine max* and reported that elevated level of CO_2 may compensate the damaging effect of UV-B on growth and development of plants. However the damage caused by UV-B on flower, pollen morphology, production, germination and tube length can not be ameliorated by enhanced CO_2 (Koti et al. 2005). In C_3 plant *Dimorphotheca pluvialis* elevated CO_2 altered reproductive phenology (delayed) and reproductive success and this effect may be mitigated by enhanced UV-B conversely and no any interaction was observed under combined tretment (Wand et al. 1996). Different parameters of cotton plant responded differentially towards elevated UV-B and CO_2. Zhao et al (2003) have not found elevated CO_2 to be helpful in ameliorating the adverse effect of UV-B on growth and physiology of cotton plants especially in ball retention. However, on similar plant no interaction was reported for photosynthetic parameters by Zhao et al. (2004). Response on photosynthesis was very interesting; under the ambient UV-B condition acclimation was reported by elevated CO_2. Net photosynthesis was increased when elevated dose of both the factors were applied simultaneously and this response may be due to more utilization of photosynthate in protective measures. Similarly, Kakani et al. (2004) have also not found any interaction between UV-B and CO_2 in cotton plant. However, Qaderi et al. (2007) have reported that some of adverse effect of UV-B on reproductive parameters can be mitigated by elevated CO_2 in *Brassica napus*. In C_3 plant Helianthus annuus, Mark and Tevini (1997) have reported that doubling of CO_2 concentration may compensate or surpass the harmful effect of UV-B. Likewise Zhao et al. (2004), Staaij et al. (1993) have found elevated CO_2 acclimation under ambient UV-B and reverting the value of NAR back to the low CO_2 level while under elevated level of UV-B reduction in growth was reported and NAR value remained high which checks the negative feedback mechanism of an invasive plant *Elymus*

athericus. Teramura et al. (1990) have observed that in combination, enhanced UV-B has eliminated CO_2 induced increase in seed yield of wheat *seed yield* and total biomass of rice, however both were increased in soybean plants. Similar to the above result of rice Ziska and Teramura (1992) have also found elimination of CO_2 induced enhancement in biomass by elevated UV-B. In contrast to biomass yield was increased with elevated CO_2 and UV-B suggesting that yield can be the most conservative parameter with respect to CO_2 and UV-B interaction whereas the relative decrease in biomass would be more as compared to the present scenario of UV-B and CO_2. Unlike the other studies Deckmyn et al. (2001) also used two different levels of UV-B which are less than ambient (82 and 88%) under enhanced level of CO_2 and observed that elevated level of CO_2 stimulated growth at reduced level of UV-B (88%) in Trifolium repens.

Several mechanisms may be involved in modification of plant response to UV-B due to CO_2 enrichment. Elevated CO_2 induces the production of more leaves and thus enhances leaf area and in turn productivity of plants. UV-B induced damage to photosynthetic apparatus can also be compensated by enhancement of CO_2 by increasing carbon availability, water use efficiency, and Rubisco activity and also by reducing photosynthetic respiration (Sullivan and Teramura, 1994). Elevated CO_2 is also known to enhance secondary metabolism which may increase the amount of UV-B absorbing compounds (flavonoids, tannins, lignins etc.) which may reduce plant sensitivity towards UV-B (Rozema et al. 1997, Penuelas et al. 1997). Two hypotheses may function behind the CO_2 induced secondary metabolite synthesis. According to “carbon-nutrient balance hypothesis”, increases in C/N ratio stimulate more production of carbon based secondary compounds (Bryant et al. 1983). Similarly the “growth differentiation balance hypothesis" says that any environmental condition (like elevated CO_2) which differentially affects photosynthesis (source) and growth (sink) will change the available carbon pool and synthesis of carbon based secondary compounds (Loomis, 1932). Increasing atmospheric CO_2 increases the strength of source and available carbon pool which in turn stimulate synthesis of secondary metabolites (Penuelas and Estiarte, 1998). Increase in the level of carbon based secondary compounds (tannin, lignin) provide protection to the plants against enhanced UV-B damage (Fig. 1).

UV-B and nutrient interaction

Various anthropogenic activities (industrial and agricultural) have significantly altered the global nutrient cycle. Excessive loading and deficiency both can strongly affect the sensitivity of plants towards other stresses. Mineral stress is defined as sub-optimal availability of essential nutrient or toxicity due to excess of nutrients to plants (Lynch and Clair, 2004). Majority of world agriculture is facing the problem of sub-optimal availability of nitrogen (N) and phosphorus (P). However N deposition is increasing in many European countries, north-eastern United States and China (Yao and Liu, 2006). Nitrogen is a major component for all the biochemical processes operating in plants and also important limiting factor in those zones where UV-B fluence rate are normally high (Riquelme et al. 2007). Some studies pertaining to interactive effect of UV-B and nutrients on tree plants reported that under low nutrient supply plants show tolerance against UV-B increment (Musil and Wand, 1994 on *Dimorphotheca pluvialis*), more than with optimal nutrients (De la Rosa et al. 2003 on *Betula pendula*) and with high nutrient supply (Tosserams et

al. 2001 *Plantago lanceolata*). Similar response was reported by Yao and Liu (2006) on tree species Acer mono maxim in which N supply made plant more sensitive towards UV-B. Nitrogen helped to increase the growth, antioxidants, lower the level of reactive oxygen species (ROS) and intensity of harm but was not able to totally alleviate the effect of UV-B. Gymnosperm plant *Picea asperata,* also responded similarly under same dose of UV-B (14.33 KJ/m^2/day) and N (20 g/m^2/area) (Yao and Liu, 2007). However, Yao et al (2008) doesn't found excess N to help in photosynthetic impairment in similar plant. These responses are also species dependent. Levizou and Manetas (2001) have noticed that slow growing *Ceratonia siliqua* doesn't respond against low/high nutrients in presence of UV-B and this may be due to the requirement of longer exposure time of both the stresses in order to get significant response. However, fast growing species *Phlomis fruticosa* showed improved growth under high nutrient and enhanced UV-B. Inherently slow growing species under nitrogen deficiency invest more carbon based secondary metabolites and their growth promotion by additional nutrients would result in less investment into phenolics and make plants more vulnerable to enhanced UV-B (Bryant et al. 1983, Levizou and Manetas, 2001). It is suggested that low nutrient availability induces synthesis of phenolics, condensed tannins and flavonoids (querecitin, myricitin) which may afford protection against UV-B radiation (De la Rosa et al. 2001., Lambers et al. 1993) According to carbon (C)/ nutrients balance hypothesis by Bryant et al. (1983), deficiency of nutrients affect growth of plant more than photosynthesis which result in diversion of assimilated carbon to production of secondary metabolites (phenolics/terpenoids). However the study of Lavola et al. (2003) made on a gymnosperm plant i.e. *Pinus sylvestris* reported that certain level of high nutrients (4 and 6%) may deliver protection against ambient and near ambient UV-B by increasing flavonoids and flavonols but carbon allocation to other branches of flavonoid pathway (catechin and tannin formation) remain unchanged. Mineral stress negatively affects the sink strength which favors synthesis of carbon based secondary compounds however according to Yeoman and Yeoman (1996) deficiency of N causes growth limitation which enhances the level of secondary metabolite (Fig 1). Enhanced level of secondary metabolite provides protection to plants against UV-B damage. Wheat is one of the most important cereal crops. And three different studies on wheat showed that increased level of nutrients provided protection against UV-B damage (Rathore et al. 2003), at both recommended and 1.5 times recommended NPK (Agrawal et al. 2004) however Agrawal and Rathore (2007) found only recommended dose of NPK helpful in ameliorating the negative effect of UV-B in wheat plants. Similar response was noticed by Singh et al. (2009) on *Amaranthus tricolor* in which 1.5 times recommended dose of NPK helped to minimize negative effect of UV-B while in *Solanum tuberosum* only recommended dose of NPK was found to be the best for reducing the effect of enhanced UV-B (Singh et al. 2010). They suggested that high nutrient supply enhanced the growth and thus invested more photosynthate for protection. Plants have strategies to trade off between productivity and tolerance to stress. Since high dose NPK increased plant tolerance to UV-B thus sustained higher yield (Singh et al. 2009). Correia et al. (2000, 2005) have observed that reduced N supply helped to minimize negative effect of UV-B on growth, photosynthesis and yield of maize plants. Nitrogen stressed plants generally have smaller leaves and low mersitematic activity. Since reduced level of cell division increases opportunity for repairement of DNA dimmers before cell enters its synthesis phase thus UV-B induced TT dimmers can be repaired to minimize its negative impact (Correia et

al., 2000). Similar response was noticed even in case of leguminous crops. Nitrogen stress rendered plant more tolerant towards UV-B by reducing leaf area and increasing amount of UV-B absorbing compounds in *Phaseolus vulgaris* (Requilme et al. 2007, Pinto et al.1999). Musil et al. (2003) have supplemented *Podolyria calyptrate* with nitrate which enhanced active metabolism (photosynthesis and respiration) and made plant more sensitive towards UV-B. However, Agrawal and Rathore (2007) have found recommended dose of NPK helping to alleviate the deleterious effect of UV-B in *Vigna radiata.* A conclusion could be drawn from the results of all the studies performed for low nutrient conditions especially N is a favoring condition to minimize the harmful effect of UV-B radiation. Pinto et al. (1999) has given a hypothesis that under low N, synthesis of protein was partially suppressed and turnover and catabolic protein degradation were favored which in turn stimulated the deamination of L-phenylalanine leading to overproduction of ammonia and cinnamic acid. Ammonia can be recycled into new proteins and cinnamic acid is used as substrate in phenyl propanoid pathway for synthesis of flavonoids, anthocyanin and various other secondary metabolites. Like NPK, iron (Fe) is an essential plant nutrient involved in synthesis of various antioxidants (SOD), non-specific peroxidases, ascorbate peroxidase and ascorbate-glutathione cycle. Zancan et al. (2008) have reported on *Hordeum vulgare* that Fe deficient conditions also make plant sensitive towards UV-B. Unlike the response of terrestrial plants to nutrients and UV-B, marine organisms showed a different trend. Under low level of N, *Myriophyllum spicatum* and *Dunaliella tertiolecta* both showed increased sensitivity towards enhanced UV-B (Li et al., 2005, Shelly et al., 2005).

UV-B and heavy metal interaction

Various studies have been conducted worldwide to evaluate the interactive effect of UV-B with different heavy metals and they faced that in general heavy metals have ameliorating effect to minimize the harmful effect of UV-B (Larsson et al., 2001, Liang et al., 2006, Chanjuan et al., 2006). On the other hand Rai et al. (1995, 1998) have studied effect of two metals Cu and Pb with UV-B on a cyanobacteria *Anabaena doliolum* and reported synergism between their responses. UV-B exposed cells lead to changes in membrane permeability by peroxidation of lipids and thus facilitated the uptake of Cu and Pb. Lipid peroxidation was identified to be the main phenomenon behind the synergistic interaction of UV-B with Cu and Pb (Rai et al. 1998). UV-B and Cu also altered the energy transfer system of phycobilisome, photosystem I and II, respiration rate and Na+ and K+ leakage (Rai et al. 1995). UV-B and Cd have reduced synergistically the level of photosynthetic pigments and in turn the photosynthetic electron transport activity and oxygen evolution of *Plectonema boryanum* (Prasad and Zeeshan, 2005). They suggested that involvement of similar and multiple sites of action by UV-B and Cd may be the possible reason for their synergistic interaction. Bryophytes also impart sensitivity to various changes in climate. Prasad et al. (2004) have reported additive effect of Cd and UV-B on *Riccia* sp. but the response was modified when the high concentration of Cd was applied in presence of similar dose of UV-B. Both the stress altered the photosynthetic activity of *Riccia* but the inhibition of PS II was only reported in case of UV-B while the water splitting complex was more susceptible towards Cd. Some other studies made with UV-B and Ni interaction on temperate leguminous plants showed some very interesting outcomes. Prasad et al. (2005) have noticed significant reduction in physiological characteristics and biomass production of soybean but

their mode of interaction was less than additive except catalase (CAT) which showed suppressed activity. However, Singh et al. (2009) have reported antagonistic response of UV-B and Ni on pigments, proteins and antioxidants of pea except CAT which showed synergistic response. Similar result was also reported by Mishra and Agrawal (2009) with UV-B and Cd on pea in which CAT showed its additive response against both the stress. Nandi et al. (1984) have suggested that degradation of tetrameric CAT molecule into monomeric subunits during stress may be a major reason for decreased activity of CAT. Utilization of CAT in hydrogen peroxide detoxification and its inactivation may be responsible for reduced CAT activity. In two different studies of Larsson et al (1998, 2001) on two members of Brassicaceae family *Brassica napus* and *Arabidopsis thaliana,* Cd was reported to be the more dominant stress as compared to UV-B and many of the stimulatory effects of UV-B were overridden by Cd. UV-B and Cd altered the balance of various nutrients such as Mg, Ca, P, Cu and K which was increased in shoots of both the test plants while the concentration of S decreased in *Brassica napus.* Larsson et al (1998) have also reported the reduction in concentration of UV screening pigments due to phytochelatin synthesis in presence of Cd. GSH acts as signal transducer of UV-B stimuli for induction of UV screening pigments, on the other hand GSH also act as precursor for phytochelatin synthesis therefore the simultaneous application of both Cd and UV-B may lower the level of UV screening pigments (Kalbin et al., 1997). The most pronounced effect of Cd+UV-B was reported on chl a/b ratio and non photochemical quenching in rapeseed which may be explained by the inhibition in activity of violaxanthin de-epoxidase in presence of Cd+UV-B (Larsson et al., 1998). Likewise the response of *Riccia,* Shukla et al. (2002) have also reported that low concentration of Cd (1 ppm) did not respond significantly in presence of UV-B however the higher dose (2.5, 5 ppm) caused retardation in growth and chlorosis of wheat plants. In another study made by Mishra and Agrawal (2006) on a leafy vegetable spinach, interactions of two heavy metals Ni and Cd individually and in combination with UV-B were evaluated and observed that their mode of interaction was always less than additive. Among both the metals Cd was found to be more deleterious as compare to Ni when provided with UV-B. To assess the effect of UV-B and heavy metal (Cd++), Nedunchezhian and Kulandaivelu (1995) have isolated chloroplast from *Vigna unguiculata* and observed that UV-B supported the inhibitory effect of all applied doses (3,6,9 mM). Both UV-B and Cd induced the severe loss of 17, 23, 33 and 43 kDa proteins which are responsible to inactivate oxygen evolving complex and thus affecting PS II activity. On the other hand PS I activity was only marginally affected. Rare earth metals are not serious environmental pollutants. Acidic condition can cause mobilization leading to their enrichment in ground water, river water etc. Neal et al (2005) have reported increased concentration of lanthanum (La), cerium (Ce), yttrium (Y) and praseodymium (Pr) in rain fall, cloud water and ground water in mid Wales, U.K. Some studies have also been conducted on interactive effect of rare earth metal and UV-B on plants (Chanjuan et al. 2006 a, b, Liang et al. 2006). In the study of Chanjuan et al. (2006 a, b) on soybean and rapeseed Ce helped to lower or alleviate the damage caused by low level of UV-B. In soybean Ce was capable of enhancing the capability of enzymes to scavenge free radicals and thus protected the membrane system. Similar response was also reported by Liang et al (2006) on soybean where La provided resistance to soybean towards UV-B with the help of increased levels of flavonoids, chlorophyll content and PAL (phenylalanine ammonia lyase) activity.

Both UV-B and heavy metal follow more or less similar pathways for signaling inside the plant cell. Being a nonionizing radiation UV-B infers both photomorphogenic and nonphotomorphogenic response which can be low and high fluence dependent. However the existence of UV-B receptors is potent question for decades. Previously it was thought that phytochromes and cryptochromes are putative UV-B receptor. But the study of mutants which are devoid of these photoreceptors showed influence of UV-B on hypocotyl elongation (Frohnmeyer and Staiger, 2003; Bocalandro et al. 2001). Inferences from some important studies suggest that UV-B receptor consist of a protein with a bound pterin or flavin as chromophores (Frohnmeyer and Staiger, 2003) or they can be a factor like ULI3 (found in Brassicaceae family) which encodes an unknown protein containing putative heme and diacylglycerol binding sites (Lariguet and Dunand, 2005). Evidence of some membrane bound cell surface receptors, SR 160 (a peptide systemin) was also given by Stratmann (2003) which is phosphorylated on the intracellular kinase domain in response to UV-B resulting in activation of several defense signaling steps. After the perception of signal photomorphogenesis can be induced by either UV Resistance Locus 8 (UVR8), Elongandated hypocotyl (HY5) or HY5 Homolog (HYH) dependent or independent pathways (Kaiserli and Jenkins, 2007; Brown and Jenkins, 2008).

Besides these undefined UV-B photoreceptors, existence of some cell surface bound receptors has also been noticed. NOS (Nitric oxide synthase) was also identified as factor responsible for upregulation of gene encoding chalcone synthase (CHS) (Jordan, 2002; Brosche and Strid, 2003). NADPH oxidase gene GP31 that encode a plasma membrane protein showed Ca^{++} dependent signaling of ROS in plants (Keller et al. 1998). NADPH induced ROS signaling has been noticed in case of both UV-B (Rao et al. 1996; Jordan, 2002) and heavy metal (Foreman et al. 2003; Maksymiec, 2007). Heavy metal induces H_2O_2 accumulation either by stimulating OXO (oxalate oxidase), NADPH oxidase or by displacing the transition metals from metallochaperones or metalloenzymes and these released transition metals induces oxidative stress (Polle and Schutzendubel, 2003). These transition metals can also activates genes responsible for chperones and metallothioneins. In case of UV-B these ROS perform signaling for the synthesis of jasmonic acid (JA), salicylic acid (SA) and ethylene (Mackerness et al. 1999). JA along with ethylene synergistically induces expression of pathogenesis related PDF 1.2 genes (Pannickx et al. 1998). However SA along with ethylene upregulate the expression of PR genes (Jordan, 2002). Heavy metal induced H_2O_2 accumulation can also trigger the mitogen activated protein kinase (MAPK) cascade involving histidine kinase which in turn activate transcription of defense genes (Polle and Schutzendubel, 2003). Some undefined cell receptors have also been recognized with UV-B which follows MAPK pathway (Fig 2).

UV-B and water stress interaction

Water stress is one of the most obvious global issues like temperature and salinity that affects the survival of agricultural crops. Drought is itself a metrological term that defines a particular period of an area without significant rain fall. Generally drought arises when available water in soil is reduced however the surrounding atmospheric condition causes continuous loss of water either through transpiration or evaporation. The International Water Management Institute estimates that by the year 2025, one third of the world population will inhabit regions of severe water stress scarcity (IWMI, 2005). Since UV-B and water stress are globally accepted

concurring problems of many parts of the world, their interaction should be discussed extensively. Numerous studies have been conducted worldwide on the interactive effect of UV-B and water stress on wheat (Feng et al. 2007, Alexiva et al. 2001), leguminous plants (Teramura et al., 1984, Allen et al., 1999) and aromatic plants (Nogues and Baker, 2000) and noticed various types of interactions. Net effects of these stresses are sometimes synergistic (wheat), additive (soybean), adaptive (sunflower) or without any interaction (lavender, rosemary). Table 4. represents overall type of interaction in different studies conducted so far. Teramura et al. (1984) have found that UV-B more effectively changed biomass allocation however water stress reduced leaf and node number of *Glycine max* and their combined effect was additive on dry matter production and photosynthesis. However, Sullivan and Teramura (1990) have reported that UV-B and water stress showed less than additive effect on photosynthetic parameters of same test plant. Water stress induced masking of effect of UV-B may be due to anatomical or biochemical adjustments (pigment accumulation) which ostensibly protect plants from UV-B through screening mechanism. Drought may also delay cell divison and reduces cell elongation (Boyer, 1970). Since UV-B directly affects cell division thus delay in cell divison may provide protection against UV-B. Another possibility is the development of reduced level of phosphorus in plant due to water stress. In soybean plant Sullivan and Teramura (1990) have reported that phosphorus deficiency in soybean plants directly reduces sensitivity against UV-B. On the other hand, Ren et al. (2009) have observed antagonistic response of UV-B and water stress induced response on yield of soybean. Another leguminous plant *Pisum sativum* showed differential response in photosynthesis and productivity under water stress and UV-B. Nogues et al. (1998) noticed synergistic mode of interaction of both the stresses in flavonoid production but UV-B induced severity of photosynthesis was delayed by UV-B through reducing water loss rates, stomatal conductance and leaf area. On the other hand, Allen et al. (1999) have observed that upto 30 % increase of UV-B doesn't affect the photosynthesis and productivity under well watered and droughted plants of pea. In the study of Yang et al. (2007) two different populations of a leguminous plant *Hippophae rhamnoides* were showed that water stress had moderate response of UV-B which is more pronounced in species growing at high altitude as compare to low altitude. In wheat, UV-B and water stress synergistically induced specific changes in leaf morphology and water relation leading to improved water economy which maintains photosynthetic performance, biomass and yield (Feng et al. 2009). This synergism doesn't show any detrimental effect as compared to their individual response. Increased root shoot ratio in response to UV-B may help to offset water deficit while reduction in leaf area, LAI and induction of flavonoids may help to counter balance effect of UV-B. However, Tian and Lei (2007) have reported that both the stresses produced excessive ROS production leading to increased oxidative stress. UV-B produced more severe response but their interactive response showed additive effect on wheat. Similar response was also reported by Zhao et al. (2009) at 15% field capacity in water relation of wheat plants. However, negative effect of UV-B was alleviated by mild water stress (0.5 MPa) in both pea and wheat plants (Alexieva et al. 2001). Cechin et al. (2008) have also noticed alleviation of negative effect of drought by UV-B on photosynthesis and transpiration. Cucumber is relatively susceptible to unfavorable environmental conditions and is often chosen for studies investigating the reaction to one or more stress factors. Kubis and Zajac (2008) have measured antioxidative system of cucumber and reported synergistic response of UV-B and water stress.

Enhanced activity of syringaldazine peroxidase (SPX) suggests intensification of cell wall component synthesis and consequent increase in cell wall rigidity which provides tolerance against drought stress. In Qurecus petraea two type of differential response were reported. UV-B and water stress showed positive correlation in reducing fluorescence of oak while Meszaros et al. (2005) have observed that UV-B radiation caused hardening of oak which ultimately provided tolerance against water stress. Ren et al. (2007) have also studied response of two species of Populas and reported that *P. kangdingensis* which is already adapted to drought condition exhibit more tolerance to UV-B as compared to *P. cathayana* found at lower altitude. However, another tree species *Salix myrsinifolia* showed additive effect on growth parameters (Turtola et al., 2006). They have taken hybrids of *Salix* (fast growing and slow growing) and found that fast growing species was more susceptible as compared to slow one. This response may be due to better adaptability towards UV-B because of slow growth. Exposure of drought stressed species to UV-B showed more allocation of biomass to root which improved water relation of plant and provided protection against UV-B. Study of Schmidt et al. (2000) also showed that exposure of UV-B moderates the response of water stress in *Arabidopsis* plants and mechanism behind this response underlies in the maintenance of leaf water relation due to induced biosynthesis of stress proteins and compatible osmolytes. On other hand Nogues and Baker (2000) have reported no any significant interaction of UV-B and water stress on three Mediterranean plants lavender, olea and rosemary.

Both UV-B and water stress alter the morphology, anatomy, photosynthesis and metabolism of plant however their mechanism and site of action may be different. Both the stress affects the light and dark reaction of photosynthesis at various steps; however their sites of action may be different. The major mode of UV-B induced damage to photosynthesis is photomodification of various components while for water stress the main deciding factor is stomatal limitation leading to carbondioxide deficiency and alteration of some structural components. Ability of any plant to tolerate stress condition also depends on multiple biochemical pathways and their important products (active metabolite and specific proteins) that may help to maintain plant homeostasis and to sustain their life. Plants have a common strategy for protection against water stress is by accumulating compatible solutes and electrolytes (osmolyte). Osmolyte are a group of biochemically inert compound which helps to maintain osmotic balance necessary for growth and cellular metabolism under dehydration. Water stress induces important metabolic changes including synthesis and accumulation of various polyamines, polyols, proteins, pigments, amino acids, sugar, phenolics and amines. Accumulation of these compounds in high concentrations raise cytoplasmic osmotic pressure without perturbing cellular function and they also stabilize enzymes and membranes of plants (Rathinasabapathi et al., 2000) which in turn provides protection against UV-B (Fig 3).

UV-B and O_3 interaction

Our present state of knowledge on combined effect of UV-B and O_3 on plants is very limited. Earlier studies reported more reduction after sequential treatment of UV-B and O_3 in pollen tube growth of *Nicotiana tobaccum* and *Petunia hybrida* as compared to their individual effect (Feder and Shrier). However, Rao and Ormorod (1995) have reported that pre-exposure of O_3 to Arabidopsis thaliana made plant more sensitive towards UV-B. Table 5. have summarized

effect of UV-B and O_3 interaction on some plant species along with their dose and experimental condition. Booker et al. (1994) have conducted three year field study (1989 to 1991) to assess the effect of UV-B and O_3 on soybean plant. UV-B was not reported to be harmful for growth and yield of soybean but O_3 showed significant reduction for all the studied parameters. UV-B reduced the intensity of O_3 induced visible injuries initially but in last year no such interaction was reported. Growth and yield parameters also showed no significant interaction between UV-B and O_3 of the same plant. Ozone treatment consistently induced visible injury suppressed net carbon exchange rate, growth, yield and accelerated reproductive development however enhanced UV-B didn't suppress any of the above parameters. To study the mechanism of differential response of both the factors, Rao et al. (1996) have used *Arabidopsis thaliana* and its flavonoid deficient mutant for separate exposure of UV-B and O_3 and reported that both the stresses induced oxidative stress and ROS production. UV-B preferentially enhanced NADPH-oxidase and peroxidase related enzymes while O_3 induced SOD and enzymes of ascorbate-glutathione cycle. Staaij et al. (1997) have studied effect of reciprocal exposure of UV-B and O_3 on *Elymus athericus* and found both the stresses negatively affecting the growth of plant. However, the mode of interaction was not clear but their combined response supported the hypothesis that when changes in climatic condition will subject the plants to elevated levels of UV-B and rising concentrations of tropospheric O_3, the total result of both stress factors on plant growth may be of an additive nature. Baumbusch et al. (1998) also explained that low UV-B induced the protection against elevated O_3 in two gymnospermic plant (pines and spruce) and found that pine was more sensitive however spruce is was protected by low level of UV-B. Similar response of amelioration of O_3 response even in presence of ambient UV-B was observed by Schnitzler et al. (1998) on similar coniferous plants. All these studies clearly indicate that amelioration of effect may be seen only when concentration of single factor is elevating and the other remain at ambient level. In another study of Tripathi et al. (2011) and Tripathi and Agrawal (2012) simultaneously exposed linseed plants with elevated dose of both the stresses and reported that these stresses lowered their negative effect in interaction as compared to individual exposures.

Among all the studies considered in the present review, most of them were performed under controlled and indoor conditions. Indoor experiments generally don't have sufficient photosynthetically active radiation and thus exhibit reduced photolyase activity and DNA repairing process (Caldwell et al. 1995). Since these studies are performed under laboratory conditions and controlled practices which are little different from what plants experience in natural field, further detailed research studies are needed to deepen the role of these abiotic stress factors in the adaptive or changed response of plants to an UV-B enriched environment.

From these studies it can be predicted that the overall response of UV-B may be modified in natural field conditions which is species specific. However from few studies, it is not possible to predict a clear conclusion whether the response will be additive, synergistic or antagonistic. Future interaction based studies are needed in natural filed conditions before we come to definite conclusion.

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Table 1. Interactive effects of UV-B radiation and carbondioxide on different plants

Plant material	Growth Conditions	UV-B dose	CO_2 dose	Result of different parameters				Conclusion	Reference
				Morphological	Growth and physiological	Biochemical	Yield		
Vicia faba	Pot experiment	Ambient	700 µmol mol^{-1}	Shoot length, leaf area and dry weight (+)	LWR, RSR (+) RWR,LAR,SLA (-) gs and Pn (-)	carbohydrate, starch (+)	-	UV-B modified the response of elevated CO_2	Visser *et al* (1997)
Vicia faba	Green house	10.6 kJ m^{-2} day^{-1}	750 µmol mol^{-1}	Biomass, number of leaves (+), leaf area (-)	LWR, SLA LAR, Pn and g_s (-), (-) RWR (+)	Carbohydrate and starch content (-)	-	No stimulatory response of CO_2 under UV-B	Tosserams *et al* (2001)
Glycine max	SPAR chambers	10 kJ m^{-2} day^{-1}	720 µmol mol^{-1}	Size of floral organs (-)	-	-	-	amelioration	Koti *et al* (2005)
Glycine max	SPAR chambers	10 kJ m^{-2} day^{-1}	720 µmol mol^{-1}	Plant height and leaf area (-)	Pn (+)	chlorophyll, phenolics and wax contents (−)	-	Amelioration	Koti *et al* (2007)
Gossypium hirsutum	SPAR Chambers	15.1 kJ m^{-2} day^{-1}	720 µmol mol^{-1}	Stem elongation, branch length, leaf area, number of balls and dry weight (-), fruit abscission and number of fruiting branches (+)	Gs and net Pn (-)	Chlorophyll, carotenoid and non structural carbohydrate content (-)	-	Elevated CO_2 could not alleviate the detrimental effect of UV-B	Zhao *et al* (2003)
Gossypium hirsutum	SPAR chambers	16 kJ m^{-2} day^{-1}	720 µmol mol^{-1}	Canopy leaf area (-)	Pn, g_s, transpiration rate, water use efficiency, leaf dark respiration (-)	Starch and non structural carbohydtare (+)	-	No interaction of UV-B and CO_2	Zhao *et al* (2003)
Gossypium hirsutum	SPAR chambers	15.1 kJ m^{-2} day^{-1}	720 µmol mol^{-1}	-	Leaf Pn, g_s (-)	total chlorophyll, carotenoids (-), phenolics (+)	-	No interaction of UV-B and CO_2	Kakani *et al* (2004)
Betula pendula	Green house Pot experiment	8.16 kJ m^{-2} day^{-1}	700 µmol mol^{-1}	Biomass accumulation (+)	RSR (+)	Phenolics flavonoid, condensed tannins, PAL and POD activity	-	Elevated CO_2 may ameliorate the effects of UV-B radiation	Lavola *et al* (2000)
Betula pendula	Closed top chamber	7.95 kJ m^{-2} day^{-1}	700 ppm	-	-	Peroxidase, polyphenol oxidase, total polyamines (+) while Chl a, Chl b and soluble protein (-)	-	Synergistic	Tegelberg *et al* (2008)
Pinus taeda	Green house	13.8 kJ m^{-2} day^{-1}	650 µmol mol^{-1}	Needle, root and stem biomass (-)	RSR (+) while SLW, Fv/Fm, O_2 evolution, Pn (-)	Total chlorophyll (+)	-	Elevated CO_2 may modified UV-B response	Sullivan and Teramura (1994)

Brassica napus	Green house	4.2 kJ m^{-2} day^{-1}	700 µmol mol^{-1}	-	CO_2 assimilation and water use efficiency (+) while transpiration (-)	Total chlorophyll, UV screening pigments (+)	Seed weight (-)	amelioration	Qaderi *et al* (2007)
Trifolium repens	Green house	Reduced level 82% and 88% than ambient	520 µmol mol^{-1}	UV-B favored shoot growth and CO_2 favored root growth . both enhanced number of flowers	-	-	-	Both stress enhanced their response	Deckmyn (2001)
Elymus athericus	Green house	16.8 kJ m^{-2} day^{-1}	720 µmol mol^{-1}	Plant dry weight, number of leaves, leaf area, shoot number and shoot length (-)	RSR, SLW, LAR (-) while SLA, NAR, RGR (+)	-	-	CO_2 modified response of UV-B	Staaij *et al* (1993)
Oryza sativa	Green house	13.8 kJ m^{-2} day^{-1}	660 µbars	biomass (+) number of tillers, leaf area and leaf weight (-)	RSR, SLW, Amax (+) while ACE and stomatal limitation (-)	Concentration of UV-B absorbing compound (+)	harvest index and yield (+)	UV-B modified the response of CO_2	Ziska and Teramura (1991)
Dimorphotheca pluvialis	Open top chamber	11.13 kJ m^{-2} day^{-1}	650 µmol mol^{-1}	Biomass, number of buds, open flowers and reproductive structure (+)	Pn, WUE (–) while g_s(-)	UV-B absorbing compound (+)	-	synergistic	Wand *et al* (1996)
Oryza sativa *Glycine max* *Triticum aestivum*	Green house	10% ozone depletion	650 µmol mol^{-1}	-	Pn (+) in wheat and soybean while (-) in rice	UV-B absorbing compounds (+)	Seed yield of rice, wheat (-) soybean(+)	UV-B modified the response of CO_2	Teramura *et al* (1990)

Negative impact (-), positive effect (+), non significant (ns)

Table 2. Interactive effect of UV-B and mineral nutrient stress along with experimental conditions on different plants

Plant material	Growth Conditions	UV-B dose	Nutrient dose	Results				Conclusion	Reference
				Morphological	Growth and physiological	Biochemical	Yield		
Acer mono maxim	Pot experiment	14.33 $KJm^{-2}day^{-1}$	20 $g\,m^{-2}\,a^{-1}$ (Nitrogen)	total biomass, number of leaves, SLA (-)	Pn and gs and chlorophyll (-)	H_2O_2, O_2^-, Proline, POD, SOD, CAT, APX, GR (+)	-	N-supply made plant more sensitive to enhanced UV-B	Yao and Liu (2006)
Hordeum vulgare	Pot experiment	21 $KJm^{-2}day^{-1}$	100 µM (Iron)	Fresh and dry weight (-)	-	Zeaxanthin (+), H_2O_2, ascorbate, protein, CAT (-) APX (+)	-	UV-B enhances oxidative stress in iron deficient condition	Zancan et al. (2008)

Ceratonia siliqua* *Phlomis fruticosa	field study	15% ozone depletion	10 mg N, 1 mg P, 1.3 mg K	No interaction on growth and morphology of *Ceratonia siliqua* However strong positive interaction on *Phlomis fruticosa*	-	Total phenolics and chlorophyll (+) in *Phlomis fruticosa* While decreases in *Ceratonia siliqua*	-	Low nutrient condition provide protection against UV-B stress	Levizou and Manetas (2001)
Betula pendula	Green house	7.3 KJ m^{-2} day^{-1}	Nutrient deficiency	% injury (+)	-	No interaction of UV-B and N on nutrient content of leaf and phenol except myricitin	-	additive	De la Rosa et al. (2003)
Plantago lanceolata	Green house and pot experiment	0, 4.6, 7.6 and 10.6 KJ m^{-2} day^{-1}	Low nutrient 0.5 g dm^{-3} High nutrient 4 g dm^{-3}	Root shoot and leaf biomass reduced at high N and UV-B	-	Chlorophyll and UV-B absorbing compounds (+)	-	amelioration	Tosserams (2001)
Pinus sylvestris	Green house	0-13.07 KJ m^{-2} day^{-1}	3.2–36.3 mg N L^{-1}	Shoot and needle weight were (+) at high UV-B	-	Low nutrient availability changes concentration of flavonoids and tannins	-	synergistic	Lavola et al. (2003)
Phaseolus vulgaris l.	Green house	3.2 KJ m^{2} day^{-1}	12 or 1 mM nitrate	No change in leaf area in low N condition	Gs, Rubisco activity (-)	Starch, UV absorbing compound (+) chlorophyll (ns)	-	adaptation	Riquelme et al. (2007)
Picea asperata	Open semi field	−11.0 kJ m^{-2} day^{-1}	20 gm^{-2} a^{-1} nitrogen	Plant height, basal diameter (-) total biomass (-)	Pn, gs, transpiration rate, chlorophyll (-)	H_2O_2, O, MDA, proline enzymatic activity (+)	-	synergistic	Yao and Liu (2007)
Picea asperata	Open semi field	14.33 kJ m^{-2} day^{-1}	20 gm^{-2} N	Plant height, basal diameter (-) biomass (-)	Pn, chlorophyll accumulation (-)	-	-	amelioration	Yao et al. (2008)
Amaranthus tricolor	Field experiment	+7.2 kJ m^{-2} d^{-1}	Different NPK doses	Root, shoot length leaf area, biomass (-) number of leaves (+)	SLA (-) while SLW, NAR, RGR, (-)	-	Yield (+) only in 1.5 times recommended NPK while (-) in rest two nutrient doses	1.5 times recommended NPK showed amelioration	Singh et al. (2008)
Solanum tuberosum	Field experiment	−7.2 kJ m^{-2} d^{-1}	Different NPK doses	Root length, shoot length ,leaf number, area and biomass (-)	Growth indices altered		Yield and quality deteriorated	No amelioration	Singh et al. (2010)
Zea mays	Field experiment	+ 6.84 kJ m^{-2} d^{-1}	N_0, N_{100} N_{200} N_{300} (nitrogen)	-	Pn, gs, transpiration rate (-)	chlorophyll, carotenoid, protein, soluble sugar, starch (-)	-	No amelioration	Correia et al. (2005)

Triticum aestivum ***Vigna radiata***	Field experiment	~7.1 kJ m^{-2} d^{-1}	Recommended dose of NPK and without NPK	Nutrient deficiency and UV-B results into maximum (-) biomass	-	Nutrient deficiency and UV-B result into more damage of chlorophyll and in thiol, SOD and POD (+)	-	Amelioration	Agrawal and Rathore (2007)
Triticum aestivum	Field experiment	Ambient+7.1) KJ m^{-2} day^{-1}	without NPK, Recommended NPK, 1.5 times NPK, 2 times NPK	Root, shoot length and biomass (-)	growth indices were minimum in additional NPK	-	Yield and harvest index (-) in UV-B and NPK amended plants	Mineral nutrient specially 1.5 times NPK is most suitable UV-B dose to overcome the effect of	Agrawal et al (2004)
Zea mays	Field experiment	3.16(+ 6.84) KJ m^{-2} day^{-1}	N_0, N_{100}, N_{200}, N_{300} (nitrogen)	Maximum reduction in biomass in N0T	LAR, LWR, SLA (+) while NAR (-)	-	Ear length, ear perimeter, grain number, grain weight and grain yield (-)	UV-B lowered positive effect of N	Correia et al. (2000)
***Cucumis sativus* L.**	UV-B transparent green house in Perlite pots	3.1(12.5) KJ m^{-2} day^{-1}	four nitrogen treatments: 0.5, 2.0, 5.0, 10.0 mol m^{-3} of nutrient solution	Plant height, leaf area, total biomass reduced while epidermal thickness of leaf (-)	Fluorescence (-)	Chlorophyll and carotenoids (-) upto N level 5 mol m^{-3}	-	amelioration	Hunt and McNeil (1998)
***Dimorphotheca pluvialis* (L.)**	Green house and pot experiment	0, 10, 20, 30% ozone depletion	Low and high nutrient dose N-5.8 mg, P-0.8 mg, K-1.7 mg	Biomass (-) in low N at 30% while number of leaves, leaf area (-) in high N at 30%	growth (ns), number of diaspore, inflorescence (-)	Foliar C, N have no effect while foliar P, thickness (-)	-	Low nutrient level enhances the effect of (-) UV-B	Musil and Wand (1994)
Myriophyllum spicatum (L)	Aquarium	0.0.3 W/m^2	0.3.3 mg/L of nitrogen	Growth (-)	-	phenolic content (ns)	-	Low N enhances the effect of UV-B	Li et al (2005)
Dunaliella tertiolecta	Auxenic culture	0.4W/ m^2	P starvation	Growth rate (-)	Pn and quantum yield reduced	-	-	Low P enhances the sensitivity towards UV-B	Shelly et al. (2005)

Negative impact (-), positive effect (+), non significant (ns)

Table 3. Interactive effects of UV-B radiation and heavy metals along with experimental conditions on different plants

Plant material	Growth Conditions	UV-B dose	Heavy metal dose	Result of different parameters				Conclusion	Reference
				Morphological	Growth and physiological	Biochemical	Yield		
Riccia sp.	Growth chamber	0.4 W m^{-2}	1-1000 mM (Cd)	Growth (-)	Oxygen evolution, PS2 activity and electron transport chain (-), respiration (+)	Chl a, b, carotenoids and phycocyanin (-), MDA content, SOD, CAT activity (+)	-	synergistic effect	Prasad *et al* (2004)
Triticum aestivum	Pot experiment	0.4 W m^{-2}	0.25-5.0 ppm (Cd)	Shoot length, fresh and dry weight (-)	-	Chl a, b, carotenoids soluble sugar (-) protein, free amino acid and starch content content (+)	-	amelioration	Shukla *et al. (2002)*
Spinacea olererea	Pot experiment	+7.1 KJ m^{-2}	68 µ mol kg^{-1} Cd and Ni	Biomass (-)	-	Chl, carotenoid, ascorbic acid content, catalase activity (-) anthocyanin, flavonoid content, LPO, proline and peroxidase activity (+)	-	less than additive	Mishra and Agrawal (2006)
Glycine max	Growth chamber experiment	0.4 W m^{-2}	0.01, 0.10, 1.00 mM (Ni)	Height, leaf area, fresh weight and biomass (-)	PS I and II inhibited	Chl a,b, ascorbic acid and CAT activity (-) Carotenoid, H_2O_2, O_2^- ,proline, MDA content, electrolyte leakage, SOD and POD (+)	-	less than additive	Prasad *et al.* (2005)
Arabidopsis thaliana	Growth chamber	6 KJ m^{-2} day^{-1}	0,1 µM Cd	-	O_2 evolution, potential and maximum photochemical yield (-)	Total chlorophyll and carotenoid content (-), nutrient content affected Ca, Mg content (-)	-	amelioration	Larsson *et al* (2001)
Anabaena doliolum	Culture media	12.9 mW m^{-2}	0.3, 0.5 µg ml^{-1} Cu	Specific growth rate (-)	C-fixation, PS II and PS I, ATP pool, chlorophyll fluorescence and ETS (-) respiration rate (↑) and complete loss of O_2^- evolution	LPO and Cu uptake (−)	-	Synergistic effect	Rai *et al.*(1995)
Anabaena doliolum	Culture media	12.9 mW m^{-2}	Cu 8.0 m mo l^{-1} Pb 70 m mol l^{-1}	-	-	Uptake of urea, NH_4, $NO_3^{-5}$and PO_4^{-3} (-)	-	synergistic	Rai *et al.* (1998)

Glycine max	Pot experiment	0.15, 0.45 W m^{-2}	La 20 mg/L	-	-	Pigments (-), flavonoid content and PAL activity (+) -	amelioration	Bin *et al* (2006)
Pisum sativum	field experiment	+ 7.1 KJ m^{-2} day^{-}	Cd 68 µmol kg^{-1}	Shoot length and biomass (-)	-	Chl, car, ascorbic acid and catalase (-) SOD,POD, thiol, proline and LPO (+) Yield (-)	synergistic	Agrawal and Mishra (2007)
Plectonema boryanum	Culture media	0.4 W m^{-2}	2, 8 µM Cd	Growth and survival reduced	Pn, O_2 evolution, PS I and PS II activity (-) respiration (−)	Chl, car and phycocyanin (-) SOD, LPO, CAT (↑) -	synergistic	Prasad and Zeeshan (2005)
Pisum sativum	field experiment	+ 7.1 KJ m^{-2} day^{-}	Ni 68 µmol kg^{-1}	-	-	Total chl, car, flavonoids (+), ascorbic acid, thiol, phenol, proline, LPO, SOD, POX (+) while protein and CAT activity (-) -	antagonistic	Singh *et al* (2009)
Brassica napus	green house	15 KJ m^{-2} day^{-1}	0, 0.5, 2, 5 µM Cd	Leaf area root dry weight (-)	Fv/Fm, non photochemical quenching and photochemical yield (-)	Chl a, b, carotenoids (-) some nutrients (Cd, P,S,Cu, Zn) (+) some (-) (Mn) -	synergistic	Larrsson *et al* (1998)
Brassica juncea	Pot experiment	0.15, 0.35 W m^{-2}	Ce 12 mg/L	-	-	Chlorophyll (-), membrane permeability, SOD, CAT, POD activity (+) -	amelioration	Chanjuan *et al* (2006)
Glycine max	Pot experiment	0.15, 0.45W m^{-2}	Ce 20 mg/L	-	All photosynthetic processes (-)	- -	antagonistic	Chanjuan *et al* (2006)

Negative impact (-), positive effect (+), non significant (ns)

Table 4. Interactive effects of UV-B radiation and water stress along with experimental conditions on different plants

Plant material	Growth Conditions	UV-B dose	Water stress	Result of different parameters				Conclusion	Reference
				Morphological	Growth and physiological	Biochemical	Yield		
Pisum sativum	field study	2.4 kJ m^{-2} d^{-1}	-	Dry weight, height, leaf area, shoot number (+) Number of leaves (-)	Root shoot ratio (+)	Flavonoid and anthocynain (+)	-	No effect	Allen *et al* (1999)
Triticum aestivum	field study	4.25 kJ m^{-2} d^{-1}	15 % field capacity	Flowering, ripening delayed Growth, biomass (-)	Water potential (-) while relative water content (+)	Chlorophyll (-) while MDA and flavonoid (+)	Yield (-)	amelioration	Feng et al (2007)
Pisum sativum Triticum aestivum	Growth chamber	49 kJ m^{-2} d^{-1}	-0.5 MPa	Fresh, Dry weight, height (-)	relative water content (-)	Chlorophyll (-) anthocyanin, phenols, LPO, electrolyte leakage, proline (+) CAT, SOD, H_2O_2 (−)	-	synergistic effect	Alexieva *et al* (2001)
Triticum aestivum	Pot experiment	13.1 kJ m^{-2} day^{-1}	15 % field capacity	-	Water use efficiency, water consumption (-)	-	-	synergistic	Zhao *et al* (2009)
Glycine max	Green house	2.88 kJ m^{-2} day^{-1}	-2 MPa	Plant height, number of nodes, leaves, leaf area and dry weight(-)	SLW, net photosynthesis, stomatal conductance, dark respiration (-)	Chlorophyll a, b (-) UV-B absorbing pigments (+)	-	additive	Teramura *et al* (1984)
Glycine max	Field study	13.6 kJ m^{-2} day^{-1}	-2 MPa	Plant height, leaf area and dry weight (-)	SLW (+), AQE, g_s, photosynthesis and carboxylation efficiency (-)	-	Number of pods, seed number and seed yield (-)	additive	Sullivan and Teramura (1990)
Populus kangdingensis P. cathayana	Pot experiment	4.4 kJ m^{-2} day^{-1}	50% field capacity	Plant height, leaf number and leaf area (-)	Specific leaf mass (−)	UV-B absorbing pigments, proline, SOD, APX, CAT (+)	-	synergistic	Ren *et al* (2007)
Helianthus annuus	Green house	8.6 W m^{-2}		Stem, root, leaf dry weight (-)	Stomatal conductance, transpiration, internal CO_2 and Fv/Fm (-)	Chlorophyll a,b (-) and POD, MDA and proline (+)	-	amelioration	Cechin *et al* (2008)
Qurecus petraea	Controlled chambers	150 µW m^{-2}		-	Water content, Sm, Fv/Fm (-), water potential (−)	Chlorophyll a,b (-) and carotenoids specially lutein (+)	-	amelioration	Meszaros *et al*

Lavandula stoechas Olea europea Rosmarinus officinalis	glass house	24 kJ m^{-2} day^{-1}		Plant height, dry weight, number of leaves, leaf area (-)	RWC, Ψw, Asat, Vc max, Fv/Fm and Φ_{II} (-), stomatal limitation and transpiration (+) SLA, LWR, LAR plant, soil water content (-)	Anthocyanin (−), flavonoid (−) in olive while (-) in other two	-	No interaction	Nogues and Baker (2000)
Salix myrsinifolia	glass house	7.2 kJ m^{-2} day^{-1}	20% field capacity	total biomass and stem height (-)	RSR (+)	-	-	additive effect	Turtola *et al* (2006)
Glycine max	Pot experiment	4.33, 12.8% UV-B	40%, 80 % water volume	-	-	-	yield (-)	antagonistic	Ren *et al.* (2009)
Pisum sativum	Green house	32 kJ m^{-2} day^{-1}	-	Biomass and growth (-)	LAR, RSR, plant water content all (-) photosynthetic (ns)	Anthocyanin and flavonoid contents (+)	-	UV-B radiation delayed effect of water stress	Nogues and Baker (1998)
Cucumis sativus	Growth chamber	16 kJ m^{-2} day^{-1}	40% water holding capacity	Dry weight (-)	Relative water content (-)	SPX, GR, GPX, SOD (+)	-	Synergistic	Kubis and Zajac (2008)
Arabidopsis thaliana	Controlled environment chamber	6 kJ m^{-2} day	-	No significant effect on biomass	Maintained leaf water content	Induction of some proteins	-	amelioration	Schmidt *et al.* (2000)
Quercus petraea	Phytotronic chamber	150 μW m^{-2}	-	-	Chlorophyll fluorescence (+)	xanthophyll cycle (−)	-	synergistic	Szollosi *et al.* (2008)
Hippophae rhamnoides	Green house	+8 kJ m^{-2} day	25 % field capacity	Total dry weight, leaf area (-)	SLA (-), RSR (+)	MDA, electrolyte leakage, proline, anthocyanin (+) , ABA (-)	-	Synergistic	Yang *et al.* (2005)
Triticum aestivum	Controlled environment	3.5 kJ m^{-2} day	- 5.0 MPa	Shoot growth (-)	-	H_2O_2, TBARS, CAT, APX, GPX, SOD,	-	additive effect	Tian and Lei (2007)

Negative impact (-), positive effect (+), non significant (ns)

Table 5. Interactive effects of UV-B radiation and Ozone along with experimental conditions on different plants

Plant material	Growth Conditions	UV-B dose	O_3 dose	Result of different parameters				Conclusion	Reference
				Morphological	Growth and physiological	Biochemical	Yield		
Glycine max	Open top chamber study	35 , 37 % depletion	83 nL L^{-1}	Visible injury reduced	Biomass (ns)	-	yield (ns)	No interaction	Miller et al. (1994)
Arabiodopsis thaliana	Growth chamber	18 kJ $m^{-2}d^{-1}$	200 ppb	Reduced growth	-	Enhanced SOD, GR, APX, POD	-	enhanced oxidative stress	Rao et al. (1996)
Elymus athericus	Growth chamber	16 kJ $m^{-2}d^{-1}$	190 µg m^{-3}	Number of shoots and leaves (-)	Pn (-)	-	-	additive effect	Staaij et al. (1997)
Pinus sylvestris Picea abies	Phytochambers	1.2 kJ $m^{-2}d^{-1}$	43 nL L^{-1}	-	-	POD, CAT, SOD, LPO, ascorbate, glutathione (+)	-	amelioration	Baumbusch et al. (1998)
Pinus sylvestris Picea abies	Growth chamber	1.2 kJ $m^{-2}d^{-1}$	Twice ambient	Visible injury (-)	Pn (-)	-	-	amelioration	Schnitzler et al. (1999)
Pinus sylvestris	Growth chamber	0.8 kJ $m^{-2}d^{-1}$	Twice ambient (52 to 192 nL L^{-1})	Visible injury (+)	-	Secondary metabolites (+)	-	additive	Zinsser et al. (2000)
Triticum aestivum	Field study	+7.6 kJ $m^{-2}d^{-1}$	0.07 µmol mol^{-1}	Biomass (-)	Photosynthesis, chlorophyll, carotenoids (-) anthocyanin , flavonoid (+)	CAT, phenol, POX (+) ascorbic acid (-)	Yield (-)	less than additive	Ambasht and Agrawal (2003)
Linum usitatissimum	Field study	+7. kJ $m^{-2}d^{-1}$	+ 10 ppb	Biomass (-)	-	antioxidants (+), protein profile and DNA showed alterations -	-	less than additive	Tripathi et al. (2011)
Linum usitatissimum	Field study	+7. kJ $m^{-2}d^{-1}$	+ 10 ppb	-	-		Seed yield, seed and oil quality (-)	less than additive	Tripathi and Agrawal (2011)

Negative impact (-), positive effect (+), non significant (ns)

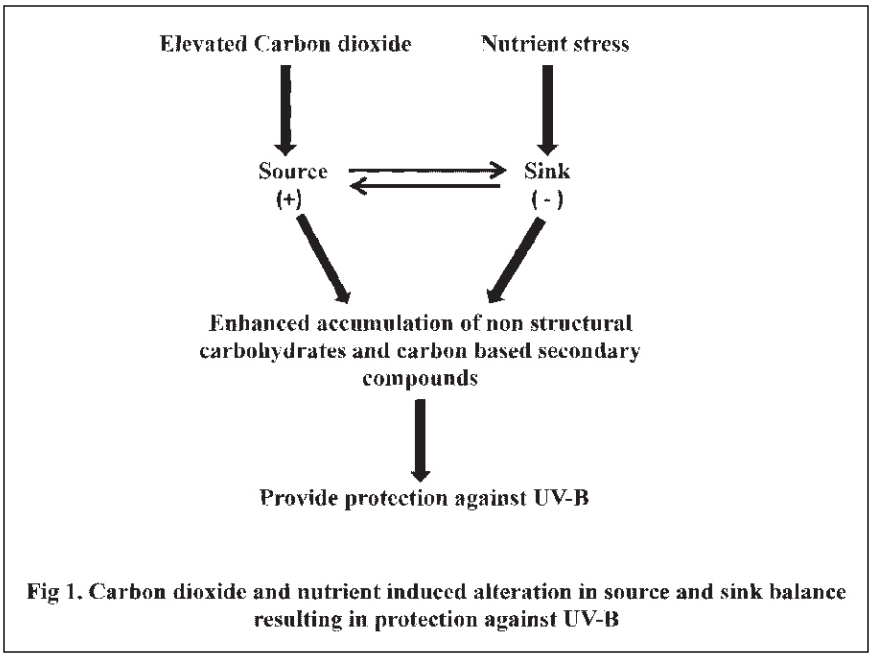

Fig 1. Carbon dioxide and nutrient induced alteration in source and sink balance resulting in protection against UV-B

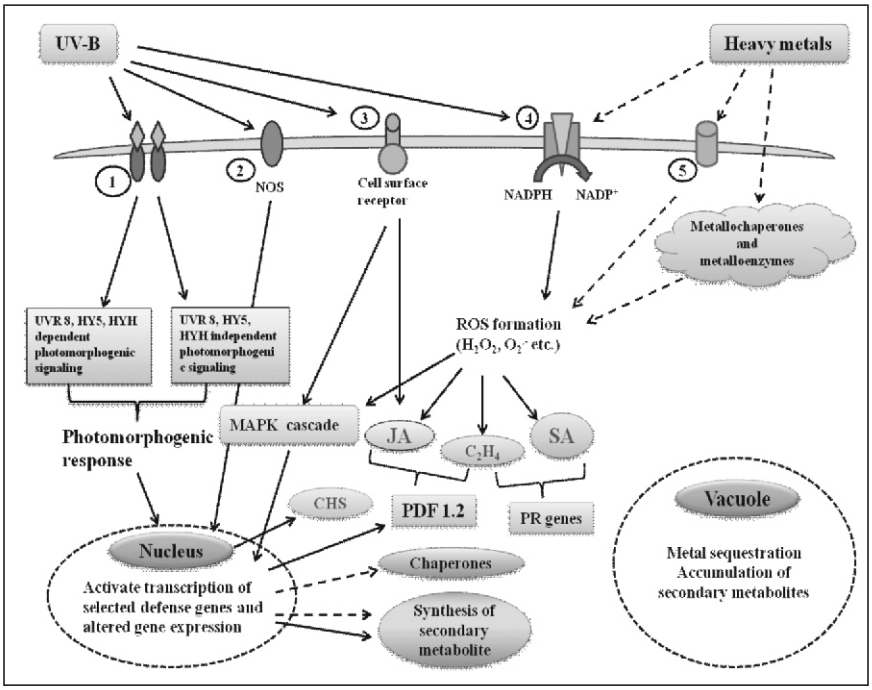

Fig 2. UV-B and heavy metal induced signaling in plant cell.

(Abbreviations; 1. Photoreceptors, 2.Nitric oxide synthase, 4. NADPH oxidase, 5. Oxalate oxidase, UVR 8; UV Resistance Locus 8, HY5; Elongandated hypocotyls, HYH; HY5 Homolog, MAPK; mitogen activated protein kinase, JA; jasmonic acid, SA; salicylic acid, C_2H_4; ethylene, ROS; reactive oxygen species, CHS; chalcone synthase)

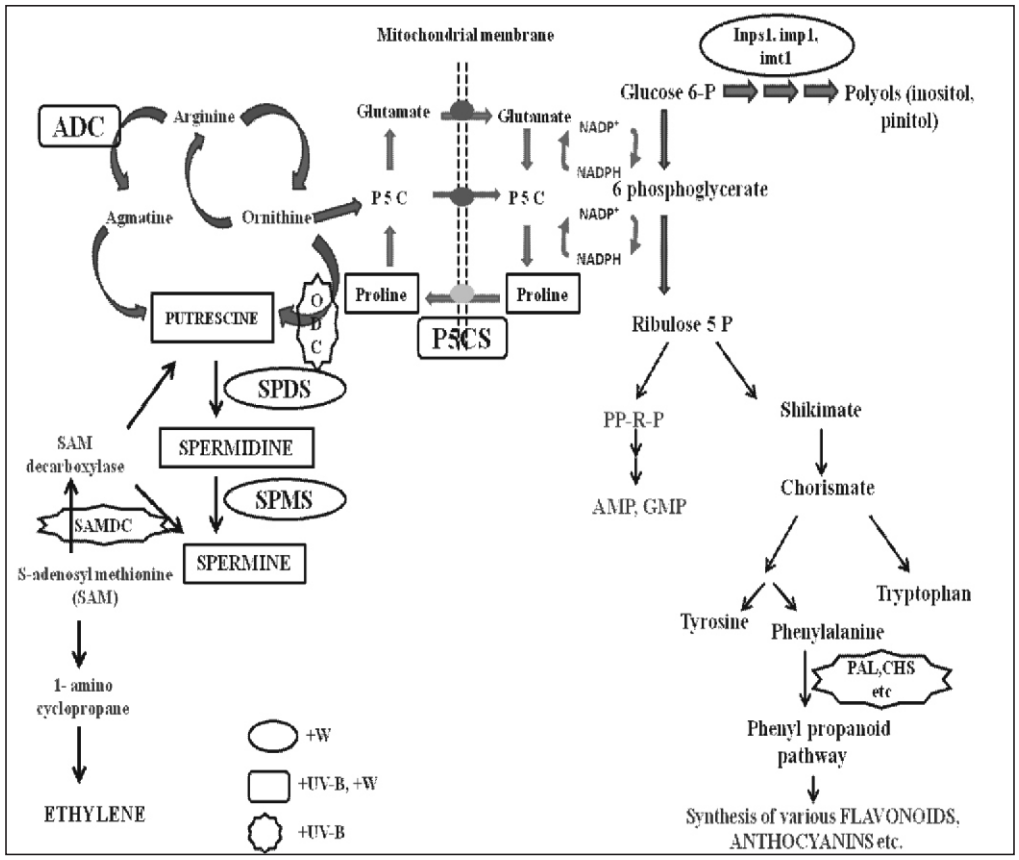

Fig 3. Induction of various enzymes after UV-B and water stress in synthesis of secondary metabolites.

(Abbreviations; SAMDC; S- adenosyl methionine decarboxylase, SPMS; spermine synthase, SPDS; spermidine synthase, P5C, ^{1}-pyrroline-5-carboxylate, P5CS; pyrroline-5-carboxylate synthetase, P5CR; pyrroline-5-carboxylate reductase, PP-R-P; phosphoribosyl pyrophosphatase, inps1; Inositol1-phosphate synthase, imp1, inositol monophosphatase, imt 1; inosititol O-methyltransferase, ADC; arginine decarboxylase, ODC; ornithine decarboxylase, PAL; phenyl alanine ammonia lyase, CHS, chalcone synthase)