Response of Crop Plants to Enhanced UV-B Radiation and Possible Implications on the Rice Crop

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ABSTRACT

Increases in solar UV, particularly UV-B (280-320 nm) waveband, have been observed due to the erosion of the stratospheric ozone layer by gases like chlorofluorocarbons. Ozone depletions of as much as 10% on a global scale and 4% in tropical rice-growing areas have been detected. The consequent increase in UV-B radiation may affect agricultural production in general and rice production in particular. UV-B has been shown to affect growth, photosynthesis, plant pigments, morphology and anatomy of plants, while interspecific and intraspecific differences have been reported.

Much of the research on UV-B in the past decade centered on the physiological and biochemical responses and environmental conditions. Few studies were undertaken under field conditions. Information is still insufficient to assess the risks of UV-B to rice. Results show varietal differences in rice response varying from: stunting; increased silica wax and flavonoid content of leaves; degradation of stomates, etc.. The resulting effect of these changes in the rice plant and the possible venues for the mitigation of and adaptation to the effects of UV-B are discussed.

The stratospheric ozone layer is decreasing at an alarming rate. This is mainly the result of the use of chlorofluorocarbons (CFC), the most common chemical for refrigerants and aerosols. Current estimates of ozone depletion during the next century range between 5 and 9% (**87**). The stratospheric ozone is the primary attenuator of solar ultraviolet radiation. A reduction of the ozone layer results in a very specific increase in shortwave radiation (UV-B, 280-320 nm). Absorption by ozone of shorter wavelengths (UV-C, 200-280 nm) is so great that a small fraction of the present ozone layer is sufficient to block radiation of UV-C. The absorption by ozone of longer wavelengths (UV-A, 320- 400 nm) is so weak that changes in ozone are of no consequence. The main concern, therefore, is the UV-B radiation.

In the rice growing regions of Asia, ozone column thickness has declined to 1-4% over the past 20 years (**140**). The highest UV-B levels at the earth's surface are found in the tropics, where the ozone layer is naturally thinnest and prevailing solar angles are highest. With ozone depletion, UV-B levels in the tropics are expected to exceed those experienced in recent history (**37**).

The most obvious effect of UV-B on human beings is skin cancer. UV-B is also known to cause cataracts and wrinkles on the skin. In plants, a wide variety of responses have been recorded. The biological effects of UV-B on plants have been reviewed by several scientists (**35, 61**). For field crops in particular, the effect of UV-B has been reviewed by Teramura in 1983 (**112**). This review is an update of Teramura's review with emphasis on the implications of enhanced UV-B irradiance on the rice crop, one of the most widely planted crops in the world under diverse environmental situations. Rice is planted in plains and high- altitude areas, under dry and flooded conditions (even in more than two meters of water), using a large and diverse group of cultivars.

This would mean that a wide range of cultivar differences from UV-B irradiance may be expected.

Studies involving the whole range of UV radiation were made in the early thirties and even in the late seventies (**61**). More recent studies indicate very definite responses between UV-B and UV-C so that earlier studies where UV-B and UV-C were not differentiated in the treatments would be difficult to interpret. This review deals mainly with UV-B. To date, very little work has been conducted under field conditions for crop plants,even less on their yield and only a handful on rice. While most of the described UV-B effects were destructive or inhibitory to the plant system, plants also showed nondamaging responses to UV-B. These responses may be a protection from UV damage.

The responses recorded by different workers using different plant species or cultivars are summarized in Table 1 (after Teramura **112**). UV-B radiation affects the photosynthetic processes, through both photosystems I and II, the carboxylating enzymes, stomatal resistance, chlorophyll concentration, soluble leaf proteins,lipids and carbohydrate pools. UV-B radiation has also been shown to affect the anatomy and morphology of the plant, such as plant stunting, reduction in leaf area and increase in leaf thickness. Cell and tissue damage such as chlorosis, bronzing and necrosis also occur in sensitive plants. The best documented effect of UV-B radiation is the stimulation of flavonoid biosynthesis which is thought to be a protective response to the deleterious effects of UV-B. Flavonoids are UV-B-absorbing compounds found in the epidermal layer of plants.

Results of many experiments using a variety of plants definitely show alteration in plant growth and physiological processes with increased levels of UV-B. Generalizations were made in this review. However, one must bear in mind that the UV-B influence rate and dose used varied and that reactions may differ with cultivar, stage of growth and condition of the plants.

A. Physiological and biochemical effects

Photosynthesis. Among species and among cultivars, large differences in response to UV-B irradiation occurred. Nevertheless, the general result is the reduction in net photosynthesis by UV-B radiation through the primary photochemical events and electron transport reactions, the dark reactions fixing carbon into reduced compounds, the dark respiration, stomatal resistance and the attendant CO_2 exchange (Table I). All these can affect the carbon balance of the crops although species and cultivar differences have been reported.

In comparing photosynthetic rates of leaves with similar chronological ages, some caution must be observed. In soybean, UV-B irradiation resulted in earlier attainment of leaf maturity and maximum photosynthetic capacity (**114**). Thus, low photosynthetic rates at later stages of growth may be recorded for plants exposed to UV-B since the peak level has been reached and the plants are senescing when compared to the control plants. The reduction in photosynthetic activity paralleled the decrease in Hill activity, indicating the sensitivity of Photosystem II (PSII) to UV-B radiation (**12, 136**). Although cyclic photophosphorylation (PSI) was also somewhat sensitive to UV-B radiation, the primary effect involved PSII. The net reduction in photosynthesis also coincided with structural damage to the chloroplast. The reduction in photosynthesis with enhanced UV-B was manifested through reduction of photosynthetic pigments, protein and RUPB carboxylase activity (**138**). These led to less growth in UV-B-sensitive crop plants. PEP carboxylase activities in *Zea mays* L. (cv Golden Cross Bantam) have been reported to be suppressed with large dosages of UV-B; they were, however, only enhanced by low dosages (**137**).

Most early studies on the effect of UV on photosynthesis used lights with broader spectrum (**112, 142**). Different wavebands of the UV spectrum have shown different effects so that earlier findings were difficult to interpret and were excluded from this review. However, the studies were cited in Table I.

A reduction in photosynthesis was accompanied by a significant increase in respiration rate. In *Rumex patientia* L., dark respiration rates were significantly higher in UV-B-treated plants (**102**).

Electron micrographs of *Pisum sativum* L. exposed to UV-B radiation indicated structural damage to chloroplasts as well as other organelles (**33**). This was not so in *Rumex patientia* L. where chlorophyll concentration remained unaltered even after 22 days of UV-B treatment (**102**).

The reaction of the rice crop to high UV-B irradiation in terms of net photosynthesis is complicated since growth stages, canopy reactions, levels of visible radiation before and during treatment, cultivar differences and other factors have to be considered. For example, many plant species are more sensitive to UV-B irradiation when grown under low levels of visible radiation (**76, 122**) and this would be the case with the rice crop grown during the wet season (as compared with that grown during the dry season).

In soybean, stomatal conductance was reported to have been increased and, at another stage, to have been decreased by UV-B (**81**). Varietal differences in reaction were noted.

In rice, we found that stomatal resistance increased with enhanced UV-B (**39**). This is partly the result of stomatal closure and the collapse of the stomata especially in UV-B-sensitive cultivars. Stomates of rice plants exposed to UV-B opened later than those in the control plants when returned to normal conditions (**39**). This response may indicate less efficient CO_2 exchange and lower transpiration rates in UV-B-sensitive rice plants. With closed stomates, the attendant higher leaf temperatures and lower CO_2 decrease the photosynthetic rates and eventual biomass production in rice.

Soluble proteins/DNA. UV-B is readily absorbed by nucleic acid and protein chromophores so that these substances are easily damaged by UV-B. Their participation in the plant response to UV-B has been documented (**35, 85, 52**). Our studies showed that total amounts of nucleic acid and soluble proteins were reduced significantly in UV-B-sensitive rice cultivars (Table 2). Studies have also shown that plants have the ability to repair UV-induced DNA damage (**74**).

Carbohydrates. UV-radiation significantly reduced total nonstructural carbohydrates in tomato, cabbage and collard but had no effect on peanut and corn (**50**). Nothing had been reported on rice.

Nonphotosynthetic pigments. Flavonoids in the leaf epidermis selectively filter sunlight so that much of the damaging UV-B radiation is removed while most of the photosynthetically active radiation is transmitted. The increase in the production of flavonoids in the leaf tissue due to UV-B irradiance can reduce the UV-B flux received at potentially sensitive sites such as chloroplasts and nuclei. This may represent an adaptive response to UV-B radiation. Much of the UV-B attenuation on the leaf epidermis was removed upon methanolic extraction of the epidermis, suggesting that phenolic compounds such as flavonoids are important in the absorption of UV-B radiation. Flavonoids are ideal UV screens since they are nearly transparent in the visible region and thus allow PAR while possessing high absorption coefficient in the UV region. Resistant cultivars generally produce more flavonoids with UV-B radiation (**78, 112, 128**). However, in radish seedlings, the increase in flavonoids could not protect them from high UV-B radiation levels (**78**).

Epidermal transmission of UV-B was lowest in plants growing in regions with high, naturally occurring UV-B flux; it then increased as UV-B radiation diminished along a latitudinal gradient (**112**). SInce rice plants are cultivated in such places as Uruguay, South America (35^{0} S latitude), Northeastern China (50^{0} N latitude) and from altitudes below sea level in Kerala, India to above 2000 m in Kashmir (**148**), great variability in response may be expected from this wide ecologial distribution. This aspect requires more extensive investigation.

The results for UV-B-induced anthocyanin formation in corn (**16**) and sorghum (**43**) show that the response of various cultivars may vary considerably within a single species. Large quantities of anthocyanins were found not only in the shoots but also in the roots of corn seedlings (**49**).

Some reports indicate that UV-B irradiation induced flavonoid synthesis and that a blue light photoreceptor may also be involved (**16, 42, 44, 144**). Flavonoid increase in rice leaves has been reported (**39**) and the increase is greater in the tolerant cultivars.

Plant hormones. UV-B treatment of spinach leaves showed lower endogenous gibberellin activities at the period of active growth of the plants (**70**). UV-B had no significant effect on the amount of abscisic acid in *Rumex patientia* L. (**69, 133**).

Ion transport. The amount of ^{65}Zn translocated from the cotyledons of cotton seedlings to the newly developing shoot was twice as great in control seedlings as that in UV-B-treated plants (**3**). In UV-B-treated rice plants, the reduction in electrical conductivity of leaves measured after boiling may be an indirect evidence of ion transport inhibition (**39**). Such an inhibition would affect the nutrition of the rice plant and the subsequent biomass production.

Cellular/chromosome. The rate at which cell division occurs is determined generally by the sequence of DNA replication. Since DNA, RNA and proteins are UV-B chromosomes (**52**), these are likely targets of UV radiation. In *Rumex patientia* L., UV-B primarily affects cell division rather than cell expansion. Less number of cells results in a smaller leaf. The cell size of the palisade and the epidermis are similar in the control and treated plants (**41**).

UV-B increased water permeability in *Allium cepa* (**67**) and the UV- B dose necessary was much higher than those affecting the cytomorphological parameters of the cell. In *Allium cepa*, low dosage of UV-B resulted in plasmolysis, acceleration of protoplasmic streaming and rounding of mitochondria. Higher dosages resulted in decreased protoplasmic streaming, swelling of the endoplasmic reticulum and increased water permeability.

B. Morphological/anatomical effects

Stunting. One of the most commonly observed effects of UV-B radiation on seedling growth is stunting or dwarfing (Table 1). This is primarily due to the decrease in internode length. In cereals, stunting may also be due to shorter leaf blade and leaf sheath since the measure of plant height depends on the length of leaf sheath and blade. The decrease in leaf area is accompanied by a decrease in leaf length.

UV-B-induced growth reductions are associated with changes in cell division and/or cell elongation. An interaction with growth regulator indole-3-acetic-acid (IAA) was demonstrated in hypocotyls of sunflower seedlings. IAA absorbs UV-B and can be converted to various photo-oxidation products (**126**). One of these products, 3-methyl-oxindole, inhibits hypocotyl growth when applied exogenously.

According to Biggs and Kossuth (**19**), rice height was unaffected by UV-B but Basiouny (**11**) reported shorter plant height for variety 'Caloro'. Our preliminary observations showed a wide range of responses by different rice cultivars. Nine out of 30 cultivars had stunting with Amarelao and IR45 showing the greatest reduction while Fujisaka 5, Cafuringa 1 and ROK5 showed the greatest increase in height (**6**).

If UV-B reduces internode elongation, this would be critical for deepwater rice cultivars since internode elongation is necessary for their survival. Deepwater rice is planted in around 20 million hectares, mostly in India, Bangladesh, Thailand and Vietnam. SInce it is the only crop planted during the monsoon season, survival of the crop means survival of the farmer.

Leaf area. Leaves are sensitive to environmental stresses such as low and high temperatures, drought, mineral deficiency and toxicity and excess salt. It is not surprising that UV-B radiation generally reduces leaf area (Table 1). In a growth chamber study using over 70 unrelated crop species and cultivars, it was found that leaf area was significantly reduced in over 60% of the plants (**19**). However, UV-B had little effect on rice and other cereals. In the most sensitive plants, 60-70% reduction in leaf expansion was recorded. Such large reductions were found only in studies utilizing very low PAR (**19**). Under field conditions, leaf expansion was substantially increased by moderate UV-B radiation in rice (**20**). In some species, apparently different responses were obtained among growth chamber-vs-field grown crops. Our preliminary findings showed both decreases and increases in leaf area in 30 rice cultivars (**6**).

Specific leaf weight (SLW). Plants adapt to UV-B radiation by increasing the SLW; the upper leaf tissue layers thus act as anatomical screens or filters. Thicker leaves have a greater proportion of their chloroplasts at greater depths in the leaf tissue and they are better shielded from UV-B radiation. However, increase in SLW did not always correspond with UV-B radiation resistance (**19**). This is to be expected in as much as different species have different or many mechanisms for tolerating UV-B radiation. Therefore, increase in SLW alone cannot be assumed to be an indicator of UV radiation stress. In soybean, visible irradiation during leaf development is important in altering UV-B sensitivity of the photosynthetic system. The thicker leaves produced at high visible irradiation or outside the greenhouses and growth chambers had less damage from subsequent UV-B radiation (**13,32,36,47,102,139**).

Leaf structural characteristics and protective pigment levels, rather than chloroplast characteristics, appear to be responsible for tolerance to UV-B among species and among cultivars. If additional flavonoids can be induced by increased solar UV-B radiation, the sensitivity to UV-B of field-grown plants could be reduced further.

Epidermal transmission/wax content. Attenuation of damaging UV-B radiation (280-320 nm) in the upper epidermis reduces the penetration of UV-B radiation to the mesophyll where damage to physiologically sensitive targets can occur. The epidermis can attenuate up to 95% of the incident UV-B radiation and yet transmit between 70 and 89% of the visible radiation of 400-700 nm (**96**). In *Oenothera stricta*, a high-elevation tropical plant, no significant reduction in epidermal transmittance of visible radiation was observed as a result of UV-B exposure (**96**). The plasticity in epidermal UV-B transmittance results from production of flavonoid and related phenolic compounds in the tissue. After UV-B exposure, the absorbance of UV-B radiation in flavonoid extract solutions from epidermal and mesophyll tissues significantly increased by as much as 100 and 35%, respectively, without reduction in epidermal transmittance of visible radiation.

Most leaf waxes do not absorb within the UV and the visible wavebands and are excellent leaf protectants against microorganisms and water loss. Waxes also enhance light reflectance and scattering. UV-B irradiation increased the total wax on the leaf surface by about 25% in barley, bean and cucumber seedlings (**108**). The aldehydes, detected as minor constituents of the wax, increased twofold, mostly on the adaxial surface on the leaf. The wax layer might be thicker merely as a consequence of smaller leaf area and of constant endogenous wax production.

In the wax biosynthesis of cucumber leaves, the distribution pattern of alkanes was greatly influenced by UV-B irradiation. Short-chain alkanes were increased while long-chain alkanes were depressed (**123**) by UV-B irradiation.

Preliminary studies on rice leaf epidermis using scanning electron microscopes showed that enhanced UV-B treatment tended to increase wax content of the leaves (**40**). Since the UV-B treatment also decreased the leaf area, the increase may be a consequence of the smaller leaf area. The increase in leaf surface wax may be important if increase in temperature accompanies increase in UV-B irradiance.

Leaf bronzing, glazing and chlorosis. According to Teramura's review (**112**), UV-B radiation produces bronzing, scorching, glazing or chlorosis in leaves of susceptible plants such as soybean, pea, cotton and cucumber (Table 1). However, these symptoms are nearly always associated with plants grown under either high UV-B (**128**) or moderate UV-B but low PAR. Scanning electron microscopy of leaf surface showed deformed epidermal structures in plants showing scorching (**128**). Basiouny (**11**) reported leaf necrosis in the rice cultivar 'Caloro'. In field studies with high UV-B supplied by unfiltered lamps, these symptoms have not been reported. Our studies showed no chlorosis in rice cultivars for the levels of treatment used (**39**).

Seedling emergence and growth. UV-B radiation had no effect on the percentage of seed germination in the species tested (**11,63**). This may be due to the inability of UV-B to penetrate the growing media or the seed coat. However, once the seed has germinated, seedling emergence was delayed 2-3 days by UV-B radiation in almost all the species tested (**11**). The cotyledons in some plants emerged late from the seed. Extended UV-B exposure can result in abnormal seedling growth in many species and, consequently, cause short, stubby roots, increased pigmentation and abnormal curvatures of the shoots (**63**). Although germination is not particularly sensitive to UV-B, the developing seedling is extremely sensitive.

Total chlorophyll and chorophyll a/b ratios were reduced in UV-B- irradiated plants during the vegetative stage. In contrast, total chlorophyll was increased by UV-B during the reproductive stage (**121**). Under natural conditions, plants will probably be more sensitive to UV-B during the early stages of growth than at later stages.

No significant changes in chlorophyll content were reported in different cultivars of rice at the seedling stage by the Spad method (**39**) while chlorophyll content by the acetone method increased (Table 2). The effect of UV-B irradiation on the chlorophyll content of rice at the later growth stages is not known.

Biomass production/partitioning. Total biomass represents a long- term integration of all growth processes and subtle effects of UV-B radiation may accumulate and result in significant effects. Unfortunately, most studies on UV-B radiation do not include the root biomass so that one of the effects of UV-B -- which may be in the distribution of the biomass -- is not reflected in the results. Nevertheless, studies showed that the total plant dry weight was often substantially reduced by UV-B radiation (**17,102,112, 133, 135**).

Rice variety 'Caloro' produced less fresh and dry weight per plant and also less ash weight per plant as a result of UV-B irradiation (**11,133**). Our studies in rice showed that in general, total dry weight (which included the root biomass) was reduced by UV-B radiation in 30 cultivars. Marked decreases in shoot weight were observed mostly in IR cultivars. UV-B also induced a shift in biomass partitioning with enhanced allocation to the leaves during the vegetative stage. Reduction in total biomass was not always correlated with reduction in plant height or leaf area, especially in grasses where leaves were oriented vertically rather than horizontally (**9**).

Crop Yield. Ultimately, we are interested in the effect of UV-B irradiation on crop yield or the economic yield of a crop. Very few studies have been conducted under field conditions. Most experiments using crop plants were conducted in growth chambers or in greenhouses and, because of space limitation, the plants were usually not grown to maturity. The crop yield response is the key factor in assessing the impact of partial stratospheric ozone depletion.

Of the 10 crop species tested, yield was unaffected in nine crops despite massive UV-B doses and only a significant reduction in fruit number of pepper was observed in one of two experiments (**54**). In another study using eight crops, only broccoli was affected (**4**); still in another experiment using six crops, no significant effect was reported (**46**). No effect in bean and tomato was reported (**10**) although yield of corn was significantly greater. However, other workers said that corn yield was not affected (**4**, **54**). Until these discrepancies are resolved, the field experiments, to date, are of limited use (**112**).

Studies of Biggs and Kossuth (**20**) showed no effect of low levels of UV-B irradiation on yield of rice and other crops. However, yield was consistently reduced at the highest UV-B enhancement level for all test crops. The possible effect of UV-B irradiation on rice crop yield is difficult to predict since cultivar differences and environment parameters are most diverse in this crop compared with other major crops.

Plant type. Using different models, leaf area indices and leaf angles, it was predicted that penetration of UV-B radiation would be much greater in erect-leaf than in horizontal-leaf canopies (**1**). This simulation has definite implications to the rice plant type -- erect leaves for the modern, high-yielding varieties in contrast to the long and droopy leaves of the traditional varieties. The modern cultivars have a canopy that would be more receptive not only to solar radiation but also to the attendant UV-B radiation. In this case, the deleterious effects of UV-B might be greater.

In developing a rice cultivar tolerant of high UV-B radiation, the different plant traits responsible for tolerance should be incorporated and each trait should be examined independently. This is similar to the development of flood-resistant rice cultivars. Many morphological and physiological factors are involved and as many positive traits as possible should be incorporated.

Most of the rice traits measured in terms of response to enhanced UV-B radiation showed a wide range of cultivar differences, thus selection can be made and breeding for a plant type tolerant of UV-B is possible.

Reproduction. Flowering responses of plants to UV-B irradiance have been reported in several crops. It was found that more flowers were produced when UV-B was excluded by mylar plastic films or glass in *Melilotus* (**60**), *Trifolium dasyphyllum* (**34**) and *Tagetes* (**62**). A clear UV-B fluent rate and fluence-dependent inhibition of photoperiodic flower induction were observed in the long-day *Hyoscyamus niger* (**92**). In contrast, no significant effect was found on the flowering of *Petunia*, on the tassling of maize or on heading of *Sorghum bicolor* (**54**).

In soybean, the transition period between vegetative and reproductive growth was the stage most sensitive to enhanced UV-B radiation (**116**). The time of flowering was delayed by 1-3 days by UV-B radiation in all species tested by Basiouny (**11**). The flowers of UV-B-irradiated plants were smaller, fewer and less vital than flowers of untreated plants.

Specific leaf weight increased during vegetative growth but was unaffected by UV-B during reproductive growth (**116**).

Since UV-B may cause inhibition of elongation, panicle exsertion in the rice plant may also be delayed by UV-B irradiation or panicles may not be fully exserted as a consequence. This would make threshing difficult.

C. Differences in response

Interspecific differences. There are large differences in response to UV-B radiation between genera and species (**19**). Since a variety of responses has been recorded, a combination of morphological, anatomical and physiological processes can easily provide different sensitivities in different species. It has been reported, however, that monocotyledons as a whole seem to be less affected by UV-B than dicotyledons (**111, 128, 132**). This difference might be partially due to the vertical leaf orientation and the basal leaf sheaths which provide protection to the meristematic region in the monocots (**132**). Some broad-leafed species with C_3 type of carbon assimilation were more susceptible to UV-B than the narrow-leafed species with C_4 type of photosynthesis (**12**).

Some plant families like the Cruciferae have many species which are extremely sensitive to UV-B while the Poaceae (a grass family) has relatively resistant species (**19**). Also, alpine species are more resistant than lowland species (**110**). Epidermal transmission of UV-B was lowest in plants growing in regions of high, naturally occurring UV-B flux; it increased as UV-B radiation diminished along a latitudinal gradient.

Variations in plant responses may be the results of changes in microclimate, differences in repair or protection mechanisms, diversity in conditions prevailing during the growing season and stage of plant development.

Intraspecific differences. The more important aspect in the mitigation of UV-B is the large varietal differences in response to UV-B within species (**4, 17, 29, 45, 112, 135**). In cucumber, the intraspecific differences in UV-B sensitivity are related to inherent differences in the accumulation of UV-absorbing compound (**82**). This suggests that there is a potential for genetically modifying future cultivars to minimize the deleterious effects of UV-B or to optimize possible beneficial effects. Biggs and Kossuth (**19**) reported cultivar differences in rice. The reasons for the cultivar variability are not completely understood.

Our studies of four rice cultivars showed cultivar differences in the response of rice to enhance UV-B (**39**). Differences in plant height, leaf area and length, dry weight, as well as in chlorophyll, soluble protein, nucleic acid, flavonoid, silica, root-oxidizing activity and ion concentration in the leaves were observed (Table 2).

D. Environmental interactions

Visible radiation. The greatest differences in total dry matter production resulting from UV-B radiation were found in moderately shaded conditions for soybean but in full sunlight for wheat (**111**). The study emphasized the importance of the interaction between UV-B and PAR and the need to measure PAR to critically evaluate the effects of UV-B radiation on plant growth under natural conditions.

Leaves that developed under reletively low visible radiation (as in cloudy weather) are generally thinner and are, therefore, more susceptible to inhibition of photosynthesis by UV-B radiation (**76, 133, 139**). The implication is if the visible radiation is low during UV-B irradiation, this will result in greater photosynthetic depression than when visible irradiation is high. However, radiation during pretreatment can play a larger role in altering UV-B sensitivity of photosynthesis than the visible flux applied during the UV-B irradiation, as found in soybean (**139**). High visible flux given concomitantly with UV-B after low visible radiation treatment resulted in greater photosynthetic depression than when low visible flux was presented with the UV-B irradiation. High visible flux alone resulted in no detectable photosynthesis inhibition.

During the monsoon season, the rice plant may be subjected to a week of low visible irradiation followed by high visible irradiation concomitant with high UV-B irradiation. The damage from UV-B to the new leaves formed, which are thinner, is expected to be higher, based on the findings in soybean.

Water stress. UV-B had no effect on the internal water relations of soybean (**118**). However, in *Allium cepa,* UV-B increased water permeability in the cell (**67**) through membrane lipid and plasmalemma breakdown.

In soybean, the intraspecific response differences in UV-B treatments between two seasons of planting were thought to be related to the frequency of drought and overcast skies (**81**). In another study, increased levels of UV-B in soybean had no effect on leaf area, total plant dry weight and net photosynthesis in plants subjected to water stress (**80**). The insensitivity may be related to anatomical and biochemical changes induced by water stress, such as increase in the concentration of UV-B-absorbing compounds in the leaves and leaf thickening, both of which can lessen UV-B penetration to the photosynthetic system.

Water deficit in rice plants is common in upland and rainfed lowland rice. There is, therefore, a need for intensive research on the effect of enhanced UV-B irradiance on the water relations of the rice plant.

Ecology/competition. Predicted penetration of UV-B radiation was much greater in erect-leaf than in horizontal-leaf canopies. This finding would indicate that the modern, high-yielding rice cultivars with erect leaves would have UV-B radiation penetrating down to the lower leaves. Whether the lower leaves are more sensitive or not would also determine the effect of UV-B radiation. The lower, more mature rice leaves have lower photosynthetic rates (**149**) and the effect of UV-B may not be as critical.

In pine, the effects of enhanced UV-B were less for those species indigenous to higher elevations, implying the presence of natural adaptations to UV-B (**110**).

Competitive interaction studies show that smaller species usually benefited under UV-B stress, presumably as a result of relatively reduced UV-B flux in the shade of the taller species (**53**). In many communities, complex species interrelationships invalidate the concept of discrete, competing species pairs. However, a ricefield with serious infestation of broad-leaf weeds may show greater damage to the rice crop than to the broad-leaf weeds. The possible stunting of the rice crop, a general effect on all cultivars so far (**39**), and the reduction of UV-B flux to the weeds by the relatively taller rice plants will probably result in greater domination of the weed species especially those less sensitive to UV-B.

UV-B has shown deleterious effects on the morphology, anatomy and physiology of the rice plants. However, cultivar differences were noted and this provides strong indications of mitigating the effect of elevated UV-B in the future.

Table1. Summary of the effects of UV-B radiation on crop growth (Modified from Teramura 1983)

	References
Physiological/biochemical effects	
Photosynthesis	2, 7, 12, 17, 18, 21, 33, 37, 47, 71, 76, 78, 80, 81, 90, 96, 100, 101, 102, 103, 104, 112, 113, 114, 117, 121, 122, 125, 133, 136, 139
Hill reaction	2, 12, 33, 50, 65, 73, 90, 136
Electron transport	33, 58, 65, 90, 93, 94
RuBP carboxylase	2, 25, 50, 76, 130, 137, 138
PEP carboxylase	2, 137
Dark respiration	21, 33, 102, 117, 121
Transpiration/stomatal resistance	17, 18, 21, 33, 47, 76, 80, 81, 88, 89, 101, 102, 112, 113, 117, 118, 120, 121, 122
Photosynthetic pigments	2, 12, 24, 33, 50, 57, 70, 76, 80, 81, 90, 101, 102, 114, 121, 122, 125, 128, 136, 138, 139
Soluble proteins/DNA	2, 12, 14, 15, 35, 47, 49, 59, 74, 84, 86, 91, 98, 105, 127, 128, 131, 134, 137, 138, 142
Lipids	46, 72, 107, 112, 128, 129
Carbohydrates	3, 4, 46, 50, 112
Nonphotosynthetic pigments	5, 7, 14, 15, 16, 24, 36, 37, 42, 43, 44, 47, 49, 55, 56, 57, 68, 71, 74, 75, 76, 77, 78, 80, 82, 84, 90, 96, 97, 100, 113, 114, 122, 127, 128, 136, 138, 139, 142, 143, 144, 145, 147
Plant hormones	23, 25, 37, 69, 70
Ion transport	3, 93
Cellular/chromosome	2, 38, 41, 61, 67, 80, 134

Table 1. Cont . . .

Morphological/anatomical effects	
Stunting	2, 8, 11, 12, 29, 48, 79, 80, 82, 110, 112 115, 116, 122, 124, 135, 136, 138, 142
Leaf area	2, 8, 21, 28, 29, 41, 48, 66, 68, 70, 76, 80, 81, 82, 84, 100, 102, 103, 111, 112, 114, 115, 116, 121, 122, 128, 135
Specific leaf weight	7, 29, 47, 66, 76, 80, 82, 84, 112, 114, 116, 121, 139
Epidermal transmision/wax content	1, 22, 47, 51, 74, 96, 97, 104, 108, 109, 123
Bronzing/glazing/chlorosis	2, 17, 28, 29, 55, 63, 95, 117, 128
Growth stages	11, 55, 61, 63, 81, 106
Biomass production/partitioning	8, 9, 11, 12, 17, 19, 20, 21, 28, 29, 33, 48, 53, 66, 70, 72, 79, 80, 82, 84, 100, 102, 106, 110, 111, 112, 113, 115, 116, 121, 122, 124, 133, 135, 136
Crop yield	20, 30, 70, 112, 115, 119, 122
Plant type	1, 141
Reproduction	11, 20, 26, 27, 37, 116, 122
Response differences	
Interspecific (species differences)	2, 8, 11, 12, 19, 20, 28, 50, 63, 79, 110, 112, 113, 128, 133, 135, 137
Intraspecific (cultivar differences)	16, 28, 29, 64, 71, 82, 84, 112, 113, 115
Environmental interactions	
Visible radiation	7, 10, 29, 48, 76, 102, 111, 113, 117, 122, 133, 139, 146
Water stress/microclimate	67, 76, 80, 81, 113, 116, 118, 120, 121, 122, 127
Ecology/competition	1, 7, 8, 9, 18, 37, 48, 53, 96, 99, 110, 122, 133
Mineral stress	31, 83, 113, 122

Table 2. Physiological changes of rice in response to enhanced UV-B treatment for 4 weeks. Each value is average of 24 plants (39).

Parameter	Cultivar			
	IR30	IR45	IR64	IR74
Plant height (cm)	-*	-*	-*	-*
Maximum root length (cm/plant)	-	+	-	-
Root volume (cm^3/plant)	+	-	-	-**
Tillers (no./plant)	+	-	+	-**
Leaf area (cm^2/plant)	-	-*	-	-**
Leaf dry weight (g/plant)	-	-*	-	-**
Sheath dry weight (g/plant)	-*	-*	-	-**
Root dry weight (g/plant)	-	-*	-*	-**
Shoot dry weight (g/plant)	-*	-*	-	-**
Dry weight (g/plant)	-	-*	-	-**
Specific leaf weight (g/m^2)	+	-	+*	+
Relative growth rate (mg/g/d)	-	-*	-*	-**
Net assimilation rate ($g/m^2/d$)	-*	-**	+*	-*
Shoot/root ratio	+	-	+	+**
Chlorophyll content (mg/g fresh weight)	+*	+	+*	+
Root activity (mg α-naphthylamine/h/g)	-*	-*	-*	-*
Soluble protein (mg/g fresh weight)	-**	-*	-*	-**
Nucleic acid (g/g fresh weight)	-	-*	-	-*

*, ** Significant at the 0.05, and 0.01 levels, respectively, according to Student's T-test.

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