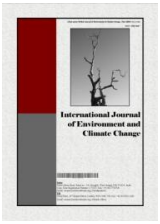

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Changes in Morpho-physiological and Yield Parameters of Rice (*Oryza sativa* L.) in Response to Ultraviolet-B (UV-B) Radiation

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Authors' contributions

This work was carried out in collaboration between both authors. Author YSW conducted the research work, interpreted the data and prepared the manuscript. Author KBN provided the guidance for conducting the experiment and critically reviewed the manuscript. Both authors read and approved the final manuscript.

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ABSTRACT

A rice variety Jyothi (PTB 39) is a red kernelled with bold grain, popular in the region of Kerala, India used in the study. Plants were grown in pots under three different conditions, natural solar UV-B conditions, UV-B excluded condition using UV-B filters and supplemental UV-B using UV-B lamps along with ambient solar radiation. During the study period, UV-B radiation was in the range of 1.30 to 3.58 Wm^2 which affected the productivity of the crop under open solar condition. A decrease in morphological traits like plant height, number of tillers, flag leaf angle and increase in leaf thickness were observed. Physiological parameters, leaf gas exchange parameters and biochemical constituents such as chlorophyll content also recorded less value under high UV-B condition along with the high content of protective compounds such as flavonoid content, catalase and PAL activity. The phenophases of the crop were also delayed by 4-5 days under UV-B

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radiation exposed conditions. All these negative impacts of UV-B radiation on crop leads to restricted filling of grain, lesser harvest index and grain development leading to a decrease in yield and yield attributing characters.

Keywords: UV-B radiation; rice; morphology; phenology; photosynthesis; Canopy Temperature Depression (CTD); flavonoid; yield.

1. INTRODUCTION

The solar radiation reaches to earth's surface is mainly divided into two main spectra i.e. photosynthetically active radiation (PAR) (400 to 700 nm) and Ultraviolet radiation (UV) (100 to 400 nm). UV radiation contains three groups of radiation UV-C (100 to 280), UV-B (280 to 320 nm) and UV-A (320 to 400 nm). Among these, the UV-B region is selectively attenuated by the stratospheric ozone layer [1]. In contrast, the UV-A and PAR radiation are affected by light scattering. The most biologically damaging wavelength UV-C is absorbed almost completely by the atmosphere and therefore, not a significant factor for biological processes under natural conditions [2]. A decrease in stratospheric ozone layer due to man-made ozone-depleting pollutants, such as halogenated hydrocarbon and other chemicals could lead to a significant increase in incoming ultraviolet-B (UV-B) radiation (280-320 nm) and shift in the spectral ultraviolet (UV) radiation composition reaching the surface of the earth [3-5]. In spite of the current global efforts going on to restrict the manufacture and use of ozone-depleting substances, increase perforation of UV-B radiation to the earth's surface will continue for decades [6-8].

UV-B can influence plant processes either through direct damage or *via.* various regulatory effects [9-11]. It has considerable consequences including anatomy, morphology, physiology, biochemistry, phenology and yield and these responses vary markedly within and between species [12-14]. The intraspecific variation to enhanced or supplemental UV-B radiation in terms of morphological parameters has been determined in many important crop species, such as barley [15,16], maize [17,18], wheat [19,20], rice [21,22] cucumber [23], pea [14], Amaranthus [24] and soybean [25-27]. The structure of the photosynthetic apparatus is the major UV-B target among all the plant systems. Impacts on a wide number of photosynthetic components have been reported such as the decline in chlorophyll synthesis, the inactivation of oxygen evolution, LHCII, photosystem (PSII) reaction center and thylakoid electron flux, would contribute to a reduction in photosynthesis and yield [21,28-30].

About 3 billion population in Asia is mostly dependent on rice [31]. Rice is grown in tropical regions, where it is known that UV-B radiation is highest because the solar angles are higher and the stratospheric ozone layer is high latitudes, which consists mostly of developing countries. In the previous decade, many studies showed that the enhanced UV-B radiation causes a momentous reduction in the total biomass in several rice cultivars, along with a reduction in tiller number and photosynthetic capacity of plants [32-34]. UV-B radiation also cause changes in the ultrastructure of the leaf of rice crop, which included an increased thickness of the leaf, reduced intracellular spaces and destruction of chloroplast [35]. A study showed that the yield and yield attributes such as tiller number, dry mass, panicle number, grain yield and grain size were significantly reduced under elevated UV-B radiation [36]. The inference from these studies and reviews is that rice and other crop plants are sensitive to UV-B radiation. Therefore, the present study was conducted to understand the effect of UV-B radiation on morpho-physiological and yield in rice (*Oryza sativa* L.).

2. MATERIALS AND METHODS

2.1 Plant Materials and Growth Conditions

A rice variety Jyothi was grown in pots under three different conditions; i) natural solar condition (T_1) ii) reduced UV-B condition (T_2) and iii) enhanced UV-B condition (T_3) during December, 2014 to April, 2015. Plants under treatment T_2 and T_3 were grown under polyhouse conditions where polyhouse cladded with a polyester filter which excludes spectrum UV-B and another compartment of polyhouse covered by polyethylene sheet which transmits spectrum UV-B respectively. In T_3 condition, UV-B fluorescent tubes (230 nm to 312 nm; TL-D18W/52 2G- Made in Holland) were installed to enhance UV-B radiation effect. These tubes were

fixed on an adjustable frame and the distance maintained from plant canopy was 30 cm. The lamps were switched on from 10 am to 2 pm daily (4 hrs. daily). The UV-B radiation inside and outside of polyhouse was measured using the UV-B meter (Model-PMA2200 Single-Input Radiometer, Solar Light Company, Inc. USA) daily throughout the growing period (between 10 am to 4 pm at 2 hr interval) and expressed as Wm^{-2}.

2.2 Growth Data Collection

The growth data was recorded at tillering and flowering stage of the crop. The plant height was measured from ground level to tip of the longest leaf of the plant and expressed in centimeter. Leaf thickness was recorded as leaf dry weight per unit leaf area and expressed in mg/cm^2 at both tillering and flowering stages [37]. Flag leaf angle was measured near the collar as the angle of attachment between the flag leaf blade and the main panicle axis using protractor vertically at flowering stage of the crop [37] and is measured in degrees. Phenophases of plants which are; day to heading, days to 50% flowering and days to harvestable maturity were recorded after transplanting at respective growth phases of the crop.

2.3 Leaf Gas Exchange Parameters and Canopy Temperature Depression (CTD)

To measure leaf gas exchange parameters such as photosynthesis rate, stomatal conductance and transpiration rate, portable photosynthesis system (Model - LI-6400 of ICOR inc. Lincoln, Nebraska, USA) was used. Canopy Temperature Depression (CTD) was measured using an infrared thermometer (Model-6110L AGRITHERM III^{TM} by Everest Interscience INC. Tuscon, USA). Leaf gas exchange and CTD measurements were taken in the morning from 09-11 am at tillering and flowering.

2.4 Biochemical Analysis

The chlorophyll pigments were estimated using DMSO (Dimethyl sulphoxide) [38]. Flavanoids were extracted and quantified with 80% acidified methanol (methanol:water: HCl 79:20:1) for 12 hours in dark [39]. Catalase (EC 1.11.1.6) activity was assessed by using the titration method against 0.01 M $KMnO_4$ [40]. Phenylalanine ammonia lyase (PAL) (EC 4.3.1.24) was determined by the method suggested by Bruseke [41]. All the biochemical analysis was done at tillering and the flowering stage.

2.5 Yield-related Parameters

Yield-related parameters such as panicle length, number of panicles per plant, number of spikelets per panicle, filled grain per panicle, spikelet sterility, 1000 grain weight and harvest index (HI) were measured after harvest of the crop.

3. RESULTS

3.1 UV-B Analysis

The daily observation recorded at 2 hr interval from 10 am to 4 pm during the growth period (Dec. to April) of crop showed a maximum value of UV-B at 12 noon during March (3.581 Wm^{-2}) and a minimum of 2.822 Wm^{-2} during April in T_1 condition. The lowest value of UV-B radiation ranged from 1.304 Wm^{-2} to 1.671 Wm^{-2} at 4 pm in all the months observed in open condition. Variation in UV-B radiation from 10 am to 4 pm was significant in all the months throughout the growing period (Table 1).

3.2 Morphological and Phenological Characters of the Crop

The mean plant height of the crop was significantly higher under T_2 condition at the tillering stage (54.400 cm) and flowering stage (105.286 cm) (Table 2). The lowest plant height was recorded (30.667 cm) at the tillering stage and flowering stage (78.357 cm) under conditions T_3 and T_1 respectively (Table 2). A number of tillers were significantly higher in UV-B free condition (T_2) at tillering stage (8.871 per plant) and lesser in a solar natural condition (T_1) (7.243 per plant) (Table 2). However, at the flowering stage, the number of tillers was non-significant. There was no significant variation in leaf thickness at the tillering stage but at flowering stage treatment T_1 (5.200 mg/m^2) showed significantly higher value and the treatment T_2 (4.271mg/cm^2) showed the minimum value (Table 2). The flag leaf angle was significantly wider under UV-B excluded condition (T_2) than natural solar (T_1) and supplementary UV-B (T_3) conditions by 112% and 68% respectively (Table 3).

Natural solar condition (T_1) took significantly more number of days to accomplish their phenophases such as days to heading, days to 50% flowering and days to harvestable maturity than condition T_2 and T_3 (Table 3). However, condition T_2 and T_3 were not significant (Table 3).

Table 1. Data on UV-B radiation has taken at different treatments and different time throughout the growing period of the crop

December	10 am	12 noon	2 pm	4 pm
T_1	2.4503	3.2483	2.6822	1.3036
T_2	0	0	0	0
T_3	0.1187	0.1726	0.1301	0.0511
t-Value	22.246	88.592	15.335	14.115
January				
T_1	2.0994	3.2913	2.7056	1.3331
T_2	0	0	0	0
T_3	0.1319	0.1960	0.1620	0.0693
t-Value	29.403	25.867	13.989	17.536
February				
T_1	1.9579	3.0207	2.8594	1.44469
T_2	0	0	0	0
T_3	0.1270	0.1872	0.1519	0.0721
t-Value	16.763	14.920	17.060	20.290
March				
T_1	2.1895	3.5811	3.2416	1.6714
T_2	0	0	0	0
T_3	0.1599	0.2555	0.1842	0.0814
t-Value	24.027	29.516	28.917	29.007
April				
T_1	1.7421	2.8220	2.5218	1.3407
T_2	0	0	0	0
T_3	0.1749	0.2770	0.2008	0.0863
t-Value	7.930	9.481	9.288	25.387

Table 2. Mean plant height (cm), number of tillers per plant and leaf thickness (mg/cm^2) at different UV-B levels. (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

	Tillering stage		
	Plant height (cm)	**No. of Tillers/ plant**	**Leaf thickness (mg/cm^2)**
T_1	38.271	7.243	4.971
T_2	54.400	8.871	4.514
T_3	30.657	7.871	4.671
CD (0.05)	3.667	1.112	NS
	Flowering stage		
	Plant height (cm)	**No. of Tillers/ plant**	**Leaf thickness (mg/cm^2)**
T_1	78.357	27.286	5.200
T_2	105.286	25.857	4.271
T_3	100.257	24.143	4.529
CD (0.05)	13.428	NS	0.740

Table 3. Mean data on flag leaf angle (°), Days to heading, Days to 50% flowering and Days to harvestable maturity at different UV-B levels. (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

	Flag leaf angle (°)	Days to heading	Days to 50% flowering	Days to harvestable maturity
T_1	12.455	69.971	76.971	106.971
T_2	26.427	65.514	72.514	102.514
T_3	15.710	65.229	72.229	102.229
CD (0.05)	4.656	2.911	2.911	2.911

Table 4. Mean photosynthetic rate (µmol CO_2 $m^{-2}s^{-1}$), Stomatal conductance (mol H_2O $m^{-2}s^{-1}$), Transpiration rate (mmol H_2O $m^{-2}s^{-1}$) and CTD (°C) of rice under different UV-B levels. (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

	Tillering stage			
	PN. Rate (µ mol $CO_2m^{-2}s^{-1}$)	Stoml. Cond. (mol H_2O $m^{-2}s^{-1}$)	Trasp. Rate (mmol $H_2Om^{-2}s^{-1}$)	CTD (°C)
T_1	31.100	0.382	4.304	-1.774
T_2	36.174	0.568	4.760	-3.212
T_3	22.225	0.260	3.562	-1.787
CD (0.05)	3.921	0.136	0.567	0.428
	Flowering stage			
	PN. Rate (µ mol $CO_2m^{-2}s^{-1}$)	Stoml. Cond. (mol H_2O $m^{-2}s^{-1}$)	Trasp. Rate (mmol $H_2Om^{-2}s^{-1}$)	CTD (°C)
T_1	27.600	0.367	4.284	-3.157
T_2	28.923	0.424	4.420	-3.229
T_3	26.571	0.341	3.700	-1.929
CD (0.05)	1.834	0.057	NS	0.866

Table 5. Mean Chlorophyll "a" (mg g^{-1} FW.), Chlorophyll "b" (mg g^{-1} FW), Total chlorophyll (mg g^{-1} FW), Flavanoid (A_{300} g^{-1} FW), Catalase (1µ mol of H_2O_2 per min g^{-1} FW) and PAL (µmol t-cinnamic g^{-1} FW) of rice under different UV-B levels. (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

	Tillering stage					
	Chl 'a'	Chl 'b'	Total chl	Flavonoid	Catalase	PAL
T_1	2.729	0.802	3.564	44.268	10.220	1.041
T_2	2.877	0.981	3.824	41.446	7.791	0.621
T_3	2.494	0.931	3.476	43.328	7.893	0.633
CD (0.05)	NS	NS	NS	NS	1.507	0.087
	Flowering stage					
	Chl 'a'	Chl 'b'	Total chl	Flavonoid	Catalase	PAL
T_1	1.597	0.731	2.609	57.535	26.558	0.595
T_2	2.085	0.542	2.630	48.218	10.625	0.137
T_3	1.880	0.389	1.981	50.654	13.357	0.412
CD (0.05)	0.353	0.234	0.318	2.436	2.498	0.119

Table 6. Mean number of panicle per hill, Panicle length(cm), Number of spikelets per panicle, Filled grain per panicle and spikelet sterility (%), Grain yield (g), 1000 grain weight (g) and Harvest index (%)of rice under different UV-B levels. (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

	Panicle no/ hill	Panicle length (cm)	No. of Spikelets / Panicle	Filled grain/ Panicle	Sterile grain (%)/ Panicle	Grain Yield (Gm)	1000 grain weight (Gm)	Harvest Index
T_1	17.557	18.359	54.949	17.866	67.208	8.914	22.974	6.831
T_2	15.629	22.147	118.840	98.900	16.956	84.194	25.429	48.607
T_3	15.386	21.230	99.053	78.449	20.980	80.714	24.189	47.654
CD (0.05)	1.510	0.922	15.631	14.395	5.837	11.361	1.723	4.111

3.3 Physiological Characters of the Crop

UV-B excluded condition (T_2) recorded 16% significantly higher photosynthetic rate than open solar condition (T_1) and 62% higher value than UV-B supplemented condition (T_3) at the tillering stage (Table 4). Stomatal conductance also recorded significantly higher value in T_2 condition by 49% and 118% under T_1 and T_3 conditions respectively at the tillering stage (Table 4). A similar trend was seen at the flowering stage where photosynthesis rate and stomatal conductance recorded higher values under T_2 condition (28.923 µmol CO_2 $m^{-2}s^{-1}$ and 0.424 mol H_2O $m^{-2}s^{-1}$ respectively) and lower values at T_3 condition (26.571 µmol CO_2 $m^{-2}s^{-1}$ and 0.341 mol H_2O $m^{-2}s^{-1}$ respectively) (Table 4).

At tillering stage UV-B free condition (T_2) showed a significantly higher level of transpiration rate (4.760 mmol H_2O $m^{-2}s^{-1}$). But the lower transpiration rate was recorded (3.562 mmol H_2O $m^{-2}s^{-1}$) when the crop was subjected to the supplementary UV-B lamp (T_3) (Table 4). However, at the flowering stage transpiration rate was non-significant. Condition T_2 recorded significantly higher CTD than the rest of the conditions at both growing stages i.e. -3.212°C and -3.229°C respectively. But at the tillering stage, lower CTD was found under T_1 condition (-1.774 °C) and at the flowering stage under T_3 condition (-1.929 °C) (Table 4).

3.4 Biochemical Characters of the Crop

Chlorophyll pigments were not significantly affected due to UV-B radiation at the tillering stage. However, at the flowering stage, T_2 condition showed considerably higher chlorophyll "a" content by 30.5% and 11% than the rest of the two conditions (T_1 and T_3). Chlorophyll "b" content was higher under natural solar condition by (T_1) 35% and 88% than UV-B excluding condition (T_2) and UV-B supplementary condition (T_3) respectively (Table 5). Total chlorophyll content found significantly higher under T_2 (2.630 mg g^{-1} FW) than T_3 condition (1.981 mg g^{-1} FW) but there was not much difference noticed when compared to T_1 condition (2.609 mg g^{-1} FW) (Table 5). Flavonoid content had no such effect during the tillering stage but there was highly significant variation during the flowering stage, where high flavonoid content was recorded in condition T_1 (57.535 A_{300} g^{-1} FW) followed by T_3 (50.654 A_{300} g^{-1} FW) and the least value was recorded in condition T_2 (48.218 A_{300} g^{-1} FW) (Table 5).

Enzyme activities of catalase and PAL were significantly higher in natural solar condition at both growing stages. At the tillering, stage, catalase activity was found higher in T_1 (10.220 1 µmol of H_2O_2 per min g^{-1} FW) than the rest of the conditions by 31% and 29% in T_2 and T_3 respectively (Table 5). The same trend was observed at flowering where catalase activity was higher by 150% and 99% in T_2 and T_3 respectively (Table 5). Like catalase activity, PAL activity was also higher under T_1 condition than T_2 (68%) and T_3 (64%) conditions at tillering stage and at flowering stage (334% and 44%) respectively (Table 5).

3.5 Yield and Yield-related Parameters

A significantly higher number of panicles were recorded under open solar condition (T_1) (17.557 panicles per hill) than the rest of the conditions (Table 6). The length of the panicle was recorded significantly higher under UV-B excluded condition (T_2) (22.147 cm) (Table 6). The number of panicles recorded was significantly higher in T_1 condition (17.557 per plant) than the remaining conditions (T_2- 15.629 per plant and T_3- 15.386 per plant) (Table 6). The number of spikelets per panicle and filled grains per panicle were found significantly higher in plants where UV-B was excluded (T_2) (118.840 per panicle and 98.90 per panicle) respectively. However, the lowest values were recorded in open natural solar condition (T_1) (54.949 per panicle and 17.866 per panicle respectively). The percentage of sterile grains was also found higher in natural solar condition (69.208% per panicle) and lesser in plants which not subjected to UV-B (T_2- 16.956% per panicle) (Table 6). Grain yield was very high in a condition where the crop was grown in UV-B free condition as compared to natural solar and supplementary UV-B condition (Table 6). Thousand (1000) grain weight was higher along with harvest index under UV-B excluded condition (T_2), 25.429 gm and 48.607 respectively than solar open condition (T_1) and supplementary UV-B condition (Table 6).

4. DISCUSSION

4.1 UV-B Radiation Measurements

The present investigation shows that during the study period ambient UV-B radiation was 2.822 to 3.580 Wm^{-2} (Table 1), which had a negative effect on rice crop growth, physiology and yield. A similar effect was reported in other rice varieties when they exposed to 4 Wm^{-2} UV-B radiation [42].

4.2 Morphological Characters Influenced by UV-B Radiation

UV-B radiation induces many morphogenic changes, such as inhibition of hypocotyls, stem and leaf expansion, reduction in growth along the adaxial-abaxial axes [43]. Our result showed that ambient UV-B radiation has affected the growth and development of rice as indicated by lesser plant height and reduced tiller number (Table 1). Similarly reduced plant height by 5% and the tiller number by 25% was observed in rice at the ambient level of UV-B radiation [34]. Many studies have indicated that an increase in leaf thickness is typically a UV-B induced response [43,44]. In *Indigofera tinctoria* L. seedlings, the leaf thickness was observed to increase with increasing time of exposure to UV-B radiation treatment [45]. The present study also corroborated this inference that leaf thickness increased under an open solar condition that received more UV-B radiation.

In rice, the flag leaf angle has an important effect on rice yield. Modification of flag leaf angle has been emphasized as a means of obtaining better light utilization with more upright leaf permitting penetration of solar energy into lower leaves. For enhancing grain yield in rice, flag leaf angle must be wider and vertical [46]. The observations taken at 50% flowering stage showed that the flag leaf was very erect under T_1 and T_3 conditions as they might have received low relative light intensity. However, T_2 condition had a better horizontal inclination. Both steeper leaf angle and increased wider angle i.e. self-shading leaf angle might have reduced the potential carbon gain by decreasing total light penetration which resulted in reduced yield (Fig. 1).

4.3 Phenological Characters Influenced by UV-B Radiation

The result of the present study indicates that the UV-B radiation alters the phenophases such as days to heading, days to 50% flowering and days to harvestable maturity and also it prolongs the time to achieve the respective growth phases under natural solar condition (T_1) than UV-B excluded condition (T_2). The delay might have been due to the increased sensitivity of plants to UV-B damage which resulted in their reduced growth *via.* lesser photosynthesis rate. At the tillering, stage the photosynthesis rate was more under the T_2 condition when compared to the flowering stage (Table 4). This higher photosynthetic rate at the vegetative stage could be attributed to the difference in photoassimilates accumulation to attain sufficient physiological maturity for flowering and other phenophases of growth. A similar finding such as delay in achieving growth phases like flowering was reported in crops like bush bean and green gram under high UV-B radiation [47,48]. In pea crop, the flowering was delayed by 2-5 days when exposed to UV-B [14]. Sikuku et al*.* [49] also reported that environmental stresses to plants took a longer time for flowering and to mature as compared to a crop grown under optimum growth conditions.

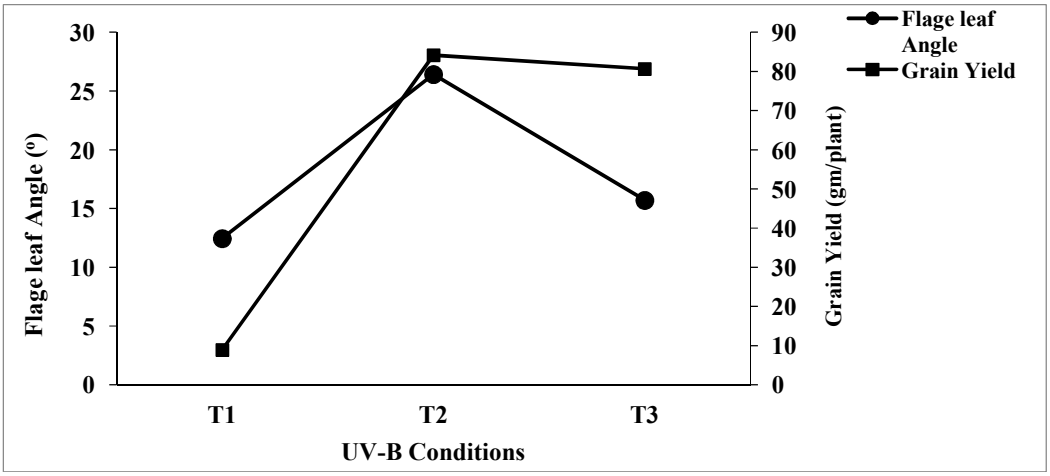


Fig. 1. Effect of UV-B radiation on Flag leaf angle (°) and Grain yield (gm/plant) under UV-B condition (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

4.4 Physiological Characters Influenced by UV-B Radiation

Photosynthesis is the most important metabolic process of plants essential for the production of biomass. The gas exchange measurements indicated a significant reduction in photosynthesis and transpiration rate accompanied by a decrease in stomatal conductance under open condition (T_1) (Table 4). This finding is consistent with the result obtained in barely [50] and lettuce [51]. Reduction in photosynthetic rates mainly due to inactivation of PSII, decreased levels of chlorophylls, carotenoids and reduced activity of Rubisco. UV-B radiation also responsible for the down-regulation of photosynthetic genes, decreased thylakoid integrity and altered chloroplast ultrastructure [52]. In the present study decreased chlorophyll content was observed (Fig. 2) and also a decrease in stomatal conductance was found in plants exposed to UV-B radiation. Similar results were observed in *Matricaria chamomilla* [53]. Stomatal closure by enhanced UV-B radiation and increased leaf diffusive resistance has also been demonstrated with the action spectrum peaking below the wavelength of 290 nm [54]. In the present study, the increased plant growth and dry matter accumulation in the UV-B excluded crop (T_2) might have been primarily due to the result of increased photosynthesis.

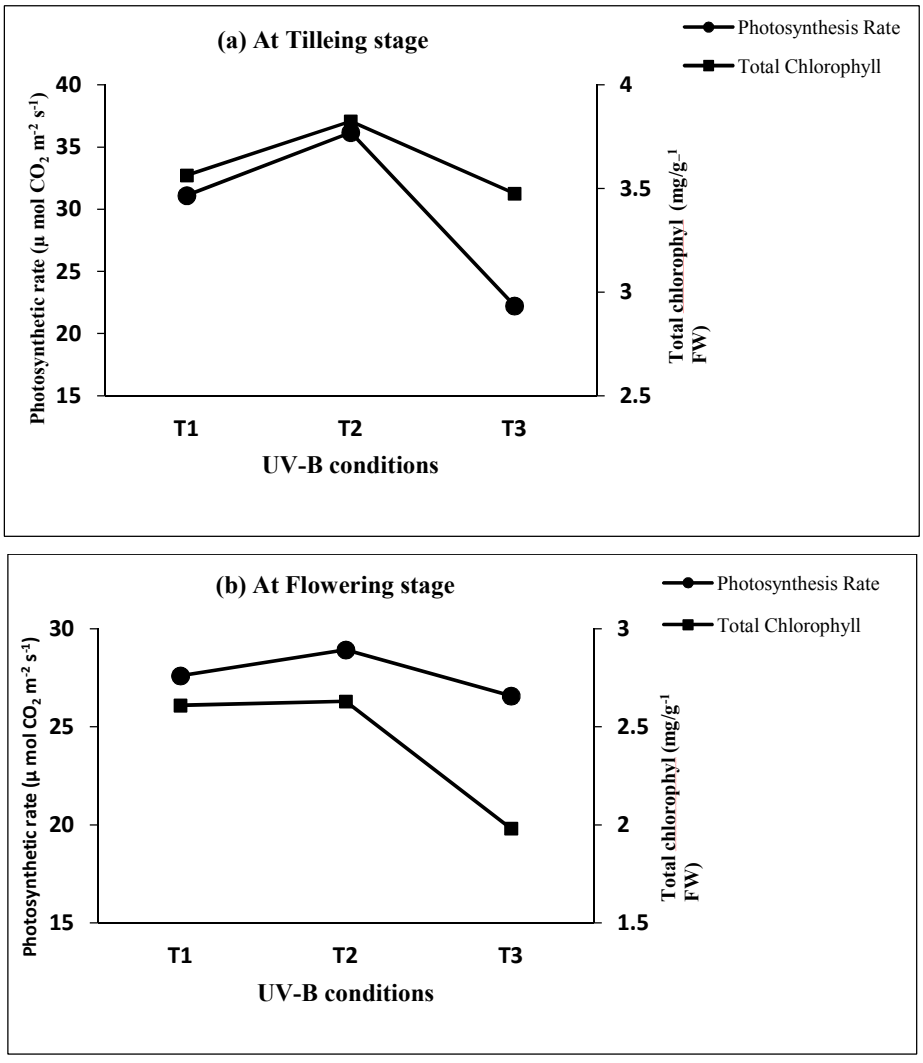


Fig. 2. Effect of UV-B radiation on Photosynthetic rate (µmol CO_2 $m^{-2}s^{-1}$) and Total chlorophyll (mg g^{-1} FW) under UV-B condition (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

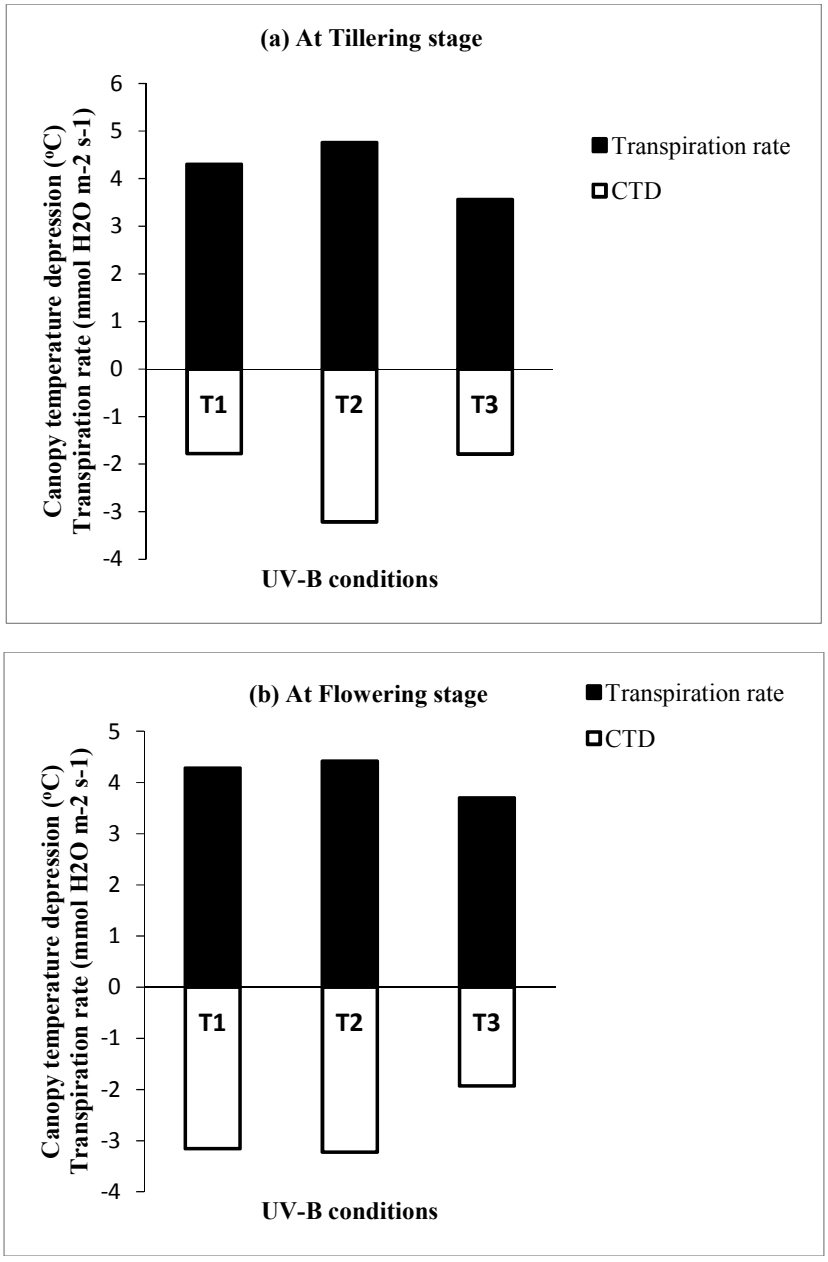


Fig. 3. Effect of UV-B radiation on Transpiration rate (mmol H_2O $m^{-2}s^{-1}$) and CTD (°C) under UV-B condition (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

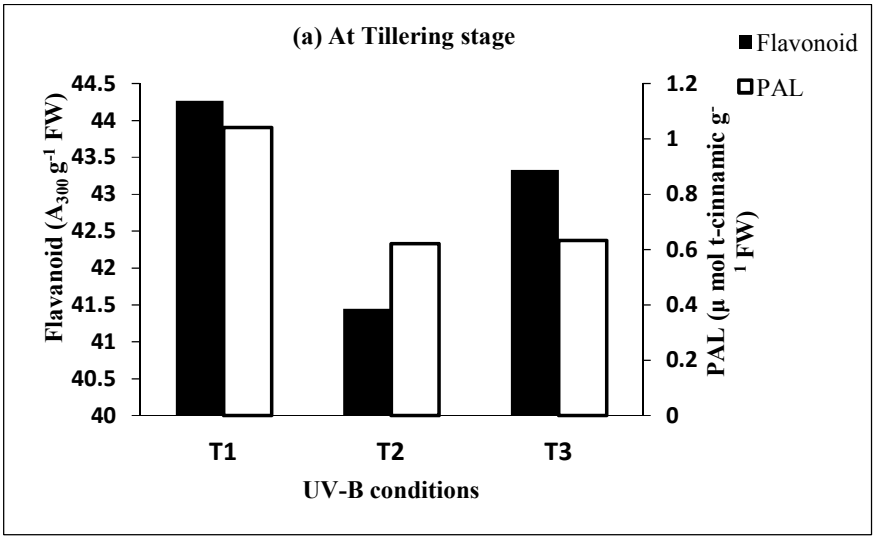
The present investigation also indicates that under UV-B excluded condition (T_2) there is more canopy cooling and high leaf temperature in the remaining two conditions. This is related to the higher transpiration rate in T_2 which in turn leads to high CTD whereas, in the remaining two conditions UV-B radiation caused less transpiration rate there by maintaining higher leaf temperature (Fig. 3). On correlating CTD with transpiration rate and stomatal conductance, the CTD could be used as selection criteria under any environmental stress conditions [55]. There are reports that suggested an adjustment of microclimate like cool canopy during grain filling period in wheat plays an important role in stress tolerance [56].

4.5 Biochemical Characters Influenced by UV-B Radiation

The decrease in chlorophyll pigment content was evident under exposure of the plants to the UV-B radiation, where they received more UV-B radiation (Table 5). Similar results have been reported in rice [30] and annual desert plants [57]. The decrease in chlorophyll content was observed under higher UV-B radiation in pea due to a reduction in expression of chlorophyll a/b binding protein [58]. UV-B radiation also affects the chlorophyll pigment, either through inhibition of their synthesis or effects on the enzymes involved in the biosynthetic pathway and degradation of its precursors [59-61].

Flavonoids perform a function as a protective pigment in leaves and shoots of the plants by attenuating the impinging UV-B radiation and their specific location is in the epidermal layer, protects cell and cell organelles [62,63]. Flavonoids also possess free-radical scavenging activity [64]. In this investigation, the flavonoid level was found significantly higher in natural solar condition (T_1) at flowering stage of plants and this might be due to the higher UV-B radiation received at canopy level under a T_1 condition in March where the crop was at flowering stage. The flavonoid concentration reduces UV-B penetration and protects the photosynthetic apparatus to some extent depending on the threshold level of UV-B radiation. The present observation is in agreement with the findings in rice [65-67].

UV-B radiation induces oxidative stress in the plants by producing reactive oxygen species (ROS), which are very harmful to the plants [68,69]. To cope with oxidative stress, various ROS-scavenging system assist in plant and among them, catalase is the most efficient antioxidant enzyme which protects plants by scavenging free radicals and H_2O_2. Our present study also indicated higher catalase activity when plants were subjected to UV-B radiation at tillering and flowering stages (Table 5). This finding correlated in soybean [70] and rice [71]. The enhanced catalase enzyme activity upon UV-B radiation indicates that plants had built a larger capacity to remove ROS as a tolerance mechanism to UV-B stress [72]. In the present study, PAL activity decreased from tillering to flowering stage (Table 5). Though significantly more activity was observed at the initial stage in all treatments, maximum PAL activity was observed under open condition in both tillering and flowering stages. This might be due to the reason that UV-B radiation enhanced the PAL activity where it produced more phenolic compounds and later gets modified through phenylpropanoid metabolism to form the precursor of secondary metabolites including flavonoids [73]. This is also evident from the increase in flavonoid content at the flowering stage in the present study under UV-B radiation treated condition (Fig. 4). Earlier reports also indicate a similar trend [74,75].



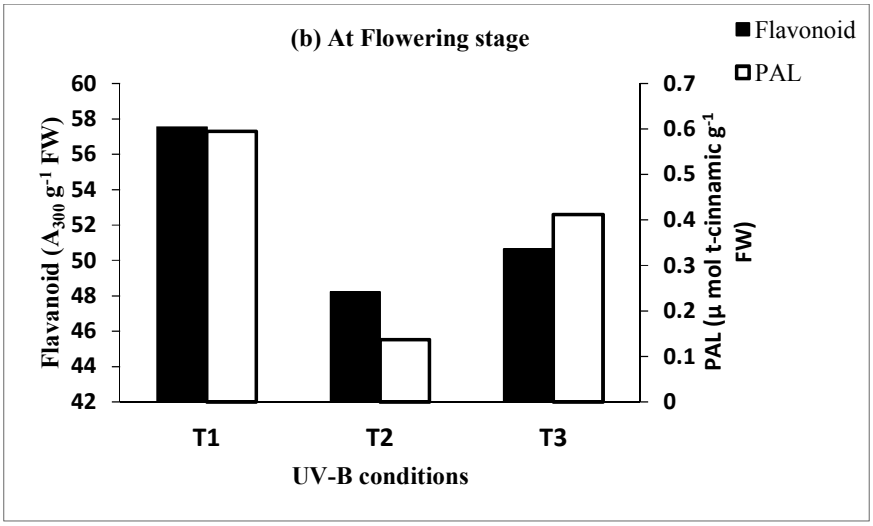


Fig. 4. Effect of UV-B radiation on Flavanoid (A_{300} g^{-1} FW) and PAL (µmol t-cinnamic g^{-1} FW) under UV-B condition (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

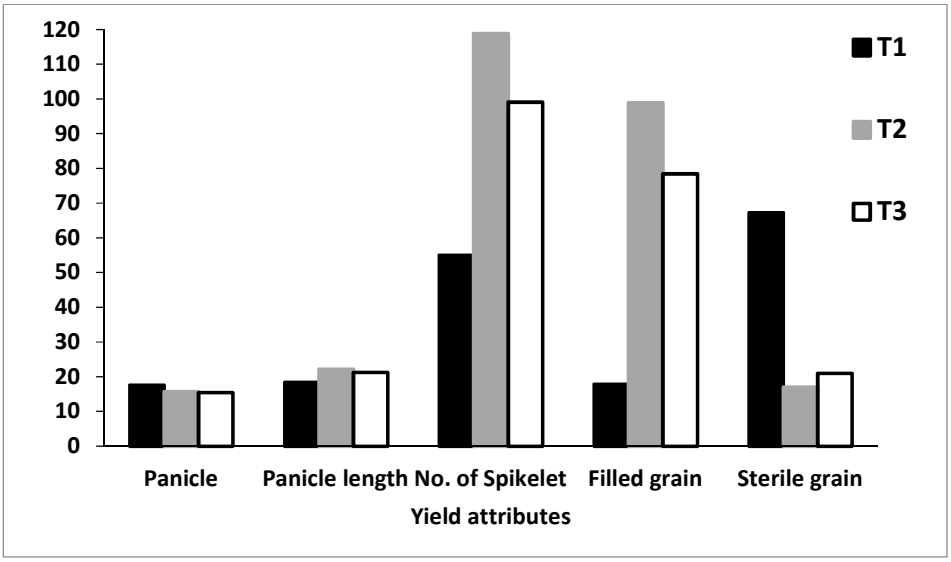


Fig. 5. Effect of UV-B radiation on panicle per hill, Panicle length (cm), Number of spikelets per panicle, Filled grain per panicle and spikelet sterility (%) under UV-B condition (T_1- Natural solar UV-B condition. T_2- Reduced UV-B radiations using UV-B filters (which measures UV-B as zero). T_3- 85% ambient radiation including UV-B in polyhouse + UV-B supplemented with UV-B lamps)

4.6 Yield and Yield-related Parameters Affected by the UV-B Radiation

In the present study, yield and yield attributes were affected by the high UV-B radiation which leads to lesser yield in the crop where they were subjected to UV-B radiation except that the number of panicles per hill was higher where the plants were grown under natural solar radiation (Table 6). Though the number of panicles was higher it did not result in a higher yield in open solar condition because the length of panicles, number of spikelets per panicle and filled grains per panicle were very less with very high spikelet

sterility (Table 6) (Fig. 5) compared to the UV-B excluded condition. This might have been due to more panicle length, higher photosynthetic rate, stomatal conductance, and more chlorophyll content and low flavonoid content under UV-B excluded condition (T_2). Similar results were reported in wheat [76] and soybean [25]. Under open condition UV-B radiation affected the grain development by restricting grain filling which leads to a lesser number of filled grains per panicle and thousand grain weight. Similar observations of the spikelet sterility on prolonging exposure to UV-B radiation in rice were reported [42]. This investigation also suggested that a decrease in grain yield may often be accompanied by a substantial modification in the partitioning of biomass into different components of plant organs under UV-B radiation. A similar conclusion in wheat had been reported [76,77]. The reproductive stage is the most important period to achieve higher grain yield but in the present study, the grain yield decreased due to high UV-B received in open condition (T_1) at flowering stage, which in turn decreased the harvest index.

5. CONCLUSION

The chemical profile of the atmosphere has been changed during a few decades due to anthropogenic activity, which arose as a serious threat to agriculture, reducing the productivity of major crops. The depletion of the stratospheric ozone layer due to ozone-depleting substances results in an increase in UV-B radiation reaching the earth's surface. UV-B radiations have high energy and potential for causing reversible or irreversible biological damages. In the present study, exposure of rice plants to UV-B radiation reduced the growth and development of the plants by affecting morphological characters such as plant height, tiller number, leaf thickness and flag leaf angle. UV-B radiation also resulted in changes in the phenophases of rice where the plants took more time to achieve respective phenophases. Physiological and biochemical parameters also were highly influenced and all these awful changes in rice plants resulted in lesser yield under UV-B radiation exposed conditions.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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