



Special issue on Recent advances in photomodulation in higher plants, algae, and bryophytes

Intraspecific variation in photosynthetic efficiency in soybean (*Glycine max* L.) varieties towards solar ultraviolet radiations

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Abstract

In the current study, we used four soybean varieties PK-1029, PK-472, NRC-7, and Hardee to examine the effect of exclusion of solar UV radiation on photosynthetic efficiency and to test possible variety-dependent sensitivity to ambient UV (280–400 nm). Plants that were grown under UV exclusion filters had higher chlorophyll *a* and *b*, efficiencies of PSII and more active reaction centers indicated that PSII were substantially affected by solar UV radiation. The significant increase in net photosynthesis was linked to increased stomatal conductance and lower intercellular concentration of CO₂ in UV-excluded plants. The exclusion of solar UV increased seed mass per plant in all soybean varieties as compared to the control; this indicates that ambient UV exclusions boost photosynthetic efficiency and improve soybean yield. The overall cumulative stress response index of four varieties implies that Hardee and PK-472 were more sensitive whereas NRC-7 and PK-1029 were resistant to ambient UV radiations.

Keywords: chlorophyll fluorescence; OJIP transient; photosynthesis; PSII efficiency; soybean; UV exclusion.

Introduction

In natural sunlight, exposure to ultraviolet (UV) radiation is inevitable as the need for plants to capture light for photosynthesis. UV radiation is composed of three wavelength ranges: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm) (Björn 2015). UV-C and a larger

part of the UV-B radiations of the solar spectrum are absorbed by the ozone layer, while UV-A and a little portion of UV-B reach at the Earth's surface and are absorbed by the plants (Kataria *et al.* 2014, Bornman *et al.* 2019). The reduction of stratospheric ozone has appeared to be the foremost reason for the prominent rise in UV-B radiation (Ballaré *et al.* 2011, McKenzie *et al.* 2011).

Highlights

- Intraspecific variations in photosynthetic performance were studied in soybean
- UV-B exclusion upregulates chlorophyll, PSII efficiency, and photosynthesis
- UV-B sensitivity is greater in soybean variety Hardee/PK-472 than NRC-7/PK-1029

Received 16 September 2022

Accepted 14 November 2022

Published online 21 December 2022

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Abbreviations: ABS – absorbance; Chl – chlorophyll; C_i – intercellular CO₂ concentration; CSRI – cumulative stress response index; DI₀/RC – dissipation per reaction center; DMSO – dimethyl sulfoxide; ET₀/RC – electron transport per reaction center; F₀ – minimal Chl *a* fluorescence; F_m – maximal Chl *a* fluorescence; F_v – variable fluorescence; F_v/F₀ – the activity of PSII; F_v/F_m – maximum photochemical efficiency of PSII; g_s – stomatal conductance; PEA – plant efficiency analyzer; PI_(ABS) – performance index at absorption basis; P_N – net photosynthesis; RC – reaction center; TR₀/RC – trapping per reaction center; UV-B – ultraviolet-B.

Conflict of interest: The authors declare that they have no conflict of interest.

UV-B radiation has an inexplicably large photobiological effect due to its absorption by pivotal classes of biomolecules (proteins, lipids, and nucleic acids) causing their photoexcitation, and may endorse changes in various biological processes (Jenkins 2009, Hideg *et al.* 2013). In higher plants, UV-B causes many detrimental effects at the cellular, molecular, and organism level (Caldwell *et al.* 2007, Jenkins 2009, Wang *et al.* 2012, Reddy *et al.* 2013).

Compared to temperate regions, plants are exposed to high levels of UV-B radiation in tropical regions (Jansen 2002, Semerdjieva *et al.* 2003). The effects of UV-B radiations on plants are decreased biomass (Vandenbussche *et al.* 2018), abnormal growth (Searles *et al.* 2001, Robson *et al.* 2015, Zhu and Yang 2015), and damage to photosynthetic apparatus, in particular to PSI and PSII (Liu *et al.* 2013). UV-triggered physiochemical changes can finally decline seed quality and yield of major crop plants (Kataria *et al.* 2014, Bais *et al.* 2018). It was observed that plant growth declines by ~1% for every 3% rise in UV-B (Ballaré *et al.* 2011), however, this could be more remarkable in genotypes sensitive to UV-B radiations (Hakala *et al.* 2002, Hidema and Kumagai 2006, Zhu and Yang 2015, Kataria and Guruprasad 2018).

Optimization of photosynthesis is one of the utmost significant approaches for environmental suitability to increase crop yield and acclimatize plants to adverse abiotic stress conditions (Brestic *et al.* 2018, 2021; Allakhverdiev 2020). Photosynthesis is the foremost sensitive physiological process influenced by UV-B radiation in photosynthetic organisms (Kataria *et al.* 2014, Sharma *et al.* 2019, Joshi-Paneri *et al.* 2020), as it is directly linked to biomass production and yield; therefore, it is essential to deepen the knowledge of the impact of UV-B stress on plant photosynthesis (Lidon and Ramalho 2011, Lidon *et al.* 2012). Direct effects of enhanced UV-B on photosynthesis are reduced chlorophyll content (Surabhi *et al.* 2009), loss in integrity of the thylakoid membranes (Swarna *et al.* 2012), damage of PSII (Dobrikova *et al.* 2013), decline in Rubisco activity (Allen *et al.* 1997), CO₂ fixation, and O₂ evolution (Çiçek *et al.* 2012).

Under high UV-B radiation, the decrease in chlorophyll content was due to damage in the structural integrity of chloroplasts which ultimately leads to reduction of photosynthesis. Indirect effects of high UV-B on photosynthesis include changes in gas-exchange efficiency, stomatal closure (Nogués *et al.* 1999), canopy morphology (Zhao *et al.* 2004), and leaf color which ultimately results in desiccation, chlorosis, and necrosis of the leaves (Visser *et al.* 1997). UV-B can stimulate the opening or closing of stomata (Jansen and van den Noort 2000). Chlorophyll fluorescence (ChlF) is used to study the changes that affect the photosynthetic apparatus under different environmental conditions (Goltsev *et al.* 2016). The investigation of fluorescence signals provides thorough information on the function of PSII, light-harvesting complexes, donor and acceptor sides of PSII (Kalaji *et al.* 2014, Rastogi *et al.* 2019, 2020).

Studies on the exclusion of UV-B radiation can provide helpful information on the adaptation of tropical plants to

higher UV-B. Moreover, studies on UV exclusion using specific filters to eliminate UV radiation have usually focused on the effect of ambient UV-B on the growth and development of plants (Rousseaux *et al.* 2004, Kataria *et al.* 2013). Experiments on UV-B exclusion studies have shown that solar UV affects the growth, photosynthesis, yield, and seed quality of plants (Kataria *et al.* 2013, Kataria and Guruprasad 2014, 2015; Ferreira *et al.* 2016). These studies indicated that ambient UV-B declines growth, dry matter accumulation, photosynthesis, and yield of some plant species, such as cucumber, *Trigonella*, barley, sorghum, *Vigna*, soybean, *Amaranthus*, wheat, and cotton (Amudha *et al.* 2005, Baroniya *et al.* 2011, Dehariya *et al.* 2012, Kataria and Guruprasad 2012a,b; 2014, 2015; Kataria *et al.* 2013, Sharma *et al.* 2019). These studies suggested that the response of plants to UV-B does not only vary among the species but also varies considerably among the genotypes of the same plant species (Kataria and Guruprasad 2012a,b; 2014, 2015; Kataria *et al.* 2013). It is of our interest to add information about intraspecific variations to solar UV-A/UV-B amongst soybean varieties in terms of their photosynthetic performance. Soybean is the most widely cultivated seed legume (Jumrani and Bhatia 2018, 2019a,b). Previously an intraspecific difference in growth, nitrogen, and antioxidants has been reported in soybean, however, this is the first study in which the intraspecific variations in soybean genotypes was investigated for their photosynthetic efficiency (Chl *a* fluorescence and gas exchange) in response to ambient UV radiations. In the present study, the experiments were performed to measure the influence of UV-A/UV-B on the sensitivity of four soybean varieties and to calculate the cumulative stress response index (CSRI) to assess the physiological responses of soybean genotypes to ambient UV radiations by the elimination of solar UV under field conditions.

Materials and methods

Plant material: Soybean (*Glycine max* L.) varieties PK-1029, PK-472, NRC-7, and Hardee seeds were obtained from IISR (the Indian Institute of Soybean Research), Indore (M.P.), India. These are commonly grown varieties in the central part of India, and these were reported to have significant physiological changes in response to ambient UV-B (Baroniya *et al.* 2011, 2014).

Experimental design for UV exclusion experiment: All field tests were carried out outdoors in the open air in the Devi Ahilya University's botanical garden in Indore (latitude: 22.71°N), India. The seeds were surface sterilized with 0.01% HgCl₂ for 2 min, then washed 4 to 5 times with distilled water. After that, seeds were inoculated with *Rhizobium japonicum* slurry before they were planted in the 120 × 90 cm field rows. The soil of the study site was black; it was clayey in nature and rich in alumina, lime, iron, and magnesia. Seeds were planted 0.3 m apart with 0.06 m plant spacing inside each row under iron cages measuring [1.21 m L × 0.91 m W × 1.21 m H] coated with polyester filters (*Garware Polyesters Ltd.*, Mumbai) that excluded

either UV-B (280–315 nm) or UV-A/B (200–400 nm). The control plants were grown under a polythene screen that allowed UV-B and UV-A from the sun to pass through. The transmission characteristics of the UV cut-off filters as well as clear polythene were measured by *Shimadzu (UV-1601)* spectrophotometer (Fig. 1S, *supplement*).

The transmission properties of the filters did not change during the experiment, and they did not produce any fluorescence in the visible range. During the day, the metal cages were exposed to direct sunlight with no shade. The seedlings were exposed to sunlight right after they emerged. There was no discernible change in temperature between the UV-excluded and filter-control chambers due to the horizontal holes constructed in the filters wrapped in the metal cages for air ventilation. Three replicates of each treatment were used in the randomized block design of the trials.

Radiation measurement: A radiometer was used to calculate the solar irradiances in all treatments (*Solar Light-PMA 2100*, Glenside, PA, USA). During the experiment, the midday solar irradiance was 1,450 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$; the reduction in light intensity caused by the UV-B exclusion filter was 14% [1,240 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$]; the reduction in light intensity caused by the UV-A/B exclusion filter was 19% [1,180 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$]; and the reduction in light intensity caused by the polyethylene filter transmissible to UV was 4% [1,390 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$].

Chlorophyll (Chl) content: The dimethyl sulfoxide (DMSO) method was used to determine the amount of total Chl (*Hiscox and Israelstam 1979*). Leaves (50 mg), freshly cut and thoroughly cleaned, were diced and added to 10 ml of DMSO in a test tube for the extraction of Chl. After being diluted with DMSO to a volume of 10 ml, the mixture was incubated at 65°C for 3 h. After allowing the material to settle, the absorbance was recorded with a *Shimadzu UV/VIS 1601* spectrophotometer at 663, 646, and 470 nm. The calculations for concentrations of Chl *a*, Chl *b*, total Chl, and carotenoids were done using equations of *Wellburn and Lichtenthaler (1984)*.

Chl fluorescence measurements: *Plant Efficiency Analyzer (Hansatech Instruments, King's Lynn, Norfolk, UK)* was used to measure the Chl fluorescence in the third trifoliolate leaves of soybean plants. Measurements were done in three replicates ($n = 3$) of five plants each replica. The red light was focused on the leaf surface in the clips on a point of 4 mm in diameter to give uniform illumination over the exposed region of the sample, producing 600 W m^{-2} (3,200 $\text{E m}^{-2} \text{s}^{-1}$) of red light (peak at 650 nm) that caused the transients. Data were acquired every 10 s for the first 2 ms and every 1 ms after that. They were recorded for 1 s with a 12-bit resolution (*Strasser and Strasser 1995*). All measurements were taken at $25 \pm 1^\circ\text{C}$. The fluorescence rise kinetics was polyphasic when the Chl *a* fluorescent transient was displayed on a logarithmic scale (OJIP phase). When all reaction centers are opened, the fluorescence intensity was considered to be

F_0 (O phase) at 20 microseconds, J phase at 2 milliseconds, I phase at 30 milliseconds, and P phase at the maximum fluorescence (F_m) (since the excitation intensity is strong enough to ensure the closure of all PSII reaction centers, F_p is equal to F_m in this instance).

The following quantum efficiencies were determined (*see Appendix*): proportional to the activity of the water-splitting complex on the donor side of the PSII (F_v/F_0); maximum quantum yield of primary photochemistry (ϕ_{P_0}) = $(\text{TR}_0/\text{ABS}) = (F_v/F_m)$; the efficiency with which an electron living on Q_A^- will enter the intersystem electron transport chain (ET_0/TR); and the quantum yield of electron transport (ET_0/ABS). $\text{PI}_{(\text{ABS})}$ (performance index on absorption basis), which reflects the efficiency of the overall energy flow, and $\text{SFI}_{(\text{ABS})}$, which serves as a measure of PSII 'structure and functioning', were the other parameters calculated. Using the tool *Bioolyzer HP 3*, models for energy pipelines and leaves were created (*Bioenergetics Laboratory, University of Geneva, Switzerland*).

Gas-exchange parameters: Using a portable photosynthesis system infra-red gas analyzer (IRGA, *LICOR 6200*, Lincoln, Nebraska, USA) in the third trifoliolate leaves of soybean plants, the following parameters were measured in 45-d-old plants on cloudless days at 11:00 h: net photosynthesis (P_N [$\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$]), stomatal conductance (g_s [$\text{mmol}(\text{H}_2\text{O}) \text{m}^{-2} \text{s}^{-1}$]), and intercellular CO_2 concentration (C_i [$\mu\text{mol mol}^{-1}$]).

Cumulative stress response index (CSRI): CSRI is calculated by adding the relative individual component responses for each treatment (*Kataria and Guruprasad 2012a,b*). The CSRI was calculated to evaluate the physiological response of several soybean cultivars to ambient UV radiations, including total biomass, total Chl content, performance index, rate of photosynthesis, and seed production. CSRI was determined using the formula: $\text{CSRI} = \{[(\text{TBM}_c - \text{TBM}_t)/\text{TBM}_c] + [(\text{TC}_c - \text{TC}_t)/\text{TC}_c] + [(\text{PI}_c - \text{PI}_t)/\text{PI}_c] + [(P_{Nc} - P_{Nt})/P_{Nc}] + [(SY_c - SY_t)/SY_c]\} \times 100$, where TBM is total plant biomass, PI is performance index at absorption basis, P_N is photosynthetic rate, TC is total chlorophyll content, and SY is the plant's seed yield under T (treatment implies -UVB or -UVA/B) and C (means filter control which receives ambient UV). Based on the total CSRI from all treatments, the varieties were divided into those that were less vulnerable to ambient UV and those that were the most sensitive.

Crop yield and yield components: Three replicates of five plants each were utilized to harvest the crop, and yield metrics including the number of pods and mass of seeds per plant were measured. All yield indicators were evaluated for the four soybean types at harvest maturity.

Statistic evaluation: Results were analyzed using one-way analysis of variance (*ANOVA*) and a post hoc *Newman-Keuls* multiple comparison test ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$) using *Graph Pad* software (La Jolla, CA, USA), using a trial version of the *Windows* software *Prism 4*. The data are provided as a mean \pm SE ($n = 3$).

Results

Photosynthetic pigments: The exclusion of UV enhanced the amount of Chl *b* as compared to Chl *a* (Table 1). Maximum enhancement in Chl *a* was observed in Hardee (~33 and 36% by UV-B and UV-A/B exclusion, respectively), and minimum in PK-1029 (~2 and 3% by UV-B and UV-A/B exclusion, respectively) as compared to control (Table 1). Chl *b* was promoted to a maximum in Hardee (~33 and 54% by UV-B and UV-A/B exclusion, respectively). Minimal influence on Chl *b* by UV-B and UV-A/B exclusion was on PK-1029 (~8 and 11%, respectively; Table 1). Total Chl was enhanced to a maximum in Hardee (by 32 and 38%, respectively, by UV-B and UV-A/B exclusion). Minimum enhancement was observed in PK-1029 (~3 and 5%; Table 1). Chl *a/b* ratio decreased in all the varieties because of higher enhancement in Chl *b* by both UV-B and UV-A/B exclusion (Table 1).

Chlorophyll fluorescence: Chl *a* fluorescence was measured to assess the effect of UV exclusion on the photochemical efficiency of PSII in four soybean varieties. Higher fluorescence yield was recorded in UV-excluded plants in var. Hardee and PK-472 (Fig. 1). In control plants of all the varieties, a significant reduction in maximum Chl fluorescence (F_m) indicated a decline in the quantity of PSII centers which can reduce Q_A . In our study, lower fluorescence was observed in control plants because of the delay in the flow of electrons rather than a decline in the absorption cross-section area. The fluorescence yield at the I and P phase were higher in the UV-excluded plants as compared to control plants (Fig. 1). In variety Hardee the difference in fluorescence yield decreased by 15 and

12% at the O phase, 8 and 5% at the J level, and it showed an enhancement of 0 and 17% at the I phase, 6 and 18% at the P phase (F_m) in plants that were grown under UV-B and UV-A/B cutoff filters, respectively, over control plants (Fig. 1). In other varieties as well, the trend was similar and the promotion in fluorescence yield varied between 0 to 18%. In variety PK-1029, it decreased slightly by 2–3% (Fig. 1). The F_v/F_0 was enhanced in all the varieties studied after the exclusion of UV and the maximum rise was in Hardee, and the minimum was observed in PK-1029 (Table 2). There was also an enhancement in PSII quantum efficiencies, such as TR_0/ABS , ET_0/ABS , and ET_0/TR , in plants grown under UV-exclusion filters in comparison to control plants in all four varieties. Maximum promotion in these quantum efficiencies was recorded in Hardee and minimum in PK-1029. The effect was more pronounced in UV-A/B-excluded plants (Table 2).

The most susceptible parameter derived by the equations of the JIP-test is $PI_{(ABS)}$ which is an indicator of sample vitality (Srivastava *et al.* 1999). $PI_{(ABS)}$ was enhanced significantly by the exclusion of solar UV components (Table 2). Enhancement in $PI_{(ABS)}$ after the UV-B and UV-A/B exclusion was recorded as 92 and 137%, respectively, over the control in soybean var. Hardee. Minimum enhancement by UV-B exclusion was observed in NRC-7 and PK-1029 by 10 and 18%, respectively. By exclusion of UV-A/B minimum enhancement (37%) was observed in PK-1029 (Table 2). $SFI_{(ABS)}$, a sign of PSII's structure and functioning, also increased in all varieties of soybean after UV-B and UV-A/B exclusion from solar radiation (Table 2).

Change of PSII energy fluxes in response to ambient UV and exclusion of solar UV was obtained by energy pipeline models of leaves (Fig. 2A). The energy fluxes

Table 1. Changes in photosynthetic pigment content [$\text{mg g}^{-1}(\text{FM})$] in leaves of soybean varieties after exclusion of UV-B and UV-A/B from solar radiation. Data are presented as mean \pm SE ($n = 3$) and values are significantly different at * $P < 0.05$ ** $P < 0.01$ from filter control (Newman-Keuls multiple comparison test).

Photosynthetic pigment	Soybean varieties	Control	-UV-B	-UV-A/B
Chl <i>a</i>	Hardee	3.48 \pm 0.07	4.62 \pm 0.08*	4.74 \pm 0.08*
	PK-1029	3.03 \pm 0.04	3.10 \pm 0.08	3.13 \pm 0.01
	NRC-7	3.69 \pm 0.09	4.12 \pm 0.07*	4.04 \pm 0.15
	PK-472	3.61 \pm 0.09	4.29 \pm 0.02*	4.84 \pm 0.21*
Chl <i>b</i>	Hardee	0.81 \pm 0.02	1.08 \pm 0.01*	1.24 \pm 0.03**
	PK-1029	0.36 \pm 0.03	0.39 \pm 0.03	0.40 \pm 0.04
	NRC-7	0.49 \pm 0.04	0.61 \pm 0.03*	0.61 \pm 0.06*
	PK-472	0.43 \pm 0.08	0.57 \pm 0.06*	0.64 \pm 0.07*
Chl <i>a/b</i>	Hardee	4.33 \pm 0.09	4.28 \pm 0.09	3.79 \pm 0.11*
	PK-1029	8.41 \pm 0.02	7.85 \pm 0.11*	6.97 \pm 0.03*
	NRC-7	7.49 \pm 0.05	6.73 \pm 0.09	6.63 \pm 0.10*
	PK-472	8.37 \pm 0.02	7.22 \pm 0.04*	7.52 \pm 0.27*
Total Chl	Hardee	4.28 \pm 0.10	5.65 \pm 0.07*	5.92 \pm 0.16*
	PK-1029	3.38 \pm 0.85	3.48 \pm 0.27	3.56 \pm 0.58
	NRC-7	4.17 \pm 0.30	4.70 \pm 0.18	4.62 \pm 0.09
	PK-472	4.02 \pm 0.81	4.86 \pm 0.59*	5.46 \pm 0.33**

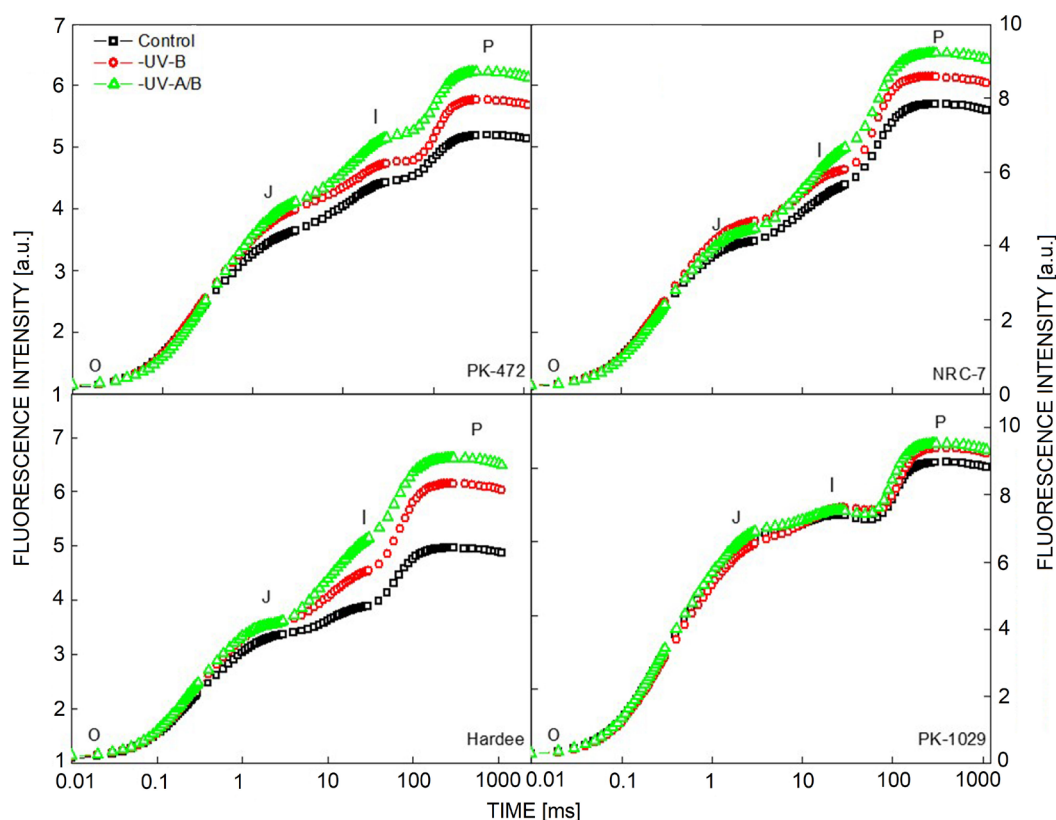


Fig. 1. Fluorescence emission transient of third trifoliolate leaves of soybean varieties Hardee, PK-1029, NRC-7, and PK-472 normalized at F_0 after exclusion of solar UV-B and UV-A/B. Control; -UV-B – UV-B-excluded plants; -UV-A/B – UV-A/B-excluded plants.

Table 2. Summary of parameters, formulae, and their description using data extracted from the fast fluorescence transient OJIP for soybean varieties Hardee, PK-1029, NRC-7, and PK-472. ET – flux of electrons from Q_A^- into the intersystem electron transport chain; ϕ_{P_0} – maximal quantum yield of primary photochemistry; ϕ_{E_0} – quantum yield of electron transport; ψ_0 – efficiency with which a trapped excitation can move an electron in the electron transport chain further than Q_A ; RC – concentration of reaction centers; TR – excitation energy flux trapped by a RC and utilized for the reduction of Q_A to Q_A^- ; $PI_{(ABS)}$ – performance index on absorption basis; $SFI_{(ABS)}$ – an indicator of PSII ‘structure and functioning’; F_v/F_0 – a value that is proportional to the activity of the water-splitting complex on the donor side of the PSII. Adapted and reorganized from Strasser *et al.* (2000) and (2004). Data are presented as mean \pm SE ($n = 3$) and values are significantly different at * $P < 0.05$ ** $P < 0.01$ from filter control (Newman–Keuls multiple comparison test).

Soybean varieties	Treatments	F_v/F_0	$\phi_{P_0} = TR_0/ABS$	$\psi_0 = ET_0/TR$	$\phi_{E_0} = ET_0/ABS$	$PI_{(ABS)}$	$SFI_{(ABS)}$
Hardee	Control	2.951 ± 0.057	0.746 ± 0.015	0.450 ± 0.009	0.336 ± 0.007	9.024 ± 0.174	1.256 ± 0.025
	-UV-B	$3.820 \pm 0.074^*$	0.792 ± 0.016	$0.533 \pm 0.011^*$	0.422 ± 0.009	$17.291 \pm 0.333^*$	$1.672 \pm 0.033^*$
	-UV-A/B	$4.100 \pm 0.080^*$	$0.804 \pm 0.016^*$	$0.577 \pm 0.012^*$	$0.464 \pm 0.009^*$	$21.400 \pm 0.413^{**}$	$1.770 \pm 0.035^*$
PK-1029	Control	2.921 ± 0.057	0.745 ± 0.015	0.309 ± 0.006	0.230 ± 0.005	5.330 ± 0.103	0.938 ± 0.019
	-UV-B	3.010 ± 0.058	0.750 ± 0.015	$0.335 \pm 0.007^*$	0.251 ± 0.005	$6.281 \pm 0.122^*$	1.041 ± 0.021
	-UV-A/B	3.101 ± 0.066	0.760 ± 0.015	$0.380 \pm 0.008^*$	0.290 ± 0.006	$7.330 \pm 0.142^*$	$1.111 \pm 0.022^*$
NRC-7	Control	3.421 ± 0.066	0.774 ± 0.015	0.516 ± 0.010	0.399 ± 0.008	13.410 ± 0.259	1.465 ± 0.029
	-UV-B	3.740 ± 0.073	0.789 ± 0.016	0.498 ± 0.020	0.393 ± 0.008	14.870 ± 0.287	$1.572 \pm 0.031^*$
	-UV-A/B	$4.070 \pm 0.079^*$	$0.803 \pm 0.016^*$	0.557 ± 0.011	$0.447 \pm 0.009^*$	$20.852 \pm 0.402^*$	$1.818 \pm 0.036^*$
PK-472	Control	3.001 ± 0.058	0.750 ± 0.015	0.325 ± 0.009	0.319 ± 0.007	8.130 ± 0.157	1.165 ± 0.023
	-UV-B	$3.390 \pm 0.066^*$	0.772 ± 0.015	$0.426 \pm 0.009^*$	0.329 ± 0.007	$10.100 \pm 0.195^*$	$1.318 \pm 0.026^*$
	-UV-A/B	$3.810 \pm 0.074^*$	$0.792 \pm 0.016^*$	$0.457 \pm 0.009^{**}$	$0.362 \pm 0.007^*$	$14.011 \pm 0.271^*$	$1.579 \pm 0.031^*$

ratios ABS/RC , TR_0/RC , and ET_0/RC increased and DI_0/RC decreased in soybean var. Hardee and PK-472 after solar UV exclusion (Fig. 2A). A phenomenological leaf model showed more active reaction centers per unit area of the leaf in UV-excluded plants (Fig. 2B). Open circles symbolize the active reaction center and closed circles symbolize the inactive reaction center, broader widths of the arrow indicated higher efficiency of electron transport in the leaf models (Fig. 2B).

Gas-exchange parameters: Differences in photosynthetic pigments and PSII efficiency indicates that the exclusion of UV resulted in better carbon fixation in soybean. The enormous increase in the P_N was observed in the UV-excluded plants of soybean variety Hardee ~83% (-UV-B) and 93% (-UV-A/B), whereas this was promoted to only 10 and 15%, respectively, in variety PK-1029 (Table 3). This was associated with an enhancement in g_s and a decline in C_i . The increase in these parameters was

higher in the UV-A/B-excluded plants in comparison to UV-B-excluded plants (Table 3).

In soybean var. Hardee, the enhancement in stomatal conductance was by 34% in -UV-B and 72% in -UV-A/B plants. In PK-1029, stomatal conductance was enhanced to a lower extent with a slight decrease in C_i while the decrease in C_i was more apparent in var. Hardee by the exclusion of solar UV-B and UV-A/B in comparison to var. PK-1029 (Table 3).

Seed yield: Seed mass per plant increased by the elimination of UV-B alone and UV-A/B in comparison to control in all four varieties of soybean (Table 4). The maximum increase was observed in Hardee and PK-472 by 46 and 36%, respectively, by the exclusion of UV-B. By eliminating UV-A/B, Hardee and PK-472 promotion in seed mass were 62 and 56%, respectively, in comparison to their controls (Table 4).

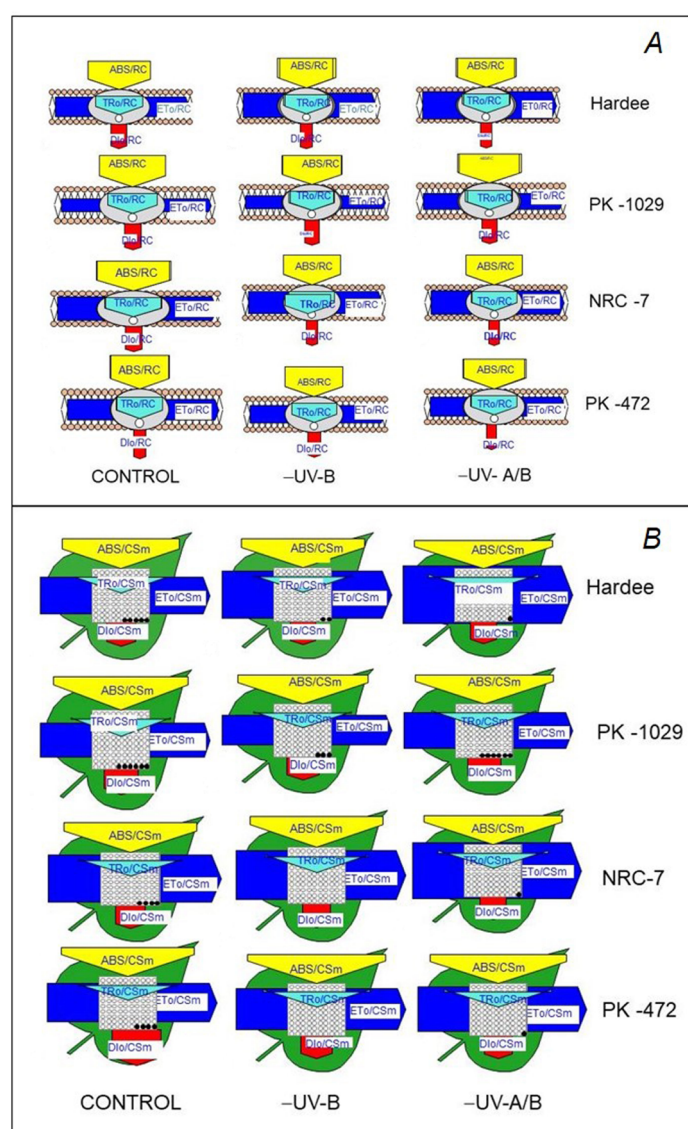


Fig. 2. (A) Membrane model shows the specific activities per unit reaction center (RC) in third trifoliolate leaves of soybean varieties Hardee, PK-1029, NRC-7, and PK-472 after exclusion of solar UV-B and UV-A/B. The small hatched circles represent newly synthesized units. The arrows indicate fluxes for light absorbance (ABS), excitation energy trapping (TR_0), energy dissipation (DI_0), and electron transport (ET_0) beyond Q_A^- . The width of each arrow denotes the relative size of the fluxes or the antenna. (B) Phenomenological energy fluxes per excited cross-section (CS) in leaf models of third trifoliolate leaves of soybean varieties Hardee, PK-1029, NRC-7, and PK-472 after exclusion of solar UV-B and UV-A/B. TR_0/CS_m – trapped energy per CS; ABS/CS_m – absorption flux per CS approximated by F_m ; ET_0/CS_m – electron transport flux per CS; DI_0/CS_m – dissipated energy per CS. All comparative values are characterized by the magnitude of the proper parameters (arrow), empty circles indicate reducing Q_A reaction centers (active), and full black circles indicate nonreducing Q_A reaction centers (inactive or silent).

Table 3. Changes in rate of CO₂ assimilation (P_N), intercellular CO₂ concentration (C_i), and stomatal conductance (g_s) in leaves of different varieties of soybean after exclusion of UV-B and UV-A/B from solar radiation. Data are presented as mean \pm SE ($n = 3$) and values are significantly different at * $P < 0.05$ /** $P < 0.01$ from filter control (*Newman-Keuls* multiple comparison test).

Soybean varieties	Treatment	P_N [$\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$]	C_i [$\mu\text{mol mol}^{-1}$]	g_s [$\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2}\text{s}^{-1}$]
Hardee	Control	9.01 \pm 0.41	301.10 \pm 2.01	0.61 \pm 0.04
	-UV-B	16.46 \pm 0.78*	271.61 \pm 5.52*	0.82 \pm 0.06*
	-UV-A/B	17.41 \pm 0.95**	273.83 \pm 4.96*	1.05 \pm 0.12**
PK-1029	Control	7.28 \pm 0.58	277.81 \pm 4.27	0.33 \pm 0.01
	-UV-B	8.01 \pm 0.38	268.30 \pm 2.82*	0.34 \pm 0.01
	-UV-A/B	8.41 \pm 1.17*	267.20 \pm 5.88	0.37 \pm 0.01
NRC-7	Control	23.30 \pm 1.06	283.81 \pm 4.52	0.58 \pm 0.02
	-UV-B	26.52 \pm 1.03	278.31 \pm 3.55	0.86 \pm 0.01*
	-UV-A/B	28.41 \pm 1.05	277.52 \pm 6.02	0.94 \pm 0.02**
PK-472	Control	14.60 \pm 1.09	295.31 \pm 5.27	0.56 \pm 0.03
	-UV-B	19.80 \pm 1.06*	283.73 \pm 3.97**	0.74 \pm 0.02*
	-UV-A/B	22.72 \pm 1.07**	281.90 \pm 4.85**	0.81 \pm 0.02**

Cumulative stress response index (CSRI): The CSRI is a combination of the physiological traits of soybean genotypes to ambient UV-A and UV-B. It is an integration of the effects of solar UV on total biomass, total chlorophyll content, $PI_{(ABS)}$, P_N , and seed yield of soybean genotypes to the UV radiation. All four varieties of soybean had negative CSRI (Table 5) representing that they were negatively affected by ambient UV radiation. The CSRI ranged from (-44) for the tolerant genotype PK-1029 to (-292) for the sensitive genotype Hardee under UV-B stress (Table 5). For ambient level of UV-A/B, PK-1029 showed CSRI (-86) and Hardee showed CSRI (-384) (Table 5).

Discussion

The reduced photosynthetic efficiency, slower development, and metabolic changes in carbon and nitrogen are all consequences of high UV-B radiation (Kataria *et al.* 2014, Dotto and Casati 2017, Piccini *et al.* 2020). Additionally, it has been noted that increased UV-B radiation affects plant height, leaf morphology, mass and area, and total biomass accumulation (Zuk-Golaszewska *et al.* 2003, Yao and Liu 2009). The UV-B radiations drastically decreased the stomatal conductance, so the rate of CO₂ assimilation and water loss through transpiration were also severely affected in the plants (Koubouris *et al.* 2015). Moreover, excessive UV-B irradiation affects PSII (Zlatev *et al.* 2012), photosynthetic pigments (Lidon and Ramalho 2011, Machado *et al.* 2017), the integrity of thylakoids and chloroplasts (Kataria *et al.* 2013), the activity of Rubisco (Kataria *et al.* 2013, Dias *et al.* 2018, Piccini *et al.* 2021), and transcription of photosynthetic genes (Strid *et al.* 1994). In field conditions, excluding UV components from solar radiation led to higher plant growth, leaf area, and total biomass accumulation in some plant species including soybean (Kataria and Guruprasad 2012a,b; 2014, 2015; Kataria *et al.* 2013, 2014).

Table 4. Seed mass per plant [g] after exclusion of UV-B and UV-A/B from solar radiation in soybean varieties. Data are presented as mean \pm SE ($n = 3$) and values are significantly different at * $P < 0.05$ /** $P < 0.01$ from filter control (*Newman-Keuls* multiple comparison test).

Soybean varieties	Control	-UV-B	-UV-A/B
Hardee	14.1 \pm 1.0	20.6 \pm 1.2*	22.9 \pm 1.1*
PK-1029	12.4 \pm 1.1	12.9 \pm 1.0	13.8 \pm 1.1
NRC-7	5.9 \pm 1.0	6.9 \pm 1.1	6.6 \pm 0.1
PK-472	10.7 \pm 1.2	14.5 \pm 1.0*	16.7 \pm 0.1*

Table 5. Cumulative stress response index (CSRI) for sensitivity of soybean varieties to ambient level of UV-B and UV-A/B radiation by the exclusion of solar UV-B and UV-A/B. The CSRI was determined by adding the changes in leaf mass area ratio, total chlorophyll content, performance index at absorption basis, rate of photosynthesis, and seed yield by ambient UV radiation as compared to the exclusion of solar UV components.

Soybean varieties	-UV-B	-UV-A/B
Hardee	-291.51	-384.32
PK-1029	-44.29	-85.90
NRC-7	-76.19	-117.91
PK-472	-169.18	-269.93

Chlorophylls are pivotal pigments for the plant photosynthetic process. Chl content and ratio are vital keys for plants to regulate several environmental variables. The UV-B and UV-A/B exclusion showed improvement in Chl *a*, Chl *b*, and total Chl content per unit leaf fresh mass. Chl *a/b* ratio was reduced as the increase in Chl *b* was higher than that in Chl *a* (Table 1). According to earlier

studies (Barsig and Malz 2000, Ranjbarfordoei *et al.* 2006, Shweta and Agrawal 2006), a lower concentration of Chl *b* has been discovered as a more frequent sign of UV-B radiation stress. This is because UV-B stress inhibits the production of both Chl *a* and *b* (Musil *et al.* 2002). In contrast, UV exclusion increases the total Chl by a higher increase in Chl *b* rather than Chl *a* in *Gossypium hirsutum* (Dehariya *et al.* 2011), *Fagus sylvatica* (Láposi *et al.* 2008), *Helianthus annuus* (Cechin *et al.* 2007), *Triticum aestivum*, *Sorghum bicolor* (Kataria *et al.* 2013), and *Cyamopsis* (Amudha *et al.* 2005).

UV-B can cause the production of reactive oxygen species (ROS) which can lead to lipid peroxidation, and damage to DNA and proteins (Hollósy 2002, Kliebenstein *et al.* 2002). According to Baroniya *et al.* (2013), the generation of ROS in soybean decreased in the absence of UV components. It may be possible that lowering the quantity of ROS in the leaves may improve the PSII capacity to harvest light by UV exclusion in the present study. The JIP-test is sensitive to detect stress and provide details on several scales of the PSII photosynthetic machinery's performance (Rastogi *et al.* 2020, Kataria *et al.* 2021). As with CO₂ assimilation, it has been shown that the PI indexes are influenced by an accumulation of factors that affect the functionality of the photosynthetic apparatus (Van Heerden *et al.* 2003). Under ambient UV stress, soybean quantum efficiencies decreased, clearly suggesting a marginally reduced efficiency to process light energy through PSII.

However, the results with the OJIP curve showed that the PSII components are significantly hampered by ambient UV-B. All the examined parameters were altered more dramatically when UV-B and UV-A were excluded together than when only UV-B was excluded. Potential photochemical efficiency or F_v/F_0 measures a plant's ability to use light to produce energy. It refers to the potential activity of PSII photoreaction centers (Lichtenthaler *et al.* 2007, Faseela *et al.* 2020). Plants have a greater ability to utilize light energy when F_v/F_0 and F_v/F_m are higher (Maxwell and Johnson 2000). When it comes to the particular fluxes per active PSII RCs, ambient UV had a larger ABS/RC (absorption flux of photons per active RC) value (Fig. 2A). Possibly, this may be a result of the greater size of the antenna per PSII RC. The antennae size is considered to average values as total absorbing Chl per total fully active PSII RCs (Q_A reducing) (Strasser and Strasser 1995, Van Heerden *et al.* 2003). Due to the increasing antenna size of active RCs, the antenna size of an active reaction center (ABS/RC) decreased in plants cultivated in UV-exclusion filters (Fig. 2A). The maximum rate at which an exciton is captured by the RC, lowering Q_A , is represented by the ratio, TR_0/RC . An increase in this ratio showed that all of the Q_A has been reduced, but due to UV stress, it is unable to oxidize back, inhibiting the ability of Q_A to transfer electrons to Q_B effectively and causing the most energy to be wasted in dissipation. The largest rise in this ratio by excluding solar UV-B and UV-A/B was found in soybean var. Hardee because ET_0/RC is solely represented by active centers. The ratio of the total untrapped excitation energy dissipation from

all RCs to the number of active RCs is known as DI_0/RC . The ratios of active/inactive RCs affect dissipation. In the presence of UV-B stress (control), it was observed that the DI_0/RC ratio was higher in the leaves of soybean varieties Hardee, PK-1029, and NRC-7 as the number of inactive centers increased. This occurs as a result of the photon not being captured by the inactive centers, which led to an enhancement in the number of untrapped photons. Thus, it demonstrates that the collective response of individual fluxes per active PSII RCs into $PI_{(ABS)}$, confirms the lesser performance of control plants. A greater potential for electron transport capacity per leaf CS in UV-B and UV-A/B-excluded plants is evident from the higher electron transport per active PSII RC (ET_0/RC) and the increased number of active PSII RCs per leaf CS in UV-excluded plants (Fig. 2B). This view is in line with earlier studies conducted on *Salix arctica* by Albert *et al.* (2005) and C₃ and C₄ plants by Kataria *et al.* (2013) under ambient and UV-excluding conditions.

The productivity of photosynthetic metabolites is correlated with the quantum yield of electron transport (Φ_{E_0}) and $PI_{(ABS)}$ both of which were significantly greater in UV-excluded soybean plants (Strasser *et al.* 2000). They provide a method for diagnosing the capacity for biomass production. An increase in fresh and dry mass also shows the addition of biomass as a result of increased protein and carbohydrate accumulation (Guruprasad *et al.* 2007). The considerable reprogramming from primary to secondary metabolism seems to be stimulated by UV radiation (Jordan 2002). Despite, several studies demonstrating PSII sensitivity to UV-B radiation (Melis *et al.* 1992), the impairment in the Calvin cycle, which may be mediated by Rubisco, is more likely to be the cause of the reduced CO₂ assimilation caused by UV-B (Nogués and Baker 1995, Lesser *et al.* 1996, Allen *et al.* 1999, Kataria *et al.* 2013).

The performance indices incorporate variations in response patterns for quantum efficiency and phenomenological fluxes. Their enhancement determines clearly that UV-B and UV-A/B-excluded plants use light energy more efficiently overall per CS of the leaf sample. The PI indices are sensitive and overall integrating criteria for PSII performance is therefore supported by these response patterns (Clark *et al.* 2000, Strasser *et al.* 2000). These results collectively showed that the chloroplasts of plants exposed to ambient UV-B radiations have a decreased capacity for electron transport capability and PSII performance.

Overall, all the soybean varieties analyzed in the present experiments showed higher values of stomatal conductance and net photosynthesis with solar UV exclusion. Similar findings of increased net photosynthesis have also been shown in poplar (Schumaker *et al.* 1997), maize and mung bean (Pal *et al.* 1997), wheat and pea (Pal *et al.* 2006), and cotton (Dehariya *et al.* 2011). In pea, *Commelina communis*, and *Brassica napus*, stomatal conductance is directly affected by UV-B (Nogués *et al.* 1999). The reduced photosynthetic rate for plants exposed to actual UV-B irradiation is consistent with other earlier studies (Baker *et al.* 1997, Keiller

and Holmes 2001, Keiller *et al.* 2003) that demonstrate field-based photosynthesis suppression. Arguments have been made that these decreases are the result of unreasonably high UV-B irradiances (Allen *et al.* 1998). As a result, Lee *et al.* (1999) showed *in vivo* on the plant *Capsicum annuum* that a restriction on photosynthetic ability only becomes apparent after a 40% loss of functioning PSII complexes. In this work, it was shown that solar UV-B diminishes the potential of primary photochemistry due to reduced phenomenological fluxes, quantum efficiencies, performance indices, and the number of active RCs. Of note, the UV-triggered loss of P_N was attributable to both mesophilic (reduction of photochemistry performance) and stomatal limitations (constraint of g_s values and reduction in CO_2 uptake) in individuals of Hardee, NRC-7, and PK-472 varieties. Conversely, because of the slight changes observed in g_s for PK-1029 individuals subjected to UV exclusion, it is conceivable that only in this variety the mesophyll limitations were the main determinant undergoing the decline of P_N when subjected to UV exposure.

On the bases of the higher amplitude of the reduction in P_N values observed between control *vs.* UV-excluded plants of each variety, it seems reasonable to hypothesize that Hardee (–45.3% in control *vs.* UV-B and UV-A/B on average) and PK-472 (–35.7% in control *vs.* UV-B and UV-A/B on average) were the most sensitive varieties to UV exposure than PK-1029 (–13.4%) and NRC-7 (12.8%).

In earlier research, the cumulative stress response index was thought to be a trustworthy sign of plant sensitivity to ambient UV-B radiation (Kataria and Guruprasad 2012a,b). The present finding revealed that all four varieties of soybean had negative CSRIs, indicating a detrimental effect of UV-B on soybean. The four varieties of soybean studied were ranked according to their CSRI values, with Hardee being the most sensitive (CSRI of –384) and PK-1029 being the least susceptible (CSRI of –85) when UV-A/B were excluded from sun radiations. PK-1029 had a CSRI of –44 when solar UV-B was excluded, and Hardee has a CSRI of –292. As a result, PK-1029 was more susceptible to ambient UV-B levels, Hardee was more sensitive to both UV-B and UV-A levels. These results demonstrated that ambient UV exclusions increased soybean genotype photosynthetic efficiency and channeled the additional carbon fixation into greater biomass accumulation, which improved the soybean crop yield.

Conclusion: Our results confirmed that UV exclusions enhanced the efficiency of PSII and photosynthesis in soybean varieties and increased carbon fixation towards enhanced dry matter accumulation and improvement of yield. This may be due to increased light-utilization efficiency as indicated by Chl *a* fluorescence data. The present results give the information that the presence of UV-B and UV-A components in sunlight was the reason for the decline in carbon assimilation and alteration in photosystem components in soybean varieties. These responses showed intraspecific variations in soybean varieties towards the UV-B and UV-A/B radiations.

The soybean varieties Hardee and PK-472 showed more responsiveness in photosynthetic parameters after solar UV exclusion and it indicates that these varieties are more sensitive to the current level of UV-B radiations as compared to other varieties PK-1029 and NRC-7.

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Appendix. Some parameters used in studying Chl fluorescence.

ABS/RC – light absorption flux (for PSII antenna chlorophylls) per reaction center (RC)

DI₀/RC – dissipation energy flux per reaction center (RC) (at t = 0)

ET₀/RC – maximum electron transport (maximum) flux (further than Q_A⁻) per reaction center (RC) (at t = 0)

TR₀/RC – trapped (maximum) energy flux (leading to Q_A reduction) per reaction center (RC) (at t = 0)

F_v/F₀ – a value that is proportional to the activity of the water-splitting complex on the donor side of the PSII

φ_{p₀} = TR₀/ABS = F_v/F_m = [1 - (F₀/F_m)] – maximum quantum yield of primary photochemistry

PI_(ABS) – performance index that is calculated as: (RC/ABS) × [φ_{p₀}/(1 - φ_{p₀})] × [ψ₀/(1 - ψ₀)], where RC is for reaction center; ABS is for absorption flux; φ_{p₀} is for maximal quantum yield for primary photochemistry; and ψ₀ is for the quantum yield for electron transport

SFI_(ABS) – an indicator of PSII ‘structure and functioning’, calculated as (RC/ABS) × φ_{p₀} × ψ₀