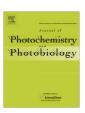
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Assessing genotypic variability of cowpea (Vigna unguiculata [L.] Walp.) to current and projected ultraviolet-B radiation

Shardendu K. Singh a, Giridara-Kumar Surabhi a, W. Gao b, K. Raja Reddy a,*

^a Mississippi State University, Department of Plant and Soil Sciences, 32 Creelman Street, Box 9555, Mississippi State, MS 39762, USA

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ABSTRACT

The current and projected terrestrial ultraviolet-B (UV-B) radiation affects growth and reproductive potential of many crops. Cowpea (Vigna unguiculata [L.] Walp.), mostly grown in tropical and sub-tropical regions may already be experiencing critical doses of UV-B radiation due to a thinner ozone column in those regions. Better understanding of genotypic variability to UV-B radiation is a prerequisite in developing genotypes tolerant to current and projected changes in UV-B radiation. An experiment was conducted in sunlit, controlled environment chambers to evaluate the sensitivity of cowpea genotypes to a range of UV-B radiation levels. Six cowpea genotypes [Prima, California Blackeye (CB)-5, CB-27, CB-46, Mississippi Pinkeye (MPE) and UCR-193], representing origin of different geographical locations, were grown at 30/22 °C day/night temperature from seeding to maturity. Four biologically effective ultraviolet-B radiation treatments of 0 (control), 5, 10, and 15 kJ m $^{-2}$ d $^{-1}$ were imposed from eight days after emergence to maturity. Significant genotypic variability was observed for UV-B responsiveness of eighteen plant attributes measured. The magnitude of the sensitivity to UV-B radiation also varied among cowpea genotypes. Plants from all genotypes grown in elevated UV-B radiation were significantly shorter in stem and flower lengths and exhibited lower seed yields compared to the plants grown under control conditions. Most of the vegetative parameters, in general, showed a positive response to UV-B, whereas the reproductive parameters exhibited a negative response showing the importance of reproductive characters in determining tolerance of cultivars to UV-B radiation. However, all cultivars, except MPE, behaved negatively to UV-B when a combined response index was derived across parameters and UV-B levels. Based on the combined total stress response index (C-TSRI) calculated as sum of individual vegetative, physiological and reproductive component responses over the UV-B treatments, the genotypes were classified as tolerant (MPE), intermediate (CB-5, CB-46 and UCR-193) and sensitive (CB-27 and Prima) to UV-B radiation. The differences in sensitivity among the cowpea genotypes emphasize the need for selecting or developing genotypes with tolerance to current and projected UV-B radiation.

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1. Introduction

Even though ultraviolet-B (UV-B, 280–320 nm) represents a small fraction of total electromagnetic spectrum, exposure to UV-B at the current and projected levels is known to elicit a variety of responses by all living organisms including crop plants [1,2]. The amount of UV-B radiation received on the Earth's surface is closely correlated with the thickness of the stratospheric ozone (O₃) column. Relative to the 1970s, the midlatitudes O₃ column losses for the 2002–2005 periods are approximately 3% in the Northern and 6% in the Southern hemispheres [3]. Current global distribution of mean erythemal daily doses of UV-B radiation be-

tween the latitude 40 °N and 40 °S during summer ranges from 2 to 9 kJ m $^{-2}$ [4] which are comparatively higher than the earlier measurement of 2–6 kJ m $^{-2}$ d $^{-1}$ in 1994 [5]. The three-dimensional Chemistry-Climate models estimates indicate that ground-level UV-B radiation is currently near its maximum levels and is expected to revert to the pre-1980s level at the midlatitudes by 2040–2070, if all member countries implement the Montreal Protocol [3]. Non-compliance by member countries to implement the protocol would delay the recovery or even prevent the recovery of the ozone layer. Therefore, depletion of stratospheric O_3 and consequent increase in the terrestrial UV-B radiation has and will continue to raise interest in understanding the deleterious effects of UV-B radiation on plants.

Cowpea plays an important role in the cropping systems of tropical and sub-tropical, arid and semi-arid regions that cover a wide range of latitudes (45 °N–35 °S) on the globe [6,7]. Typically, the daily doses of UV-B radiation in the cowpea growing regions in

b USDA-UV-B Monitoring Network, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

^{*} Corresponding author. Tel.: +1 662 325 9463; fax: +1 662 325 9461. E-mail address: krreddy@pss.msstate.edu (K.R. Reddy).

¹ Present address: Division of Biology, Kansas State University, Manhattan, KS 66506. USA

USA ranges from 0.02 to 8.75 kJ m $^{-2}$ d $^{-1}$ [8], however, on the global scale, maximum UV-B radiation could reach up to 8–10 kJ m $^{-2}$ d $^{-1}$ [9].

Previous reviews and published studies clearly demonstrate the extent of damage caused by both ambient [10-13] and elevated UV-B radiation [2,11,14-16] on morphological, physiological, biochemical, and molecular level processes of crop plants which varied widely among species and among cultivars of the same species. In a recent review, Kakani et al. [2] reported that enhanced UV-B radiation affects most crop growth processes directly through several first order effects including reductions in photosynthesis and vegetative growth, leading to lower yield. Moreover, UV-B in combination with other abiotic stressors can drastically modify the magnitude and direction of plant responses [14]. Premkumar and Kulandaivelu [17] reported that enhanced UV-B, simulating 20% O₃ depletion, markedly alleviated the adverse effect of magnesium deficiency in cowpea, whereas, the impacts of elevated UV-B aggravated the negative effects of temperature on growth and development of soybean [18].

In general, plants may tolerate small increases in UV-B by protective mechanisms such as reducing the transmittance of UV-B through the epidermis by producing UV-B absorbing compounds, scattering and reflecting light, quenching free radicals and photorepair of sensitive systems such as nucleic acids [12,15,17]. Most defense mechanisms appeared to be light dependent such as photo-repair system for DNA and the biosynthesis of UV-B absorbing compounds [15,19,20]. Despite the known importance of photosynthetically active radiation (PAR), studies utilizing an unrealistic and unbalanced UV-B and PAR ratio for plant growth are not uncommon resulting in unrealistic plant responses [21]. However, many species appeared to be more sensitive to the UV-B radiation than others even under ambient PAR and such crop species may already be experiencing UV-B stress [10].

Crop economic yield is an important trait for selection of cultivar for a niche environment. Increased concern about the UV-B radiation effects on crops has prompted developing screening tools and methods for tolerance in crop populations [2,22]. The large differences among cultivar responses to UV-B radiation offer a valuable tool for selection process in response to UV-B radiation [2]. Many crops have been screened using various UV-B response indices which were derived from short-term plant growth responses to UV-B [18,22,23]. The reproductive growth and seed yield are important components of plant growth responses to UV-B radiation [18], but have received little attention. Therefore, a seasonlong UV-B exposure on crop plants is needed to understand the mechanisms and causes for crop yield losses.

Noticeable uncertainties exist concerning influence of UV-B radiation on tropical legumes including cowpea plants exposed to both above and below ambient levels of UV-B radiation [9,10,13,24–29]. For instance, cowpea plants did not exhibit a significant change in plant height, leaf area and dry matter when grown under elevated UV-B simulating 15–25% O₃ depletion [26,27]. Contrary to this, studies simulating a similar O₃ depletion caused pronounced decrease in biomass production and photosynthesis [10,28,29]. These inconsistencies could be partially explained by genotypic differences, different growth environments, intensity and duration of UV-B supplementation [2,21]. The supplied UV-B radiation in these studies represents very small additions of absolute energy capable of inducing a variety of responses in biological systems.

Cowpea, a traditional source of livelihood to many rural African populations, has been reported as highly sensitive to UV-B radiation [14,28]. Musil et al. [28] found that cowpea was exceptionally sensitive to UV-B (15% $\rm O_3$ depletion) among the evaluated 17 species native to or largely grown in South Africa. Earlier studies evaluating the UV-B responsiveness of cowpea represented a smaller set of

plant attributes usually measured from part of a plant organ and/or growth stage involving either vegetative, physiological and/or molecular responses expressed for a part of a growing season [17,26–29]. To our knowledge, there are no reports on screening the responses of cowpea genotypes to UV-B radiation based on both vegetative and reproductive growth processes. We hypothesized that UV-B tolerant characteristics are present in cowpea with genotypic variability and when exposed to UV-B, the vegetative traits respond dissimilarly in comparison to the reproductive characteristics. The objectives of this study were to determine the vegetative, physiological and reproductive responses of cowpea genotypes to a range of UV-B radiation and to identify the genotypic variability using several plant attributes and statistical methods.

2. Materials and methods

2.1. Experimental facility

The experiment was conducted in four sunlit, controlled environment chambers known as soil-plant-atmosphere-research (SPAR) units located at the R.R. Foil Plant Science Research Center, Mississippi State (33° 28' N 88° 47' W), Mississippi, USA. SPAR units have the capacity to precisely control temperature, CO₂ concentration, UV-B radiation, and the recommended nutrient and irrigation regimes at determined set points for plant growth studies under near ambient levels of PAR. Each SPAR chamber consists of a steel soil bin (1 m deep by 2 m long by 0.5 m wide) to accommodate the root system, a Plexiglas chamber (2.5 m tall by 2 m long by 1.5 m wide) to accommodate aerial plant parts and a heating and cooling system connected to air ducts that pass the conditioned air through the plant canopy with sufficient velocity (4.7 km h⁻¹) to cause leaf flutter, mimicking field conditions. Variable density black shade cloths around the edge of the plant canopy were adjusted regularly to match the height and to eliminate the need for border plants. The Plexiglas chambers are completely opaque to solar UV-B radiation and transmit 12% UV-A, and more than 95% incoming PAR [30]. During the experiment, the incoming solar radiation (285-2800 nm) outside of the SPAR units measured with a pyranometer (Model 4-8; The Eppley Laboratory Inc., Newport, RI, USA) ranged from 1.5 to 24 MJ m⁻² d⁻¹ with an average of $18 \pm 4 \,\mathrm{MJ}\,\mathrm{m}^{-2}\,\mathrm{d}^{-1}$. The measured solar radiation on most of the days except few cloudy days were above 15 MJ m^{-2} d^{-1} , 3 days $<10 \text{ MJ m}^{-2} \text{ d}^{-1}$ or 6 days $<15 \text{ MJ m}^{-2} \text{ d}^{-1}$. The data acquisition and control systems are networked to provide automatic acquisition and storage of the data from the SPAR units, monitoring the SPAR environments every 10 s throughout the day and night. The operational details and controls of the SPAR chambers have been described by Reddy et al. [31].

2.2. Plant culture

Six genotypes of cowpea representing diverse sites of origin; California blackeye (CB)-5 and CB-46 (University of California, Davis, USA), CB-27 (University of California, Riverside, USA), Mississippi Pinkeye; MPE (Mississippi State University, Mississippi, USA), Prima (Nigeria), and UCR-193 (India) were used in present study [32–34]. The genotypes were seeded in 15 cm diameter and 15 cm deep plastic pots filled with fine sand on 26 July, 2005. After emergence, seven days after sowing, thirty pots having healthy plants, five pots for each genotype and three plants in each pot, were transferred and arranged randomly into each SPAR chamber. The temperature and $\rm CO_2$ were maintained at $\rm 30/22~^{\circ}C$ (day/night) and $\rm 360~\mu L~^{-1}$, respectively, in all chambers. Plants were watered three times a day with full-strength Hoagland's nutrient solution delivered 8:00, 12:00, and 17:00 h to ensure opti-

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