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Exclusion of solar UV components improves growth and performance of *Amaranthus tricolor* varieties

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ABSTRACT

A field experiment was conducted to study the influence of exclusion of solar UV components on the growth responses, gas exchange rates, chlorophyll fluorescence, pigmentation, carboxylation enzymes and foliage yield of four *Amaranthus tricolor* varieties; Arka arunima, Arka suguna, Pusa lalchaulai and Pusa kiran. The plants were grown in specially designed UV exclusion chambers, wrapped with filters that excluded UV-B (<315 nm), UV-A/B (<400 nm) or transmitted ambient UV or lacked filters. Plants grown under ambient UV radiation (280–400 nm) were compared with those grown without UV-B or UV-A/B. The results indicated increased plant height, leaf weight ratio, specific leaf weight and foliage yield in all the four varieties of *A. tricolor* grown without UV-B and UV-A/B compared with those grown under ambient UV. Exclusion of UV significantly increased the total chlorophyll while Chl *a*/*b* ratio decreased. The efficiency of PS II (F_v/F_m), rate of photosynthesis and stomatal conductance significantly enhanced along with a remarkable increase in Carbonic anhydrase, PEP carboxylase and total soluble proteins. Thus UV excluded plants have higher reducing power and increased CO_2 fixation and decreased UV-B absorbing compounds, channelling the additional fixation of carbon towards the improvement of yield in *A. tricolor* varieties. The response for UV exclusion was higher in variety Arka arunima and Arka suguna compared with Pusa kiran and Pusa lalchaulai. UV sensitivity of the *A. tricolor* varieties was in the following sequence – Pusa lalchaulai > Pusa kiran > Arka suguna > Arka arunima. Thus Arka arunima and Arka suguna were most sensitive and Pusa lalchaulai and Pusa kiran the least sensitive varieties to ambient level of UV. The least sensitive varieties may be used in the development of UV-B tolerance mechanisms and also developing new varieties tolerant to higher levels of UV-B in future attempts in plant breeding programmes.

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1. Introduction

Ultraviolet-B radiation (UV-B; 280–315 nm) is an important component of the environment acting as an ecophysiological factor with the potential to alter plant growth and photosynthesis (Ballaré et al., 2011). A global depletion of the stratospheric ozone layer, largely due to the release of chlorofluorocarbons (CFCs) caused by human activities, has resulted in an increase of solar UV-B radiation at the earth's surface. As CFCs can remain in the upper atmosphere, with a half-life ranging from 50 to 150 years, it will take until 2065 to return to the pre-1980 levels providing no further release occurs (UNEP, 2007). Although the UV-B level varies with several factors as latitude, season, time of the day, altitude, cloud cover, surface reflectance and the thickness of the vegetation canopy (Jenkins, 2009). Plants grown in low latitudes are exposed to higher flux of UV-radiation due to greater solar angle as compared with high latitude. A substantial part of India lies in the low stratospheric ozone belt and is expected to receive high flux of UV-B radiation which may injure plants. Sahoo et al. (2005) observed a significant decline in the total ozone column (TOC) at numerous stations in northern India.

UV-B radiation has considerable consequences at many levels, including anatomy, morphology, physiology, biochemistry, phenology and yield, even though these responses varied markedly within and between species (Searles et al., 2001; Kakani et al., 2003). The intraspecific variation to enhanced or supplemental UV-B in terms

Abbreviations: BSA, bovine serum albumin; CA, carbonic anhydrase; DTT, dithiothreitol; EDTA, ethylene diamine tetraacetic acid; FC, filter control; LWR, leaf weight ratio; F_v/F_m, maximum quantum yield of primary photochemistry; OC, open control; Pn, net photosynthesis; $MgSO_4$, magnesium sulphate; MDH, malate dehydrogenase; NADH, nicotinamide adenine dinucleotide; PAR, photosynthetic active radiation; PEP, phosphoenolpyruvate; PEPcase, phosphoenolpyruvate carboxylase; PS II, photosystem II; PVP, polyvinylpyrrolidone; RC, reaction centre; $NaHCO_3$, sodium bicarbonate; SLW, specific leaf weight; gs, stomatal conductance; UAS, UV-B absorbing substances; −UV-B, UV-B exclusion; −UV-A/B, UV-A and UV-B exclusion.

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of morphological parameters has been determined in many crop species, such as barley (Mazza et al., 1999), maize (Correia et al., 1998), wheat (Li et al., 2000), rice (Mohammed and Tarpley, 2011), cucumber (Tapia et al., 2010), buckwheat (Yao et al., 2008) and soybean (Li et al., 2002). Amongst the major UV-B targets are the photosynthetic apparatus. Photosystem (PS II), rather than PS I, is considered to be the most vulnerable target of UV-B (Tyystjärvi, 2008; Yu et al., 2013). Reductions in CO_2 assimilation rate by UV-B may be further mediated through the suppression of chlorophyll synthesis (Kulandaivelu et al., 1991), the inactivation of oxygen evolution, reduction in light-harvesting complexes and disruption of thylakoid membrane integrity, reduction in Rubisco activity (Cicek et al., 2012; Yu et al., 2013).

Much of the early work concerning the effects of UV-B radiation on terrestrial plants was conducted indoors using growth chamber or greenhouse. Many of these reports of UV-B effect were exaggerated and that extrapolation of these results to field responses was not appropriate (Kotilainen et al., 2011). Therefore, more research is needed to assess the impact of UV-B irradiance under more natural or realistic conditions. Experiments using UV-B exclusion by specific filters to remove much of the radiation at shorter wavelength from solar spectrum are most suited to assessing the effects of present day UV-B radiation at particular latitudes (Rousseaux et al., 2004). No information is available in this respect for *Amaranthus*. Earlier studies have shown that *Amaranthus* is a potentially UV-B sensitive species and the growth and yield of *Amaranthus* plants were adversely influenced under supplemental UV-B and ambient UV-B (Singh et al., 2009, 2013; Kataria et al., 2013).

Amaranthus species are being cultivated since centuries as a leafy vegetable, as well as an important subsidiary food grain crop in many parts of the world (Shukla et al., 2003). *Amaranthus* is a C_4 dicot plant, in C_4 photosynthetic carbon metabolism, the initial carboxylation reaction is catalysed by phosphoenolpyruvate carboxylase (PEPcase). PEPcase utilizes bicarbonate rather than CO_2 as the inorganic substrate (O'Leary, 1982). To sustain this process, atmospheric CO_2 entering the mesophyll cells must be rapidly converted to HCO_3^- and this reaction is the critical first step of C_4 photosynthesis (Hatch and Burnell, 1990). Carbonic anhydrase (CA) plays an important role in the acceleration of carbon assimilation, by catalysing the reversible interconversion of CO_2 and HCO_3^-.

To date, there is not enough information about the influence of ambient UV on intraspecific variations in terms of PS II efficiency and enzymes involved in C_4 carbon metabolism like CA and PEP carboxylase. For all these reasons, the present study was intended to assess the impact of ambient level of solar UV by the exclusion of UV-B and UV-A/B on intraspecific variation in *Amaranthus tricolor* varieties. The four varieties of *A. tricolor* namely – Pusa Kiran, Pusa lalchaulai, Arka arunima and Arka suguna were evaluated for their sensitivity to ambient UV radiation in terms of (i) growth, biomass accumulation and yield, (ii) photosynthetic performance (Pigments, PS II efficiency, gas exchange parameters and C_4 carbon metabolism enzymes like; Carbonic anhydrase/PEP carboxylase). We hypothesized that ambient UV-B radiation would affect crop growth, photosynthetic performance and yield of *A. tricolor* varieties. These changes will result in intraspecific differences in morphological, physiological and biochemical changes to UV-B radiation under field conditions.

2. Materials and methods

2.1. Plant material and growth conditions

A field experiment was conducted under natural sunlight at Botanical garden of School of Life Sciences, Devi Ahilya Vishwavidyalaya, Indore (22°44′ N), India. The experiments were carried out during March 2012 to April 2012. Four varieties of *A. tricolor* viz., Pusa Kiran, Pusa lalchaulai, Arka arunima and Arka suguna were grown in the field conditions. The seeds of Pusa Kiran and Pusa lalchaulai were obtained from IARI, New Delhi, India and the seeds of Arka arunima and Arka suguna were obtained from Indian Institute of Horticultural Research, Banglore, India.

The seeds of all the four varieties of *A. tricolor* were sown in the field area of 120 cm × 120 cm in 120 cm rows planted 23 cm apart with 5 cm plant spacing within the row under iron cages of dimensions [150 cm L × 150 cm W × 170 cm H]. Recommended doses (250 kg ha^{-1}) of nitrogen, phosphorus and potassium as urea, super phosphate and muriate of potash (12:32:16) were applied to all plots. The experiment was conducted in a randomized block design and there were three replications each for control and treatments (−UV-B and −UV-A/B). Irrigation was given as and when required for optimal growth of the crops.

2.2. Solar UV-B and UV-A/B exclusion

The iron cages were wrapped with UV cut-off Polyester filters (Garware polyester Ltd., Mumbai) that selectively cut-off UV-B (<315 nm) and UV-A/B (<400 nm) radiation. Two types of control were taken for the present study; plants were grown either in the cages covered with polythene filter that transmits all the ambient solar radiation (filter control FC) or in open field without any filters, exposed to natural solar radiation (open control OC). The transmission characters of these filters were measured by Shimadzu Spectrophotometer (UV-1601) and illustrated in Fig. 1. The filters were erected from the time of germination and were maintained until maturity. The filters were replaced every two weeks as they became brittle because of solarization. The bottom sides of all the cages (0.35 m above ground) were left uncovered to allow normal ventilation. The frames received full solar radiation for most of the day without any shading. Temperatures both inside and outside each enclosure were monitored daily using max/min thermometers. The average temperature at outside raised from 25 °C to 32 °C during the growing period. No significant increase in the temperature was measured inside the chambers compared with ambient air due to the passive ventilation system.

2.3. Radiation measurement

Absolute solar irradiance with and without UV-B or UV-A/UV-B was measured using a radiometer (Solar light Co. Inc. (PMA 2100), Glenside, PA, USA) with the help of three detectors; PAR (PMA-2132), UV-A (PMA-2110) and UV-B (PMA-2106) under all treatments between 11.30 am and 12.00 pm during the

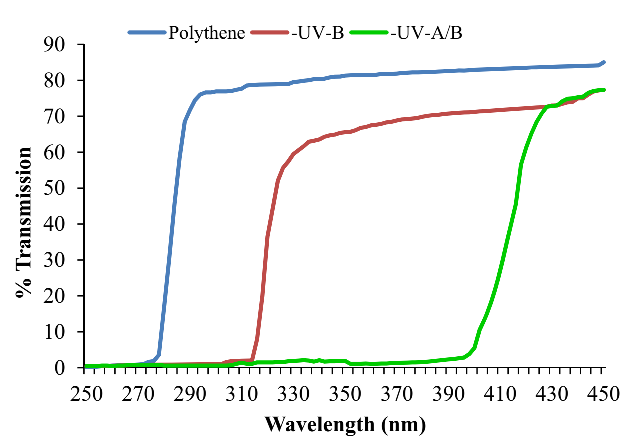

Fig. 1. Transmission spectra of UV cut off filters and polyethne filter used for raising *Amaranthus tricolor* varieties under field conditions.

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