



Cotton responses to ultraviolet-B radiation: experimentation and algorithm development

K. Raja Reddy^{a,*}, V.G. Kakani^a, D. Zhao^a, A.R. Mohammed^a, Wei Gao^b

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

^b USDA UV-B Monitoring and Research Program, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

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Abstract

The potential impact of an increase in solar ultraviolet-B (UV-B) radiation due to human activity on higher plants has been the subject of many studies. Little work has been carried out so far on cotton responses to enhanced UV-B radiation. The objective of this study was to determine whether or not the current and projected increases in UV-B levels affect cotton growth and development, and to quantify and develop UV-B radiation functional algorithms that can be used in simulation models. Two experiments were conducted during the summer of 2001 using sunlit plant growth chambers in a wide range of UV-B radiations under optimal growing conditions. Leaves exposed to UV-B radiation developed chlorotic and necrotic patches depending on the intensity and length of exposure. Along with changes in visible morphology, cotton canopy photosynthesis declined with increased UV-B radiation. The decline in canopy photosynthesis was partly due to loss of photosynthetic pigments and UV-B-induced decay of leaf-level photosynthetic efficiency (maximum photosynthesis) and capacity (quantum yield) as the leaves aged. The total leaf area was less due to smaller leaves and fewer leaves per plant. Less plant height was closely related to a shorter average internode length rather than a fewer mainstem nodes. The UV-B did not affect cotton major developmental events such as time taken to square, time to flower, and leaf addition rates on the mainstem. Lower biomass was closely related to both smaller leaf area and lower photosynthesis. The critical limit, defined as 90% of optimum or the control, for stem elongation was lower (8.7 kJ m^{-2} per day UV-B) than the critical limit for leaf expansion (11.2 kJ m^{-2} per day UV-B), indicating that stem elongation was more sensitive to UV-B than leaf expansion. The critical limits for canopy photosynthesis and total dry weight were 7 and 7.3 kJ m^{-2} per day, respectively. The identified UV-B-specific indices for stem and leaf growth and photosynthesis parameters may be incorporated into cotton simulation models such as GOSSYM to predict yields under present and future climatic conditions.

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1. Introduction

Global climate is the result of a complex system of atmospheric processes and their products. Past and

present-day anthropogenic activities are clearly causing major changes in the atmospheric chemistry and climate. The concentration of carbon dioxide ($[\text{CO}_2]$) in the atmosphere has increased by more than 28% since the beginning of the Industrial Revolution mainly because of the burning of fossil fuels and deforestation (Houghton et al., 2001; Reicosky et al., 2000). The most recent and future scenarios of greenhouse

* Corresponding author. Tel.: +1-662-325-9463;

fax: +1-662-325-9461.

E-mail address: krreddy@ra.msstate.edu (K.R. Reddy).

gases in the atmosphere indicate that $[\text{CO}_2]$ could increase from current levels of approximately $360 \mu\text{l l}^{-1}$ to between 540 and $970 \mu\text{l l}^{-1}$ by the end of the 21st century (Houghton et al., 2001). Furthermore, global circulation models (GCMs) project that the increase in global surface air temperature could range from 1.4 to 5.8°C because of a projected increase in the concentrations of all greenhouse gases by the end of the 21st century. In addition to their contribution to global warming, chlorofluorocarbons (CFCs) also deplete the earth's protective stratospheric ozone layer (Molina and Rowland, 1974; Dentener et al., 2001). Continued depletion of the earth's stratospheric ozone layer is of concern as the ozone column is the primary attenuator of solar ultraviolet-B (UV-B) radiation (280–320 nm). Reductions in the ozone column have led to substantial increases in UV-B radiation at earth's surface with the amount dependent on atmospheric and geographic factors (Madronich et al., 1998; WMO, 1995). As CFCs can remain in the upper atmosphere for 40–150 years (Molina and Rowland, 1974), it is probable that terrestrial plants will experience increased levels of UV-B for many more years, and stratospheric O_3 recovery is not expected much before 2010 (Hofmann and Pyle, 1999). Current growth rates however, are slightly negative for CFC-11 and CFC-113 (Prinn et al., 2000).

The UV-B radiation is readily absorbed by biomolecules such as amino acids, pigments and nucleic acids (Caldwell and Flint, 1994; Sullivan and Teramura, 1989). In addition to the intensive investigations on growth and physiological responses to UV-B radiation on many field crops such as bean (*Phaseolus vulgaris* L.) (Deckmyn et al., 1994), maize (*Zea mays* L.) (Correia et al., 1998, 1999; Mark and Tevini, 1996), pea (*Pisum sativum* L.) (Day et al., 1996; Mepsted et al., 1996), rice (*Oryza sativa* L.) (Dai et al., 1992; Teramura et al., 1990), soybean [*Glycine max* (L.) Merr.] (Miller et al., 1994; Sinclair et al., 1990; Teramura et al., 1990), sunflower (*Helianthus annuus* L.) (Battaglia and Brennen, 2000), and wheat (*Triticum aestivum* L.) (Li et al., 2000; Teramura et al., 1990), several reviews have recently summarized the effects and consequences of UV-B radiation on major agricultural and horticultural crops, and nonagricultural species (Allen, 1990, 1994; Allen et al., 1998; Caldwell et al., 1998; Groth and Krupa, 2000; Krupa and Kickert, 1989; Teramura and Sullivan, 1994). The inferences from these studies and reviews are that

plant sensitivities to UV-B radiation differ among species and cultivars within a species; however, little is known about the responses of cotton (*Gossypium hirsutum* L.), a major economic crop grown on over 32 Mha worldwide and over 5 Mha in the United States (<http://www.ers.usda.gov/briefing/cotton>).

Cotton and all other crops cultivated between 40°N and 40°S latitudes are already experiencing UV-B doses of $2\text{--}10 \text{ kJ m}^{-2}$ per day depending on location and season (http://www.toms.gsfc.nasa.gov/ery_uv/ery_uv1.html). The UV-B radiation is projected to further increase in the future. It is hypothesized that current and projected increases in UV-B radiation can alter cotton growth and development. An understanding of the effects of solar UV-B radiation on cotton would provide information about the causes of changes in growth, development, and physiology. Therefore, the objectives of this study were to examine the effects of enhanced UV-B radiation on cotton morphology, phenology, growth, and physiology, and to quantify and develop UV-B radiation-specific functional algorithms that can be used in cotton simulation models.

2. Materials and methods

2.1. Soil–plant–atmosphere-research (SPAR) units

Two experiments were conducted at the Mississippi Agriculture and Forestry Experiment Station, Mississippi State ($33^\circ 28' \text{N}$, $88^\circ 47' \text{W}$), Mississippi, USA in 2001 using SPAR units (Fig. 1). Details of the SPAR unit operation and control have been described by Reddy et al. (2001). The SPAR units are located outdoors and use solar radiation as the light source. Temperature and CO_2 can be controlled at predetermined set points. Each SPAR unit consists of a steel soil bin (1 m deep, 2 m long, 0.5 m wide) to accommodate the root system, and a Plexiglas chamber (2.5 m tall, 2.0 m long, 1.5 m wide) to accommodate aerial plant parts, a heating and cooling system, and an environmental monitoring and control system. The Plexiglas allows 97% of the visible solar radiation to pass without spectral variability in absorption and is opaque to solar ultraviolet radiation.

Air ducts located on the northern side of each SPAR unit connect the heating and cooling devices to



Fig. 1. Naturally lit controlled-environment chambers known as SPAR units used in the study.

each unit. Conditioned air is passed through the plant canopy with sufficient velocity to cause leaf flutter (4.7 km h^{-1}) and is returned to the air-handling unit just above the soil level. Chilled ethylene glycol is supplied to the cooling system via several parallel solenoid valves that open or close depending on the cooling requirement. Two electrical resistance heaters provide short pulses of heat, as needed, to fine-tune the air temperature. Chamber air temperature, $[\text{CO}_2]$, and soil watering in each SPAR unit, as well as continuous monitoring of all-important environmental and plant gas exchange variables, were controlled by a dedicated computer system (Digital, Pro 380, Digital Equipment, Maynard).

Temperatures in all units were maintained at $30/22^\circ\text{C}$ (day/night) during the experiments. Air temperature in each SPAR unit was monitored and adjusted every 10 s throughout the day and night and maintained within set points $\pm 0.5^\circ\text{C}$. The daytime temperature was initiated at sunrise and returned to the nighttime temperature 1 h after sunset. The $[\text{CO}_2]$

in each SPAR unit was monitored and adjusted every 10 s throughout the day, and maintained within set points $360 \pm 10 \mu\text{l l}^{-1}$ during the daylight hours.

2.2. Plant culture

Cotton cv. NuCOTTN 33B, a midseason Upland cotton variety, was used in both the experiments. The seeds were sown on 4 June 2001 in Experiment I and on 1 August 2001 in Experiment II in the soil bins, filled with fine sand, of the SPAR units. Each SPAR unit had three rows of five plants per row, with each row 0.67 m apart. Fifty percent emergence was observed 5 days after sowing in both experiments.

Plants were irrigated three times a day with half-strength Hoagland's nutrient solution delivered at 0800, 1200 and 1700 h with an automated, and computer-controlled drip system to provide favorable nutrient and water conditions for plant growth (Hewitt, 1952). Variable-density shade cloths placed around the edges of plants at emergence were adjusted regularly to

match plant heights, simulating the presence of other plants and eliminating the need for border plants.

2.3. UV-B radiation treatments

In Experiment I, five UV-B radiation treatments, zero (control, no UV-B), and a total daily dose of biologically effective UV-B radiation of 4, 8, 12 and 16 kJ m^{-2} were imposed soon after emergence. In Experiment II, three UV-B treatments of zero (control, no UV-B), and two total daily doses of biologically effective UV-B radiation of 8 and 16 kJ m^{-2} per day were imposed from emergence as in Experiment I. The UV-B doses imposed in Experiment I simulated 5, 10, 15 and 30% depletion of stratospheric ozone (Madronich et al., 1998). The 8 kJ m^{-2} per day treatment is near natural solar UV-B levels during June–July months in Mississippi (http://www.toms.gsfc.nasa.gov/ery_uv/ery_uv1.html; <http://www.uvb.nrel.colostate.edu/UVB/>). Although the square-wave UV-B supplementation systems in controlled environments provide disproportionate spectral conditions on cloudy days, they are particularly useful for quantifying the growth and developmental responses of plants to allow modeling the impact of UV-B without the interacting effects of other variables.

In both experiments, UV-B radiation was delivered to plants for 8 h from 0800 to 1600 h by UV-313 lamps (Q-Panel Company, Cleveland, OH) driven by 40 W dimming ballasts. To filter UV-C radiation ($<280 \text{ nm}$), the lamps were wrapped with solarized 0.07 mm cellulose diacetate (CA) film (JCS Industries Inc., La Mirada, CA). The CA on the lamps was changed at regular intervals to account for the degradation of the CA properties. Eight UV-B lamps were arranged on the aluminum frame to provide a uniform UV-B radiation over the canopy. The UV-B energy delivered at the top of the plant canopy was checked daily with a UVX digital radiometer (UVP Inc., San Gabriel, CA) and calibrated against an Optronic Laboratory (Orlando, FL) Model 754 Spectroradiometer, which was used to initially quantify lamp output. The lamp power was adjusted, as needed at 1000 h to maintain the respective UV-B radiation levels. The distance from lamps to the top of plants was always maintained at 0.5 m throughout the experiment. In the control units, unilluminated bulbs with frame were placed. The average

daily doses of biologically effective UV-B during the experiments were 4.04 ± 0.03 , 7.81 ± 0.04 , 11.64 ± 0.08 and $15.29 \pm 0.12 \text{ kJ m}^{-2}$ per day for the intended 4, 8, 12 and 16 kJ m^{-2} per day UV-B radiation treatments, respectively in Experiment I and 7.63 ± 0.05 and $15.19 \pm 0.08 \text{ kJ m}^{-2}$ per day for the intended 8 and 16 kJ m^{-2} per day UV-B treatments, respectively in Experiment II.

2.4. Growth and developmental measurements

Nodes were counted and plant heights were measured on nine plants from the three rows (three plants per row) in each unit at 3-day intervals. Daily observations were made for appearance of first square and first flower. Leaf lengths were measured on all expanding mainstem leaves at 3-day intervals on nine plants. The leaf length measurements were subsequently converted to leaf areas by developing a relationship between the lengths of different leaves and leaf areas measured using the LI-3100 leaf area meter (LI-COR Inc., Lincoln, NE). The leaf area was calculated using the equation, $A = 7.4585 - 0.1688L + 0.097L^2$ ($R^2 = 0.99$), where A is the area in cm^2 and L the length in mm.

Final harvest was carried out 43 days after emergence (DAE) in Experiment I and 66 DAE in Experiment II. The harvested plants were separated into different plant components, dried to constant weight and weighed to determine biomass. Bolls and squares were counted at the end of the study in both experiments.

2.5. Leaf photosynthesis

In the second experiment, net photosynthetic rates (P_n) of the uppermost, fully expanded mainstem leaves from five plants in each treatment were measured between 1000 and 1200 h using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE) at regular intervals starting 20 DAE. When measuring P_n , the photosynthetic photon flux density (PPFD), provided by a 6400-02 LED light source, was set to $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The temperature in the leaf cuvette was set to 30°C , and $[\text{CO}_2]$ was set to $360 \mu\text{l l}^{-1}$. In addition to the temporal trends in leaf photosynthesis measurements, photosynthetic light responses were measured at 38 DAE.

To determine the influence of UV-B radiation on leaf aging, leaf maximum net photosynthesis was measured at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ from three leaves from three different plants starting from 5 days after leaf unfolding. The measurements were continued for 35 days. Photosynthetic light response curves were also generated 24 days after leaf unfolding in each treatment. Quantum yield was determined from the initial slope of the light response curves when the light was limiting and expressed as $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon.

2.6. Canopy photosynthesis

In both experiments, canopy photosynthesis was measured employing a mass balance approach in each chamber throughout the experiment (Reddy et al., 1995; Acock et al., 1985). Each SPAR growth chamber and a fan-coil box formed a semi-closed system for the measurement of CO_2 fluxes. The Plexiglas chamber containing the plants, ducts, and cooling system was sealed. The $[\text{CO}_2]$ within a SPAR unit was monitored at 10 s intervals and controlled at predetermined levels. An absolute infrared gas analyzer, calibrated weekly, was used to monitor and control $[\text{CO}_2]$ to within $\pm 10 \mu\text{l CO}_2 \text{l}^{-1}$ air of the set point. Commercial grade CO_2 was injected through a system including a pressure regulator, solenoid and needle valves, and a calibrated flowmeter. The flowmeters were calibrated with a Brooks's gas displacement apparatus at the beginning and at the end of each experiment. The time intervals during which the solenoid valves opened were monitored by the computer indicating the amount of gas injected. Carbon dioxide flow rates were recorded three times a day and converted into mass quantity using gas corrections for temperature and pressure. A leakage test was performed each night to derive a correction factor for losses of CO_2 from the chamber (Acock and Acock, 1989). All CO_2 exchange rate data were obtained every 10 s and integrated over 900 s intervals throughout the day-lit period. The corresponding incident PPFD was also measured by monitoring with a 200 SB pyranometer (LI-COR Inc., Lincoln, NE) and summarized with a data acquisition system at 900 s intervals. Data for canopy net CO_2 exchange rates (P_n) were summarized over the same time intervals. The curves of P_n vs. PPFD were fitted with

a quadratic equation, and canopy photosynthesis, expressed as $\text{mg CO}_2 \text{m}^{-2} \text{s}^{-1}$, at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD was estimated from the light response curves during the last 10 days in each of the experiment.

2.7. Analysis of data

Statistical analysis was conducted by using analysis of variance (ANOVA) procedures (SAS Institute Inc., 1997). The least significant difference (LSD) tests at $P = 0.05$ were employed to distinguish among treatments for the growth and physiological parameters measured in the study. The standard errors of each mean were also calculated and presented in the graphs and tables as error bars. Regression analysis was carried out for determining the UV-B radiation indices for various growth and developmental processes (SAS Institute Inc., 1997).

3. Results and discussion

3.1. Photosynthetic light response curves

Measuring and analyzing the functional responses of CO_2 assimilation to light allow one to assess the influence of UV-B radiation on photosynthetic damage. The light response curves on the topmost, fully expanded leaves on the mainstem indicated a 60% decrease in net photosynthesis (P_n) in 16kJ m^{-2} per day (high) UV-B treatment compared to the control (Fig. 2A). Photosynthetic rate saturated at a lower light intensity at the high UV-B radiation treatment, approximately $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. However there was not a significant ($P > 0.05$) difference between the control and the 8kJ m^{-2} per day of UV-B treatments, and P_n saturated at about $1700 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD in both the treatments (Fig. 2A).

3.2. Temporal photosynthesis trends

The daily effects of UV-B radiation and cumulative dose response on leaf gas exchange can be readily seen in Fig. 2B. Temporal trends of P_n of the topmost, fully expanded leaves on the mainstem, measured at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, indicated no significant ($P > 0.05$) differences between the control and the

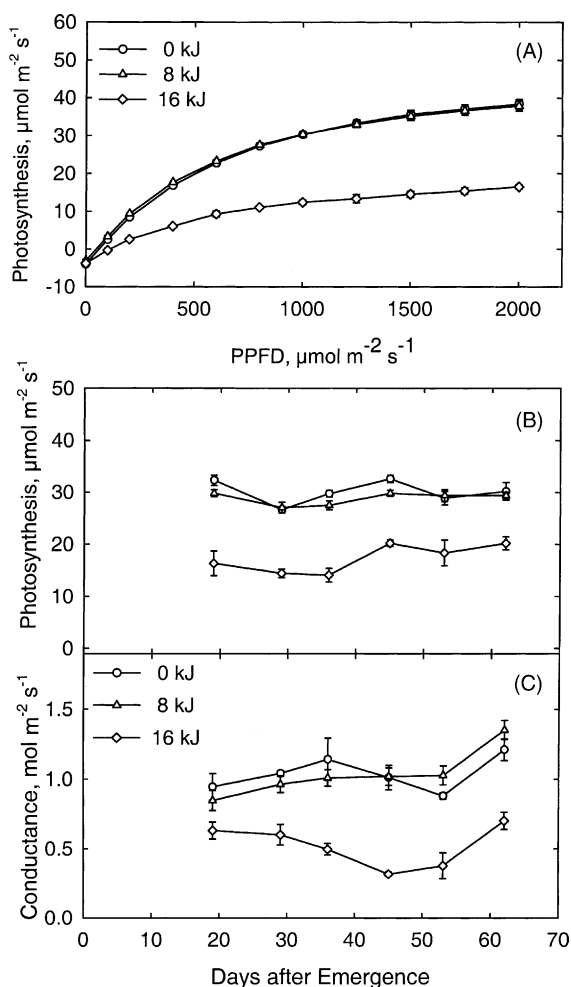


Fig. 2. Influence of (A) UV-B radiation and PPFD on cotton photosynthetic light response curves of topmost, fully expanded leaves on the mainstem, and temporal trends of (B) photosynthesis and (C) stomatal conductance measured at 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD of the same leaves. Each vertical bar indicates \pm S.E. of five observations (Experiment II).

8 kJ m^{-2} per day UV-B treatment similar to the observations from the light response curves. Stomatal conductance followed similar declines as that of the P_n rates of topmost, fully expanded leaves (Fig. 2C). At the high UV-B treatment, there was significantly ($P < 0.05$) lower P_n and stomatal conductance, 43% compared to the control (Fig. 2B and C). Intercellular CO_2 concentration, on the other hand, did not differ among the UV-B treatments (Table 1).

Based on the fact that higher UV-B radiation lowers the light utilization efficiency (Fig. 2A), maximum photosynthesis (Fig. 2B) and conductance (Fig. 2C), it is concluded that higher UV-B radiation (16 kJ m^{-2} per day) has both direct and indirect effects on cotton leaf photosynthesis. Similar reductions in photosynthesis were observed in other crop species such as soybean (Vu et al., 1981) and rice (Teramura et al., 1990). Noguez et al. (1999) also reached a similar conclusion that there is a direct effect of UV-B radiation on stomatal conductance in addition to that caused by changes in mesophyll photosynthesis of pea, Asiatic dayflower (*Commelina communis* L.), and oilseed rape (*Brassica napus* L.) plants. Decreased leaf photosynthesis and stomatal conductance were not associated with intercellular $[\text{CO}_2]$ (C_i) (Table 1). Therefore, elevation of C_i is indirect evidence that mesophyll photosynthetic capacity was reduced. This is also evident from lower light utilization efficiency in the higher UV-B radiation treated plants compared to the plants without the UV-B radiation treatment. Factors limiting cotton leaf photosynthesis may be associated with changes in activities of enzymes involved in carbon assimilation or the capacity for regeneration of RuBP (Ziska and Teramura, 1992; Allen et al., 1997), although we did not investigate these physiological processes. Other investigations in similar studies have indicated that high UV-B radiation caused the loss of RuBP regeneration (Ziska and Teramura, 1992), Rubisco (Allen et al., 1997) or PSII damage (Correia et al., 1999) in several other species.

3.3. Photosynthesis and leaf age relationships

To study age and photosynthesis relationships, leaf gas exchange measurements were monitored on 10th leaf on the mainstem from 5 to 35 days after leaf unfolding (Fig. 3A and B). Averaged across measurement days, there was 72% lower photosynthesis in the high UV-B treated plants compared to the control. The slopes appear similar over time (Fig. 3B). Therefore, the leaf P_n decreased as plants aged. Photosynthetic rate saturated at a much lower light level, 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, compared to the light saturation observed for the control and 8 kJ m^{-2} per day UV-B treatments. Similar to the topmost, fully expanded leaf measurements, there was no significant difference between the control and the 8 kJ m^{-2} per

Table 1

Effects of UV-B radiation on leaf photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$), internal CO_2 concentration ($\mu\text{l l}^{-1}$) and light-use efficiency ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}^{\text{a}}$)

Parameter	UV-B radiation (kJ m^{-2} per day)		
	0	8	16
Photosynthesis	$30.10 \pm 0.90 \text{ a}^{\text{b}}$	$28.80 \pm 0.50 \text{ a}$	$17.30 \pm 1.12 \text{ b}$
Conductance	$0.90 \pm 0.10 \text{ a}$	$0.90 \pm 0.10 \text{ a}$	$0.50 \pm 0.10 \text{ b}$
Internal CO_2 concentration	$259.60 \pm 7.10 \text{ a}$	$264.70 \pm 7.40 \text{ a}$	$271.70 \pm 6.10 \text{ a}$
Light-use efficiency	$0.10 \pm 0.00 \text{ a}$	$0.10 \pm 0.00 \text{ a}$	$0.03 \pm 0.00 \text{ b}$

^a The light-use efficiency was estimated from the leaf-level light response curves on the topmost fully expanded cotton leaves.

^b Means with the same letter within a row are not significantly different ($P > 0.05$).

day UV-B radiation treatment, and saturation occurred approximately at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Fig. 3A).

Quantum yields determined from the initial slope of the light response curves under light limited con-

ditions, showed a decline in plants grown with the high UV-B radiation ($0.032 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$) similar to maximum photosynthesis (P_{max}). The quantum yields however, were not significantly different between the control and the 8 kJ m^{-2} per day UV-B treatments ($0.063 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ for the control and $0.062 \mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photon}$ for the 8 kJ m^{-2} per day UV-B).

The temporal trends of P_n at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for the 10th mainstem leaf indicated that P_{max} increased up to 15 days of leaf unfolding in the control plants and 10 days after leaf unfolding in the 8 kJ m^{-2} per day UV-B treatment, and then declined linearly as leaves aged (Fig. 3B). However, photosynthetic capacity in the high (16 kJ m^{-2} per day) UV-B treated plants showed a continuous and substantial decline with age from 5 days after leaf unfolding. Thirty days after leaf unfolding, P_n declined to half of maximum capacity for the control and the 8 kJ m^{-2} per day UV-B treatment and to one third of the maximum for the 16 kJ m^{-2} per day UV-B treatment (Fig. 3B). Decline in photosynthetic capacity and efficiency with leaf age irrespective of the light environment in which they were grown was observed in cotton by Sassenrath-Cole et al. (1996) similar to the results observed in this study. The rate and extent of decay of P_{max} and capacity (quantum yield) with high UV-B radiation indicated an alteration and deterioration of physiological function associated with carbon assimilation as the leaves aged.

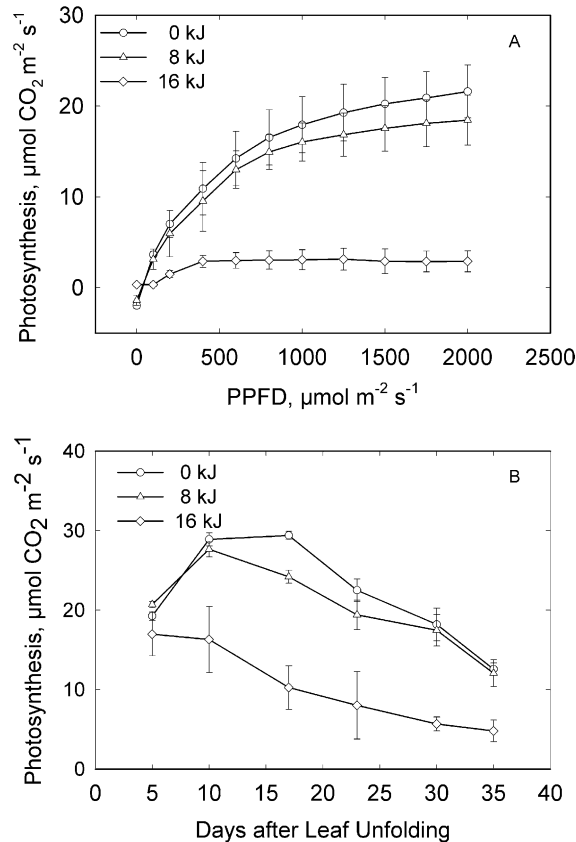


Fig. 3. Influence of (A) UV-B radiation and PPFD on cotton leaf photosynthetic light responses of leaf 10 on the mainstem, 24 days after leaf unfolding, and (B) temporal trends in photosynthesis of the same leaf. Each bar indicates \pm S.E. of five observations (Experiment II).

3.4. Canopy photosynthesis

To study the overall effect of UV-B radiation on photosynthesis, canopy-level net photosynthesis was measured in both experiments and presented in Figs. 4 and 5. Cotton canopies grown continuously in elevated

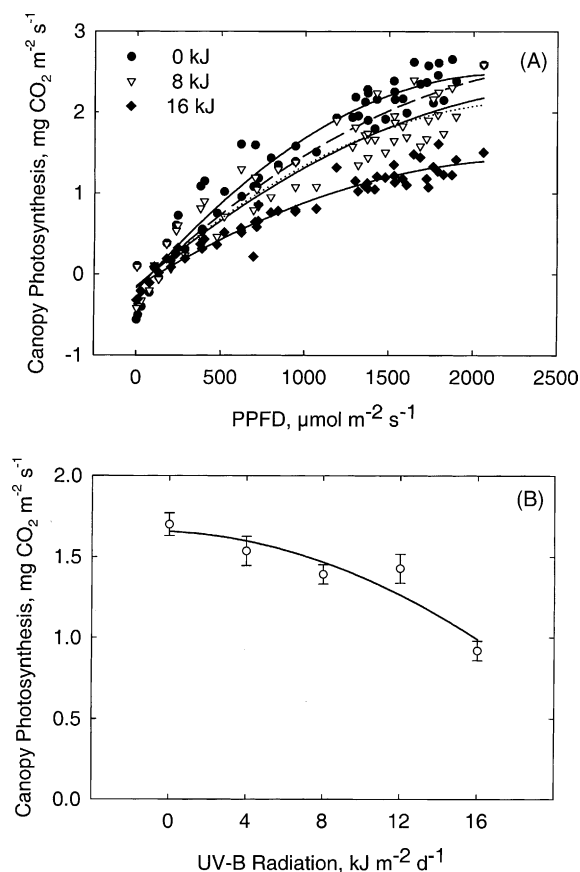


Fig. 4. Effects of UV-B on cotton canopy photosynthesis. (A) Light response curves and (B) means of photosynthesis rate for 10 days at the end of the Experiment I estimated from the light response curves at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. The regression lines were estimated by quadratic fit of the 900 s data points collected throughout the day for each treatment. For clarity, individual points are presented only for 0, 8 and 16 kJ of UV-B treatments in (A) and each vertical bar in (B) indicates \pm S.E. of 10 observations (Experiment I).

UV-B radiation responded to increases in PPFD with smaller increases in the rates of photosynthesis (Figs. 4A and 5A). Both the initial slopes of the light response curves and the asymptotes were lower in plant canopies grown in elevated UV-B radiation. That result was similar to the leaf-level photosynthesis responses to increasing PPFD.

From these light responses curves, canopy photosynthesis was estimated from the daily light response curves at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD in both the experiments, and correlated with UV-B radiation (Figs. 4B

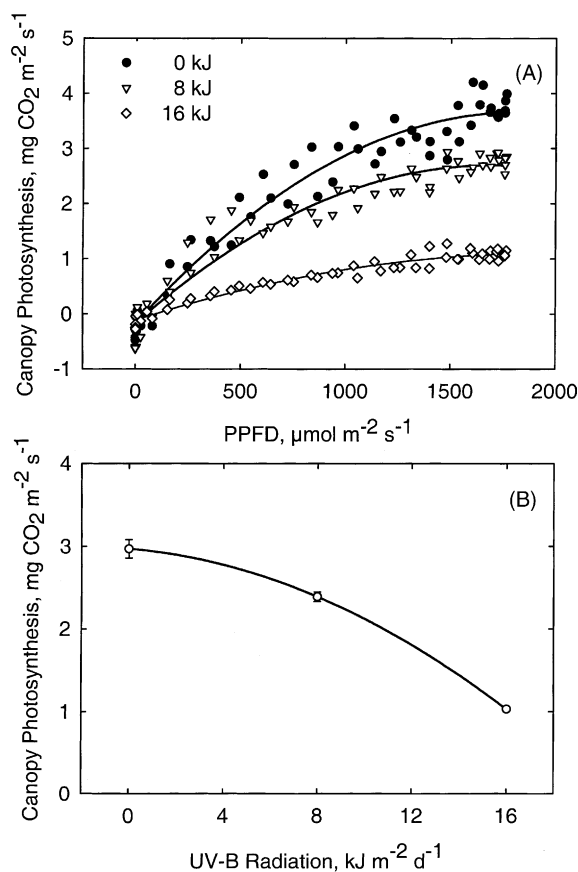


Fig. 5. Effects of UV-B on cotton canopy photosynthesis. (A) Light response curves and (B) mean of photosynthesis rate for 10 days at the end of the Experiment II estimated from the light response curves at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. The regression lines were estimated by quadratic fit of the 900 s data points collected throughout the day for each treatment. Each vertical bar in (B) indicates \pm S.E. of 10 observations (Experiment II).

and 5B). Such an analysis allows one to estimate the rates of canopy photosynthesis daily and they can be expressed as a function of UV-B treatment. Although, the absolute rates of canopy photosynthesis were different due to age of the canopy in those respective experiments, the trends were similar in both experiments in response to UV-B radiation, and declined quadratically with increases in UV-B radiation.

In Experiment I, there was a 46% decline in canopy photosynthesis at the 16kJ m^{-2} per day UV-B radiation treatment and 65% decline in Experiment II compared to the respective controls. The difference in the extent of damage to canopy photosynthesis in the two

experiments was due to ages of the canopies at the time of measurements. In Experiment I, the canopies were 34–43 DAE, and in Experiment II, they were 57–66 DAE when the data were obtained. Unlike the leaf-level net photosynthesis of the topmost fully expanded leaves on the mainstem (Fig. 2B), a 18% decline in canopy photosynthesis was observed even in the 8 kJ m^{-2} per day UV-B radiation treatment compared to the control. The decline in the rate of canopy photosynthesis indicated some damage to the photosynthesis system, particularly as the leaves aged since canopy photosynthesis integrates leaf photosynthetic capacities of various age groups. It is also consistent with the evidence that damage to younger leaves becomes progressively more severe with age as shown by visual symptoms (Fig. 8). Canopy photosynthesis was positively and linearly correlated with biomass accumulation rates (data not shown), indicating that changes in canopy photosynthesis are being reflected in biomass accumulation. Reddy et al. (1989) found from carbon balance estimates that canopy photosynthesis summations were in close agreement with structural carbon when adjusted for tissue constituents indicating that canopy photosynthetic rates are more likely predictors of dry matter production than photosynthetic rates of individual leaves. The decline in the photosynthetic capacity may be due to both direct and indirect effects of UV-B radiation on photosynthesis system as discussed earlier.

The limitations of canopy carbon assimilation with leaf age under the elevated UV-B radiation due to loss of individual leaf CO_2 uptake will have substantial effects on yield. Landivar et al. (1983) reported that a decline in canopy photosynthesis, due to loss of individual leaf photosynthesis, was directly correlated with lint yield. They suggested that maintaining the photosynthetic capacity of leaves by an additional 10 days would significantly increase lint yield. Thus, the UV-B radiation effects on cotton photosynthesis will have major consequences on growth, development and finally yield.

3.5. Effects of UV-B on cotton phenology

If changes in phenological events occur, they will have major effects on the number of leaves and fruiting structures produced, and they may influence the sizes of leaves, internodes and thus overall canopy size and

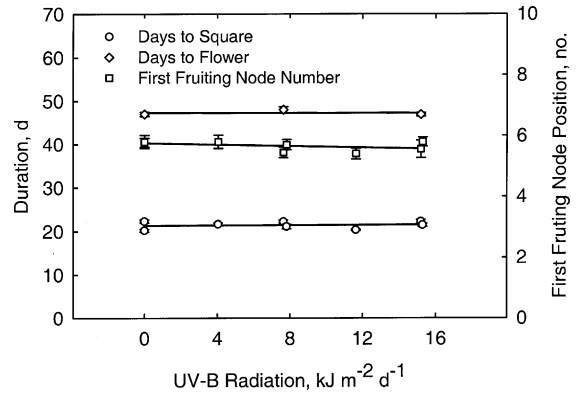


Fig. 6. Influence of UV-B radiation on reproductive phenology of cotton, first fruiting branch position on the mainstem, days from emergence to squaring and emergence to flowering. The data are means \pm S.E. of nine observations from each experiment.

structure, and finally biomass production and subsequent seed cotton yield. Phenology, study of periodic biological phenomena (Reddy et al., 1997), is the time between like and unlike events, or the duration of a process. Like events include the time intervals between mainstem leaves and branch leaves on a plant. Unlike events include the intervals between plant emergence and formation of a flower bud, flower or mature fruit. Duration of a process might include the period between unfolding of leaves and the time required for a leaf or internode to reach maximum size.

The sixth node was the first fruiting node in all the treatments (Fig. 6). There were no variations among treatments with respect to days-to-square and days-to-flower. First square appeared 22 DAE and the time interval between squaring and flowering was 25 days. The time required for the formation of flower buds, and flower in cotton was also not sensitive to UV-B radiation. These results are similar to the study conducted by Sampson and Cane (1999), where UV-B did not affect flowering phenology in meadow foam (*Limnanthes alba* L.).

A leaf was considered emerged when three main veins were clearly visible. Cotton plants, when grown at optimum temperature, $30/22^\circ\text{C}$ day and night, produced a mainstem leaf every 3 days (Fig. 7) similar to prior observations for several other cotton cultivars grown under similar conditions (Reddy et al., 1997, 2000). UV-B radiation did not affect either vegetative development such as mainstem leaf development

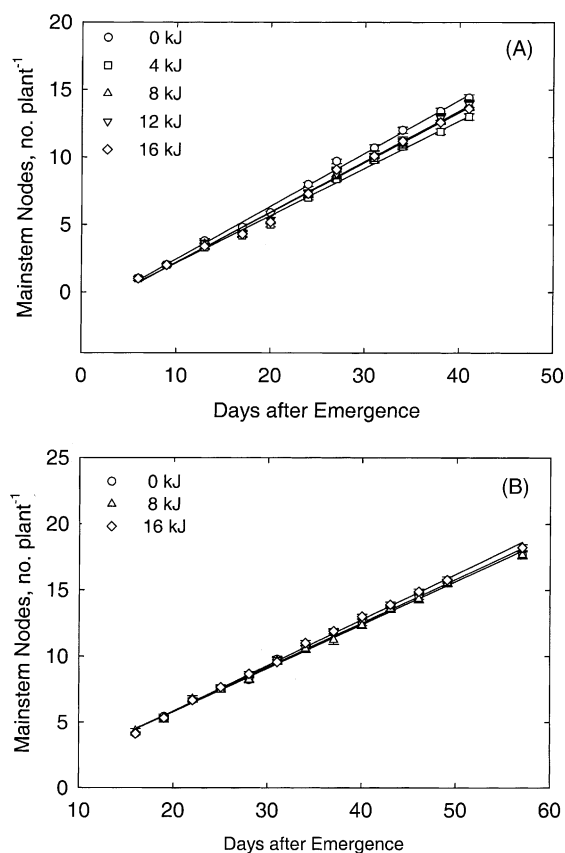


Fig. 7. Influence of UV-B radiation on production of mainstem cotton nodes: (A) Experiment I; (B) Experiment II. Each vertical bar indicates \pm S.E. of nine observations.

rate, or reproductive development such as the first fruiting node and time intervals between emergence to square, emergence to flower and square to flower. Similar observations were noticed in meadow foam by Sampson and Cane (1999) and Hart et al. (1975) in several other species, flowering in garden petunia (*Petunia hybrida* L.), tasseling in maize and heading

in sorghum (*Sorghum bicolor* L.). From our results and from the published evidence, it is inferred that the elevated UV-B radiation may not have any effects on major phenostages such as squaring, flowering and mainstem leaf addition rates. However, total fruiting sites produced (Tables 2 and 3) were reduced due to insufficient carbohydrate availability in the high UV-B radiation-grown plants. Reddy et al. (2000) reported that carbon demand/supply alters the number of fruiting sites produced on the branches, thus resulting in variation in the total number of leaves and fruiting structures.

3.6. Effect of UV-B on cotton morphology

In contrast to the effects of UV-B radiation on photosynthesis and growth, much less is known about the foliar injury symptoms of elevated UV-B radiation exposures on crops other than a few morphological deformations and necrosis (Groth and Krupa, 2000). In this study, leaves showed yellowing along the mid-veins and between the veins in UV-B irradiated plants. Depending upon the intensity and the length of exposure to UV-B radiation, these yellow patches later turned into necrotic regions. These visible damage symptoms were seen much earlier as the UV-B doses increased. It took about 14 days for symptoms to appear in the high UV-B treatment, but required about 25–30 days in the other treatments (Fig. 8). Similar results were observed in Experiment II (data not shown). Changes in leaf color on exposure to enhanced UV-B radiation have been reported in other species. In pea leaves, visible signs such as bronzing of irradiated leaves appeared as quickly as 2 days after exposure to UV-B (Strid and Porra, 1992). Appearance of black leaf symptom, a leaf disorder in grape (*Vitis vinifera* L.), was also observed on exposure to UV-B (Lang et al., 2000). Appearance of the chlorotic and

Table 2

Effect of UV-B radiation on vegetative and reproductive dry weights and square numbers of cotton plants, 43 DAE in Experiment I

Parameter	UV-B radiation (kJ m^{-2} per day)				
	0	4	8	12	16
Total weight (g per plant)	55.4 \pm 3.2 a ^a	40.5 \pm 2.4 b	42.8 \pm 4.0 b	39.3 \pm 3.2 b	27.3 \pm 1.9 c
Squares (no. per plant)	23.0 \pm 1.4 ab	18.9 \pm 1.4 b	24.4 \pm 1.3 a	20.3 \pm 2.0 ab	14.0 \pm 1.3 c
Square weight (g per plant)	2.0 \pm 0.2 a	1.0 \pm 0.1 c	1.4 \pm 0.2 b	1.1 \pm 0.1 c	0.9 \pm 0.1 c

^a Means followed by the same letter within a row are not significantly different ($P > 0.05$).

Table 3

Influence of UV-B radiation on vegetative and reproductive dry matter production and boll retention of cotton plants, 66 DAE in Experiment II

Parameter	UV-B radiation (kJ m ⁻² per day)		
	0	8	16
Total weight (g per plant)	119.6 ± 10.3 a ^a	113.0 ± 5.1 a	37.1 ± 3.9 b
Square weight (g per plant)	2.0 ± 0.3 a	2.2 ± 0.1 a	1.0 ± 0.2 b
Boll weight (g per plant)	18.4 ± 2.1 a	14.3 ± 1.4 b	2.1 ± 0.7 c
Retained bolls (no. per plant)	18.0 ± 0.1 a	15.0 ± 0.1 b	5.0 ± 0.1 c

^a Means followed by the same letter within a row are not significantly different (*P* > 0.05).

necrotic patches could be attributed to the decrease in leaf chlorophyll content (up to 40%) on exposure to UV-B, which is widely reported (Smith et al., 2000; Strid and Porra, 1992; Vu et al., 1981).

3.7. Effects of UV-B on cotton growth

Plant growth and development plays a pivotal role in crop production systems, controlling the production rate of new leaves, the duration of leaf area expansion of each leaf, the total number of leaves and fruiting

sites produced, and plant height extension. Although the influence of several environmental and nutritional aspects on cotton growth and development were extensively studied (Reddy et al., 1997, 2000), the influence of UV-B radiation on cotton growth processes has not been studied so far. Therefore, it is useful to better understand the response of cotton growth and development to changes in UV-B radiation. Growth is defined as the increase in length, area, or weight of the whole plants or of individual organs (Reddy et al., 1997). Plant height and leaf area expansions are

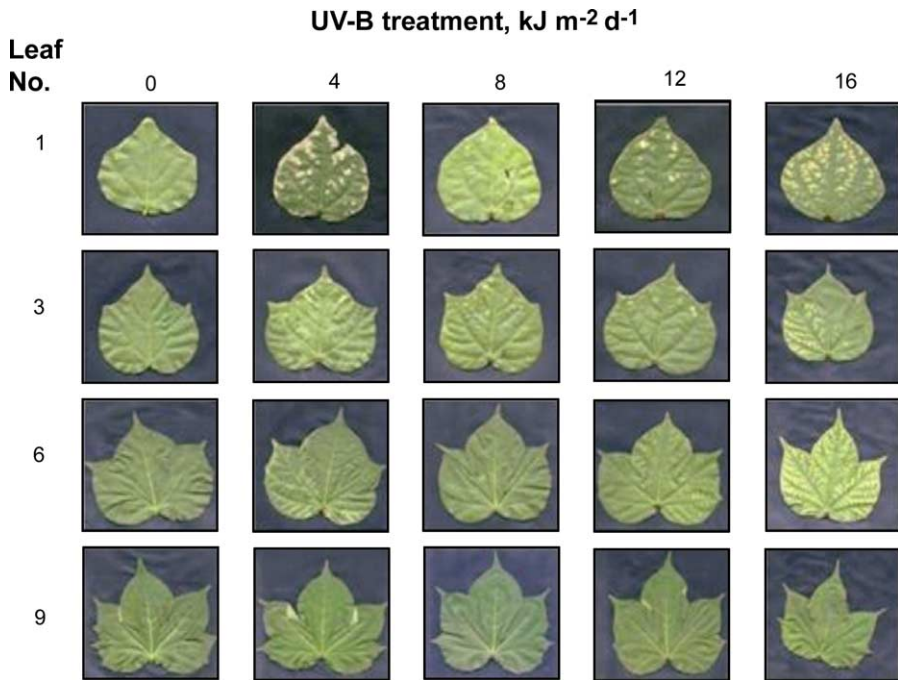


Fig. 8. Foliar symptoms showing the damage caused by UV-B radiation. The cotton leaves were photographed when there were 13–14 leaves on the mainstem (Experiment I). Leaf number is from plant bottom to the top.

recognized as the basic phenomena of shoot morphogenesis and growth. Internodes elevate other organs, particularly leaves for effective interception and capture of photosynthetically active radiation.

Prior studies indicated an inhibition of plant growth by UV-B in soybean (Kramer et al., 1992) and Scot pine (*Pinus sylvestris* L.) (Fernbach and Mohr, 1992). In addition, others reported inhibition of plant height and seedling length in pine plants because of UV-B exposure (Tevini and Teramura, 1989). Our results indicate that plants grown in the UV-B-free environment were significantly different and taller than plants with UV-B exposure. There were no significant ($P > 0.05$) differences among the 4, 8 and 12 kJ m^{-2} per day UV-B treatments with respect to plant height. However, the 16 kJ m^{-2} per day UV-B treatment plants were significantly ($P < 0.05$) shorter than the plants grown in the rest of the UV-B treatments. When plants were exposed to 16 kJ m^{-2} per day UV-B levels, there was a 34% decrease in plant height compared to the control, 43 DAE (Fig. 9A). For the 8 kJ m^{-2} per day UV-B treatment, a 16% decrease in plant height was observed compared to the control, 43 DAE.

In Experiment II, there was no significant difference between plants in the control and 8 kJ m^{-2} per day UV-B treatment. However, at the 16 kJ m^{-2} per day UV-B, plants were only half the size of the control plants (Fig. 9B). A previous study on aheahea and tassel flower, indicates 16 and 12%, respectively, reduction in plant height when exposed to UV-B (23.1 kJ m^{-2} per day, Sullivan et al., 1992). Trends in plant height differed in both experiments with respect to the 8 kJ m^{-2} per day UV-B treatment. In Experiment I, the 8 kJ m^{-2} per day UV-B treatment plants were significantly ($P < 0.05$) shorter than those in the control at the end of the experiment. However, in Experiment II, there was no significant difference for the same treatments at the end of the experiment. This may be due to an increase in duration of exposure in Experiment II. Similar results were seen in loblolly pine when exposed to UV-B, simulating a 25% decrease in ozone level. The UV-B treated plants were shorter initially, but the plants later recovered in shoot growth (Sullivan and Teramura, 1989).

In the present study, plant height was less due to shorter stem internodes. In both experiments, UV-B had no effect on the number of mainstem nodes per plant and hence no effect on the node addition rates.

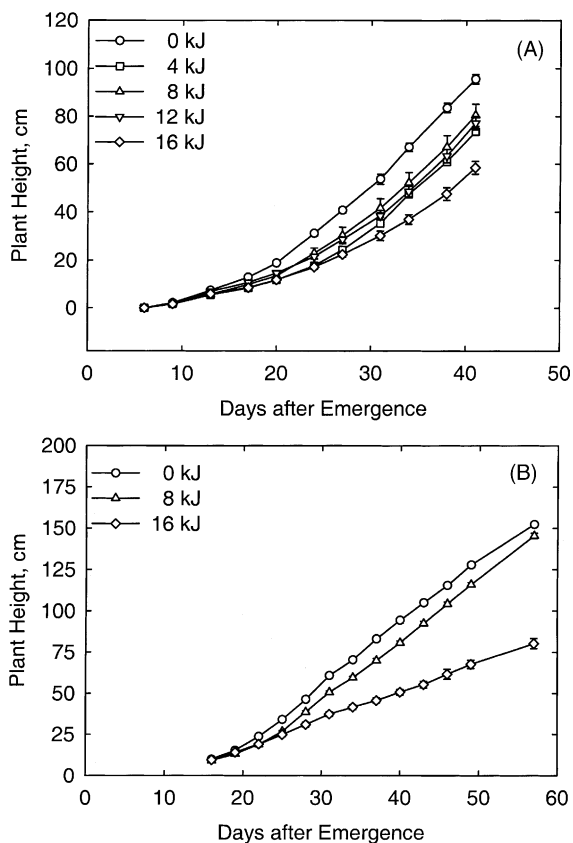


Fig. 9. Influence of UV-B radiation on cotton plant height: (A) Experiment I; (B) Experiment II. Each vertical bar indicates \pm S.E. of nine observations.

It is reported that UV-B radiation directly interacts with the metabolism of plant growth regulators, such as indole acetic acid (IAA) and alters plant growth (Curry et al., 1956).

Ultraviolet-B radiation has been reported to cause a reduction in leaf area in several crops. A significant reduction in leaf area was observed in several horticultural crops such as cucumber and radish (Tevini et al., 1983). Also, sunflower (Tevini and Teramura, 1989), pumpkin (*Cucurbita pepo* L.) (Sisson, 1981) and field crops such as soybean (Teramura and Murali, 1986) had less leaf area when exposed to UV-B. In the present study, plants treated with UV-B radiation had a significantly smaller canopy leaf area. Among the 4, 8 and 12 kJ m^{-2} per day UV-B treatments, there were no statistical differences with regard to mainstem leaf area, but they were significantly different from

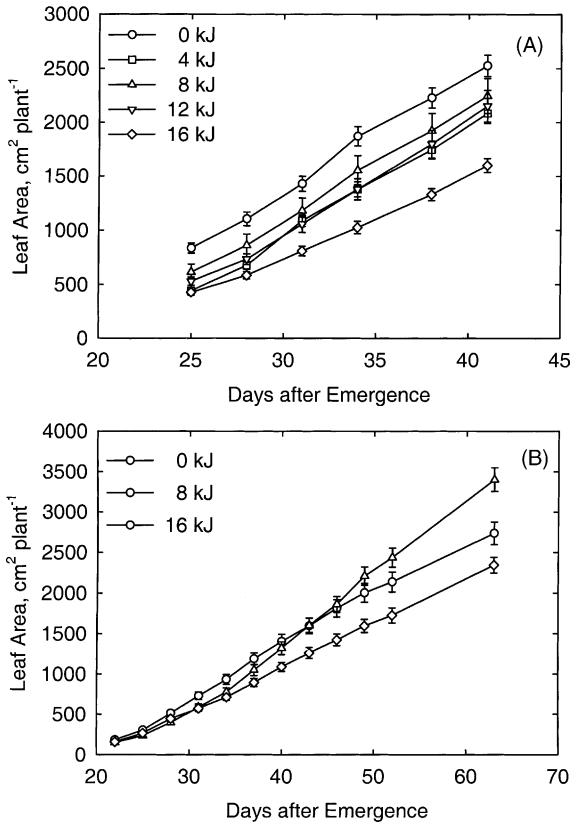


Fig. 10. Influence of UV-B radiation on cotton mainstem leaf area development: (A) Experiment I; (B) Experiment II. Each vertical bar indicates \pm S.E. of nine observations.

the control and the 16 kJ m^{-2} per day UV-B treatments (Fig. 10A). The mainstem leaf area measured, 43 DAE, was 46% less in the high UV-B treated plants compared to the control (Fig. 10A and B). Leaf area responses to UV-B radiation were similar to the reductions observed in plant height. In Experiment I, leaf area of the control plants was significantly greater than plants in the 8 kJ m^{-2} per day UV-B treatment. However, in the second experiment, there was no significant difference between the control and the 8 kJ m^{-2} per day UV-B treatment at the end of the experiment, which may be due to additional time. The extended growth period may have allowed the leaves of UV-B irradiated plants to expand more completely and partially catch up with the nonirradiated plants. Cotton plants slowdown and even stop producing new leaves during fruit growth, but begin producing new leaves

as fruits mature. Therefore, if UV-B reduces available resources or through some other mechanism causes lower fruit production comparisons of leaf area growth in response to UV-B may be confounded and meaningless. However, comparisons during the vegetative growth period can be meaningful. Similar results were observed in a previous study on eggplant (Latimer and Mitchell, 1987). They found that leaf area decreased by 16% at 5 days after treatment. However, when irradiated for 12 days, there was no significant decrease in leaf area. In our experiments, at the high UV-B radiation, leaf area was reduced significantly (50%) compared to the control plants, 66 DAE (Fig. 10B). Barnes et al. (1990) reported a reduction in mainstem leaf area in monocots when exposed to UV-B simulating a 20% decrease in ozone levels. This reduction in leaf area can also be attributed to a corresponding decrease in the number of leaves under UV-B irradiated conditions. A previous study by Ballare et al. (1996) in long spine thorn apple indicates inhibition of leaf expansion by UV-B radiation. Smaller leaf area in plants grown in high UV-B may have also been a reason for lower canopy photosynthesis. The smaller leaves would allow greater penetration of UV-B into the lower canopy. This would result in continued accelerated aging of the older leaves and to their further demise (Figs. 4 and 5).

Previous work on the effects of UV-B radiation on crop growth indicates a reduction in biomass accumulation (Song et al., 1999; Krupa and Kickert, 1989). There was a 51% reduction in total dry matter, 43 DAE at high UV-B radiation compared to the control in our first experiment and a reduction of 64% in the second experiment at 66 DAE (Tables 2 and 3). Barnes et al. (1993) reported a decrease in dry matter production in rice when exposed to UV-B, simulating 5% depletion in ozone level. The reduction in dry matter production was due to a decrease in both leaf area and canopy photosynthesis. The decrease was more prominent in fruit dry matter than vegetative dry matter. Seed biomass was reduced when black pine (*Pinus contorta* L.) and loblolly pine were irradiated with UV-B (Sullivan and Teramura, 1989).

In our second experiment, reproductive dry weights measured at 66 DAE showed 19 and 85% reductions at the 8 and 16 kJ m^{-2} per day UV-B treatments, respectively, compared to the control (Table 3). This reduction in reproductive dry matter was due to a decrease

in the biomass of squares and bolls; boll biomass decreased by 88% whereas square biomass decreased by 52% at 66 DAE when exposed to 16 kJ m^{-2} per day UV-B radiation (Table 3). The decrease in fruit dry weight was due to a decrease in the number and size of the bolls at high UV-B treatments. Increased fruit abscission observed at the 8 kJ m^{-2} per day UV-B radiation treatment seemed to be mainly associated with changes in leaf net photosynthesis as leaves aged and thus lowered canopy photosynthesis resulting in fruit loss at the 8 kJ m^{-2} per day UV-B radiation treatment due to insufficient carbon supply.

3.8. UV-B indices for cotton growth processes

To date, quantitative relationships between various growth and developmental processes of cotton as a function of UV-B radiation are not available for developing models to study current and projected changes in UV-B radiation and their interactions with other projected changes in the climate (Reddy et al., 2002; Doherty et al., 2003). One way to quantify the effects of UV-B radiation on cotton is to develop UV-B radiation-specific growth and developmental indices as proposed by Nobel (1991). Potential growth, development or photosynthesis is defined as the rate/amount of an individual process that takes place under optimum environmental conditions without the UV-B radiation. Then, by accounting for UV-B radiation-specific reduction factors or indices, the effects of UV-B radiation on cotton can be quantified and modeled (Fig. 11). The corresponding regression parameters and coefficients are presented in Table 4.

Table 4

Regression parameters and coefficients of various growth and developmental environmental productivity indices of cotton as affected by UV-B radiation ($y = 1 + ax + bx^2$, where y is the plant parameter and x the UV-B dosage)

Plant parameter	Regression parameter		Determination coefficient, r^2
	a	b	
Leaf area expansion	0.0157	-0.0022	0.86
Stem elongation	0.0101	-0.0025	0.93
Photosynthesis	-0.00038	-0.002	0.86
Dry matter accumulation	-0.00116	-0.0017	0.81

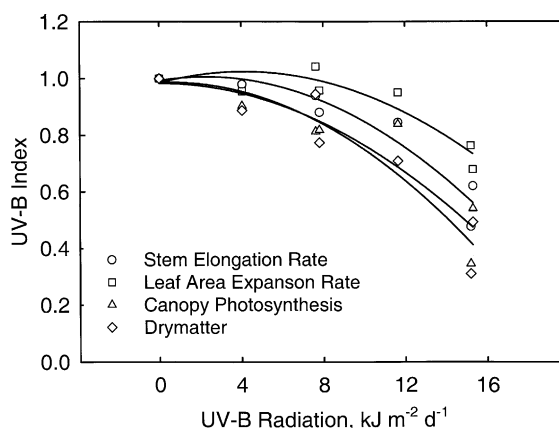


Fig. 11. UV-B radiation indices for various growth processes of cotton.

All the indices, ranging from 0 when the given environment stress is totally limiting that particular development, growth or photosynthesis process, to 1 when it does not limit that parameter, represent the fractional limitation due to the UV-B radiation. These processes decrease as the effect of UV-B radiation stress becomes more severe. This way, the effects of UV-B radiation on cotton growth, development and photosynthesis in a changing UV-B radiation environment can be quantified without the interference of other biotic and environmental stresses when grown in an essentially stress-free environment. But, more importantly, the effects of UV-B radiation can be incorporated into a mechanistic model that responds appropriately to environmental conditions and accurately predicts cotton responses to weather variables.

The critical limit defined as 90% of optimum or the control, for stem elongation (8.7 kJ m^{-2} per day UV-B) was lower than the critical limit for leaf expansion (11.2 kJ m^{-2} per day UV-B), indicating that stem elongation was more sensitive to UV-B than leaf expansion (Fig. 11). The critical limits for canopy photosynthesis and total dry weight were 7 and 7.3 kJ m^{-2} per day, respectively. A decrease in canopy photosynthesis was accompanied by a corresponding decrease in total dry matter indicating the dependence of total dry matter production on canopy photosynthesis. In general, reproductive dry matter was more sensitive to UV-B than vegetative dry matter.

From the database (Fig. 11 and Table 4), it seems that developing functional algorithms for canopy

photosynthesis, leaf and stem growth will account for most of the UV-B effects on cotton growth and development. The major life-cycle reproductive events (Fig. 6) were not affected by UV-B, and there is no need to have any reduction factors for those events. It is also true for leaf addition rate on the mainstem, and critical limit for leaf addition rate is 18.1 kJ m^{-2} per day (Fig. 7). The UV-B-specific photosynthesis index will be sufficient to account for fruit loss and dry matter partitioning and production as the rates of reduction in photosynthesis and total dry matter production go hand in hand as UV-B radiation increased. The identified UV-B-specific indices for stem and leaf growth, and photosynthesis parameters should be useful and can be incorporated into mechanistic cotton simulation models, which accounts for variations in temperature as well as water and nutrient stresses. Models such as GOSSYM (Hodges et al., 1998; Reddy et al., 1997, 2001) can be used to predict yields and to improve management practices under present and future enhanced UV-B radiation levels in production environments.

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