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Field crop responses to ultraviolet-B radiation: a review

V.G. Kakani*, K.R. Reddy, D. Zhao, K. Sailaja

Department of Plant and Soil Sciences, Mississippi State University, Mississippi State, MS 39762, USA

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Abstract

This paper provides an overview of existing literature on the ultraviolet-B (UV-B) radiation effects on field crops. Earlier reviews on field crop responses to UV-B considered few physiological processes or crops. For this review, we easily located about 129 studies on 35 crop species published since 1975. Here, we report the effects of UV-B radiation on visual symptoms, leaf ultrastructure and anatomy, photosynthetic pigments, UV-B absorbing compounds, photosynthesis, growth and development, yield, genotypic differences, and finally, interactions of UV-B with abiotic and biotic factors of crop plants. Experiments conducted in glasshouses, in closed and open top chambers, and under field conditions, with varying source (solar or artificial) and intensity of photosynthetically active radiation (PAR, 50–1800 μmol m^{-2} s^{-1}) and UV-B (0–50 kJ m^{-2} per day) are included. It is easy to conduct experiments that purport to evaluate the effects of projected UV-B intensities on crop species by providing supplemental irradiance with lamps or by reducing UV-B with filters; however, it is very difficult to simulate UV-B irradiance spectral changes that are likely to occur in nature. Collated results for each process are presented as percent change from control along with the experimental conditions in tabular format. Many of the studies showed dramatic effects of UV-B radiation, but under conditions with supplemental UV-B irradiance that was higher than would ever occur outside experimental conditions or in which the longer wavelengths in the PAR and UV-A, which moderate UV-B effects, were greatly reduced. Only 25 of the studies reviewed used experimental conditions and supplemental UV-B irradiance that approached realism. However, unrealistic the experimental conditions might be, an increase in understanding of basic plant physiology was gained from most of the studies.

Visual symptoms consisting of chlorotic or necrotic patches on leaves exposed to UV-B were not unique. Both vegetative and reproductive morphology were altered by UV-B radiation. Leaf anatomy was altered due to changes in thickness of epidermal, palisade, and mesophyll layers. Enhanced UV-B generally decreased chlorophyll content (10–70%), whereas it increased UV-B absorbing compounds (10–300%) in many crops. Decrease in photosynthesis (3–90%), particularly at higher UV-B doses, was due to both direct (effect on photosystem) and indirect (decrease in pigments and leaf area) effects. The decreases in chlorophyll pigments and photosynthesis resulted in lower biomass and yield of most crop plants. Genotypes of crop species exhibited variability in leaf wax layer thickness, loss of chlorophyll, and increase in phenolics as mechanisms of tolerance to enhanced UV-B radiation resulting in changes in biomass/yield. Results from the few studies on interaction of UV-B with other abiotic and biotic factors did not lead to useful conclusions. Studies are needed to quantify the effects of UV-B radiation on crops in order to develop dose response functions that can facilitate development of dynamic simulation models for use in UV-B and other environmental impact assessments.

Keywords: Crop yield; Leaf pigments; Leaf wax; Phenology; Photosynthesis; Plant development

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* Corresponding author. Tel.: +1-662-325-9466; fax: +1-662-325-9461.
E-mail address: vgk3@ra.msstate.edu (V.G. Kakani).

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1. Introduction

Understanding of relationships between crop and environment has substantially improved during the last few decades of the 20th century. Anthropogenic factors are continuously changing the environment, and projections are that atmospheric CO_2 concentrations ($[CO_2]$) will double and temperatures will increase by 5.5 °C by the end of current century (Houghton et al., 2001). However, the associated uncertainty with these projected changes is very high. In contrast to the uncertainty of predicted global climate changes, scientific assessment of ozone depletion (UNEP, 2002) provides clear evidence that stratospheric ozone for the period of 1997–2001 was 3–6% less than the pre-1980 average values. Ozone depletion is primarily due to the chlorine- and bromine-containing compounds released into the atmosphere due to anthropogenic activities during the later part of the 20th century (Blumthaler and Ambach, 1990; Kerr, 1993; Manney et al., 1994; Butler et al., 1999). The CFCs (CFC-11, CFC-12, and CFC-113) are gases with the largest potential to deplete ozone and have a half-life ranging from 50 to 150 years, and continue to deplete the ozone layer (Dentener et al., 2001). However, the current growth rates are slightly negative for these CFCs (Prinn et al., 2000). Therefore, stratospheric ozone recovery is not expected before 2010 (Jackman et al., 1996; Hofmann and Pyle, 1999) and recovery would be slower due to the effect of greenhouse gas emissions (Weatherhead et al., 2000), and decreased ozone levels are expected to recover to the pre-1970 levels by 2050, if all member countries implement the Montreal Protocol (UNEP, 2002). Non-compliance by member countries to implement the protocol would delay the recovery or even prevent the recovery of the ozone layer.

Evolution of life, from under water unicellular forms to animals and plants on Earth's surface, was possible due to the formation of an ozone layer that reduced ultraviolet-B (UV-B) radiation received on the Earth surface by about 10,000 times (Rozema et al., 1997b; Canuto et al., 1983). Therefore, the most important consequence of stratospheric ozone depletion is the increase in the amount of UV-B radiation harmful to life on the Earth's surface (Farman et al., 1985). Current stratospheric ozone levels are at the lowest point since measurements began in 1970s and global terrestrial UV-B radiation levels range between 0 and 12 $kJ\,m^{-2}$ on a given day with near Equator and mid-latitudes receiving higher doses (Total Ozone Mapping Spectrometer, 2002, http://toms.gsfc.nasa.gov/ery_uv/euv.html). The changes in ozone and UV-B are not uniform over the Earth's surface. The ozone concentrations in the high latitudes (comprising Antarctic and Arctic regions) are 40–50% lower than the pre-1980 values; in the mid-latitudes (35–60°N and 35–60°S) are 3–6% lower than pre-1980 values; and at the Equator show minimum changes (UNEP, 2002). Due to the ozone depletion, UV-B radiation on the Earth's surface has increased since early 1980s by 6–14% (UNEP, 2002). The amount of UV-B received at a location depends on several atmospheric factors like the amount of ozone, position of the sun, and cloud cover. Land factors such as sand, snow, and water also influence the total amount of UV-B. Relative to the 1979–1992 conditions, for the 2010–2020 time period, the GISS model results indicate a springtime enhancement of erythmal UV doses of up to 14% in the Northern hemisphere and 40% in the Southern hemisphere (Taalas et al., 2000). Spectral studies on UV-B radiation indicated a 35% increase in intensity at 300 nm wavelength, while there was no change in intensity at 320 and 325 nm wavelengths due to wavelength dependence of absorption coefficient of ozone (Kerr and McElroy, 1993). Although, the UV-B radiation comprises only a small portion of the electromagnetic spectrum, it has a disproportionately large photobiological effect on both plants and animals due to its absorption by important biological molecules such as proteins and nucleic acids (Jansen et al., 1998). As plants lack locomotion, adaptation or tolerance to increased levels of UV-B radiation is essential.

Several reviews have been published summarizing the effects of UV-B radiation on crop plants. Corlett et al. (1997) compared the results from controlled environments, glass houses, and field experiments, but only a few case studies were discussed in the study. In a review of agricultural crops sensitivity to UV-B, Krupa et al. (1998) classified crop plants based only on crop dry weights, but several other crop physiological and growth parameters sensitive to UV-B were not addressed. In a recent review, Searles et al. (2001) carried out a meta-analysis using 62 field-based papers and identified only a few subtle responses for physiological and growth parameters on exposure to enhanced UV-B simulating 10–20% stratospheric ozone depletion. In their review, however, about 44% of the studies were non-agricultural and 60% were from regions of 35–45°N latitude where the current ambient UV-B levels are low, creating an inherent bias towards sites, studies and species.

A thorough understanding of the UV-B radiation levels across agricultural lands of the world and the effects of these levels on crop species is essential to design crops that can produce food, fiber and other raw materials for the increasing world population. Current levels of UV-B during the cropping season are anywhere between 2 and 12 $\mathrm{kJ\,m^{-2}}$ per day on the Earth's surface, which includes an increase of 6–14% of UV-B radiation (UNEP, 2002) over the pre-1980 levels. A 30% increase in UV-B results in a maximum dose of 2.44 $\mathrm{kJ\,m^{-2}}$ per day in UK (Allen et al., 1999), but such low levels of UV-B radiation are very uncommon during the cropping season in several parts of the world. For example, in the Cotton Belt of USA, current UV-B radiation levels are 4–11 $\mathrm{kJ\,m^{-2}}$ per day during the summer season (Frederick et al., 2000), and the predicted UV-B levels based on Taalas et al. (2000) would be 4.56–12.54 $\mathrm{kJ\,m^{-2}}$ per day. In China, ambient UV-B levels during soybean cropping period averaged to 8.85 $\mathrm{kJ\,m^{-2}}$ per day (Li et al., 2002). A 30% increase in UV-B levels would seriously affect crop production in these and several parts of the world.

Predicted climate changes for future, even though uncertain, are inevitable due to continued anthropogenic activities. Along with elevated UV-B radiation, field crops would be grown in doubled [CO_2] and 5.5 °C higher temperatures (Houghton et al., 2001). Therefore, an understanding of the effects of environmental factors that mimic the future would be useful to assess growth and productivity of agricultural crops. The aim of this review is to summarize the results of the numerous studies of physiological, growth, and yield characteristics of agricultural crops to UV-B radiation. The review also focuses on effects of UV-B radiation on agricultural crops and its interaction with other environmental factors.

2. Methodologies

A comprehensive list of published experimental studies was collated from the CAB (Commonwealth Agricultural Bureau) and AGRICOLA (AGRICultural Online Access) electronic databases for major food and fiber crops grown across the world. Many of the major cereal, oilseed, fiber, and protein crops listed in Table 1 were evaluated for their response to enhanced UV-B radiation. The keywords used for the database search were the common and Latin names of the crop and UV-B. Studies selected were not subjected to any type of constraint as far as the UV-B treatments are concerned. The UV-B radiation studies varied in dosage, duration, stage of crop, crop species, location, and experimental conditions. Studies listed in this review contain experiments carried out in controlled environment (CE), growth chambers (GC), greenhouses or glasshouses (GH or GLH), open top chambers (OTC), and field (F) conditions. The published studies were conducted under a range of UV-B doses from 0 $\mathrm{kJ\,m^{-2}}$ per day to as high as 49 $\mathrm{kJ\,m^{-2}}$ per day depending on the researcher's objectives. The duration of the imposed UV-B treatments was anywhere from a few days to the entire crop season. Several stages of crop growth, including seedling, vegetative, reproductive, and maturity, were examined for the effects of UV-B radiation. The UV-B radiation treatments other than the ambient were usually imposed using UV-B emitting fluorescent bulbs placed 0.5–0.7 m above the canopy and small amounts of UV-C emitted were filtered by cellulose diacetate plastic film wrapped around the bulbs. In most field studies, the control treatment plants were exposed to ambient UV-B radiation. However, in some, the control consisted of no UV-B radiation, either by growing plants in chambers whose casing filters solar UV-B radiation or by using Mylar sheet placed over the crop canopy to filter UV-B radiation.

Results collated in this review are largely from single factor experiments, i.e. effects of enhanced UV-B radiation on a crop species. In the future, enhanced UV-B radiation may coincide with projected changes in several environmental factors. Hence, results from two-factor studies where an interaction between UV-B radiation and other major environmental variables, temperature, CO_2, water-deficit, and ozone depletion, have been also reviewed in this study. We concentrate on the impact of UV-B radiation on visual symptoms, leaf ultrastructure and anatomy, photosynthetic pigments, UV-B absorbing

Table 1
Total world area harvested, yield, and production, from FAOSTAT online (FAO, 2001) and total number of references for primary row crop species

Crop	Area harvested (ha)	Yield (Mt ha^{-1})	Production (Mt)	Number of UV-B references
Cereal crops				
Wheat (*Triticum* spp.)	213443943	2.75	587561753	40
Rice paddy (*Oryza sativa* L.)	154140174	3.90	600638089	56
Maize (*Zea mays* L.)	138738942	4.27	592999083	39
Barley (*Hordeum vulgare* L.)	53096972	2.52	133933386	17
Sorghum (*Sorghum* spp.)	41964377	1.38	57964600	12
Millet (*Pennisetum glaucum* (L.) R. Br.)	36315592	0.72	26281789	1
Maize for forage + silage	17793750	26.51	471768130	0
Oats (*Avena sativa* L.)	12849939	2.03	26086195	9
Rye (*Secale cereale* L.)	9745081	2.02	19694254	8
Sorghum for forage + silage	1119288	23.31	26091154	0
Tuber crops				
Potatoes (*Solanum tuberosum* L.)	19940259	16.45	328050784	5
Cassava (*Manihot esculentum* Crantz)	17032269	10.38	176784378	3
Sweet potatoes (*Ipomea batatus* (L.) Lam.)	9111974	15.24	138848631	0
Yams (*Diascorea* spp.)	4050247	9.46	38304339	0
Oil crops				
Soybeans (*Glycine max* (L.) Merr.)	74102000	2.18	161229850	40
Rapeseed (*B. napus* L. var napus)	25721381	1.54	39516424	21
Groundnuts in shell (*Arachis hypogaea* L.)	24290847	1.42	34515701	3
Sunflower seed (*Helianthus* spp.)	21081016	1.24	26168523	5
Safflower seed (*Carthamus tinctorius* L.)	878619	0.79	690488	2
Fiber crops				
Seed cotton (*Gossypium hirsutum* L.)	31607367	1.73	54590370	6
Jute (*Corchorus capsularis* L.)	1391036	1.91	2651030	0
Hemp fiber and tow (*Cannabis sativa* L. subsp. *sativa*)	53347	1.07	57074	2
Sugar crops				
Sugarcane (*Saccharum officinarum* L.)	19185566	65.60	1258530680	1
Sugar beets (*Beta vulgaris* L. subsp. *vulgaris*)	5968770	41.12	245419567	2
Protein crops				
Beans, dry (*V. faba* L.)	24138243	0.71	17152464	24
Chick-peas (*Cicer arietinum* L.)	9968944	0.79	7839795	0
Cowpeas, dry (*Vigna ungiculata* (L.) Walp. subsp. *ungiculata*)	9867865	0.30	2969599	7
Peas, dry (*Pisum* spp.)	6048281	1.78	10791302	51
Peas, green	939079	7.92	7433459	–
Beans, green	680925	6.91	4702660	–

compounds, photosynthesis, growth and development, and yield. Studies where genotypes differed in tolerance to UV-B radiation are reviewed and characters for UV-B tolerance are listed. Collated results for each process were presented as percent change from control along with the experimental conditions in tabular format.

3. Results and discussion

3.1. UV-B and visual symptoms

Plants under stress show unusual growth patterns and coloration called symptoms and UV-B radiation is no exception in producing symptoms. Changes in leaf color and form were reported in several species. Initially, bronze or brown spots appear on the leaf surface that later result in chlorosis, necrosis, and desiccation of the leaves (Ambler et al., 1975; Strid and Porra, 1992; Dai et al., 1994a; Visser et al., 1997a; Krizek et al., 1993). On continued exposure to UV-B, leaves become involuted or cup-shaped and dry up (Ambler et al., 1975; Santos et al., 1993). In cotton, initially the leaves developed chlorotic patches in the interveinal region, which became brown spots and later became necrotic, and resulted in early senescence of leaves (Kakani et al., 2003; Reddy et al., 2003, Fig. 10). Appearance of chlorotic and necrotic patches was attributed to the decrease in leaf chlorophyll content (up to 40%) on exposure to UV-B (Smith et al., 2000; Strid and Porra, 1992; Vu et al., 1981). Such chlorotic and necrotic symptoms are not unique to UV-B radiation, plants deficient in mineral nutrients (N, K, Mg, Fe, Mn, Cu, Cl and Ni) (Fageria et al., 1997) and those exposed to environmental pollutants like ozone (Krupa et al., 2001) also produce similar symptoms.

3.2. *UV-B and leaf ultrastucture and anatomy*

Changes in leaf ultrastructure due to enhanced UV-B would modify the light attenuation by the leaf and in turn affect photosynthesis. Of the incident solar UV-B radiation, leaf reflects 3–6% (Gao et al., 1996; Yang et al., 1995) to 10–40% from pubescent or glaucous surface (Robberecht and Caldwell, 1980), and leaf epidermis transmits anywhere between <0.1 and 5% of the incident UV-B radiation (Robberecht and Caldwell, 1980; Yang et al., 1995). An increase in incident UV-B radiation would increase the amount transmitted if no additional reflection occurs at leaf surface. Plant species differed in their anatomical responses to UV-B radiation, while increase in leaf thickness due to UV-B was common (Nagel et al., 1998; Bornman and Vogelman, 1991), a decrease in leaf thickness along with an increase in number of palisade layers was observed in cotton (Kakani et al., 2003). The increase in leaf thickness was due to addition of spongy mesophyll cells. The palisade cells from UV-B irradiated leaves of these species were wider and shorter. Weston et al. (2000) investigated palisade development in the wild type and blue-light-perception mutant of *Arabidopsis thaliana*, at high light intensity. A second and even a third palisade layer were formed due to supplemental UV-B in the blue light sensitive mutant. The increase in cell number would increase the cell wall surface area, which blocks and prevents the harmful UV-B radiation from reaching the abaxial photosynthetically active mesophyll. The increased palisade cell number would also increase the amount of air–cell wall interfaces, an important parameter that affects reflectance (Knipling, 1970) and transmission of the incident radiation through the leaf surface (Bornman and Vogelman, 1991). Further studies are needed to verify the effects of altered leaf anatomy on reflectance and transmittance of UV-B radiation.

On exposure to enhanced UV-B radiation, leaf cell structure in susceptible rice cultivars was damaged by UV-B radiation of 15–16 $\mathrm{kJ\,m^{-2}}$ per day; the granal stacks were disrupted and the chloroplast envelope ruptured (Cassi-Lit et al., 1997). In maize leaves, UV-B radiation of 9 $\mathrm{kJ\,m^{-2}}$ per day caused collapse of the adaxial epidermis in the distal region of the leaf and decrease in fractional volume of chloroplasts in several species (Santos et al., 1993; Fagerberg and Bornman, 1997). Other changes produced by enhanced UV-B included more trichomes on the abaxial leaf surface (Barnes et al., 1996), a reduction in number and diameter of xylem tubes, decreased stomatal frequency and distorted leaf area (Lingakumar and Kulandaivelu, 1993). These adverse effects of UV-B on leaf anatomy would inhibit the uptake of CO_2 and in turn assimilate production.

3.3. *UV-B and photosynthetic pigments*

A decrease in chlorophyll content was evident on exposure to enhanced UV-B radiation in most of the crop species reviewed (Table 2). Ultrastructural damage to chloroplasts and changes in photosynthetic pigments result in reduction of photosynthesis (Sullivan and Rozema, 1999). Crop species differed in their ability to tolerate UV-B radiation and retain leaf chlorophyll (Table 2). Chlorophyll reduction on exposure to UV-B in major crop species ranged from as low as 10% (Mirecki and Teramura, 1984; Pal et al., 1999; Tevini et al., 1981) to as high as 70% (Tevini et al., 1981; He et al., 1993) and the reduction being higher among the dicot species (10–78%) compared to that in monocot species (0–33%). The

Table 2
Effects of UV-B radiation and experimental conditions on photosynthetic (Pn) pigments and UV-B absorbing compounds in different crop species

Crop	UV-B$_{BE}$ (kJ m^{-2} per day)	Simulating O$_3$ depletion (%)	PAR (μmol m^{-2} s^{-1})	Experimental condition	Pn pigments	UV-B absorbing compounds	References
Alfalfa	6.3	6		CE	↓ (13)	↓ (15–21)	Bornman and Vogelman (1991)
Barley	8.84, 13.56	5, 25	200	GC	–	↑ (12)	Liu et al. (1995)
	2.2, 4.2, 8.3				↓ (30)	↑ (60)	Tevini et al. (1981)
Bean	6.17			CE	↑ (20)	–	Cen and Bornmann (1990)
	0.25–1.66	?	50, 100, 250	GC	↑ (13)	–	Deckmyn et al. (1994)
	4.7, 6.5, 7.2, 12.2	6–36	A	F	–	↑ (5–12)	Flint et al. (1985)
	12			GH	–	↑	Meijkamp et al. (2001)
	10.08	15	A	F	↓ (42)	↑ (10)	Singh (1995)
	2.2, 4.2, 8.3				↓ (70)	↑ (15)	Tevini et al. (1981)
Brassica	6.3	6		CE	↓ (13–27)	↑ (15–21)	Bornman and Vogelman (1991)
Cassava	13.9	15	A	F	–	–	Ziska et al. (1993)
Cowpea	12.2	20	A	F	↑↓ (5–40)	↑ (5–300)	Premkumar and Kulandaivelu (2001)
Greengram	11.02	15	A	F	↓	↑ (11–24)	Pal et al. (1999)
	10.08	15	A	F	–	↑ (24)	Singh (1995)
Maize		20	A	F	↑ (50)	↑↓	Ambasht and Agrawal (1995)
	9		700	GC	↓ (25)	↑	Santos et al. (1993)
	2.2, 4.2, 8.3				↓ (10)	–	Tevini et al. (1981)
Pea	49		160–180	GC	↓ (30)	↑ (150–200)	Alexieva et al. (2001)
	18.0			GH	↓	↑	Day and Vogelmann (1995)
	2.3, 4.6, 6.9, 9.2			CE		↑	Gonzalez et al. (1998a)
	2.2, 9.9		850–950	CE		↑ (21)	Gonzalez et al. (1998b)
	2.4		800–1200	GH	↓ (78)	↑ (15)	He et al. (1993)
	1.38, 1.92	A, 15	A	F	–	↑ (6)	Stephen et al. (1999)
	2.5 × A		?	GC	↓ (35)	↑ (15–100)	Strid and Porra (1992)
		0, 9, 21, 36	480–500	GH	↓ (50)		Vu et al. (1984)
Rapeseed	4.3		400–700	GC	–	↑ (150)	Greenberg et al. (1996)
	2.6		70	CE	–	↑ (80–120)	Wilson and Greenberg (1993)
Rice	2.4		800–1200	GH		↑ (60)	He et al. (1993)
	3 UV-B lamps		800–1000	GH	↓ (10–15)		Huang et al. (1993)
	2.8, 3.9, 6.5	A, 27, 38	A	F	↓	–	Kim et al. (1996)
	8.8, 15.7	A, 10		GH	↑↓	↑	Teramura et al. (1990a)
Rye	2–6			GC	–	↓	Deckmyn and Impens (1997a)
Sorghum	7.1	20	A	F	↓ (23%)	↑ (33)	Ambasht and Agrawal (1998)
Soybean	9.5	36	A	F		↑ (18)	Caldwell et al. (1994)
	0, A		A	F		↑	Mazza et al. (2002)
	10.7, 14.1	15, 30	1300–1600	GH	↓	↑	Middleton and Teramura (1993)
	2.6		1400–1800	GH	↓ (10)	↑ (15)	Mirecki and Teramura (1984)
		0, 9, 21, 36	480–500	GH	↓ (50)		Vu et al. (1984)
Wheat	8.8, 15.7	A, 10		GH		↑	Teramura et al. (1990b)
	49		160–180	GC	↓ (30)	↑ (150–200)	Alexieva et al. (2001)
	3.17	15	A	F		↑↓	Li et al. (1998)

Values in parenthesis indicate percentage change. A: ambient level; CD: cultivar dependant; F: field; GC: growth chamber; GH: greenhouse; GLH: glasshouse; CE: controlled environment chambers; MD: mid-day; OTC: open top chamber; ?: information not available. The ↓, ↑ and – represent that parameter was decreased, increased and unaffected by elevated UV-B radiation, respectively, compared to the control.

differential responses between these two groups can be attributed to the orientation of leaves; narrow leaves with vertical orientation result in lower attenuation of the incoming solar UV-B compared with plants having wider leaves and horizontal leaf orientation resulting in greater attenuation of incoming UV-B radiation (He et al., 1993). Variation in the amount of chlorophyll reduced among crop species can also be attributed to UV-B radiation doses (2.6–49 $\mathrm{kJ\,m^{-2}}$ per day) and the light regimes (photosynthetically active radiation (PAR) of 150–1800 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) under which the studies were conducted. This variation in PAR/UV-B ratio is also known to alter the extent of damage caused by UV-B radiation to crop plants (discussed in detail in Section 3.9).

Reduction in chlorophyll content was due to a breakdown of the structural integrity of chloroplasts on exposure to UV-B radiation as discussed earlier. The chlorophyll components, thylakoids and grana were sensitive to the incoming solar radiation (Cassi-Lit et al., 1997; He et al., 1994; Tevini et al., 1991). An increase in UV-B radiation resulted in rupture of the thylakoids and grana due to the disintegration of the membranes. Photobleaching was dependent on the length and intensity of UV-B radiation (Huang et al., 1993). Thus, cultivars/species with greater membrane stability under enhanced UV-B radiation might offer some tolerance.

3.4. UV-B and plant protective mechanisms

3.4.1. UV-B and waxes

Epicuticular wax layer is an important leaf surface character that responds to environmental stresses (Bondada et al., 1996; Rao and Reddy, 1980; Baker, 1982) and acts as an interface between environment and leaf internal structures providing the first line of defense. Only a few studies have reported of UV-B effects on epicuticular waxes of crop plants. Increased wax might provide a protective mechanism as the epicuticular wax reflects from 10% (Caldwell et al., 1983) to 30% of the incident UV-B radiation in eucalyptus (Holmes, 1997). As early as 1975, Clark and Lister confirmed that epicuticular wax increases reflectance markedly in the ultraviolet and blue regions of the spectrum. Enhanced UV-B irradiation produced 23 and 28% increase in wax content on leaf area basis in barley and bean, respectively (Steinmuller and Tevini, 1985), however, ambient barley leaves had five times higher amount of wax than bean. In a study with six pea genotypes differing in their surface waxiness, an increase in wax content was observed when the genotypes were exposed to UV-B radiation of 6.5 $\mathrm{kJ\,m^{-2}}$ per day (Gonzalez et al., 1996), but this increased wax content did not alter the amount of UV-B reflected in the study. Soybean N-15 cultivar canopy with higher quantities of epicuticular waxes reflected more UV-B compared with cultivar BM-15 that had low wax content (Grant, 1999). The presence of epicuticular waxes, however, did not modify the PAR reflectance in either of the genotypes. In cotton, exposure to UV-B resulted in 200% increase of epicuticular wax content (Kakani et al., 2003). Enhanced UV-B radiation not only altered the quantity but also chemical composition of leaf surface wax (Tevini and Steinmuller, 1987; Barnes et al., 1996) that modified leaf reflectance of UV-B. From these studies, it can be concluded that wax is a secondary metabolite produced in larger quantities when plants are exposed to UV-B radiation. The role of epicuticular waxes in filtering UV-B radiation and genotypic variability requires further investigation before its role in leaf protection from UV-B is understood.

3.4.2. UV-B and secondary metabolites

Another adaptive mechanism to enhanced UV-B radiation is increased production of secondary metabolites in leaf tissues under enhanced UV-B radiation. The studies indicated that UV-B absorbing compounds increase from 10 to 300% in agronomic crops (Table 2). The UV-B radiation transmitted after reflection by epicuticular wax layer reaches the epidermal layer. The epidermal layer is known to accumulate most of the secondary metabolites, such as phenolics and flavonoids that absorb/screen UV-B radiation and shield the underlying tissues against harmful UV-B radiation (Cen and Bornman, 1993; Cen et al., 1993; Liu et al., 1995; Olsson et al., 1998).

A greater increase in the leaf UV-B absorbing compounds occurred when the plants were grown in relatively low PAR/UV-B (Wilson and Greenberg, 1993; Alexieva et al., 2001). The data in Table 2 suggests that high PAR allowed the plants to offset some effects caused by UV-B radiation. UV-B absorption was increased in peas after a 10 h exposure (Strid and Porra, 1992). However, UV-B-induced reduction of assimilate production (Zhao et al., 2003) leading to lower efficacy of the biosynthetic system producing secondary metabolites might reduce the amount of UV-B absorbing compounds. Hence, UV-B absorbing compounds might not offer a continued protection at increasingly higher levels of UV-B radiation. Thus, identifying crop species or genotypes that can continue to produce UV-B absorbing compounds at high intensities of solar UV-B radiation and under prolonged exposure is essential in areas prone to and projected to have high UV-B radiation levels.

3.5. *UV-B and photosynthesis*

Photosynthetic response to UV-B radiation depends on crop species, cultivars, experimental conditions, UV-B dosage, and the ratio of PAR to UV-B radiation. In general, leaf photosynthesis of crop plants was decreased more by enhanced UV-B radiation under growth chamber or glasshouse conditions than under field conditions due to low PAR or a low ratio of PAR to UV-B in the chambers (Table 3). Battaglia and Brennan (2000) reported that treatment with 194 kJ m^{-2} UV-B radiation delivered over a period of 16 h led to significantly reduced cotyledon CO_2 fixation rates in cucumber, but had no such effect in sunflower. Correia et al. (1999) found that under field conditions, a 30% increase in UV-B radiation from ambient level significantly decreased leaf photosynthesis of most corn cultivars (25–46%), but the photosynthetic rates of two cultivars did not change compared to the control. Therefore, both species and cultivar differences exist in tolerance of UV-B radiation.

In a recent review, Allen et al. (1998) summarized the mechanisms of UV-B-induced inhibition of photosynthetic capability. Numerous studies have demonstrated that in photophosphorylation processes, photosystem II (PSII) is the most sensitive component of the thylakoid membrane of photosynthetic apparatus on exposure to UV-B radiation (Brandle et al., 1977; Noorudeen and Kulandaivelu, 1982; Renger et al., 1989; Kulandaivelu et al., 1991; Melis et al., 1992; Chaturvedi et al., 1998; Correia et al., 1999; Bolink et al., 2001; Savitch et al., 2001). Several other investigations (Ziska and Teramura, 1992; Middleton and Teramura, 1993; Allen et al., 1997) suggest that UV-B inhibition of PSII photochemistry was not a ubiquitous primary limitation to photosynthesis. In the Calvin cycle of CO_2 fixation, enhanced UV-B radiation caused reductions in both Rubisco activity and content in many field crops (Vu et al., 1982, 1984; Strid et al., 1990; Nedunchezhian and Kulandaivelu, 1991; Jordan et al., 1992; He et al., 1993, 1994; Huang et al., 1993; Kulandaivelu and Nedunchezhian, 1993; Mackerness et al., 1997b; Correia et al., 1999; Savitch et al., 2001). In addition, the RuBP regeneration (Allen et al., 1997; Savitch et al., 2001) and the amount of sedoheptulose 1,7-bisphosphatase (Allen et al., 1998) were also decreased by UV-B radiation. Caldwell et al. (1994) pointed out that UV-A appeared to be particularly effective in mitigating UV-B damage when PAR was low. Recently, Savitch et al. (2001) investigated the effect of UV-B with or without UV-A radiation on the mechanisms of UV-B reduced photosynthesis of *Brassica napus* using 200 μmol m^{-2} s^{-1} PAR and suggested that the decrease in the CO_2 assimilation capacity for PAR + UV-B treated plants was not associated with limitation at the level of PSII electron transport, but rather with a decreased capacity for sucrose biosynthesis, limited triose-P utilization, and a decreased capacity for RuBP regeneration. In contrast, decreased CO_2 assimilation capacity for PAR + UV-A + UV-B treated plants was associated with an inhibition of PSII photochemistry and a decreased supply of ATP. Therefore, UV-A radiation appeared to induce feedback-limited photosynthesis and did not enhance resistance of the crop to UV-B radiation (Savitch et al., 2001).

Stomatal regulation is another important process limiting leaf photosynthesis. Although some earlier studies have shown that UV-B radiation does not affect stomatal conductance in soybean (Teramura et al., 1984; Murali and Teramura, 1985, 1987) and snapbean (Agrawal et al., 1991), several other studies have demonstrated reduced stomatal conductance in response to UV-B radiation (Dai et al., 1992; Middleton and Teramura, 1993; Pal et al., 1998, 1999). However, the direct UV-B effect on stomatal conductance was not a major limitation for CO_2 assimilation in several crops (Agrawal et al., 1991; Teramura et al., 1991a; Ziska and Teramura, 1992; Zhao et al., 2003). The decrease in stomatal conductance was much smaller than the decrease in net photosynthetic rate, and the intercellular CO_2 concentration of plants exposed to UV-B radiation was not

Table 3
Field crop leaf photosynthesis (Pn) response to elevated UV-B radiation

Crop	UV-B_{BE} (kJ m^{-2} per day)	Simulating O$_3$ depletion (%)	PAR (μmol m^{-2} s^{-1})	Experimental condition	Pn	References
Barley	8.84, 13.56	5, 25	800–1000	GC	↓	Liu et al. (1995)
Blackgram	A + 10.08	15	A	F	↓ (88)	Singh (1995)
Cassava	A + 5.5	15	A	F	–	Ziska et al. (1993)
Corn	1, 2 W m^{-2}	?	200–250	GH	↓↑	Rozema et al. (1991)
	125% of A	15	?	GC	↓	Tevini et al. (1991)
	140% of A	20	A	F	–	Ambasht and Agrawal (1995)
	130% of A	?	∼A	GC	↓	Mark and Tevini (1997)
Cotton	8	∼A	∼A	Sunlit chamber	–	Zhao et al. (2003)
	15	30	∼A	Sunlit chamber	↓ (33–38)	Zhao et al. (2003)
Cowpea	1.8	?	250	GC	↓ (60)	Lingakumar and Kulandaivelu (1993)
	0, 4.6, 7.6, 10.6	?	250	GH	–	Tosserams et al. (2001)
Faba bean	2.8, 6.0 (A)	?	A	OTC	–	Visser et al. (1997a)
Mung bean	A + 10.08	15	A	F	↓ (45)	Singh (1995)
	A + 11.02	15	A	F	↓ (21)	Pal et al. (1997, 1999)
Pea	∼5.9	?	150	GC	↓ (90)	Strid et al. (1990)
	18	?	>800	GH	↓ (17)	Day and Vogelmann (1995)
	40, 50	?	450	GH	↓ (30)	Nogues and Baker (1995)
	∼7	?	150–350	GC	↓ (10–90)	Mackerness et al. (1997a)
	32	?	500	GH	–	Nogues et al. (1998)
	2.3, 4.6, 6.3, 9.2	A, A, 22, 45	850–950	GC	–	Gonzalez et al. (1998b)
	130% of A	18	A	F	–	Allen et al. (1999)
	7.7	?	?	GH	–	Skorska (2000a)
Rapeseed	2.6	?	70	GC	–	Wilson and Greenberg (1993)
	32	?	>500	GH	↓	Allen et al. (1997)
	11.2	?	?	?	↓	Skorska (2000b)
	34	?	200	GC	↓ (40)	Savitch et al. (2001)
Rice	8.8, 15.7	A, 10	1400–1700 (MD)	GH	–	Teramura et al. (1990b)
	8.8, 13.8	A, 25	1400–1700 (MD)	GH	↓	Ziska and Teramura (1992)
	140% of A	20	A	F	↓	Ambasht and Agrawal (1997)
Rye	0.28, 0.42	?	700	GC	↓ (17–19)	Deckmyn and Impens (1997a,b)
Soybean	3	25	1400	GH	↓	Teramura et al. (1984)
	A + 0.7–1.2	?	A	F	–	Murali and Teramura (1985)
	A + 3 or 5.1	16 or 25	A	F	–	Murali and Teramura (1986b)
	A + 5.1	25	A	F	↓ (14)	Sullivan and Teramura (1990)
	8.8, 15.6	A, 10	1400–1700 (MD)	GH	–	Teramura et al. (1990b)
	10.7–14.1	?	1300–1600 (MD)	GH	↓ (6–21)	Middleton and Teramura (1993)
	2.5–9.3	20–37	A	F	–	Miller et al. (1994)
Snapbean	11.7	?	300	GC	↓	Agrawal et al. (1991)
	0.25–1.66	?	50, 100, 250	GC	↓ (3–22)	Deckmyn et al. (1994)
	8% increase	?	?	GH	–	Deckmyn and Impens (1995)
	11	15	A	F	↓ (18)	Pal et al. (1999)
	11.2	?	?	?	↓	Skorska (2000b)
Sunflower	125% of A	15	?	GC	↓	Tevini et al. (1991)
	130% of A	?	∼A	GC	↓	Mark and Tevini (1997)
	194 (16 h)	?	?	GH	–	Battaglia and Brennan (2000)
Wheat	9.6–17.9	20–45	∼A	GH	–	Beyschlag et al. (1988)
	Modulated	20	A	F	–	Beyschlag et al. (1988)
	8.8, 15.6	A, 10	1400–1700 (MD)	GC	–	Teramura et al. (1990b)
	1, 2 W m^{-2}	?	200–250	GH	↓	Rozema et al. (1991)

Values in parenthesis indicate percentage change. A: ambient level; CD: cultivar dependant; F: field; GC: growth chamber; GH: greenhouse; GLH: glasshouse; CE: controlled environment chambers; MD: mid-day; OTC: open top chamber; ?: information not available. The ↓, ↑ and – represent that parameter was decreased, increased and unaffected by elevated UV-B radiation, respectively, compared to the control.

different or even higher than that of untreated control plants (Agrawal et al., 1991; Zhao et al., 2003). The mechanism of UV-B-induced stomatal closure is not clearly understood yet (Allen et al., 1998). In a recent study, Jansen and van-den-Noort (2000) found that high UV-B stimulated either stomatal opening or closing in *Vicia faba*, depending on the metabolic state. Once stomata were exposed to UV-B radiation, they were unable to readjust their aperture in response to environmental stimuli and speculated that UV-B may impact reactions that facilitate the solute fluxes leading to stomatal opening, such as those from the plasmalemma-based enzyme complexes.

3.6. UV-B and phenology and growth

Only a few studies have documented the effect of UV-B radiation on crop phenology or developmental rates. Enhanced UV-B radiation delayed both seedling emergence and flowering of several crop plants under controlled growth chamber conditions (Basiouny, 1986; Saile-Mark and Tevini, 1997; Santos et al., 1998) and in field (Li et al., 1998). On the other hand, under field conditions, soybean flowering and podding dates were unaffected by a 32% enhanced exposure to UV-B radiation (Sinclair et al., 1990). Similarly, days from emergence to the first floral bud and from the first floral bud to first flower for cotton plants did not differ between the UV-B radiation treatments in a sunlit chamber study (Reddy et al., 2003). Based on these studies, current and projected UV-B levels may not affect crop phenology to an extent that would call for changes in cultivation and management of the crops.

Numerous studies have been conducted to determine the impact of UV-B radiation on crop growth (Table 4). Overall, enhanced UV-B radiation reduces mainstem and branch elongation rates, resulting in more compact and shorter plants. Decreased plant height was mainly due to shorter internodes rather than fewer nodes (Tevini and Teramura, 1989; Barnes et al., 1993; Santos et al., 1993; Searles et al., 1995; Li et al., 1998; Gonzalez et al., 1998b; Zhao et al., 2003). Mark and Tevini (1996) speculated that the mechanism for reduced stem elongation by UV-B might be due to changes in the phytohormone levels, especially IAA which plays a role in stem elongation. Few studies indicated a break down of IAA on exposure to UV-B radiation (Ros and Tevini, 1995; Huang et al., 1993). Gonzalez et al. (1998a) pointed out that the shorter internodes for UV-B-treated pea plants were due to fewer cells rather than reduced cell length. Other UV-B-induced effects on stems include coiling of both attached and detached tendrils in peas that could be used as markers for selecting UV-B tolerant genotypes (Brosche and Strid, 2000).

Similar to plant height, leaf area is also a very sensitive growth parameter that responded to elevated UV-B radiation (Table 4). Under most experimental conditions, leaf area was less due to both smaller and lesser number of leaves when plants were exposed to enhanced UV-B radiation (Nogues et al., 1998; Zhao et al., 2003) that serve as a protective mechanism (Bornman and Teramura, 1993). The reduction in leaf area was caused by a reduction in cell size and/or a change in leaf structure (Tevini et al., 1983), reduction in cell number (Gonzalez et al., 1998a) and by both cell division and cell expansion (Hofmann et al., 2001), and the UV-B effect on cell division was greater than on the cell expansion (Nogues et al., 1998; Hofmann et al., 2001). In contrast, Nedunchezhian and Kulandaivelu (1997) reported that, under field conditions, slightly enhanced UV-B radiation (1.8 $\mathrm{kJ\,m^{-2}}$ per day) increased leaf area of cowpea. Even high UV-B-treated (13.4–63.3 $\mathrm{kJ\,m^{-2}}$ per day) broad bean and wheat plants had higher leaf area than the untreated control plants (Al-Oudat et al., 1998). Along with reduced leaf area, heliotropism also helps to reduce the amount of UV-B intercepted by leaves and could be used to characterize tolerant and susceptible cultivars to UV-B radiation (Grant, 1999).

Out of the 40 studies using 23 crop species in the last 18 years under greenhouse, growth chamber, or field conditions, reduced biomass by elevated UV-B radiation was recorded in 54% of studies, about 35% of the studies reported no effect on dry weight, and a few (5%) studies demonstrated increases in crop dry matter accumulation (Table 4). The differences were probably associated with crop species, genotypes (see Section 3.8), UV-B doses, and PAR:UV-A:UV-B ratio. Crop biomass production in response to UV-B radiation was highly UV-B dosage-dependent. In a sunlit chamber study (Zhao et al., 2003), cotton plants exposed to near ambient UV-B (8 $\mathrm{kJ\,m^{-2}}$ per day) radiation from emergence to 66 days showed no difference in total biomass from the control plants

Table 4
Effects of UV-B radiation on plant height, leaf area, and biomass accumulation of field crops

Crop	UV-B$_{BE}$ (kJ m^{-2} per day)	Simulating O$_3$ depletion (%)	PAR (μmol m^{-2} s^{-1})	Experimental condition	Plant height	Leaf area	Biomass	References
Barley	8.84, 13.56	5, 25	800–1000	GC	–	–	–	Liu et al. (1995)
	0, A	?	A	F	?	?	↓ (20–32)	Mazza et al. (1999)
	130% of A	?	A	F	–	?	–	Hakala et al. (2002)
Blackgram	A + 10.08	15	A	F	↓ (22)	↓ (35)	↓ (31)	Singh (1995)
Cassava	A + 5.5	15	A	F	–	↑ (18)	–	Ziska et al. (1993)
Corn	5.4	50	400	GC	↓ (12)	?	↓ (17)	Basiouny (1986)
	125% of A	15	?	GC	↓	↓	↓	Tevini et al. (1991)
	72	?	700	GC	↓ (25)	↓ (42)	?	Santos et al. (1993)
	130% of A	?	∼A	GH	↓	↓	↓	Mark and Tevini (1997)
	A + 18.7	?	A	F	–	↓ (14)	↓ (21)	Correia et al. (1998)
	A + 3.16	20	A	F	?	?	↓ (30)	Correia et al. (2000)
Cotton	17.5	?	?	GC	?	↓ (40–90)	↓ (68–70)	Ambler et al. (1975)
	A + 11.5, 22	?	A	F	↓	↓	↓	Song et al. (1999)
	8	A	∼A	Sunlit chamber	–	–	–	Zhao et al. (2003)
	15	30	∼A	Sunlit chamber	↓ (44)	↓ (50)	↓ (69)	Zhao et al. (2003)
Cowpea	A + 1.8	16	A	F	↑	↑	↑	Nedunchezhian and Kulandaivelu (1997)
	A + 2.2	20	A	F	–	–	–	Premkumar and Kulandaivelu (2001)
Broad bean	13.4–63.3	10	A	F	↑ (35)	↑ (20)	↑ (14)	Al-Oudat et al. (1998)
Bush bean	0.25–1.66	?	50, 100, 250	GC	↓ (0–12)	↓ (0–15)	↓ (11–32)	Deckmyn et al. (1994)
	A, 92% of A	4–5	∼A	GH	↓	↓	CD	Saile-Mark and Tevini (1997)
Groundnut	5.4	50	400	GC	↓ (22)	?	–	Basiouny (1986)
Linseed	? (1 h per day)	?	A	?	?	?	–	Goyal et al. (1991)
	? (4 h per day)	?	A	?	?	?	↓	Goyal et al. (1991)
Mung bean	A + 10.08	15	A	F	↓ (20)	↓ (33)	↓ (60)	Singh (1995)
	11.02	15	A	F	↓ (18)	↓ (18)	↓ (15)	Pal et al. (1999)
Mustard	11.02	15	A	F	↓	↓	↓	Pal et al. (1998)
Pea	?	15	A	F	↓	?	↓	Mepsted et al. (1996)
	6.5	20	850–950	GC	↓ (30–38)	↓ (20–30)	↓ (25)	Gonzalez et al. (1996)
	2.3–9.2	A–45	850–950	GC	↓ (25)	↓ (30)	↓ (6–30)	Gonzalez et al. (1998b)
	130% of A	18	A	F	–	–	–	Allen et al. (1999)
	32	?	500	GH	?	↓	↓	Nogues et al. (1998)
Oat	5.4	50	400	GC	↓ (35)	?	↓ (21)	Basiouny (1986)
	125% of A	15	?	GC	–	–	–	Tevini et al. (1991)
	130% of A	?	A	F	–	?	–	Hakala et al. (2002)
Rice	5.4	50	400	GC	↓ (9)	?	↓ (39)	Basiouny (1986)
	19	?	?	GH	↓	↓	↓	Coronel et al. (1990)
	10.3	5	∼974	GH	↓ (7)	↓ (12)	↓ (5)	Barnes et al. (1993)
	0.8–22.1	?	A	F	–	?	–	Nouchi and Kobayashi (1995)
	13	?	940	GH	↓ (−2 to 32)	↓ (−30 to 34)	↓ (−32 to 35)	Dai et al. (1994a,b)
	3.8–6.5	27–38	A	F (pot)	–	–	–	Kim et al. (1996)
	A + 6.5	20	A	F	–	?	–	Dai et al. (1997)
	?	?	A	F	?	?	↓	Kumagai et al. (2001)
Rye	5.4	50	400	GC	↓ (26)	?	–	Basiouny (1986)
	125% of A	15	?	GC	↓	↓	↓	Tevini et al. (1991)
Soybean	5.4	50	400	GC	–	?	–	Basiouny (1986)
	10.1	16	∼A	F, GH	CD	CD	CD	Teramura and Murali (1986)

Table 4 (*Continued*)

Crop	UV-B$_{BE}$ (kJ m^{-2} per day)	Simulating O$_3$ depletion (%)	PAR (μmol m^{-2} s^{-1})	Experimental condition	Plant height	Leaf area	Biomass	References
	132% of A	16	A	F	–	–	–	Sinclair et al. (1990)
	136	25	1200	GH	↓ (19)	↓ (20)	↓ (17)	Reed et al. (1992)
Sugar beet	6.91	?	106	GC	?	↑ (17)	–	Panagopoulos et al. (1992)
Sugarcane	?	?	?	GH	↓	↓	↓	Elawad et al. (1985)
Sorghum	5.4	50	400	GC	↓ (25)	?	↓ (59)	Basiouny (1986)
Sunflower	125% of A	15	?	GC	↓	↓	↓	Tevini et al. (1991)
	130% of A	?	~A	GC	↓	↓	↓	Mark and Tevini (1997)
Tobacco	5.4	50	400	GC	↓ (21)	?	–	Basiouny (1986)
Wheat	13.4–63.3	10	A	F	↑ (10)	↑ (12)	↑ (11)	Al-Oudat et al. (1998)
	A + 2.5, 4.3, 5.3	12, 20, 25	~A	F	↓ (7–16)	↓ (45)	↓ (37)	Li et al. (1998)
	130% of A	?	A	F	–	–	–	Hakala et al. (2002)

Values in parenthesis indicate percentage change. A: ambient level; CD: cultivar dependant; F: field; GC: growth chamber; GH: greenhouse; CE: controlled environment chambers; MD: mid-day; OTC: open top chamber; ?: information not available. The ↓, ↑ and – represent that parameter was decreased, increased and unaffected by elevated UV-B radiation, respectively, compared to the control.

(0 kJ UV-B), but the biomass of 15 kJ UV-B-treated plants was decreased by 69% compared to the control. Deckmyn and Impens (1997a) investigated the effect of UV-B/PAR ratio on the sensitivity of rye to increased UV-B radiation under growth chamber conditions, and concluded that plants grown under higher total irradiance levels developed leaves that were more tolerant to UV-B damage, while low PAR levels increased the sensitivity of plants to the UV-B radiation.

The effects of enhanced UV-B radiation on plant growth and dry mass accumulation in field conditions were usually much smaller than on those in growth chamber or greenhouse conditions (Caldwell et al., 1994; Olszyk et al., 1996). Further interpretations of these differences can be found in two related publications by Olszyk et al. (1996) and by Dai et al. (1997). In field conditions, UV-B caused decreases in total aboveground production of soybean when PAR and UV-A were reduced to less than half their flux in sunlight (Caldwell et al., 1994). The UV-A radiation appears to have a strong ameliorating effect when PAR is not high (refer to Caldwell et al., 1994 for further explanation).

3.7. UV-B and crop yield

The main concern for producers and agricultural scientists is whether or not enhanced UV-B radiation due to stratospheric O$_3$ depletion reduces economic yields and product quality of field crops. The UV-B radiation modifies the reproductive or floral morphology of crop plants and affects reproductive processes that lead to final yield formation. Flowering increased when UV-B was excluded by covering plants with Mylar sheet that filters UV-B radiation (Caldwell, 1968). Cotton flowers produced on plants exposed to UV-B treatments were smaller due to reduced petal and bract size, and had reduced anther number (Kakani et al., 2003). As cotton floral morphology is sensitive to enhanced UV-B radiation, pollination, boll formation and development, and finally, the lint yield could also be affected. The decrease in anther number would also hamper the commercial cotton hybrid production. Evidence from in vitro experiments shows that pollen germination was inhibited by exposure to enhanced UV-B (Chang and Campbell, 1976; Caldwell, 1979; Flint and Caldwell, 1984). In a study with 34 plant species, Torabinejad et al. (1998) showed that UV-B radiation reduced pollen germination, but more severely the pollen tube growth. They reported that pollen tube lengths of crop species (corn, rye and tobacco) were reduced by 10–25%, depending on crop species, which would severely limit fertilization and the yield forming capability of these crops. Further studies are needed to evaluate the effects of UV-B on pollen of crop plants.

Many studies evaluating the impact of enhanced UV-B on crop yields were carried out in both field and/or greenhouse conditions (Table 5). Almost half of the studies showed that enhanced UV-B radiation decreased yield, the other half showed no UV-B effect

Table 5
Field crop economic yield response to elevated UV-B radiation

Crop	UV-B_{BE} (kJ m^{-2} per day)	Simulating O_3 depletion (%)	PAR (μmol m^{-2} s^{-1})	Experimental condition	Yield	References
Barley	Modulated	15	A	F	–	Stephen et al. (1999)
	0, A	?	A	F	↓ (17–31)	Mazza et al. (1999)
	130% of A	?	A	F	–	Hakala et al. (2002)
Blackgram	A + 10.08	15	A	F	↓ (63)	Singh (1995)
Cassava	A + 5.5	15	A	F	↓ (32)	Ziska et al. (1993)
Corn	7.83	?	700	GC	↓	Santos et al. (1999)
	A + 3.16	20	A	F	↓ (22–33)	Correia et al. (2000)
Cotton	A + 3.5, 13.2	?	A	F	↓	Giller (1991)
	A + 11.5, 22	?	A	F	↓	Song et al. (1999)
Broad bean	13.4–63.3	10	A	F	–	Al-Oudat et al. (1998)
Bush bean	A, 92% of A	?	?	GH	↑	Deckmyn and Impens (1995)
	A, 92% of A	4–5	∼A	GH	CD	Saile-Mark and Tevini (1997)
Forage	133, 166% of A	?	A or ∼A	F, GH	↑	Papadopoulos et al. (1999)
	?	25	A	F	–	Gwynn-Jones (2001)
	130% of A	?	A	F	–	Hakala et al. (2002)
Linseed	? (1 h per day)	?	A	?	↑	Goyal et al. (1991)
	? (4 h per day)	?	A	?	↓	Goyal et al. (1991)
Mung bean	A + 10.08	15	A	F	↓ (76)	Singh (1995)
Pea	?	15	A	F	↓	Mepsted et al. (1996)
	Modulated	15	A	F	–	Stephen et al. (1999)
Oat	?	15	A	F	↓	Yue and Wang (1998)
	130% of A	?	A	F	–	Hakala et al. (2002)
Rapeseed	?	15–32	?	?	–	Demchik and Day (1996)
Potato	130% of A	?	A	F	–	Hakala et al. (2002)
Rice	8.8, 15.6	A, 10	1400–1700 (MD)	GH	–	Teramura et al. (1990b)
	3.8–6.5	27–38	A	F (pot)	–	Kim et al. (1996)
	A + 6.5	20	A	F	–	Dai et al. (1997)
	?	?	A	F	↓	Kumagai et al. (2001)
Soybean	10.1	16	A or ∼A	F, GH	CD (−41 to 46)	Teramura and Murali (1986)
	132% of A	16	A	F	–	Sinclair et al. (1990)
	A + 3 or A + 5.1	16 or 25	A	F	↓ (−16 to 32)	Teramura et al. (1990a)
	8.8, 15.6	A, 10	1400–1700 (MD)	GH	–	Teramura et al. (1990b)
	13.6	25	1200(MD)	GH	CD (0–37)	Reed et al. (1992)
	2.5–9.3	4, 20, 32, 35, 37	A	OTC	–	Miller et al. (1994)
Wheat	8.8, 15.6	A, 10	1400–1700 (MD)	GH	–	Teramura et al. (1990b)
	A + 2.5, 4.3, 5.3	12, 20, 25	∼A	F	↓ (43)	Li et al. (1998)
	A + 13.4–63.3	10	A	F	↑ (15)	Al-Oudat et al. (1998)
	?	15	A	F	–	Yue and Wang (1998)
	A + 5.0	20	A	F	CD	Li et al. (2000)
	130% of A	?	A	F	–	Hakala et al. (2002)

Values in parenthesis indicate percentage change. A: ambient level; CD: cultivar dependant; F: field; GC: growth chamber; GH: greenhouse; CE: controlled environment chambers; MD: mid-day; OTC: open top chamber; ?: information not available. The ↓, ↑ and – represent that parameter was decreased, increased and unaffected by elevated UV-B radiation, respectively, compared to the control.

on the yield, and a few studies showed UV-B enhancement increased yields. The UV-B radiation supplied in these studies varied considerably (2.5–63 kJ m^{-2} or 10–50% of stratospheric O_3 depletion).

Final yield or biomass is influenced by various parameters that are affected by UV-B radiation. Decreases in chlorophyll concentration, photosynthesis, leaf area, and fruit retention result in yield reduction. From the compiled data, a significant relationship ($R^2 = 0.7$) was found only between leaf area and final biomass as leaf area encompasses the effect of UV-B on changes in leaf ultrastructure, pigments and canopy photosynthesis. Hence, future studies should record all the important physiological and growth parameters to estimate the effect of each parameter in reducing final biomass or yield.

3.8. Genotype variation

Increased yield and yield stability are the characters responsible for the acceptability of a genotype in a given environment. The increased concern about UV-B radiation effects on crop plants has prompted plant physiologists and breeders to look for UV-B tolerance in crop populations. Genotypes of several crop species were screened for tolerance to UV-B radiation. Decreased total accumulated biomass, photosynthetic pigments and photosynthetic rate, and increased UV-B absorbing compounds were the main characters used to classify the genotypes for tolerance to UV-B radiation.

Genotypes of rice were extensively screened for their tolerance to UV-B radiation. Rice genotypes were classified as tolerant, intermediate, or susceptible to UV-B radiation on the basis of the observed damage (Cassi-Lit et al., 1997), variation in phenolic concentration, and shoot dry weight (Dai et al., 1994a,b, 1995). Of the 188 rice cultivars screened in response to UV-B radiation (13 kJ m^{-2} per day) in a phytotron study, total shoot dry weight ranged from −35 to +32% compared to no UV-B control (Dai et al., 1994a,b, 1995). However, when evaluated under field conditions, cultivar differences for yield disappeared due to higher PAR (Dai et al., 1995, 1997). Among 16 rice cultivars screened by Teramura et al. (1991b), total plant dry weight varied from −41 to +23% with enhanced UV-B (15.7 kJ m^{-2} per day) compared to check plants. Other parameters such as net photosynthesis varied from −26 to +24%, total chlorophyll content varied between −20 and +44%, while the UV-B absorbing compounds ranged from −19 to +46% among the genotypes compared to control plants. A sensitivity index, calculated by summing the percent changes in plant dry weight, shoot height and leaf area in a study of 21 rice genotypes (Barnes et al., 1993), classified genotypes into insensitive (−9.9 to +3.0), intermediate (−29.6 to −11.9) and sensitive (−50.4 to −32.0). These studies showed that the origin and adaptation of the rice genotypes to niche environments determines their ability to tolerate UV-B radiation.

Wheat, an important cereal crop grown throughout the world, has had no extensive screening of genotypes for UV-B radiation. In a study of 20 wheat cultivars, exposed to 5 kJ m^{-2} per day of UV-B radiation simulating 20% stratospheric ozone depletion, differences were seen in chlorophyll and UV-B absorbing compounds among the cultivars. The change in chlorophyll content was −56% to +0.53% of the control plants, while for UV-B absorbing compounds it was between −40 and +16% of control plants (Li et al., 2000). Correia et al. (1998) evaluated eight maize genotypes to determine growth and morphological effects of UV-B radiation under field conditions. The sensitivity index, based on changes in plant dry weight, plant height, and leaf area, was −7 in the most tolerant and −56 in the most susceptible genotype compared to the control. Plant height and leaf number were not affected in this study.

Among oilseed crops, soybean and rapeseed received more attention for genotype responses to enhanced UV-B radiation than peanuts, sunflower and safflower. Soybean genotypes varied widely in response to UV-B and were character specific (Teramura and Murali, 1986; Reed et al., 1992). The genotypes varied for plant height, leaf area, total dry weight, seed yield. Percent variation of individual character, plant height (−44 to +21%), leaf area (−87 to +186%), total dry weight (−46 to +64%), and seed yield (−41 to +46%), varied among the genotypes. Genotypes tested under both greenhouse and field conditions showed greater responses under greenhouse conditions (−38 to +84%) than under field conditions (−22 to +14%). Two soybean cultivars, Essex (susceptible) and Williams (tolerant) were studied in detail to understand plant responses to UV-B radiation (D'Surney et al., 1993; Kramer et al., 1992; Teramura et al., 1990a; Teramura and Murali, 1986; Murali and Teramura, 1986b). Experiments in both greenhouses and field conditions established the relative tolerance of soybean cultivars that can be exploited to breed more UV-B tolerant genotypes. Genotypic variability was also detected in peas (Gonzalez et al., 1996).

Crop yields represent an integration of the variability due to environmental factors, and their interaction. Therefore, the yield variation caused by UV-B radiation may depend on species sensitivity to UV-B radiation and all other biological and environmental factors. Since these environmental factors vary seasonally and annually, the degree of UV-B effects on crop yield may vary considerably among locations, and even from year to year (Teramura et al., 1990a). Therefore, the interactive effects of UV-B radiation and other environmental factors on crop growth and yield under field conditions should be investigated.

3.9. UV-B interaction with abiotic and biotic factors

3.9.1. UV-B interaction with abiotic factors

Studies showed both positive and negative interactive effects on crops with UV-B radiation along with other environmental factors. The overall UV-B effect was aggravated and in some cases ameliorated by some environmental factors (Caldwell et al., 1998; Krupa et al., 1998). The combined effects of elevated UV-B, [CO_2], surface O_3, temperature, moisture, diseases and insect pests on crops are dealt in this section in an integrated manner (Table 6). Advanced computer technologies and complex models are yet to be developed to understand the interaction in detail (Groth and Krupa, 2000).

The measured physiological and biochemical parameters indicated that UV-B has a stronger stress effect than drought on growth (Alexieva et al., 2001), but UV-B had little effect on biomass under drought conditions compared to well-watered condition (Teramura et al., 1990a). Similar results were recorded for photosynthesis (Murali and Teramura, 1986a; Sullivan and Teramura, 1990) and photosynthesis and nitrate reductase activity (Eswaran et al., 1993). In contrast, Premkumar et al. (1993) found significant increase in growth and biochemical parameters in water-deficit and UV-B-treated plants over control greengram plants. Plants in water-deficit conditions produced higher amounts of flavonoids (112%) that provided protection against UV-B (Murali and Teramura, 1986a) by dissipating energy and protecting sensitive organelles (Cen et al., 1993; Liu et al., 1995; Olsson et al., 1998). UV-B was also found to increase the surface wax production (Steinmuller and Tevini, 1985), which has an important implication for water conservation. In summary, a pre-application of either UV-B or drought stress reduced the damage caused by the subsequent application of other stress.

The plant growth responses to atmospheric [CO_2] and UV-B radiation generally are in opposite directions when they occur independently. To date, few studies have investigated the possible interaction between [CO_2] and UV-B (Table 6). Some studies with elevated [CO_2] and UV-B interaction indicated that increased growth and seed yield of crops resulting from [CO_2] enrichment were negated or reduced or unaffected by UV-B radiation (Teramura et al., 1990a,b; Ziska and Teramura, 1992; Bjorn et al., 1997; Gwynn-Jones et al., 1997; Sullivan, 1997; Tosserams et al., 2001). A combination of UV-B and [CO_2] is also known to affect biomass partitioning (Sullivan, 1997). Xiu-Ming et al. (1997) found that a higher dose of UV-B (13.1 $\mathrm{kJ\,m^{-2}}$ per day) resulted in more severe damage at 600 $\mu\mathrm{l\,l^{-1}}$ of [CO_2] than at ambient [CO_2]. A study by Zhao et al. (2003) showed that elevated [CO_2] did not ameliorate the adverse effects of UV-B on cotton growth, physiology and particularly boll retention. Interaction of [CO_2] and UV-B modified leaf optical properties, and the combined effects differed from single stress effects (Visser et al., 1997a). In a study by Deckmyn et al. (2001), 88% of ambient UV-B radiation combined with elevated [CO_2] (521 $\mu\mathrm{l\,l^{-1}}$) increased growth and flowering of white clover indicating the important role played by UV-B under present day climates.

Studies evaluating temperature and UV-B interaction indicate that temperature alleviates the UV-B effects (Table 6). Mark and Tevini (1996) found that reduced growth due to enhanced UV-B radiation was alleviated by 4 °C increase in temperature. The alleviation was attributed to higher net photosynthetic rates that could be due to some unidentified photorepair mechanism (Teramura, 1980) or an increased accumulation of flavonoids that filter UV-B radiation (Tevini et al., 1991). Nedunchezhian and Kulandaivelu (1996)

Table 6
UV-B interactions with biotic and abiotic factors

Crop	UV-B_{BE} (kJ m^{-2} per day)	Simulating O_3 depletion (%)	Interaction factor	PAR (μmol m^{-2} s^{-1})	Experimental condition	References
Water stress						
Cucumber	12, 24	–	?	400	CE	Yang et al. (2000)
Cucumber	?	–	Mild	A	Hydroponics	Al-Wakeel (1998)
Greengram	?	–	?	?	CE	Premkumar et al. (1993)
Maize	?	–	?	A	GH	Eswaran et al. (1993)
Mustard	6, 17	45	Mild	552	GH	Conner and Zangori (1998)
Pea	32	–	Mild	A	GH	Nogues et al. (1998)
Pea	1.9, 2.4	18	?	A	F	Allen et al. (1999)
Pea	49	–	Moderate	A	GC	Alexieva et al. (2001)
Soybean	8.5, 13.6	25	?	A	F	Sullivan and Teramura (1990)
Soybean	–	25	?	A	F	Teramura et al. (1990a)
Soybean	5.1, 8.5	25	?	A	F	Murali and Teramura (1986a)
Soybean	–	23	Mild	A	CE	Teramura et al. (1984)
Wheat	49	–	Moderate	A	GC	Alexieva et al. (2001)
CO_2 ($\mu l\, l^{-1}$)						
Cotton	8, 16	–	360, 720	A	SPAR	Zhao et al. (2003)
Faba bean	3.2, 6.0	–	350, 750	600	OTC	Visser et al. (1997b)
Faba bean	4.6, 7.6, 10.6	–	380, 750	600	GH	Tosserams et al. (2001)
Peas			350, 700	?	CE	Rozema et al. (1990)
Rice	8.8, 15.7	10	350, 650	A	GH	Teramura et al. (1990b)
Rice	8.8, 13.8	25	360, 660	1800	GH	Ziska and Teramura (1992)
Soybean	8.8, 15.7	10	350, 650	3000	GH	Teramura et al. (1990a)
Tomato	2.7, 7.2, 13.1	–	380, 600	A	CE	Xiu-Ming et al. (1997)
Tomato	–	28	350, 706	?	CE	Rozema et al. (1990)
Wheat	8.8, 15.7	10	350, 650	A	GH	Teramura et al. (1990b)
White clover	7, 21	–	371, 521	A	GH	Deckmyn et al. (2001)
Nutrients and minerals						
Cowpea	–	20	Potassium	A	CE	Premkumar and Kulandaivelu (1996)
Cowpea	2.2, 10, 12.2	20	Magnesium	A	CE	Premkumar and Kulandaivelu (1999, 2001)
Maize	3.2, 6.9	20	Nitrogen	A	F	Correia et al. (2000)
Mustard	15	–	Cadmium	800	GH	Larsson et al. (1998)
Rapeseed	6	–	Sulfur/P/K		CE	Skorska and Murkowski (1997)
Rye	2.8, 4.2	–	Nitrogen	A	GC	Deckmyn and Impens (1997b)
Soybean	11.5	–	Phosphorus		CE	Murali and Teramura (1987)
Wheat	2, 4	–	Cadmium	?	GH	Shukla et al. (2002)
Light (μmol m^{-2} s^{-1})						
Bean	11.2	–	?	–	CE	Skorska (2000b)
	6.17	5	230, 500, 700		CE	Cen and Bornmann (1990)
	11.3	–	1200	1200	GC	Bolink et al. (2001)
	0, 12	–	250, 600	250, 600	CE	Meijkamp et al. (2001)
Maize			14, 300		?	Drincovich et al. (1998)
Mustard	4.6	–	1600		CE	Olsson et al. (2000)
Pea	11.2	–	?	?	CE	Skorska (2000a)
	11.3	–	1200	1200	GC	Bolink et al. (2001)
Rapeseed	13	–	200, 700		?	Fagerberg et al. (1995), Fagerberg and Bornman (1997)
	11.2	–	?	–	CE	Skorska (2000b)
Rye	2, 4.1	–	780, 1585	1600	GC	Deckmyn and Impens (1997b)
Wheat	–	20, 30, 45	?	?	GH, F	Beyschlag et al. (1988)
Temperature (°C)						
Sunflower, maize	–	12	32	A	GC	Mark and Tevini (1996)
Cowpea	4.5, 3.2	?	10, 20, 30, 40	A	GC	Nedunchezhian and Kulandaivelu (1996), Kulandaivelu and Nedunchezhian (1993)

Table 6 (*Continued*)

Crop	UV-B_{BE} (kJ m^{-2} per day)	Simulating O_3 depletion (%)	Interaction factor	PAR (μmol m^{-2} s^{-1})	Experimental condition	References
Ozone (nl l^{-1})						
Soybean	–	37	14–83	A	OTC	Miller et al. (1994)
Tobacco	16	?	12	A	GH	Feder and Shrier (1990)
Insects/diseases						
Rice	?	–	*Pyricularia gyrisea*	?	CE	Finckh et al. (1995)
Soybean	A	–	*Anticarsia gemmatalis*	?	F	Zavala et al. (2001)
White clover	13.3	25	Army and cut worms	?	GC	Lindroth et al. (2000)
Pea	?	–	*Autographa gamma*	?	GC	Hatcher and Paul (1994)
Sugar beet	6.91, ?	9	*C. beticola*	?	GC	Panagopoulos et al. (1992)
Weeds						
Wheat		20	*Avena fatua*	?, 1600	Field, GH	Barnes et al. (1995, 1988)
Wheat		20	*A. fatua*	?, 1600	Field, GH	Beyschlag et al. (1988)
Wheat		20	*A. fatua*	?	GH	Barnes et al. (1990)
Oat			*Setaris viridus*			
Maize			*Triticum cylindricum*			
Pea, faba bean		20	*Chenopodium album*	?	GH	Barnes et al. (1990)
Sunflower			*Amaranthus retroflexus*, *Kochia scoparia*			

A: ambient level; CD: cultivar dependant; F: field; GC: growth chamber; GH: greenhouse; CE: controlled environment chambers; MD: mid-day; OTC: open top chamber; ?: information not available.

recorded reduction in growth of pea by UV-B at 30 °C and only a marginal reduction at 20 and 40 °C. With the available few studies on temperature and UV-B interactions, it can be inferred that with temperatures up to 30 °C, crops are able to withstand UV-B radiation and are able to reduce the damage caused by the UV-B radiation. Studies are needed to evaluate the UV-B radiation and high temperature effects on the sensitive reproductive processes and final yield.

The combined effect of high ground-level ozone and UV-B could put plants at greater risk than is expected from their individual effects, but they do not co-occur (Groth and Krupa, 2000). Soybean showed sensitivity to ozone, but not to UV-B supplements (Miller et al., 1994). Increasing concentrations of ozone reduced the levels of UV-B absorbing pigments in the plant tissues. The increased phytotoxicity of the combination was deleterious to plants. Effect of these two stressors was increased when imposed simultaneously. The combined reduction by O_3 and UV-B of pollen tube growth in tobacco appeared to be additive rather than synergistic (Feder and Shrier, 1990). As concluded by Groth and Krupa (2000), experimental methods and exposure protocols must be more realistic to understand this interaction in detail.

Nutrient uptake and translocation within the plant can be affected by elevated UV-B radiation (Murali and Teramura, 1985; Ros, 1995; Musil and Wand, 1994). Nitrogen concentrations in plant tissues can increase under elevated UV-B (Hatcher and Paul, 1994; Rousseaux et al., 1998). However, nitrogen deficiency and enhanced UV-B in rye decreased biomass production by 24–33% (Deckmyn et al., 2001). Lower K supplied either independently or in combination with UV-B significantly reduced shoot, leaf biomass and leaf area in the combined stress treatment (Premkumar and Kulandaivelu, 1996). Electron transport activities and net CO_2 uptake declined in seedlings subjected to combined stresses although the concentration of photosynthetic pigments remained unchanged. Higher UV-B doses in cadmium-polluted soils severely reduced chlorophyll, photosynthesis, biomass and yield (Eriksson et al., 1995; Larsson et al., 1998; Shukla et al., 2002). Premkumar and Kulandaivelu (1999, 2001) reported that stem elongation was stimulated in magnesium-deficient cowpea when treated with UV-B, as the physiological nutritional imbalance was minimized. Studies are required to understand the dynamics of UV-B radiation in modifying the nutrient uptake and nutritional balance of crop plants, as only few studies were conducted in this area.

Changes in light environment were well tolerated by plants as long as UV-B/PAR ratios were constant (Deckmyn and Impens, 1997a). High PAR levels compensated the effects of UV-B radiation (Sisson and Caldwell, 1976; Teramura, 1980; Warner and Caldwell, 1983; Adamse and Britz, 1992). In most of the studies, PAR levels in the greenhouse and climate-controlled chambers were lower than ambient (Table 6). Therefore, when results from the glasshouse are extrapolated to the field, an overestimation of the UV-B effects was predicted (Kramer et al., 1992; Barnes et al., 1996; Rozema et al., 1997a; Caldwell et al., 1998). Short duration exposure to UV-B in darkness reduced chlorophyll fluorescence parameters indicating reductions in photosynthesis (Skorska, 2000b; Bolink et al., 2001). Adamse and Britz (1992) found no visible damage with 18 kJ m^{-2} per day of UV-B in combination with a PAR of 1000 μmol $m^{-2} s^{-1}$. High PAR (1600 μmol $m^{-2} s^{-1}$) also induced photoinhibitory effect and increase in UV-B radiation serves as additional stress (Olsson et al., 2000). Effective scavenging capabilities of flavonoids (Bors et al., 1990) could have contributed directly to the enhanced photoprotection of UV-B-treated plants in high PAR, as flavonoids in chloroplasts (Saunders and McClure, 1976) serve as antioxidants (Takahama, 1982). Some UV-B effects such as shorter plants, thick leaves, and enhanced concentration of phenolics were also observed at high PAR levels (Teramura, 1980; Ballare et al., 1996). Therefore, the threshold of UV-B damage is dependent on quantity and quality of PAR.

3.9.2. UV-B interaction with biotic factors

The extent of damage caused by biotic factors (pests, pathogens and weeds) on growth and development of crop plants was modified by abiotic factors such as UV-B radiation in the present context (Table 6). The interaction between UV-B and biotic factors depended on species, cultivars, plant tissue composition, developmental stage and plant age. Sugar beet grown under elevated UV-B radiation and infected with *Cercospora beticola* reported a deleterious additive effect from the two stressors (Panagopoulos et al., 1992). Prior exposure of cucumber plants to UV-B radiation made the plants more susceptible to *Colletotrichum lagenarium* and *Cladosporium cucumerinum* (Orth et al., 1990). Current level of solar UV-B radiation could substantially reduce insect herbivory of crop foliage mediated through changes in plant secondary chemistry or alterations in plant nitrogen or sugar content (Ballare et al., 1996; Rousseaux et al., 1998; Zavala et al., 2001). Reduced herbivory by insects under elevated UV-B radiation was attributed to increased host plant tissue nitrogen content and an increase in efficiency with which larvae utilized the food (Hatcher and Paul, 1994), higher levels of soluble phenolics and lower levels of lignin (Zavala et al., 2001), lowered sucrose content of the foliage (Yazawa et al., 1992), increased furanocoumarin content of plant tissue that resulted in slower development of during early stages of the larvae (McCloud and Berenbaum, 1994). This was further confirmed by exclusion of solar UV-B that resulted in two-fold increase of feeding by various species of chewing insects in soybean (Zavala et al., 2001). In contrast, winter moth larvae consumed most of the leaves of European silver birch (*Betula pendula*) seedlings irradiated with UV-B, irrespective of [CO_2] (Lavola et al., 1998). Their study also showed, through a diet choice experiment that increase in flavonoids was not the only reason for the preference by the larvae. The changes in insect herbivory and disease severity caused by alterations of solar UV-B can be sizeable and they can operate in different directions with certain diseases being less damaging, while increased severity of other diseases has been observed.

There was an alteration in the balance or competition between plant species when they were exposed to enhanced levels of UV-B (Table 6; Fox and Caldwell, 1978). Enhanced UV-B was shown to alter competitive balance indirectly by influencing competition for light (Barnes et al., 1995). Significant shifts in the competitive balance of *Amaranthus*–*Medicago* and *Poa* (bluegrass)–*Geum* were observed. In both cases, UV-B caused a shift in favor of the crop (alfalfa and bluegrass) over the weed species. Barnes et al. (1990) also found a competitive advantage for the crop species (wheat) and increased UV-B enhancement in the wheat–wild oat and wheat–goat grass (*Aegilops cylindrica*) mixtures. These competitive shifts were associated with differential effects of UV-B on shoot morphology (Barnes et al., 1988). Barnes et al. (1990) suggest that crop-weed competition balance under elevated UV-B may be shifted to crops when monocots dominate the weed species in a given crop. These studies, however are inconclusive, as interaction does not favor either crops or weeds, and also there is no change in total radiation intercepted.

4. Summary and conclusions

The responses of agricultural crops to current and projected increases in UV-B radiation and its interactions with other environmental factors that affect crop growth, development and finally, economic yield are fairly complex, but we suggest, based on existing knowledge, the following conclusions.

Enhanced UV-B radiation affected most crops studied and the degree of damage was contingent on experimental conditions (greenhouse, sunlit chambers, and field), UV-B dosimetry and genotypic tolerance. Most of the UV-B studies were conducted under fairly high UV-B radiation levels (>15 $\mathrm{kJ\,m^{-2}}$ per day), that are likely to be unusual in the future climates (Tables 1–5) as current levels of UV-B during the cropping season vary anywhere between 2 and 12 $\mathrm{kJ\,m^{-2}}$ per day on the Earth's surface, which includes an increase of 6–14% of UV-B radiation (UNEP, 2002) over the pre-1980 levels. Another important concern for UV-B dosimetry studies is the unequal change in intensity of wavelengths in UV-B spectra (280–325 nm). The ozone absorbs more at lower wavelengths (<300 nm) of the UV-B spectra and hence ozone depletion would significantly increase intensity at the lower wavelengths (Kerr and McElroy, 1993). Therefore, future studies evaluating UV-B effects on plants should not only focus on realistic UV-B levels but also account for spectral differences.

It is clear from the field experiments that ambient PAR (1000–1600 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) is able to ameliorate the effects of UV-B radiation as high as 18 $\mathrm{kJ\,m^{-2}}$ per day (Adamse and Britz, 1992). However, some crop species appeared to be more sensitive to elevated UV-B than others even under ambient PAR and such crops might already be experiencing UV-B radiation stress effects. Thus, experiments evaluating the effects of UV-B on photosynthesis, biomass and yield should be carried out under ambient PAR levels at the location.

This review revealed that both square wave (SQ) and modulated (MOD) methods of exposure to UV-B radiation were used in the experimental studies (Tables 1–5), though there were only a few MOD studies. Even though the MOD delivery method mimics realistic diurnal and temporal trends in UV-B radiation (Musil et al., 2002), it is farfetched to reach a general conclusion from the few studies that one system of delivery is superior to the other. The dosages between the two systems were different in the few studies where the delivery methods were evaluated along with the experimental settings (greenhouse versus field). Therefore, designing methodological comparison experiments in the future should focus on delivering the same levels of UV-B in both the systems. It would be highly desirable to conduct experiments with several UV-B levels so that one can extrapolate from the dose response functions in determining the suitability of the delivery system for UV-B studies.

In most systems of exposure, enhanced UV-B radiation affected crop growth directly through several first order effects. These include leaf photosynthesis (photosystems, thylakoid and grana membrane integrity) and photomorphogenic systems (developmental rates), upregulation of pathways producing defense compounds (flavonoids and related phenolic compounds or waxes), decreased vegetative growth, and decreased developmental times. These primary effects have led to a myriad of secondary and tertiary effects resulting in altered crop growth and development, which in turn affected light interception that lowered canopy photosynthesis, reduced fruit numbers and retention, and finally, biomass and yield reductions.

Plant responses to enhanced UV-B radiation varied markedly within and between species. The recent introduction of genetically modified cultivars and species often with superior traits designed to increase growth and yield under narrow, but well-defined conditions promote narrow genetic makeup of cultivars used in production agriculture. Breeders will be hard pressed to accommodate climate change including UV-B radiation into their breeding programs because of technical difficulties involved in the methods and approaches in this area of research. If climate change is small and slow, production agriculture will adapt to changes projected in climate, but if changes in climate are rapid with more frequent occurrence of extreme climate episodes, production agriculture may not be able to adapt to such changes in climate.

Although the mechanisms of UV-B radiation effects on plant systems have been well understood, our abilities to assess the consequences of current and projected changes in UV-B radiation on crop production have been hampered by lack of responses requiring quantification of several important processes in interaction with other environmental factors. As the UV-B dose response studies with more than three levels of UV-B radiation for growth and development of crop plants (Gonzalez et al., 1998a; Tosserams et al., 2001) and those that studied all the physiological, growth and development characters (Reddy et al., 2003) were very few, future studies should utilize ambient PAR (Reddy et al., 2001, 2003) to study the effects of UV-B on crop plants without the interference of other abiotic and biotic factors.

As growth reductions were not always correlated to the observed reductions at the whole plant-level, caution is needed in drawing conclusions based on just leaf-level photosynthetic processes. Future studies should take into consideration canopy and whole plant processes as affected by UV-B. These studies will provide meaningful information that can ultimately be used to develop process-level crop models to study the impacts of global environmental change including UV-B at different scales. From the few studies addressing the interactions of UV-B and other environmental factors such as atmospheric [CO_2], temperature, drought and ozone, it was not possible to predict the consequences and even the direction of changes as both ameliorating and aggravating effects have been reported. Future studies should address understanding of plant responses to the interactions of UV-B radiation and other climate change variables, particularly atmospheric [CO_2], temperature, ozone, drought conditions, and mineral deficiencies.

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