



## Field crop responses to ultraviolet-B radiation: a review

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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  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and UV-B (0–50  $\text{kJ m}^{-2}$  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.

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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<sub>2</sub> concentrations ([CO<sub>2</sub>]) 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<sup>-2</sup> 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](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 erythral 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 kJ m<sup>-2</sup> 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 kJ m<sup>-2</sup> 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 kJ m<sup>-2</sup> 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 kJ m<sup>-2</sup> per day. In China, ambient UV-B levels during soybean cropping period averaged to 8.85 kJ m<sup>-2</sup> 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<sub>2</sub>] 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 kJ m<sup>-2</sup> per day to as high as 49 kJ m<sup>-2</sup> 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<sub>2</sub>, 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 <sup>-1</sup> )	Production (Mt)	Number of UV-B references
<b>Cereal crops</b>				
Wheat ( <i>Triticum</i> spp.)	213443943	2.75	587561753	40
Rice paddy ( <i>Oryza sativa</i> L.)	154140174	3.90	600638089	56
Maize ( <i>Zea mays</i> L.)	138738942	4.27	592999083	39
Barley ( <i>Hordeum vulgare</i> L.)	53096972	2.52	133933386	17
Sorghum ( <i>Sorghum</i> spp.)	41964377	1.38	57964600	12
Millet ( <i>Pennisetum glaucum</i> (L.) R. Br.)	36315592	0.72	26281789	1
Maize for forage + silage	17793750	26.51	471768130	0
Oats ( <i>Avena sativa</i> L.)	12849939	2.03	26086195	9
Rye ( <i>Secale cereale</i> L.)	9745081	2.02	19694254	8
Sorghum for forage + silage	1119288	23.31	26091154	0
<b>Tuber crops</b>				
Potatoes ( <i>Solanum tuberosum</i> L.)	19940259	16.45	328050784	5
Cassava ( <i>Manihot esculentum</i> Crantz)	17032269	10.38	176784378	3
Sweet potatoes ( <i>Ipomea batatas</i> (L.) Lam.)	9111974	15.24	138848631	0
Yams ( <i>Dioscorea</i> spp.)	4050247	9.46	38304339	0
<b>Oil crops</b>				
Soybeans ( <i>Glycine max</i> (L.) Merr.)	74102000	2.18	161229850	40
Rapeseed ( <i>B. napus</i> L. var <i>napus</i> )	25721381	1.54	39516424	21
Groundnuts in shell ( <i>Arachis hypogaea</i> L.)	24290847	1.42	34515701	3
Sunflower seed ( <i>Helianthus</i> spp.)	21081016	1.24	26168523	5
Safflower seed ( <i>Carthamus tinctorius</i> L.)	878619	0.79	690488	2
<b>Fiber crops</b>				
Seed cotton ( <i>Gossypium hirsutum</i> L.)	31607367	1.73	54590370	6
Jute ( <i>Corchorus capsularis</i> L.)	1391036	1.91	2651030	0
Hemp fiber and tow ( <i>Cannabis sativa</i> L. subsp. <i>sativa</i> )	53347	1.07	57074	2
<b>Sugar crops</b>				
Sugarcane ( <i>Saccharum officinarum</i> L.)	19185566	65.60	1258530680	1
Sugar beets ( <i>Beta vulgaris</i> L. subsp. <i>vulgaris</i> )	5968770	41.12	245419567	2
<b>Protein crops</b>				
Beans, dry ( <i>V. faba</i> L.)	24138243	0.71	17152464	24
Chick-peas ( <i>Cicer arietinum</i> L.)	9968944	0.79	7839795	0
Cowpeas, dry ( <i>Vigna unguiculata</i> (L.) Walp. subsp. <i>unguiculata</i> )	9867865	0.30	2969599	7
Peas, dry ( <i>Pisum</i> 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 ultrastructure 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 Vogelmann, 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 Vogelmann, 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 kJ m<sup>-2</sup> 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 kJ m<sup>-2</sup> 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<sub>2</sub> 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 <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	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 2.2, 4.2, 8.3	5, 25	200	GC	– ↓ (30)	↑ (12) ↑ (60)	Liu et al. (1995) Tevini et al. (1981)
Bean	6.17 0.25–1.66 4.7, 6.5, 7.2, 12.2 12 10.08 2.2, 4.2, 8.3	? 6–36 15	50, 100, 250 A A	CE GC F GH F	↑ (20) ↑ (13) – – ↓ (42) ↓ (70)	– – ↑ (5–12) ↑ ↑ (10) ↑ (15)	Cen and Bornmann (1990) Deckmyn et al. (1994) Flint et al. (1985) Meijkamp et al. (2001) Singh (1995) Tevini et al. (1981)
<i>Brassica</i>	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 10.08	15 15	A A	F F	↓ –	↑ (11–24) ↑ (24)	Pal et al. (1999) Singh (1995)
Maize	9 2.2, 4.2, 8.3	20	A 700	F GC	↑ (50) ↓ (25) ↓ (10)	↑↓ ↑ –	Ambasht and Agrawal (1995) Santos et al. (1993) Tevini et al. (1981)
Pea	49 18.0 2.3, 4.6, 6.9, 9.2 2.2, 9.9 2.4 1.38, 1.92 2.5 × A	A, 15 0, 9, 21, 36	160–180 850–950 800–1200 A ? 480–500	GC GH CE CE GH F GC GH	↓ (30) ↓ – – ↓ (78) – ↓ (35) ↓ (50)	↑ (150–200) ↑ ↑ ↑ (21) ↑ (15) ↑ (6) ↑ (15–100)	Alexieva et al. (2001) Day and Vogelmann (1995) Gonzalez et al. (1998a) Gonzalez et al. (1998b) He et al. (1993) Stephen et al. (1999) Strid and Porra (1992) Vu et al. (1984)
Rapeseed	4.3 2.6		400–700 70	GC CE	– –	↑ (150) ↑ (80–120)	Greenberg et al. (1996) Wilson and Greenberg (1993)
Rice	2.4 3 UV-B lamps 2.8, 3.9, 6.5 8.8, 15.7	A, 27, 38 A, 10	800–1200 800–1000 A	GH GH F GH	– ↓ (10–15) ↓ ↑↓	↑ (60) – – ↑	He et al. (1993) Huang et al. (1993) Kim et al. (1996) 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 0, A 10.7, 14.1 2.6	36 15, 30 0, 9, 21, 36	A A 1300–1600 1400–1800 480–500	F F GH GH GH	– – ↓ ↓ (10) ↓ (50)	↑ (18) ↑ ↑ ↑ (15)	Caldwell et al. (1994) Mazza et al. (2002) Middleton and Teramura (1993) Mirecki and Teramura (1984) Vu et al. (1984)
Wheat	8.8, 15.7 49 3.17	A, 10 15	160–180 A	GH GC F	– ↓ (30) –	↑ ↑ (150–200) ↑↓	Teramura et al. (1990b) Alexieva et al. (2001) 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 kJ m<sup>-2</sup> per day) and the light regimes (photosynthetically active radiation (PAR) of 150–1800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) 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 kJ m<sup>-2</sup> 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  $194 \text{ kJ m}^{-2}$  UV-B radiation delivered over a period of 16 h led to significantly reduced cotyledon  $\text{CO}_2$  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  $\text{CO}_2$  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; Nedunchezian and Kulandaivelu, 1991; Jordan et al., 1992; He et al., 1993, 1994; Huang et al., 1993; Kulandaivelu and Nedunchezian, 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  $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PAR and suggested that the decrease in the  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  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 <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	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 <sup>-2</sup>	?	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 (16h)	?	?	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 <sup>-2</sup>	?	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, Nedunchezian and Kulandaivelu (1997) reported that, under field conditions, slightly enhanced UV-B radiation ( $1.8 \text{ kJ m}^{-2}$  per day) increased leaf area of cowpea. Even high UV-B-treated ( $13.4\text{--}63.3 \text{ kJ m}^{-2}$  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 ( $8 \text{ kJ m}^{-2}$  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 <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	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	↑	↑	↑	Nedunchezian 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 <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	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<sub>3</sub> 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 <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	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	↑	Papadopoulou 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 ( $2.5\text{--}63\text{ kJ m}^{-2}$  or 10–50% of stratospheric  $\text{O}_3$  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 ( $13\text{ kJ m}^{-2}$  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 ( $15.7\text{ kJ m}^{-2}$  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  $5\text{ kJ m}^{-2}$  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<sub>2</sub>], surface O<sub>3</sub>, 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 con-

trol 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<sub>2</sub>] and UV-B radiation generally are in opposite directions when they occur independently. To date, few studies have investigated the possible interaction between [CO<sub>2</sub>] and UV-B (Table 6). Some studies with elevated [CO<sub>2</sub>] and UV-B interaction indicated that increased growth and seed yield of crops resulting from [CO<sub>2</sub>] 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<sub>2</sub>] is also known to affect biomass partitioning (Sullivan, 1997). Xiu-Ming et al. (1997) found that a higher dose of UV-B (13.1 kJ m<sup>-2</sup> per day) resulted in more severe damage at 600 μl l<sup>-1</sup> of [CO<sub>2</sub>] than at ambient [CO<sub>2</sub>]. A study by Zhao et al. (2003) showed that elevated [CO<sub>2</sub>] did not ameliorate the adverse effects of UV-B on cotton growth, physiology and particularly boll retention. Interaction of [CO<sub>2</sub>] 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<sub>2</sub>] (521 μl l<sup>-1</sup>) 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). Nedunchezian and Kulandaivelu (1996)

Table 6  
UV-B interactions with biotic and abiotic factors

Crop	UV-B <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	Interaction factor	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	Experimental condition	References
<b>Water stress</b>						
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)
<b>CO<sub>2</sub> (μl l<sup>-1</sup>)</b>						
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)
<b>Nutrients and minerals</b>						
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)
<b>Light (μmol m<sup>-2</sup> s<sup>-1</sup>)</b>						
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 Bornmann (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)
<b>Temperature (°C)</b>						
Sunflower, maize	–	12	32	A	GC	Mark and Tevini (1996)
Cowpea	4.5, 3.2	?	10, 20, 30, 40	A	GC	Nedunchezian and Kulandaivelu (1996), Kulandaivelu and Nedunchezian (1993)



Table 6 (Continued)

Crop	UV-B <sub>BE</sub> (kJ m <sup>-2</sup> per day)	Simulating O <sub>3</sub> depletion (%)	Interaction factor	PAR (μmol m <sup>-2</sup> s <sup>-1</sup> )	Experimental condition	References
Ozone (nl l <sup>-1</sup> )						
Soybean	–	37	14–83	A	OTC	Miller et al. (1994)
Tobacco	16	?	12	A	GH	Feder and Shrier (1990)
Insects/diseases						
Rice	?	–	<i>Pyricularia grisea</i>	?	CE	Finckh et al. (1995)
Soybean	A	–	<i>Anticarsia gemmatalis</i>	?	F	Zavala et al. (2001)
White clover	13.3	25	Army and cut worms	?	GC	Lindroth et al. (2000)
Pea	?	–	<i>Autographa gamma</i>	?	GC	Hatcher and Paul (1994)
Sugar beet	6.91, ?	9	<i>C. beticola</i>	?	GC	Panagopoulos et al. (1992)
Weeds						
Wheat		20	<i>Avena fatua</i>	?, 1600	Field, GH	Barnes et al. (1995, 1988)
Wheat		20	<i>A. fatua</i>	?, 1600	Field, GH	Beyschlag et al. (1988)
Wheat		20	<i>A. fatua</i>	?	GH	Barnes et al. (1990)
Oat			<i>Setaria viridis</i>			
Maize			<i>Triticum cylindricum</i>			
Pea, faba bean		20	<i>Chenopodium album</i>	?	GH	Barnes et al. (1990)
Sunflower			<i>Amaranthus retroflexus</i> , <i>Kochia scoparia</i>			

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<sub>3</sub> 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<sub>2</sub> 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  $18 \text{ kJ m}^{-2}$  per day of UV-B in combination with a PAR of  $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . High PAR ( $1600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) 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  $[\text{CO}_2]$  (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 ( $>15 \text{ kJ m}^{-2}$  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  $12 \text{ kJ m}^{-2}$  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 ( $<300 \text{ nm}$ ) 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 ( $1000\text{--}1600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) is able to ameliorate the effects of UV-B radiation as high as  $18 \text{ kJ m}^{-2}$  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<sub>2</sub>], 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<sub>2</sub>], temperature, ozone, drought conditions, and mineral deficiencies.

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### References

- Adamse, P., Britz, S.J., 1992. Amelioration of UV-B damage under high irradiance. I. Role of photosynthesis. *Photochem. Photobiol.* 56, 645–650.
- Agrawal, M., Agrawal, S.B., Krizek, D.T., Kramer, G.F., Lee, E.H., Mirecki, R.M., Rowland, R.A., 1991. Physiological and morphological responses of snapbean plants to ozone stress as influenced by pretreatment with UV-B radiation. In: Abrol, Y.P., Govindjee, Wattal, P.N., Ort, D.R., Gnanam, A., Teramura, A.H. (Eds.), *Impact of Global Climatic Changes on Photosynthesis and Plant Productivity*. Proceedings of the Indo-US Workshop, New Delhi, 8–12 January 1991. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, pp. 133–146.
- Alexieva, V., Sergiev, I., Mapelli, S., Karanov, E., 2001. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant Cell Environ.* 24, 1337–1344.
- Allen, D.J., McKee, I.F., Farage, P.K., Baker, N.R., 1997. Analysis of limitations to CO<sub>2</sub> assimilation on exposure of leaves of two *Brassica napus* cultivars to UV-B. *Plant Cell Environ.* 20, 633–640.
- Allen, D.J., Noguez, S., Baker, N.R., 1998. Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? *J. Exp. Bot.* 49, 1775–1788.
- Allen, D.J., Noguez, S., Morison, J.I.L., Greenslade, P.D., McLeod, A.R., Baker, N.R., 1999. A 30% increase in UV-B has no impact on photosynthesis in well-watered and droughted pea plants in the field. *Global Change Biol.* 2, 235–244.
- Al-Oudat, M., Baydoun, S.A., Mohammad, A., 1998. Effects of enhanced UV-B on growth and yield of two Syrian crops wheat (*Triticum durum* var. Horani) and broad beans (*Vicia faba*) under field conditions. *Environ. Exp. Bot.* 40, 11–16.
- Al-Wakeel, S.A.M., 1998. Growth and metabolic changes in *Cucurbita pepo* L., under water stress and ultra-violet B radiation. *Egypt. J. Physiol. Sci.* 22, 171–187.
- Ambasht, N.K., Agrawal, M., 1995. Physiological responses of field grown *Zea mays* L. plants to enhanced UV-B radiation. *Biotronics* 24, 15–23.
- Ambasht, N.K., Agrawal, M., 1997. Influence of supplemental UV-B radiation on photosynthetic characteristics of rice plants. *Photosynthetica* 34, 401–408.
- Ambasht, N.K., Agrawal, M., 1998. Physiological and biochemical responses of *Sorghum vulgare* plants to supplemental ultraviolet-B radiation. *Can. J. Bot.* 76, 1290–1294.
- Ambler, J.E., Krizek, D.T., Semeniuk, P., 1975. Influence of UV-B radiation on early seedling growth and translocation of <sup>65</sup>Zn from cotyledons in cotton. *Physiol. Plant* 34, 177–181.
- Baker, E.A., 1982. Chemistry and morphology of plant epicuticular waxes. In: Cutler, D.F., Alvin, K.L., Price, C.E. (Eds.), *The Plant Cuticle*. Academic Press, London, pp. 139–166.
- Ballare, C.L., Scopel, A.L., Stapelton, A.E., Yanovsky, M.J., 1996. Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate and attractiveness to herbivore insects in *Datura ferox*. *Plant Physiol.* 112, 161–170.
- Barnes, P.W., Jordan, P.W., Gold, W.G., Flint, S.D., Caldwell, M.M., 1988. Competition, morphology and canopy structure in wheat (*Triticum aestivum* L.) and wild oat (*Avena fatua* L.)

- exposed to enhanced ultraviolet-B radiation. *Funct. Ecol.* 2, 319–330.
- Barnes, P.W., Flint, S.D., Caldwell, M.M., 1990. Morphological responses of crop and weed species of different growth forms to ultraviolet-B radiation. *Am. J. Bot.* 77, 1354–1360.
- Barnes, P.W., Maggard, S., Holman, S.R., Vergara, B.S., 1993. Intraspecific variation in sensitivity to UV-B radiation in rice. *Crop Sci.* 33, 1041–1046.
- Barnes, P.W., Stephen, D.F., Caldwell, M.M., 1995. Early season effects of supplemented solar UV-B radiation on seedling emergence, canopy structure, simulated stand photosynthesis and competition of light. *Global Change Biol.* 1, 43–53.
- Barnes, P.W., Ballare, C.L., Caldwell, M.M., 1996. Photomorphogenic effects of UV-B radiation on plants: consequences for light competition. *J. Plant Physiol.* 148, 15–20.
- Basiouny, F.M., 1986. Sensitivity of corn, oats, peanuts, rice, rye, sorghum, soybean and tobacco to UV-B radiation under growth chamber conditions. *J. Agron. Crop Sci.* 157, 31–35.
- Battaglia, P.R., Brennan, T.M., 2000. Differential effects of short-term exposure to ultraviolet-B radiation upon photosynthesis in cotyledons of a resistant and a susceptible species. *Int. J. Plant Sci.* 161, 771–778.
- Beyschlag, W., Barnes, P.W., Flint, S.D., Caldwell, M.M., 1988. Enhanced UV-B irradiation has no effect on photosynthetic characteristics of wheat (*Triticum aestivum* L.) and wild oat (*Avena fatua* L.) under greenhouse and field conditions. *Photosynthetica* 22, 516–525.
- Bjorn, L.O., Callaghan, T.V., Johnsen, I., Lee, J.A., Manetas, Y., Paul, N.D., Sonesson, M., Wellburn, A.R., Coop, D., Heid Jorgensen, H.S., Gehrke, C., Gwynn-Jones, D., Johanson, U., Kyparissis, A., Lezovou, E., Nikolopoulos, D., Petropoulou, Y., Stephonou, M., 1997. The effects of UV-B radiation on European heathland species. *Plant Ecol.* 128, 252–264.
- Blumthaler, M., Ambach, W., 1990. Indication of increasing solar ultraviolet-B radiation flux in alpine regions. *Science* 248, 206–208.
- Bolink, E.M., van-Schalkwijk, I., Posthumus, F., van-Hasselt, P.R., 2001. Growth under UV-B radiation increases tolerance to high-light stress in pea and bean plants. *Plant Ecol.* 154, 149–156.
- Bondada, B.R., Oosterhuis, D.M., Murphy, J.B., Kim, K.S., 1996. Effect of water stress on the epicuticular wax composition and ultrastructure of cotton (*Gossypium hirsutum* L.) leaf, bract, and boll. *Environ. Exp. Bot.* 36, 61–69.
- Bornman, J.F., Teramura, A.H., 1993. Effect of ultraviolet-B radiation on terrestrial plants. In: Young, A.R., Bjorn, L.O., Moan, J., Nultsch, W. (Eds.), *Environmental UV Photobiology*. Plenum Press, New York, pp. 427–472.
- Bornman, J.F., Vogelmann, T.C., 1991. Effect of UV-B radiation on leaf optical properties measured with fiber optics. *J. Exp. Bot.* 41, 547–554.
- Bors, W., Heller, W., Michel, C., Saran, M., 1990. Flavonoids as antioxidants: determination of radical-scavenging efficiencies. *Methods Enzymol.* 186, 343–355.
- Brandle, J.R., Campbell, W.F., Sisson, W.B., Caldwell, M.M., 1977. Net photosynthesis, electron transport capacity, and ultrastructure of *Pisum sativum* L. exposed to ultraviolet-B radiation. *Plant Physiol.* 60, 165–169.
- Brosche, M., Strid, A., 2000. Ultraviolet-B radiation causes tendril coiling in *Pisum sativum*. *Plant Cell Physiol.* 41, 1077–1079.
- Butler, J.H., Battle, M., Bender, M.L., Montzka, S.A., Clark, A.D., Saltzman, E.S., Sucher, C.M., Severinghaus, J.P., Elkins, J.W., 1999. A record of atmospheric halocarbons during the 20th century from polar firn air. *Nature* 399, 749–755.
- Caldwell, M.M., 1968. Solar ultraviolet radiation as an ecological factor for alpine plants. *Ecol. Monogr.* 38, 243–268.
- Caldwell, M.M., 1979. Plant life and ultraviolet radiation: some perspectives in the history of the Earth's UV climate. *Bioscience* 29, 520–525.
- Caldwell, M.M., Robberecht, R., Flint, S.D., 1983. Internal filters: prospects for UV acclimation in higher plants. *Physiol. Plant* 58, 445–450.
- Caldwell, M.M., Flint, S.D., Searles, P.S., 1994. Spectral balance and UV-B sensitivity of soybean: a field experiment. *Plant Cell Environ.* 17, 267–276.
- Caldwell, M.M., Bjorn, L.O., Bornmann, J.F., Flint, S.D., Kulandaivelu, G., Teramura, A.H., Tevini, M., 1998. Effect of increased solar UV-B on terrestrial ecosystems. *J. Photochem. Photobiol. B: Biol.* 46, 40–52.
- Canuto, V.M., Levine, J.S., Augustsson, T.R., Imhoff, C.L., Giampapa, M.L., 1983. The young sun and the atmosphere and photochemistry of the early Earth. *Nature* 305, 281–286.
- Cassi-Lit, M., Whitecross, M.J., Nayudu, M., Tanner, G.J., 1997. UV-B irradiation induces differential leaf damage, ultrastructural changes and accumulation of specific phenolic compounds in rice cultivars. *Aust. J. Plant Physiol.* 24, 261–274.
- Cen, Y.P., Bornmann, J.F., 1990. The response of bean plants to UV-B radiation under different irradiances of background visible light. *J. Exp. Bot.* 41, 1489–1495.
- Cen, Y.P., Bornman, J.F., 1993. The effect of exposure to enhanced UV-B radiation on the penetration of monochromatic and polychromatic UV-B radiation in leaves of *Brassica napus*. *Physiol. Plant* 87, 249–255.
- Cen, Y.P., Weissonbock, G., Bornmann, J.F., 1993. The effects of UV-B radiation on phenolic compounds and photosynthesis in leaves of *Brassica napus*. In: *Physical Biochemical and Physiological Effects of Ultraviolet Radiation on Brassica napus and Phaseolus vulgaris*. Ph.D. thesis, Lund, Sweden.
- Chang, D.C.N., Campbell, W.F., 1976. Responses of *Tradescantia* stamen hairs and pollen to UV-B (ultraviolet) irradiation. *Environ. Exp. Bot.* 16, 195–199.
- Chaturvedi, R., Shyam, R., Sane, P.V., 1998. Steady state levels of D1 protein and psbA transcript during UV-B inactivation of photosystem II in wheat. *Biochem. Mol. Biol. Int.* 44, 925–932.
- Clark, J.B., Lister, G.R., 1975. Photosynthetic action spectra of trees. II. The relationship of cuticle structure to the visible and ultraviolet spectral properties of needles from four coniferous species. *Plant Physiol.* 55, 407–413.
- Conner, J.K., Zangori, L.A., 1998. Combined effects of water, nutrient and UV-B stress on female fitness in *Brassica*. *Am. J. Bot.* 85, 925–931.
- Corlett, J.E., Stephen, J., Jones, H.G., Woodfin, R., Mepsted, R., Paul, N.D., 1997. Assessing the impact of UV-B radiation on the growth and yield of field crops. In: Lumsden, P.J. (Ed.),

- Plants and UV-B: Responses to Environmental Change. Society for Experimental Biology, Seminar Series 64. Cambridge University Press, Cambridge, pp. 195–211.
- Coronel, V.P., Dai, Q.J., Vergara, B.S., Teramura, A., 1990. Preliminary study on response of rice seedlings to enhanced UV-B radiation. *Int. Rice Res. Newslett.* 15, 37.
- Correia, C.M., Areal, E.L.V., Torres-Pereira, M.S., Torres-Pereira, J.M.G., 1998. Intraspecific variation in sensitivity to ultraviolet-B radiation in maize grown under field conditions. I. Growth and morphological aspects. *Field Crops Res.* 59, 81–89.
- Correia, C.M., Areal, E.L.V., Torres-Pereira, M.S., Torres-Pereira, J.M.G., 1999. Intraspecific variation in sensitivity to ultraviolet-B radiation in maize grown under field conditions. II. Physiological and biochemical aspects. *Field Crops Res.* 62, 97–105.
- Correia, C.M., Coutinho, J.F., Bjorn, L.O., Torres, P.J.M.G., 2000. Ultraviolet-B radiation and nitrogen effects on growth and yield of maize under Mediterranean field conditions. *Eur. J. Agron.* 12, 117–125.
- Dai, Q., Coronel, V.P., Vergara, B.S., Barnes, P.W., QUINTOS, A.T., 1992. Ultraviolet-B radiation effects on growth and physiology of four rice cultivars. *Crop Sci.* 32, 1269–1274.
- Dai, Q., Peng, S., Chavez, A.Q., Vergara, B.S., 1994a. Intraspecific response of 188 rice cultivars to enhanced ultraviolet-B radiation. *Environ. Exp. Bot.* 34, 433–442.
- Dai, Q., Vergara, B.S., Chavez, A.Q., Peng, S., 1994b. Response of rice plants from different regions to ultraviolet-B radiation. *Int. Rice Res. Notes* 19, 15–16.
- Dai, Q., Peng, S., Chavez, A.Q., Vergara, B.S., Peng, S., Ingram, K.T., Neue, H.U., Ziska, L.H., 1995. Effect of enhanced ultraviolet-B radiation on growth and production of rice under greenhouse and field conditions. In: Peng, S., Ingram, K.T., Neue, H.U. (Eds.), *Climate Change and Rice*. Springer-Verlag, Berlin, pp. 189–198.
- Dai, Q.J., Peng, S.B., Chavez, A.Q., Miranda, M.L.L., Vergara, B.S., Olszyk, D.M., 1997. Supplemental ultraviolet-B radiation does not reduce growth or grain yield in rice. *Agron. J.* 89, 793–799.
- Day, T.A., Vogelmann, T.C., 1995. Alterations in photosynthesis and pigment distribution in pea leaves following UV-B exposure. *Physiol. Plant* 94, 433–440.
- Deckmyn, G., Impens, I., 1995. UV-B increases the harvest index of bean (*Phaseolus vulgaris* L.). *Plant Cell Environ.* 18, 1426–1433.
- Deckmyn, G., Impens, I., 1997a. The ratio UV-B/photosynthetically active radiation (PAR) determines the sensitivity of rye to increased UV-B radiation. *Environ. Exp. Bot.* 37, 3–12.
- Deckmyn, G., Impens, I., 1997b. Combined effects of enhanced UV-B radiation and nitrogen deficiency on the growth, composition and photosynthesis of rye (*Secale cereale*). *Plant Ecol.* 128, 235–240.
- Deckmyn, G., Martens, C., Impens, I., 1994. The importance of the ratio UV-B/photosynthetically active radiation (PAR) during leaf development as determining factor of plant sensitivity to increased UV-B irradiance: effects on growth, gas exchange and pigmentation of bean plants (*Phaseolus vulgaris* cv. Label). *Plant Cell Environ.* 17, 295–301.
- Deckmyn, G., Caeyenberghs, E., Ceulemans, R., 2001. Reduced UV-B in green houses decreases white clover response to enhance CO<sub>2</sub>. *Environ. Exp. Bot.* 46, 109–117.
- Demchik, S.M., Day, T.A., 1996. Effect of enhanced UV-B radiation on pollen quantity, quality, and seed yield in *Brassica* rape (Brassicaceae). *Am. J. Bot.* 83, 573–579.
- Dentener, F., Derwent, R., Dlugokencky, E., Holland, E., Isaksen, I., Katima, J., Kirchhoff, V., Matson, P., Midgley, P., Wand, M., 2001. Atmospheric chemistry and greenhouse gases. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), *Climate Change 2001: The Scientific Basis. Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York, 881 pp.
- Drincovich, M.F., Casati, P., Andreo, C.S., Donahue, R., Edwards, G.E., 1998. UV-B induction of NADP-malic enzyme in etiolated and green maize seedlings. *Plant Cell Environ.* 21, 63–70.
- D'Surney, S.J., Tschaplinski, T.J., Edwards, N.T., Shugart, L.R., 1993. Biological responses of two soybean cultivars exposed to enhanced UV-B radiation. *Environ. Exp. Bot.* 33, 347–356.
- Elawad, S.H., Allen Jr., L.H., Gascho, G.J., 1985. Influence of UV-B radiation and soluble silicates on the growth and nutrient concentration of sugarcane. *Proc. Soil Crop Sci. Soc. Fla.* 44, 134–141.
- Eriksson, J., Soderstorm, M., Anderson, A., 1995. Cadmium contents in the plough layer of Swedish agricultural soils. *Swed. Environ. Prot. Agency* 4450, 24–28.
- Eswaran, K., Premkumar, A., Kulandaivelu, G., 1993. Impact of enhanced UV-B on photosynthetic and biochemical characteristics of maize under water stress. *Plant Physiol. Biochem.* 20, 36–40.
- Fagerberg, W.R., Bornman, J.F., 1997. Ultraviolet-B radiation caused shade type ultrastructural changes in *Brassica napus*. *Physiol. Plant* 101, 833–844.
- Fagerberg, W.R., Bornman, J.F., Mathis, P., 1995. Short term exposure of *Brassica napus* to 13 kJ m<sup>-2</sup> per day weighted UV-B irradiance and different PAR induces a shade type response in palisade cells. In: *Proceedings of the 10th International Photosynthesis Congress, Montpellier*, pp. 175–178.
- Fageria, N.K., Baligar, V.C., Jones, C.A., 1997. *Growth and Nutrition of Field Crops*, second ed. Marcel Dekker, New York, 85 pp.
- FAO, 2001. FAOSTAT online. <http://apps.fao.org/page/collections?subset=agriculture> (verified on 5 May 2003).
- Farman, J.C., Gardiner, B.G., Shanklin, J.D., 1985. Large losses of total ozone in Antarctica reveal seasonal ClO<sub>x</sub>-NO<sub>x</sub> interaction. *Nature* 315, 207–210.
- Feder, W.A., Shrier, R., 1990. Combination of UV-B and ozone reduced pollen tube growth more than either stress alone. *Environ. Exp. Bot.* 30, 451–454.
- Finckh, M.R., Chavez, A.Q., Dai, Q., Teng, P.S., 1995. Effects of enhanced UV-B radiation on the growth of rice and its susceptibility to rice blast under glasshouse conditions. *Agric. Ecosyst. Environ.* 52, 223–233.

- Flint, S.D., Caldwell, M.M., 1984. Partial inhibition of in vitro pollen germination by simulated solar ultraviolet-B radiation. *Ecology* 65, 792–795.
- Flint, S.D., Jordan, P.W., Caldwell, M.M., 1985. Plant protective response to enhanced UV-B radiation under field conditions: leaf optical properties and photosynthesis. *Photochem. Photobiol.* 41, 95–99.
- Fox, F.M., Caldwell, M.M., 1978. Competitive interaction on plant populations exposed to supplementary UV-B radiation. *Oecologia* 36, 173–190.
- Frederick, J.E., Slusser, J.R., Bigelow, D.W., 2000. Annual and interannual behavior of solar ultraviolet irradiance revealed by broadband measurements. *Photochem. Photobiol.* 72, 488–496.
- Gao, W., Grant, R.H., Heisler, G.M., 1996. Spectral radiative properties of various tree species in ultraviolet wavelengths and irradiance modeling implications. In: Proceedings of the 22nd Conference on Agricultural and Forest Meteorology with Symposium on Fire and Forest Meteorology, American Meteorological Society, Boston, MA, pp. 417–418.
- Giller, Y.E., 1991. UV-B effect on the development of photosynthetic apparatus, growth and productivity of higher plants. In: Abrol, Y.P., Wattal, P.W., Ort, D.R., Gnanam, A., Teramura, A.H. (Eds.), *Impact of Global Climatic Changes on Photosynthesis and Plant Productivity*. Proceedings of the Indo-US Workshop, New Delhi, 8–12 January 1991. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, pp. 77–93.
- Gonzalez, R., Paul, N.D., Percy, K., Ambrose, M., McLaughlin, C.K., Barnes, J.D., Areses, M., Wellburn, A.R., 1996. Responses to ultraviolet-B radiation (280–315 nm) of pea (*Pisum sativum*) lines differing in leaf surface wax. *Physiol. Plant* 98, 852–860.
- Gonzalez, R., Mepsted, R., Wellburn, A.R., Paul, N.D., 1998a. Non-photosynthetic mechanisms of growth reduction in pea (*Pisum sativum* L.) exposed to UV-B radiation. *Plant Cell Environ.* 21, 23–32.
- Gonzalez, R., Wellburn, A.R., Paul, N.D., 1998b. Dose responses of two pea lines to ultraviolet-B radiation (280–315 nm). *Physiol. Plant* 104, 373–378.
- Goyal, A.K., Jain, V.K., Ambrish, K., 1991. Effect of supplementary ultraviolet-B radiation on the growth, productivity and chlorophyll of field grown linseed crop. *Indian J. Plant Physiol.* 34, 374–377.
- Grant, R.H., 1999. Potential effect of soybean heliotropism on ultraviolet-B irradiance and dose. *Agron. J.* 91, 1017–1023.
- Greenberg, B.M., Wilson, M.I., Gerhardt, K.E., Wilson, K.E., 1996. Morphological and physiological responses of *Brassica napus* to ultraviolet-B radiation: photomodification of ribulose-1,5-bisphosphate carboxylase/oxygenase and potential acclimation processes. *J. Plant Physiol.* 148, 78–85.
- Groth, J.V., Krupa, S.V., 2000. Crop ecosystem response to climate change: interactive effects of ozone, ultraviolet-B radiation, sulphur dioxide and carbon dioxide on crops. In: Reddy, K.R., Hodges, H.F. (Eds.), *Climate Change and Global Crop Productivity*. CAB International, Wallingford, pp. 387–405.
- Gwynn-Jones, D., 2001. Short-term impacts of enhanced UV-B radiation on photo-assimilate allocation and metabolism: a possible interpretation for time-dependent inhibition of growth. *Plant Ecol.* 154, 67–73.
- Gwynn-Jones, D., Lee, J.A., Callaghan, T.V., 1997. Effects of enhanced UV-B radiation and elevated carbon dioxide concentrations on a sub-Arctic forest heath system. *Plant Ecol.* 128, 242–249.
- Hakala, K., Jauhiainen, L., Hoskela, T., Kayhko, P., Vorne, V., 2002. Sensitivity of crops to increased ultraviolet radiation in northern growing conditions. *J. Agron. Crop Sci.* 188, 8–18.
- Hatcher, P.E., Paul, N.D., 1994. The effect of elevated UV-B radiation on herbivory of pea by *Autographa gamma*. *Entomol. Exp. Appl.* 71, 227–233.
- He, J., Huang, L.K., Chow, W.S., Whitecross, M.I., Anderson, J.M., 1993. Effects of supplementary ultraviolet-B radiation on rice and pea plants. *Aust. J. Plant Physiol.* 20, 129–142.
- He, J., Huang, L.K., Chow, W.S., Whitecross, M.I., Anderson, J.M., 1994. Responses of rice and pea plants to hardening with low doses of ultraviolet-B radiation. *Aust. J. Plant Physiol.* 21, 563–574.
- Hofmann, D.J., Pyle, J.A., 1999. Predicting future ozone changes and detection of recovery. In: WMO/UNEP Scientific Assessment of Ozone Depletion: 1998. Global Ozone Research and Monitoring Project Report no. 44, Geneva, Chapter 12, pp. 1–57.
- Hofmann, R.W., Campbell, B.D., Fountain, D.W., Jordan, B.R., Greer, D.H., Hunt, D.Y., Hunt, C.L., 2001. Multivariate analysis of intraspecific responses to UV-B radiation in white clover (*Trifolium repens* L.). *Plant Cell Environ.* 24, 917–927.
- Holmes, M.G., 1997. Action spectra for UV-B effects on plants: monochromatic approaches for analyzing plant responses. In: Lumsden, P.J. (Ed.), *Plants and UV-B: Responses to Environmental Change*. Society for Experimental Biology, Seminar Series 64. Cambridge University Press, Cambridge, pp. 31–50.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Xiaosu, D. (Eds.), 2001. *Climate Change 2001: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, 944 pp.
- Huang, L.K., He, J., Chow, W.S., Whitecross, M.I., Anderson, J.M., 1993. Responses of detached rice leaves (*Oryza sativa* L.) to moderate supplementary ultraviolet-B radiation allow early screening for relative sensitivity to ultraviolet-B irradiation. *Aust. J. Plant Physiol.* 20, 285–297.
- Jackman, C.H., Fleming, E.L., Chanra, S., Considine, D.B., Rosenfield, J.E., 1996. Past, present and future modeled ozone trends with comparison to observed trends. *J. Geophys. Res.* 101, 28753–28767.
- Jansen, M.A.K., van-den-Noort, R.E., 2000. Ultraviolet-B radiation induces complex alterations in stomatal behavior. *Physiol. Plant* 110, 189–194.
- Jansen, M.A.K., Gaba, V., Greenberg, B.M., 1998. Higher plants and UV-B radiation: balancing damage, repair and acclimation. *Trends Plant Sci.* 3, 131–135.
- Jordan, B.R., He, J., Chow, W.S., Anderson, J.M., 1992. Changes in mRNA levels and polypeptide subunits of ribulose 1,5-bisphosphate carboxylase in response to supplementary ultraviolet-B radiation. *Plant Cell Environ.* 15, 91–98.

- Kakani, V.G., Reddy, K.R., Zhao, D., Mohammed, A.R., 2003. Ultraviolet-B radiation effects on cotton (*Gossypium hirsutum* L.) morphology and anatomy. *Ann. Bot.*, pp. 817–826.
- Kerr, R.A., 1993. The ozone hole reaches a new low. *Science* 262, 501.
- Kerr, J.B., McElroy, C.T., 1993. Evidence for large upward trends of ultraviolet-B radiation linked to ozone depletion. *Science* 262, 1032–1034.
- Kim, H.Y., Kobayashi, K., Nouchi, I., Yoneyama, T., 1996. Enhanced UV-B radiation has little effect on growth, delta <sup>13</sup>C values and pigments of pot-grown rice (*Oryza sativa*) in the field. *Physiol. Plant* 96, 1–5.
- Knipling, E.B., 1970. Physical and physiological basis for the reflection of visible and near-infrared radiation from vegetation. *Remote Sens. Environ.* 1, 155–159.
- Kramer, G.F., Krizek, D.T., Mirecki, R.M., 1992. Influence of photosynthetically active radiation and spectral quality on UV-B induced polyamine accumulation in soybean. *Phytochemistry* 31, 1119–1125.
- Krizek, D.T., Kramer, G.F., Upadhyaya, A., Mirecki, R.M., 1993. UV-B response of cucumber seedlings grown under high pressure sodium/deluxe lamps. *Physiol. Plant* 88, 350–358.
- Krupa, S.V., Kickert, R.N., Jager, H.J. (Eds.), 1998. Elevated UV-B Radiation and Agriculture. Academic Press, San Diego, 296 pp.
- Krupa, S.V., McGrath, M.T., Andersen, C.P., Booker, F.L., Burkey, K.O., Chappelka, A.H., Chevone, B.I., Pell, E.J., Zilinskas, B.A., 2001. Ambient ozone and plant health. *Plant Dis.* 85, 4–12.
- Kulandaivelu, G., Nedunchezian, N., 1993. Synergistic. Photosynthetic effects of ultraviolet-B enhanced radiation and growth temperature on ribulose 1,5-bisphosphate and <sup>14</sup>CO<sub>2</sub> fixation in *Vigna sinensis* L 29, 377–383.
- Kulandaivelu, G., Nedunchezian, N., Annamalaiathan, K., 1991. Ultraviolet-B (280–320 nm) radiation induced changes in photochemical activities and polypeptide components of C<sub>3</sub> and C<sub>4</sub> chloroplasts. *Photosynthetica* 25, 333–339.
- Kumagai, T., Hidema, J., Kang, H.S., Sato, T., 2001. Effects of supplemental UV-B radiation on the growth and yield of two cultivars of Japanese lowland rice (*Oryza sativa* L.) under the field in a cool rice-growing region of Japan. *Agric. Ecosyst. Environ.* 83, 201–208.
- Larsson, E.H., Bornmann, J.F., Asp, H., 1998. Influence of UV-B radiation and Cd<sup>2+</sup> on chlorophyll fluorescence, growth and nutrient content in *Brassica napus*. *J. Exp. Bot.* 49, 1031–1039.
- Lavola, A., Julkunen Titto, R., Roininen, H., Aphalo, P., 1998. Host-plant preference of an insect herbivore mediated by UV-B and CO<sub>2</sub> in relation to plant secondary metabolites. *Biochem. Syst. Ecol.* 26, 1–12.
- Li, Y., Yue, M., Wang, X.L., 1998. Effects of enhanced ultraviolet-B radiation on crop structure, growth and yield components of spring wheat under field conditions. *Field Crops Res.* 57, 253–263.
- Li, Y.A., Zu, Y.Q., Chen, H.Y., Chen, J.J., Yang, J.L., Hu, Z.D., 2000. Intraspecific responses in crop growth and yield of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions. *Field Crops Res.* 67, 25–33.
- Li, Y., Zu, Y., Chen, J., Chen, H., 2002. Intraspecific responses in crop growth and yield of 20 soybean cultivars to enhanced ultraviolet-B radiation under field conditions. *Field Crops Res.* 78, 1–8.
- Lindroth, R.L., Hofman, R.W., Campbell, B.D., McNabb, W.C., Hunt, D.Y., 2000. Population differences in *Trifolium repens* response to ultraviolet-B radiation: foliar chemistry and consequences for two lepidopteron herbivores. *Oecologia* 122, 20–28.
- Lingakumar, K., Kulandaivelu, G., 1993. Changes induced by ultraviolet-B radiation in vegetative growth, foliar characteristics and photosynthetic activities in *Vigna unguiculata*. *Aust. J. Plant Physiol.* 20, 299–308.
- Liu, L., Gitz, D.C.III, McClure, W., 1995. Effects of UV-B on flavonoids, ferulic acid, growth and photosynthesis in barley primary leaves. *Physiol. Plant* 93, 725–733.
- Mackerness, S.A.H., Surplus, S.L., Jordan, B.R., Thomas, B., 1997a. Ultraviolet-B effects on transcript levels for photosynthetic genes are not mediated through carbohydrate metabolism. *Plant Cell Environ.* 20, 1431–1437.
- Mackerness, S.A.H., Thomas, B., Jordan, B.R., 1997b. The effect of supplementary ultraviolet-B radiation on mRNA transcripts, translation and stability of chloroplast proteins and pigment formation in *Pisum sativum* L. *J. Exp. Bot.* 48, 729–738.
- Manney, G.L., Froidevaux, L., Waters, J.W., Zurek, R.W., Read, W.G., Elson, L.S., Kumer, J.B., Mergenthaler, J.L., Roche, A.E., O'Neill, A., Harwood, R.S., Mackenzie, I., Swinrack, R., 1994. Chemical depletion of ozone in the Arctic lower stratosphere during winter 1992–1993. *Nature* 370, 423–429.
- Mark, U., Tevini, M., 1996. Combination effects of UV-B radiation and temperature on sunflower (*Helianthus annuus* L., cv. Polstar) and maize (*Zea mays* L., cv. Zenit 2000) seedlings. *J. Plant Physiol.* 148, 49–56.
- Mark, U., Tevini, M., 1997. Effects of solar ultraviolet-B radiation, temperature and CO<sub>2</sub> on growth and physiology of sunflower and maize seedlings. *Plant Ecol.* 128, 225–234.
- Mazza, C.A., Battista, D., Zima, A.M., Szwarcberg, B.M., Giordano, C.V., Acevedo, A., Scopel, A.L., Ballare, C.L., 1999. The effects of solar ultraviolet-B radiation on the growth and yield of barley are accompanied by increased DNA damage and antioxidant responses. *Plant Cell Environ.* 22, 61–70.
- Mazza, C.A., Boccacandro, H.E., Giordano, C.V., Battista, D., Scopel, A.L., Ballare, C.L., 2002. Functional significance and induction by solar radiation of ultraviolet-absorbing sunscreens in field-grown soybean crops. *Plant Physiol.* 122, 117–125.
- McCloud, E.S., Berenbaum, M.R., 1994. Stratospheric ozone depletion and plant-insect interactions: effects of UV-B radiation on foliage quality of *Citrus jambhiri* for *Trichipulsi* ni. *J. Chem. Ecol.* 20, 525–539.
- Meijkamp, B.B., Doodeman, G., Rozema, J., 2001. The response of *Vicia faba* to enhanced UV-B radiation under low and near ambient PAR levels. *Plant Ecol.* 154, 137–146.
- Melis, A., Nemson, J.A., Harrison, M.A., 1992. Damage to functional components and partial degradation of photosystem II reaction center portents upon chloroplast exposure to ultraviolet-B radiation. *Biochem. Biophys. Acta* 1109, 312–320.
- Mepsted, R., Paul, N., Stephen, J., Noguez, S., Corlett, J.E., Baker, N.R., Jones, H.G., Ayres, P.G., 1996. Effects of enhanced UV-B radiation on pea (*Pisum sativum* L.) grown under field conditions. *Global Change Biol.* 2, 325–334.



- Middleton, E.M., Teramura, A.H., 1993. The role of flavonol glycosides and carotenoids in protecting soybean from ultraviolet-B damage. *Plant Physiol.* 103, 741–752.
- Miller, J.E., Booker, F.L., Fiscus, E.L., Heagle, A.S., Pursley, W.A., Vozzo, S.F., Heck, W.W., 1994. Ultraviolet-B radiation and ozone effects on growth, yield, and photosynthesis of soybean. *J. Environ. Qual.* 23, 83–91.
- Mirecki, R.M., Teramura, A.H., 1984. Effects of ultraviolet-B irradiance on soybean. V. The dependence of plant sensitivity on the photosynthetic photon flux density during and after leaf expansion. *Plant Physiol.* 74, 475–480.
- Murali, N.S., Teramura, A.H., 1985. Effects of ultraviolet-B irradiance on soybean. VII. Biomass and concentration and uptake of nutrients at varying P supply. *J. Plant Nutr.* 8, 177–192.
- Murali, N.S., Teramura, A.H., 1986a. Effectiveness of UV-B radiation on the growth and physiology of field grown soybean modified by water stress. *Photochem. Photobiol.* 44, 215–219.
- Murali, N.S., Teramura, A.H., 1986b. Effects of ultraviolet-B radiation on the growth and physiology of field-grown soybean. *Environ. Exp. Bot.* 26, 233–242.
- Murali, N.S., Teramura, A.H., 1987. Insensitivity of soybean photosynthesis to ultraviolet-B radiation under phosphorus deficiency. *J. Plant Nutr.* 10, 501–515.
- Musil, C.F., Wand, S.J.E., 1994. Differential stimulation of an arid-environment winter ephemeral *Dimorphotheca pluvalis* by ultraviolet-B radiation under nutrient limitation. *Plant Cell Environ.* 17, 245–255.
- Musil, C.F., Bjorn, L.O., Scourfield, M.W.J., Bodeker, G.E., 2002. How substantial are ultraviolet-B supplementation inaccuracies in experimental square-wave delivery systems? *Environ. Exp. Bot.* 47, 25–38.
- Nagel, L.M., Bassman, J.H., Edwards, G.E., Robberecht, R., Franceschi, V.R., 1998. Leaf anatomical changes in *Populus trichocarpa*, *Quercus rubra*, *Pseudotsuga menziesii* and *Pinus ponderosa* exposed to enhanced ultraviolet-B radiation. *Physiol. Plant* 104, 385–396.
- Nedunchezian, N., Kulandaivelu, G., 1991. Effects of UV-B enhanced radiation on ribulose 1,5-bisphosphate carboxylase in leaves of *Vigna sinensis* L. *Photosynthetica* 25, 431–435.
- Nedunchezian, N., Kulandaivelu, G., 1996. Effects of ultraviolet-B enhanced radiation and temperature on growth and photochemical activities in *Vigna unguiculata*. *Biol. Plant* 38, 205–214.
- Nedunchezian, N., Kulandaivelu, G., 1997. Changes induced by ultraviolet-B (280–320 nm) radiation to vegetative growth and photosynthetic characteristics in field grown *Vigna unguiculata* L. *Plant Sci. Limerick* 123, 85–92.
- Nogues, S., Baker, N.R., 1995. Evaluation of the role of damage to photosystem II in the inhibition of CO<sub>2</sub> assimilation in pea leaves on exposure to UV-B radiation. *Plant Cell Environ.* 18, 781–787.
- Nogues, S., Allen, D.J., Morison, J.I.L., Baker, N.R., 1998. Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. *Plant Physiol.* 117, 173–181.
- Noorudeen, A.M., Kulandaivelu, G., 1982. On the possible site of inhibition of photosynthetic electron transport by ultraviolet-B (UV-B) radiation. *Physiol. Plant* 55, 161–166.
- Nouchi, I., Kobayashi, K., 1995. Effects of enhanced ultraviolet-B radiation with a modulated lamp control system on growth of 17 rice cultivars in the field. *J. Agric. Meteorol.* 51, 11–20.
- Olsson, L.C., Veit, M., Weissonbock, G., Bornmann, J.F., 1998. Differential flavonoid response to enhanced UV-B radiation in *Brassica napus*. *Phytochemistry* 4, 1021–1028.
- Olsson, L.C., Fraysee, L., Bornmann, J.F., 2000. Influence of high light and UV-B radiation on photosynthesis and D1 turnover in atrazine-tolerant and -sensitive cultivars of *Brassica napus*. *J. Exp. Bot.* 51, 265–274.
- Olczyk, D., Dai, Q.J., Teng, P., Leung, H., Luo, Y., Peng, S.B., 1996. UV-B effects on crops: response of the irrigated rice ecosystem. *J. Plant Physiol.* 148, 26–34.
- Orth, A.B., Teramura, A.H., Sisler, A.D., 1990. Effects of ultraviolet-B radiation on fungal disease development in *Cucumis sativus*. *Am. J. Bot.* 77, 1188–1192.
- Pal, M., Sharma, A., Abrol, Y.P., Sengupta, U.K., 1997. Exclusion of UV-B radiation from normal solar spectrum on the growth of mungbean and maize. *Agric. Ecosyst. Environ.* 61, 29–34.
- Pal, M., Jain, V., Sengupta, U.K., 1998. Influence of enhanced UV-B radiation on mustard: cultivar response. *Indian J. Plant Physiol.* 3, 188–193.
- Pal, M., Sengupta, U.K., Srivastava, A.C., Jain, V., Meena, R.C., 1999. Changes in growth and photosynthesis of mungbean induced by UV-B radiation. *Indian J. Plant Physiol.* 4, 79–84.
- Panagopoulos, I., Bornman, J.F., Bjorn, L.O., 1992. Response of sugar beet plants to ultraviolet-B (280–320 nm) radiation and *Cercospora* leaf spot disease. *Physiol. Plant* 84, 140–145.
- Papadopoulos, Y.A., Gorden, R.J., McRae, K.B., Bush, R.S., Belanger, G., Butler, E.A., Fillmore, S.E.A., Morrison, M., 1999. Current and elevated levels of UV-B radiation have few impacts on yields of perennial forage crops. *Global Change Biol.* 5, 847–856.
- Premkumar, A., Kulandaivelu, G., 1996. Influence of ultraviolet-B enhanced solar radiation on growth and photosynthesis of potassium deficient cowpea seedlings. *Photosynthetica* 32, 521–528.
- Premkumar, A., Kulandaivelu, G., 1999. Influence of increased ultraviolet-B radiation on magnesium deficient cowpea seedlings: changes in the photosynthetic characteristics. *Photosynthetica* 36, 21–29.
- Premkumar, A., Kulandaivelu, G., 2001. Influence of increased ultraviolet-B radiation on magnesium deficient cowpea seedlings: changes in growth and foliar constituents. *Plant Sci.* 161, 1–8.
- Premkumar, A., Eswaran, K., Kulandaivelu, G., 1993. Growth, biochemical and photosynthetic responses of greengram seedlings under water stress to ultraviolet-B radiation. *Plant Physiol. Biochem.* 20, 31–35.
- Prinn, R.R., Weiss, R.F., Fraser, P.J., Simmonds, P.G., Cunnold, D.M., Alyea, F.N., Doherty, S.O., Salameh, P., Miller, B.R., Huang, J., Wang, R.H.J., Hartley, D.E., Harth, C., Steele, L.P., Sturrock, G., Midgley, P.M., McCulloch, A., 2000. A history of chemically and radioactively important gases in air

- deduced from ALE/GAGE/AGAGE. *J. Geophys. Res.* 105, 17751–17792.
- Rao, J.V.S., Reddy, K.R., 1980. Seasonal variation in leaf epicuticular wax of some arid shrubs. *Indian J. Exp. Biol.* 18, 495–499.
- Reddy, K.R., Read, J.J., Baker, J.T., McKinion, J.M., Tarpley, L., Hodges, H.F., Reddy, V.R., 2001. Soil–plant–atmosphere research (SPAR) facility—a tool for plant research and modeling. *Biotronics* 30, 27–50.
- Reddy, K.R., Kakani, V.G., Zhao, D., Mohammed, A.R., Gao, W., 2003. Cotton responses to ultraviolet-B radiation: experimentation and algorithm development. *Agric. For. Meteorol.* 120, 249–265.
- Reed, H.E., Teramura, A.H., Kenworthy, W.J., 1992. Ancestral US soybean cultivars characterized for tolerance to ultraviolet-B radiation. *Crop Sci.* 32, 1214–1219.
- Renger, G., Volker, M., Eckert, H.J., Fromme, R., Hohm-Veit, S., Graber, P., 1989. On the mechanism of photosystem II deterioration by UV-B irradiation. *Photochem. Photobiol.* 49, 97–105.
- Robberecht, R., Caldwell, M.M., 1980. Leaf ultraviolet optical properties along a latitudinal gradient in the Arctic-alpine life zone. *Ecology* 61, 612–619.
- Ros, J., 1995. Synergistic and antagonistic effects of enhanced (reduced) UV-B radiation at various nitrogen levels in crop plants. In: Bauer, H., Nolan, C. (Eds.), *Proceedings of the First European Symposium on the Effects of Environmental UV-B Radiation*, Brussels, Luxembourg, pp. 245–252.
- Ros, J., Tevini, M., 1995. UV-radiation and indole-3-acetic acid: interaction during growth of seedlings and hypocotyl segments of sunflower. *J. Plant Physiol.* 146, 295–305.
- Rousseaux, M.C., Ballare, C.L., Scopel, A.L., Searles, P.S., Caldwell, M.M., 1998. Solar ultraviolet-B radiation affects plant–insect interactions in a natural ecosystem of Tierra del Fuego. *Oecologia* 116, 528–535.
- Rozema, J., Lenssen, G.M., Van De Staij, J.W.N., 1990. The combined effect of increased atmospheric CO<sub>2</sub> and UV-B radiation on some agricultural and salt marsh species. In: *Proceedings of the International Workshop on Primary Productivity of European Agriculture and the Greenhouse Effect*, Wageningen, pp. 68–71.
- Rozema, J., Van-de, S.J., Costa, V., Pereira, J.T., Broekman, R., Lenssen, G., Stroetenga, M., 1991. A comparison of the growth, photosynthesis and transpiration of wheat and maize in response to enhanced ultraviolet-B radiation. In: Abrol, Y.P., Govindjee, Watal, P.W., Ort, D.R., Gnanam, A., Teramura, A.H. (Eds.), *Impact of Global Climatic Changes on Photosynthesis and Plant Productivity*. Proceedings of the Indo-US Workshop, New Delhi, 8–12 January 1991. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, pp. 163–174.
- Rozema, J., Lenssen, G.M., Van de Staij, J.W.M., Tosserrams, M., Visser, A.J., Broekman, R.A., 1997a. Effects of UV-B radiation on terrestrial plants and ecosystems: interaction with CO<sub>2</sub> enrichment. *Plant Ecol.* 128, 183–191.
- Rozema, J., Van de Staij, J., Bjorn, L.O., Caldwell, M.M., 1997b. UV-B as an environmental factor in plant life: stress and regulation. *Trends. Ecol. E* 12, 22–28.
- Saile-Mark, M., Tevini, M., 1997. Effects of solar UV-B radiation on growth, flowering and yield of central and southern European bush bean cultivars (*Phaseolus vulgaris* L.). *Plant Ecol.* 128, 115–125.
- Santos, I., Almeida, J.M., Salema, R., 1993. Plants of *Zea mays* L. developed under enhanced UV-B radiation. I. Some ultrastructural and biochemical aspects. *J. Plant Physiol.* 141, 450–456.
- Santos, A., Almeida, J.M., Santos, I., Salema, R., 1998. Biochemical and ultrastructural changes in pollen of *Zea mays* L. grown under enhanced UV-B radiation. *Ann. Bot.* 82, 641–645.
- Santos, I., Almeida, J.M., Salema, R., 1999. Maize seeds developed under enhanced UV-B radiation. *Agron. Lusitana* 47, 89–99.
- Saunders, J.A., McClure, J.W., 1976. The distribution of flavonoids in chloroplasts of 25 species of vascular plants. *Phytochemistry* 15, 809–810.
- Savitch, L.V., Pockock, T., Krol, M., Wilson, K.E., Greenberg, B.M., Huner, N.P.A., 2001. Effects of growth under UV-A radiation on CO<sub>2</sub> assimilation, carbon partitioning, PSII photochemistry and resistance to UV-B radiation in *Brassica napus* cv. Topas. *Aust. J. Plant Physiol.* 28, 203–212.
- Searles, P.S., Caldwell, M.M., Winter, K., 1995. The response of five tropical dicotyledon species to solar ultraviolet-B radiation. *Am. J. Bot.* 82, 445–453.
- Searles, P.S., Flint, S.D., Caldwell, M.M., 2001. A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127, 1–10.
- Shukla, U.C., Joshi, P.C., Poonam, K., 2002. Synergistic action of ultraviolet-B radiation and cadmium on the growth of wheat seedlings. *Ecotoxicol. Environ. Saf.* 51, 90–96.
- Sinclair, T.R., N'Diaye, O., Biggs, R.H., 1990. Growth and yield of field-grown soybean in response to enhanced exposure to ultraviolet-B radiation. *J. Environ. Qual.* 19, 478–481.
- Singh, A., 1995. Influence of enhanced UV-B radiation on tropical legumes. *Trop. Ecol.* 36, 249–252.
- Sisson, W.B., Caldwell, M.M., 1976. Photosynthesis, dark respiration, and growth of *Rumex patientia* L. exposed to ultraviolet irradiance (288–315 nm) simulating a reduced atmospheric ozone column. *Plant Physiol.* 58, 563–568.
- Skorska, E., 2000a. Responses of pea and triticale photosynthesis and growth to long-wave UV-B radiation. *Biol. Plant* 43, 129–131.
- Skorska, E., 2000b. Comparison of responses of bean, pea and rape plants to UV-B radiation in darkness and in light. *Acta Physiol. Plant* 22, 163–169.
- Skorska, E., Murkowski, A., 1997. The effect of UV-B irradiation on photosynthesis of rape leaves growing under deficit of some mineral elements. *Rosliny Oleiste* 18, 111–118.
- Smith, J.L., Burritt, D.J., Bannister, P., 2000. Shoot dry weight, chlorophyll and UV-B-absorbing compounds as indicators of a plant's sensitivity to UV-B radiation. *Ann. Bot.* 86, 1057–1063.
- Song, Y.Z., Zhang, Y.F., Wan, C.J., Wang, C.H., Zhang, F.C., 1999. Impact of intensified ultraviolet radiation on cotton growth. *J. Nanjing Inst. Meteorol.* 22, 269–273.
- Steinmuller, D., Tevini, M., 1985. Action of ultraviolet radiation (UV-B) upon cuticular waxes in some crop plants. *Planta* 164, 557–564.

- Stephen, J., Woodfin, R., Corlett, J.E., Paul, N.D., Jones, H.G., Ayres, P.G., 1999. Response of barley and pea crops to supplementary UV-B radiation. *J. Agric. Sci.* 132, 253–261.
- Strid, A., Porra, R.J., 1992. Alterations in pigment content in leaves of *Pisum sativum* after exposure to supplementary UV-B. *Plant Cell Physiol.* 33, 1015–1023.
- Strid, A., Chow, W.S., Anderson, J.M., 1990. Effects of supplementary ultraviolet-B radiation on photosynthesis in *Pisum sativum*. *Int. J. Biochem. Biophys.* 1020, 260–268.
- Sullivan, J.H., 1997. Effects of increasing UV-B radiation and atmospheric CO<sub>2</sub> on photosynthesis and growth: implications for terrestrial ecosystems. *Plant Ecol.* 128, 194–206.
- Sullivan, J.H., Rozema, J., 1999. UV-B effects on terrestrial plant growth and photosynthesis. In: Rozema, J. (Ed.), *Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*. Backhuys Publishers, Leiden, pp. 39–57.
- Sullivan, J.H., Teramura, A.H., 1990. Field study of the interaction between solar ultraviolet-B radiation and drought on photosynthesis and growth in soybean. *Plant Physiol.* 92, 141–146.
- Taalas, P., Kaurola, J., Kylling, A., Shindell, D., Sausen, R., Dameris, M., Grewe, V., Herman, J., Damski, J., Steil, B., 2000. The impact of greenhouse gases and halogenated species on future solar UV radiation doses. *Geophys. Res. Lett.* 27, 1127–1130.
- Takahama, U., 1982. Suppression of carotenoid photobleaching by kaempferol in isolated chloroplasts. *Plant Cell Physiol.* 23, 859–864.
- Teramura, A.H., 1980. Effects of ultraviolet-B irradiances on soybean. I. Importance of photosynthetically active radiation in evaluating ultraviolet-B irradiance effects on soybean and wheat growth. *Physiol. Plant* 48, 333–339.
- Teramura, A.H., Murali, N.S., 1986. Intraspecific differences in growth and yield of soybean exposed to ultraviolet-B radiation under greenhouse and field conditions. *Environ. Exp. Bot.* 26, 89–95.
- Teramura, A.H., Forseth, I., Lydon, J., 1984. Effects of ultraviolet-B radiation on plants during mild water stress. IV. The insensitivity of soybean internal water relations to ultraviolet-B radiation. *Physiol. Plant* 62, 384–389.
- Teramura, A.H., Sullivan, J.H., Lydon, J., 1990a. Effects of UV-B radiation in altering soybean yield: a 6-year field study. *Physiol. Plant* 80, 5–11.
- Teramura, A.H., Sullivan, J.H., Ziska, L.H., 1990b. Interaction of elevated ultraviolet-B radiation and CO<sub>2</sub> on productivity and photosynthetic characteristics in wheat, rice, and soybean. *Plant Physiol.* 94, 470–475.
- Teramura, A.H., Sullivan, J.H., Abrol, Y.P., Govindjee, Watal, P.W., Ort, D.R., Gnanam, A., 1991a. Field studies of UV-B radiation effects on plants: Case histories of soybean and loblolly pine. In: Abrol, Y.P., Govindjee, Watal, P.W., Ort, D.R., Gnanam, A. (Eds.), *Impact of Global Climatic Changes on Photosynthesis and Plant Productivity*. Proceedings of the Indo-US Workshop, New Delhi, 8–12 January 1991. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi, pp. 147–161.
- Teramura, A.H., Ziska, L.H., Szein, A.E., 1991b. Changes in growth and photosynthetic capacity of rice with increased UV-B radiation. *Physiol. Plant* 83, 373–380.
- Tevini, M., Steinmuller, D., 1987. Influence of light, UV-B radiation, and herbicides on wax biosynthesis of cucumber seedlings. *J. Plant Physiol.* 131, 111–121.
- Tevini, M., Teramura, A.H., 1989. UV-B effects in terrestrial plants. *Photochem. Photobiol.* 50, 479–487.
- Tevini, M., Iwanzik, W., Thoma, U., 1981. Some effects of enhanced ultraviolet irradiation on the growth and composition of plants: barley, maize, kidney beans, radishes. *Planta* 153, 388–394.
- Tevini, M., Thoma, U., Iwanzik, W., 1983. Effects of UV-B radiation on germination, seedling growth, leaf anatomy and pigments of some crop plants. *Z. Pflanzenphysiol.* 109, 435–448.
- Tevini, M., Mark, U., Saile-Mark, M., 1991. Effects of enhanced solar UV-B radiation on growth and function of crop plant seedlings. *Curr. Top. Plant Biochem. Physiol.* 10, 13–31.
- Torabinejad, J., Caldwell, M.M., Flint, S.D., Durham, S., 1998. Susceptibility of pollen to UV-B radiation: an assay of 34 taxa. *Am. J. Bot.* 85, 360–369.
- Tosserams, M., Visser, A., Groen, M., Kalis, G., Magendans, E., Rozema, J., 2001. Combined effects of CO<sub>2</sub> concentration and enhanced UV-B radiation on faba bean. *Plant Ecol.* 154, 197–210.
- Total Ozone Mapping Spectrometer (TOMS), 2002. Atmosphere Chemistry and Dynamics Branch (Online). Available at [http://toms.gsfc.nasa.gov/ery\\_uv/euv.html](http://toms.gsfc.nasa.gov/ery_uv/euv.html) (verified 5 May 2003).
- UNEP, 2002. Executive Summary. Final of UNEP/WMO Scientific Assessment of Ozone Depletion: 2002. Prepared by the Scientific Assessment Panel of the Montreal Protocol on Substances that Deplete the Ozone Layer. UNEP, Nairobi (released 23 August 2002).
- Visser, A.J., Tosserams, M., Groen, M.W., Kalis, G., Kwant, R., Magendans, G.W.H., Rozema, J., 1997a. The combined effects of CO<sub>2</sub> concentration and enhanced UV-B radiation on faba bean. 3. Leaf optical properties, pigments, stomatal index and epidermal cell intensity. *Plant Ecol.* 128, 208–222.
- Visser, A.J., Tosserams, M., Groen, M.W., Magendans, G.W.H., Rozema, J., 1997b. The combined effects of CO<sub>2</sub> concentration and solar UV-B radiation on faba bean grown in open-top chambers. *Plant Cell Environ.* 20, 189–199.
- Vu, C.V., Allen Jr., L.H., Garrard, L.A., 1981. Effects of supplemental UV-B radiation on growth and leaf photosynthetic reactions of soybean (*Glycine max*). *Physiol. Plant* 52, 353–362.
- Vu, C.V., Allen Jr., L.H., Garrard, L.A., 1982. Effects of supplemental UV-B radiation on primary photosynthetic carboxylating enzymes and soluble proteins in leaves of C<sub>3</sub> and C<sub>4</sub> crop plants. *Physiol. Plant* 55, 11–16.
- Vu, C.V., Allen Jr., L.H., Garrard, L.A., 1984. Effects of enhanced UV-B radiation (280–320 nm) on ribulose-1,5-bisphosphate carboxylase in pea and soybean. *Environ. Exp. Bot.* 24, 131–143.
- Warner, C.W., Caldwell, M.M., 1983. Influence of photon flux density in the 400–700 nm waveband on inhibition of photosynthesis by UV-B (280–320 nm) irradiation in soybean

- leaves: separation of indirect and immediate effects. *Photochem. Photobiol.* 38, 341–346.
- Weatherhead, E.C., Reinsel, G.C., Tiao, G.C., Jackman, C.H., Bishop, L., Hollandsworth Frith, S.M., DeLuisi, J., Keller, T., Ottmans, S.J., Fleming, E.L., Wuebbles, D.J., Kerr, J.B., Miller, A.J., Herman, J., McPeters, R., Nagatani, R.M., Frederick, J.E., 2000. Detecting the recovery of total column ozone. *J. Geophys. Res.* 105, 22.
- Weston, E., Thorogood, K., Vinti, G., Lopez-Juez, E., 2000. Light quantity controls leaf-cell and chloroplast development in *Arabidopsis thaliana* wild type and blue-light-perception mutants. *Planta* 211, 807–815.
- Wilson, M.I., Greenberg, B.M., 1993. Protection of D1 photosystem II reaction center protein from degradation in ultraviolet radiation following adaptation of *Brassica napus* L. to growth in ultraviolet-B. *Photochem. Photobiol.* 57, 556–563.
- Xiu-Ming, H., Hale, B.A., Ormford, D.P., Hao, X.M., 1997. The effects of ultraviolet-B radiation and carbon dioxide on growth and photosynthesis of tomato. *Can. J. Bot.* 75, 213–219.
- Yang, X., Heisler, G.M., Montgomery, M.E., Sullivan, J.H., Whereat, E.B., Miller, D.R., 1995. Radiative properties of hardwood leaves to ultraviolet irradiation. *Int. J. Biometeorol.* 38, 60–66.
- Yang, Z., Zheng, S.J., Hu, A.T., Zheng, Y.F., Yan, J.Y., 2000. Response of cucumber plants to increased UV-B radiation under water stress. *J. Environ. Sci.* 12, 236–240.
- Yazawa, M., Shimizu, T., Hirao, T., 1992. Feeding response of the silkworm to UV irradiation of mulberry leaves. *J. Chem. Ecol.* 18, 561–569.
- Yue, M., Wang, X.L., 1998. A preliminary study of the responses of wheat and oat reproductive characteristics to enhanced UV-B radiation. *China Environ. Sci.* 18, 68–71.
- Zavala, J.A., Scopel, A.L., Ballare, C.L., 2001. Effects of ambient UV-B radiation on soybean crops: impact on leaf herbivory by *Anticarsia gemmatalis*. *Plant Ecol.* 156, 121–130.
- Zhao, D., Reddy, K.R., Kakani, V.G., Read, J., Sullivan, J., 2003. Growth and physiological responses of cotton (*Gossypium hirsutum* L.) to elevated carbon dioxide and ultraviolet-B radiation under controlled environment conditions. *Plant Cell Environ.*, pp. 771–782.
- Ziska, L.H., Teramura, A.H., 1992. CO<sub>2</sub> enhancement of growth and photosynthesis in rice (*Oryza sativa*). *Plant Physiol.* 99, 473–481.
- Ziska, L.H., Teramura, A.H., Sullivan, A.H., McCoy, A., 1993. Influence of ultraviolet-B (UV-B) radiation on photosynthetic and growth characteristics in field-grown cassava (*Manihot esculentum* Crantz). *Plant Cell Environ.* 16, 73–79.