

13 Solar UV-B Radiation and Global Dimming: Effects on Plant Growth and UV-Shielding

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Abstract Atmospheric aerosols and other particulates have been linked to reductions in shortwave radiation (global dimming). While much research has focused on the effects on plants caused by ambient and elevated UV-B (290 nm – 320 nm), the direct effects of global dimming, and those mediated by associated changes in UV-B radiation, have not been effectively assessed. We conducted an experiment in the high-UV environment of Mauna Kea, Hawaii to compare the effects of UV-B reduction with a simulation of global dimming (accomplished with 13% shading). Using fava beans, (*Vicia faba*), we found that structural differences due to the treatments were minimal in this high light environment. Most surprising was the minimal effect of UV-B on plant growth given the high UV-B environment. However, both UV-B and shading significantly influenced epidermal UV transmittance, suggesting that changes that occur in secondary chemistry can affect epidermal transmittance for UV. Additional experiments suggest that the change in epidermal transmittance due to shading would most likely occur with foliage in high-shade environments. Such changes in secondary chemistry have the potential to affect herbivory, nutrient cycling, and plant response to pathogens. While there are few experimental studies that specifically address possible reductions in radiation due to global dimming, many UV reduction experiments have been conducted in recent decades. Attempts to generalize latitudinal responses from these studies, however, are frustrated by a number of factors. Chief among them are different methodologies (reduction of different UV wavebands in different experiments) and a lack of reporting UV irradiance levels.

Keywords global dimming, UV-A epidermal transmittance, UV reduction experiment, leaf optical properties, UV-A and UV-B absorbing pigments, UVA-PAM, *Vicia faba*

13.1 Introduction

Total solar radiation reaching the surface of the earth depends on sunlight reaching the top of the atmosphere and the transparency of the atmosphere. Recent research has indicated solar radiation reaching the surface of the earth has decreased globally by 4%–6% during the period of 1960–1990 (Wild et al., 2005) and 10% over the past 50 years (Stanhill and Cohen, 2001). This phenomenon has been termed “global dimming.” However, since about 1990, this trend at the global scale has reversed and “global brightening” has been measured at a rate averaging 0.10% per year (Pinker et al., 2005; Wild et al., 2005; Norris and Wild, 2007). These multi-year trends suggest that the total radiation reaching the earth’s surface, as affected by changes in atmospheric transparency, can fluctuate over periods of 20–50 years (Roderick, 2006).

Sunlight reaching the top of the atmosphere is affected by solar output and earth orientation, while cloudiness and both natural and anthropogenic sources of particulate and aerosol material affect atmospheric transparency. Declines in atmospheric transparency have been linked to volcanic activity (Roderick et al., 2001; Lohmann et al., 2006), increased cloud cover (Cutforth and Judiesch, 2007) and air pollution (Jauregui and Luyando, 1999; Alpert et al., 2005; Ramana and Ramanathan, 2006), while decreased cloudiness related to global warming (Nazarenko and Menon, 2005) and improved air quality (Schiermeier, 2005; Black et al., 2006; Norris and Wild, 2007) have been touted as increasing atmospheric transparency. Potential ecological effects of changes in solar radiation reaching the surface of the earth include changes in plant productivity (Roderick et al., 2001; Stanhill and Cohen, 2001; Black et al., 2006) and alteration of the hydrological cycle (Cohen et al., 2002; Roderick and Farquhar, 2002; Liepert and Romanou, 2005; Brutsaert, 2006; Robock and Li, 2006; Li et al., 2007).

13.1.1 Global Dimming and UV-B: Potential Effects on Plants

Reductions in shortwave radiation with increased atmospheric aerosols and other particulates are well established. This reduction of total shortwave radiation also coincides with an increase in the diffuse portion of the shortwave radiation (Black et al., 2006; Roderick, 2006) as aerosols and particulates increase the scatter of direct beam radiation (Fig. 13.1). Surface ultraviolet radiation (UV; <400 nm) levels are also influenced by atmospheric aerosols and other pollutants, both causing varying degrees of attenuation and scattering of the radiation. While increased levels of UV-B radiation due to ozone depletion during the latter part of the 20th century are unquestioned (McKenzie et al., 2007), reductions in surface-level UV radiation due to pollution are ubiquitous over some surprisingly large areas of the Northern Hemisphere (McKenzie et al., 2001) and can cancel the increased

UV-B radiation from ozone depletion (Ma and Guicherit, 1997). At present, since stratospheric ozone levels are already showing signs of recovery, UV levels would be expected to decrease in the near future (McKenzie et al., 2007), even without global dimming.

Much is known about the effects of ambient and elevated UV-B (290 nm – 320 nm) on plants (see reviews by Barnes et al., 2005; Caldwell et al., 2007; and others), but the direct effects of global dimming on plants and those mediated by associated changes in UV-B radiation have not been effectively assessed. In particular, experiments specifically designed to assess changes in UV-B under global dimming have not been conducted. Interactions between quantities of photosynthetically active radiation (PAR; 400 nm – 700 nm) and UV on plant performance are known (e.g., Krizek, 2004), but are further complicated by the nature of PAR and UV radiation. Because solar UV radiation has a greater diffuse component than the longer wavelengths of sunlight, the penetration of PAR and UV into plant canopies is different (Flint and Caldwell, 1998). In particular, it has been shown that the ratio of PAR to UV in a canopy differs dramatically depending on whether solar radiation is measured in a sunfleck or the shade (Flint and Caldwell, 1998). Not surprisingly, therefore, generalizations on how total solar radiation changes, as occurs with global dimming and brightening, interact with recovery from ozone depletion are lacking.

Research previously conducted that examined plant responses to changes in total solar radiation, as might be expected under global dimming, involved both modeling and experimental efforts. Modeling studies have generally shown increases in canopy photosynthesis with global dimming as a result of increased penetration of diffuse PAR into the canopy. For example, a substantial increase in the proportion of diffuse radiation following the eruption of Mt. Pinatubo appears to have increased photosynthesis to the same extent that atmospheric CO₂ showed an unexpected decline (Roderick et al., 2001). Experimental studies to assess plant effects resulting from changes in total solar radiation have typically involved manipulation of total sunlight. However, these studies often use substantial amounts of shade (e.g., 30% and 60% shade, Raveh et. al., 2003), which is a much greater change in solar radiation than occurs with global dimming. Therefore, results from these studies make extrapolation to global dimming scenarios tenuous. Results from a limited number of experiments using minimal shading (e.g., 13% used by Fischer, 1975) suggest that some effects can be seen due to even limited shade levels, and may be more affected in plant communities that are light-limited (Black et al., 2006).

13.1.2 Assessing Global Dimming and UV-B Effects on Plant Growth

To provide some insight into the effects of global dimming on plant growth, the

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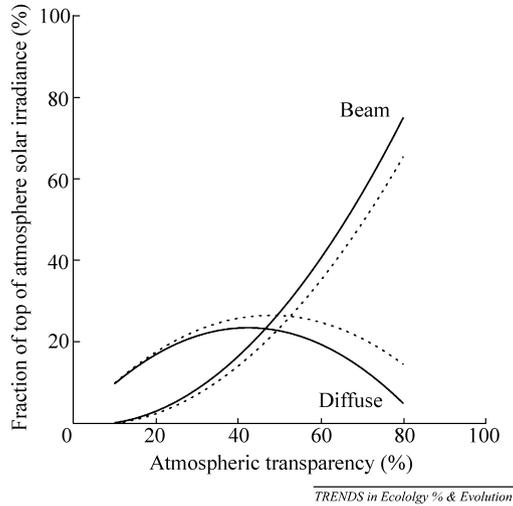


Figure 13.1 Idealized changes in diffuse and direct beam radiation reaching the Earth as a function of atmospheric transparency (reprinted from Roderick 2006). Solid lines represent standard atmospheric conditions; dotted lines show the immediate effect of the Mt. Pinatubo volcanic eruption in June 1991

role of UV-B in this response, and a comparison of the magnitude of the responses to dimming and UV-B, we conducted a field experiment using minimal shading levels approximating the reduction in solar radiation observed under these conditions (e.g., Stanhill and Cohen, 2001). We specifically examined whether there could be direct influences of global dimming and altered solar UV-B on various aspects of leaf development (e.g., leaf optical properties or leaf mass per unit area), which are important traits that influence light penetration into the canopy and which often influence plant responses to UV-B. We further evaluated whether these possible changes in light penetration or other effects of shade could influence overall plant growth in this experiment. These effects were put into perspective with UV-B radiation effects by simultaneously conducting a UV-B screening experiment at the same site (Mauna Kea, Hawaii). This served two purposes: (1) it permitted comparisons between these two global environmental factors, and (2) enabled us to assess whether UV radiation effects are sufficiently large such that a potential reduction in UV accompanied by global dimming could have measurable effects on plants. Finally, we examined whether reports in the literature suggest trends in the effects of UV-B radiation, contrasting UV screening experiments at higher latitudes (lower UV-B) with lower-latitude (higher UV-B) sites, and we compared the responses of other species at high-UV sites with our results.

13.2 Methods

13.2.1 Field Site

Studies were conducted during summer at a field site located on the south slope of Mauna Kea, Hawaii, USA (2,800 m elev.; 19°45'N, 155°27'W). Climate at the study site is Mediterranean, with warm relatively dry summers and cooler, wetter winters. Average summer high temperatures are ca. 20°C–22°C and annual precipitation is ca. 400 mm. The light climate is characterized by high PAR (max clear day ca. 2,100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and very high UV-B and UV-A levels (max clear day ca. 5.1 and 69 W m^{-2} , respectively). Additional measurements were conducted at an experimental site located in North Logan, UT, USA (1,408 m elev.; 41°30'N, 111°48'W).

13.2.1.1 Experimental Plots

Vicia faba L. cv. Broad Windsor (fava bean) were grown under horizontal filters with three primary treatments (three replicate filters per treatment) to simulate ambient radiation and dimming conditions: (1) near ambient full spectrum radiation (+UV-B, full sun); (2) full spectrum radiation reduced by 13% (+UV-B, reduced sun); and (3) full spectrum radiation reduced by 13% with UV-B wavelengths removed (-UV-B, reduced sun). A UV-transparent film (Aclar type 22 A, 0.038 mm thick, Honeywell, Pottsville, PA, USA) was used for treatments 1 and 2, and UV-B blocking (<320 nm) film (0.051 mm polyester (Mylar); DuPont Teijin Films U.S., LLP, Hopewell, VA, USA) was used for treatment 3 (Fig. 13.2). Reduced sun treatments were made using three different fine mesh nettings: 4 cm squares, 2.4 cm squares, and mesh with diagonal openings 2 cm per side. A layer of all three mesh nettings was used for treatment 2, while only the 2.4 cm mesh was used for treatment 3 because of the lower transmittance of Mylar. Transmittances for photosynthetically active radiation (PAR, 400 nm–700 nm) were 92.9%, 81.0% and 80.7% and for broadband UV (UV-A and UV-B) were 88.1%, 74.0% and 50.9% for treatments 1, 2, and 3, respectively, as measured with a quantum sensor (Li-185, Li-COR, Inc., Lincoln, NE, USA) and broadband UV sensor (Skye UV-B; Skye Instruments, Ltd., Powys, UK). Filters and netting were mounted on 1.3 cm diameter electrical conduit in 1.1 m×1.0 m horizontal filter frames and mounted on four metal corner rods 38 cm above the ground. Filters were periodically moved upward to maintain a distance of ca. 15 cm height above growing plants. A fourth treatment (-UV-B, “full” sun) was constructed using only polyester filter material (0.051 mm Mylar); PAR transmittance was 87.2% and broadband UV was 58.8%. Because of the differences in transmittance for PAR, this treatment could not be considered a true -UV-B, full sun treatment for comparing plant growth. This treatment was used only for assessing leaf epidermal transmittance for UV.

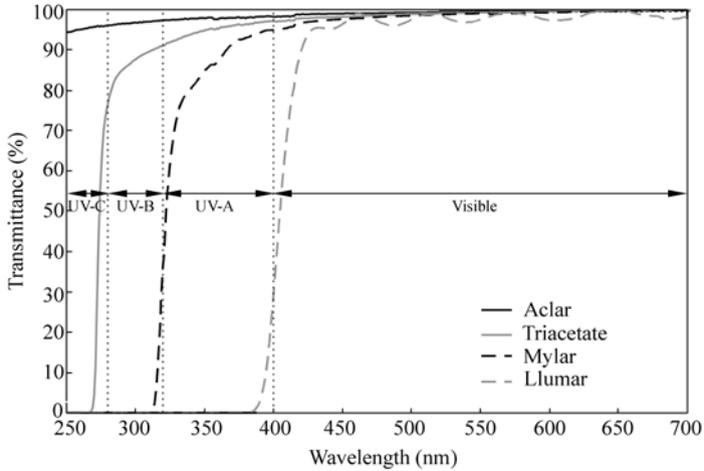


Figure 13.2 Relative spectral transmittance for four commonly used plastic filters used in UV-exclusion experiments. Transmittance is relative to the maximum transmittance (100%) for each filter across the range from 250 nm – 700 nm (see text for filter descriptions)

Vicia faba were grown in cone-shaped pots (Ray Leach Cone-tainers: 0.15 L volume, 205 mm length, 40 mm top diameter; Stuewe and Sons, Corvallis, Oregon, USA) placed in racks holding 49 (7×7) pots with 5 mm edge separation to simulate plants growing in a canopy. This resulted in a plant density of 494 plants m⁻². Single seeds were planted (June 2, 2005) at 2 cm – 3 cm depth in each cone-tainer containing organic potting soil and racks of cone-tainers were placed under moderate shade (<500 μmol m⁻² s⁻¹ max PAR) until emergence 13 days later (June 15). Roughly double the necessary cone-tainers were planted so that seedlings of uniform size could be selected and randomly assigned to treatments. Upon emergence, plants were sorted by size to create three full racks of plants per treatment with similar-sized plants. Each rack of cone-tainers was then placed under a single filter frame. Plants were watered with tap water 1–2 times daily to minimize water stress and grown for 30 days (until July 15) under the filters.

13.2.2 Structural and Biomass Measurements

After 30 days of growth, plants were removed from under the filter and taken indoors for structural and epidermal transmittance measurements and then destructively harvested for biomass quantification. Structural measurements included total height (soil surface to top of terminal bud), number of internodes, and height of each internode. Plants were then harvested and sorted into components (leaf, stem, branches), oven dried at 60°C for 24 hours and weighed for dry mass determinations. Leaf mass per area was determined by cutting a leaf

disk (1 cm^2) from a mature leaf at the time of harvest using a cork-borer. The leaf disk was dried at 60°C and weighed.

13.2.3 UV-A Epidermal Transmittance Measurements

Non-invasive measurements of epidermal UV-A transmittance were made on intact mature leaves of plants at the time of harvest with a field-portable pulse amplitude modulation (PAM) chlorophyll fluorometer (UVA-PAM; Gademann Instruments, Würzburg, Germany). The UVA-PAM provides non-destructive estimates of epidermal UV-A transmittance through fluorescence yields of chlorophyll induced by UV-A (375 nm) and blue (470 nm) radiation pulses (Kolb and Pfündel, 2005). Fluorescence induced by UV-A (F_{UV}) from the mesophyll is compared to fluorescence induced by blue light (F_{BL}). By standardizing the ratio F_{UV}/F_{BL} to unity for an epidermis-free leaf (represented by a blue plastic standard, Heinz Walz GmbH, Effeltrich, Germany), absorbance of UV by the epidermis will proportionately reduce F_{UV} with the resulting ratio equivalent to the transmittance for UV-A. Since UV-A transmittance is a dynamic plant characteristic responding to changing environmental factors (Barnes et al., 2008), these measurements were taken on plants that had been moved indoors.

The UVA-PAM measures the changes in transmittance associated with changes in UV-A absorbing pigments (375 nm peak). To determine the relationship between UV-A and UV-B absorbing compounds in *Vicia faba*, we measured epidermal transmittance and UV-absorbing compounds from additional plants grown in varying light environments in North Logan, Utah. Epidermal transmittance for UV-A was measured on mature intact leaves using the UVA-PAM. The leaves in this study had developed under different densities of shade cloth and under premium cellulose triacetate (0.13 mm thick, Liard Plastics, Salt Lake City, UT, USA) and Lumar (0.13 mm thick, part no. UVCLSRPS, cutoff near 390 nm; CP Films, Inc., Martinsville, VA, USA) to create unfiltered and UV-screened environments (Fig. 13.2), respectively, of different levels of PAR and UV. Subsequently, leaf disks (1 cm^2) were collected from each leaf, dried at 60°C for 24 hours and weighed. Samples were ground, placed in an acidified methanol solution (5 ml of 70% methanol, 29% H_2O , and 1% HCl) in the dark at 20°C for 24 hours. Absorbances at 305 nm (approximate midpoint of UV-B spectrum) and 360 nm (midpoint of UV-A spectrum) of the extracts were measured with a scanning UV/visible spectrophotometer (Model DU640; Beckman Coulter, Inc., Fullerton, CA, USA).

13.2.4 Solar UV and PAR Irradiance

Measurements of ambient solar UV and PAR were made using a broadband UV

sensor (Skye UV-B; Skye Instruments, Ltd., Powys, UK) and quantum sensor (LI-185, Li-COR, Inc., Lincoln, NE, USA), respectively, at the Mauna Kea field site during the experiments. Clear-day data during the experiment were regressed against biologically-weighted estimates calculated from solar UV irradiance measured at the USDA UV-B monitoring station UVMFRS radiometer located at the Mauna Loa Meteorological Observatory (3,397 m elevation; ca. 30 km from our field site on Mauna Kea, <http://uvb.nrel.colostate.edu/UVB>). Biologically effective UV-B irradiances were reported for three generalized spectral weighting functions from Caldwell (1971; UV-BBE71), Flint and Caldwell (2003; UV-BBE03), and McKinlay and Diffey (1987; erythemal). We reported the erythemal (reddening of human skin) weighting as sometimes this is the only weighted irradiance available to researchers and is occasionally reported in plant studies. The UV-BBE data were adjusted for elevation differences between the Mauna Loa station and the Mauna Kea study site using a regression equation generated from data by Nullet and Juvik (1997). Reported integrated UV-A (321 nm–400 nm) irradiances were not adjusted for elevation, as differences would be minimal.

13.2.5 Statistical Analyses

ANOVA (General Linear Model) was used to test for differences among treatments, and pair-wise comparisons were made using the Tukey-Kramer multiple-comparison test. We initially tested for differences in plant metrics among treatment replicates (three replicates per filter treatment) and found none, but did find highly significant differences among individual plants within container racks due to the red/far-red ratio growth response of plants (tallest plants were in the center of the rack, smallest on the outer margin). Due to this, data were blocked by treatment and by position in the cone-tainer racks (1–25); highly significant position effects were found ($p < 0.00001$). Linear regression was used to test for significance of various trends. NCSS Statistical Software (NCSS, 2007; release Aug. 2007; NCSS, Orem, UT, USA) was used for all statistical analyses.

13.3 Results

13.3.1 UV-A Epidermal Transmittance

Epidermal transmittance for UV-A for fava beans grown in a high UV environment on Mauna Kea was found to be significantly affected by both the

dimming treatment and UV-B screening (Table 13.1; Fig. 13.3). On average, measured transmittances increased 6.6% with a 13% reduction in PAR (+UVB full sun vs. +UVB reduced sun). Screening of UV-B further increased epidermal

Table 13.1 Summary of 2-way ANOVA of the global dimming and UV-B reduction experiment conducted with fava bean at the Mauna Kea, HI, USA field station. Dosimetry and meteorological data as described in Fig 13.3. Treatments are described in the text. “mse” refers to mean square error from ANOVA; *n* is the total number measurements per treatment. Not all plants had internodes 7–9

Metric	Units	<i>n</i>	Treatments			mse	<i>p</i> -value
			+UVB full sun	+UVB reduced sun	–UVB reduced sun		
UVA transmittance	%	150	4.521	4.819	5.516	0.097	<0.0001
Total height	cm	75	19.223	19.191	19.309	0.223	0.927
Total biomass	g	75	0.814	0.804	0.803	0.018	0.903
Leaf biomass	g	75	0.402	0.393	0.388	0.014	0.783
Stem biomass	g	75	0.245	0.229	0.227	0.008	0.221
Branch biomass	g	75	0.162	0.177	0.184	0.016	0.609
Leaf mass per area	g cm ⁻²	75	0.0044	0.0044	0.0043	0.0001	0.796
Number of internodes	n	75	7.68	7.91	8.00	0.10	0.081
Number of branch nodes	n	75	2.49	2.56	2.69	0.10	0.330
Number of leaf nodes	n	75	5.19	5.35	5.31	0.08	0.360
Length of 1st internode	cm	75	0.376	0.415	0.324	0.041	0.294
Length of 2nd internode	cm	75	1.420	1.395	1.227	0.094	0.291
Length of 3rd internode	cm	75	2.405	2.273	2.144	0.114	0.272
Length of 4th internode	cm	75	3.020	2.935	2.840	0.107	0.496
Length of 5th internode	cm	75	2.716	2.584	2.761	0.086	0.319
Height of 1st internode	cm	75	0.068	0.088	0.064	0.017	0.547
Height of 2nd internode	cm	75	0.444	0.503	0.388	0.050	0.275
Height of 3rd internode	cm	75	1.864	1.897	1.615	0.131	0.253
Height of 4th internode	cm	75	4.269	4.171	3.759	0.229	0.250
Height of 5th internode	cm	75	7.289	7.105	6.599	0.308	0.262
Height of 6th internode	cm	75	10.005	9.689	9.360	0.316	0.354
Height of 7th internode	cm	73-75	11.991	11.594	11.406	0.282	0.330
Height of 8th internode	cm	41-50	13.238	12.359	12.443	0.316	0.104
Height of 9th internode	cm	10-22	14.101	12.828	13.036	0.551	0.335

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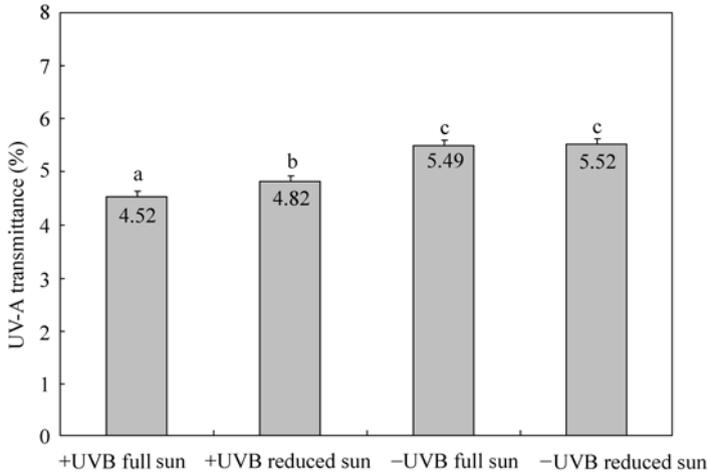


Figure 13.3 Epidermal transmittance for UV-A (375 nm) for mature fava bean leaves grown under simulated global dimming and UV-B exclusion environments at the Mauna Kea, HI field site (see Section 13.2.1). Epidermal transmittance was measured non-destructively with a UVA-PAM fluorometer. Error bars represent 1 standard error. Bars with different letters are significantly different at $p < 0.05$. Average daily biologically weighted UV doses were: erythemal = $8.97 \text{ kJ m}^{-2} \text{ d}^{-1}$ (sd. 1.28, min. 4.90, max. 10.06); UV-BBE71 = $13.8 \text{ kJ m}^{-2} \text{ d}^{-1}$ (sd. 2.0, min. 7.5, max. 15.4); and UV-BBE03 = $37.7 \text{ kJ m}^{-2} \text{ d}^{-1}$ (sd. 5.4, min. 20.6, max. 42.3). Daily total PAR averaged $46.6 \text{ mol m}^{-2} \text{ d}^{-1}$ (sd. 8.3) and daily maximum PAR averaged $2,024 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ (sd. 332). Daily air temperature averaged 11.8°C (sd. 1.5), daily maximum temperature averaged 17.8°C (sd. 2.0), and daily minimum temperature averaged 5.9°C (sd. 2.1)

transmittance by an additional 14.5% under a 13% reduction in PAR (-UVB reduced sun), and a total 22.1% increase in transmittance from the full sun treatment (vs. +UVB full sun). Screening of UV-B under a 6.1% reduction in PAR resulted in a 21.5% (-UVB, “full” sun) increase in epidermal transmittance for UV-A from the full sun treatment (+UVB full sun).

To determine the relationship between maximum ambient PAR and UV exclusion on leaf epidermal transmittance for UV, we grew fava beans under different PAR and UV environments in Utah. For these plants, relatively small but steady increases in transmittance were observed with declining PAR until maximum daily PAR exposure went below $200 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ where transmittances were observed to increase rapidly per unit quanta. This pattern was found to be consistent whether UV was present or absent, although leaves not exposed to UV radiation had slightly higher transmittances for all levels of PAR exposure (Fig. 13.4 upper). A similar pattern (Fig. 13.4 lower) was found for quaking aspen (*Populus tremuloides*) leaves grown in Utah under different levels of PAR without UV exclusion.

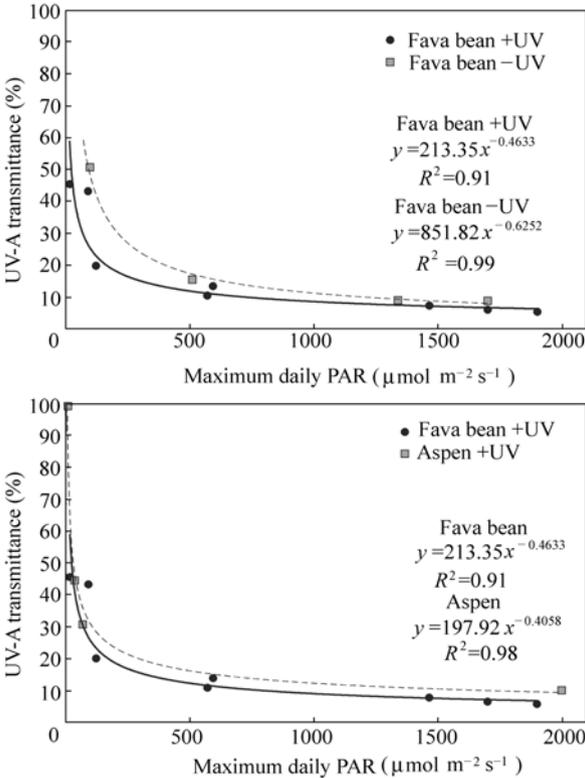


Figure 13.4 Epidermal transmittance for UV-A (375 nm) for mature fava bean (upper and lower panels) and quaking aspen leaves (lower panel only) grown under different PAR intensities in Logan, Utah measured non-destructively with a UVA-PAM fluorometer. Changes in UV exposure were commensurate with changes in PAR. Both UV-A and UV-B were shielded under the UV exclusion treatment (-UV)

The relationship between the concentration of UV absorbing pigments and UV-A epidermal transmittance as measured with the UVA-PAM was also evaluated for the fava beans grown in Utah. Highly significant relationships ($p < 0.0001$) were found among concentrations of extracted UV absorbing pigments and UV-A epidermal transmittance for both UV-A (Fig. 13.5, upper left) and UV-B (Fig. 13.5, lower left) absorbing compounds. In addition, concentrations of UV-A and UV-B absorbing compounds were highly correlated ($R^2 = 0.93$, $p < 0.0001$) and linear in relationship (Fig. 13.5, upper right). The relationship between the concentration of UV-B absorbing compounds and epidermal transmittance were consistent with a relationship (Fig. 13.5, lower right) found for a single quaking aspen growing in Utah.

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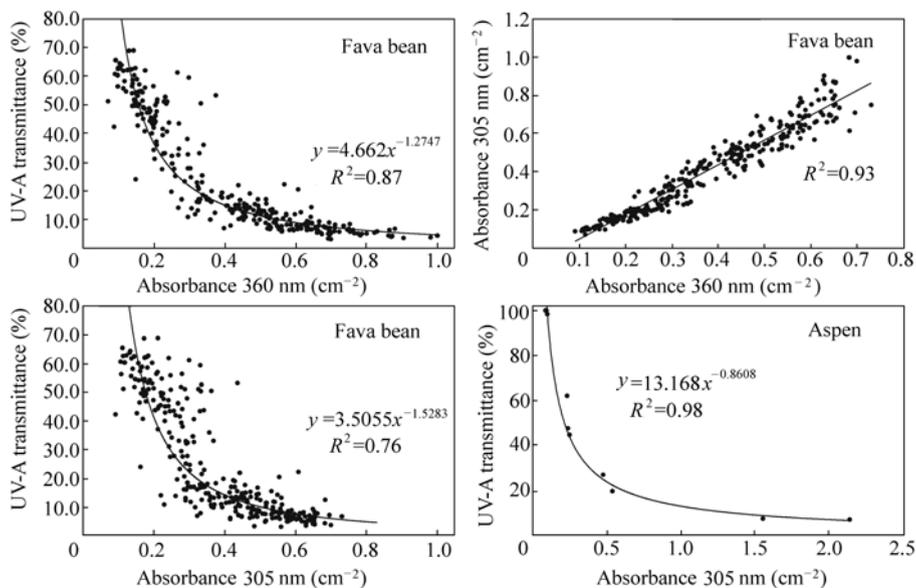


Figure 13.5 Relationship between UV-A transmittance (375 nm) as measured with a UVA-PAM fluorometer and absorbance (at 305 and 360 nm) of flavonoids extracted from same leaves for fava bean (left panels) and quaking aspen growing in Logan, Utah (lower right panel). The relationship between extract absorbance at 305 nm and 360 nm for fava bean is shown in the upper right panel. The quaking aspen relationship was derived from a single tree, while multiple individuals of fava bean were used

13.3.2 Dimming Effects on Biomass and Structure

Changes in structure and biomass of seedling fava beans were assessed with simulated dimming and UV-B exclusion in Hawaii. For total height, internode lengths, specific leaf weight and total, leaf, stem and branch biomass, no statistically significant differences were found between plants grown in full sun and under the dimming treatment, either with or without UV-B exclusion (Table 13.1; Fig. 13.6, upper, middle). Non-significant decreasing trends ($p > 0.05$) from full sun to reduced sun with UV-B exclusion were found for biomass and for many internode heights. One exception to this was a non-significant increase along the same radiation gradient for branch biomass. Evidence that more branching may have been induced with UV-B exclusion were obtained by assessing the number of plants with 8–10 internodes and the number of leaf and branch internodes. More plants grown under the dimming treatment with UV-B excluded had 8–10 internodes (Fig. 13.6, lower), and more branches per plant and greater branch biomass were measured (although not significant) for this treatment (Fig. 13.7).

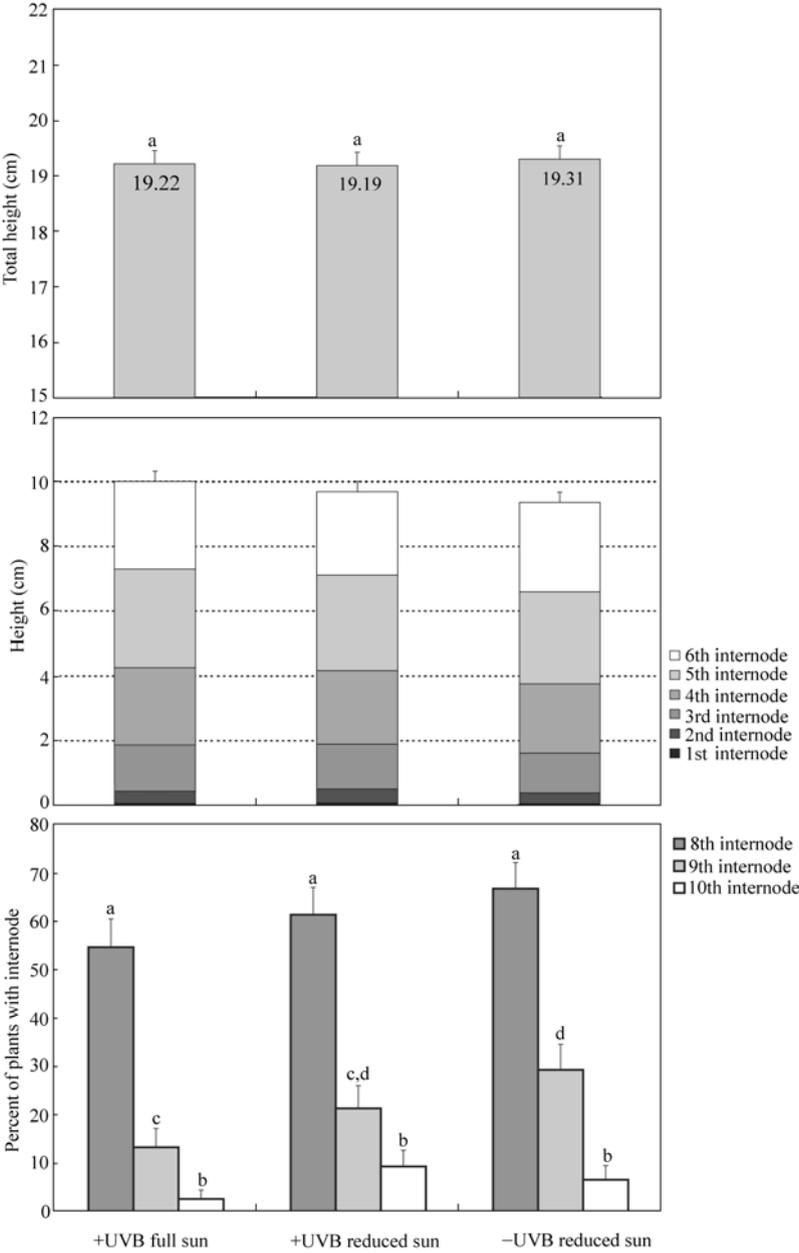


Figure 13.6 Total plant height (upper), height of internodes 1 – 6 (middle) and portion of experimental plants with internodes 8 – 10 (lower) for fava beans grown under simulated global dimming and UV-B exclusion at the Mauna Kea, Hawaii field site. Error bars represent 1 standard error. Values with same letter designation are not significantly different ($p > 0.05$). No significant differences were found among internode heights (middle panel). Dosimetry and meteorological data as in Fig. 13.3

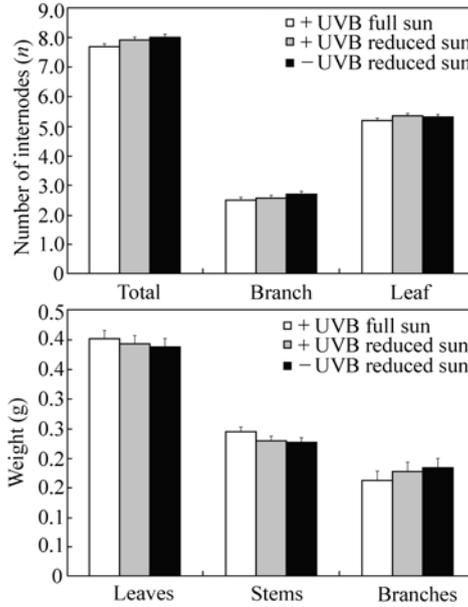


Figure 13.7 Average total number of internodes, number of branches and number of leaf insertions (upper) and weight of leaves, stems and branches (lower) for fava bean plants grown under simulated global dimming and UV-B exclusion at the Mauna Kea, Hawaii field site. Error bars represent 1 standard error. No significant differences ($p > 0.05$) were found among treatments for the number of internodes and weights of plant parts. Dosimetry and meteorological data as in Fig. 13.3

13.4 Discussion

Our results with fava bean (*Vicia faba*) indicated little change in plant structure or biomass under an experimental global dimming environment where ambient PAR was reduced approximately 13%. We also found minimal additional differences with UV-B exclusion in the same environment. However, we found significant changes in leaf optical properties related to UV transmittance in both the reduced PAR and UV-B treatments.

The growth response to UV-B exclusion in this experiment was less than expected for a temperate-latitude crop grown at a high-elevation tropical location with high solar UV. Biologically effective UV radiation increases substantially from high to low latitudes, and there is also an increase with elevation (Caldwell et al., 1980). Because of its elevation and latitude, the study site on Mauna Kea, Hawaii, experiences some of the highest effective UV doses on the planet (Bodhaine et al., 1996). Thus, we were somewhat surprised that attenuation of these high UV fluxes had minimal effect on fava bean growth and morphology. Some small morphological changes in fava bean, without accompanying changes

in above-ground mass, have been reported with UV-B exclusion in the Netherlands (Visser et al., 1997) and in a greenhouse UV-B supplementation experiment (Barnes et al., 1990a). However, under field UV-B supplementation at mid-latitudes, this variety of fava bean showed changes in leaf optical properties, but no changes in photosynthesis (Flint et al., 1985).

13.4.1 Global Dimming and UV-B Effects on Leaf Optical Properties

Small increases of epidermal transmittance for UV in fava bean leaves were found under the 13% reduction in PAR and with UV-B exclusion. These results are consistent with increases in leaf UV-absorbing compounds with increased UV-B exposure (Mazza et al., 2000; Searles et al., 2001; Coleman and Day, 2004). Over a wide range of solar radiation regimes, we found that only small differences in epidermal transmittance occurred over large ranges of PAR ($500 - 2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$), and that this relationship held even for leaves developed under full UV-B and UV-A exclusion (Fig. 13.4). These findings suggest that the primary effect on changes in leaf epidermal transmittance due to global dimming will likely occur for leaves developed in shaded environments ($< 200 \mu\text{mol m}^{-2} \text{s}^{-1}$) where reductions in ambient PAR and UV are related to large changes in epidermal transmittance.

We also observed that changes in levels of whole-leaf UV-absorbing compounds were not linearly correlated with measurements of UV-A transmittance. Rather, this relationship was curvilinear whereby leaves with low UV-A transmittance exhibited a range of whole-leaf absorbance values (Fig. 13.5). In addition, the relationship more closely fit a power function ($y = bx^a$), rather than exponential ($y = be^{ax}$), indicating that the distribution of the absorbing compounds did not approximate a random distribution of particles as in the Beer-Lambert law of light absorbance through particles suspended in a medium (Kostinski, 2001). Krause et al. (2003) also reported constant levels of UV-A transmittance over a wide range of whole-leaf absorbance values in leaves from tropical tree crowns. The non-random distribution of UV-absorbing compounds in the epidermis (Day et al., 1993) may help explain the broad range of whole-leaf absorbance values for a given quantity of epidermal transmittance.

13.4.2 Global Dimming and UV-B Effects on Productivity

The lack of a significant growth response under reduced PAR is not totally unexpected in the high light environment of Mauna Kea where clear sky ambient PAR levels can routinely exceed $2,200 \mu\text{mol m}^{-2} \text{s}^{-1}$. Light saturation would be expected for many of the leaves of the experimental plants even in early stages of

canopy development. Furthermore, reductions in total available PAR have little effect in the nearly linear portion of the photosynthetic light response curve often observed for C₃ photosynthesis at high levels of PAR (e.g., Lambers et al., 1998). In addition, these results are consistent with those reported by Stanhill and Cohen (2001) for many crops in high-radiation, arid climates. They concluded that there would be minimal negative effects of global dimming on crop productivity due to shade tolerance and anticipated reductions in water stress. Thus, our results did not agree with previous research indicating increased productivity associated with increased diffuse radiation in light-limited canopies (Roderick et al., 2001; Black et al., 2006) under global dimming, and likely reflect a nearly light saturated canopy within the experimental setup. Our results further suggest that reduced leaf photosynthesis resulting from high light exposure (e.g., photoinhibition, Demmig-Adams, 1990) did significantly reduce productivity (Werner et al., 2001).

Many plant responses to a global dimming environment are not necessarily linked to overall plant productivity. In experiments with wheat, Fischer (1975) found that shading reduced dry matter production approximately in proportion to the percent shade, even at the lowest (13%) shade levels used. However, grain production was less influenced by shading, most likely because shading reduced tillering, but enhanced tiller survival (Fischer, 1975). The response of wheat to shade was considerably greater than the growth responses we observed in fava bean, but may relate to higher leaf area and greater canopy self-shading in the wheat experiment. Although not significant, our data suggested a possible increase in branching rate with reduced PAR and UV-B exclusion. Over an entire growing season, such morphological differences might affect productivity as more energy put into branch structures likely results in less energy and carbon allocated to other plant parts.

13.4.3 Ecological Implications

The body of evidence to date indicates that changes in UV effects on plants are often relatively subtle, but these small changes may have important ecological implications, particularly by secondary or indirect effects (Caldwell et al., 2007). The small changes in leaf optical properties and secondary chemistry, and minimal differences in productivity under simulated global dimming and UV-B reduction found in our study, are consistent with this perspective.

Changes in the quantity of UV exposure by plants have been shown to affect morphology in ways that can affect competitive interactions, with changes in biomass among species corresponding to changes in the quantity of UV-B radiation (Barnes et al., 1990b; Ryel et al., 1990; Robson et al., 2003). Changes in yield, as have been observed under small changes in PAR (e.g., Fischer, 1975), and changes in root:shoot allocation (Zaller et al., 2002; Rinnan et al., 2005) may

affect competitive interactions (Rinnan et al. 2006). Exposure to UV-B radiation also may affect herbivory rates (Ballaré et al., 1996; Zavala et al., 2001). Changes in concentrations of UV-B absorbing pigments have also been linked to both negative and positive plant responses to pathogens, (e.g., Raviv and Antignus, 2004). Different levels of secondary compounds related to changes in UV-B absorbing pigments may have additional below-ground effects on soil microorganisms by affecting carbon and other nutrient availability (Robson et al., 2005). All these examples show potential mechanisms for UV-B to influence competitive interactions.

Effects of global dimming on plants may also interact with other environmental changes, including temperature and precipitation patterns, in complex and synergistic ways. These interactive effects include increases in UV-absorbing secondary compounds associated with drought (Milchunas et al., 2004; Yang et al., 2005). These may change plant performance by reducing UV-induced damage, and affecting herbivory rates and soil processes, as discussed above.

13.4.3.1 UV Exclusion Studies

Portions of this study involved using filters to selectively exclude UV-B (and in one experiment all UV) from the incident radiation spectrum. Results from UV exclusion studies have varied widely, and the importance of excluding various portions of the UV spectrum on these biological effects has been debated. At temperate locations, many species often fail to respond to UV-B exclusion (e.g., Cybulski and Peterjohn, 1999). Properly designed UV exclusion experiments at lower latitudes with higher ambient levels of UV-B, but similar levels of PAR, might be expected to show greater effects than similar experiments at higher latitudes. On the other hand, species of low latitudes may be adapted to cope with high levels of ambient solar UV-B and thus, might be expected to show less of a response to solar UV-B exclusion than high latitude species. The examples discussed below show that, while trends of responses to UV exclusion cannot now be easily seen from simple comparisons, improvements in methodology may permit generalizations to be made in the future.

Exclusion studies at low latitudes comprise a small number of the total exclusion studies in literature and show that species exhibit a variety of growth responses to ambient levels of UV-B. An examination of five tropical species at 9°N latitude in Panama (four tree species and the crop cassava) found substantial growth responses in two species and smaller or no growth responses in others (Searles et al., 1995). Rice (*Oryza* sp.) exhibited no significant growth responses in four seasons of UV-B exclusion experiments in the Philippines at 15°N (Dai et al., 1997). However, other crop experiments did show responses. When comparing the responses of maize (*Zea mays*) and the mung bean (*Vigna* sp.) to UV-B removal at New Delhi (28.6°N), Pal et al. (1997) found the bean to be much more responsive to UV-B than the maize. *Vigna unguiculata* grown under a

similar UV-B exclusion at 10°N latitude, where we assume UV-B could be more intense, responded to UV-B to a lesser extent (Lingakumar et al., 1999).

The category of UV-absorbing pigments was the most responsive characteristic in a meta-analysis of UV-supplementation studies (Searles et al., 2001) and is a characteristic that often responds in UV exclusion studies. Four of the five species examined by Searles et al. (1995) in Panama showed significant changes in levels of these compounds in response to UV-B exclusion. The only other low-latitude study examining UV-absorbing compounds in response to UV-B exclusion used the bean *Vigna unguiculata* and saw an approximate 60% increase in these compounds under near-ambient radiation compared to the UV-B exclusion (Lingakumar et al., 1999).

Since UV-exclusion experiments appear less technically complex than lamp-supplementation experiments, it is tempting to use multiple studies at different latitudes or elevations to examine response. One potential comparison uses wheat: Becwar et al. (1982) grew wheat under UV-B exclusion at 3,000 m elevation in the Rocky Mountains at 39.2°N latitude, while Häder (1996) studied several wheat cultivars exposed at 2,400 m elevation in the Andes at 22.8°S latitude. However, the latter study did not use a filter over the ambient UV plants, so the true UV-B effect may be confounded as the lack of a filter induces a host of microclimate differences besides the UV treatment (Flint et al., 2003). A latitudinal gradient study of *Salicornia* along the Atlantic coast of South America (Costa et al., 2006) had the potential to provide an overview of how this genus responds to varied UV environments, but interpretation is complicated. Experiments in one location lacked filters over the ambient-UV plots, preventing a true evaluation of UV effects as discussed above. In another location in this study, both UV-B and UV-A were removed from the UV exclusion treatment, while all the other sites only excluded UV-B, considerably complicating comparisons (see below).

Selection of different wavebands of interest may complicate comparisons of results between studies. Among the 100 or so published exclusion studies, exclusion has included removing all UV-B wavelengths, removing only a portion of the UV-B waveband, and removing all UV-B and simultaneously some or all of the UV-A. While many studies use polyester (often referred to as Mylar) which removes most UV-B wavelengths (Fig. 13.2), other studies use different techniques or materials to remove more limited wavebands. This is illustrated by experiments with maize at a low-latitude site (28.6°N), where Pal et al. (1997) used the standard polyester filter and saw only some limited change in plant growth with UV-B removal. Several varieties of maize grown further north (38.7°N latitude), under filters that removed only a narrower waveband of UV-B, often seemed to show greater effects (Mark et al., 1996). This is unexpected, both in terms of the direction of the latitudinal response and the larger response to the smaller UV radiation difference between the two treatments.

There is also increasing evidence of the importance of portions of the UV-A

spectrum. Several recent spectral weighting functions extend into the UV-A region (Quaite et al., 1992; Ibdah et al., 2002; Flint and Caldwell, 2003; also see discussion of UV-A exclusion experiments in Flint and Caldwell, 2003). Thus experiments excluding portions of the UV-A spectrum would be expected to produce different results than exclusions of only UV-B and are not directly comparable; in some instances solar UV-A invokes different responses than UV-B (Kotilainen et al., 2008).

Latitudinal comparisons are sometimes further complicated because the latitude of the experiments is not reported. Also, in some studies, the dates of plant growth are not presented. As many UV-exclusion experiments are short-term studies, and UV levels can vary considerably over the course of the growing season in many areas, these two problems make even crude estimates of irradiance levels problematic.

Perhaps the greatest aid for reconciling exclusion experiments in different areas would be the presentation of UV dosimetry integrated over the course of the experiment, although a characterization of representative clear-day radiation would be preferable to a complete lack of dosimetry. Biologically-weighted UV radiation with more than one common weighting function is preferable to unweighted values, as comparisons of weighted and unweighted radiation, or radiation weighted with different spectral weighting functions, are seldom possible. For example, both of the *Vigna* studies referred to above provide dosimetry, but use different weighting functions. Thus, it is not possible to use the available dosimetry to help understand the unexpected response to latitude when these two studies are compared.

13.5 Concluding Remarks

Global dimming, in addition to affecting the amount of visible radiation, will affect the amount of UV radiation reaching the earth's surface. Our experiment using fava beans (*Vicia faba*) grown in the high UV environment of Mauna Kea, Hawaii, was designed to detect whether a 13% reduction in visible radiation (and associated reduction in UV radiation), a level similar to global dimming, could influence plant growth and leaf optical properties for UV-transmittance. We found that structural differences were minimal in this high light environment, but changes that can occur in secondary chemistry can affect epidermal transmittance for UV. Our results, and those of other researchers, suggest that the primary effects of global dimming on plants may be mediated through changes in secondary chemistry, and would be most likely to occur with foliage in high-shade environments. Such changes have the potential to affect herbivory, nutrient cycling, and plant response to pathogens. Future research to further understand global dimming effects on ecosystem function should continue with a focus on secondary compounds of plants.

Experiments involving UV filtration need to have sufficient methodological detail that comparisons can be made between different venues. Methodology need not be ponderous, but needs to include: (1) latitude and elevation of the experimental site, (2) dates of plant growth, (3) dosimetry of UV radiation during the experiment, and (4) filter descriptions. Filter transmittance needs mention if non-standard materials are used, and filter geometry should not be neglected. For example, flat filter sheets permit some radiation to reach plants in the filtered wavelength region while tents or tunnels exclude all filtered wavelengths. With this standardized reporting of experimental conditions, comparisons of experiments between locations will be facilitated and may lead not only to generalizations on plant responses, but may also assist in the evaluation of spectral weighting functions.

Acknowledgements

This research was supported by the US Department of Agriculture UV-B Monitoring and Research Program (USDA-CSREES No. 2004-34263-14270 to Utah State University via subcontract with Colorado State University), the Utah Agricultural Experiment Station, the Loyola University J.H. Mullahy Endowment in Environmental Biology, and a Loyola University Faculty Research Grant. We are grateful to S. Kelly, M. Spriggs and V. Del Bianco for their assistance, and R. Koehler, D. Byrne, A. Teramura, and J. Juvik and the Mauna Kea Support Services for logistical support in Hawaii. Heinz Walz GmbH, Effeltrich, Germany and Gademann Instruments, GmbH, Würzburg, Germany are gratefully acknowledged for their technical assistance and loan of instruments.

References

- Alpert P, Kishcha P, Kaufman and YJ, Schwarzbard R (2005) Global dimming or local dimming?: Effect of urbanization on sunlight availability. *Geophysical Research Letters* 32: L17802
- Ballaré CL, Scopel AL, Stapleton AE, and Yanovsky M J (1996) Solar ultraviolet-B radiation affects seeding emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insects in *Datura ferox*. *Plant Physiology* 112: 161 – 170
- Barnes PW, Flint SD, and Caldwell MM (1990a) Morphological responses of crop and weed species of different growth forms to ultraviolet-B radiation. *American Journal of Botany* 77: 1354 – 1360
- Barnes PW, Beyschlag W, Ryel RJ, Flint SD, and Caldwell MM (1990b) Plant competition for light analyzed with a multi-species canopy model. III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat. *Oecologia* 82: 560 – 566
- Barnes PW, Shinkle JR, Flint SD, and Ryel RJ (2005) UV-B radiation: photomorphogenesis and plant-plant interactions. *Progress in Botany* 66: 313 – 340

UV Radiation in Global Climate Change: Measurements, Modeling and Effects on Ecosystems

- Barnes PW, Flint SD, Slusser JR, Gao W, and Ryel RJ (2008) Diurnal changes in epidermal transmittance of plants in naturally high UV environments. *Physiologia Plantarum* 133: 363 – 372
- Becwar MR, Moore III FD, and Burke MJ (1982) Effects of deletion and enhancement of ultraviolet B (280 – 315 nm) radiation on plants grown at 3000 m elevation. *Journal of the American Society for Horticultural Science* 107: 771 – 774
- Black K, Davis P, Lynch P, Jones M, McGettigan M, and Osborne B (2006) Long-term trends in solar irradiance in Ireland and their potential effects on gross primary productivity. *Agricultural and Forest Meteorology* 141: 118 – 132
- Bodhaine BA, McKenzie RL, Johnston PV, Hofmann DJ, Dutton EG, Schnell RC, Barnes JE, Ryan SC, and Kotkamp M (1996) New ultraviolet spectroradiometer measurements at Mauna Loa Observatory. *Geophysical Research Letters* 23: 2121 – 2124
- Brutsaert W (2006) Indications of increasing land surface evaporation during the second half of the 20th century. *Geophysical Research Letters* 33: L20403
- Caldwell MM (1971) Solar ultraviolet radiation and the growth and development of higher plants. In: Giese AC (ed) *Photophysiology*, Vol 6. Academic Press, New York, pp.131 – 177
- Caldwell MM, Robberecht R, and Billings WD (1980) A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic-alpine life zone. *Ecology* 61: 600 – 611
- Caldwell MM, Bornman JF, Ballaré CL, Flint SD, and Kulandaivelu G (2007) Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. *Photochemical and Photobiological Sciences* 6: 252 – 266
- Cohen S, Ianetz A, and Stanhill G (2002) Evaporative climate changes at Bet Dagan, Israel, 1964 – 1998. *Agricultural and Forest Meteorology* 111: 83 – 91
- Coleman RS and Day TA (2004) Response of cotton and sorghum to several levels of subambient solar UV-B radiation: a test of the saturation hypothesis. *Physiologia Plantarum* 122: 362 – 372
- Costa C, Armstrong R, Detres Y, Koch EW, Bertiller M, Beeskow A, Neves LS, Tourn GM, Bianciotto OA, Pinedo LB, Blessio AY, and San Roman N (2006) Effect of ultraviolet-B radiation on salt marsh vegetation: trends of the genus *Salicornia* along the Americas. *Photochemistry and Photobiology* 82: 878 – 886
- Cutforth HW and Judiesch D (2007) Long-term changes to incoming solar energy on the Canadian Prairie. *Agricultural and Forest Meteorology* 145: 167 – 175
- Cybulski WJ and Peterjohn WT (1999) Effects of ambient UV-B radiation on the above-ground biomass of seven temperate-zone plant species. *Plant Ecology* 145: 175 – 181
- Dai Q, Peng S, Chavez AQ, Miranda MLL, Vergara BS, and Olszyk DM (1997) Supplemental ultraviolet-B radiation does not reduce growth or grain yield in rice. *Agronomy Journal* 89: 793 – 799
- Day TA, Martin G, and Vogelmann TC (1993) Penetration of UV-B radiation in foliage: evidence that the epidermis behaves as a non-uniform filter. *Plant, Cell and Environment* 16(6): 735 – 741
- Demmig-Adams B (1990) Carotenoids and photoprotection: A role for the xanthophyll zeaxanthin. *Biochimica et Biophysica Acta* 1020: 1 – 24
- Fischer RA (1975) Yield potential in a dwarf spring wheat and the effect of shading. *Crop*

13 Solar UV-B Radiation and Global Dimming: Effects on Plant Growth and UV-Shielding

Science 15: 607 – 613

- Flint SD and Caldwell MM (1998) Solar UV-B and visible radiation in tropical forest gaps: measurements partitioning direct and diffuse radiation. *Global Change Biology* 4: 863 – 870
- Flint SD and Caldwell MM (2003) A biological spectral weighting function for ozone depletion research with higher plants. *Physiologia Plantarum* 117: 137 – 144
- Flint SD, Jordan PW, and Caldwell MM (1985) Plant protective response to enhanced UV-B radiation under field conditions: Leaf optical properties and photosynthesis. *Photochemistry and Photobiology* 41: 95 – 99
- Flint SD, Ryel RJ, and Caldwell MM (2003) Ecosystem UV-B experiments in terrestrial communities: a review of recent findings and methodologies. *Agricultural and Forest Meteorology* 120: 177 – 189
- Häder DP (1996) Effects of solar radiation on local and German wheat seedlings in a Chilean high mountain station. *Journal of Photochemistry and Photobiology B: Biology* 35: 181 – 187
- Ibdah M, Krins A, Seidlitz HK, Heller W, Strack D, and Vogt T (2002) Spectral dependence of flavonol and betacyanin accumulation in *Mesembryanthemum crystallinum* under enhanced ultraviolet radiation. *Plant, Cell and Environment* 25: 1145 – 1154
- Jauregui E and Luyando E (1999) Global radiation attenuation by air pollution and its effects on the thermal climate in Mexico City. *International Journal of Climatology* 19: 683 – 694
- Kostinski AB (2001) Extinction of radiation by a homogeneous but spatially correlated random medium. *Journal of the Optical Society of America* 18: 1929 – 1933
- Kolb CA and Pfündel EE (2005) Origins of non-linear and dissimilar relationships between epidermal UV absorbance and UV absorbance of extracted phenolics in leaves of grapevine and barley. *Plant, Cell and Environment* 25: 580 – 590
- Kotilainen T, Tegelberg R, Julkunen-Tiitto R, Lindfors A and Aphalo PJ (2008) Metabolite specific effects of solar UV-A and UV-B on alder and birch leaf phenolics. *Global Change Biology* 14: 1294 – 1304
- Krause GH, Galle A, Gademann R, and Winter K (2003) Capacity of protection against ultraviolet radiation in sun and shade leaves of tropical forest plants. *Functional Plant Biology* 30: 533 – 542
- Krizek DT (2004) Influence of PAR and UV-A in determining plant sensitivity and photomorphogenic responses to UV-B radiation. *Photochemistry and Photobiology* 79: 307 – 315
- Lambers H, Chapin III FS, and Pons TL (1998) *Plant Physiological Ecology*. Springer, New York, Berlin, Heidelberg. p.540
- Li HB, Robock A, and Wild M (2007) Evaluation of Intergovernmental Panel on Climate Change Fourth Assessment soil moisture simulations for the second half of the twentieth century. *Journal of Geophysical Research-Atmospheres* 112: D06106
- Liepert BG and Romanou A (2005) Global dimming and brightening and the water cycle. *Bulletin of the American Meteorological Society* 86: 622 – 623
- Lingakumar K, Amudha P, and Kulandaivelu G (1999) Exclusion of solar UV-B (280 nm – 315 nm) radiation on vegetative growth and photosynthetic activities in *Vigna unguiculata* L. *Plant Science* 148: 97 – 103

UV Radiation in Global Climate Change: Measurements, Modeling and Effects on Ecosystems

- Lohmann S, Schillings C, Mayer B, and Meyer R (2006) Long-term variability of solar direct and global radiation derived from ISCCP data and comparison with reanalysis data. *Solar Energy* 80: 1390 – 1401
- Ma J and Guicherit R (1997) Effects of stratospheric ozone depletion and tropospheric pollution on UV radiation in the troposphere. *Photochemistry and Photobiology* 66: 346 – 355
- Mark U, Saile-Mark M, and Tevini M (1996) Effects of solar UVB radiation on growth, flowering and yield of central and southern European maize cultivars (*Zea mays* L.). *Photochemistry and Photobiology* 64: 457 – 463
- Mazza CA, Boccacandro HE, Giordano CV, Battista D, Scopel AL, and Ballaré CL (2000) Functional significance and induction by solar radiation of ultraviolet-absorbing sunscreens in field-grown soybean crops. *Plant Physiology* 122: 117 – 125
- McKenzie RL, Seckmeyer G, Bais AF, Kerr JB, and Madronich SA (2001) Satellite retrievals of erythemal UV dose compared with ground-based measurements at northern and southern midlatitudes. *Journal of Geophysical Research D* 106: 24051 – 24062
- McKenzie R, Aucamp P, Bais A, Björn L, and Ilyas M (2007) Changes in biologically-active ultraviolet radiation reaching the Earth's surface. *Photochemical and Photobiological Sciences* 6: 218 – 231
- McKinlay AF, and Diffey BL (1987) A reference action spectrum for ultraviolet induced erythema in human skin. *CIE Journal* 6: 17 – 22
- Milchunas DG, King JY, Mosier AR, Moore JC, Morgan JA, Quirk MH, and Slusser JR (2004) UV radiation effects on plant growth and forage quality in a shortgrass steppe ecosystem. *Photochemistry and Photobiology* 79: 404 – 410
- Nazarenko L and Menon S (2005) Varying trends in surface energy fluxes and associated climate between 1960 and 2002 based on transient climate simulations. *Geophysical Research Letters* 32: L22704
- Norris JR and Wild M (2007) Trends in aerosol radiative effects over Europe inferred from observed cloud cover, solar “dimming” and solar “brightening”. *Journal of Geophysical Research-Atmospheres* 112: D08214
- Nullet D and Juvik JO (1997) Measured altitudinal profiles of UV-B irradiance in Hawaii. *Physical Geography* 18: 335 – 345
- Pal M, Sharma A, Abrol Y, and Sengupta U (1997) Exclusion of UV-B radiation from normal solar spectrum on the growth of mung bean and maize. *Agriculture, Ecosystems, and Environment* 61: 29 – 34
- Pinker RT, Zhang B, and Dutton EG (2005) Do satellites detect trends in surface solar radiation? *Science* 308: 850 – 854
- Quaite FE, Sutherland BM, and Sutherland JC (1992) Action spectrum for DNA damage in alfalfa lowers predicted impact of ozone depletion. *Nature* 358: 576 – 578
- Ramana MV and Ramanathan V (2006) Abrupt transition from natural to anthropogenic aerosol radiative forcing: Observations at the ABC-Maldives Climate Observatory. *Journal of Geophysical Research-Atmospheres* 111: D20207
- Raveh E, Cohen S, Raz T, Yakir D, Grava A, and Goldschmidt E (2003) Increased growth of young citrus trees under reduced radiation load in a semi-arid climate. *Journal of*

13 Solar UV-B Radiation and Global Dimming: Effects on Plant Growth and UV-Shielding

Experimental Botany 54: 365 – 373

- Raviv M and Antignus Y (2004) UV radiation effects on pathogens and insect pests of greenhouse-grown crops. *Photochemistry and Photobiology* 79: 219 – 226
- Rinnan R, Keinänen MM, Kasurinen A, Asikainen J, Kekki TK, Holopainen T, Ro-Poulsen H, Mikkelsen TN, and Michelsen A (2005) Ambient ultraviolet radiation in the Arctic reduces root biomass and alters microbial community composition but has no effects on microbial biomass. *Global Change Biology* 11: 564 – 574
- Rinnan R, Gehrke C, and Michelsen A (2006) Two mire species respond differently to enhanced ultraviolet-B radiation: effects on biomass allocation and root exudation. *New Phytologist* 169: 809 – 818
- Robock A and Li HB (2006) Solar dimming and CO₂ effects on soil moisture trends. *Geophysical Research Letters* 33: L20708
- Robson TM, Pancotto VA, Flint SD, Ballaré CL, Sala OE, Scopel AL, and Caldwell MM (2003) Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytologist* 160: 379 – 389
- Robson TM, Pancotto VA, Scopel AL, Flint SD, and Caldwell MM (2005) Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland. *Soil Biology and Biochemistry* 37: 2205 – 2215
- Roderick M (2006) The ever-flickering light. *Trends in Ecology and Evolution* 21: 3 – 5
- Roderick ML and Farquhar GC (2002) The cause of decreased pan evaporation over the past 50 years. *Science* 298: 1410 – 1411
- Roderick ML, Farquhar GD, Berry SL, and Noble IR (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* 129: 21 – 30
- Ryel RJ, Barnes PW, Beyschlag W, Caldwell MM, and Flint SD (1990) Plant competition for light analyzed with a multispecies canopy model. I. Model development and influence of enhanced UV-B conditions on photosynthesis in mixed wheat and wild oat canopies. *Oecologia* 82: 304 – 310
- Schiermeier Q (2005) Cleaner skies leave global warming forecasts uncertain. *Nature* 435: 135 – 135
- Searles PS, Caldwell MM, and Winter K (1995) The response of five tropical dicotyledon species to solar ultraviolet-B radiation. *American Journal of Botany* 82: 445 – 453
- Searles PS, Flint SD, and Caldwell MM (2001) A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127: 1 – 10
- Stanhill G and Cohen S (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. *Agricultural and Forest Meteorology* 107: 255 – 278
- Visser AJ, Tosserams M, Groen MW, Magendans GWH, and Rozema J (1997) The combined effects of CO₂ concentration and solar UV-B radiation on faba bean grown in open-top chambers. *Plant, Cell and Environment* 20: 189 – 199
- Werner C, Ryel RJ, Correia O, and Beyschlag W (2001) Effects of photoinhibition on whole-plant carbon gain assessed with a photoinhibition model. *Plant, Cell and Environment* 24: 27 – 40

UV Radiation in Global Climate Change: Measurements, Modeling and Effects on Ecosystems

- Wild M, Gilgen H, Roesch A, Ohmura A, Long CN, Dutton EG, Forgan B, Kallis A, Russak V, and Tsvetkov A (2005) From dimming to brightening: Decadal changes in solar radiation at Earth's surface. *Science* 308: 847 – 850
- Yang Y, Yao Y, Xu, G, and Li C (2005) Growth and physiological responses to drought and elevated ultraviolet-B in two contrasting populations of *Hippophae rhamnoides*. *Physiologia Plantarum* 124: 431 – 440
- Zaller JG, Caldwell MM, Flint SD, Scopel AL, Sala OE, and Ballaré CL (2002) Solar UV-B radiation affects below-ground parameters in a fen ecosystem in Tierra del Fuego, Argentina: implications of stratospheric ozone depletion. *Global Change Biology* 8: 867 – 871
- Zavala J, Scopel AL, and Ballaré CL (2001) Effects of ambient UV-B radiation on soybean crops: Impact on leaf herbivory by *Anticarsia gemmatalis*. *Plant Ecology* 156: 121 – 130