A survey of ultraviolet-B radiation in forests

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Summary

1 Ultraviolet-B radiation (UV-B, 280–320 nm) was surveyed in a mixed deciduous forest in Maryland, USA, using a Robertson–Berger meter. A smaller number of comparable measurements were made in closed-canopy forests in Chile, Panama, and Washington State, USA, and under two canopies recently disturbed by hurricanes, in Virginia, USA, and Mexico. Simultaneous measurements of photosynthetically active radiation (*PAR*, 400–700 nm) were also made.

2 UV-B near the forest floor was generally low compared to UV-B incident on the outer canopy, and had a positively skewed frequency distribution. Under closed canopies, geometric mean UV-B transmittance was only 1–2% of incident radiation; under disturbed canopies, 8–17%. In Maryland, geometric mean UV-B transmittance increased to 30% during the leafless season. Gaps received larger UV-B exposures over time than shaded understorey locations. Thus UV-B transmittance depends strongly on canopy structure. UV-B transmittance did not, however, have a detectable dependence on solar elevation. The vertical extinction of UV-B through a closed canopy was rapid: in Maryland, about 40–70% of incident UV-B was absorbed by the top 25% of the canopy.

3 The spatial and temporal variation in UV-B and *PAR* within the canopy were qualitatively similar. However, UV-B varied less dramatically than *PAR*, and the two wavebands also had different patterns of variation in canopy space. These differences were probably due to the greater diffuse component of incident UV-B, and led to wide fluctuations of UV-B:*PAR* ratios. The UV-B:*PAR* ratio was low in sunflecks and high in some partially shaded areas such as gap edges. In Panama and the two disturbed sites, UV-B transmittance was significantly greater than *PAR* transmittance; in the other sites no significant differences were found.

4 These results were combined with a published model of the atmospheric transmission of UV-B to estimate present and future UV-B exposures in the Maryland forest, assuming a decline in stratospheric ozone. The greatest increases in UV-B exposure should come in the summertime in the upper canopy, and in the spring in the lower canopy.

Keywords: canopy, photosynthetically active radiation, Robertson–Berger meter, UV-B, gap

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Introduction

The amount of ultraviolet-B radiation (UV-B, wavelengths 280–320 nm) reaching the earth's surface is widely expected to increase in the future, as a result

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of damage to the ozone layer by pollution (e.g. Kerr & McElroy 1993). Elevated levels of UV-B could have a considerable effect on plant life, because UV-B affects the basic chemistry of photosynthesis and is a mutagen (Caldwell 1979). Field experiments have shown that elevated UV-B may suppress photosynthesis, growth, and flowering (Tevini & Teramura 1989), alter plant morphology (Barnes *et al.* 1988),

and change the competitive balance of species (Gold & Caldwell 1983; Barnes *et al.* 1988).

The ecological consequences of elevated UV-B are nonetheless difficult to predict. Such predictions require knowledge of the response of organisms to various levels of UV-B and an ecologically realistic reckoning of the future UV-B environment. Experimental studies like those mentioned above can provide the first kind of information, while field observations of the present UV-B environment can provide the basis for the second. Many observations of UV-B from meteorological stations have recently been published (e.g. Scotto *et al.* 1988; Blumthaler & Ambach 1990; Correll *et al.* 1992; Kerr & McElroy 1993). However, meteorological observations do not necessarily reflect the radiation environment of living things realistically. In particular, plant canopies modify the radiation environment by absorbing, reflecting, and transmitting radiation, creating considerable variation in radiation flux across distance, time, and spectrum.

Attempts to measure UV-B within canopies have been fragmentary. Grant (1991) found that a large proportion – > 80% at some sensor orientations – of the incident ultraviolet radiation (305–350 nm) reached the floor of a senescing corn canopy. Lee & Downum (1991) reported that UV-B irradiances (300–320 nm) under a 'subtropical canopy' were indistinguishable from zero. DeLucia *et al.* (1991) found that about 10% of diffuse UV-B reached the oldest leaves of *Picea engelmannii* saplings in a clearcut. Yang *et al.* (1993) found that on average, 25% of biologically weighted UV-B (255–325 nm) reached the bottom of a partially defoliated hardwood canopy. Allen, Gausman, & Allen (1975) published a theoretical treatment of UV-B in forests of different structures.

This paper presents a collection of observations describing UV-B conditions within several forest canopies. Because little was known on the subject, the objective was to find and survey the sources of variation in forest UV-B, rather than to provide a complete statistical breakdown of that variation. In place of exhaustive systematic sampling, a series of simple surveys was performed. Photosynthetically active radiation (*PAR*, wavelengths 400–700nm) was usually measured simultaneously with UV-B, because the effects of UV-B on plants may depend strongly on *PAR* (Teramura 1986).

The results give preliminary answers to the following questions: How much UV-B do forest canopies transmit? Within the canopy, how does UV-B vary through horizontal and vertical space, over the course of the day, and through the seasons? And what are the relative amounts of UV-B and *PAR* in the forest? Finally, some of these results were combined with a published model of the atmospheric transmission of UV-B, to project how one forest UV-B regime might change if stratospheric ozone declines.

Materials and methods

STUDY AREAS

Most of the observations were made in a temperate deciduous forest on the western shore of the Chesapeake Bay in Maryland, USA, and described in Parker, O'Neill & Higman (1989). Some comparable measurements were made in the states of Washington and Virginia in the USA, in Panama, southern Chile, and the Yucatan Peninsula of Mexico. The sites are compared in Table 1. The Virginia and Yucatan sites were recently disturbed by hurricanes and have broken canopies with numerous overstorey gaps.

APPROACH

While the methods of the surveys varied, several general guidelines applied. All readings were taken while walking or climbing through the canopy with portable UV-B and *PAR* sensors. The sensors were always held level and UV-B and *PAR* readings were taken as concurrently as possible. Measurements were made only during very clear or slightly hazy periods, to remove the complication of clouds. Importantly, every observation made in the forest was standardized against the simultaneous irradiance, measured or estimated, incident on top of the canopy. The 'transmittance' of the canopy to UV-B or *PAR* (abbreviated T_{UV-B} and T_{PAR}) was defined as the irradiance recorded within the canopy divided by the simultaneous incident irradiance. The 'transmittance ratio' (T_{UV-B}/T_{PAR}) and the 'flux ratio' (UV-B irradiance/*PAR* irradiance) were also calculated for each observation.

In this paper, results will often be expressed as T_{UV-B} or the transmittance ratio. While these variables describe the way that the canopy filters radiation, it is important to note that they may not, by themselves, be biologically meaningful. Actual fluxes of UV-B and *PAR* within the canopy will depend not only on transmittance, but also on incident radiation, which may change with latitude, season, solar angle, and weather.

RADIATION SENSORS

A Robertson–Berger-type meter ('R-B meter', Model 2D, Solar Light, Inc., Philadelphia, PA, USA) was used to measure UV-B. This device was extremely portable and had instantaneous response, both advantageous for field surveys. Unfortunately, the R-B meter gives no information about the UV-B spectrum; it weights incoming UV-B by an action spectrum similar to the one for human sunburn, and displays a single weighted sum as output (Berger 1976). The weighting function helps make a broadband UV-B figure biologically meaningful (Caldwell *et al.* 1986). The meter's output is in nominal 'minimal erythemal doses' per hour (MED/h); these units cannot

Table 1 Comparison of the UV-B and *PAR* transmittance of six forest canopies. α = solar elevation angle. Symbols to the right of the T_{UV-B}, T_{PAR}, and transmittance ratio columns represent sites (all data lumped) that are significantly different ($P < 0.05$) according to the Ryans-Q multiple range test (SAS 1990). For T_{UV-B} and T_{PAR}, this analysis was performed on the log-transformed data; for the ratio, on normalized rank scores. Within sites, transects were often significantly different from one another (Ryans-Q test, results not shown). More results from Maryland can be found in the text. *PAR* was not recorded in Chile. Botanical authorities are given in Croat (1978), Hitchcock & Cronquist (1978), Radford *et al.* (1979), Hoffmann (1982) and Garcia & Olmsted (1987)

Site and description (name, forest type, canopy height, typical genera, remarks)	latitude longitude altitude	Date	α (°)	GMT (%)			Incident Flux			
				T_{UV-B}	T_{PAR}	MTR	UV-B	*PAR*	*N*	
North Bend, Washington, USA	47°27'N	19 Sep '92	44	1.3‡	1.4†	1.1‡	2.34	1245	144	
temperate coniferous; 50 m;	121°45' W									
Pseudotsuga	135 m									
Chiloé, Chile	43°30'S	15 Feb '92	31	1.9‡	NA	NA	1.15	NA	200	
temperate broadleaf evergreen; 30 m;	73°W		35	1.9	NA	NA	1.49	NA	200	
Aetoxicon, Eucryphia, Laurelia	100 m		51	1.1	NA	NA	3.76	NA	200	
			53	1.0	NA	NA	4.00	NA	200	
			61	1.2	NA	NA	5.11	NA	200	
Edgewater, Maryland USA	38°53'N	30 Sep '91	49	0.8§	1.1‡	0.9‡	2.69	1400	247	
temperate mixed deciduous; 40 m;	76°33'W	6 Aug '91	68	0.8	0.8	1.1	4.71	1859	250	
Liriodendron, Quercus, Carya	11 m	26 May '91	73	1.1	1.3	0.8	4.28	1827	228	
Mountain Lake, Virginia, USA	37°30'N	19 Aug '92	34	13.0*	7.8*	1.9†	1.00	724	110	
temperate mixed deciduous; 18 m;	80°37'W		43	12.0	8.3	1.8	1.83	1014	104	
Quercus, Carya, Acer; disturbed	1190 m		44	11.9	9.7	1.4	1.90	1037	110	
by Hurricane Hugo in Sept. 1989			52	11.0	7.2	1.8	2.71	1263	107	
			62	9.8	7.1	1.7	3.78	1519	108	
			65	10.3	7.7	1.6	4.02	1574	107	
Quintana Roo, Mexico	20°49'N	27 Apr '91	29	7.5*	4.8*	1.9†	1.08	928	200	
semi-evergreen dry subtropical; 12 m;	87°7'W	27 Apr '91	54	13.9	9.2	1.9	4.09	1660	195	
Manilkara, Brosimum, Gymnanthes;	4 m	1 May '91	55	16.1	12.2	1.4	4.17	1674	120	
dist'd by Hurricane Gilbert in Sept. 1988		1 May '91	82	16.7	12.9	1.4	6.88	2086	198	
Barro Colorado Island, Panama	9°9'N	17 Jan '92	60	2.1†	0.9‡	2.5*	6.87	1704	164	
tropical moist; 35 m;	79°51'W									
Alseis, Poulsenia, Tachigalia	30 m									

GMT = geometric mean transmittance. MTR = median transmittance ratio. UV-B = ultraviolet-B radiation (MED/h); PAR = photosynthetically active radiation (μmol m^{-2} s^{-1}). NA = not available.

be reliably converted into standard energy units, because the same MED reading could be produced by many different spectra. The R-B meter responds significantly to some wavelengths above 320 nm. An experiment using Schott cutoff filters and a range of natural light conditions showed that 8–14% of the response of the R-B meters used in this study was due to flux of wavelengths > 320 nm. Thus the results presented here are not strictly of UV-B, but also include some UV-A (320–400 nm).

The R-B meter's response is also reportedly dependent on temperature (Kennedy & Sharp 1992). In this work no temperature corrections were applied. Because the sensors were usually being moved rapidly through the changing environment of the subcanopy, the effective temperature of the sensor would be very complicated to determine. Also, the possible range of errors was small considering the purposes of this work and the UV-B literature (e.g. Lee & Downum 1991; Webb 1991).

PAR in the field was recorded with a Li-Cor quantum sensor attached to a Li-Cor photometer (models LI-190 SB and LI-189, Li-Cor, Lincoln, Nebraska, USA). The UV-B and *PAR* sensors were mounted as close as possible to one another (3 cm, centre to

centre). The quantum sensor is probably better corrected for cosine error (Li-Cor, Inc. 1981) than is the R-B meter (Berger 1976).

THE FIELD SURVEYS

A summary of the field surveys follows. More information is given in the text and figure captions when necessary.

To measure the UV-B transmittance of the entire canopy and UV-B conditions on the forest floor, walking transects were established at every site. The investigator paced along the transect, holding the sensors approximately 1m above the ground and making measurements every few steps. Paces were converted to metres. When possible, these transects were repeated at intervals over the day to investigate diurnal trends. To examine seasonal trends in the transmittance of a deciduous canopy, such transects were repeated 22 times over the course of 1991 at the Maryland site; all these observations were made within 1 hour of solar noon. To assess more precisely the effects of time of day and position in the understorey, 24 fixed points, 0.5 m above the forest floor at the

Maryland site, were studied over the course of a single day (May 22, 1992).

To evaluate the vertical extinction of radiation through the canopy, UV-B was repeatedly measured along a single permanent transect at the Maryland site – a diagonal (elevation angle 52°) guy wire support for a forest meteorological tower that rises up through the canopy. The sensors were mounted on a small wheeled trolley which was hauled up the guy wire with a calibrated rope. The data were recorded by a video camcorder riding on the trolley. This transect was performed 8 times over the course of one day (Sept. 9, 1992) and 19 times at solar noon over the course of a year (1991). As this transect is only a single line through canopy space, the spatial variation in canopy transmittance was checked on one occasion with replicate transects along three other guy wires for the same tower.

The special radiation environment in forest gaps was investigated in several ways at the Maryland site. One special walking transect was conducted straight through the middle of a canopy gap. On several occasions the instruments were left in the middle of canopy gaps, 0.5m above the forest floor, and sampled repeatedly there through the day. Another survey was made of radiation near the forest floor in a gridded area around a canopy gap, allowing the creation of a UV-B 'map.'

Finally, to investigate the effect of trees on the spatial distribution of radiation in a simple situation, a similar map was made of radiation near the ground around a single tree standing alone in a Maryland schoolyard.

ASSESSING INCIDENT RADIATION

For field surveys in Maryland in 1992, incident radiation was recorded with a duplicate R-B meter and Li-Cor quantum sensor, attached to a data logger (model CR21X, Campbell Scientific, Utah, USA) and mounted atop a meteorological tower rising above the canopy within 500 m of the field sites. Incident radiation was sampled once per second and recorded in one-minute averages. The tower-top UV-B and *PAR* meters were standardized to the field meters with correction equations derived from a set of measurements where all the meters were exposed to identical conditions.

In other cases, there were no duplicate meters and therefore a different procedure was used to estimate simultaneous incident radiation. For Maryland in 1991, only a few tower-top incident values were recorded per day. These observations were always within 1 hour of solar noon, and their average was used to estimate incident radiation for every forest observation on that day, which in 1991 were all also within 1 hour of solar noon. For all sites other than Maryland, $\geqslant 15$ UV-B and *PAR* measurements were taken in open areas around the times of the forest surveys. The function

$$y = a \times \sin^b(\alpha) \qquad (1)$$

was fitted through the points with a nonlinear regression (NLIN, SAS 1990), where y is the predicted incident radiation, α is the solar elevation angle; and a and b are parameters optimized by the regression. Diurnal curves can be generated from this equation, since solar angle is a function of time. This functional form yields realistically shaped diurnal incident radiation curves (for cloudless conditions) from only a few points.

Results

SPATIAL AND DIURNAL VARIATION IN UV-B AT THE FOREST FLOOR

Some excerpts from walking transects are a useful introduction to the statistical and spatial variation found in UV-B and *PAR* at the forest floor (Fig. 1). Figure 1(a) demonstrates the pattern found in the closed-canopy sites, Fig. 1(b) an extreme example of the gap effect, and Fig. 1(c) the pattern found in the disturbed ('broken') sites.

In general, little UV-B is transmitted through the canopy to the forest floor. The mean UV-B transmittance (T_{UV-B}) for the excerpts in Fig. 1(a,c) are 6.6% and 34%, respectively, although T_{UV-B} reaches as high as 78% in the gap shown in Fig. 1(b). However, the mean transmittance for UV-B or *PAR* can be deceptive, because in the forest understorey, frequent low values are punctuated by a few high values and frequency distributions are usually strongly positively skewed. Though the mean transmittance effectively describes the proportion of incident radiation filtering through the entire canopy, it overestimates the median and modal transmittance. Median T_{UV-B} for the excerpts in Fig. 1(a,c) are 3.5% and 17%. Log-transforming T_{UV-B} and T_{PAR} data results in frequency distributions considerably closer to normality. Therefore this paper will sometimes refer to the log-transformed data or the geometric mean (the antilog of the mean of the log-transformed data).

The spatial variation in UV-B on the forest floor imitates the familiar pattern of *PAR*, staying low but increasing greatly in the occasional sunfleck or gap. However, UV-B varies less drastically than *PAR*; the direct beam radiation found in sunflecks and gaps increases T_{UV-B} less than it does T_{PAR}. A close inspection of Fig. 1(c) suggests that the UV-B pattern differs from that of *PAR* in space as well as magnitude: the curves for T_{UV-B} are smoother and more gradual than those of T_{PAR}. These differences between the wavebands lead to wide fluctuations in the UV-B:*PAR* transmittance ratio. For example, in Figs 1a & 1b, the ratio is low (≈ 0.85) in sunflecks and the gap centre,
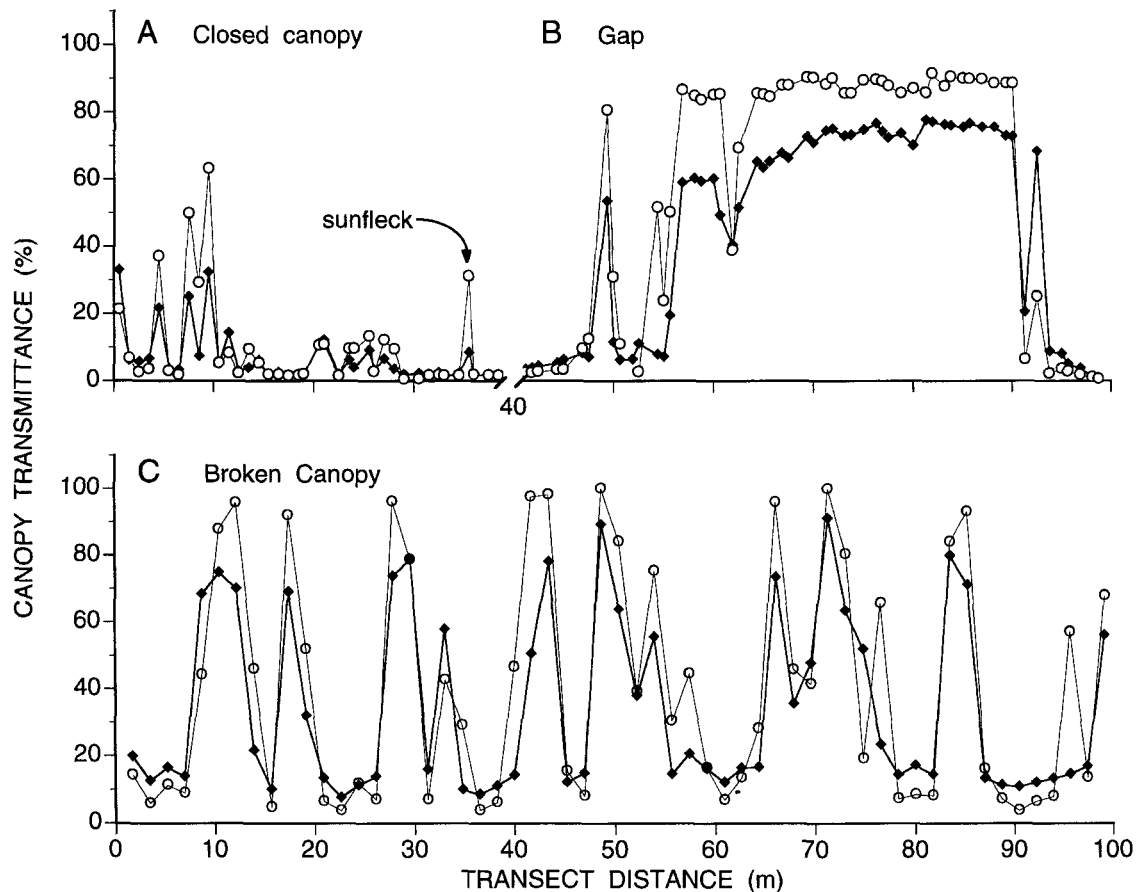
Fig. 1 Transmittance of canopies to UV-B (♦) and *PAR* (○), taken from three walking transects along the forest floor: (A) a closed broadleaf canopy in Maryland (21 May 1992; $\alpha = 72°$), with one sunfleck labelled as an example; (B) a very large (about 35 m in diameter) canopy gap near the same site (21 May 1992; $\alpha = 71°$); and, (C) a hurricane-damaged forest in Quintana Roo, Mexico (1 May 1991; $\alpha = 79°$).

higher in the dark understorey (≈ 1.15), and highest in the shady edges of the gap (≈ 1.65).

These effects are clearer in the two more systematic surveys shown in Fig. 2. The shadow of UV-B cast by a lone tree in a schoolyard clearly follows from the direction of the sun's beam and the shape of the tree's crown. The *PAR* shadow (not shown) is smaller in area, darker (including $T_{PAR}s < 20\%$), and has a steeper gradient from sun to full shade. This leads to the high transmittance ratios shown in the bottom left panel. When a more realistic, but considerably more irregular, canopy situation is examined – by studying UV-B around a very small gap – the considerable complexity of the forest floor radiation environment becomes obvious. As expected, a pool of high T_{UV-B} results from the hole in the canopy, and a similar pool with a higher peak transmittance (not shown) occurs for T_{PAR}. Within the hole in the canopy, the transmittance ratio is high in an area outside the direct beam of the sun. But outside the hole, the ratio is extremely irregular, probably due to details of canopy structure that were too fine to measure. It is important to remember that the high ratios outside the hole involve very low fluxes.

Figure 3 illustrates the differences between under-

storey and gap fluxes over the course of a single clear day. UV-B flux in all the environments studied – incident, gap centre, and understorey – varies as expected with solar elevation. The gap centre UV-B flux is always many times higher than that of almost all of the understorey points. Although the brightest sunfleck in the understorey may occasionally have a flux as high as that in the gap centre, these events are short-lived: the brightest understorey location shifted many times over the course of the day. The integrated daily UV-B flux for the 24 understorey points averaged 0.8 MED, or only 2.7% of the integrated daily incident flux; about 75% of this sum came in the middle 6 hours of the day, though the duration of daylight was 14 hours.

In comparison the gap centre receives considerably more exposure: there the daily integrated flux was 5.1 MED, or 17% of the incident integrated flux. Another Maryland gap centre (diameter ≈ 15 m, not shown), studied a few weeks later, had a daily integrated flux that was $\approx 20\%$ of incident. During some times of the year, the direct beam of the sun may never strike the centre of a gap during the entire day. One situation like this was studied in Maryland in September 1992 (gap diameter ≈ 13 m, not shown), before leaf fall.
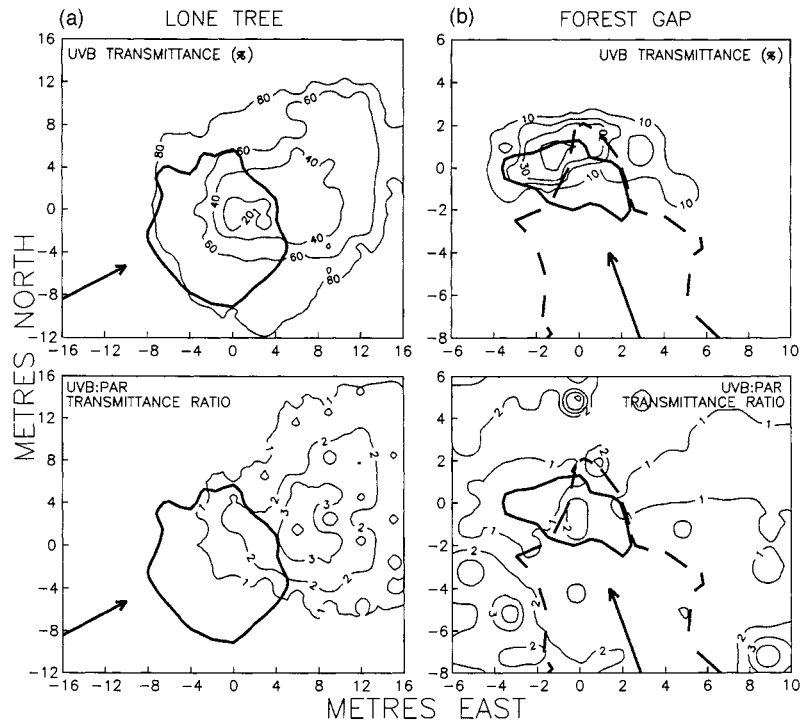
Fig. 2 Contour maps of T_{UV-B} and the UV-B:PAR transmittance ratio, measured at 1 m above ground in two situations. Arrows denote the direction of the sun's beam during the measurements. (a) The shade cast by a solitary tree (*Quercus alba*) in a Maryland schoolyard. The bold outline marks the limit of tree's crown (11 September 1992; $n = 152$, $\alpha \approx 43°$). (b) Radiation penetrating into a very small canopy gap at the Maryland site. This gap was created when a treefall opened up a large gap (projected area $\approx 130 \, \text{m}^2$, bold dashed line) in the overstorey. An irregular understorey then grew in, resulting in a gap centre that was small enough to map. The solid bold line marks the limit of this gap within a gap (11 June 1992; $n = 156$, $\alpha \approx 73°$).

There, the daily integrated flux at the gap centre was only 4% of incident.

The diurnal course of the UV-B:PAR flux ratio seems more complicated (Fig. 3b). The flux ratio is higher in the gap centre than it is for the incident radiation, except for those periods when the gap centre is illuminated by the direct beam of the sun, when the ratio drops sharply. In the understorey, where in general fluxes are much lower, the ratio varies greatly in space and time.

SEASONAL VARIATION IN THE TRANSMITTANCE OF A DECIDUOUS CANOPY

Figure 4(a) shows a very clear example of the effect of canopy structure on the forest floor UV-B environment: the seasonal variation of T_{UV-B} in response to deciduous-forest leaf area phenology. Arithmetic mean T_{UV-B} declined quickly with the spring leaf emergence, stayed < 3% through the summer, and rose quickly again during autumn leaf fall. Note that even in the leafless season, T_{UV-B} remains much less than 100% (about 30%) owing to the presence of trunks and branches. T_{UV-B} was often lower but not significantly different from T_{PAR} over the year ($P > 0.05$; paired t-test on means of log-transformed data). Moreover, during the fully-leaved season (days 150–275), the log mean T_{UV-B} and T_{PAR} at solar noon were unrelated to solar elevation (Pearson product-moment correlation, $P > 0.05$). Figure 4b shows how the seasonal pattern in canopy transmittance might interact with a modelled seasonal trend in incident radiation, leading to high springtime UV-B fluxes on the forest floor.

TRANSMITTANCE OF SIX FULLY LEAVED CANOPIES

Table 1 compares the UV-B and PAR transmittance of six different forest canopies during their growing seasons, as measured in walking transects on the forest floor. With geometric mean T_{UV-B} of 8–17%, the disturbed canopies admitted significantly more UV-B than the undisturbed sites, with geometric means 0.8–2.1%. Each of the disturbed canopies also transmitted significantly more UV-B than PAR ($P < 0.05$, ANOVA on log-transformed data), while the Washington and Maryland canopies did not. The single transect from the Panamanian site also shows an unusually high transmittance of UV-B compared to PAR.

Within sites, transects were often significantly different from one another. However, in the sites where it could be tested, log mean T_{UV-B} did not vary systematically with solar elevation ($P > 0.05$, Pearson product-moment correlation). The one exception was Virginia ($P < 0.05$), where transmittance was inversely correlated with solar elevation.
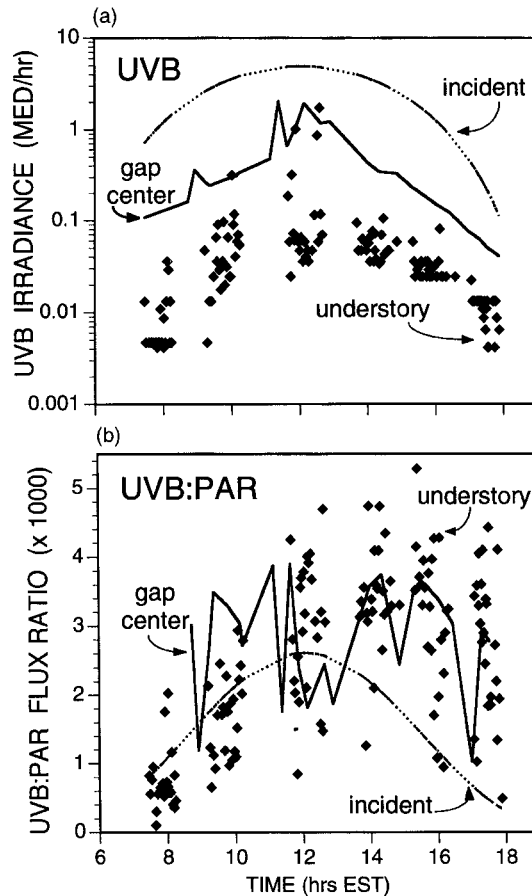
Fig. 3 UV-B flux, and the UV-B:*PAR* flux ratio, over the course of a single clear day in three canopy environments at the Maryland site. The dashed line is the incident radiation hitting the top of the canopy; the diamonds are 24 fixed points 0.5 m above the forest floor on the same day (22 May 1992). The solid line connects 24 observations made at a single fixed point in the middle of a nearby forest gap (also 0.5 m above the ground) on another clear day (1 June 1992). The gap data has been standardized to the diurnal incident curve of 22 May to make the gap and understorey irradiances comparable. Each forest floor point was sampled six times over the day – in 'groups' centered on 8, 10, 12, 14, 16, and 18 hours EST, and each sample is actually the mean of five observations taken over approximately 1 minute – thus the few observations which are less than the detection limit of the R-B meter, 0.01 MED/h. Both location and 'group' were significant sources of variation in understorey UV-B flux (ANOVA on log-transformed data, $P < 0.001$ for both effects).

VERTICAL VARIATION OF UV-B

The finding that only a few per cent of incident UV-B reaches the forest floor suggests that UV-B is very effectively absorbed or reflected by the upper canopy. The remaining results explore the vertical variation of UV-B in the Maryland deciduous canopy.

Figure 5 shows the vertical extinction of UV-B along several different transects rising through the same canopy, and the rough relationship of vertical extinction to canopy structure. All the transects show an immediate decline in UV-B – a drop of 40–70% in the top 25% of the canopy. The general decline in UV-B is often punctuated by small zones of very low
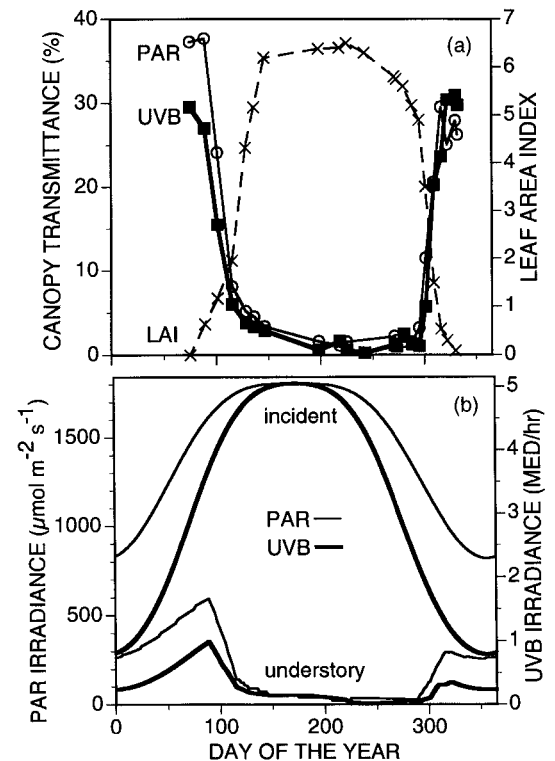

Fig. 4 (a) Seasonal variation in arithmetic mean solar noon UV-B and *PAR* transmittance at 1 m above the forest floor in the Maryland deciduous canopy in 1991, and the seasonality in leaf area index (*LAI*). *N* for each point ranges from 110 to 278. Leaf area phenology was generated from measurements of litterfall and canopy cover (G. G. Parker, unpublished data). (b) Seasonal variation in modelled, clear-day, solar-noon irradiance, both incident on the canopy roof and the arithmetic mean at the forest floor. Modelled incident UV-B and *PAR* came from a modification of eqn 1. Forest floor irradiances were predicted by multiplying the measured and interpolated transmittances by the modelled incident irradiances.

or high irradiance, created by the peculiarities of local shading. There is spatial variation in vertical extinction, but in absolute terms this declines with depth in the canopy. *PAR*, though noisier than UV-B (see, e.g. Fig. 1), showed similar patterns. As on the forest floor (Figs 2 and 3), the vertical dimension of canopy space shows considerable variation in the ratio of UV-B:*PAR*.

Figure 6 summarizes results of repeating one such transect eight times over the course of a single day. As expected, UV-B irradiances were generally highest in the middle of the day and at the highest elevations, and declined quickly towards the forest floor. However, the interactions of irregular canopy structure and changing solar angle created some deviations from these general trends – for example, high UV-B irradiance around a height of 25 m at 10 a.m. EST. Thus locations in the lower canopy can receive high UV-B fluxes, but only for a limited time. When the results were expressed as transmittances instead of fluxes, they were remarkably consistent over the course of the day.
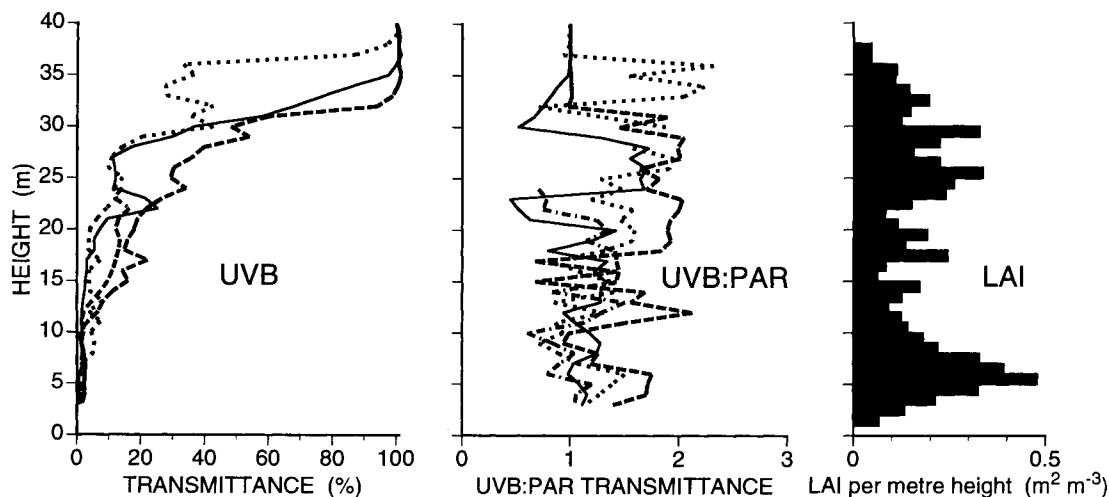
Fig. 5 Spatial variability in the vertical gradient of UV-B transmittance and the UV-B:*PAR* transmittance ratio in a Maryland broadleaf canopy, compared to the vertical profile of *LAI* (Parker *et al.* 1989). Each line represents a different diagonal transect rising through the canopy, all made within one hour of solar noon on 9 September 1992 ($\alpha \approx 56°$). Two observations of transmittance were made per metre of canopy height and then averaged. One transect is incomplete because of equipment failure. The vertical gradients in radiation and *LAI* are not precisely comparable because the former are from unique transects and the latter is a stand-wide average. The solid line represents the single permanent transect used to create Figs 6 and 7.
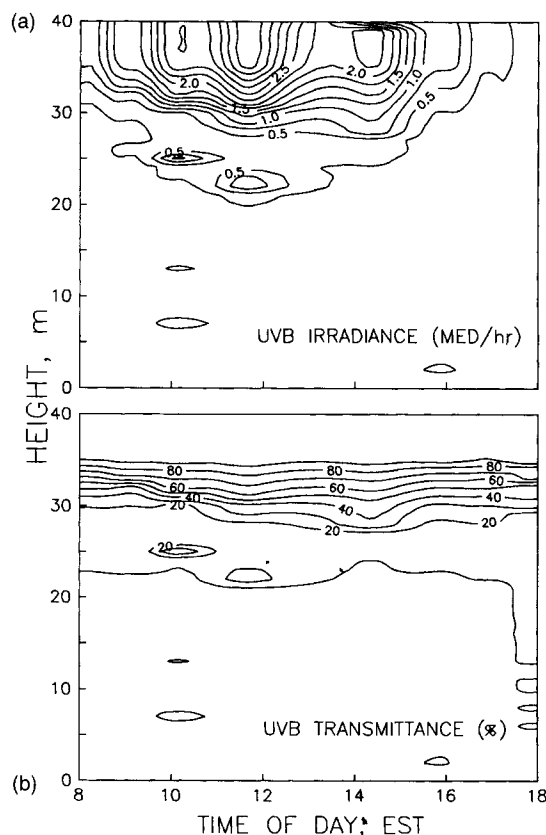

Fig. 6 UV-B irradiance (a) and transmittance (b) at different heights in a Maryland canopy, over the course of a single clear day (9 September 1992). Generated from 8 runs of $N = 78$ to 85 on a single permanent transect rising diagonally through the canopy.

Canopy reflectance was also measured several times during the same day (not shown) along the same transect, but with the sensors pointed downwards. UV-B reflectance was extremely low. Upwelling UV-B irradiances were < 2% of the downwelling radi-

ation at elevations above the canopy, and, moving down through the canopy, quickly declined to below detectable levels. Since transmittance to the forest floor is usually 1–2%, the summertime Maryland canopy is apparently absorbing > 96% of the incident UV-B.

Repeating this transect 19 times over the course of the year, at solar noon, provided a description of the Maryland site's seasonal UV-B regime (Fig. 7). The upper panel shows that the vertical gradient in T_{UV-B} depends very strongly on the presence of the deciduous leaf canopy over the course of the year. For example, the canopy height with $\geq 40\%$ UV-B transmittance changes from $\approx 4m$ in the dormant season to $\approx 30m$ in the growing season. The few deviations from this strong seasonal pattern probably reflect the use of only a single transect through canopy space, not a stand-wide average.

If one assumes that, as in Fig. 6, canopy transmittance is relatively consistent over the course of a day, then the product of modelled incident radiation and transmittances can predict UV-B exposure at any canopy height or day of the year. Several such calculations, for clear days (middle and bottom panels of Fig. 7), summarize this paper's results in units often used by researchers investigating the effects of elevated UV-B on plants. The estimated incident radiation comes from Green's model (Green *et al.* 1980; Shippnick & Green 1982) and is weighted by Caldwell's (1971) generalized plant action spectrum. One scenario models the Maryland site under current ozone conditions, and another under a 20% ozone reduction.

In both scenarios, the seasonal trend in canopy transmittance interacts with the seasonal changes in incident radiation to create relatively high lower-canopy UV-B exposures in the spring. The ratio of UV-
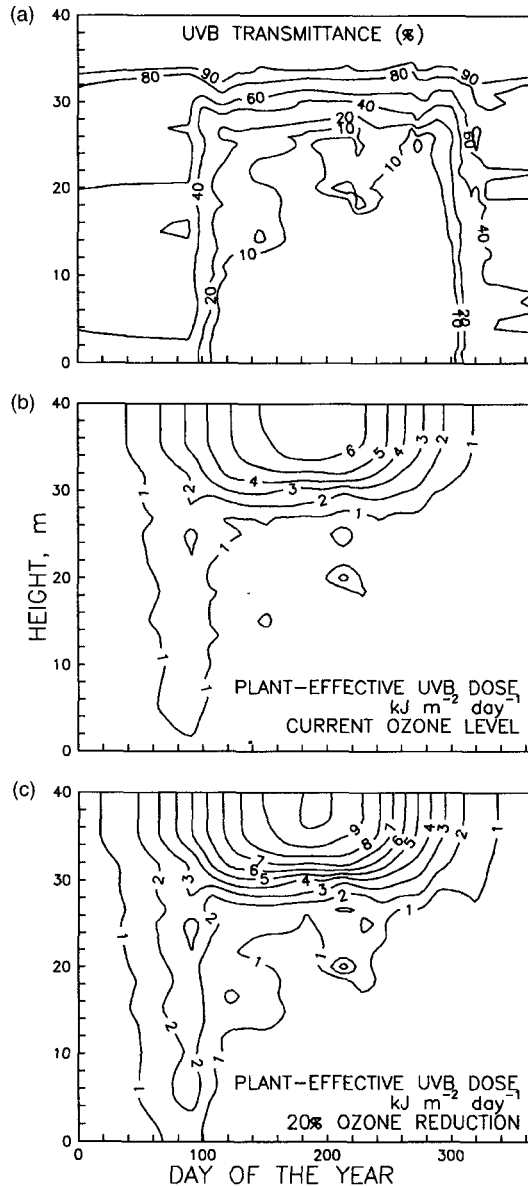
Fig. 7 (a) Seasonal variation in solar noon UV-B transmittance at different heights in the Maryland canopy. Generated from 19 runs of $N = 360$ to 420 spread over the course of a year on a single permanent transect rising diagonally through the canopy. (b,c) Seasonal variation in modelled daily biologically effective UV-B exposures, at different heights in the Maryland canopy under two ozone regimes. Exposures were generated by multiplying the measured transmittances (see a) by the spectral incident irradiances from the model of Green *et al.* (1980) and Shippnick & Green (1982). The modelled spectral forest irradiances, calculated for each hour of the year and metre of canopy height, were weighted by Caldwell's (1971) generalized plant action spectrum, summed across the UV-B band, and integrated over each day. The ozone parameter for the current ozone regime (annual mean of 0.329 atm-cm) was varied seasonally, according to a sine model fit through Dobson ozone data from 1976–1990 at 39°N, 76°W (Atmospheric Environment Service 1993). For the ozone reduction scenario (c) the ozone parameter was set 20% lower.

B exposure to *PAR* exposure (not shown) is by far greatest in the summer, because of the greater seasonal variation in biologically effective incident UV-B. Comparing present and future, the top of the canopy experiences the biggest absolute increases in UV-B dose, though the length and peak intensity of the spring incursion of UV-B into the subcanopy also increases.

Discussion

FACTORS AFFECTING FOREST UV-B CONDITIONS

Little UV-B is transmitted to the lower levels of any forest canopy – the geometric mean T_{UV-B} to near the forest floor was only 1–2% in four widely varying forests, and even the recently disturbed canopies had geometric mean $T_{UV-B} < 20\%$ (Table 1). In broad terms, these results agree with 2.5–17% arithmetic mean transmittances predicted by the model of Allen *et al.* (1975) for a more limited range of canopy structures. When expressed as arithmetic means, the results from the disturbed sites agree well with those of Yang *et al.* (1993), who found biologically weighted $T_{UV-B} \approx 25\%$ and $T_{PAR} \approx 30\%$ in a canopy damaged by the moth *Lymantria dispar*. The vertical extinction of UV-B is rapid, with most of the incident radiation being lost in the top of the canopy (Figs 5 and 6). Furthermore, it is likely that almost all of the UV-B not transmitted is absorbed by the canopy. Our few measurements of the gross UV-B reflectance of the canopy were very low. Though not directly comparable, most laboratory measurements of the UV-B reflectance of leaves are typically low, usually between 3–9% (Rodriguez & Gausman 1977; Gausman *et al.* 1975).

The lower variation of UV-B compared to *PAR*, and its slightly different pattern of variation in space, are very likely due to the large diffuse component of incident UV-B (e.g. Webb 1991) compared to *PAR*. These differences between the wavebands, interacting with complex canopy structure and constantly changing solar angles, lead to considerable spatial and temporal variation in UV-B:*PAR* ratios (Figs 2, 3 and 5). Although some of the variation in the UV-B:*PAR* ratios shown in these figures is probably instability due to equipment limitations (e.g. in the low fluxes of the subcanopy, the R-B meter was operating near its detection limit) the effect is consistent enough to suggest an extremely complex radiation environment within the canopy compared to the incident radiation recorded in meteorological work. Yang *et al.* (1993) also found considerable variation in subcanopy UV-B:*PAR* ratios.

In general, canopy locations exposed to diffuse radiation only, such as gaps during the morning or evening, will be relatively rich in UV-B. Exposure to direct beam radiation, such as in a sunfleck or in a gap

during the middle of the day, means a comparative richness in *PAR*. Expanded to a larger scale, these effects probably explain the high transmittance ratios in the disturbed sites compared to two closed canopy forests (Table 1). Moreover, the small range of T_{UV-B} values for the undisturbed sites is interesting in light of the sites' rather disparate character and species composition. A relatively small amount of leaf area seems to intercept a great deal of the incoming UV-B (Figs 5 and 6). Thus the simple structural feature of canopy openness to skylight is probably the greatest single influence on transmitted UV-B.

The few data from the Panamanian forest show the highest UV-B transmittance for a closed-canopy situation, with a median transmittance ratio of 2.5 (Table 1). Though it is tempting to suspect instrument error in this case, the most likely instrument errors (e.g. temperature dependence of the R-B sensor) would tend to decrease or leave unchanged the UV-B transmittance. If the data are reliable, then there may be some real differences in the UV-B-optical properties of temperate and tropical forests, conceivably due to high tropical incident UV-B fluxes. This warrants further work.

RELEVANCE OF THESE MEASUREMENTS

These results need to be put into several kinds of perspective. First, it is important to remember the strong geographical and seasonal variation in biologically effective and low-wavelength incident UV-B (Caldwell, Robberecht & Billings 1980; Webb 1991). For example, though UV-B optical properties (the UV-B transmittance and the UV-B:*PAR* transmittance ratio) do not differ between the Mexico and Virginia sites (Table 1), the UV-B flux and UV-B:*PAR* flux ratio probably do. The range of geographic variation may sometimes be greater than projected changes in UV-B exposure due to ozone loss. For example, we predict an approximate 47% increase in midsummer incident UV-B exposure in Maryland under a 20% ozone reduction. However, Caldwell *et al.* (1980) calculate that under present conditions, the UV-B exposure in Panama is 70% more than in Maryland.

The R-B meter has some shortcomings as a sensor of UV-B. Some of the incident fluxes in Fig. 4b and Table 1 seem high, even given a positive temperature dependence, since Berger (1976) expects a maximum reading of 5 MED/h under an overhead sun. However, there are few published reports of R-B meter flux (as opposed to long-term sums, e.g. Scotto *et al.* 1988) with which to compare these results. Given this uncertainty, the transmittances we have reported are probably more reliable than the fluxes.

More importantly, though it is likely that there were differences in the UV-B spectrum within the canopy space, these were not detectable in this study, because the R-B meter reports only a single sum after

weighting by a particular action spectrum. Since action spectra for different biological responses to UV-B vary in shape (Rundel 1983; Caldwell *et al.* 1986), the exact relevance of any broad-band meter for any particular biological response is unclear. There is a need for spectral ultraviolet measurements within canopies. These would require a sensor that was portable, that was sensitive enough to detect very low levels of UV-B, that reported results in energy units, and that responded quickly enough across wavelengths to capture common transient phenomena of forest radiation, like sunflecks.

THE FOREST UV-B ENVIRONMENT OF THE FUTURE

Ultimately, the ecological implications of this work depend on the mechanisms of photobiology. For example, if stratospheric ozone declines, with a consequent increase in incident UV-B, how would we expect forests to change?

If either high fluxes or accumulated doses of UV-B induce biological responses, then the upper surface of the canopy is the most likely site for ecological change. Since the structure and composition of the outer canopy have a strong influence on the forest below, effects in this zone may have strong implications for forest composition and succession. If, on the other hand, high ratios of UV-B:*PAR* can induce biological responses even in the absence of extreme fluxes (as has been suggested by Wilson & Greenberg 1993), then several more canopy locations might be affected: gap edges and other 'broken' sites that admit much skylight but relatively little direct radiation. The spatial and temporal complexity of the spectral radiation environment in the forest raises several relevant questions: What is the relative influence of UV-B dosage and peak irradiance ('dose-rate reciprocity,' de Gruijl *et al.* 1986)? How do the effects of UV-B depend on concurrent levels of *PAR* (Teramura 1986)?

Combining our results with some data from the literature suggests at least one possible scenario for ecological change in forests. Sullivan & Teramura (1992) have shown in field experiments that *Pinus taeda*, a frequent invader of old fields and important lumber species in the south-eastern United States, suffered significant biomass reductions at doses like those in the upper canopy of Fig. 7 (ozone reduction scenario). Meanwhile, similar experiments show that the hardwood *Liquidambar styraciflua*, a weedy competitor in young *P. taeda* stands, suffers either no changes in biomass or some increase in leaf area under elevated UV-B (J. Sullivan, personal communication). Together, these observations suggest that, under elevated UV-B, *L. styraciflua* could gain some competitive advantage relative to *P. taeda*, conceivably leading to an entirely different forest association. Barnes *et al.* (1988) showed that in a mixture of two cereal species,

elevated UV-B could alter canopy structure and thereby the relative competitive status of species. Whether or not increased UV-B will lead to environmental catastrophe, it seems quite possible that it could change entire communities.

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