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ULTRAVIOLET-B RADIATION AND THE ROCKY MOUNTAIN ENVIRONMENT: MEASUREMENT OF INCIDENT LIGHT AND PENETRATION INTO FOLIAGE

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I. Introduction

The unprecedented rate of degradation of stratospheric ozone (3 to 5% per decade, 14) associated with anthropogenic release of chlorofluorocarbons and oxides of nitrogen is predicted to increase the flux of UV-B radiation (280-320 nm) impinging on terrestrial and aquatic ecosystems (3). It is established that enhanced levels of UV-B radiation causes reductions in growth and yield of a broad spectrum of agronomic species (19) and there is heightened concern about the potential effects of increased UV-B radiation on the productivity and function of natural ecosystems. Our understanding of the potential responses of native ecosystems, including forests, to enhanced UV-B is limited. Forest trees contribute up to 80% of net global primary productivity and are of enormous economic importance yet UV-sensitivity of only 15 temperate tree species has been examined (19). A goal of our research is to understand ecophysiological effects of enhanced UV-B radiation on high elevation forest species of the Rocky Mountains.

Subalpine conifers are sensitive to atmospheric pollutants, and increasing evidence indicates that acid precipitation and other pollutants are changing the structure and productivity of high elevation forests. Recent studies suggest that certain conifer species are also susceptible to damage induced by increased UV-B radiation (18); however, the mechanism of damage and basis for

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interspecific differences in susceptibility are not known. The reliance on a wide span of needle ages for seasonal carbon gain forms the basis of our prediction that subalpine conifers may be particularly susceptible to UV damage. Depending on the species, individual trees may retain foliage for 5 to 20 years. In the fairly open canopies typical of subalpine forests these older needles may therefore accumulated large lifetime doses of UV-B radiation. Additionally, the short duration of the growing season at high elevations combined with wind abrasion can limit cuticle development and erode needle surfaces (11). The cuticle and epicuticular waxes may contain important UV-absorbing compounds and provide a first line of defence against enhanced UV-B light (22,4).

A number of features of high elevation habitats increase UV-B doses independently of changes in stratospheric ozone levels. Low absolute humidity, air pressure, and aerosol levels increase atmospheric transmission of UV-B and visible light, and reflected light from snow may further increase light incident on foliage (5,6). High elevation habitats in the Rocky Mountains are characterized by frequent cloud cover and it is unknown how this may influence the relative doses of UV and visible light. Our understanding of the interactions of UV-B light and clouds or plant canopies has been limited, in part, by the unavailability of a commercial UV-radiometer that has an ecologically relevant spectral response. The objectives of this preliminary study were threefold: 1) We tested a commercially available UV-B radiometer for field measurement of biologically effective UV-B radiation; 2) We measured diurnal patterns and crown penetration of UV-B light in a subalpine habitat; and 3) Using fiber optic microprobes, we investigated the depth of penetration of UV-B and visible light into foliage of several conifer species and a number of other species of different physiognomy.

II. Measurement of UV, Solar, and Photosynthetically Active Radiation

Measurement of ecologically relevant UV-B doses under field conditions has been limited by lack of appropriate light sensors. Although a number of UV-radiometers (broad-band sensors) are commercially available, their spectral responses do not conform to the generalized plant-damage action spectrum (8). Field measurement of UV-B radiation is most often made with a scanning spectroradiometer. There are, however, a number of logistical difficulties associated with using this type of instrument under rigorous field conditions-- temperature fluctuation of the photomultiplier tube and thermal expansion/contraction of mechanical linkages in the monochrometer are two critical examples. Moreover, the long scan time of spectroradiometers using mechanical monochrometers precludes making instantaneous measurements necessary to characterize rapid light fluctuations during cloudy conditions or within plant canopies. We tested an affordable commercially available UV-B radiometer that circumvents a number of these problems.

Biologically effective UV-B irradiance was measured with a UV radiometer (SED240, International Light, Inc. Newburyport, MA). The detector was a solar-blind vacuum photodiode with a spectral range of 190 to 320 nm (equipped with a ACTS270 filter and W-type diffuser from the manufacturer). An input voltage of 4.5 V was provided to the sensor, and output from the radiometer under ambient UV conditions ranged from 0 to 25 nA. The input voltage and output signal were provided and measured with a LI-1000 datalogger (LiCOR, Inc., Lincoln, NE). The spectral response of the radiometer compared favorably with the generalized plant-damage action spectrum of Caldwell (8) (Figure 1).

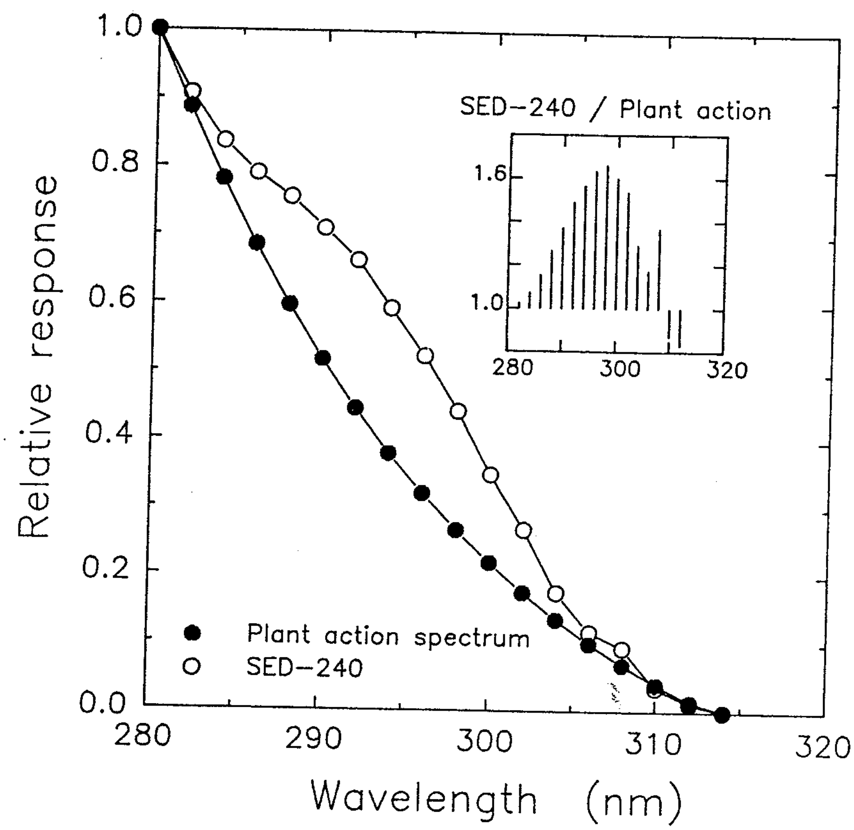


Figure 1. Relative spectral response of the SED240 UV radiometer equipped with an ACT270 filter and W-type diffuser (open circles) and the generalized plant-damage action spectrum (8) (closed circles) normalized to 280 nm. The absolute ratio of the spectral response of the radiometer/action spectrum is illustrated in the inset.

The maximum response of the radiometer was at 240 nm (data not shown). Light below *ca.* 290 to 300 nm, however, does not typically penetrate the atmosphere. Thus, under ambient light the maximum sensor response occurred at the minimum wavelengths penetrating the atmosphere. Radiometer output declined to near zero at 314 nm, which is the cutoff for UV damage defined by the generalized plant action spectrum. The radiometer significantly over-weighted light from 290 to 302 nm. Assuming that major spectral shifts in light relative to the calibration source do not occur, over-weighting by the radiometer at mid-UV-B wavelengths should not cause significant error in estimation of integrated UV-B doses.

The UV-radiometer was calibrated in the field under full sun using a portable UV/VIS spectroradiometer (OL 752, Optronics Lab, Inc., Orlando, FL). The spectroradiometer employs a double monochrometer with dual holographic gratings and was configured with 0.25 mm slits which produced a nominal half band width of 1.5 nm. Prior to measurements, the spectroradiometer was calibrated with a NIST-traceable 200W tungsten halogen lamp, and the wavelength alignment was checked against the mercury-emission lines from a fluorescent bulb. The UV-radiometer was calibrated at solar noon (1145 - 1215) on 22 June, in an alpine meadow at 3000 m above sea level. It was mounted next to the input optics of the spectroradiometer and measurements were made while holding different layers of screen over the sensors. Output from the radiometer was linear over the range of ambient UV-B levels (Figure 2). Recent studies use the plant action spectrum normalized to 300 nm. We also generated a calibration curve normalized to 280 nm to facilitate comparison of our measurements with the older literature. Calibration of the radiometer under very high UV doses generated by artificial light sources (fluorescent tubes or a xenon lamp) can produce significant

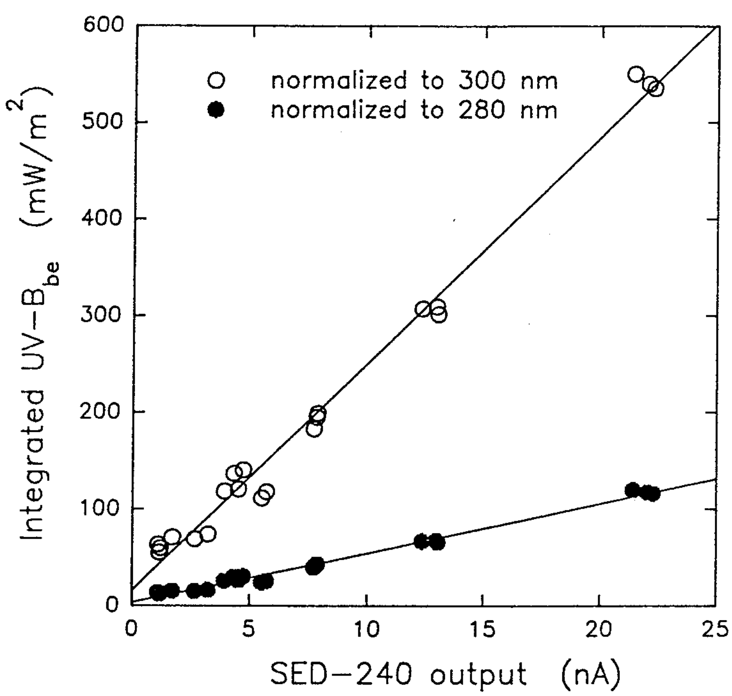


Figure 2. Typical calibration curves for the SED240 UV-B radiometer. Biologically effect UV-B (UV-B_{be}) and sensor output were measured in the field with a portable UV/VIS spectroradiometer. The regression equations for UV-B_{be} normalized to 280 and 300 nm, respectively are: UV-B_{be280} = 5.1769 (SED240 output) + 2.5616, and UV-B_{be300} = 23.797 (SED240 output) + 11.78219.

nonlinearity in the sensor output (data not shown). This can be alleviated by providing higher input voltages (up to -13 V).

The cosine response of the SED240 radiometer was examined by orienting the sensor at different angles from the sun. Appreciable deviation from the "true" cosine response was observed at angles > 10° from the sun (Figure 3). Addition of a teflon diffuser (T-type, International Light) greatly improved the cosine response but attenuated sensor output by a factor of 8.29 (±0.19 SD), thus making measurements in plant canopies difficult.

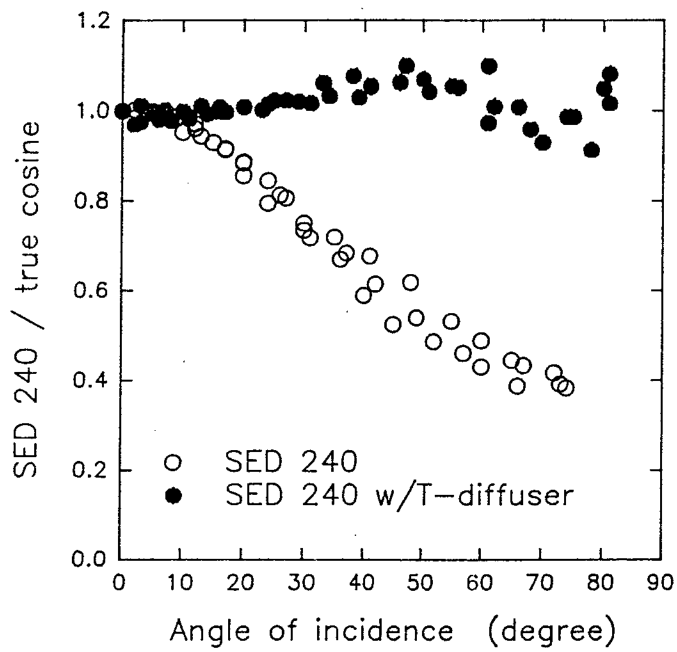


Figure 3. Cosine response of the SED240 UV-B radiometer as a ratio of the true cosine response. Measurements were made in the field with (closed circles) or without (open circles) the addition of a teflon diffuser. High levels of sky diffuse light caused significant errors at large angles therefore data were not collected at angles > 80° from the sun.

III. The UV and Visible Light Environment in Subalpine Habitats.

Measurements of diurnal patterns and canopy penetration of UV-B_{be280}, photosynthetic photon flux density (PPFD), and solar radiation were made by mounting the SED240, a quantum sensor (Li 190SB, LiCOR), and pyranometer (Li 200SB, LiCOR) on the end of a wand fitted with a level. All sensor outputs were either logged manually or automatically with the datalogger.

The diurnal pattern of PPFD, solar radiation, and biologically effective UV-B (UV-$B_{be\ 280}$) were measured near the summer solstice in Libby Flats, an alpine meadow in the Medicine Bow Mountains of southeastern Wyoming. The traces show a high frequency of small clouds occluding

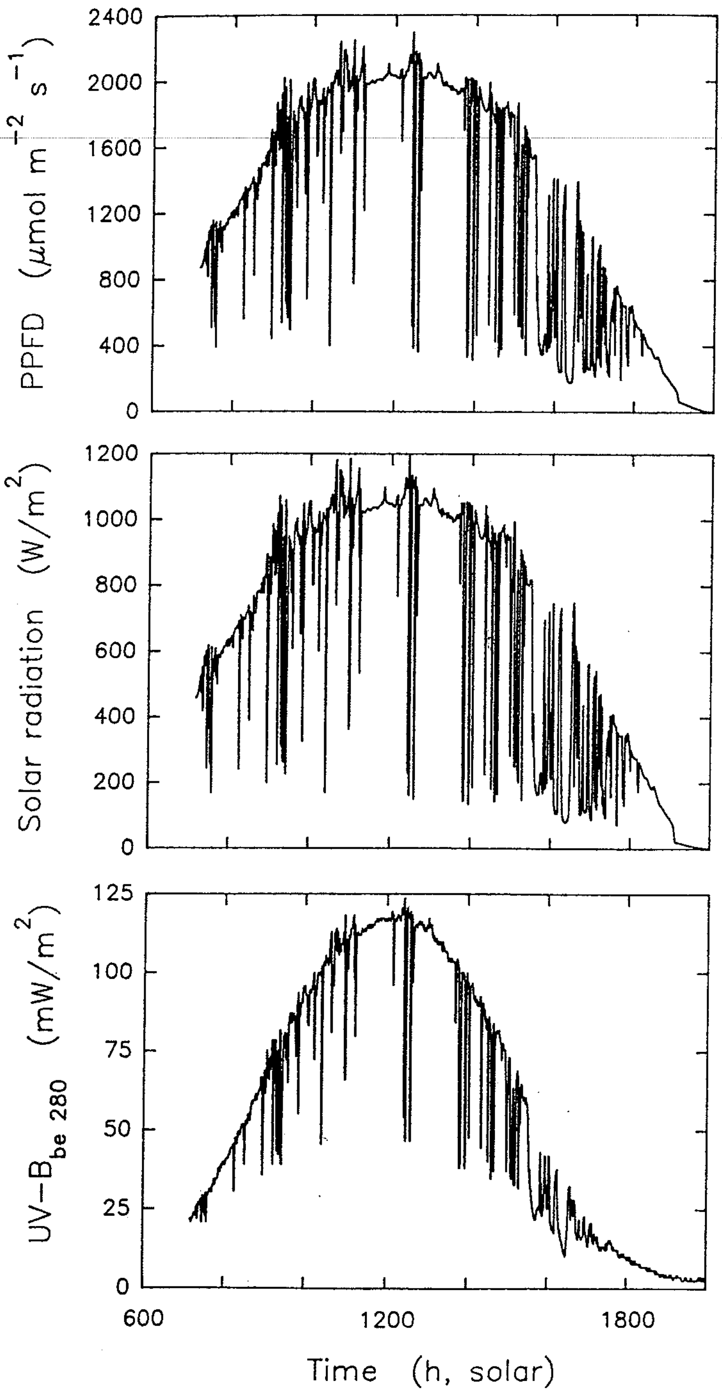


Figure 4. Diurnal pattern of photosynthetic photon flux density (PPFD), solar radiation, and biologically effective UV-B radiation weighted by the generalized plant action spectrum and normalized at 280 nm ($UV\text{-}B_{be280}$). Measurements were made in an alpine meadow (3000 m above sea level) in the Medicine Bow Mountains, Wyoming, on 27 June 1990. The horizon was < 15° from horizontal at all azimuths.

the sun (Figure 4). This pattern of incident irradiance is typical of high elevation sites, particularly during mid-morning through afternoon when convective clouds form as warm air masses move up-slope (23). As small rapidly moving cumulus clouds approach the sun, reflected light increased causing transient increases of short and long-wavelength light. These cloud enhancements were followed by large decreases in light as the cloud occluded the solar disk. If the cloud was small light measured during a shade event represented the diffuse component of global radiation. Cloud events at midday indicated that diffuse light was *ca.* 40% of global UV-B radiation and *ca.* 20% of PPFD and solar radiation. Similar high proportions of UV-B in the diffuse component have been reported for other high elevation sites (5) and are predicted by the wavelength-dependence of Rayleigh scattering (13). At large zenith angles the effective ozone column is increased resulting in a more rapid decrease in incident UV-B than PPFD or solar radiation (Figure 4).

The rapid attenuation of UV-B at large zenith angles resulted in a non-linear relationship between UV-B_{be280} and solar radiation (Figure 5) or PPFD (data not shown). Particularly at low values of solar radiation (< 400 W/m^2), considerable enhancement of UV-B_{be280} was evident. Points falling to the left and above the UV-B_{be280}/Solar radiation curve resulted from cloud events causing enhancement of diffuse light which is enriched in the UV-B portion of the solar spectrum. Points falling to the right and below the curve resulted from cloud enhancement events that increase the direct portion of global radiation, which is depleted in short wavelengths. Cloud enhancement of longer wavelengths is small relative to UV-B enrichment during the time the cloud occludes the sun. Thus, the rapid movement of small clouds past the sun may greatly increase the daily integrated ratio of UV-B to solar radiation and PPFD. This may be significant insofar as longer wavelength light (>320 nm) drives photoreactivation and photorepair processes (2).

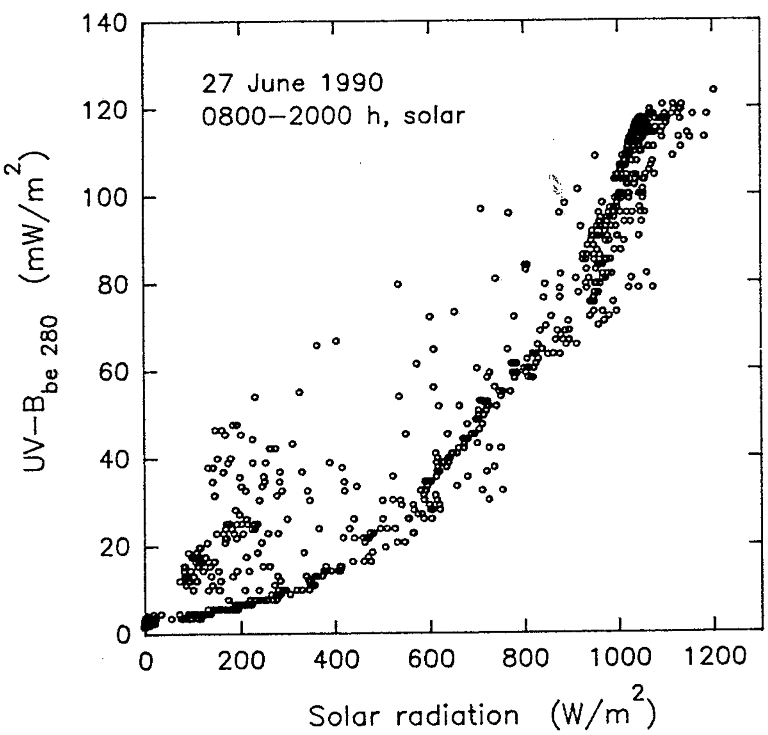


Figure 5. Integrated biologically effective UV-B radiation (UV-B_{be280}) as a function of solar radiation. Data are from Figure 4.

We predicted that differential absorption and reflection would alter the relative proportion of visible and UV-B radiation reaching older foliage within the crown of conifers. Profiles of PPFD and $UV\text{-}B_{be280}$ were measured along individual branches of *Picea engelmannii* and *Pinus contorta.* Trees were 2-3 m in height and were growing in an open clear-cut at 2700 m elevation. Measurements were made in 10-cm increments from the branch tip toward the bole with a UV-B radiometer and quantum sensor mounted on a 1-m long wand. Data were taken under diffuse light conditions on south-facing branches.

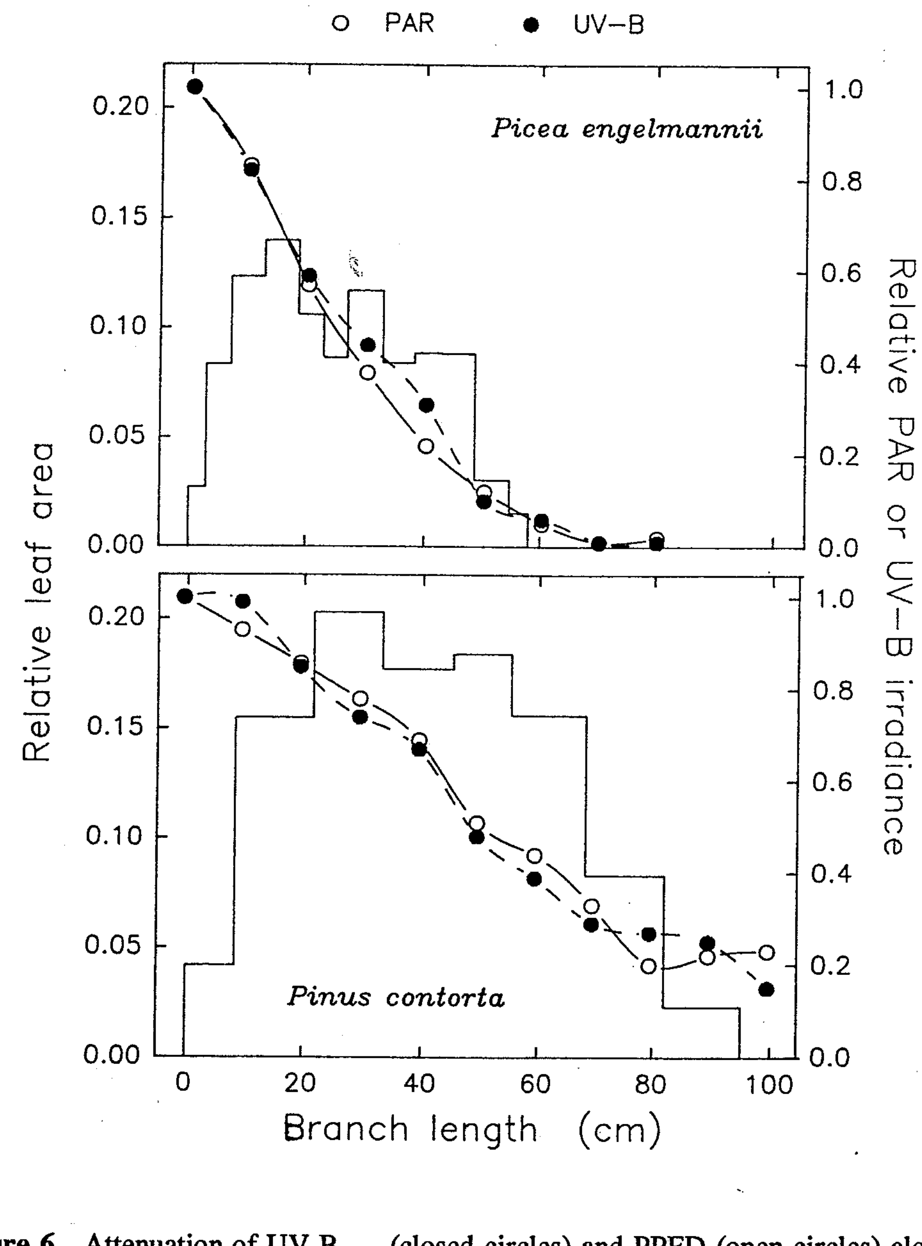


Figure 6. Attenuation of $UV\text{-}B_{be280}$ (closed circles) and PPFD (open circles) along individual branches of *Picea engelmannii* and *Pinus contorta.* The relative leaf area in each needle cohort is illustrated by the histograms. Measurements were made under diffuse light conditions.

The foliated-branch lengths for *Picea* and *Pinus* were *ca.* 58 and 95 cm, respectively, and these species maintained 12 and 9 foliage cohorts (Figure 6). Light attenuation along branches of both species was steep. Only *ca.* 10% of incident PPFD reached the oldest needles of *Picea*. The more open crown of *Pinus* permitted greater light penetration. In this species *ca.* 20% of incident light reached the oldest foliage cohort. In contrast to our initial prediction that differential absorption and reflection of visible and UV-B radiation may alter the ratio of these wavelengths in the crown, we found that penetration of PPFD and $UV\text{-}B_{be280}$ were proportional (Figure 7). Greater absorption of UV-B than visible light by foliage may offset the higher proportion of UV-B in the diffuse light component, thus explaining the equal attenuation of these wave bands in the canopy.

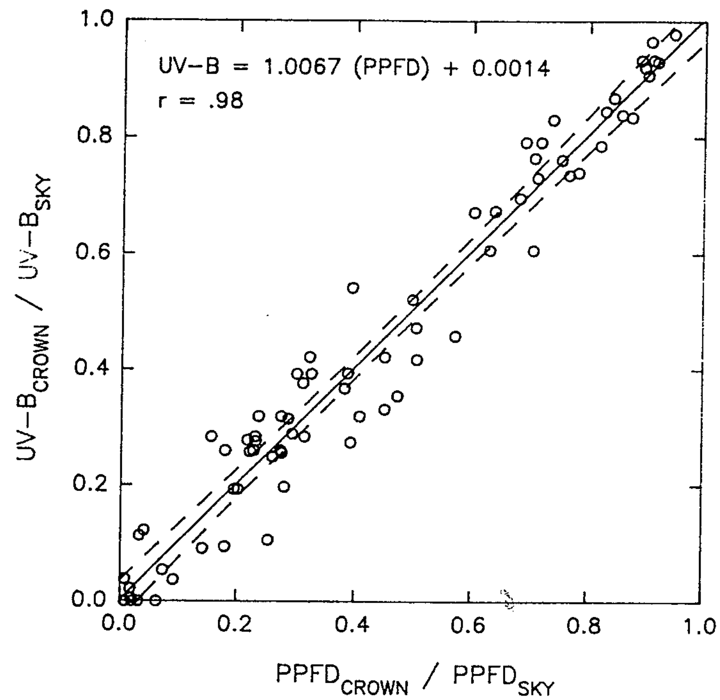


Figure 7. Relative crown penetration of $UV\text{-}B_{be280}$ as a function of crown penetration of PPFD. Data are for both species in Figure 6. The dashed line designates the 99% confidence interval.

Surface reflectance (albedo) of features in the microenvironment of conifer saplings were measured in early summer. Measurements were made by orientating the UV radiometer and quantum sensor normal to the sky and then the substrate. Albedos ranged from *ca.* 8 to 58% for PPFD and <1 to 23% for UV-B (Table I). Reflectance was consistently greater for PPFD than for UV-B, and the highest reflectances were from old snow-- 58 and 23% for PPFD and UV-B, respectively. Iqbal (13) reported reflectance values of greater than 80% across a wide range of wavelengths, including the UV-B, for fresh snow.

Table I. Microsite albedo for tree seedlings. Reflectance of visible (400-700 nm) and UV-B_{be280} radiation from features in the microsite of tree seedlings in a subalpine habitat.

Substrate	Description	PAR%	UV-B (be)%
Dry Ground	Soil derived from till w/small stones	8.1 ± 0.1	2.1 ± 0.8*
Subalpine meadow	Cover of low stature alpine perennials	5.0 ± 0.4	0.7 ± 0.2*
Wet meadow	Same as above but w/ standing water	3.3 ± 0.4	0.9 ± 0.5*
Standing water	Standing water (*ca.* 10 cm), no vegetation	4.9 ± 0.5	2.8 ± 0.4*
Wood	Large spruce bole w/o bark	11.6 ± 1.9	3.8 ± 0.9*
Scree	Large-facet granitic rock	24.1 ± 0.1	5.3 ± 0.6*
Old snow	Large wet grain w/ plant debris	58.3 ± 3.8	23.1 ± 2.1*
New snow	Fresh fallen, dry	82[1]	

*t-test, $P < 0.05$
[1]Iqbal (1983)

IV. Penetration of UV and Visible Light Into Foliage.

Assessment of the potential impact of UV-B radiation on native plants is difficult. The generation of meaningful UV enhancements in the field is often prohibitively expensive and in the case of large forest trees impossible. As a first step in assessing the potential impact of enhanced UV-B levels on the productivity of subalpine forests, we have developed a novel method for measuring UV penetration into intact foliage using fiber optic microprobes. With this technique we have measured the amount of UV radiation reaching the photosynthetic apparatus and other sensitive chromophores in the mesophyll of foliage. We have made preliminary measurements on a number of important Rocky Mountain conifers and have extended this survey to other woody plants and forbs.

Fused-silica fiber-optic microprobes were used to directly measure light penetration into foliage as in Vogelmann (20,21). Multimode fused-silica step-index fibers (125 μm OD) were tapered by stretching the fibers at constant force while heating with a thin hydrogen-oxygen flame. The tapered region was coated with chromium and truncated with a diamond knife thereby producing a microprobe with a tip diameter of 10 to 15 μm. The chromium coating eliminated light from outside the acceptance angle of the tip from entering the probe. Acceptance angles of the microprobes were determined in air and water, and the probes had near-perfect Gaussian curves and 50% band widths of 14 to 32°.

A microprobe was mounted on a stepper motor and advanced through a leaf or needle toward the light source from the abaxial (lower) to adaxial (upper) surface at 12 μm/s. Foliage was irradiated on the adaxial surface with a xenon-arc lamp, and photons entering the microprobes were counted with UV/VIS spectroradiometer (Optronics model 742). The lamp supplied a weighted irradiance at the leaf or needle surface of 3,222 mW/m^2 biologically effective UV-B, using the generalized plant-damage action spectrum normalized to 280 nm. Following measurements of light penetration, leaf thickness and the depth of various cell layers were measured on fresh transverse section using an ocular micrometer at 100X. Plant material was collected by severing branches under water to maintain hydration or by transporting whole plants back to the laboratory. Measurements were made within 6 hours from the time of collection.

As exemplified by *Picea engelmannii*, UV-B was completely absorbed in the epidermis of

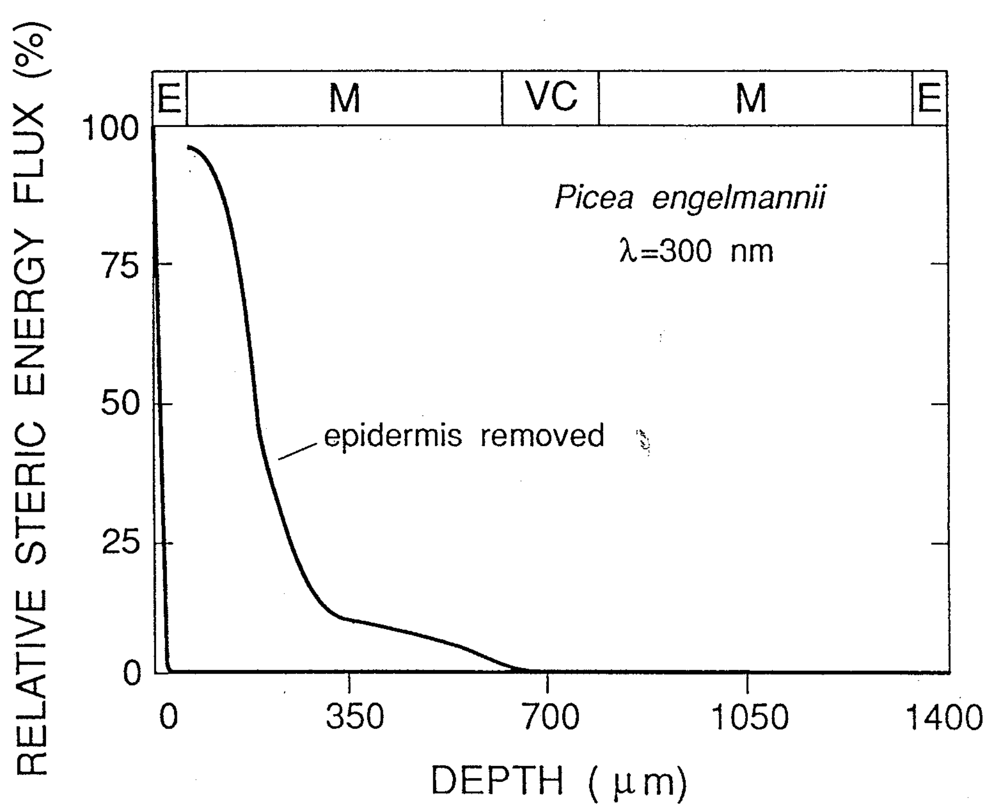


__Figure 8.__ Flux (as a percentage of incident light) of 300 nm light as a function of depth in a one-year-old needle of *Picea engelmannii*. Measurements were made with or without the epidermis removed. The horizontal bar at the top of the graph denotes the thickness of various tissue layers: E (cuticle, epidermis, and hypodermis), M (mesophyll), and VC (vascular cylinder).

conifer needles (Figure 8). In the 5 species of conifers examined penetration of 300 nm light was limited to the adaxial 2 to 18 μm. Initially, we thought the highly developed cuticle of conifer needles was responsible for the rapid attenuation of UV light, and a number of experiments were performed to test this prediction. These experiments included physical and chemical degradation of the cuticle and measurement of light attenuation in old highly ice-abraded needles from krummholz plants. No differences in the patterns of UV-B penetration were observed. Removal of the epidermis did, however, greatly enhance the depth of UV-penetration (Figure 8). Thus, for the conifer species examined the epidermis of mature needles effectively screens out all UV-B and protects the photosynthetic mesophyll from damage. Effective screening of UV-B radiation by the epidermis has been reported in a number of different species (7,9,10,15,16,17). Pigments including flavonoids and ferulic acid in the cuticle, cell wall, or cytosol of the epidermis may be responsible for this UV-B screening. These pigments are nearly transparent to longer wavelength light and permit penetration of photosynthetically active radiation to the mesophyll (Figure 9).

Examination of foliar light penetration for a number of different species representing a wide

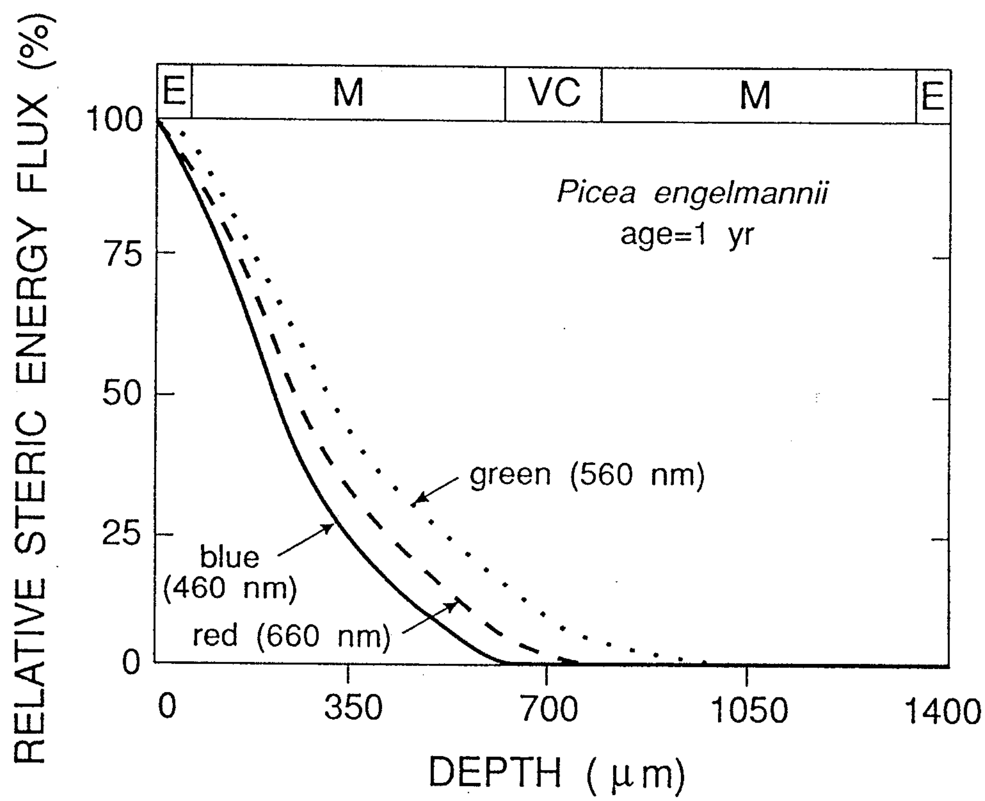


Figure 9. Flux (as a percentage of incident light) of visible light as a function of depth in a one-year-old needle of *Picea engelmannii*. The horizontal bar at the top of the graph denotes the thickness of various tissue layers: E (cuticle, epidermis, and hypodermis), M (mesophyll), and VC (vascular cylinder).

array of growth forms revealed substantial interspecific variation in the depth of UV-penetration. Woody dicots and grasses had significantly greater UV-B penetration than the conifers. *Salix planifolia*, for example, had measurable levels of 300 nm light at 40-um depth, well into the palisade parenchyma (Figure 10). Herbaceous dicots, as illustrated by *Aster foliaceus*, were least effective in screening UV-B from the mesophyll (Figure 11). This species permitted considerable UV-B light to pass through the upper palisade layer and enter the lower palisade. Thus, penetration of 300 nm light to the mesophyll which was not measurable in foliage of conifers, was *ca.* 5-8% of incident irradiance for woody dicots and grasses, and was in excess of 25% for most of the herbaceous dicots (Figure 12).

We postulate that UV-screening ability may be related to leaf longevity. The species measured represent a gradient of leaf longevity-- conifer foliage is typically functional for 5-20 years, the woody dicots retain foliage for a complete growing season, and grasses and forbs maintain functional foliage for only part of the growing season. More effective UV-B screening in long-lived conifer needles may be an evolutionary response to the potential for cumulative damage caused by

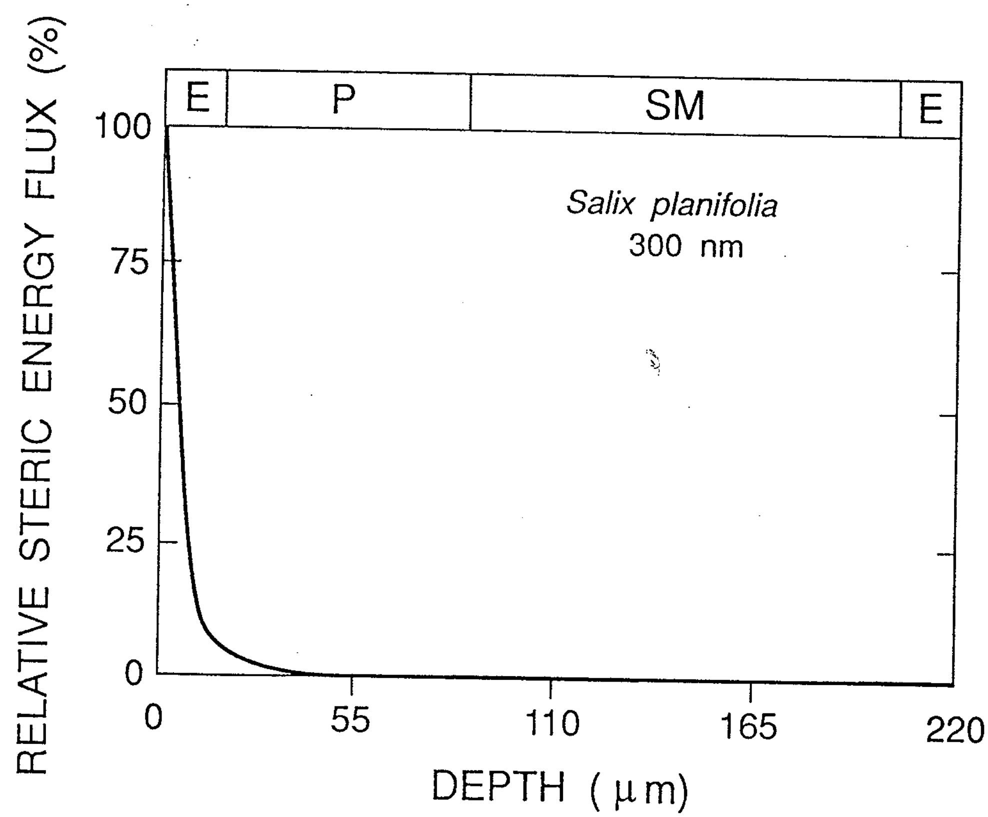


Figure 10. Flux (as a percentage of incident light) of 300 nm light as a function of depth in a leaf of *Salix planifolia*, a woody dicotyledenous shrub. The horizontal bar at the top of the graph denotes the thickness of various tissue layers: E (cuticle and epidermis), P (palisade mesophyll), and SM (spongy mesophyll).

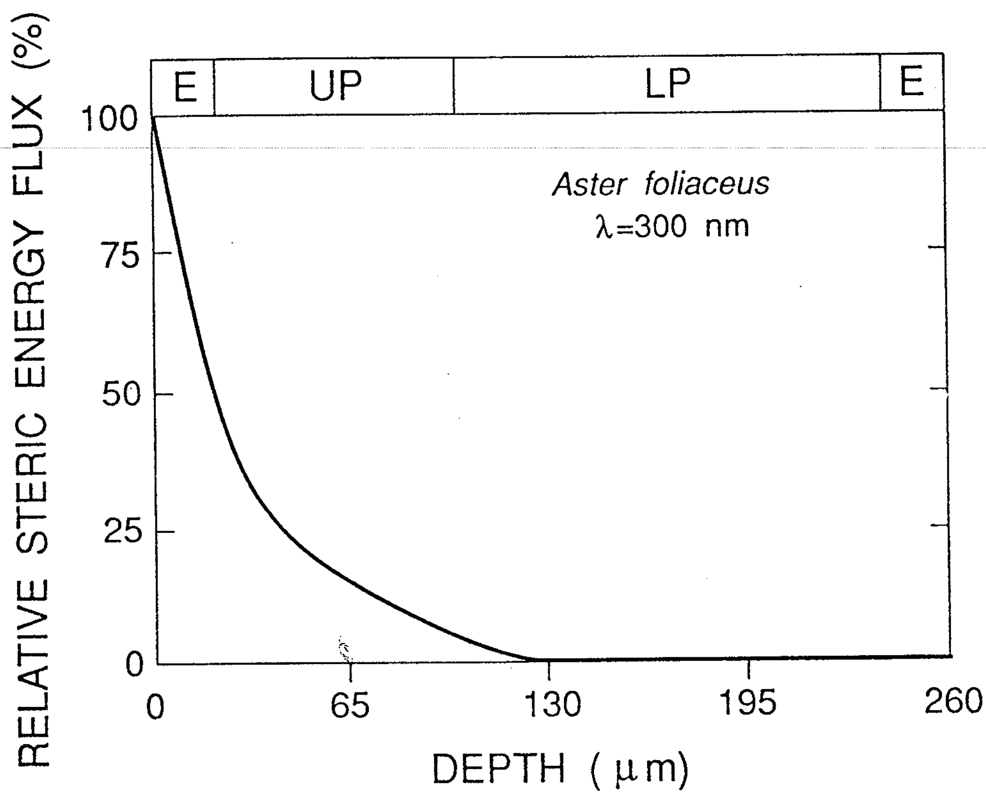


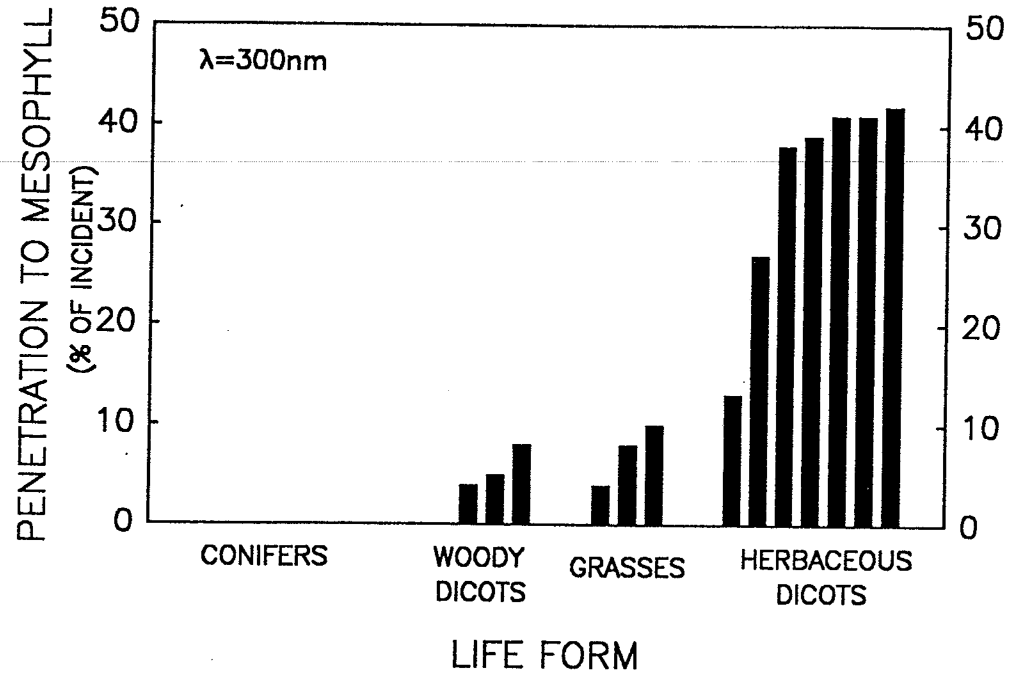
Figure 11. Flux (as a percentage of incident light) of 300 nm light as a function of depth in a leaf of *Aster foliaceus,* an alpine forb. The horizontal bar at the top of the graph denotes the thickness of various tissue layers: E (cuticle and epidermis), UP (upper palisade mesophyll), and LP (lower palisade mesophyll).

large life-time doses of UV-B. Though incident UV-B levels may be high, the short life of the foliage of alpine forbs may obviate the need for effective UV-B screening and would reduce the expense to the plant of producing UV-screening pigments.

V. Summary

The ability to make instantaneous measurements of biologically effective UV-B radiation in the open and within plant canopies will greatly enhance our understanding of the potential effects of UV-B on natural ecosystems. The SED240 UV radiometer is affordable and can be run and sampled continuously with a datalogger. The instrument requires additional cosine correction which is achieved by adding a teflon diffuser. However, a limitation of radiometers employing vacuum photodiodes is low output signal (23 nA under full sun without the cosine diffuser). This problem can be circumvented by use of additional amplification.

Frequent intermittent clouds and the dynamic nature of light within plant canopies increases the relative proportion of diffuse to direct irradiance incident on foliage in alpine and subalpine



<u>Figure 12</u>. Penetration into the mesophyll of 300 nm light for different montane trees, shrubs, grasses, and forbs growing in the Medicine Bow Mountains of southeastern Wyoming. Results are means of ten microprobe measurements. Most plants were growing unshaded in a subalpine meadow 3310 m above sea level. Some plants were collected from lower montane meadow and adjacent forest understory (2880 M elevation) and are noted by LM (lower meadow) or LU (lower understory). From left to right the species are: (conifers) *Abies lasiocarpa, Pinus flexilis, Pinus contorta* (LM), *Juniperus communis* (LM), *Picea pungens* (LM); (woody dicots) *Mahonia repens* (LU), *Populus tremuloides, Salix planifolia*; (grasses) *Phleum aplinum, Deschampsia caespitosa, Festuca ovina*; (herbaceous dicots) *Rumex densiflorus* (LU), *Sibbaldia procumbens, Plygonoum bistortoides, Aster foliaceus, Gentianella detonsa, Heracleum lanatum* (LU), *Orthilia secunda* (LU). Nomenclature follows R.D. Dorn, *Manual of Vascular Plants of Wyoming*, Garland Publ., N.Y., Vols. I & II.

habitats. Diffuse light is enriched in short wavelength UV-B radiation. Therefore, increasing the proportion of diffuse relative to direct light increases the proportion of UV-B to visible and UV-A light. We speculate that increasing the ratio of UV-B to visible light will increase the ratio of physiological damage to repair processes. The importance of absolute UV-B dose versus the ratio of UV-B/visible light in causing damage to photosynthesis and other physiological processes is not well understood and is an important avenue of future research.

Using fiber optic microprobes to directly measure light attenuation in foliage, we observed that the photosynthetic tissue of mature foliage of subalpine conifers is exceptionally well protected from UV-B radiation. No measurable light below 300 nm penetrated through the epidermis of conifer needles, and the ability to absorb UV-B was independent of the thickness or the integrity of the cuticle. In future studies we will examine the development of UV-B screening capacity during leaf emergence. Budbreak for subalpine conifers occurs in early to late June when there is still abundant snow. UV incident on foliage is greatly increased by reflection from snow and needles may be vulnerable to high doses of UV-B radiation during emergence from the bud scales.

Interspecific variation in the ability of leaves to screen UV-B prior to reaching and potentially damaging the photosynthetic apparatus and other metabolic chromophores was high. Epidermal transmittance ranged from < 1% for conifers to 42% for alpine forbs. These values are similar to the range (< 1% to 25%) of UV-B transmittances measured on isolated epidermal peels (7,9,10,15,17). Our data suggest a trend for long-lived foliage to have lower epidermal transmittances than short-lived foliage. More data is needed to establish evolutionary relationships in the ability to absorb UV-B light in the leaf epidermis. Whether the high doses of UV-B reaching the mesophyll of alpine forbs will induce damage is unknown. It is possible that these species protect sensitive photosynthetic chromophores by localizing UV-absorbing pigments in the chloroplast outer membrane (12). The substantial interspecific differences in the ability to screen UV-B from the photosynthetic apparatus may result in differences in susceptibility of carbon gain and plant growth to enhanced UV-B. Thus, we predict that enhanced levels of UV-B radiation may alter competitive relationships among species in high elevation habitats (1).

Acknowledgements

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