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Internal Filters : Prospects for UV-Acclimation in Higher Plants

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Internal filters: Prospects for UV-acclimation in higher plants

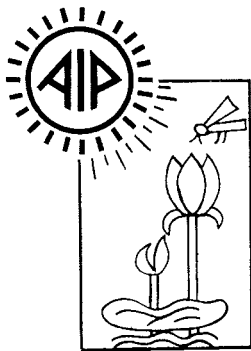Martyn M. Caldwell, Ronald Robberecht and Stephan D. Flint

Caldwell, M. M., Robberecht, R. and Flint, S. D. 1983. Internal filters: Prospects for UV-acclimation in higher plants. – Physiol. Plant. 58: 445–450.

Wavelength-selective absorption of solar radiation within plant leaves allows penetration of visible radiation (400–700 nm) to the chloroplasts, while removing much of the damaging ultraviolet-B (UV-B, 280–320 nm) radiation. Flavonoids are important in this wavelength-selective absorption. Induction of flavonoid synthesis by solar radiation, and specifically by UV-B radiation, is discussed as this relates to the potential acclimation of plants to enhanced solar UV-B radiation that would result from stratospheric ozone reduction.

Additional key words – Epidermal transmittance, flavonoids, ozone reduction, ultraviolet-B.

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Introduction

Photosynthetically active radiation penetrates effectively into the mesophyll and is attenuated by as little as 20 to 30% as it passes through the epidermis of some plant leaves (McCree 1981, Robberecht and Caldwell 1983). Chloroplasts as well as nuclei are organelles where primary lesions can result from UV-B irradiation (Brandle et al. 1977, Iwanzik et al. 1983, Howland 1975). Thus, radiation should be selectively filtered to remove the short wavelength UV component before it reaches the chloroplasts, while at the same time providing minimal attenuation in the 400–700 nm waveband which is effectively utilized by the photosynthetic system. The existence of selective filtration in plant leaves makes it unlikely that most plants in their natural habitats are suffering reduced photosynthetic capacity or significant nucleic acid damage due to solar UV-B irradiation (Caldwell 1981). This selective filtration is, however, imperfect. Damage to the photosynthetic system of many plant leaves can be readily demonstrated when intact leaves are exposed to UV-B radiation from lamps (Sisson and Caldwell 1977, Teramura et al. 1980). On the other hand, some of the photosynthetically active radiation (UV-A, violet, and blue) may be absorbed by the epidermis (McCree 1981).

The ecological question of acclimation to increased solar UV-B radiation, as would occur with a reduced ozone layer, or acclimation of species invading regions of naturally higher solar UV-B irradiation will be addressed in this paper. One plausible mechanism of acclimation would be the change in UV optical properties of plant leaves, resulting in the reduction of effective UV fluence reaching physiological targets. This not only would reduce the total number of damaging photons reaching chromophores, but at these lower fluence rates nucleic acid repair systems could function more efficiently (Murphy 1975, Soyfer 1979).

Abbreviations – UV-B, 280–320 nm; UV-A, 320–400 nm.

Attenuation of UV radiation in plant tissues

Leaf orientation has little influence on the total global (direct beam + diffuse) UV-B irradiance reaching the leaf surface since the diffuse component, which tends to be isotropic, is a large part of the total UV-B radiation (Caldwell 1981). At least 90% of the UV-B radiation that does reach the surface of plant leaves is attenuated before reaching the mesophyll tissues and very little radiation in this waveband penetrates completely through the mesophyll tissue (Fig. 1).

For most species, UV-B reflectance from the leaf surface is less than 5% and most of the attenuation is the result of absorption and scattering within epidermal tissues (Gausman et al. 1975, Caldwell 1971). There are a few species which do exhibit leaf surface reflectance on the order of 20 to 70% in the UV waveband. This has been reported for some species that have a dense glaucous surface such as *Dudleya brittonii* (Mulroy 1979) and *Picea pungens* (Clark and Lister 1975), or for certain species with dense pubescence (Robberecht et al. 1980). This reflectance does not appear to be wavelength selective, i.e., those species with high UV reflectance also have approximately the same reflectance in the visible part of the spectrum. [*Picea pungens* exhibits some wavelength specificity in that UV-B reflectance is approximately twice that of visible reflectance (Clark and Lister 1975)]. High visible radiation reflectance from the leaf surface necessarily limits the efficiency of photosynthesis for such species (Ehleringer et al. 1976) by reducing the fluence of photosyntheti-
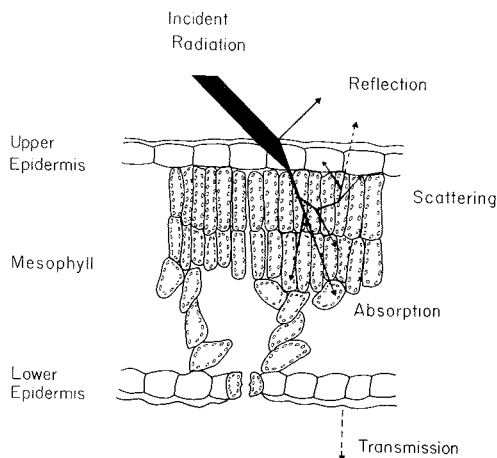

Fig. 1. Partitioning of UV-B radiation incident on a glabrous leaf surface based on a survey of 100 species (Robberecht and Caldwell 1978, Robberecht et al. 1980, R. Robberecht, unpublished). Widths of arrows indicate the magnitude of reflectance from the leaf surface (less than 5%), and attenuation in the epidermis (90% average, with a range of 75 to 95%). Further scattering and absorption within the mesophyll results in less than 1% of the incident UV radiation leaving the mesophyll and entering the lower epidermis. No detectable UV flux passes through the entire leaf.

cally active radiation (400–700 nm) reaching the chloroplasts. The wavelength selectivity of absorption in the epidermis of most plant species is much more pronounced and, as will be discussed later, can often be attributed to flavonoids and related UV-absorbing pigments (Robberecht and Caldwell 1978).

Since many of the UV-absorbing compounds of plant cells are contained within the vacuole (McClure 1975), this is the site for much of the UV absorption in the epidermis. Ultraviolet-absorbing compounds such as flavonoids can also occur within specific organelles such as chloroplasts (Weissenböck et al. 1976). Unless there are compounds such as flavonoids or phenolic derivatives incorporated within the cuticular membrane or the cell walls, there would be little UV absorption in these structures since lipids and cellulose have little UV absorbance. While there can be substantial UV attenuation by scattering in these structural components, there is no consistent correlation between epidermal thickness and UV transmittance of this tissue layer (Robberecht and Caldwell 1978).

To differentiate between UV attenuation by cellular UV-absorbing pigments as opposed to attenuation by the cuticular membrane and cell walls of the epidermal tissue, a simple procedure can be followed. Transmittance of fresh epidermal samples can be measured, then extracted with an acidified methanol-water solvent which readily removes most of the soluble UV-absorbing compounds such as flavonoids and related phenolics. The UV transmittance can then be measured for the remaining constituents of the extracted epidermis: cuticular membranes, cell wall structure and residual cellular constituents (Robberecht and Caldwell 1978). Some results of such experiments are shown in Fig. 2 for six high-altitude Hawaiian species. These species occur in an environment of naturally high solar UV-B irradiation (Caldwell et al. 1980) and all species examined in such environments exhibit very low epidermal UV transmittance (Robberecht et al. 1980). Three of these species possess a dense leaf pubescence and three are glabrous. Epidermal transmittance of fresh and extracted epidermal tissue is shown for each species. The samples were collected from these species in their normal habitat and analyzed within a few hours. For the glabrous species, at least 50% of the total epidermal UV attenuation could be attributed to the extractable component. In contrast, species with a dense pubescence underwent little change in epidermal transmittance following the extraction of UV absorbing pigments. Much of the attenuation in these species, especially *Argyroxiphium sandwicense* and *Sophora chrysophylla*, apparently occurs in the pubescence and structural components of the epidermis.

Potential sites of UV damage other than leaves can also be considered in the context of protective filtration by plant tissues. The gametophytic tissues of higher plants are a case in point. Prior to flower opening, corollas of most plants provide nearly complete screen-
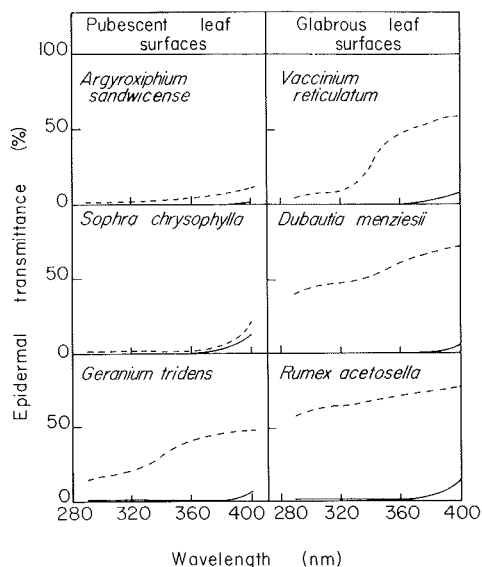
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Fig. 2. Transmittance of UV radiation through the fresh epidermal tissue (solid line), and through the epidermal tissue from which flavonoids and related phenolic compounds were extracted (dashed line). These species were collected from high UV-B irradiance habitats on the Haleakala Crater, Maui, Hawaii between 2 000 and 3 000 m elevation.

ing from UV-B radiation. After flower opening, pollen is still well protected in the anther sacs since the anther walls attenuate UV-B radiation by at least 98% (S. D. Flint and M. M. Caldwell, unpublished). Even the pollen grain wall is effective in attenuating UV-B radiation by at least 80% (Uber 1939). The relatively thick ovary wall should also serve to effectively protect the ovules, although this has not been specifically investigated. Most floral structures including pollen grains contain flavonoids and related pigments (Wiermann 1968, Martin 1970) which may be responsible for some UV attenuation.

Flavonoids as variable filters

Flavonoids and related phenolic compounds fulfil the role of wavelength-selective pigments for UV filtration very well. A diverse array of these compounds occurs in higher plants, and virtually all terrestrial species thus far examined possess flavonoids of some variety (McClure 1975). Flavonoids that occur in plant leaves generally have substantial UV absorbance and very little absorption in the visible waveband. Anthocyanins are a notable exception in that they have substantial absorption in the visible waveband and rather little in the UV-B (E. Wellmann, unpublished).

The quantities of different plant flavonoids vary among plant species, with developmental state, and often between epidermal and mesophyll tissues of the

same leaf. The flavonoid content and composition is usually altered by environmental conditions as well. The light environment is particularly influential. Flavonoid synthesis can be induced by radiation through the phytochrome system, and in response to high intensity blue, green or red light (McClure 1975). Specific induction of flavonoids by UV radiation has also been clearly demonstrated by Wellmann (1974, 1982). The manner in which flavonoid synthesis can be induced by light of different wavebands is dependent not only on the species under consideration, but also on factors such as the developmental stage of the plant (McClure 1975, Mohr and Drumm-Herrel 1983). It is expected that a terrestrial plant grown in sunlight, even without the UV component, will possess some flavonoids, although E. Wellmann (unpublished) has graphically demonstrated that recently-germinated seedlings of certain species exposed to light with the UV component removed can be free of flavonoids and easily damaged when subsequently irradiated with UV-B. In such cases, UV induction of flavonoid synthesis, which occurs within the span of several hours, would be of obvious benefit to the plant. For seedlings in nature, which are beyond these first critical days and already possess flavonoids, UV-specific induction of additional flavonoids may also play a useful role in acclimation to increased solar UV radiation under certain circumstances.

Once synthesized, the flavonoid pool is not static but undergoes some turnover and total flavonoid concentrations will vary with time (McClure 1975). Again, total flavonoid concentrations will depend on the radiation environment as well as on other factors. Fluctuations in flavonoid pools in outer tissue layers such as the leaf epidermis have been suggested (Peyron and Tissut 1981), and there is also some indirect evidence that these epidermal flavonoid pools do vary. Lautenschlager-Fleury (1955) was one of the first to consider the leaf epidermis as a UV filter for higher plant leaves. Her work showed that UV epidermal transmittance of *Vicia faba* growing under field and glasshouse conditions varied considerably – even within the course of 24 h. After a few overcast days, UV epidermal transmittance of glasshouse-grown plants was considerably greater than following a few days of clear weather with intense solar radiation. When grown in a glasshouse in winter under overcast conditions the epidermal transmittance could reach values as great as 50%. She could remove much of the UV-absorbing component of the epidermis by extraction with distilled water for 24 h, and it was this component that varied with radiation conditions. Furthermore, epidermal transmittance in the visible waveband underwent little change following water extraction. She also claimed that the visible, and not the UV component of the solar spectrum, was responsible for these pigment alterations.

Irradiation of plants with UV-B has been shown to result in reduced epidermal UV transmittance for some species under glasshouse conditions as opposed to
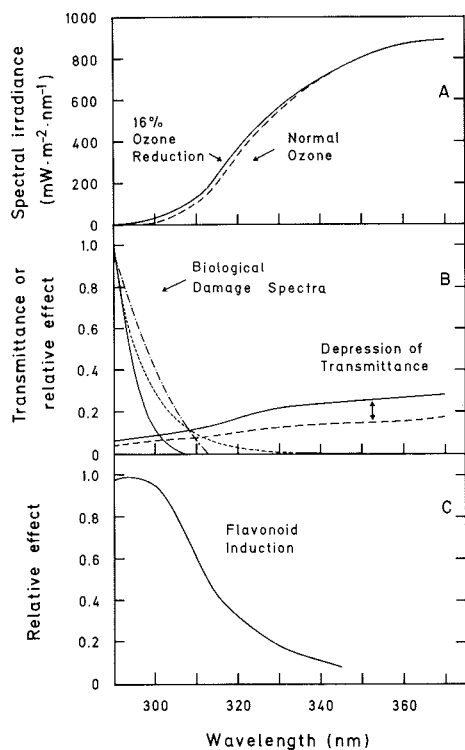
Fig. 3. Solar spectral UV irradiance at midday in the summer (temperate latitudes, sea level). This is depicted for an average ozone thickness of 0.32 atm·cm and for an ozone layer reduction of 16% (A). Biological damage action spectra appropriate for plants are portrayed in (B). These include a DNA-damage spectrum (Setlow 1974) (solid line), a provisional photosynthetic inhibition spectrum (M. M. Caldwell, C. W. Warner and S. D. Flint, unpublished; dashed line) and a generalized plant damage action spectrum (Caldwell 1971; dash-dot line). The change in epidermal UV transmittance of *Oenothera stricta* following UV-B irradiation under glasshouse conditions (Robberecht and Caldwell 1983) is also depicted in (B). The action spectrum for flavonoid induction in parsley and maize seedlings (Wellmann 1982) is shown in (C).

plants growing in the absence of UV-B radiation under identical conditions (Robberecht and Caldwell 1978, 1983). This UV-B-specific induction of altered epidermal transmittance is apparently due to a change in UV-absorbing flavonoids since this attenuation is primarily in the extractable component of the epidermis. Such evidence, along with the demonstration that synthesis of certain flavonoids in some species can be specifically induced by UV-B radiation (Wellmann 1982), suggest that plants under field conditions might respond to enhanced solar UV-B radiation with decreased epidermal transmittance. This might constitute a means of acclimation to enhanced solar UV-B radiation in the absence of change in other parts of the solar spectrum, as would be the case with stratospheric ozone reduction. Nevertheless, many questions remain.

Stratospheric ozone reduction would result in radia-

tion intensification primarily in the UV-B, and it is unknown whether this supplemental UV-B radiation would induce still more flavonoid synthesis, especially since the solar spectrum already contains UV-B radiation. That is, is the induction of flavonoid synthesis in those species that do respond to UV-B radiation a quantitative or simply a quantal effect? The waveband where solar UV-B radiation would be most enhanced as a consequence of ozone reduction is also the waveband where UV-B is most damaging as indicated by the biological damage action spectra shown in Fig. 3 (Caldwell 1981). Epidermal transmittance can be decreased following UV-B irradiation, although a relatively larger decrease usually occurs in the UV-A [320–400 nm; Robberecht and Caldwell 1978, 1983); (Fig. 3, this paper)] because many flavonoids have absorbance maxima in the UV-A waveband. Also shown in Fig. 3 is an action spectrum for flavonoid induction in parsley and maize seedlings as determined by Wellmann (1982). Within the UV-B waveband, flavonoid induction increases with decreasing wavelength as does the relative enhancement of solar UV-B radiation and the relative effectiveness of UV-B radiation to inflict biological damage (Fig. 3). Nevertheless, it is not clear how many species would respond to enhanced UV-B radiation by increased synthesis of flavonoids, and whether the consequent increase in absorption of UV-B in the epidermis and other tissues would be sufficient to compensate for the increased incident UV-B radiation.

To address such questions, field experiments are now underway to determine if supplemental UV-B irradiation, modulated to simulate enhanced solar UV-B radiation due to ozone reduction (Caldwell et al. 1983), will result in reduced epidermal UV transmittance of plants growing under field conditions. Preliminary results with *Vicia faba* suggest that such reduction of UV epidermal transmittance may occur in the field.

Although an increase in epidermal flavonoid pigments probably affords increased protection of the mesophyll, most of these pigments are contained within the vacuoles. Thus one might expect that changes in UV transmittance of the epidermis would not vary according to Beer's law with changes in flavonoid concentration of this tissue. As portrayed in Fig. 4, the epidermal tissue is not an homogeneous filter, and increased flavonoid concentrations in the vacuoles, although causing a decrease in epidermal UV transmittance, would not uniformly decrease the UV penetration to the mesophyll. Some chloroplasts in the upper mesophyll tissue might still receive sufficient flux to suffer damage. Increased UV-B absorbing pigments within the mesophyll tissues following UV-B irradiation have also been documented (Robberecht and Caldwell, 1983) and thus this protective reaction appears to occur in these deeper tissue layers as well.

Little attention has been directed to the epidermis itself as a target. Certainly, intense UV-B radiation can result in profound damage to epidermal tissues
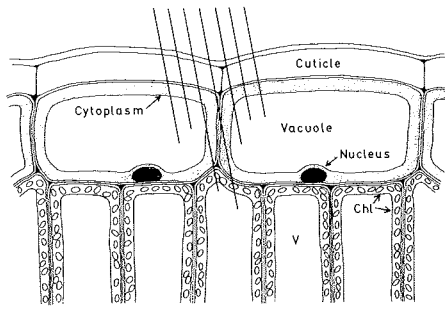
Fig. 4. Depiction of the epidermis as a non-uniform filter of UV-B radiation (inclined parallel lines). Ultraviolet-absorbing pigments should occur principally in the vacuoles, although some compounds such as leucoanthocyanins may be bound to the cell wall. (E. Wellmann, personal communication).

(Caldwell 1968, Tevini et al. 1981) resulting in alterations of the cuticular wax layer and leaf surface morphology as well as eventual cell death. There is no suggestion that such damage ever occurs in nature. With moderate intensification of solar UV-B radiation it is not clear if epidermal cells, including guard cells, might be affected. The nucleus in epidermal cells is depicted as safely tucked beneath the vacuole (Fig. 4), but its real location would need to be considered as well as the exposure of other organelles and guard cell chloroplasts. Whether cell membranes themselves are targets of solar UV-B radiation is still unclear (Murphy 1983). Even within organelles such as chloroplasts, UV radiation may be attenuated significantly. It has been suggested that the innermost thylakoid membranes may not be damaged even following prolonged UV irradiation (Bornman et al. 1982). Flavonoids have been reported in chloroplasts (Weissenböck et al. 1976, Plesser and Weissenböck 1977) and these may serve as a useful UV filter within these organelles.

Apparent acclimation to UV-B radiation

As an indication that at least some species might acclimate to increased solar UV-B radiation by changes in leaf optical properties, it is instructive to examine a natural gradient of solar UV-B radiation on the Earth's surface. A steep gradient exists in the arctic-alpine life zone over a latitudinal span from the arctic tundra at sea level in northern Alaska to the Andes at high elevations and low latitudes. Maximum biologically effective UV-B irradiance varies tenfold and total daily UV-B irradiation by 7-fold over this gradient, even though total solar radiation flux undergoes comparatively little change (Caldwell et al. 1980). At temperate and arctic latitudes, where solar UV-B radiation is less intense, there is considerable variability among species in epidermal UV transmittance. However, in high UV-B radiation alpine environments at equatorial and tropical

latitudes, the UV epidermal transmittance of all species is consistently very low – an average value of less than 2% (Robberecht et al. 1980). This includes several temperate latitude species that have been introduced to these low latitude environments.

The existence of exotics from temperate latitudes in these low latitude, high elevation environments where biologically effective solar UV-B radiation is more than 3-fold greater than would occur if the ozone layer were reduced by 16% at temperate latitudes (Caldwell et al. 1980) attests to the acclimation capacity of these species. While one cannot argue with the success of these temperate latitude exotics that do exist in tropical highlands, nothing is known about the degree to which solar UV radiation prevented the establishment of temperate latitude species that do not occur in these high UV flux environments. Whether the capacity to tolerate intense solar UV-B radiation has been accomplished solely through alterations of leaf optical properties is not known. Furthermore, possible genetic changes in these populations of exotics introduced to low latitude environments have not been explored. Thus, considerable caution is warranted in attempts to generalize about the capacity of entire floras to tolerate enhanced solar UV-B radiation in the event of ozone reduction.

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Edited by L. O. Björn and J. F. Bornman