of the entire epidermis but the significance of these spots becomes greater with increasing difference between vacuolar and intervacuolar absorption.

The sieve effect for UV radiation was visualised using epidermal peels placed on a film which fluoresces in the blue when excited with UV radiation (Day *et al.*, 1993). Microscopic examination of the film revealed high transmission of UV radiation between epidermal cells and also through stomatal pores. The optical heterogeneity of these epidermal layers was confirmed by measurements using a fibre-optic micro-probe which revealed large spatial intensity variations below the epidermis. The sieve effect was not detected in needles of *P. pungens* and this was attributed to the presence of UV-absorbing phenolics in the cell walls of conifers but not in the herbaceous species investigated. Similarly, a quantitative relationship between epidermal UV absorbance and UV absorbance of extracted phenolics was successfully established for both barley and grapevine leaves when the sieve effect was taken into account (Kolb and Pfündel, 2005). Therefore, transparent areas between completely non-transparent vacuoles might determine the lower limit of epidermal transmittance in the UV range of many plants.

Structural colour. In addition to absorption and wavelength-dependent scattering of radiation, the optical behaviour of nanometric structures can produce a coloured appearance of plant surfaces. Leaves of *S. uncinata* exhibit blue-iridescence when grown under extreme-shade conditions but are green in response to more direct sunlight. The different appearance corresponded to higher reflectance in the blue but lower reflectance in both the green and red spectral ranges of the shaded compared with the sun-exposed leaves (Hébant and Lee, 1984). The blue colour was attributed to constructive interference caused by thin layers which are comparable in thickness to the wavelengths involved and also differ in their refractive index from the surrounding media.

Considering the wavelength of maximum reflection, and that the refractive index of the layer is always higher than that of its surroundings, Hébant and Lee (1984) predicted a thickness of about 70 nm for the optical layer in *S. uncinata* and confirmed this calculation by electron microscopy which detected two opaque layers of the appropriate thickness in the outer cell wall of the upper epidermis. Destructive interference at longer wavelengths explains why blue leaves show decreased reflectance within the green and red spectral range.

We argued (see Section 6.4.1) that peripheral reflectance does not significantly obstruct penetration of light into leaves. However, absorption of dense canopies results in extremely low light intensities and a relative enrichment of far red photons. In extreme-shade plants growing under such conditions, photosynthesis depends literally on each single photon and, hence, decreased reflection of red wavelengths by thin-film interference might play a significant role in optimising light-harvesting (Lee, 1986, 1997). Interference phenomena, comparable to *S. uncinata*, have been observed in other species of *Selaginella* and also in two remotely related flowering plant species, *Begonia pavonina* and *Phyllagathis rotundifolia*, and in the fern *Trichomanes elegans*. In *T. elegans*, however, interference is caused by