flavonoids are also bound to cell walls of conifer needles (Strack *et al.*, 1989; Schnitzler *et al.*, 1996; Hoque and Remus, 1999) and their non-polar derivatives are also constituents of wax layers on leaf surfaces (Wollenweber and Dietz, 1981; Harborne and Williams, 2000; Onyilagha and Grotewold, 2004).

Recent data, from leaves of *Phillyrea latifolia*, support the view that cuticular flavonoids may play some role in UV screening of leaves (Tattini *et al.*, 2005); however, there is no general consensus on the importance of non-vacuolar flavonoids for UV screening of leaves. Indeed, the increase in UV-A screening in leaves, induced by UV radiation, can be attributed to vacuolar flavonoids (Schnitzler *et al.*, 1996; Burchard *et al.*, 2000; Markstädter *et al.*, 2001; Kolb *et al.*, 2001; Kolb and Pfündel, 2005) while non-vacuolar flavonoids seem to play a negligible role in variable UV screening.

Flavonol glycosides have been demonstrated in the vacuoles of white *V. vinifera* berries (Moskowitz and Hradzina, 1981). Fluorescence microscopy on the berries showed that the flavonols are accumulated in the multi-layered skin of the fruit suggesting that they function as UV-screening compounds. This was confirmed by the correlation between absorption of isolated flavonoids and skin absorption in both the UV-A and UV-B regions (Kolb *et al.*, 2003). Flavonols have been suggested as UV-screening compounds in apple (*Malus pumila*) fruits (Merzlyak *et al.*, 2005). It was estimated that cuticular flavonoids accounted for approximately one third (at most) of the total flavonoid UV screening in the *M. pumila* skin (Solovchenko and Merzlyak, 2003). Further, flavonoids were located in the skin layer of olives (*Olea europaea*) (Servili *et al.*, 1999) and flavonoid precursors were found in tomato (*Lycopersicon esculentum*) fruit cuticle (Baker *et al.*, 1982) which could be consistent with a UV-screening function for flavonoids.

Substantial amounts of colourless flavonoids have been found in the epidermal vacuoles of petals from a number of plant species (Kay *et al.*, 1981). The confinement of the UV-absorbing flavonoids to only certain areas of the petal can result in patterns of UV reflection which might increase their attraction to pollinating insects with UV vision (see Section 6.4.1 and Chapter 13). Colourless flavonoids can also affect the visible colour of flowers by acting as co-pigments to anthocyanins (Harborne, 1988).

Anthocyanins. Anthocyanidins, the chromophores of anthocyanins, are formed from colourless flavan-3,4,-diols (Harborne, 1988; Koes *et al.*, 1994; Turnbull *et al.*, 2000). Formation of anthocyanin, by glycosidation of anthocyanidin, is important for stabilising the chromophore *in vivo*; consequently, the failure to glucosylate flavonoids in grape-skin tissue results in an anthocyanin-free, white *V. vinifera* berry (Boss *et al.*, 1996). At acidic pH values, anthocyanins exist as flavylium cations which absorb maximally in the green wavelengths between 500 and 550 nm with negligible absorption in the red region (Harborne, 1988; Strack and Wray, 1989; Stintzing and Carle, 2004). The absorption characteristics of anthocyanins are affected not only by the pH but also by substitution patterns, presence of co-pigments and by metal ions chelated to the anthocyanins (Harborne, 1988; Strack