epidermal cells (Hébant and Lee, 1984; Lee 1986); hence, carotenoid effects on the optical surface properties of green leaves can only arise from sub-epidermal layers.

During acclimation to cold seasons, the leaves of some gymnosperms develop red–brown colours due to synthesis of large amounts of rhodoxanthin (Ida, 1981; Weger *et al.*, 1993). This colouration by carotenoids was confined to the upper leaf side (Weger *et al.*, 1993) which is consistent with carotenoid-dependent screening of visible radiation. In fact, Han *et al.* (2003) reported less light stress during winter in rhodoxanthin-synthesising foliage of wild-type *Cryptomeria japonica* than in a non-rhodoxanthin-accumulating mutant. More spatial distribution studies of rhodoxanthin within conifer leaves are needed to determine if rhodoxanthin is accumulated in the upper mesophyll layers to form an adequate shield against light stress in the bulk mesophyll beneath. Screening of light by carotenoids in senescing leaves of Norway maple (*Acer platanoides*) was also proposed by Merzlyak and Gitelson (1995) on the basis of reflectance and transmittance spectra. Furthermore, carotenoids, located in *M. pumila* peel, have been suggested to protect the fruit against deleterious light intensities together with anthocyanins (Merzlyak *et al.*, 2002).

Carotenoid-containing chromoplasts of the yellow–red coloured petals of wallflower (*Erysimum cheiri*), are derived from chloroplasts situated in the epidermal cells of the petal (Weston and Pyke, 1999). In a survey of flowering plants, Kay *et al.* (1981) found that carotenoids are often confined to the petal epidermis. A combination of epidermally located chromoplasts with unpigmented mesophyll, which provides back-scattering of non-absorbed light (see Section 6.4.1), could intensify colour to efficiently attract pollinators.

6.4 Non-absorptive optical properties

6.4.1 Reflectance

Radiation can not only be absorbed at surfaces, but redirection of photons at transitions of phases with different refractive indices also affects the optical behaviour of plant surfaces. This subject has been reviewed by Grant (1987), Vogelmann (1993) and Barnes and Cardoso-Vilhena (1996). In brief, radiation can be reflected at the border between air and a smooth cuticle surface resulting in specular reflectance rather than diffuse reflectance which arises from a perfect matte surface (i.e. a so-called Lambertian surface). Specular reflectance exhibits polarisation and directional intensity which are both affected by the angle of incident radiation and the viewing angle (Woolley, 1971).

Natural surfaces which are composed of structures that are larger than the wavelength of the incident light can reflect radiation specularly. Surface structures which are much smaller than the wavelength of the incident radiation can, however, be much more effective in reflecting radiation of shorter rather than longer wavelengths. Radiation from this so-called Rayleigh scattering may be polarised