6.3.2 *Betalains*

Betalains (Figure 6.3) are immonium conjugates of betalamic acid comprised of yellow betaxanthins, with amino acids or amines as the conjugating moiety and red–violet betacyanins, which are conjugated to various substituted *cyclo*-Dopa (i.e. *cyclo*-dihydroxy-phenylalanine) derivatives (Strack *et al.*, 2003). Betaxanthins have an absorption peak near 480 nm and the betacyanins have a corresponding peak between 530 and 550 nm with a further peak between 270 and 280 nm due to the Dopa moiety (Pedreño and Escribano, 2000; Cai *et al.*, 2001a,b). Acylation of some betacyanins with hydroxycinnamic acids gives rise to a third absorbance maximum between 300 and 330 nm (Strack *et al.*, 2003; Stintzing and Carle, 2004).

Betalains occur only in some families of the order of *Caryophyllales* which includes other families that synthesise anthocyanins. Because the betalain and anthocyanin pathways appear to be mutually exclusive (Kimler *et al.*, 1970; Stafford, 1994; Mabry, 2001), it was suggested that betalains assume the same functions as anthocyanins (Steyn *et al.*, 2002; Stintzing and Carle, 2004). Betalains, like anthocyanins, are located in vacuoles (Stintzing and Carle, 2004) and they also accumulate in the upper leaf epidermis of ice-plant leaves (*Mesembryanthemum crystallinum*) in response to high radiation intensities (Vogt *et al.*, 1999; Ibdah *et al.*, 2002) suggesting that betalains can protect against high light intensities. Betalains also replace anthocyanins as flower and fruit pigments, presumably, to attract not only insect pollinators but also fruit-eating animals as a seed dispersal mechanism (Kay *et al.*, 1981; Kobayashi *et al.*, 2000; Cai *et al.*, 2001a,b; Butera *et al.*, 2002; Christinet *et al.*, 2004). It is unclear, however, if betalains function as light screens in fruits as has been proposed for anthocyanins.

6.3.3 *Carotenoids*

Most, but not all, plant carotenoids are made up of a C_{40} carbon skeleton including a central polyene chain and two end rings (Figure 6.3). The number of conjugated double bonds ranges between 9 and 14 giving rise to absorption of blue and blue–green light, respectively (Vetter *et al.*, 1971; Britton, 1985, 1995; van den Berg *et al.*, 2000). If the central polyene chain is in the all-*trans* configuration, the UV absorption of the carotenoid is low; with *cis* configurations, however, the UV absorption peak is higher and can reach roughly one-third of the maximum absorption in the visible range (Molnár and Szabolcs, 1980; Bialek-Bylka *et al.*, 1998; Phillip *et al.*, 1999). It is unclear, however, if accumulation of *cis*-carotenoids is sufficient to affect plant surface optics in the UV.

Carotenoids are synthesised in plastids (Lichtenthaler, 1999; van den Berg *et al.*, 2000; Hirschberg, 2001) where they are normally located. In chromoplasts, the yellow, orange or red carotenoid colours are apparent, but in the green chloroplast, these colours are masked by the green chlorophylls (Bartley and Scolnik, 1995). In green leaves, plastids are absent from epidermal cells, with the exception of stomatal guard cells, although some extreme-shade plants do possess chloroplasts in normal