Chapter 21

Delayed Greening

Delayed greening of young leaves is a phenomenon in which instead of being green, these young leaves express various conspicuous colors (white, pink, red, very light green) (Fig. 20.4), is a common phenomenon in the tropics (Richards 1996). The hypothesis that delayed greening is associated with low nutritive value in young leaves of tropical plants, and that this property defends them from herbivory (Kursar and Coley 1991, 1992, 2003; Coley and Barone 1996) is a special case of a more general hypothesis about low nutritive value as defense (Feeny 1976; Moran and Hamilton 1980; Augner 1995). A similar principle based on a very different mechanism is known to operate well as defense in many leaves, stems, and young fruit that produce high levels of tannins and other protease inhibitors that decrease protein availability during digestion (Robbins et al. 1987; Bernays et al. 1989; Ryan 1990) or in flowers with diluted nectar as defense against nectar robbers (Irwin et al. 2004).

The defensive function of delayed greening was tested in the forest by Numata et al. (2004), who showed that seedlings of various species of the genus *Shorea* (Dipterocarpaceae) that express delayed greening indeed suffered less damage from insect herbivory than species with regular greening. A second test of the possibility of a defensive potential of delayed greening and red young leaves conducted in Ecuador and Panama also showed clearly that this character is associated with reduced herbivory (Queenborough et al. 2013). A similar or related phenomenon occurs in *Conocarpus erectus* (buttonwood), which has polymorphic leaf color. In buttonwood, some individual plants are silvery and some are green, but some change from green when young to silvery later. Silvery leaves in buttonwood suffer less insect herbivory (Schoener 1987, 1988; Agrawal and Spiller 2004). Yet despite the high likelihood that delayed greening is effective, and probably also operates outside the tropics, this hypothesis has not received the attention it merits.

Lev-Yadun (2009a) proposed that the associations of being unpalatable with conspicuous colors (delayed greening *per se*, and all other colors expressed by such young leaves) may signal herbivores about the lower nutritive value, a typical aposematism. At the same time, such coloration may also undermine herbivorous insect camouflage (e.g., Lev-Yadun et al. 2004a; Lev-Yadun 2006a, 2009a).