Defensive Coloration in Plants: A Review of Current Ideas about Anti-Herbivore Coloration Strategies

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ABSTRACT

In addition to the many anti-herbivore defense mechanisms, plants have probably also adopted various types of defensive coloration: (1) undermining herbivorous insect camouflage, (2) aposematic (warning) coloration of thorny and poisonous plants, (3) camouflage, (4) insect and dead leaf mimicry, (5) various unexplained types of leaf variegation, (6) delayed leaf greening, and (7) signaling about trees' defensive quality by red and yellow autumn leaves. At this initial stage of study of defensive plant coloration, many additional types and aspects of defensive plant coloration very likely remain experimentally unexplored, and even not recognized and described. Visually oriented animals were the selective agent for such types, by attacking defended and non-defended genotypes differentially. Many of the defensive types of coloration certainly perform various physiological functions concomitantly.

1. INTRODUCTION

Plants, being sessile and the main producers of terrestrial biomass, suffer never-ending pressure of various types of herbivory and have evolved a rich arsenal of anti-herbivore defense mechanisms. Examples include chemical defenses (poisons, inhibitors of digestion, resins and gums) (Fahn 1979, Biere *et al.* 2004), mechanical means such as spines (Janzen 1986, Grubb 1992), aposematism by odor (Eisner and Grant 1981), and herbivore satiation, e.g., certain bamboos that flower only once in 120 years (Janzen 1976) or mast years in trees (Kelly and Sork 2002). Plants also use several types of defense against herbivory provided by other organisms. Thorny plant neighbors function as nurse plants (Rebollo *et al.* 2002), attacked plants may emit volatile signals to call the predators (e.g., parasitic wasps) of the herbivorous insects assailing them (Kessler and Baldwin 2001, Kappers *et al.* 2005), mutualistic ants attack herbivores that approach their host plants (Huxley and Cutler 1991), and fungal endosymbionts may provide their hosts with a chemical defense (Clay 1990).
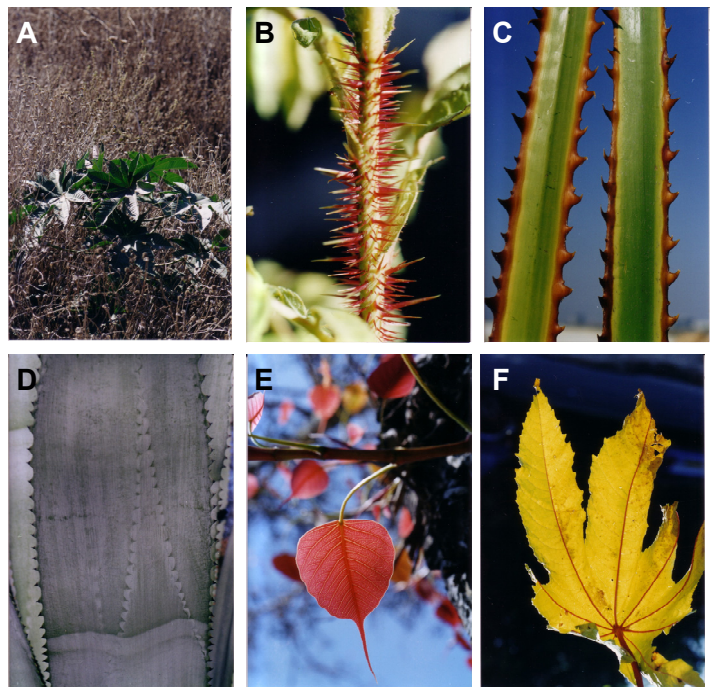

Fig. 1 (**A**) A green very poisonous young tree of *Ricinus communis* growing among dry plants in the coastal plain of Israel, an arid zone with ca. 6 dry months in the summer. Green is contrasting with the typical dry vegetation in summer, being conspicuous and may thus serve aposematism. (**B**) Red aposematic prickles of *Rosa* sp. growing in the plains of Canada, about 300 km north of Calgary. (**C**) The conspicuous aposematic spines along the petioles of the American palm *Washingtonia filifera*. A colorful panel connects the spines and enhances their conspicuousness. (**D**) Real red-brown aposematic spines along the margins of the leaves and their mimicry expressed by two rows of their printed copies along the center of the leaf in *Agave americana*, a common American ornamental in Israel. (**E**) A red young leaf of *Ficus religiosa*, a tree from India growing as an ornamental in Tel Aviv, Israel. Red young leaves are very common in the tropics, but not only there. Green or grey insects will be conspicuous to birds and other insects on such leaves if they will feed on them. (**F**) A yellow old leaf of *Ricinus communis* growing in the coastal plain of Israel. Yellow and red old leaves are very common in the temperate and other regions. Such coloration will undermine the camouflage of green or grey insects, exposing them to predators and parasites.

Before we turn to defensive plant coloration, it should be stressed that animals can see such optical signals. It was hotly debated whether mammalian or insect herbivores see colors or not, and if they do, to what degree. Recent reviews of this issue have provided enough data to conclude that they do see colors (Jacobs 1993, Dafni *et al*. 1997, Kelber 2001, Kelber *et al*. 2003). Large mammalian herbivores very likely do not see colors the way trichromatic humans do. Still, there are good reasons to conclude that even in the herbivores' dichromatic vision, colorful spines or other plant parts look different to them from regular green tissues because of their hue, saturation, or brightness (see Kelber *et al*. 2003). This view is supported by the fact that the "color-blind" cuttlefish successfully camouflage themselves in various backgrounds, possibly by using reflectance cues (Marshall and Messenger 1996). In both plants and animals, visually oriented animals were the agent that selected for defensively colored mutants, because animals see the visual patterns, change their behavior and thus, by attacking the non- or less defended genotypes more, select for the better defended ones.

Gould *et al*. (2002a), Lev-Yadun *et al*. (2002 2004), Schaefer and Wilkinson (2004) and Schaefer and Rolshausen (2006) have already proposed that plant colors serve more than a single function. Various hypotheses concerning coloration of leaves and other plant parts need not run counter to, or exclude any other functional explanation of specific types of plant coloration, and traits such as coloration that might have more than one type of benefit may be selected for by several agents. This is in accordance with Grubb`s (1992) view that plant defensive systems are not simple, and with Diamond`s (2005) view that single-factor explanations may fail when complex environmental issues are at issue. I emphasize that defensive coloration does not conflict with or exclude any other previous, current, or future defensive, reproductive, or physiological explanations of specific types of plant coloration (e.g., Lev-Yadun *et al*. 2004).

Defensive coloration has received very limited attention in plants compared with animals. In animals, it embraces various types of concealing and disruptive coloration, crypsis (including mimicry of plant parts, soil, stones, and animal droppings), aposematic (warning) coloration and mimicry of dangerous animals (e.g., Thayer and Thayer 1918, Cott 1940, Wickler 1968, Kettlewell 1973, Edmunds 1974, Majerus 1998, Merilaita 1998, Ruxton *et al*. 2004, Inbar and Lev-Yadun 2005, Merilaita and Lind 2005), described in thousands of publications (e.g., Komárek 1998). For instance, a brightly-colored animal (purple, red, orange, yellow, blue, white, black, or various combinations of such colors) is usually dangerous or unpalatable to predators - a trait that confers a selective advantage because predators learn to associate conspicuous coloration with unpleasant qualities (Cott 1940, Gittleman and Harvey 1980, Harvey and Paxton 1981, Wiklund and Järvi 1982, Ruxton *et al*. 2004, Speed and Ruxton 2005). The volume of proposed (and meagerly tested) defensive coloration in plants is much smaller, since botanists on the whole were generally reluctant to accept ideas that were commonplace for zoologists (Harper 1977, Lev-Yadun *et al*. 2002), and there is not one monograph or review on this issue. At this initial stage of study of defensive plant coloration, not only do many aspects of defensive plant coloration probably remain experimentally unexplored, but many basic facts, even at the morphological level, are without doubt not yet identified and described.

Here I will review the major hypotheses proposed concerning the role of plant coloration as defense from other organisms (mostly herbivores). Physiological aspects of plant coloration such as protection from photoinhibition and photo oxidation, have received considerable attention (e.g., Chalker-Scott 1999, Matile 2000, Hoch *et al*. 2001 2003, Lee and Gould 2002, Gould *et al*. 2002a 2002b, Close and Beadle 2003, Gould 2004) and will not be reviewed here. However, many cases of plant coloration exist for which the physiological hypotheses provide no explanation. For instance, photoinhibition and photo oxidation under high illumination, or having a moderate role in defense from UV, does not explain the common phenomenon of red, pink, purple, brown, yellow, light green, blue, or white leaf undersides, especially in deeply shaded habitats. The many well-documented cases of physiological gains of plant coloration should indeed not be ignored, but nor may the cases where physiological gains do not explain coloration, or the role of plant coloration in defense from various biotic agents be dismissed altogether. However, while the various physiological benefits are taken for granted and certainly not disregarded in this review, other, non-physiological views concerning the functions of plant coloration do exist. The understanding that many plants use visual signals to communicate with and advertise to animals is well-documented and tested. The involvement of such signals in pollination and seed dispersal has been demonstrated in many studies (e.g., Darwin 1877, Ridley 1930, Faegri and van der Pijl 1979, Willson and Whelan 1990, Weiss 1995, Clegg and Durbin 2003) and likewise will not be reviewed here. It is clear that plants regularly use signaling by color to communicate with animals.

2. HYPOTHESES AND DISCUSSION

2.1. General

Until recently, most of the few hypotheses on the operation of defensive coloration in plants were not discussed as constituting general defensive mechanisms. Hypotheses that received only little discussion were (1) aposematism in poisonous seeds (Cook *et al*. 1971, Williamson 1982), (2) aposematism in colorful poisonous flowers (Hinton 1973), (3) leaf variegation that somehow reduces herbivory (Cahn and Harper 1976), (4) red leaves as mimicry of dead or old ones or look unlike young ones (Stone 1979, Juniper 1994, Dominy *et al*. 2002, Gould 2004, Karageorgou and Manetas 2006, Manetas 2006), (5) protection from biotic factors, such as fungal attacks (Coley and Aide 1989), (6) camouflage postulated to act in pine seeds (Saracino *et al*. 1997 2004) or in plants of the genus *Lithops*, which resemble gravel in the desert (Cole 1970, Cole and Cole 2005), (7) insect mimicry by plants (mimicry of butterfly eggs, ants, aphids, poisonous caterpillars) (Rothschild 1974, Benson *et al*. 1975, Shapiro 1981, Williams and Gilbert 1981, Lev-Yadun and Inbar 2002), (8) young colorful leaves that attract herbivores and divert them from the more costly older ones (Lüttge 1997).

Several additional hypotheses on defensive coloration in plants seem to be more general: (1) delayed greening associated with low nutritive value in young leaves of tropical plants; (2) variegation in understory herbs in forests as camouflage; (3) red and yellow autumn leaves posited to signal to insects that the trees are well defended; (4) colorful or otherwise marked thorns that were proposed to be aposematic; (5) plant coloration that undermines herbivorous insect camouflage.

2.2. Delayed greening

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 1992, Coley and Barone 1996) is a special case of a more general hypothesis about low nutritive value

as defense (Moran and Hamilton 1980). A similar principle 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). Numata *et al*. (2004) showed that seedlings of various species of the genus *Shorea* (Dipterocarpaceae) that express delayed greening suffer less damage from insect herbivory than species with regular greening. Yet despite the high likelihood that this principle (delayed greening) is effective, and probably operates outside the tropics also, this hypothesis has not received the attention it merits.

2.3 Variegation

The hypothesis that variegation is common in understory herbs in the forests of New England and serves as camouflage (Givnish 1990, Allen and Knill 1991) has not received the attention it deserves either. The possibility that it operates in understory plants in the tropics or in temperate forests of Asia, Europe and South America has unfortunately not been examined. While this hypothesis seems to be true under the light regime of the forest understory, variegation in open habitats, such as grasslands, might be a different matter. For instance, the zebra-like marking of the very spiny annual rosette *Silybum marianum* (Asteraceae) is conspicuous from several up to tens of meters away (depending on leaf size and number of rosettes in a group) and was proposed to be aposematic against large mammalian herbivores (Lev-Yadun 2003a). This would appear to conflict with Givnish's (1990) conclusion that white leaf mottling serves as camouflage, but since Givnish (1990) studied understory species that grow in a habitat characterized by a mixture of dark and light spots, and not plants of open, well-illuminated areas, there is no contradiction. I therefore proposed that white mottling may act as camouflage in the forest undergrowth, as suggested by Givnish (1990), and as conspicuous aposematic coloration in open, well-lit areas (Lev-Yadun 2003a). In general, camouflage as defense in plants has enjoyed sparse attention not only regarding the shoot system, but even regarding seeds (e.g., Saracino *et al*. 1997 2004), where it is certainly an important and common defense.

2.4. Red autumn leaves

The liveliest discussion on defensive plant coloration recently has centered on the phenomenon of red autumn leaves. For many decades most people believed that these colors simply appear after the degradation of chlorophyll, which masked these pigments, and that they have no function. However, physiological benefits of autumn leaf coloration are well indicated, such as protection from photoinhibition and photo oxidation (e.g., Chalker-Scott 1999, Matile 2000, Hoch *et al*. 2001 2003, Lee and Gould 2002, Gould *et al*. 2002a 2002b, Close and Beadle 2003, Gould 2004, Ougham *et al*. 2005). Recently, the question of possible ecological benefits of this coloration has attracted considerable scientific attention. Currently, four defensive roles of this coloration against insect herbivory are proposed. The first, and most discussed, is that the bright colors of autumn leaves signal that the trees are well defended and that this is a case of Zahavi`s handicap principle operating in plants (Archetti 2000, Hamilton and Brown 2001, Hagen *et al*. 2003 2004, Archetti and Brown 2004, Archetti and Leather 2005), an idea partly or wholly discounted by some (Holopainen and Peltonen 2002, Wilkinson *et al*. 2002, Ougham *et al*. 2005, Schaefer and Rolshausen 2006). Archetti (2000) specifically rejected the possibility that the bright autumn leaf coloration is aposematic, and in the other studies favoring the signaling hypothesis (Hamilton and Brown 2001, Hagen et al. 2003 2004, Archetti and Brown 2004, Archetti and Leather 2005) aposematism is not discussed. Holopainen and Peltonen (2002) suggested that leaves that have just turned yellow are a good indication to aphids of nitrogen available in them in the form of amino acids, an attracting rather than a repealing signal. Wilkinson *et al*. (2002) held that rather than signaling defensive qualities to aphids, especially since these are drawn to yellow leaves, this coloration serves as a sun screen (a physiological role), and red colors help to warm leaves and function as antioxidants. Ougham *et al*. (2005) stressed the importance and good documentation of the physiological role of autumn leaf coloration. They argue that the signal is not costly, which, according to the most common view, is a basic feature of signals involved in the operation of Zahavi`s handicap principle. These authors also make the astute point that within-tree variation in coloration may indicate that an individual leaf approach is needed for a better understanding of the possible defensive role. Schaefer and Rolshausen (2006) postulated an upgraded and combined new hypothesis of defensive plant coloration, focusing on anthocyanins (second hypothesis). Elaborating on a previous idea by Fineblum and Rausher (1997) about the common biochemical pathways for flower color and defensive molecules, Schaefer and Rolshausen (2006) formulated the "Defense Indication Hypothesis". It posits that fewer herbivorous insects (and, I suggest, any sensitive herbivore) will feed on plants with strong anthocyanin coloration because it correlates with defensive strength. The biochemical basis for this correlation is that anthocyanins and a number of defense chemicals such as tannins stem from the same biosynthetic pathways. If the "Defense Indication Hypothesis" is accepted, and I think that there are very good reasons why it should be, I propose that it directly follows that plant parts rich in anthocyanins may serve in many cases as aposematic (warning) coloration for chemically-based unpalatability (third hypothesis). If the red-colored autumn leaves are well defended by various chemicals as proposed by Schaefer and Rolshausen (2006), or even if red and yellow autumn leaves are just of low nutritive value (two cases of unpalatability), all bright autumn leaves should be considered aposematic. Schaefer and Rolshausen (2006), however, clearly state that since according to their understanding autumn leaf coloration has evolved primarily because of physiological roles, and not as defense against herbivores, this coloration is not a signal (is not aposematic) and may be used only as a cue by the insects. The general issue of aposematic coloration in plants will be dealt in more detail later in this review. The fourth hypothesis concerning the defensive role of bright autumn coloration addresses undermining herbivorous insect camouflage. This hypothesis is general, and bright autumn leaves are a specific case to which this hypothesis is applicable. It has recently been suggested that the bright colors expose insects of green and various cryptic colors to predation (especially by birds) and that it may also cause them to avoid such leaves of unsuitable background coloration altogether (Lev-Yadun *et al*. 2004). Again, this issue will be dealt in more detail later. In sum, I propose that the evolution of autumn leaf coloration reflects several types of adaptation to internal physiological constraints and external environmental factors, as well as to biotic stresses.

2.5 Aposematism in plants - general remarks

Another major issue I discuss is aposematism in plants. The possibility that aposematism operates in plants was overlooked for over a century of intense studies of this strategy in animals. It then received very scant attention for 30 years till it was specifically suggested to be common in over a thousand thorny plant species originating in several continents (Lev-Yadun 2001). A number of authors (Cook *et al*. 1971, Hinton 1973,

Harper 1977, Wiens 1978, Rothschild 1980, Harborne 1982, Williamson 1982, Knight and Siegfried 1983; Smith 1986, Lee *et al*. 1987, Coley and Aide 1989, Givnish 1990, Tuomi and Augner 1993, Archetti 2000) all briefly mentioned a possible association between bright colors in plants and toxicity, but the scope and significance of this phenomenon was not determined. In fact, aposematic coloration was discounted in some of these studies (Knight and Siegfried 1983, Smith 1986, Lee *et al*. 1987, Coley and Aide 1989, Archetti 2000). Olfactory aposematism in poisonous plants was also proposed (Eisner and Grant 1981, Harborne 1982, Launchbaugh and Provenza 1993, Provenza *et al*. 2000), from my field experience it is probably a common phenomenon, but not much has been done to study it. Cook *et al*. (1971) referred to the grey color of poisonous seeds of *Eremocarpus setigerus* that doves (*Zenaidura macroura*) refrain from eating as "warning coloration", in contrast to non-toxic seeds with other colors. Hinton (a zoologist) (1973) suggested that the bright colors of flowers are aposematic because colorful flowers of some species are known to be poisonous to animals. This author further proposed that while the poisonous colorful species are probably aposematic, the other, non-poisonous ones perform Batesian mimicry. Flowers, however, are usually colored as advertisements for pollinators, and it is difficult to distinguish between two concurrent functions of the same coloration. We witness a case of preemptive scientific success when the understanding of the great significance of flower colors in attracting animal pollinators obstructs admitting a simultaneous function of the same coloration in repelling other groups of animals. Again, this issue deserves much more theoretical and experimental attention than it has received. Wiens (1978) briefly raised the question of whether the variegated or mottled patterns of coloration that characterize many plants, particularly their leaves, are aposematic, and gave several examples of poisonous plant parts with bright colors. Moreover, he proposed that unprotected plants might mimic the variegated patterns, but again his hypothesis, which was only a small section in his review essay, did not stimulate any broad effort of further research. Rothschild (1980) proposed that in certain poisonous plant species carotenoids might serve in aposematic coloration. Harborne (1982) proposed that the brightly colored, evil-looking purple black berries of the deadly *Atropa belladonna* warn grazing mammals of the danger to consume them. Williamson (1982) briefly proposed that brightly colored (red or red and black) seeds lacking an arillate or fleshy reward (e.g., *Erythrina*, *Ormosia*, and *Abrus*) might be aposematically colored to warn seed eaters of their toxicity. Knight and Siegfried (1983) considered whether green fruits signal unpalatability, and supposed that green does not provide enough contrast to be aposematic. This view, which seems to be correct in the green habitats they studied, might not hold in yellow desert environments where green may be aposematic (**Fig. 1A**) (Lev-Yadun and Ne'eman 2004). Smith (1986) hypothesized that leaf variegation may theoretically be aposematic, but concluded that for the vine species (*Byttneria aculeata*) he studied, the variegation was related to defense from herbivory, mimicking leaf mining damage. Although Smith (1986) rejected the aposematic hypothesis, he gave a clear and detailed formulation of the aposematic hypothesis for plants: "The benefits to the plant of chemical defense against herbivores would be greater if herbivores avoided such plants altogether, rather than testing leaves for palatability, and so causing some damage. A distinct leaf color pattern linked with chemical defense might function in this way. Polymorphism for leaf color should then coincide with polymorphisms for chemical defense. Müllerian and Batesian mimicry could result in evolution of similar patterns of variegation, with or without associated toxicity, among other species which have herbivore species in common with the model species" (p. 284). Givnish (1990) noted that Smith's (1986) rejected hypothesis regarding the aposematic value of leaf variegation should also be considered concerning leaf coloration, but did not discuss the issue further. Lee *et al*. (1987) concluded that anthocyanins in developing leaves of mango and cacao are not aposematic. Only one field experiment, by Cahn and Harper (1976), showed clearly that rumen-fistulated sheep, which could be directly sampled for diet-content, preferred unmarked leaves of *Trifolium repens* over marked ones, indicating the probable defensive value of such variegation.

2.5.1. Aposematism in plants - spiny plants

Colorful or otherwise visually marked thorns (**Figs. 1B, 1C**) were posited as aposematic (Lev-Yadun 2001 2003a 2003b, Lev-Yadun and Ne'eman 2004, Rubino and McCarthy 2004, Ruxton *et al*. 2004). This hypothesis was later applied to spiny aposematic animals (Ruxton *et al*. 2004, Inbar and Lev-Yadun 2005, Speed and Ruxton 2005), a rare instance of a hypothesis of defensive coloration originating in botany influencing zoology. This phenomenon, which seems to be very common, was described and discussed at three levels: (1) the floristic approach, studying it across large taxa (Lev-Yadun 2001) or floras or ecologies (Lev-Yadun and Ne'eman 2004, Rubino and McCarthy 2004), (2) the individual species level (Lev-Yadun 2003a), (3) mimicry of the phenomenon (Lev-Yadun 2003a 2003b). Although Midgley *et al*. (2001) did not specifically or directly refer to the typical conspicuous white thorns of many African *Acacia* trees they described as aposematic, in their study they presented enough characters of aposematism to support the aposematic hypothesis. Ruxton *et al*. (2004) and Speed and Ruxton (2005), elaborated on the principle that unlike poisons, aposematic thorns advertise their own dangerous quality (self-advertisement).

Two studies demonstrated that colorful spines might be aposematic at the broad taxa or floristic level. Lev-Yadun (2001) showed that two types of conspicuousness of thorns are typical of many plant species: (1) colorful thorns and spines, and (2) white and colorful spots and stripes associated with thorns and spines in leaves, stems, and fruits. Both types of aposematic coloration predominate the spine system of taxa rich in spiny species: cacti and the genera *Agave, Aloe,* and *Euphorbia*. It has been recorded in over a thousand species originating in several continents of the Old and the New World. The colorful thorn systems were commonly multi-colored (thorns were brown, yellow, red, white, gray, pink, black, and tan). For instance, in cacti, the spiniest taxon, in more than 50% of the species for which there were detailed data (e.g., Benson 1982), the spines were pigmented with 3-7 colors, and 88.6% of the 973 cacti species described in Preston-Mafham and Preston-Mafham (1994) had white markings associated with their spines (Lev-Yadun 2001). It has been proposed that conspicuous spines are beneficial for plants since herbivorous vertebrates remember the signal, and tend to avoid subsequent tasting of such conspicuous spiny plants. Furthermore, herbivores might pass over aposematic individuals and eat their non-aposematic neighbors, thus reducing the competition between the aposematic and neighboring plants (Lev-Yadun 2001). Rubino and McCarthy (2004) tested Lev-Yadun's (2001) aposematic hypothesis by examining the presence of aposematic coloration in thorny, spiny, and prickly vascular plants of southeastern Ohio, and because of their similar field results, reached the same conclusions (Rubino and McCarthy 2004).

2.5.2. White marking in aposematism

Concerning white aposematic marking, two evolutionary issues should be specifically mentioned. First, the significance of white marking in contrast to colorful marking, and second, the convergence of this character as expressed by geography and taxonomy. When a certain herbivore

is color-blind to a certain sector of the spectrum or is color-blind altogether; or when illumination is not strong or it has an altered color temperature for some meteorological or ecological reason - then white marking increases the possibility that the aposematic signal will still be visible. Since colorful aposematic signals associated with thorns in general and white ones in particular appear in plants of diverse geographical and taxonomic origins, it was proposed that this is an ancient signal that has been selected for many times (Lev-Yadun 2001).

2.5.3. *Aposematism in zebra-like plants*

A more focused study examined aposematism in spiny plants in a single species, comparing the strength of the aposematic signal in relation to age and size, correlating it with the strength of the defense (Lev-Yadun 2003a). The conspicuous rosette and cauline leaves of the very spiny Mediterranean winter annual *Silybum marianum* (Asteraceae) resemble green zebras. In the field, the white, large and zebra-like marking on the upper surface of the rosette leaves of *S. marianum* is conspicuous from several to tens of meters away, depending on leaf size and number of rosettes in a group. During the ontogeny of the rosette a clear positive correlation exists between the number and length of spines along the leaf margins and the extent of white variegation. The well-developed green cotyledons, several cm long, have neither spines nor variegation. In small rosette leaves, 2.8-4.0 cm long, which have up to ca 40 short (not longer than 1 mm) marginal spines, the white stripes are only ca. 1 mm wide and many of them are not continuous. By contrast, in most large, mature rosette leaves the white stripes are 4-6 mm wide and continuous. In the very large rosette leaves (70-92 cm long) the number of marginal spines in a single leaf ranges between 1,000 and 2,225. The widths of typical variegation bands proved closely correlated with leaf length, the length of the longest spines at the leaf margins, and the number of spines around the leaf circumference. Thus, there is a significant correlation between the spiny defense and strength of variegation, which means that the aposematic signal is honest (Lev-Yadun 2003a). However, such variegation may contribute physiologically to plants' fitness.

White variegation might have two additional (presently weakly supported) protective benefits against insect herbivory. The first is that the variegation serves as mimicry of tunnels of flies belonging to the Agromyzidae. The larvae of flies of this group tunnel and eat the photosynthetic tissues of leaves, which results in white variegation resembling that of *S. marianum*. The variegation might serve as mimicry of an already infected leaf to deter female Agromyzidae flies or other insects from laying eggs, or even to deter large vertebrate herbivores from eating damaged leaves that might express several defensive mechanisms following the previous damage induced by the insects (Lev-Yadun 2003a). A similar idea was proposed by Smith (1986), who hypothesized that leaf variegation in the vine species *Byttneria aculeata* was mimicry of leaf-mining damage as a defense against herbivory. Indirectly such a benefit is well indicated from the behavior of frugivores that avoid eating damaged fruit (especially in large fruit) (Janzen 1977, Herrera 1982, Manzur and Courtney 1984, Borowicz 1988). The second explanation is that such stripes may reduce insect landing on the leaves in general (Lev-Yadun 2003a). This idea was originally proposed for the evolution of zebra stripes as a defense against tsetse flies in Africa (Waage 1981, Brady and Shereni 1988, Doku and Brady 1989, Gibson 1992, Ruxton 2002). If the insect protection hypothesis is also true, the evolutionary advantage of zebra-resembling leaf variegation was two-fold and selected for by visually oriented vertebrate and invertebrate herbivores alike (Lev-Yadun 2003a).

2.5.4. *Mimicry of plant aposematism*

The last major issue I discuss concerning aposematic coloration in thorny, spiny, and prickly plants is mimicry of the phenomenon. Several authors have already proposed that mimicry operates in plants as an anti-herbivore mechanism. Wiens (1978) estimated that about 5% of land plants are mimetic, listing several types of protective plant mimicry. Butterfly egg mimicry in plants was proposed as a way to reduce egg laying by *Heliconius* butterflies (Benson *et al*. 1975, Shapiro 1981, Williams and Gilbert 1981). Stone (1979) proposed that the young reddish-brown leaves of palms growing in Malaya mimic the color of dead leaves, thus protecting them from herbivory. Mimicry of host leaf morphology is common in mistletoes and was proposed to give rise to crypsis and thus reduce herbivory (Ehleringer *et al*. 1986). Mimicry of feeding damage by caterpillars as the reason for the formation of leaf lobes in some Moraceae has also been posited (Niemelä and Tuomi 1987). Brown and Lawton (1991) postulated that the two non-spiny species *Celmisia lyalli* and *C. petriei* (Asteraceae) growing in New Zealand look rather like spiny members of the genus *Aciphylla* (Apiaceae). Three apparently novel types of visual insect mimicry have recently been described in plants (Lev-Yadun and Inbar 2002). In the first type, plants have dark spots and flecks in the epidermis of stems, branches, and petioles that resemble ants in size, shape, and pattern. In the second type, dark anthers are the size, shape, and color of aphids, and they sway in the wind like swivelling aphids. Finally, immature pods of several annual legumes have conspicuous reddish spots, arranged along the pods, causing them to look like aposematic lepidopteran caterpillars. It has been suggested that these morphological traits may serve as herbivore-repellent cues and that they are part of the plants` defense system (Lev-Yadun and Inbar 2002) and since coloration is involved, they may be considered special cases of aposematic coloration. From all these studies, it is clear that various types of mimicry may serve as defense against herbivory and that animals may be tricked into behaving according to the plant's interests by plant mimicry, as they are tricked by bee mimicry of orchid flowers during pollination (e.g., Dafni 1984).

Because the phenomenon of aposematic coloration and markings of real thorns, spines, and prickles in plants is so widespread, it is not surprising and even should be expected that mimics would have evolved. In animals, mimics of non-palatable or dangerous aposematically colored species are well known in invertebrates and vertebrates (Cott 1940, Wickler 1968, Edmunds 1974). The discussion of mimicry of thorny, spiny, and prickly plants proceeds at three levels: (1) Müllerian mimicry within the group of spiny plants, (2) weapon (spine) automimicry (within the same individual), and (3) Batesian mimicry, when non-thorny plants mimic thorny ones.

(1) When in a certain habitat the proportion of aposematic spiny plants increases for a period long enough for an evolutionary change, **Müllerian mimicry** may lead to the establishment of defense guilds (see Waldbauer 1988). Müllerian mimicry indeed seems to occur within the group of spiny plants because there are three very spiny zebra-like annual rosette plant species in the East Mediterranean region (*Silybum marianum*; *Notobasis syriaca*; *Scolymus maculatus*), and it has been proposed that a defense guild has evolved in these plants of the Asteraceae (Lev-Yadun 2003a).

(2) Weapon (spine) automimicry (within the same individual) may occur when impressions or color printing of spines on leaves of several dozens of species belonging to the genus *Agave* (**Fig. 1D**), one species of *Aloe*, and a palm species mimic their own real spines (Lev-Yadun 2003b). In most if not all *Agave* species, the developing leaves press hard against each other. The teeth along the margins press into the surface

of the same leaf, or another leaf, and the pattern of the teeth along the margins is copied and retained along the non-spiny parts of the leaves. For instance, in *Agave americana*, a common ornamental in Israel, the teeth copies are seen in many leaves. The species showing the most remarkable teeth mimicry is *A. impressa*, in which it is very conspicuous because of a white material that is printed on the false spines. The same type of colorful teeth along the margins and their mimicry by impression is obvious in the American palm *Washingtonia filifera* (Palmaceae), a common ornamental and a feral tree in Israel and in *Aloe* sp. (Liliaceae) (Lev-Yadun 2003b). This spine automimicry is a vegetal parallel to "weapon automimicry" of horns or canines known in several mammalian species (Guthrie and Petocz 1970).

(3) Batesian mimicry, when non-thorny plants mimic thorny ones by colorful elongated and pointed plant organs which despite their appearance and conspicuous coloration, are not sharp at all (Lev-Yadun 2003b). Simple mimicry by colorful thorn-like structures was found in several wild species growing in Israel. For example, in several *Erodium* sp., annuals of the Geraniaceae, the elongated fruits, several cm long, beak-like, pointed, and self-dispersing (by drilling into the soil), are red. In *Sinapis alba*, an annual of the Brassicaceae, the elongated and pointed distal part of the fruit, when fully developed but not yet ripe, looks like a spine and is colorful (yellow, red, purple, or various combinations of these). In *Limonium angustifolium*, a wild and domesticated perennial of the Plumbaginaceae, the distal part of its large leaves is red and looks like a spine although it is soft (Lev-Yadun 2003b).

There are two possible evolutionary routes toward mimicry of colorful thorns, spines, or prickles. In the first, an aposematic thorny plant may have lost its thorny character but retained the shape and aposematic signal. In the second, a non-aposematic and non-thorny plant can acquire the signal, becoming a primary mimic. Alternatively, the thorn-like structure and its coloration may have a different, unknown function. We have no field, developmental, or genetic data that may help in distinguishing between these options for any plant species.

2.6. Undermining invertebrate herbivores camouflage

Recently it has been suggested that many patterns of plant coloration may undermine the camouflage of small invertebrate herbivores (Lev-Yadun *et al.* 2004). This hypothesis attempted to provide a unifying general explanation for many of the vegetal coloration types found in nature. The essence of the hypothesis is based on a simple but new principle: that many patterns of plant coloration undermine the camouflage of invertebrate herbivores, especially insects and other small invertebrates, thus exposing them to predation, and in addition causing them to avoid plant organs with unsuitable coloration, to the benefit of the plants. This is a special case of "the enemy of my enemy is my friend", and a visual parallel of the chemical signals that plants emit to call wasps when attacked by caterpillars (Kessler and Baldwin 2001, Kappers *et al.* 2005). Moreover, this is a common natural parallel to the well-known principle basic to the phenomenon of industrial melanism (e.g., Kettlewell 1973, Majerus 1998, Cook 2000 2003, Grant and Wiseman 2002), which illustrates the great importance of plant-based camouflage for herbivorous insect survival and can serve as an independent test for the camouflage undermining defensive plant-coloration hypothesis. It was claimed that the enormous variations in coloration of leaves, petioles, and stems, as well as of flowers and fruits, undermine the camouflage of invertebrate herbivores, especially insects (Lev-Yadun *et al.* 2004). For instance, color differences between the upper and lower sides of leaves, and between the veins or petioles and the leaf blade, are common across diverse plant forms, from short annuals to tall trees, and in various habitats, from deserts to rain forests and from the tropics to the temperate region. Furthermore, leaf color frequently changes with age, season, or physiological condition. Young leaves of many tropical trees and shrubs (Richards 1996), as well as some non-tropical, are red (**Fig. 1E**) and later on become green, whereas in the temperate zones leaves of many woody species change to bright colors in autumn (**Fig. 1F**), as discussed above. Although it is generally agreed that the bright flower and fruit colors facilitate communication between plants and their pollinators and seed-dispersers (e.g., Ridley 1930, Faegri and van der Pijl 1979, Willson and Whelan 1990, Weiss 1995, Clegg and Durbin 2003, Schaefer *et al.* 2004), there is no *a priori* reason to assume that their colors cannot also serve as defense from herbivory.

Plants provide habitat and food for many animals, so it is logical to assume that visual perception of animals (both herbivores and predators) co-evolved with plants, as is well known from mutualistic plant/animal interactions. Intuitively, the common optimal camouflage for herbivorous insects should be green, and indeed, many, e.g., aphids, caterpillars, grasshoppers, have evolved green coloration (Cott 1940, Purser 2003). The effectiveness of green camouflage or colors that match barks is impaired by diverse non-green, or even a variety of green shades of plant backgrounds, as was evident with industrial melanism (Kettlewell 1973, Majerus 1998, Cook 2000 2003, Grant and Wiseman 2002). When a given leaf has two different colors - green on its upper (adaxial) side and blue, brown, pink, red, white, yellow or just a different shade of green on its lower (abaxial) side, a green insect (or one of any color) that is camouflaged on one of the sides will not be camouflaged on the other. The same is true for vein, petiole, branch, stem, flower, or fruit coloration. It has therefore been suggested (Lev-Yadun *et al.* 2004) that green or otherwise colored herbivores that move, feed, or rest during the day on plant parts that have different colorations from their own immediately become more conspicuous to their predators. Many plants are simply too colorful to enable a universal camouflage of herbivorous insects and other invertebrates to operate successfully, and they force small herbivores to cross "killing zones" with colors that do not match their camouflage. Since the variable coloration usually either is ephemeral (red young leaves or red or yellow autumn leaves) or occupies only a small part of the canopy (young leaves, petioles, flowers, and fruits), the gains for insects that have evolved to match such coloration are low (Lev-Yadun *et al.* 2004), and with low gains it is difficult to overcome this type of plant defense by evolution. The excellent color vision of many predators of insects, in particular insectivorous birds (the most common and significant predators of herbivorous invertebrates) (Van Bael *et al.* 2003), make undermining herbivores' camouflage highly rewarding for plants (Lev-Yadun *et al.* 2004). In heterogeneous habitats, optimal camouflage coloration should maximize the degree of crypsis in the microhabitats used by the prey, and herbivores may enjoy better crypsis in heterogeneous habitats (Endler 1984, Edmunds and Grayson 1991, Merilaita *et al.* 1999). Therefore, a plant with many colors may under certain conditions provide better crypsis than a unicolored one. Yet, the ratio between the size of the herbivore and the size of color patches of plants determines whether a certain coloration pattern will promote or undermine crypsis of the herbivore. Since insects are in general smaller than many of the color patches of leaves, flowers, fruits or branches, they will be exposed to predators and parasites and will not become more cryptic and better defended. I emphasize that many types of variegation that form small-scale mosaics are not considered undermining insect camouflage. This important issue has been partly addressed by Schaefer and Rolshausen (2006) and should be documented and analyzed under natural conditions to allow better understanding. The special importance of the hypothesis on herbivore camouflage-undermining (Lev-Yadun *et al.* 2004) is that it imparts a defensive function not only to the orange, pink, red, brown, blue, and black colors that stem from

anthocyanins, which are correlated with various defense chemicals (Schaefer and Rolshausen 2006), but also to light green and white colorations, which lack such an explanatory connection. Comparison of the level of insect herbivory of red or green morphs of young leaves of *Quercus coccifera* showed less herbivory of the red morph. This has been interpreted as either the outcome of lower visibility of red leaves to insects (a type of camouflage) or as the operation of the undermining of the herbivorous insect camouflage (Karageorgou and Manetas 2006).

3. CONCLUSIONS AND REMARKS

Plants have adopted a varied arsenal of defense mechanisms against herbivores. The evolutionary arms race between plants and herbivores, which caused and still causes strong selective pressures on plants, selected for not only chemical, mechanical, and temporal defenses, but also for various coloration patterns. Traits such as coloration, which often has more than one type of potential benefit, may be selected for by several agents and evolve more quickly than characters with a single type of advantage. Plant coloration can be altered by genetic engineering, or by using color mutants, and both herbivore and predator behavior can be tested. The countless patterns of coloration in plants facilitate the possibility to clone promoters with specific expression patterns that may be very valuable in biotechnology, in addition to the direct cloning of genes related to the function of colors. Color patterns and pigment molecules have considerable economic value in many agricultural products, health foods, and pharmaceutics. In this respect dealing with plant coloration is not a mere theoretical issue. In the last two decades, most talented people in plant sciences have focused on molecular issues, and most funding has been allocated to biotechnology. Therefore, field botany and organismic issues are left behind, unattended. Now is the time for ambitious scientists to pursue such issues, and make their indelible mark in botany.

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