



Weapon (thorn) automimicry and mimicry of aposematic colorful thorns in plants

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Abstract

In order to further characterize the function of coloration in plants as defense against herbivory, two types of thorn mimicry are described: (1) A unique type of weapon (thorn) automimicry (within the same individual) that was previously known only in animals, and (2) mimicry of aposematic colorful thorns, by colorful elongated and pointed plant organs (buds, leaves and fruit) that, despite their appearance, are not sharp. Some thorny plants including dozens of species of *Agave*, one species of *Aloe* and a palm species have thorn-like imprints or colorations on their leaves, constituting thorn automimicry by giving the impression of more extensive thorns. The mimicry of aposematic colorful thorns is a typical case of Batesian mimicry, but the thorn automimicry is a special intra-organismic Batesian mimicry. I propose that both types of mimicry serve as anti-herbivore mechanisms.

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1. Introduction

Cases of automimicry, i.e. mimicry of some parts in other parts of the same individual, have rarely been described. Weapon automimicry of horns or canines has been shown in several mammalian species (Guthrie and Petocz, 1970) and has been proposed to be of intraspecific threatening value. However, this intriguing idea has not been examined in plants. The best-known case of mimicry in plants is mimicry of animals by orchids of the genus *Ophrys* that mimic female bees and are thus pollinated by male bees that are attracted to them (Wickler, 1968; Wiens, 1978; Dafni, 1984). Similarly, the dark spots on the umbels of wild carrot (and several other species of Apiaceae) with dark central flowers that mimic insects are thought to attract potential insect pollinators (e.g. Eisikowitch, 1980). The same syndrome has been shown in the appearance of black spots on the ray florets of *Gorteria diffusa* (Asteraceae) that mimic resting bee flies, which tend to aggregate (Johnson and Midgley, 1997).

Several authors have proposed mimicry in plants as an anti-herbivore mechanism. Wiens (1978) estimated that about 5% of the land plants are mimetic, listing several types of protective plant mimicry. 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 reddish/brown young 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 to form crypsids and thus reduce herbivory (Ehleringer et al., 1986). Mimicry of feeding damage by caterpillars on the leaf lobes of some Moraceae has also been proposed (Niemelä and Tuomi, 1987). Brown and Lawton (1991) proposed 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 and shape. In the second type, dark anthers are the size, shape and color of aphids, and they sway in the wind

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like swivelling aphids. Finally, immature pods of several annual legumes have conspicuous reddish spots, arranged along the pods, thus they appear to mimic lepidopteran caterpillars. It has been proposed that these morphological traits may serve as herbivore repellent cues and that they are part of the defence system of the plants (Lev-Yadun and Inbar, 2002). Weeds mimic crops in both morphology and physiology, thus they can manage in agricultural ecosystems (Barrett, 1983). Launchbaugh and Provenza (1993) discussed the question of odor and taste mimicry by plants and concluded that odor is not enough to establish a good mimicry and that a combination of both is needed. From all these studies, it is clear that mimicry serves in defense against herbivory and that animals are led to behave according to the plant's interests by plant mimicry.

Because thorns provide mechanical protection against herbivory (Janzen, 1986; Grubb, 1992), it has been proposed recently that herbivores learn to identify and avoid conspicuous, harmful thorny plants (Lev-Yadun, 2001). Thorns usually differ in color from leaves, being yellow, red, black, brown and white rather than green. In addition, white spots, or white and colorful stripes, are associated with thorns in leaves and stems. Both types of aposematic coloration predominate the spine system of taxa rich with spiny species—Cacti, the genera *Agave*, *Aloe* and *Euphorbia*. This phenomenon has already been found in about 1300 species originating in several continents of both the Old and New World (Lev-Yadun, 2001). *Agave* species can have two types of thorns in their leaves: spines at the distal end or teeth along the margins (Gentry, 1982), and in many species colored stripes along the margins enhance spine and teeth visibility (Lev-Yadun, 2001). A similar leaf type with side spine morphology is common in many palm and *Aloe* species.

Fieldwork in an ecosystem that has a millennia-long history of large-scale grazing, such as the land of Israel, clearly and “sharply” indicates the ecological benefit of being spiny. A continuous blanket of spiny shrubs and thistles covers large tracts of the land, and other parts are just rich with dozens of such plant species that dominate the vegetation. This dominance clearly indicates the adaptive value of being spiny when grazing pressure is high. It does not just slow the rate of feeding, but gives a considerable advantage to such plants. Spiny plants, such as *Echinops* sp. (Asteraceae), which usually grow as individuals or in small groups, sometimes become the most common perennial plant over many acres in grazing lands.

Aposematic coloration, a well-known phenomenon in animals, has recently been shown to be common in thorny plants (Lev-Yadun, 2001). In animals, where aposematic coloration is common in unpalatable or dangerous species, there are many cases of mimicry of

ants, wasps, poisonous snakes, etc., for protection from predation (Cott, 1940; Wickler, 1968; Edmunds, 1974). Usually, warning colors are red, yellow, black and white.

Here I describe two types of thorn mimicry: (1) impressions or color printing of thorns on leaves of several dozens of species belonging to three families that mimic their real thorns, and (2) colorful elongated and pointed plant organs that, despite their appearance, are not sharp at all. I propose that they serve to reduce herbivory.

2. Methods

As part of the study of aposematic coloration in plants (Lev-Yadun, 2001) and the general ecological significance of coloration (Lev-Yadun and Inbar, 2002; Lev-Yadun et al., 2002), patterns of coloration in various plant parts were examined in Israel in the years 1995–2002 in as many wild and cultivated species as possible. Because the aposematic coloration and markings of thorns in plants are so widespread (Lev-Yadun, 2001), it was expected that mimics would have evolved, and I searched for such mimics. After the phenomenon of spine automimicry was identified during fieldwork with *Agave* species cultivated in Israel, impressions of teeth along the leaves of *Agave* species were also examined in monographs that describe *Agave* species (Gentry, 1982; Sajeve and Costanzo, 1994). Plant species that showed coloration patterns similar to those of thorny plants, but that were not thorny (although they appeared to be so on first inspection) were also recorded.

3. Results

3.1. Weapon automimicry

Several dozens of *Agave* species show spine automimicry. In *Agave* species the developing leaves are strongly pressed against one another. The teeth along the margins press against 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. In *Agave americana* L., a common ornamental in Israel, the teeth copies are seen in many leaves (Fig. 1). The species showing the most remarkable teeth mimicry is *A. impressa*, in which the teeth mimicry is made of white material and is very conspicuous. However, the specimens of *A. impressa* I saw in Israel were still young and thus smaller than the ones described in Gentry (1982). The pictures of several dozens of other *Agave* species that were published in Gentry (1982) also show teeth mimicry. The other

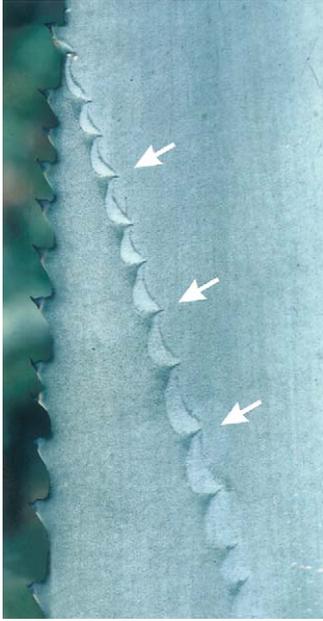


Fig. 1. A close-up of the teeth along the margins of *Agave americana* and a line of teeth pressmarks (arrows) (thorn automimicry) on the surface of the leaf.

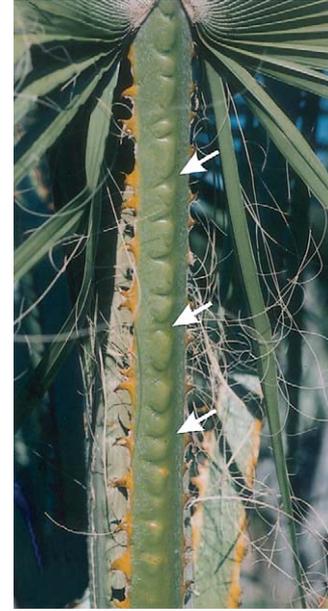


Fig. 2. The teeth pressmarks (arrows) on the surface of the petiole of a leaf of *Washingtonia filifera*.

species are *A. abrupta*, *A. applanata*, *A. avellanidens*, *A. bovicornuta*, *A. cerulata*, *A. colorata*, *A. cupreata*, *A. decipiens*, *A. deserti*, *A. flexispina*, *A. fortiflora*, *A. franzosini*, *A. gigantensis*, *A. gracilipes*, *A. guadalajara*, *A. horrida*, *A. kerchovei*, *A. macroculmis*, *A. maximiliana*, *A. mckelveyana*, *A. obscura*, *A. pachycentra*, *A. palmeri*, *A. parrasana*, *A. polyacantha*, *A. potatorum*, *A. pumila*, *A. salmiana*, *A. scabra*, *A. seemanniana*, *A. shawii shawii*, *A. sobria*, *A. victoriae-reginae*, *A. wercklei*, *A. wocomahi* and *A. zebra* (Gentry, 1982). Additional *Agave* species with such teeth mimicry are *A. ferox*, *A. lophantha*, *A. macroacantha*, *A. marmorata*, *A. parryi*, *A. triangularis*, *A. utahensis* and *A. xylonacantha* (Sajeva and Costanzo, 1994). The same type of colorful teeth along the margins and their mimicry by impression is obvious in the American palm *Washingtonia filifera* Wendl. (Palmaceae), a common ornamental and a feral tree in Israel (Fig. 2) and in *Aloe* sp. (Liliaceae) (Fig. 3).

3.2. Regular thorn mimicry

Colorful thorn-like structures were found in several wild species growing in Israel. In *Erodium laciniatum* (Cav.) Willd. subsp. *laciniatum*, an annual of the Geraniaceae, the elongated, several-cm.-long beak-like, pointed, self dispersing (by drilling into the soil), fruits are red (Fig. 4). In the small perennial desert herb *E. crassifolium* L'Her. (= *E. hirtum* Willd.), the elongated, several cm.-long beak-like, pointed fruits are partly or fully red. Another small perennial desert herb of this genus, *E. arborescens* (Desf.) Willd., has red,

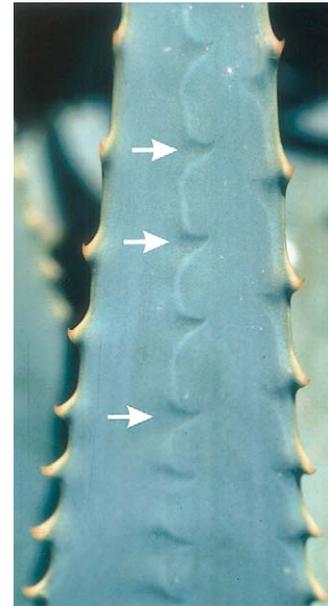


Fig. 3. The teeth pressmarks (arrows) on the leaf surface of *Aloe* sp.

elongated, several-cm.-long beak-like, pointed fruits that look like thorns although they are soft. In all these *Erodium* species, the green leaves are mixed with or very close to the colourful fruit. In *Sinapis alba* L., an annual of the Brassicaceae, the distal part of the elongated, pointed fruit, when fully developed but not yet ripe, is colorful (yellow, red, purple or various combinations of these). The pointed but soft distal ends of the new leaves of the perennial geophytes *Urginea maritima* (L.) Baker and *Asphodelus ramosus* L. of the Liliaceae are red or orange. In *Limonium angustifolium* (Tausch) Turill



Fig. 4. The red pointed but non-thorny fruit of *Erodium laciniatum* subsp. *laciniatum*.



Fig. 5. The red, spine-like but soft distal part of leaves of *Limonium angustifolium*.

[= *Limonium meyeri* (Boiss.) O. Kuntze], 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 (Fig. 5). The pointed but soft distal ends of leaves of the wild and domesticated shrub *Myrtus communis* L. (Fig. 6) of the Myrtaceae are red. The same phenomenon occurs in *Aegilops geniculata* Roth (= *A. ovata* L.), an annual of the Poaceae, in which the elongated, and several-cm.-long, spine-like but soft awns are red-purple.



Fig. 6. The pointed but soft red distal ends (arrows) of leaves of *Myrtus communis*.

The pointed distal part of the fleshy leaves of *Carpobrotus acinaciformis* L. Bol. (= *Mesembryanthemum acinaciforme* L.), a clonal perennial of the Aizoaceae, is red in many cases. Similarly, the pointed distal part of the fleshy leaves of *Aeonium decrum* Webb (= *Sempervivum decorum* Christ.), a small shrub of the Crassulaceae, is red in many cases, as it is in several other unidentified species belonging to the genus *Aeonium*. Roses (*Rosa* sp.) have colorful (whitish, yellow, orange, red, brown, black) spines along their stems. The buds that develop from suppressed buds along stems that are several years old are, temporarily while they are small and soft, the size of, spaced as and colored like the spines. It would be easy to mistake these soft buds for spines (Fig. 7).

4. Discussion

No defense system or mechanism is perfect. Assuming that a perfect defense system could exist is naive. All types of defense have a cost and an organism has to make an evolutionary and physiological decision of how much defense it can achieve at any point in time. When a new defense is established the particular organism is better defended with the new character than without it. The types of defense discussed here are no different—they are not perfect.

I am aware of the hot debate concerning whether mammalian herbivores see colors or not or to what degree. However, recent reviews provide enough data to conclude that they do (Jacobs, 1993; Kelber et al., 2003). It is quite probable that large herbivores do not see color

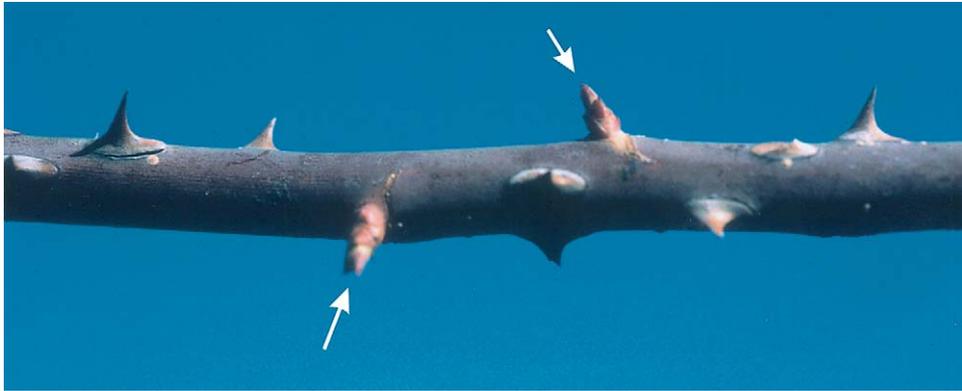


Fig. 7. The buds that develop along stems of *Rosa* sp. (arrows) are spaced and colored like the real spines.

the way we do. However, there are good reasons to think that even with dichromatic vision, colorful spines or spine mimics will look different 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). Since spines in so many species are colorful (Lev-Yadun, 2001), it is easy to accept previous proposals that a certain measure of color vision operates in large herbivores (see Janzen, 1986).

Because aposematic coloration and markings of real thorns in plants are so widespread, it is not surprising and even should be expected that mimics would have evolved. In animals, mimics of aposematically colored species are well known in both invertebrates and vertebrates (Cott, 1940; Wickler, 1968; Edmunds, 1974). There are two possible evolutionary routes toward mimicry of colorful thorns. 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 structure and coloration may have a different, unknown function. Williamson (1982) proposed that because plants are sessile, plant mimics are less likely to be mistaken for their models than animal mimics, which are mobile (a view which is only partly correct as plants, especially their leaves, move in the wind, as do light spots within the canopy). He also proposed that the autonomy of plant appendages implies that warning mimicry provides less advantage to plants than animals because plants, which can usually regenerate, suffer less than animals from sampling by naive herbivores. On the contrary, Augner and Bernays (1998) studied the conditions for an evolutionary stable equilibrium of defended signaling plants and plants mimicking these signals. The modeling showed that mimicry of plant defense signals may be common, and

even imperfect mimics could invade a population of defended signaling plants. Theoretically, selection allows the success of even poor and imperfect mimics (Edmunds, 2000).

Conspicuous thorns were proposed to be beneficial for plants as herbivorous animals would remember the signal and tend to avoid subsequent tasting of such marked plants (Lev-Yadun, 2001). I propose that the plants that mimic colorful thorns that were presented here may benefit from thorn mimicry even when this mimicry is imperfect. They are typical Batesian mimics (see Wiens, 1978 for definitions) in which non-protected organisms mimic dangerous ones. I propose that the plants that automimic thorns, but have fewer real thorns than the amount they appear to show, may benefit from thorn automimicry even if the mimicry is not perfect. This is a special case of Batesian mimicry in which protected organisms mimic dangerous ones, or in this case non-protected tissues mimic protected ones.

The pressmarks that constitute spine mimicry in *Agave*, *Aloe*, and in the palm *Washingtonia filifera* might form as a developmental constraint during leaf development. This, however, does not imply that these pressmarks, which look like real spines, have no other function or benefit. For instance, plants produce volatiles following wounding by herbivores. Wasps, however, use these cues, and approach to prey upon the herbivore insects (Baldwin et al., 2002). Thus, the use of an existing system in plants for alternative reasons, such as for defense as proposed here, is a known principle.

The spine automimicry shown here is a vegetal parallel for “weapon automimicry” of horns or canines known in several mammalian species (Guthrie and Petocz, 1970). In both plants and animals, animals were the selective agent that selected for such mutants, because animals see the visual patterns, change their behavior and thus by attacking more the non-mimic genotypes select for the mimics.

The morphologies shown here further indicate that the role of plant coloration/shape in anti-herbivore

defense deserves more attention (see Lev-Yadun et al., 2002).

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