Plant coloration undermines herbivorous insect camouflage

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Summary

The main point of our hypothesis "coloration undermines camouflage" is that many color patterns in plants undermine the camouflage of invertebrate herbivores, especially insects, thus exposing them to predation and causing them to avoid plant organs with unsuitable coloration, to the benefit of the plants. This is a common 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. Moreover, this is also a common natural version of the well-known case of industrial melanism, which illustrates the great importance of plant-based camouflage for herbivorous insects and can serve as an independent test for our hypothesis. We claim 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. We assume that the same principle might operate in certain animal–parasite interactions. Our hypothesis, however, does not contrast or exclude other previous or future explanations of specific types of plant coloration. Traits such as coloration that have more than one type of benefit may be selected for by several agents and evolve more rapidly than ones with a single type of advantage. ***BioEssays*** **26:1126–1130, 2004.**

Introduction

While flowers and fruits exhibit enormous variations in coloration, leaves, petioles and stems can also be quite colorful. Many higher plants inhabiting diverse terrestrial ecosystems worldwide exhibit remarkable interindividual and intraindividual and organ color variation. While the evolutionary role of color patterns in animals has received considerable attention,(1–4) their general adaptive value, especially in vegetative plant parts, is still unclear.(5) Thus, it is worthwhile to formulate a unifying theory that explains the adaptive significance of the many common color patterns found in plants. Here we propose a new concept (coloration undermines camouflage) in plant defense against herbivory, namely, that many of the diverse color patterns, mainly in vegetative, but also in reproductive plant organs, undermine the visual camouflage of many herbivorous invertebrates, especially insects. These patterns of coloration thus both expose them to their predators and cause them to avoid plant parts that do not match their color, to the benefit of plants. We think that the same principle might operate in certain animal–parasite interactions.

Color differences between the upper and lower sides of the leaves and between the veins or petioles and the leaf blade are common phenomena (Fig. 1A–D) across diverse plant forms, from short annuals (Fig. 1E) to tall trees (Fig. 1F), 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(6) as well as some non-tropical trees and shrubs are red and later on become green (Fig. 1G), whereas in the temperate zones, leaves of many woody species change to bright colors in the autumn, not only following the loss of chlorophyll, but also because of de novo synthesis of anthocyanins(7–9) (Fig. 1H). Although it is generally agreed that the bright flower and fruit colors facilitate communication between plants and their pollinators and seed-dispersers,(10–14) the functions of the colors of the vegetative parts are only partly understood.(5) Theoretically, such coloration may represent non-adaptive traits that exist because of developmental or physiological constraints, but several adaptive hypotheses for plant colors have been put forward. Among them are protection from UV damage and photo-inhibition,(8,15,16) mimicry of dead leaves,(17) response to low temperatures(18) or to water shortage,(19) increasing leaf temperature,(20) protection from oxygen toxicity,(21) and protection from biotic factors, such as fungal attacks(22) and herbivory.(23,24) So far no general role as to the significance of leaf coloration for plant fitness has been suggested and accepted.(25,26) The many colors of spines and spine-associated coloration have been proposed to be aposematic(27–30) and the color spots and flecks on various plant parts have been proposed as a form of insect mimicry(31) or

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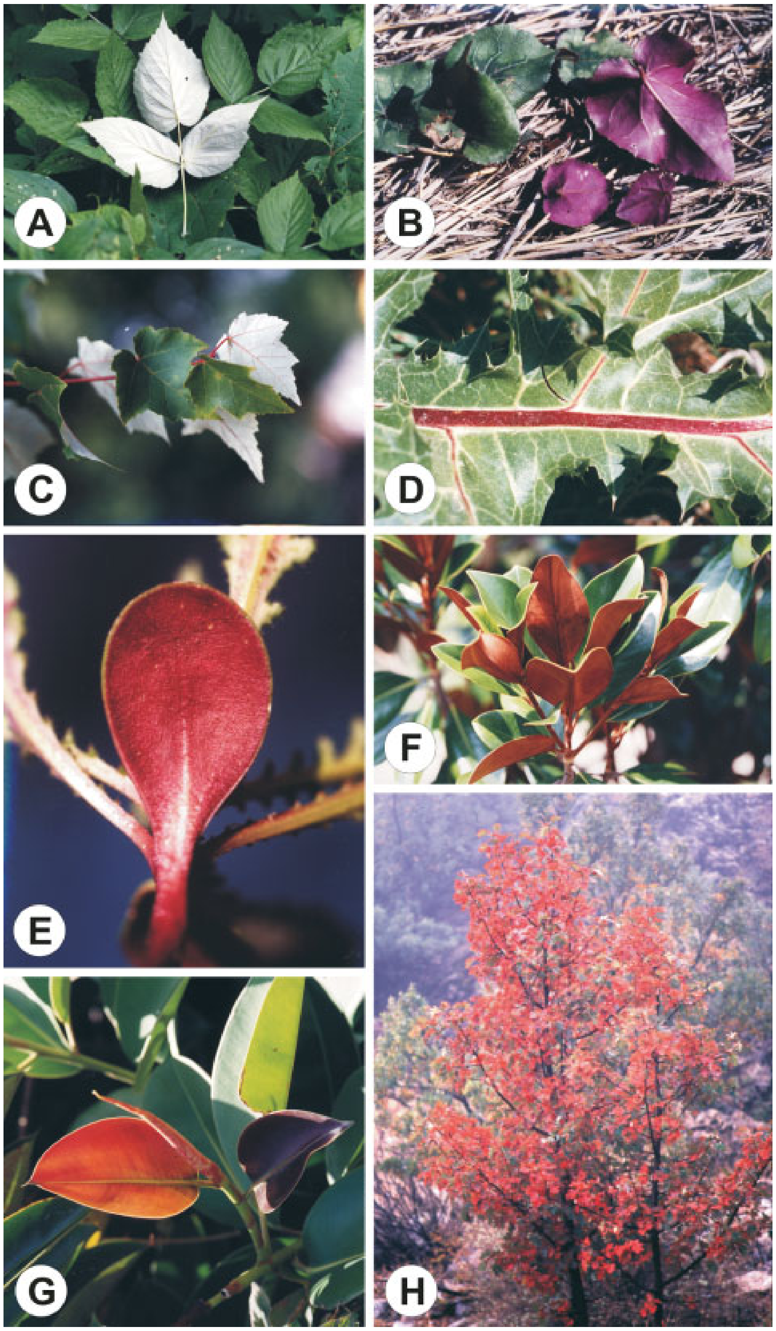

Figure 1. Demonstration of some common color patterns in plants.5 **A:** Leaves of the shrub *Rubus* sp. (Rosaceae) from Athens, Ohio, showing clear color differences between the green upper and white lower sides. **B:** Young leaves of the perennial geophyte *Cyclamen persicum* Miller (Primulaceae) from Israel, showing green variegated upper and purple lower sides. **C:** Leaves of the tree *Acer* sp. (Aceraceae) from Raleigh, North Carolina, showing green upper and white lower sides, and red petioles and veins. **D:** A leaf of the perennial hemicryptophyte *Gundelia tournefortii* L. (Asteraceae) from Israel, showing red veins. **E:** A cotyledon of the annual *Matricaria* sp. (Asteraceae) from Israel, showing its red underside. **F:** Leaves of the tree *Magnolia* sp. (Magnoliaceae) from Raleigh, North Carolina, showing green upper and brown lower sides. **G:** Red young leaves of the tropical tree *Ficus elastica* Roxb (Moraceae) from Tel Aviv, Israel. **H:** Red autumn leaves of a deciduous tree growing on Mount Hermon, Israel, at an elevation of ca 1,600 m above sea level.

camouflage in herbs of the forest understory[32] all protecting plants from herbivory. Nevertheless, the possible general adaptive value of coloration of petioles, leaf veins and barks has been overlooked. We thus propose a simple principle: plant coloration decreases herbivory by undermining herbivores' camouflage, thus having a broad ecological and evolutionary significance for plant survival, reproduction and evolution. In addition, avoidance of certain colored plant parts by herbivorous insects so as to lower visual detection by predators might add to the plant's direct benefits from predation on their herbivores. Below, we discuss several lines of evidence (industrial melanism, caterpillar and bird behavior, insect habitat selection, insect and bird vision) that support our hypothesis, which does not contradict or exclude other benefits of specific plant coloration previously proposed by others and mentioned above. The multiple benefits from improved photosynthesis, water balance, protection from UV irradiation, cooling and heating, and reduced herbivory might increase the adaptive value and enhance the rate of evolution of coloration within taxa and result in common convergence.

The ecological and evolutionary importance of coloration and camouflage for insect survival has received much attention, leading to several hypotheses and their experimental testing. Some insects adapt to plant coloration as a consequence of the evolutionary arms race between plants and herbivorous insects. Many populations of insect herbivores show a remarkable polymorphism and optimize local crypsis to fit the heterogeneity of the microhabitats of their host plants. Such intraspecific color polymorphism has been found for example in stick insects,[33] grasshoppers[34] and butterflies.[35,36] Plant organs, including leaves and stems, often change their colors with age or season. There is evidence that certain arthropods can trace these changes and modify their coloration to optimize their crypsis, e.g., the coloration of hawkmoth caterpillars is determined by the reflection of the background that they perceive soon after hatching.[37] In other lepidopterans, food content and quality are key factors in determining larval color and morphology, which enhance crypsis.[36,38] Green's[38] classic study demonstrated the importance of intra-plant variation in caterpillar coloration. On a given oak (*Quercus* sp.) host, caterpillars of *Nemoria arizonaria* may develop into a 'catkin' or 'twig' morph to maximize their camouflage. Some stick insects (Phasmatodea) may adjust their color with changes in the color of the host plant's foliage.[33] Many insects see colors, distinguish between shapes, and select their habitat accordingly.[39–44] Poisonous caterpillars are known to consume leaves at their near reach, leaving tattered edges, with no fear of being detected by birds[45,46] whereas non-poisonous caterpillars try to eliminate evidence of foraging by snipping partially eaten leaves, or by moving away from them, by keeping leaf shape intact by eating the contours, or by feeding from the lower side or at night.[45,46]

Industrial melanism[2] and the reverse process[47–50] illustrate the great importance of plant-based camouflage for herbivorous insects and can serve as an independent test for our hypothesis. Air pollution following the widespread use of coal in England and the USA in the 19th century resulted in the overall darkening of the environment, and the consequent increase in the proportion of dark morphs in many insect populations. This change was brought about by selective predation by birds of the lighter morphs, which did not match the new, darker background of tree trunks, branches and foliage.[2] The marked reduction in air pollution over the last decades and the consequent lightening of the environment was followed by the subsequent decrease in proportion of the dark morphs in both England and the USA.[47–50] This large-scale natural experiment clearly demonstrates the adaptive significance of color matching of insects and their vegetal background.[51] Experiments of selective predation of various color morphs of caterpillars, not related to industrial melanism, provided similar results.[52,53]

The hypothesis that plant coloration undermines herbivorous insect camouflage

Plants provide the habitat and food for many animals, and therefore it is logical to assume that visual perception of animals (both herbivores and predators) co-evolved with plants. In heterogeneous habitats, optimal camouflage coloration should maximize the degree of crypsis in the microhabitats used by the prey.[52,54] The efficiency of herbivore crypsis is significantly constrained because plants are heterogeneously colored. Intuitively, the common optimal camouflage for herbivorous insects should be green, and indeed, many of these, e.g., aphids, caterpillars, grasshoppers, have evolved green coloration.[1] The effectiveness of this common camouflage is compromised, however, by the patterns of diverse non-green, or even a variety of green shades of plant backgrounds. As was evident with industrial melanism, we suggest that green or otherwise colored herbivores that move, feed or rest during the day on plant parts that have different colorations, immediately become more conspicuous to their predators. 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 otherwise colored one) 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. Colorful veins make it easier for birds to detect damaged leaves, a hunting clue to search these leaves for insects, e.g.[55] 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 areas ("killing zones") with colors that do not match their camouflage. Since the variable coloration is usually either ephemeral (red young leaves or autumn red leaves) or occupies only a small part of the canopy (young leaves, petioles, flowers and fruits), the selective pressure on insects to evolve to match such coloration is low and of a limited adaptive value.

Experimental tests of the hypothesis

Of the many experiments conducted on feeding strategies of herbivores in relation to predation risks, those focusing on timing, selection of background, mimicry of plants, position of the herbivore on the leaf, modes of feeding and the concealing damage to plant tissues pertain to the presented hypothesis. In such studies, birds (mostly tits *Parus* spp.) and caterpillars or grasshoppers in large aviaries were used. Our hypothesis can be tested in such experimental setups where the colors of plant organs as well as those of caterpillar bodies can be manipulated. Consequently, the fitness of the herbivore and the efficacy of its predator can be evaluated (e.g. Refs. 56,57). A different approach would be to manipulate organ and insect coloration on photographs and monitor the behavior of potential predators, (e.g. Ref. 58). It is possible to alter plant coloration by genetic engineering, or by using color mutants, and to test both herbivore and predator behavior. Genetic engineering seems to be better as it might lower variability of other possible signals such as odor. Plants, in which the color of one side of the leaf, or that of a petiole or vein, or of the bark was changed, can be used to examine if herbivore choices concerning landing and feeding sites have changed. Similarly, birds' ability to inspect prey, and herbivore survival with changing plant colors, can be studied. There is the question of the ability of other predators of insects that use colors for crypsis from their prey and their own enemies, e.g., spiders, mantids, chameleons, snakes and frogs to prey upon insects when plant colors change. Since many birds and insects see UV,[59] testing the camouflage of many insect species in the UV, as was done for the peppered moth,[51] is essential. Moreover, we have a very fragmentary view of how plants look in the UV, and this understanding should be established for both issues of herbivory and protection from UV radiation.

Conclusions

Plants have adopted a variable arsenal of defense mechanisms against herbivores. The evolutionary arms race between plants and herbivorous insects, which caused and still causes strong selective pressures on plants, thus seems not to have been limited to chemical, mechanical and temporal defenses, but also includes the evolution of coloration patterns, specifically, to undermine herbivore camouflage. As no defense is perfect and it is certain that some animals can overcome it, protective coloration is yet another round in the arms race between vascular land plants and herbivores, which has been going on for at least 430 million years. Because it is ubiquitous, undermining the camouflage of herbivores, has probably evolved convergently many times. The excellent color vision of predators, in particular insectivorous birds, which are the most common and significant predators of herbivorous invertebrates,[60] made undermining herbivores' camouflage highly rewarding for plants. Plants are thus not a passive member in the tri-trophic system of plants–herbivores–predators, but rather an active and tricky one. This (coloration undermines camouflage) is a unifying hypothesis that may explain the various plant colorations, changes of color or differences in the contrast of seedlings, young leaves, autumn leaf coloration, leaf parts in general, stems, flowers and fruit. This hypothesis, however, does not contrast or exclude other previous or future explanations of specific plant coloration. Traits like coloration that have more than one type of benefit may be selected for by several agents and evolve more quickly than ones with a single type of advantage.

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