

This paper has been contributed in honor of Professor Abraham Fahn on the occasion of his 90th birthday.

Defensive functions of white coloration in coastal and dune plants

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ABSTRACT

Trichomes are known to have many functions, including protecting plants from excess sunlight, improving water economy, salt secretion, defense from herbivores, and signaling to animals. Additional anti-herbivore functions of trichomes, especially in coastal and desert habitats, are reviewed and proposed. Many sand-dune and sandy shore plants are white, whitish, or silver-colored because of white trichomes, because of sticky glandular trichomes to which sand grains and clay adhere, or because of light-colored waxes. The common explanation for this coloration is that it protects from irradiation, and that in addition, the glued sand defends them from abrasion by moving sand. This coloration was also proposed to camouflage the plants from herbivores. Similar coloration in animals that live in white, snow-covered habitats or light-colored sand or other soil substrates is commonly referred to as camouflage, and the same logic may also apply to plants. It has also been proposed that white plant surfaces undermine the camouflage of herbivorous insects that have other colors and expose them to predation. Three novel defensive mechanisms are proposed here: (1) because dust is a strong insect repellent and is lethal to insects, attached soil particles (especially clays) may defend plants with sticky glandular trichomes from insect herbivory; (2) in dicotyledonous plants that have sticky glandular trichomes, the attached sand may defend from herbivory by mammals by causing teeth wear as do phytoliths (silica bodies) of grasses; and (3) white coloration of leaves and branches may mimic fungal infestation. Direct experimental data for the functionality of these defensive mechanisms are missing for many of the old and all new hypotheses, but there are many indirect supporting indications.

Keywords: camouflage, crypsis, herbivory, insects, mimicry, phytoliths, sand, trichomes, white coloration

INTRODUCTION

Trichomes, the unicellular and multicellular appendages of the epidermis (Fahn, 1990), are well known for their multiple functions in plants. Trichomes may serve in protecting plants from excess sun irradiation of various wavelengths, including UV (Johnson, 1975; Ehleringer et al., 1976; Fahn and Cutler, 1992; Manetas, 2003), secrete toxic ions, especially in saline habitats (Waisel, 1972; Fahn, 1988), function in water absorption (Fahn and Cutler, 1992; Benzing, 2000), reduce transpiration (Fahn and Cutler, 1992; Werker, 2000), defend from insect or other herbivorous invertebrates by reducing ac-

cessibility or actual trapping of their legs or by chemical means (Levin, 1973; Fahn, 1979, 1988; Werker, 2000), and defend from large herbivores when they sting, as in *Urtica* (Thurston and Lersten, 1969; Levin, 1973; Fahn, 1990; Fu et al., 2006). In addition, in certain carnivorous plants such as *Drosera* and *Dionea*, they may take part in the attraction, capture, or digestion of insects (Juniper et al., 1989; Fahn, 1990).

Crypsis is a primary defense, common in many animal taxa (both vertebrates and invertebrates) of marine and terrestrial habitats, including tropical, desert,

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subtropical, temperate, and arctic habitats (Cott, 1940; Kettlewell, 1973; Edmunds, 1974; Endler, 1978, 1984; Stamp and Wilkens, 1993; Merilaita, 1998; Lev-Yadun et al., 2004; Ruxton et al., 2004; Caro, 2005). Crypsis by coloration defends against visually oriented predation or herbivory by making prey organisms indistinguishable from their background, or at least less conspicuous. There are several ways to be cryptic, and one of the most common ways is camouflage. Since the environment is usually heterogeneous, it is possible to resemble the color of a specific microhabitat, to resemble a compromise of several colors of several microhabitats, or to use disruptive coloration patterns that break up body outlines (Cott, 1940; Merilaita, 1998; Ruxton et al., 2004). There are both theoretical and experimental indications that all these strategies might operate (e.g., Cott, 1940; Kettlewell, 1973; Edmunds, 1974; Endler, 1978, 1984; Merilaita et al., 1999, 2001; Ruxton et al., 2004; Merilaita and Lind, 2005; Schaefer and Stobbe, 2006; Stevens et al., 2006).

The issue of camouflage as defense against herbivory in plants in general and their canopy in particular has received very little attention (e.g., Cole, 1970; Barlow and Wiens, 1977; Wiens, 1978; Benson, 1982; Givnish, 1990; Allen and Knill, 1991; Cole and Cole, 2005; Lev-Yadun, 2006) and even this limited attention is sometimes anecdotal. Unlike in zoology, where camouflage has been studied regularly, the possible defensive advantage of camouflage of whole plants was never an important issue in botany. When background matching has been discussed, Cole (1970) and Cole and Cole (2005) described how difficult it is to distinguish between pebbles and *Lithops* plants because of their excellent resemblance to the stone-covered ground. Wiens (1978), in an essay about mimicry in plants that was usually cited concerning deceptive pollination in orchids, proposed that light coloration, achieved by sand attached to sticky glandular trichomes, may camouflage plants from herbivores. Benson (1982) proposed that members of the cactus genus *Ariocarpus* (living rocks) are well hidden among the limestone desert pavement. A different method to camouflage was proposed by Givnish (1990), who focused on the common phenomenon of variegation in understory herbs in the forests of New England, suggesting that it serves as camouflage since the light regime there is characterized by sun-flecks, and the variegation may act as disruptive coloration. Even for seeds, which must enjoy protection by camouflage when they are dispersed on the ground, (and, according to my field experience, many species of which show excellent background matching or disruptive coloration), only a few studies of their camouflage have been conducted. However, although meager, there is clear experimental

evidence for an important role of camouflage in seed survival (e.g., Brayton and Capon, 1980; Nystrand and Granström, 1997; Saracino et al., 1997, 2004).

There are several cases in which white coloration is known (with no unequivocal explanation) to be involved in protecting plants from herbivory. 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. For instance, *Cucurbita pepo* plants with silvery leaves were found to be less susceptible to insect attacks than plants that don't express the silvery phenotype (Shifriss, 1981), an indication of the defensive potential of light-colored plant phenotypes. Smith (1986) proposed that in the vine species *Byttneria aculeata* the variegation is probably related to herbivory by mimicking leaf miner damage. Schoener (1987, 1988) showed that the silvery leaf morph of the tree *Conocarpus erectus* is more common in habitats that are more exposed to risks of leaf herbivory. Such coloration may camouflage plants from herbivores in the understory of forests (Givnish, 1990; Allen and Knill, 1991), may be aposematic, especially in open habitats (Lev-Yadun, 2001, 2003, 2006), or may undermine herbivorous insect camouflage and expose them to predation or cause them to look for other habitats in which the background fits their colors better and thus protect plants from various invertebrate herbivores (Lev-Yadun et al., 2004; Lev-Yadun, 2006).

Here, I review both well-known and forgotten hypotheses and propose novel anti-herbivory functions for white coloration and glandular trichomes in sandy or light-colored environments: (1) camouflage the plants from herbivores by background matching, (2) since dust is a strong insect repellent and even lethal for insects, its attachment to sticky glandular trichomes should defend plants from insect herbivory, (3) sand attached to plant surfaces will wear down teeth of large herbivores (and possibly also mouth parts of insects) like sand paper, probably better than phytoliths (plant silica bodies), and (4) it has been proposed that white plant surfaces undermine the camouflage of herbivorous insects that have other colors and expose them to predation.

DISCUSSION

General

The physiological functions of trichomes, which have been discussed by many, are described only briefly in the introduction. To avoid misunderstanding, I emphasize that both the physiological functions and the

defensive functions of plant trichomes may operate simultaneously. Thus, various hypotheses concerning the functions of trichomes need not conflict with or exclude any other functional explanation. Traits, such as trichomes, that might have more than one type of benefit, may have been selected for by several agents simultaneously or independently.

Light-colored plants are common in coastal and sandy habitats in the flora of Israel

Two groups of plant species that grow in sandy habitats (coastal or desert dunes) are light colored. Light-colored plants may be almost white (*Otanthus maritimus*), or have a very light green or silvery color (*Lotus creticus*). The first includes plants covered with white trichomes (most species from Israel described in Waisel et al., 1975) (*Echinops philistaeus*, *Otanthus maritimus*, Asteraceae; *Lotus creticus*, *L. lanuginosus*, *Medicago marina*, Fabaceae; *Convolvulus secundus*, Convolvulaceae; *Neurada procumbens*, Neuradaceae; *Plantago albicans*, *P. ciliata*, Plantaginaceae; *Crucianella maritima*, Rubiaceae; *Zygophyllum album*, Zygophyllaceae). This group of 11 species is 25% of the 44 coastal species described in Waisel et al. (1975), which is a much higher proportion of plants covered with dense white or silvery trichomes than in the whole Israeli flora. The second group includes plants that have glandular trichomes that secrete sticky substances that stick sand grains and clay particles to their surface (most species described in Danin, 1996) (*Aegialophila pumilio*, *Ifloga spicata*, Asteraceae; *Eremobium aegyptiacum*, Brassicaceae; *Fagonia arabica*, *F. glutinosa*, *F. mollis*, Zygophyllaceae; *Ononis serrata*, *O. natrix* subsp. *stenophylla*, *O. variegata*, Fabaceae; *Gypsophylla viscosa*, *Savignia parviflora* Brassicaceae; *Silene arabica*, *S. sedoides*, *S. succulenta*, *S. villosa*, Caryophyllaceae).

Camouflage by sand attached to sticky glandular trichomes and light-colored trichomes

Wiens (1978) proposed that light coloration achieved by sand stuck to sticky glandular trichomes may camouflage plants from herbivores. The examples that convinced him were the five species of the genus *Psammophora* (Aizoaceae) and *Crassula alpestris* (Crassulaceae) from South Africa and several other species from the deserts of North America (Wiens, 1978). In addition to Wiens' (1978) hypothesis, I propose that light coloration, achieved by non-sticky light-colored trichomes or any other light-colored surface such as cork (*Caralluma* sp.), may also camouflage plants from herbivores in light-colored or sandy habitats. Similar coloration in animals that live in white, snow-covered habitats or light-colored sand is commonly referred to

as camouflage (Cott, 1940; Hamilton, 1973; Edmunds, 1974; Endler, 1978, 1984; Cloudsley-Thompson, 1979, 1999; Owen, 1982; Majerus, 1998; Ruxton et al., 2004; Hoekstra, 2006; Rosenblum, 2006), and the same logic may also apply for plants. Being white in snowy habitats is not a common plant characteristic because many plant species have no leaves during winter.

Various invertebrates attach substrate or plant (sand, gravel, algae, lichens, mosses, dry branches) particles from the environment for better background matching as defense (Gressitt et al., 1965; Edmunds, 1974; Slocum and Lawrey, 1976; Owen, 1982; Shears, 1988; Brandt and Mahsberg, 2002; Domínguez and Jiménez, 2005) (the parallel of attaching clay or sand particles in plants by sticky glandular trichomes). For instance, the green lacewing (*Chrysopa slossonae*) attaches packets of sycamore leaf trichomes or lichen pieces. The tortoise beetle (*Gratiana pallidula*) and other insects carry feces to form a defensive packet. Caterpillars of the family Geometridae, e.g., *Synchlora* sp., cover themselves with pieces of petals of flowers they harbor (Eisner et al., 2005). As for the defensive potential of dust- and sand-covered plants, I argue that the principle is simple: the plants simply have to not look green, and this will grant them a certain level of defense from various types of visually oriented herbivores. Since plants and herbivores have co-evolved, detection of plants via visual cues is a basic aspect of herbivore life (e.g., Prokopy and Owens, 1983). The search image of plants for visually oriented herbivores should in general be green or, if the plants are dry, shades of yellow, gray, or brown. Other colors are not immediately considered by the sensory apparatus of herbivores as evidence for forage availability. It is probable that for specialized monophagous herbivores such defensive coloration will not operate well, but this coloration may defend from general herbivores that look for whatever plant they can reach. A similar principle led Stone (1979) to propose that young red leaves of certain palms mimic dead or old ones or just look unlike young edible ones, a hypothesis that has been accepted by several authors (Juniper, 1994; Dominy et al., 2002; Gould, 2004; Karageorgou and Manetas, 2006; Manetas, 2006). In addition, it has been proposed that white plant surfaces undermine the camouflage of herbivorous insects that have other colors and expose them to predation (Lev-Yadun et al., 2004; Lev-Yadun, 2006). Moreover, looking like the soil serves as excellent camouflage in members of the genus *Lithops* that grow in the desert in South Africa (Cole, 1970; Cole and Cole, 2005), members of the genus *Pseudolithos* (Lavranos, 1974), or certain cacti (Benson, 1982; Owen, 1982). I propose that when plants are light colored for whatever reason, having silvery-white trichomes or via sand or

clay cover that adheres to the sticky trichomes, they resemble the sandy soil and are thus camouflaged.

Are some light-colored coastal and desert plants aposematic?

Aposematism (warning coloration; coloration that advertises defensive or otherwise dangerous qualities) by conspicuous coloration, including white, has been proposed to operate in poisonous and thorny plants (Hinton, 1973; Lev-Yadun, 2001, 2003, 2006; Lev-Yadun and Ne'eman, 2004, 2006; Midgley, 2004; Rubino and McCarthy, 2004; Ruxton et al., 2004; Speed and Ruxton, 2005; Halpern et al., 2007). Since the light color of many coastal and sandy desert plants seems to camouflage them when they grow in a light environment, an aposematic role of their coloration should not be considered their general strategy.

Light-colored coastal and desert plants may undermine the camouflage of herbivorous invertebrates

The possibility that various plant morphological traits may make plants more accessible to predators and parasitoids had been proposed several times (Niemelä and Tuomi, 1987; Marquis and Whelan, 1996). A special, but common aspect of this type of anti-herbivory defense is the hypothesis that plant coloration may undermine herbivorous insect camouflage (Lev-Yadun et al., 2004; Lev-Yadun, 2006). White leaf undersides and other white surfaces, a common phenomenon in many floras, has been proposed (along with other types of coloration) to undermine herbivorous insect camouflage and expose them to predation or cause them to look for other habitats in which the background fits their colors better, and thus protect plants from various invertebrate herbivores (Lev-Yadun et al., 2004; Lev-Yadun, 2006). This may be one of the benefits of plants (in any habitat) that differ in color from many other plants—the common camouflage coloration (green, gray, brown) or any bright color (yellow, orange, pink, red, purple, black) of many invertebrate herbivores will not match their host color.

Dust as a strong insect repellent

Another defensive mechanism I propose is that since dust is a strong insect repellent and even may be lethal to insects (Ebeling, 1971; Cook et al., 1980; Showler, 2002, 2003), attached soil particles, especially clay, may defend plants with sticky glandular trichomes from insect herbivory. Mammals and birds take “dust baths” and by doing so receive considerable defense against ectoparasites (Ebeling, 1971). Plants with sticky glandular trichomes that are covered by soil clay particles (see Fahn and Shimony, 1996) should enjoy a similar

benefit. For instance, the ash from the eruption of Mount St. Helens on May 18, 1980 considerably damaged the insect fauna of the region because of this effect (Cook et al., 1980). Several field experiments clearly demonstrated the defensive benefits of covering plant surfaces with clay particles (Ebeling, 1971; Lapointe, 2000; Showler, 2002, 2003). This mechanism is not restricted to sandy habitats and there are good reasons to assume that it acts in many dusty habitats. Moreover, if whitish plants look to insects as if they are covered by dust even when they are not, this is a case of dust mimicry that may defend the plants from insects.

Sand may wear down the teeth of large herbivores

Plant camouflage, undermining herbivorous insect camouflage, and insect repellence seem to be only a part of the antiherbivory effect of sand and clay attachment to sticky glandular trichomes. Sand particles are commonly made of SiO_2 , a very hard material. Many plants, especially grasses, produce a large number of silica cells, known as phytoliths (Rapp and Mulholland, 1992; Meunier and Colin, 2001; Prychid et al., 2004). Plants use phytoliths (along with other biological functions of silica) to defend themselves from herbivory (Baker et al., 1959; Walker et al., 1978; McNaughton and Tarrants, 1983; McNaughton et al., 1985; Massey and Hartley, 2006). Sand attached to plant surfaces will also wear down the teeth of large herbivores probably even better than phytoliths. After all, we use sandpaper and sand spraying to polish hard materials. There are some indications that soil particles may wear teeth of mammalian herbivores more than phytoliths (Ungar et al., 1995; Mainland, 2003; Sanson et al., 2007), but this issue is very far from being well understood. I propose that especially for the dicotyledonous plants that have sticky glandular trichomes that glue sand and clay discussed here (*Aegialophila pumilio*, *Eremobium aegyptiacum*, *Ifloga spicata*, *Fagonia glutinosa*, *F. mollis*, *Ononis serrata*, *O. natrix* subsp. *stenophylla*, *O. variegata*, *Gypsophylla viscosa*, *Savignia parviflora*, *Silene arabica*, *S. sedoides*, *S. succulenta*, and *S. villosa*) but produce only small numbers of phytoliths compared to grasses, the attached sand is an external shield compensating for the low level of phytoliths, which may defend these plants from vertebrate herbivory. There is a possibility that similar damages may be caused to the hard mouth parts of insects when they eat sand-covered plants, but unlike some basic facts that are known concerning mammalian herbivores, this issue has not yet been studied in detail.

The U.V. spectrum and defense from herbivores

The physiological role of trichomes and waxes in de-

fending plants from excess sun irradiation in the U.V. spectrum is well known (e.g., Grammatikopoulos et al., 1994; Ballaré, 2003; Manetas, 2003; Paul and Gwynn-Jones, 2003). Many insects, birds, and some other vertebrates (Briscoe and Chittka, 2001; Honkavaara et al., 2002; Shi and Yokoyama, 2003) see in the UV–A wavelength range (400–315 nm). Since birds are major predators of insects (Heinrich, 1993; Honkavaara et al., 2002; Van Bael et al., 2003), an ecological role for the way insects and birds see plants in the UV band should be investigated. Reflection or absorption of UV–A from leaves should theoretically influence the behavior of insects that may choose to land and lay eggs on or consume the plants or may decide not to land on visually unsuitable surfaces. When the issue of undermining herbivorous insect camouflage by plant coloration (Lev-Yadun et al., 2004; Lev-Yadun, 2006) is considered, the possibility that this principle also operates in the UV–A should be considered. I propose that certain insects may choose to occupy or not to occupy light-colored coastal and dune plants on the basis of their appearance in the UV–A spectrum. The absorption and reflectance of plant surfaces in the UV–A, especially concerning herbivory and herbivore predation, remains largely unexplored (Paul and Gwynn-Jones, 2003). Therefore, in addition to the probable UV-related physiological roles of white or silvery coloration of many coastal and dune plants, an anti-herbivory role of this coloration in the UV–A spectrum should be considered and studied.

Whitish-colored plants may appear to be infested by fungal disease

There are many cases I found in the flora of the Near East, Europe, and North America in which plants are covered by white fungal hyphae. Many fungi produce toxic chemicals that in many cases defend their hosts from herbivory (Clay, 1988, 1990; Breen, 1994; Porter, 1994; Elmi and West, 1995; Justus et al., 1997). Fungal endophyte-mediated-alkaloids provide the basis for the acquired chemical defense against herbivory (Porter, 1994; Justus et al., 1997; Saikkonen et al., 1998). We have very good indications that plant parts that may be infested by fungi are rejected by animals. Frugivores avoid eating damaged fruits (especially large fruits) (Janzen, 1977; Herrera, 1982; Manzur and Courtney, 1984; Borowicz, 1988; Buchholz and Levey, 1990). I propose that white plant surfaces mimic fungal-infested plants and that this character may also reduce the tendency of herbivores to consume such plants.

Does Gloger's rule operate in plants?

In many animal taxa, desert animals tend to be pale compared to other members of the same taxon that in-

habit wetter environments. This phenomenon is called Gloger's rule and has been known for more than 170 years. It is considered to reflect the selection by both physiological factors such as reflecting sun irradiation, and by predation (e.g., Cloudsley-Thompson, 1999; Stoner et al., 2003a,b). The phenomenon discussed here, especially the ca. 25% of light-colored species in Israeli coastal plants and the many light-colored plants in sandy habitats or in desert habitats (e.g., *Aegialophila pumilio*, *Aerva javanica*, *Aizoon canariense*, *Artemisia judaica*, *Asteriscus graveolens*, *Blepharis ciliaris*, *Caralluma sinaica*, *C. europaea*, *Eremobium aegyptiacum*, *Fagonia glutinosa*, *F. mollis*, *Gypsophylla viscosa*, *Heliotropium maris-mortui*, *Ifloga spicata*, *Lotus lanuginosus*, *Marrubium alysson*, *Moltkiopsis ciliata*, *Moretia canescens*, *Neurada procumbens*, *Ononis serrata*, *O. natrix* subsp. *stenophylla*, *O. variegata*, *Plantago ciliata*, *Savignia parviflora*, *Scorzonera tortuosissima*, *S. judaica*, *Silene arabica*, *S. sedoides*, *S. succulenta*, and *S. villosa*, *Verbascum fruticosum*) is a good indication that Gloger's rule may also apply to plants. Such "rules" are not without exceptions in the animal kingdom and should have the same limitations in the plant kingdom. In both animals and plants the same factors seem to have been selected for lighter coloration: (1) physiological factors such as reduction of the load of sun irradiation, and (2) visually oriented predators in animals and herbivores in plants.

The problems in evaluating risk—the common view of “no damage no risk”

There are inherent theoretical difficulties in evaluation of defense by experiments. A good defense may operate so well that there are almost no attacks on the defended organism and experimental noise may be bigger than the signals. A common difficulty for many scientists is to accept the possibility that “no damage does not automatically indicate no risk”. This difficulty became clear to me first from reading the literature and later following personal discussions with scientists. Similarly, many scientists think that attacks by herbivores indicate that there is no defense. A case of no attack in spite of a high risk is demonstrated by various summer green plants growing in the Negev Desert (Israel). Several common alkaloid-rich poisonous plants (e.g., *Ephedra aphylla*, *Pergularia tomentosa*, *Anabasis setifera*, *A. syriaca*, *A. articulata*, *Asphodelus ramosus*, *Peganum harmala*, *Thymelaea hirsuta*, *Chrozophora tinctoria*, *C. obliqua*, *Nicotiana glauca*, and *Withania somnifera*) or thorny plants (e.g., *Alhagi graecorum*, *Zilla spinosa*) form green islands in the dry summer when all surrounding plants have turned yellow and in many cases have been grazed down to their roots. Even under such extreme

grazing pressure those green plants are ignored by the flocks of sheep, goats, donkeys, and camels that pass them daily (Lev-Yadun and Ne'eman, 2004). The absence of attacks on these green plants is a clear indication of their very good defensive qualities rather than of a low level of risk.

CONCLUSIONS AND OPEN QUESTIONS

Direct, plant-oriented experimental data for the functionality of the defensive mechanisms discussed here are missing or are only partial for both old and new hypotheses, as noted by Wiens (1978) almost 30 years ago. This unfortunate situation should be viewed in the light of a comment made by Harper (1977) concerning various potential defensive functions of coloration patterns of plants, namely that botanists are reluctant to accept what is commonplace for zoologists (see also Lev-Yadun et al., 2002). Only recently, since the year 2000, with the papers of Archetti (2000) and Hamilton and Brown (2001) on the possible operation of Zahavi's handicap principle in autumn leaf coloration as anti-herbivory defense, and Lev-Yadun (2001) on aposematism in thorny plants, and the responses of a growing number of scientists, defensive plant coloration has become a non-anecdotal issue in plant biology (see Lev-Yadun, 2006).

For instance, the fact that there are so many light-colored plants in the coastal and desert vegetation of Israel, an arid habitat, should be studied first in similar habitats but with a taxonomically very different flora, such as the Australian flora. It should be studied also in much colder climates and in ecosystems where light is not in excess and in coastal dunes of seas that are not salty, or exposed to lower levels of herbivory and sun irradiation, such as the Baltic Sea (a field examination of the coastal vegetation in Estonia indicated only one coastal dune species that is whitish). Only the comparative picture that emerges from such studies will enable the evaluation of the generality of the hypotheses discussed here.

The most detailed studies of plant coloration and animal vision were done on pollination biology (e.g., Chittka, 1997; Spaethe et al., 2001). The impact of the biological limitations of the visual system of herbivores in relation to defensive plant coloration was never studied in great detail. Considerable research effort in this direction is clearly needed.

It is often impossible to change individual factors when we try to isolate factors during experiments without causing unnoticed or unwanted changes in other factors. It should be taken into consideration that the per generation level of defensive advantage that can, with time, eventually lead to the evolutionary change

might be very small, so small that environmental and experimental noise may be too large to separate with affordable and manageable experimental designs. It is hoped that the new wave of studying (theoretically and experimentally) defensive plant coloration will help to narrow the broad gaps in understanding defensive plant coloration that currently exist.

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