Plants on red alert: do insects pay attention?

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Summary
Two recent hypotheses have proposed that non-green plant colouration evolved as a defence against herbivores, either as protective colouration promoting handicap signals indicating plant fitness or by undermining their crypsis. The handicap hypothesis posits a coevolutionary process between plants and herbivores, whereas the anti-crypsis hypothesis suggests that an arms race between insects and plants is the evolutionary mechanism. Both explanations assume that insects are the evolutionary origin causing plants' colouration. Here, we propose a different hypothesis, termed the "Defence Indication hypothesis". This idea focuses on the multiple protective functions of anthocyanins and carotenoids as pigments, and suggests that plant colouration evolved primarily in response to various stressors. Because pigments and defensive compounds share a common biosynthesis, the production of pigments also provides elevated defensive strengths against herbivores, a process termed priming. In effect, the Defence Indication hypothesis predicts that pleiotropic effects of the pigments and, more generally, plants' shared defence responses, explain why insects might react to plant colouration. ***BioEssays*** **28:65–71, 2006.**

Introduction

It goes without saying that the sessile nature of plants shapes their way of interacting with the environment. The particular challenges associated with a sessile lifestyle are those of combining successful reproduction and dispersal. However, the fundamental dilemma posed by immobility is that of staying alive in the face of a myriad of biotic and abiotic stress factors. Because plants cannot evade their herbivorous predators, owing to their immobility, they have evolved a variety of defence mechanisms, including those termed resistance and tolerance (see(1) for a review) to cope with both herbivory and abiotic stressors. The interaction between plants and herbivores is arguably one of the best-studied and most important interactions between disparate players. Adding a new facet to the ongoing battle between plants and herbivorous insects, Hamilton and co-workers proposed that leaf colours function to signal the defensive strength of an individual plant to herbivorous insects.(2) Alternatively, Lev-Yadun et al. recently proposed an innovative hypothesis last year,(3) that posits that the diversity of plant colouration undermines the crypsis of their herbivorous predators. Both hypotheses, however, essentially ignore the fact that the pigments producing plants' colours also serve physiological functions within the plant.(4) Here we argue that consideration of the biochemistry of plant pigments provides the key for an understanding of how and why plant colours might influence the abundance and diversity of herbivorous insects. To integrate the visual communication system between plants and animals with the biochemistry of colours, defence mechanisms and plant physiology, as we attempt to do here, represents a new and challenging research area.

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Multiple colours and cryptic herbivores

Lev-Yadun et al.(3) suggested that differently coloured plant parts make herbivorous insects more vulnerable to predation because multiple backgrounds result in less-efficient cryptic colouration on several of the various backgrounds. The hypothesis relies on an intuitively appealing conjecture: if an individual plant sports distinct colours in different or the same plant organ (e.g. veins contrasting to the rest of the leaves, see Fig. 1 in Ref. 3), it increases the matrix of unsuitable places for resting or feeding of those insects that are adapted to resemble a specific background. Likewise, if an animal is coloured so that its patterns are relatively inconspicuous against various backgrounds, it should compromise the efficiency of background matching towards each of the different backgrounds. Thus, Lev-Yadun et al. suggest that multiple colours of an individual plant undermine the cryptic colouration of insects.(3) Specifically, their hypothesis predicts that cryptic insects will suffer higher predation by visually hunting predators when these insects visit multiple coloured plants relative to unicoloured ones.

The new hypothesis is valuable because it brings multiple plant colouration, a neglected phenomenon, to the attention of scientists from various fields and links it to one of the most prolific areas of plant science: plant–herbivore interactions. However, the hypothesis also raises some theoretical concerns. An animal is defined as being cryptic if its colour pattern

Figure 1. Multiple plant colours produce variation in the background, which results in a larger number of insect species being camouflaged on that plant. To illustrate this positive relationship between the degree of plant colouration and insect diversity, we created a range of artificial insects that are cryptic on a green leaf with red veins.

resembles a random sample of the background colouration.(5) Consistent with the hypothesis, cryptic colouration leads to a reduced predation risk in a number of herbivorous insects(6) potentially explaining why so many insects are coloured in various shades of brown, grey and green (e.g. moths, grasshoppers). The central tenet of the new hypothesis is that plants reduce the number and diversity of plant-consuming insects by providing different visual backgrounds against which their herbivorous enemies stand out.

A closer inspection of the relationship between background diversity and crypsis, however, suggests otherwise: for a given background, there are a number of random samples that would be equally cryptic. The more heterogeneous the background is, the more insect patterns match a random sample of it.(7) For example, on a unicoloured green leaf, only insects matching the green colour of the leaf gain protection by crypsis. By contrast, a larger number of (differently coloured) insects is cryptic, i.e. resembles a random sample of the background, if the leaf is variegated (Fig. 1).

Theory thus predicts a *higher*, not a lower, insect abundance on heterogeneous backgrounds because differently coloured plant parts provide a variety of microhabitats for a larger number of insect species to rest and feed upon. Consequently, a positive correlation between the degree of variegation in plants and insect diversity is expected. The evolution of multiple colours seems thus an unlikely strategy for plants to reduce the herbivorous load. It has further been suggested that background heterogeneity decreases the detectability of prey by distracting the visually hunting predator,(8) but tests of this idea are scarce. However, another form of camouflage in insects, disruptive colouration, might be less dependent on background matching.(9) Disruptive colouration is produced by strongly contrasting neighbouring colour patches that disguise the animal's body outline and thereby lower the risk of detection because the animal is not perceived as a prey item.(10) Recently, two experiments in the lab and in the field documented that disruptive colouration might be as or even more effective than crypsis for avoiding attack of visually oriented predators(11,12) Disruptive colouration as another form of concealment might, therefore, lower the causal relationship between insect diversity and plant colouration. However, even if multiple plant colouration does not reduce the number of herbivores that are camouflaged on the plant, we suggest that there is indeed a relationship between non-green plant colouration and herbivores' host preferences. In this context, we discuss Hamilton's hypothesis that a co-evolutionary process between plants and insects causes plant colouration and propose a different idea, one that emphasizes that pleiotropic effects of pigments influence herbivorous insects. To develop this idea, we quickly outline the biochemistry of plant colouration and then illustrate how the colours of plants indicate their defensive strength.

Biochemistry of plant colouration

Three pigment classes, chlorophyll (green), anthocyanins (blue, red, purple, black) and carotenoids (yellow to red), contribute in various proportions to most of the colour shades produced by plants. These pigments serve multiple functions within the plant: chlorophyll is involved in photosynthesis, anthocyanins have diverse roles in protecting the photosynthetic apparatus against excess radiation and reactive oxygen species thereby facilitating the recovery of nutrients in senescing leaves,(4,13–17) whereas carotenoids function both in light capture and photoprotection of light-sensitive leaf organelles,(18–20) As acknowledged by Lev-Yadun et al. and several other researchers,(3,4,21) traits such as colour likely serve multiple roles in plants. The various adaptive explanations on the physiological functions of plant pigments do thus not preclude that colour also functions in communication to herbivores; such communication becomes an additional function, not the sole or primary one.

Here, we focus on the biochemical pathways of anthocyanin synthesis because anthocyanins produce the majority of colour diversity in the various plant parts, e.g. roots, leaves,(13) branches, stems and flowers (see Fig. 1(3)), and because this pathway is known in great detail. Anthocyanins are the most visible and therefore most widely known class of the remarkably diverse group of flavonoids,(22,23) which are ubiquitously present in angiosperms and common in gymnosperms and ferns. Other classes of flavonoids produced by the same basic biochemical pathway include flavones, flavonols and tannins (see Fig. 2), all of which contain substances that function in stress protection, see below.(23,24) Anthocyanins thus share the same precursors with various defensive compounds. For example, leucoanthocyanidins are the common precursor of anthocyanins and tannins, being the second last characterized step in tannin synthesis.(25) Because the production of defensive compounds and anthocyanins as pigments are dynamically connected by a common biosynthetic pathway, the expression of anthocyanins is intricately linked to plants' response to stress.(23)

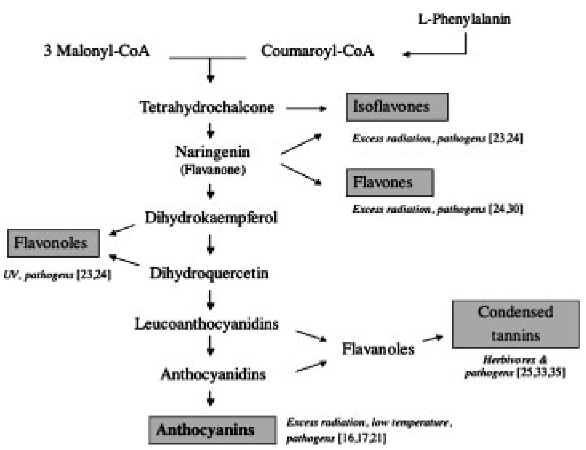

Figure 2. Schematic illustration of the biosynthetic pathway of anthocyanins and other flavonoids. Grey boxes indicate the end products of the pathway. Stressors that induce the synthesis of end products are indicated in italics, numbers refer to the respective references.

Anthocyanins provide defensive strength

The main function of anthocyanins is commonly regarded as the protection against abiotic stressors such as cold temperatures and excess light, reducing the risk of photoinhibition.(14,26) They are also active in protecting leaf tissue by scavenging reactive oxygen species.(17,27) Anthocyanins have often been assumed to be biologically active against herbivores, but the direct evidence for such activity is not very strong despite a large number of studies.(13,27) For example, artificial diets of purified anthocyanins did not affect the survival rate of herbivorous insects.(28) One study(29) documented that leaf-cutting ants avoided anthocyanic leaf extracts but did not control for total flavonoid concentrations in the extracts.(13) Other flavonoids, however, such as tannins not only function to protect plants from abiotic stress,(24) they are also active in deterring biotic stress factors, i.e. herbivores.(30–32) In fact, tannins, and more generally phenols, are considered archetypal defensive compounds that protect plants against a variety of herbivores and pathogens.(33,34) For example, the abundance and diversity of leaf-chewing herbivores are negatively correlated with condensed tannin concentrations in oak (*Quercus* sp.) leaves and variation in condensed tannin concentrations explains variation in herbivore community structure.(35) The effects of tannins on herbivores depend on the tannin structure and its interactions with other compounds such as nutrients. These effects range from pre-ingestive—e.g. inhibition of food intake—to post-ingestive such as lowering the efficiency of nutrient absorption in leaf-chewing locusts.(32,36) Owing to their common biosynthetic origin, it is not surprising that the contents of anthocyanins often correlate with those of tannins and phenols, which are avoided by herbivores.(37,38) Costa-Arbulú et al.(28) concluded, therefore, that anthocyanins were correlated with, but not responsible for, induced resistance. Interestingly, anthocyanins also correlate with the contents of secondary compounds that are not directly derived from the flavonoid pathway. For example, in the beach bur (*Ambrosia chamissonis*), a sunscreen of anthocyanins protect light-sensitive defensive compounds (thiarubrine) from photoconversion caused by excessive light.(39) Also, in the polymorphic flowers of the wild radish (*Raphanus sativus*) anthocyanin-dominant flower morphs have higher defensive compounds (indole glucosinolates) in the presence of herbivores.(40)

If the contents of anthocyanins correlate with those of various defensive compounds, which are often not coloured themselves, they are the most visible sign of defensive strength. We therefore hypothesize that insects avoid plants, which are coloured by anthocyanins, because this colouration indicates the presence of defensive compounds. This hypothesis predicts that there will be a lower number of herbivorous insects on multicoloured plants, similar to the prediction of the hypotheses by Lev-Yadun et al.(3) and Hamilton and co-workers,(2,41) but it is based on the pleiotropic effects of plant colouration rather than the direct functions of undermining camouflage or a co-evolutionary signalling system between plants and insects. As we will lay out, defence against herbivores is probably not the primary selective pressure causing leaf colouration. Hence, even though leaves might convey information about plants' defensive strength, leaf colouration is—from an evolutionary perspective—*not* a signal to herbivores because leaves did not evolve their colour because of that effect. According to our hypothesis, leaf colouration rather fits the definition of a cue, which is a feature used to make decisions, but one that is not specifically adapted to function in communication.(42)

Mechanisms of indicating defensive strength

What are the possible mechanisms responsible for such pleiotropic effects? In other words, is there more than correlative evidence for a link between defensive compounds and anthocyanin colouration? To answer such questions, it is helpful to examine the gene expression of anthocyanin production. It is a widely recognized fact that foliar anthocyanins accumulate in response to abiotic stress factors or wounding.(14,24,43,44) For example, plants challenged by low temperature or tissue damage dramatically increase the transcript levels of several of the early key enzymes i.e. phenylalanine ammonia-lyase (Pal) and chalcone synthase (Chs) in the flavonoid pathway within a few hours.(43,45) In maize seedlings (*Zea mays*), the transcript levels of these enzymes remained elevated at low temperature but returned to pre-treatment levels if the cold-stressed plants were returned to higher ambient temperature.(45) Once these transcript levels are elevated to accumulate anthocyanins, plants have an augmented capacity to mobilize a defence response against herbivores: they can synthesize flavonoids, flavones and tannins more rapidly because Pal and Chs produce early stages in the flavonoid pathway before those defensive compounds branch off. An obvious example for the connection between anthocyanin synthesis and defensive compounds is that both biotic and abiotic stress factors cause elevated levels of leucoanthocyanidins, the precursor of tannins and anthocyanins.(25,45)

By synthesizing various defensive compounds from the same precursors, plants acquire a higher resistance owing to the synergistic effects of shared defence mechanisms. This process of higher resistance against a variety of stressors is termed priming.(46) Priming not only enables a faster response to primary stressors but often also a potentiated response to the secondary stress factors(46) (e.g. herbivores) once transcript levels of enzymes producing defensive compounds are elevated by a first stressor (e.g. abiotic stressor). Interestingly, priming as the cooption between different defence mechanisms(47) might distinguish plants from animals where the effects of two stressors are considered far deadlier than that of a single one.(48) In plants, the phenomenon of priming is not restricted to specific stressors such as cold temperature or to the flavonoid pathway, but occurs more widely in response to various stressors involving the regulation of different plant defence responses.(47) Especially well-studied are the interaction between UV-B radiation and other stressors and their combined effects on plant fitness; this work has been prompted by the fear of globally increased levels of UV radiation. Many field experiments show that plants as different as southern beeches (*Nothofagus sp.*) and jimsonweed (*Datura sp.*) ward off insect herbivory (stressor 2) more effectively if they had received higher UV-B radiation (stressor 1) during plant growth e.g. see Refs. 49, 50). Both stress factors (UV-B and insect predation) activate an array of common regulatory genes(51) including those responsible for elevated flavonoid concentrations.(52) Priming thus seems to be a common phenomenon allowing for an accelerated and enhanced response when plants are challenged by the various stressors of their often unpredictable environments.(46)

Multiple colours, defence and insects

Plant defensive chemistry is certainly more complex than outlined above and we do no expect a universal correlation between the plethora of defensive compounds and anthocyanins. However, we hypothesize that multiple plant colouration produced by anthocyanins reduces insect herbivory because plants' defensive strength is correlated with and thus indicated by anthocyanin colouration. We term this hypothesis the "Defence Indication hypothesis" and readily acknowledge that this idea has been presented or implied elsewhere (for example, Ref. 22), though without this name. The hypothesis predicts that fewer herbivorous insects feed on plants that feature high anthocyanin colouration. In contrast to other hypotheses (see below), the Defence Indication hypothesis does not make specific predictions about insect behaviour i.e. at which stage they react to defensive strengths. However, insects that are sensitive to light reflecting in the red part of the spectrum might land less often on plants coloured by anthocyanins, whereas other insects might initially land on uni- and multiple-coloured plants equally and vacate the latter only after sampling.(53)

Relative to the hypothesis suggested by Lev-Yadun et al.,(3) the Defence Indication Hypothesis has the disadvantage of being focused on plant colouration produced by anthocyanins, but it may also pertain to carotenoids. Although the relationship between carotenoids as pigments and defensive compounds are generally not well known, the unmasking of yellow carotenoid colouration in senescent leaves might be related to defensive strengths. The gradual yellowing of leaves is caused by the degradation of chlorophyll, which occurs simultaneously with the upregulation of genes that produce anti-feedants inhibiting digestive tract proteases.(54) Whether and how carotenoids in other than senescent tissue relate to defensive strengths remains to be addressed.

The Defence Indication Hypothesis provides a functional explanation for the phenomenon that insects avoid brightly coloured senescent leaves in autumn.(2,55,56) As noted earlier the first workers to propose such a relationship between plant colouration and insects were Hamilton and co-workers(2,41) who suggested that the bright autumnal leaf colours of so many temperate trees are not merely a by-product of senescence but function to ward off insects. The authors suggested that a signalling system between plants and herbivorous insects evolved as a result of a co-evolutionary process between both players.(2,41) The fundamental conjecture of their hypothesis is that bright yellow and red leaf colours in autumn are a handicap signal that implies costs to the plant individual bearing the signal. This proposed signalling system would enable on one side well-defended trees to reduce their herbivorous load and on the other side insects (mainly aphids, which migrate to their hosts in autumn) to forage more efficiently because they could easily spot less-defended dull individuals. Assuming high production costs of non-green plant pigmentation, these authors speculated that only those individuals within a species are able to signal with yellow and red leaves to insects, which are also able to mount the costs of producing defensive compounds that reduce the fitness of insects landing on the plant.(2,41)

Given that plants are often not limited in carbon and energy(53) and that carotenoids and anthocyanins both function in the protection of the light-sensitive apparatus and in nutrient recovery,(14,15,57) the specific costs of producing yellow and red leaves as an explanation for this signalling system have often been questioned.(4,19,53) However, the only empirical tests of Hamilton's hypothesis revealed that less insects were found on those individuals that had a higher proportion of red or yellow leaves.(55,56,58) Yet, a negative correlation between the degree of non-green colouration and insect numbers(55,58) does not necessarily imply a co-evolutionary process between plants and insects. Such a co-evolutionary process requires that individuals of one population (e.g. plants) undergo an evolutionary change (e.g. anthocyanin accumulation) in response to an evolutionary change of a second population (insects), which is followed by an evolutionary response in the second population (e.g. avoidance of red leaves) to the change of the first population.(59) In other words, co-evolution requires that herbivorous insects are the selective pressure causing bright autumnal leaf colouration, an opinion that few plant physiologists seem to have adopted.(53,60)

A more parsimonious explanation is that a number of abiotic factors causing leaf abscission require physiological adaptations including the degradation of chlorophyll (causing the appearance of yellow leaf colour) and the upregulation of genes involved in plant defence e.g. in flavonoid biosynthesis. In this scenario, variation in the colouration between individuals of the same species and in the damage that they suffer from herbivores is explicable by strong genetic effects on leaf chemistry. In bright senescent leaves of trembling aspen (*Populus tremuloides*), for example, the concentrations of phenolics are strongly influenced by genotype and probably affect the performance of late-season herbivory.(61) Likewise, in young and expanding foliage of *Quercus coccifera*,(62) individuals vary substantially in their concentrations of phenolics. This variation is matched by the variation in anthocyanins as illustrated by the strong correlation between anthocyanins and total phenolics. In this species, leaves containing high concentrations of phenols (and anthocyanins) suffer less damage than green leaves.(62)

In conclusion, insects seem to react to a complex mosaic of physiological factors related to leaf quality, with colour being the most visible one. Considering the biochemistry of plant colouration and the variety of stressors that induce it, the evolutionary origin of plant colouration is probably not a co-evolutionary signalling system between insects and plants. The relationship between plant colours and herbivorous insects are more likely explicable as pleiotropic effects of defensive strengths caused by a common synthetic pathway that is activated in response to various stress factors.

Conclusions

Studying the signalling system between plants and animals—herbivores as well as pollinators and seed dispersers as mutualists—is an emerging research field,(63) which might open up new facets for the study of plant–herbivore interactions. The three hypotheses discussed above all expect that insects evaluate and react to plant colours, albeit for different reasons (Table 1). In the hypothesis presented by Lev-Yadun et al. plant colouration functions to undermine crypsis, while Hamilton's hypothesis and the Defence Indication hypothesis both posit that non-green plant colouration is correlated with the contents of defensive secondary compounds. The main difference is that Hamilton and co-workers assume that leaf

Table 1. Summary of the main difference between the three hypotheses on the interaction between plant colours and herbivores

Predictions	Crypsis	Co-evolution	Pleiotropic effects
Applies to	All plant colours	Red and yellow at times of host choice of insects	Anthocyanin-coloured plants and senescent yellow tissue
Number of insects	Lower on plants with multiple colours	Lower on bright red or yellow coloured plants	Lower on plants with red colours or senescent yellow plants
Selective pressure on insects	Higher predation rate on multicoloured plants (but see this article)	Lower reproductive success or survival on coloured plants	Lower reproductive success or survival on coloured plants
Relationship between colour & defensive compounds	Not required	Bright colouration implies fitness and indirectly strong defensive commitment	Bright colouration signals strength of defensive reaction directly
Insect diversity	Low on multicoloured plants	High on brightly-coloured trees(2)	Low on multicoloured plants
Proximate causation of colour	None mentioned connected to this hypothesis	Synthesis of pigments depends on individual fitness	Stress reaction induces synthesis and accumulation of pigments
Ultimate causation of colour	Arms Race: plants undermine insect camouflage	Co-evolution: Insects and plants benefit from bright colour as handicap-signal	Induced Systemic Resistance: shared biosynthesis and defence reactions protect plants against multiple stressors

colouration evolved as signals in a co-evolutionary process between plants and insects, whereas the Defence Indication hypothesis posits that plant colouration evolved in response to various stress factors and is linked to plant defence via pleiotropic effects. Tests of the hypotheses involve, on the one hand, comparisons of the predation rate of insects on multicoloured compared to unicoloured plants to evaluate whether plant colouration functions to undermine the crypsis of insects. On the other hand, investigating whether leaf colouration develops mainly in response to abiotic or biotic factors contrasts the Defence Indication hypothesis against Hamilton's co-evolutionary hypothesis. For example, if abruptly falling temperatures in autumn decrease the number of aphids migrating to their hosts, the Defence Indication hypothesis but not Hamilton's co-evolutionary hypothesis expects an increase in red leaf colouration. In contrast, if abiotic factors are held constant in greenhouse experiments, it is possible to test whether plant colouration responds solely to changes in the number of herbivorous insects. Such an experiment, however, has to establish that plant colouration develops as a signal to divert insects (as assumed by the co-evolutionary hypothesis) rather than as a result of mechanical damage caused by herbivory. Clearly, more interdisciplinary and innovative research is required to design experiments that will provide clean discriminatory predictions of these hypotheses.

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