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BOTANICAL BRIEFING

Structural colour and iridescence in plants: the poorly studied relations of pigment colour

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• *Background* Colour is a consequence of the optical properties of an object and the visual system of the animal perceiving it. Colour is produced through chemical and structural means, but structural colour has been relatively poorly studied in plants.
• *Scope* This Botanical Briefing describes the mechanisms by which structures can produce colour. In plants, as in animals, the most common mechanisms are multilayers and diffraction gratings. The functions of structural colour are then discussed. In animals, these colours act primarily as signals between members of the same species, although they can also play roles in camouflaging animals from their predators. In plants, multilayers are found predominantly in shade-plant leaves, suggesting a role either in photoprotection or in optimizing capture of photosynthetically active light. Diffraction gratings may be a surprisingly common feature of petals, and recent work has shown that they can be used by bees as cues to identify rewarding flowers.
• *Conclusions* Structural colour may be surprisingly frequent in the plant kingdom, playing important roles alongside pigment colour. Much remains to be discovered about its distribution, development and function.

Key words: Diffraction grating, flower colour, interference, iridescence, multilayer, photoprotection, pollinator attraction, structural colour.

INTRODUCTION: WHAT IS COLOUR?

The bright colours of flowers attract pollinating insects by making the floral tissue stand out against a background of vegetation. Analyses of insect visual acuity have shown that vegetation is visually very similar to bark, soil and stone from an insect's point of view, because all these materials weakly reflect light across the whole range of the insect visual spectrum (Kevan *et al.*, 1996). Flowers are different – they appear as bright colours because they selectively reflect certain wavelengths of light, which are perceptible to pollinating animals, and, usually, to humans as well.

Colour is a property of both the coloured object and the perception of the animal observing it (Fig. 1). Light arriving at an object can be transmitted through it, absorbed by it or reflected back from it. If an object reflects or transmits all wavelengths of light equally, then it is perceived as white (Fig. 1, top). If an object strongly absorbs all wavelengths of light, then it is perceived as black (Fig. 1, centre). However, if it absorbs all light except one set of wavelengths, such as the red, which it instead reflects or transmits, then it can be said to have a colour. What that colour is depends on the visual system of an animal observing the object. If it has photoreceptors that are strongly activated by red light, as vertebrates do, then the object will appear red (Fig. 1, bottom left). If it has no photoreceptors that respond to red light, the object will appear black – to that animal the object is indistinguishable from an object that absorbs all wavelengths of light. Because photoreceptors are triggered by a curve of wavelengths the situation can be more complex. So, for insects that do not have red-light receptors but whose green-light receptors respond to a curve of wavelengths with the tail of the curve in the red part of the spectrum, the object in question would appear dull green (Fig. 1, bottom right; Chittka and Raine, 2006).

Plants, like animals, achieve colour in two main ways. First, they use chemical- or pigment-based colour. Pigments are compounds which absorb subsets of the visible spectrum, transmitting and reflecting back only what they do not absorb and causing the tissue to be perceived as the reflected colours. Chlorophyll absorbs light in both the red and the blue parts of the spectrum, reflecting only green light, and causes leaves to appear green to humans. Similarly, a flower that humans perceive as red contains pigments which absorb yellow, green and blue light, leaving red light as the only wavelength visible to us which is reflected. Plant pigments have been thoroughly studied from a biochemical perspective, and their synthesis and regulation have also been characterized by molecular genetics.

However, both plants and animals have also been shown to produce structural colours. A structural colour occurs when different wavelengths of light are selectively reflected from a substance, with the remaining wavelengths transmitted or absorbed. The famous blue butterflies of the genus *Morpho* have wing scales which selectively reflect a narrow bandwidth of blue light, allowing other wavelengths to be transmitted through the wing (Fig. 2A). The wings accordingly look intensely blue to humans, even though they contain no blue pigments (Vukusic *et al.*, 1999). Structural colour has been well characterized in animals, but very little studied in plants.

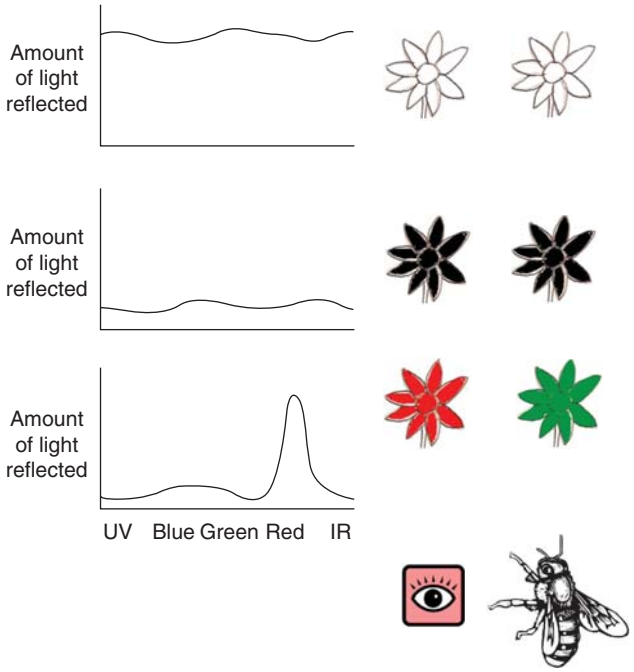

FIG. 1. Colour is a property of the light reflected by an object and the visual system of the animal observing it. If a flower reflects all wavelengths of light, it is perceived as white (top). If it absorbs all wavelengths then it appears black (centre). However, if it absorbs all wavelengths apart from one region of the spectrum, it has a colour. The flower shown in the bottom panel reflects red light. To the vertebrate eye, which has red-light receptors, the flower appears red. However, to the bee eye, which has no red-light receptors but whose green-light receptors are weakly stimulated by red light, the flower appears a dull green.

IRIDESCENCE IS A UNIQUE PROPERTY OF STRUCTURAL COLOUR

Chemical and structural colours have several different properties. They differ first in the intensity of colour that they produce. Pigments are generally not very good at absorbing all but a very few wavelengths of light. Instead, they absorb most light of a number of wavelengths, but allow quite a broad range of wavelengths to be reflected or transmitted. This results in colours which can appear dull or muted, as they consist of a mixture of different colours of light. In contrast, structural colours can appear very intense, as reflective structures can be very precise in the bandwidths that they reflect.

Chemical and structural colours also differ in the patterns that they can produce. Chemical colours are diffuse, and look the same from all angles. To produce patterns of colour, different pigments must be localized to different cells or areas of a tissue. Commonly occurring pigment patterns in plants include different coloured venation on petals, and spots of dark pigment acting as targets at the bases of petals, near the nectaries. Structural colours have the potential to generate shifting patterns of colour as the viewer moves, rather than across different regions of the tissue. Reflective structures can reflect one particular peak wavelength of light at one angle, and another peak wavelength at a second angle. Thus, as an animal moves its position relative to the structure it will see the object change from the first colour to the second colour. The phenomenon of appearing different colours when viewed from different angles is called iridescence, and it is a unique attribute of structural colour. Iridescence can cover a few or many different colours, and can be in regions of the spectrum visible to a variety of animals, including in the ultraviolet (UV).

STRUCTURAL COLOUR AND IRIDESCENCE – MECHANISMS USED BY ANIMALS

The mechanisms capable of producing structural colour in animals were described by both Hooke and Newton in the 17th and early 18th centuries, and a large body of literature has subsequently been produced, much of which is covered in several recent reviews (Parker, 2000; Vukusic and Sambles, 2003; Doucet and Meadows, 2009). A very brief overview shows that structural colour can be produced by either incoherent or coherent light scattering.

Incoherent light scattering takes place when individual light-scattering structures are randomly separated from one another by an average distance that is large when compared with the wavelength of the light. The light-scattering structures differentially scatter different visible wavelengths, but in such a way that the phase relationship of the scattered wavelengths is random. Although most structural colour in animals is produced by coherent light scattering, the blue colouration in many amphibians is attributed to incoherent scattering (Bagnara *et al.*, 2007), as is the blue colour of the sky.

The majority of structural colour, and all iridescence, in animals is produced by coherent light scattering, which occurs when the distribution of light-scattering elements, and the resulting phase relationship of reflected light waves, is precisely ordered. An ordered distribution of light scatterers can result in either constructive or destructive interference. If the phase difference between two waves is a multiple of exactly one full wavelength then the two waves constructively interfere with each other and there is a strong reflection of light at that particular wavelength. By contrast, if the phase of the reflected waves differs by half a wavelength, or an odd multiple of half wavelengths, then destructive interference occurs such that reflection of this wavelength is weak or absent.

The simplest type of coherent light scattering is that of thin-film interference, which gives the colour to soap bubbles and oil-slicked puddles. Thin-film interference occurs when two transparent layers of materials with different optical densities meet. The optical density of a material determines the extent to which light waves are slowed down as they pass through it. Light is also reflected at each side of the boundary between the two materials – both before and after passing through each individual layer. Optical density, the thickness of the material layer, and the angle and wavelength of the light all help to determine if the light reflecting from the bottom of a layer is in phase or out of phase with the light reflected from the top of the layer, which will in turn determine whether constructive or destructive interference occurs for each wavelength. Constructive interference for one wavelength and destructive interference for others results in the reflected light being of one colour. Multilayer reflectors that produce structural colour consist of ordered layers of these pairs of

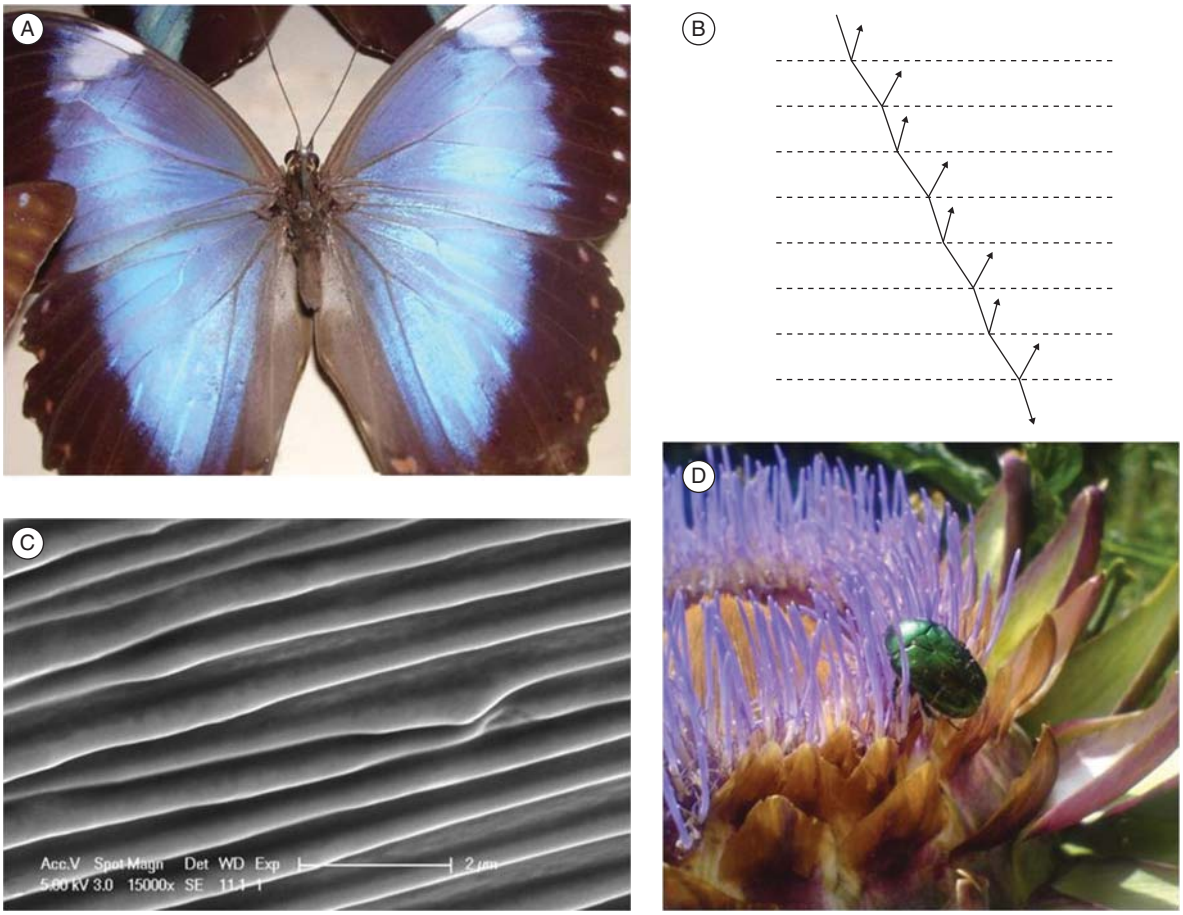

FIG. 2. Structural colour and iridescence. (A) The intense blue colour of the *Morpho* butterfly is due to reflection of light by multilayers. (B) Multilayers generate iridescence by reflecting different wavelengths of light at different angles at each boundary between layers. (C) Diffraction gratings consist of ordered parallel grooves at particular frequencies, like the cuticular striations on this tulip petal. (D) An iridescent beetle (rose chafer, *Cetonia aurata*) visits an artichoke flower.

thin films layered in series, producing even stronger constructive interference for specific wavelengths and resulting in very pure, intense colours (Fig. 2B). The classic example of multilayered structural colour in animals is shown by the blue *Morpho rhetenor* butterfly, in which the multilayered structure on its wing scales produces a vivid blue colour of such intensity that it is said to have a visibility of up to half a mile (Vukusic *et al.*, 1999; Vukusic and Sambles, 2003).

A diffraction grating consists of a reflective surface over which runs a series of ordered and precisely spaced parallel grooves (Fig. 2C). Some of the light that hits the surface is reflected as normal, but light that hits the grooves is diffracted – split into its component wavelengths – and each wavelength is reflected at a different angle. Light with longer wavelengths has a higher diffraction angle than light with shorter wavelengths, so the light separates into its component parts, producing the rainbow effect that can be easily seen over the surface of a CD. Several beetle and spider species have been found to produce iridescence through this mechanism (Parker and Hegedus, 2003; Seago *et al.*, 2009).

Iridescence can also result from the presence of photonic crystals, which are ordered three-dimensional structures. The classic example of a photonic crystal is opal, which consists of tiny spheres of silica packed together. The diffraction of light through opal is determined by the size and regularity of the spheres, which in turn determines the colours shown. Three-dimensional structures generating iridescence have been found in a wide range of animals, including comb-jellies, several butterfly species, the feathers of a number of bird species and in the annelid *Aphrodita* sp. (Parker *et al.*, 2001; Vukusic and Sambles, 2003; reviewed in Welch and Vigneron, 2007). The spines of *Aphrodita* species show a multicoloured iridescence that is caused by a structure of holes ordered in hexagonal crystal structure within the spines (Parker *et al.*, 2001). Biological photonic crystals can vary greatly in both form and method of function.

MECHANISMS OF PLANT STRUCTURAL COLOUR AND IRIDESCENCE

Structural colour and iridescence have arisen multiple times in the animal kingdom, so it is hardly surprising that they are also found in plants. All the general mechanisms used by animals to produce structural colour are also used by plants. Like animals, plants produce structural colour by both coherent and incoherent scattering. Incoherent 'Rayleigh' scattering (by particles smaller than the wavelength of light reflected) has been found in a number of plant species. The wax deposits

on blue spruce (*Picea pungens*) and chalk dudleya (*Dudleya brittonii*) scatter shorter wavelengths of light preferentially, resulting in a blue colouration to the leaves (Vogelmann, 1993).

Iridescence has been shown to be produced by both multilayers (Fig. 2B) and diffraction gratings (Fig. 2C) in plants. The first example of multilayered iridescence in plants was found in the lycophyte *Selaginella*. Two species of *Selaginella*, *S. willdenowii* and *S. uncinata*, produce a vivid blue–green iridescence on their leaves when growing in shade. In the first detailed study into the mechanisms of plant iridescence, Hébant and Lee (1984) found that *Selaginella* leaves had two layers in the outer cell wall of their epidermal cells. These layers, visible under transmission electron microscopy, were each approx. 80 nm thick, the predicted thickness to cause multilayer interference that would result in the observed iridescence. These two layers were not found in ordinary green *Selaginella* leaves grown under higher light conditions and lacking iridescence (Hébant and Lee, 1984). Other plants with iridescent leaves are also found in low light environments, and all produce a similar blue–green iridescence. Although the multilayers in *Selaginella* appear to be relatively simple, with only a few layers producing the iridescence, other plant species produce more elaborate structures. The outer epidermal cell walls of the iridescent ferns *Danaea nodosa*, *Diplazium tomentosum* and *Lindsaea lucida* have many repeated dense layers alternating with arcs of cellulose microfibrils. The layers are of the correct thickness to cause iridescence through interference in the young iridescent leaves, but these layers are missing in the older leaves, which show no iridescence. The angle of the cellulose microfibrils changes gradually through the alternating layers up to a total 180 ° rotation (Graham *et al.*, 1993; Gould and Lee, 1996; Lee, 2007). The resulting helicoidal structure is remarkably similar to the helical stack of chitin microfibrils found in some iridescent beetle species and may therefore be an example of convergent evolution (Lee, 2007; Seago *et al.*, 2009). Leaf iridescence can also be caused by multilayers within the protoplast, not just within the cell wall. In the fern *Trichomanes elegans* and the angiosperms *Phyllagathis rotundifolia* and *Begonia pavonina*, specialized plastids called 'iridoplasts' are found in the iridescent leaves. These iridoplasts are much flatter than chloroplasts, and the thylakoid stacks within them are in such close contact that they form layers that cause the interference of light, resulting in the iridescent blue colouration (Graham *et al.*, 1993; Gould and Lee, 1996; Lee, 2007).

Multilayers generating iridescence are also found in the fruits of *Elaeocarpus angustifolius* and *Delarbrea michiana*, in this case arising from a structure called an 'iridosome'. This is secreted to the region outside the cell membrane of fruit epidermal cells, and consists of layers of cellulose that are of the predicted thickness to cause interference colouration (Lee, 1991; Lee *et al.*, 2000).

Diffraction gratings were identified in plants more recently, with the first report of their presence on the petals of species including *Tulipa* sp., *Hibiscus trionum* (Fig. 3A) and *Mentzelia lindleyi* (Fig. 3E) published in 2009. In these species the petal epidermal cells are elongated and flat and the overlying cuticle produces a series of long, ordered ridges with a periodicity that acts as a diffraction grating and splits the light reflecting from the surface into component wavelengths (Fig. 3B, C; Whitney *et al.*, 2009*a*). The iridescence produced is often predominantly in the UV wavelengths, which, although invisible to the human eye, are easily visible to many animal pollinators including bees and birds. The cuticular striations creating floral iridescence can also occur in patterns overlying those caused by pigment colour (Whitney *et al.*, 2009*a*, *b*).

Flowers are also the site of the one example of a three-dimensional photonic structure that has been found in plants. The elongated hairs that cover the attractive bracts surrounding edelweiss flowers (*Leontopodium nivale* subsp. *alpinum*) have an internal structure that acts as a photonic crystal (Vigneron *et al.*, 2005). The hairs are hollow tubes with a series of parallel striations around the external surface. Through diffraction effects, the hairs absorb the majority of the UV light, effectively acting as an efficient sun-block. A variety of other epidermal cell morphologies are also known to influence light capture and reflection in petals (Kevan and Backhaus, 1998).

FUNCTIONS OF ANIMAL IRIDESCENCE

Iridescence appears to have as varied a range of functions as it does methods of production in the animal kingdom. The recent review by Doucet and Meadows (2009) gives a clear overview of the functions of animal iridescence. The most frequent role of animal iridescence appears to be in visual communication. Iridescence can relay information about the animal's species (Silberglied and Taylor, 1978), about its age if iridescence changes or deteriorates over time (Kemp, 2006; Bitton and Dawson, 2008), about sex, as in many species only one sex has iridescence (Rutowski, 1977), and nutritional status, as individuals with poor nutrition may lack the resources to produce very vivid colouration (Kemp and Rutowski, 2007). Iridescence has also been found to play an important role in mate choice in birds, butterflies and fish (Kodric-Brown and Johnson, 2002; Sweeney *et al.*, 2003; Kemp, 2007), while the depth of the blue structural colour on the testicles indicates the degree of dominance within the troop of a male vervet monkey (Prum and Torres, 2004).

As well as providing information for other animals, structural colour has also been implicated in helping animals avoid detection by their predators, either by mimicry or by camouflage. Colourful reef fish are well camouflaged against the equally colourful corals, while tiger beetles blend a range of structural colours together to produce a matt camouflage (Schultz, 1986; Schultz and Bernard, 1989; Seago *et al.*, 2009).

FUNCTIONS OF PLANT IRIDESCENCE

As with animals, structural colour in plants is important in both display and defence. However, in plants the targets of the display are not other plants but pollinating insects, and the defence may be against potentially damaging levels of light as well as animal predators.

The primary function of flower and fruit iridescence is likely to be the attraction of animals, particularly those species whose visual systems are attuned to iridescence for

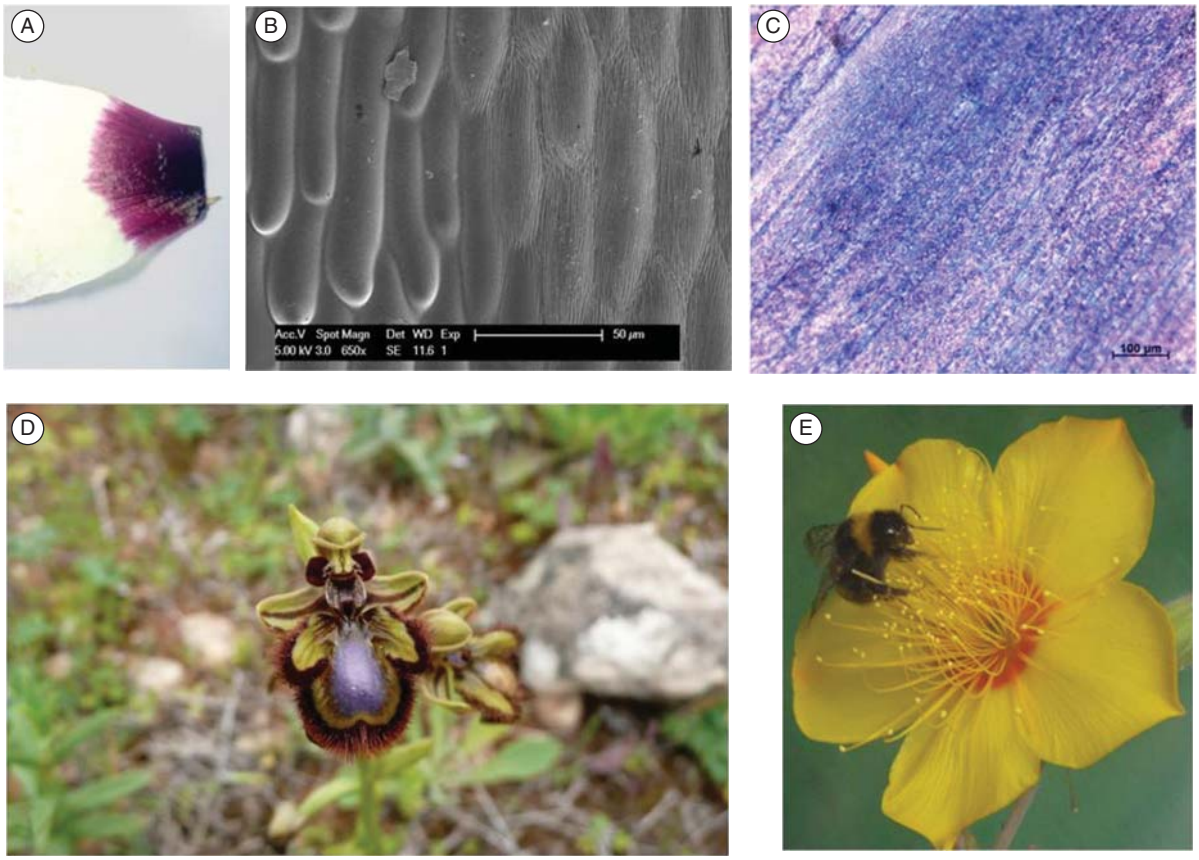

FIG. 3. Plant iridescence. (A) The inner part of the *Hibiscus trionum* petal has an oily iridescence overlying red pigmentation. (B) Scanning electron microscopy of this region shows that the cells overlying the red pigment are covered with a diffraction grating made from cuticular striations, although the cells over the white region are smooth. (C) When petal diffraction gratings are replicated in transparent optical epoxy, light reflected from the epoxy is not white but shows a range of colours. (D) The iridescent labellum of *Ophrys speculum* is thought to mimic the wings of female pollinators. (E) *Mentzelia lindleyi* is iridescent as a result of diffraction gratings, but the iridescence is only detectable in the bee-visible UV region of the spectrum.

animal–animal communication. The fruits of *Elaeocarpus* and *Delarbrea michiana* (Lee, 1991; Lee *et al.*, 2000) have an iridescence that is thought to enhance animal attraction. Iridescence has also been shown to attract pollinating insects. It has been believed for some time that iridescence is used by pseudocopulatory flowers (such as species of *Ophrys*, Fig. 3D) to mimic female insects visually, but we were able to show that iridescence can act as an ordinary, learnable cue, in the same way that flower colour or shape might (Whitney *et al.*, 2009*a*). Foraging bumblebees were trained that iridescent targets (generated by an artificial diffraction grating) contained a reward, whether they had a basic pigment colour of purple, blue or yellow, and that non-iridescent targets in the same pigment colours did not. The bees learned the iridescent cue, and were able to use it when presented with red targets to identify correctly the rewarding ones. The diffraction gratings generating floral iridescence often occur in patterns overlying those caused by pigment colour (Whitney *et al.*, 2009*b*), suggesting that they might enhance pigment-based learnable cues.

The ability of structural colour to reflect strongly in specific wavelengths is thought to provide photoprotection to leaves. The Rayleigh scattering shown by *Picea pungens* and *Dudleya brittonii* is thought to result in enhanced reflection of shorter wavelengths, and thus to give protection against UV damage (Vogelmann, 1993). Protection against UV is also thought to be the primary function of the photonic crystal hairs overlying the surface of the edelweiss bracts, which protect the reproductive tissues against the potentially mutagenic UV levels found at the altitudes where this plant grows (Vigneron *et al.*, 2005). Photoprotection may also be the function of the blue multilayer iridescence produced by understorey plants such as *Danaea nodosa*, *Diplazium tomentosum*, *Lindsaea lucida* and *Begonia pavonina*. These plants are all adapted to low light conditions, and so might be at risk of photodamage if they encountered sunflecks or other high-intensity light. The iridescent blue leaves of *Begonia pavonina* recovered significantly more rapidly from light exposure than green non-iridescent leaves, although no difference was found between the iridescent and non-iridescent leaves of *Diplazium tomentosum* (Lee, 2007).

In contrast, it has been hypothesized that the iridescence of *Selaginella* species might aid the capture of photosynthetically active wavelengths in low light conditions because the leaf iridescence may act as a natural anti-reflective coating. Such coatings (on glasses and cameras) use thin film structures, analogous to those found in the iridescent *Selaginella* leaf, to produce constructive interference for certain wavelengths,

increasing transmission of those wavelengths, but a side-effect is that the wavelengths not transmitted are strongly reflected because of destructive interference. In the same way, the iridescence in *Selaginella* could enhance blue-light reflection while enriching red-light absorption (Hébant and Lee, 1984).

OUTLOOK

Our understanding of plant structural colour and iridescence lags some way behind the work in animals, perhaps because plant pigment biochemistry has been studied so successfully or perhaps because animal structural colours are so striking. It is not surprising that similar mechanisms to generate structural colour have evolved in both plants and animals, but it will be important in the years to come to establish the molecular mechanisms underlying the development of these structures, which are likely to be very different in organisms with such basic differences in body architecture. The identification of structurally coloured plant species that are amenable to a genetic or transgenic dissection of candidate genes will be necessary to allow such work to progress rapidly. Preliminary studies suggest that some members of the Compositae, a number of petaloid monocots and certain species of Solanaceae might represent good targets for molecular and developmental analysis. It is also apparent that plant structural colour has evolved to mediate plant responses to both biotic and abiotic factors. A primary role is for communication with animals, and structures are therefore likely to target colours visible to pollinating or predatory species. One immediate challenge is to investigate how many species show structural colour (or iridescence) restricted to the UV region of the spectrum, and therefore invisible to the human eye. Investigation of the UV reflectance of flowers pollinated by insects that are themselves iridescent might be fruitful, as the visual acuity of such animals is already entrained to shifting colours, rather than to static ones. Such a study will also provide an understanding of the evolutionary lability of structural colour, and of the extent to which it appears to have co-evolved in response to interactions with particular groups of insect. Given that we do not currently have a good understanding of which plants produce structural colour, how they produce it and what they produce it for, one of the most exciting aspects of plant structural colour is the amount that still remains to be learned.

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