Plant Tissue Optics: Micro- and Nanostructures

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ABSTRACT

Plants have evolved unusual tissue optical properties, not surprising as creatures of light. These are astonishingly sophisticated, involving both micro- and nanostructures. Microstructures refract, scatter, and channel light in plant tissues, to produce concentrations and gradients of light within, and to remove undesired portions of the electromagnetic spectrum. Nanostructures use the different refractive indices of both cellulosic walls and bi-lipid membranes to interfere with light, multiple layers producing intense constructive coloration and reduced fluxes within tissues. In a tropical sedge now under analysis, structures may include silica. Recently discovered surface diffraction gratings produce strong directionally sensitive coloration that assist in pollinator visitation. Although some of these properties have obvious applications, most await appreciation by creative scientists to produce new useful devices.

Keywords: Plants, optics, energy capture, cellulose, microfibrils, leaves, interference, diffraction, fiber optics, thylakoids

1. PLANTS ARE NEGLECTED BIOINSPIRATIONS

Despite their dominance of the terrestrial world's ecosystems, plants have received less then due notice as templates of nature-inspired technology. They are passive, less charismatic, creatures and perhaps inspire less excitement than motile more human-like creatures. The stickiness of a gecko foot-pad seems more exciting than that of a root. However, there are two notable plant inspired discoveries that come to mind. The first is the discovery of Velcro™ by the inveterate Swiss inventor George de Mestral, inspired by the adherence of a cocklebur (*Xanthium* sp.) fruit during a mountain walk in the 1940's. Close inspection of the fruits led to the loop (*velour)* and hook (*crochet*) fasteners so ubiquitous today. Second is the discovery of super hydrophobicity by the German botanist Wilhelm Barthlott from his studies of water repellency in the sacred lotus (*Nelumbo nucifera*), which became known as the lotus effect[1] and has led to the development of self-cleaning surfaces. It is my task to represent the world of plants in this symposium and focus on some remarkable adaptations in their tissues, both on micro- (multi micron) and nano- (multi nanometer) scales, that relate to the capture of radiation by plants. After all, plants are creatures of light. Absorption of light is crucial for photosynthesis, the conversion of light to chemical energy. Yet, too much of certain wavelengths may be injurious to plants. Being sessile organisms with little in the way of motility as the means of responding to environmental changes, plants have evolved open plastic developmental processes[2] that facilitate environmental adaptations, and many of these relate to light absorption.

In this discussion, I'll focus on leaves as optical organs. Developmentally, flowers evolved from special reproductive axes from seed plant ancestors.[3] The accessory flower parts, petals and sepals, are both leaf-like. The reproductive structures, i.e. stamens and pistils, are both derived from leaves. The unit of structure in the development of the pistil is the carpel, which is easily seen as leaf-like in the development of the more basal flowering plants.[3] Leaves are optical organisms with a complex tissue organization that facilitates the distribution of light to tissues with differing physiological requirements for light in photosynthesis, and at the same time facilitating appropriate levels of gas exchange and water and nutrient delivery to those tissues. Pigmentation, both by chlorophylls and accessory pigments, contributes importantly to these optical properties, as also does the distribution of air spaces causing scattering and path-

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lengthening effects. A consequence of these physical properties is that the actual absorption of electromagnetic radiation by a leaf is significantly different than the absorbance spectrum of chlorophyll in solution. The packaging of pigments into organelles (as for chlorophylls and carotenoids) leads to sieving effects that reduce light capture in the regions of greatest absorbance by these pigments. The path- lengthening effects of air spaces in tissues promotes much greater absorption of electromagnetic radiation in weakly absorbed wavelengths (Fig. 1). I won't cover these points in any more detail in this discussion and refer the reader to a recently published monograph on tissue optics and plant colors.[4] Here, I will emphasize the effects of micro-structures in leaves, particularly cell shapes that refract light in ways that enhance energy absorption by plants, or otherwise promote plant fitness. Then I will discuss nano-structures, which are capable of physically interfering with light, altering interior light environments and producing brilliant colors to the exteriors of leaves, fruits and even flowers. In these discussions, I will primarily focus on the potential adaptive significances of these structures for plant survival, but will also mention what may be potentials for inventions and product development.

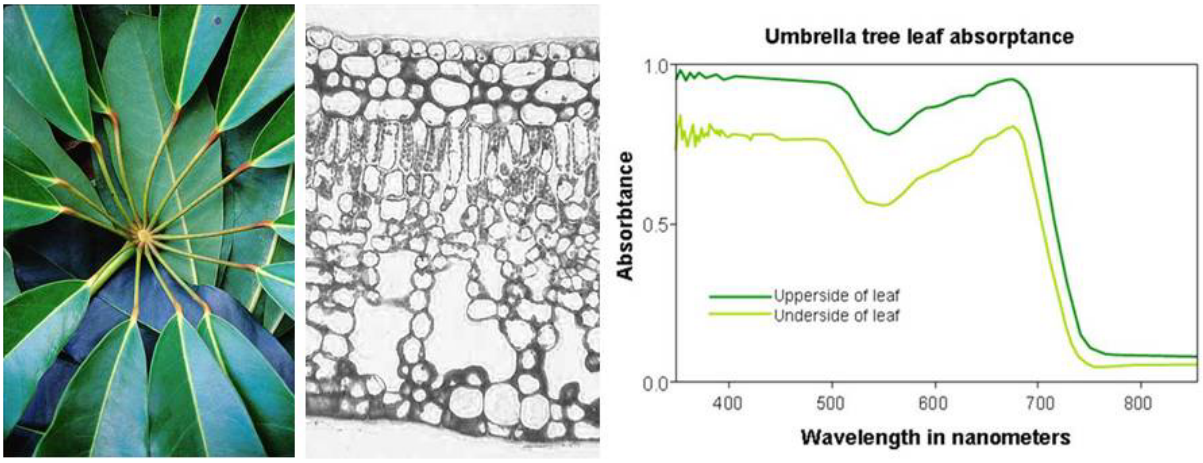

Figure 1. Leaf optics in the umbrella tree (*Schefflera actinophylla*). Left, difference between color of upper and undersurfaces is evident. This is due to leaf structure, center, which reveals air spaces mainly near the undersurface (leaf is 360 μm thick). Right, this accounts for the differences in absorption, and the relatively small reduction in green wavelengths is due to path-lengthening effects.[4]

2. MICRO-STRUCTURES IN PLANTS

Plant cells have dimensions of ~50 μm, and the shapes and distributions of cells profoundly influence the optical properties of leaves and other plant organs. Previously, I mentioned the importance of cells and air spaces, particularly in the middle of the leaf, in promoting scatter and the distribution of light within the leaf. These distributions are complex, and it is difficult to see patterns of structure that could inspire the discovery of optical devices. However, structures at the surfaces of organs have obvious optical properties and may provide some of the inspiration for which we are searching. If the surface were completely flat, transparent to most wavelengths of light, with refractive indices significantly higher than that of air, the optical properties of such a surface would be fairly predictable, with some critical angle of incidence where the surface would be a perfect reflector. Leaf surfaces are not flat and frequently produce

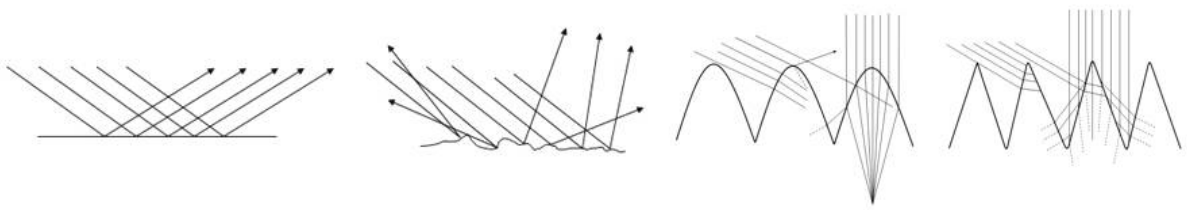

Figure 2. Diagrams of leaf and petal surfaces, describing their effects on reflectance, focusing and absorption of diffuse radiation.[4]

projections that dramatically increase scatter and reduce absorption (Fig. 2). Hairs and scales increase the back-scattering of radiation before it can be absorbed by leaf tissues (Fig. 3). They may also have additional functions, as defending against herbivory and reducing evapo-transpiration through insulation. Wax particles similarly scatter radiation and, if of sufficiently small size, will increasingly scatter shorter wavelengths through Tyndall scattering. A good example of bluish coloration from surface waxes are ornamental conifers such as the blue spruce (*Picea glauca*).

The surfaces of leaves and petals are seldom completely flat, due to the convex curvature of their epidermal cells. These vary from slightly round, to round and raised (papillose), to even sharply conical. A surface view of the surface with raised epidermal cells looks very much like the SEM photograph of the compound eye of an insect. The focusing effects

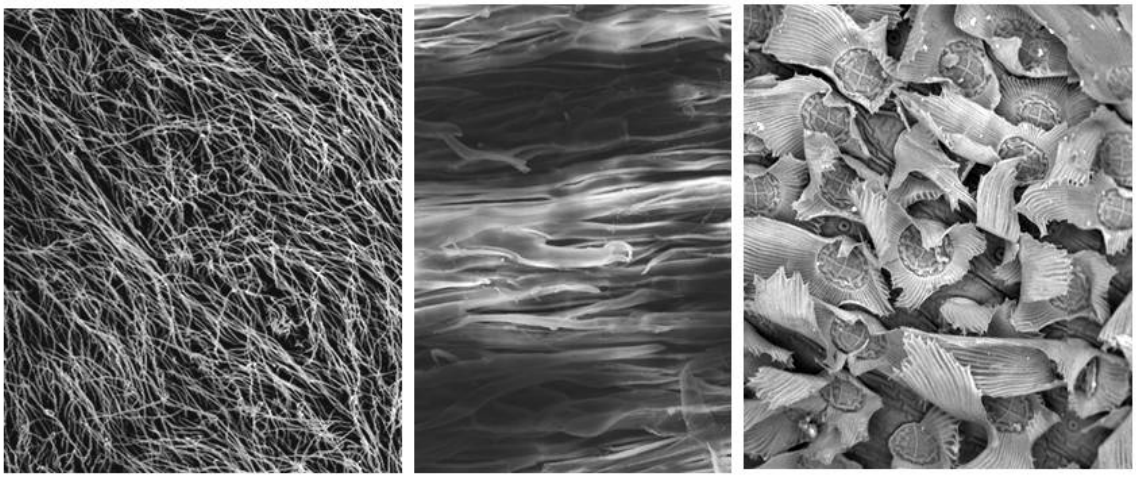

Figure 3. Surface structures on plant organs scatter radiation, reducing its absorption. Left, silver buttonwood (*Conocarpus erectus*, width 1.2 mm); center, silver thatch palm (*Coccothrinax argentata*, width 500 μm); right, ball moss (*Tillandsia recurvata*, width 1.2 mm).[4]

of such cells was commented by the European physiological plant anatomists at the end of the 19th century, but have only been modeled and examined in a quantitative fashion fairly recently. Strongly papillose cell shapes are particularly common among plants of extreme shade habitats; in such environments these cells may well focus light onto optimally positioned chloroplasts to increase photosynthetic rates in such energy poor sites.[5] The light concentrating effects of leaves has been examined in ray-tracing experiments and has been indirectly estimated by producing gel replicas of the cell surfaces.[6] These effects are dependent upon the actual surface diameters of the cells, the shape of the raised cells, and the position of chloroplasts in cell layers underneath the surface (Fig. 4).

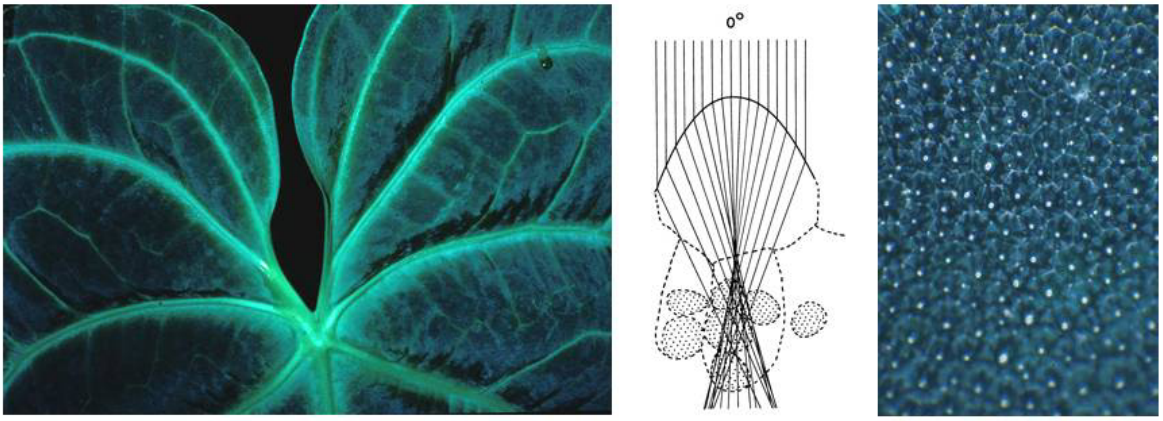

Figure 4. Epidermal lens effects in the velvet-leaved anthurium (*Anthurium warocqueanum*). Left, leaf is 15 cm across; center, cell diagram with vertical incident light modeled; right, leaf surface showing focusing effects, image width 1.1 mm.[4,5]

The radiation in extreme-shade environments, such as the understory of a tropical rainforest, is generally dominated by diffuse sources by all angles of the sky, with occasional short durations of flecks of radiation from small openings in the canopy. Leaf surface features that could increase the efficiency of absorption of diffuse light can easily be envisioned; this could consist of narrowly pointed cells that could reduce the reflection at oblique angles of incidence and could deflect vertical angles into the bases of the conical projections. However, any curvature at the tip of these projections would increase their refractive properties and reduce their ability to capture diffuse radiation.[7] These surfaces remind me of the difference of standard glass used in photographic frames, compared to those etched with hydrofluoric acid with reduced reflectance and glare.

An important means for learning about the function of structures in organisms is to find mutations in which the structure is lacking, and then compare the functioning of the two organisms. This also allows a means to determine the developmental processes that create these structures at very fine scale. Raised cell surface in petals (and presumably in leaves, too) is promoted by a gene, a Myb-related transcription factor, in several plants.[8] In plants with a mutation that disables this factor, the papillose surface is lost. This decreases the intensity of color production in flowers, and decreases pollinator visits, seed production and evolutionary fitness. However, the story may be more complicated. These raised cell surfaces also for greater ease in the attachment of insects that actually land on, and move into, the flower, obtaining their nectar award and effecting pollination.[9] The papillose cell surfaces of the sacred lotus contribute to the hydrophobicity of its leaves, but wax deposits on those surfaces are equally important. Its production is probably controlled by the same transcription factor described for flowers (Fig. 5).

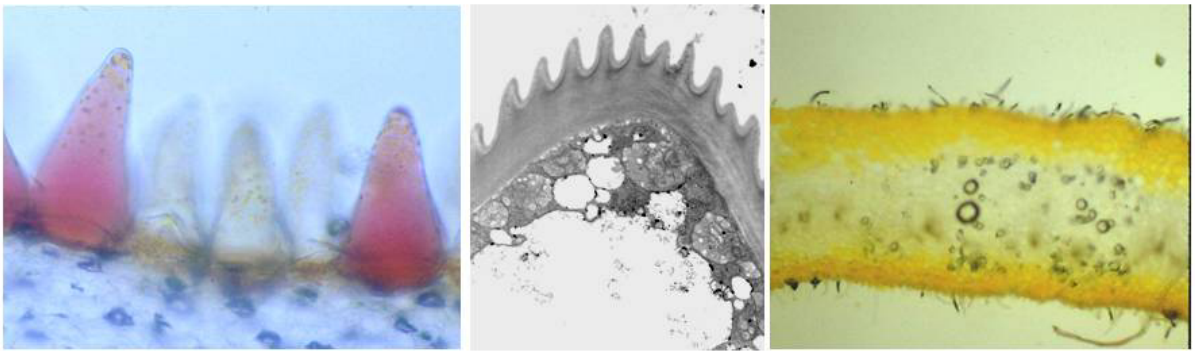

Figure 5. Raised cells affect absorption and color production in flower petals. Left, ray flowers of the French marigold (*Tagetes patula*, width of image 180 μm); center, detail of cell tip with tubercles, width 12 μm; right, pubescent petal of flame of the forest (*Butea monosperma*, thickness 170 μm).[4]

Many plants, again particularly those growing in forest understory environments, produce variegated leaves—leaves with splotches of white or colors other than green. Most plants whose leaves produce white splotches do so by destroying the chloroplasts in certain cell layers and segments of leaves. Discovery of the genetic mechanisms for variegation in many plants has led to some spectacular horticultural varieties. A minority of these white variegated plants do so without destroying photosynthetic tissue, but by more simply separating the epidermal cells from those beneath, producing a back-scattering air space, and thereby promoting the reflectance of "white" light before it has interacted with leaf pigments. Such splotches are silvery in appearance, and some species are more silvery than others.[10] I use the example of *Begonia maculata*, one of many that produce silvery variegation—but it seems particularly strong in this plant (Fig. 6). In a close up of the surface of the leaf, we see that the silvery color is conveyed to the surface by the side walls of the epidermal cells. A transverse section of the leaf shows a slight convex curvature of the epidermal cells at the surface, and a much stronger convex curvature on their abaxial side. This curvature and the associated spaces are absent from the non-variegated parts of the leaf.

I interpret this pattern of production of silver variegation in the following way. Light passes into the leaf and is scattered when it encounters the air spaces beneath the epidermal cells. This scattering funnels the light as it is reflected at oblique angles into the cell wall junctions of adjacent cells and the path out of the leaf is channeled by the side cell walls of the epidermal cells. These walls, primarily consisting of hydrated cellulose microfibrils, then function as light guides in

constraining the paths of light emitted from the leaf surface. Such structures may be homologous to safety reflectors on vehicles such as bicycles. However, perhaps the details of the variegation may inspire the design of even more efficient reflectors. For instance, emission of light by the side walls of the cell could be of a different color than that from the cell itself. There is little research on the function of plant tissues as light guides, and there may be other examples. Crystals may function in this way, or the vacuoles of elongated cells. It is quite possible that such light guides on side walls could efficiently convey light past dense collections of chloroplasts in the palisade cells into more sheltered photosynthetic cells beneath. Variegation in shade plants seems counter-intuitive. Why would plants in such shady environments reduce the absorption of light in portions of the leaf? One answer may be that such leaves are perceived as not leaf-like or as already containing herbivorous insects (as leaf minors), thus avoiding being eaten by other insects.[11] There is much about leaf structure and optics that would profit from closer observation, as inspirations for new optical devices.

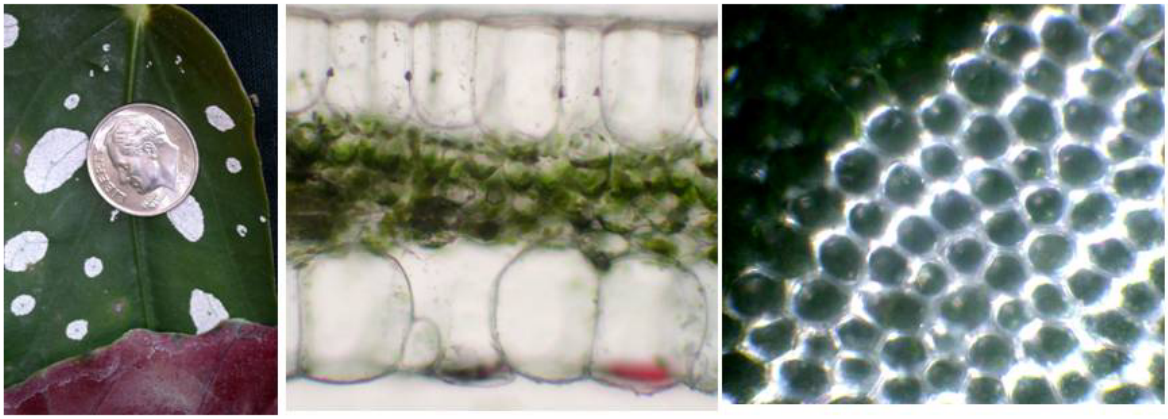

Figure 6. Silver leaf variegation in *Begonia maculata* (photographs by author). Leaf detail on left; center, transverse section, 230 μm thick; right, backscatter in side walls of epidermis, image width 500 μm.,

2. NANO-STRUCTURES IN PLANTS

In this symposium there are nine talks describing unusual structures/functions in organisms; five of these concern photonics; and this paper is the only one describing photonic systems in plants. Most of our attention in animals has and still concerns structural colors produced in a variety of ways. Structural blues are particularly noteworthy in animals; animals do not produce the pigment palette of plants, and produce blues via structures with the probable exception of a single marine fish. Greens in animals are generally caused by structural blues with superposed carotenoid-containing cells. Even those carotenoids are obtained from their diets of plant or algal materials. Various structures, including interference layers and three-dimensional structures, diffraction gratings, and small particles have been been implicating in producing structural colors. Plants can produce brilliant blue colors via modifications of anthocyanin pigments, yet they also produce structural blues via constructive interference. The following paragraphs review the nature of these structures, based on cellulose microfibrils and via thylakoid membranes of modified plastids. Very recently, diffraction gratings have been described that produce colors in flowers; This research will be reviewed at the end of this section.

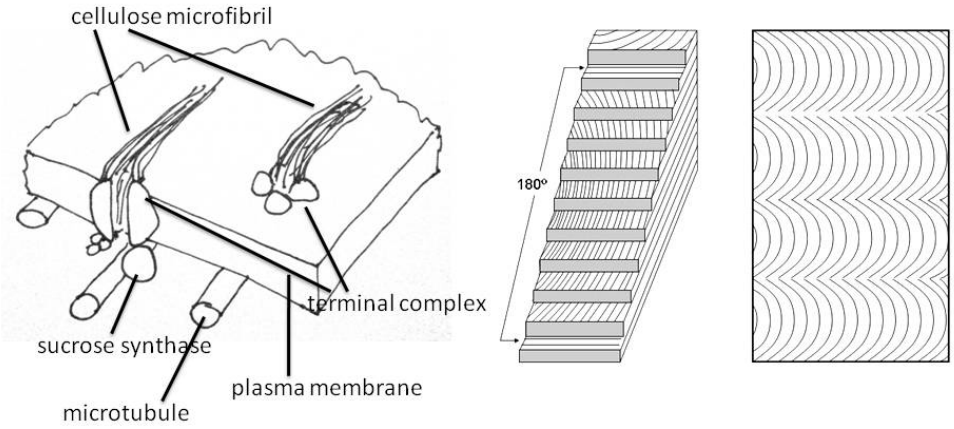

Figure 7. Cellulose deposition. Left, mechanism of microfibril production.[12] Right, changes in angle of microfibril deposition produce layers and a helicoids appearance.[4]

3.1 Interference structures based on cellulose.

Cellulose, in cell walls and also as inclusions produced outside of the cell membrane and yet inside of the cell wall, has been shown to produce brilliant blue colors through interference, in leaves and fruits of a few tropical rainforest plants. Cellulose, the most abundant polymer on earth, is particularly interesting to specialists in paper and wood chemistry. We have learned much about cellulose synthesis, microfibril assembly and cell wall deposition. Although cellulose is the most abundant component of cell walls, cross-linking components and pectins are also important.[12] Microfibrils are secreted from cell membranes on six-component cellulose synthase complexes (Fig. 7). Each component produces 3 or 6 cellulose polymers, to assemble microfibrils of 18 or 36 single polhymers. The direction of microfibril production is influenced by the orientation of cytyoskeleten components just beneath the cell membrane.[13] The orientation of microfibrils determines the expansion of the growing cell, and the final cell shape. Thus, alterations in microfibril orientation affect the ability of epidermal cells to produce lensing properties. Alternations in microfibril orientation may produce layers of the appropriate thickness and different refractive indices to produce conditions for color production through constructive interference.[14] When subsequent layers of microfibrils are deposited at a constantly different angle a helicoidal arrangement is seen in the cell walls at angles slightly deviating from a perpendicular orientation (Fig 7).[15] These layers may interfere with light and also display properties of circular polarization. Helicoidal cell walls accounting for structural blue colors have been seen in ferns of both the old and new world tropics (Fig. 8).[16,17]

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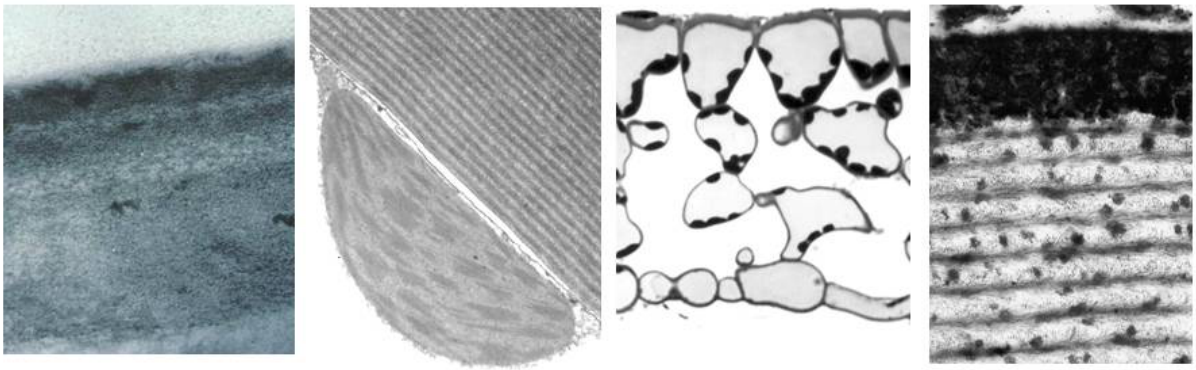

Figure 8. Cellulose cell wall structures produce blue colors through constructive interference. Left, layers in *Selaginella uncinata*, each layer ~70 nm thick; left center, transverse section of leaf of *Danaea nodosa*, with chloroplast and helicoidal layers above, image 6 μm wide; right center, transverse section of leaf of *Diplazium tomentosum*, 130 μm thick; right, section of cell wall showing helicoidal layers, vertical distance 2 μm.[4]

In rare instances fruits make structures capable of producing interference colors, blues in the examples studied thus far. In *Elaeocarpus,* an old world tropical tree genus, the fruits of most species are blue when ripe. In rudraksha, or *E. angustifolius*, the best known of these trees, the spherical fruits are a brilliant blue. This blue color is not due to

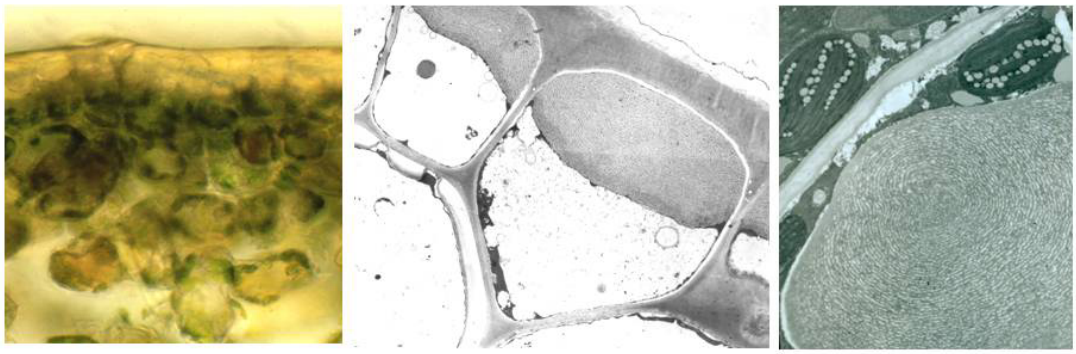

Figure 9. Interference structures in fruits. Left and center, fruit wall, with photosynthetic tissue beneath, of *Elaeocarpus angustifolius*, image height 150 μm; center, epidermal cells with iridescence structure between cell and wall, image height 30 μm; right, similar structure in *Delarbrea michieana*, image height 6 μm.

pigmentation, but to a complex structure that is secreted by the epidermal cells but lies within the outer cell wall.[18] A similar structure, again inside of the cell wall but outside of the cell membrane, is produced in the brilliant blue fruits of a queensland member of the family Araliaceae: *Delarbrea michieana*. Both of these structures are at least partly composed of cellulose, but differ considerably in structural detail from each other.[19] It is quite possible, and just poorly surveyed to date, that structural color may be more widespread in fruits, not just for blues, but for reds and other colors.

Such properties of cellulose polymers in plant cell walls are of great interest to paper and polymer chemists; one obvious use is the production of papers producing interference colors that would increase the difficulty of producing counterfeit currency. There is a large body of research in this area, some of it proprietary. When I first wrote a popular article on this subject in the American Scientist in 1998, I received an email message from a scientist at the National Institute of Standards and Technology (NIST): "It looks like mother nature beat us to the punch". Since then, cellulose has been used to produce interference colors as well as other novel optical properties.[20,21,22] Much of this research may not be familiar with materials scientists, as it is organized by the Cellulose and Renewable Materials Division of the American Chemical Society, and is conducted in institutes of polymer chemistry and pulp and paper technology.

3.2 Interference structures from thylakoid membranes.

Within cells, membranes have refractive indices similar to cellulose, both somewhat higher that aqueuous solutions in the cell, at ~1.40. In plant cells the most highly organized and planarly organized internal membranes are within the chloroplasts, the thylakoid membranes. In iridescent blue understory plants, these membranes account for blue colors in species of *Begonia* (Begoniaceae) and *Phyllagathis* (Melastomataceae) in southeast Asia[17], and a single filmy fern native to the neotropics, *Trichomanes elegans*.[16] In the Asian blue understory plants, very distinctive chloroplasts occur in the epidermal cells. These have very thin aggregations of the thylakoid membranes. These stretch for the entire length of a flat pancake-shaped organelle, uniform in thickness, and of a thickness that would account for the wavelength of the interference color. In the neotropical filmy fern, massive chloroplasts that aggregate against the adaxial surface of epidermal cells have a distinct aggregation of thylakoid membranes in short stacks. These account for the intense blue-green color produced by these plants (Fig. 10). Chloroplasts may also have a region functioning in iridescence above a region with normal thylakoid layering and better organized for photosynthesis.[23]

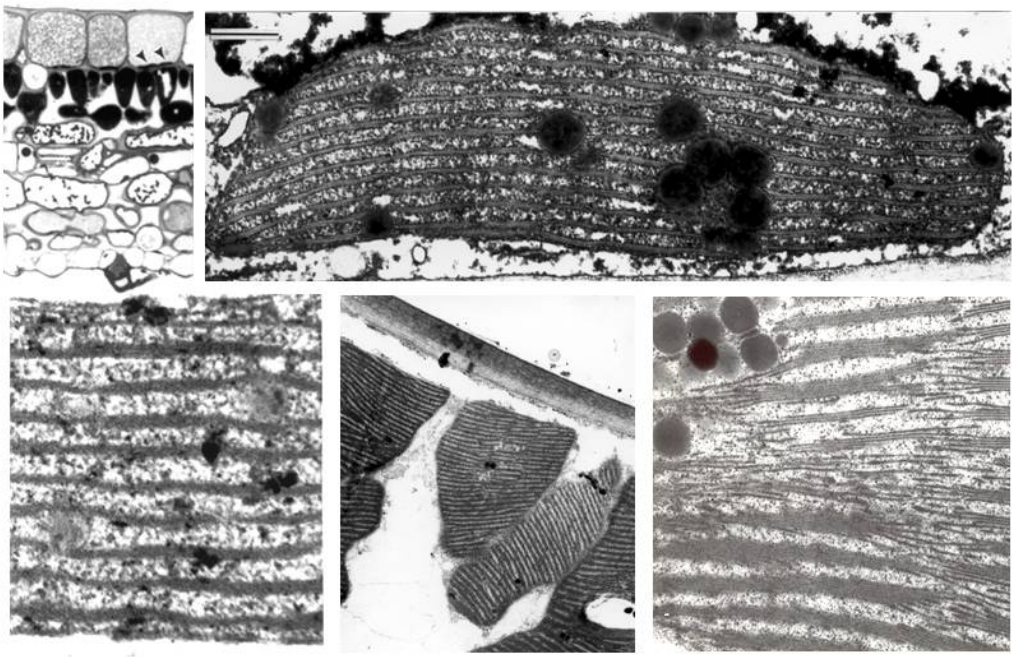

Figure 10. Thylakoid membranes produce iridescent blue colors. Top, Phallagathis rotundifolia; left, leaf transverse section (small areas indicating positions of plastids), 230 μm thick; right an intact iridoplast, image 1 μm top to bottom. Bottom left, detail of iridosome of *Begonia pavonina*; center and righ,t chloroplasts of *Trichomanes elegans*, image heights 9.8 and 2.7 μm.

3.3 Silica particles and Structural Coloration in an Asian Sedge.

I am presently collaborating with two colleagues at the University of Oklahoma, Greg Strout and Scott Russell, to determine the mechanism of structural color produced by an understory sedge (a member of the Cyperaceae). These are tough and durable plants with serrated leaf margins that can cut skin; several understory species produce intense blue colors. We are mid-stream in this analysis. The cell walls have a loose helicoidal appearance from analysis by TEM, but

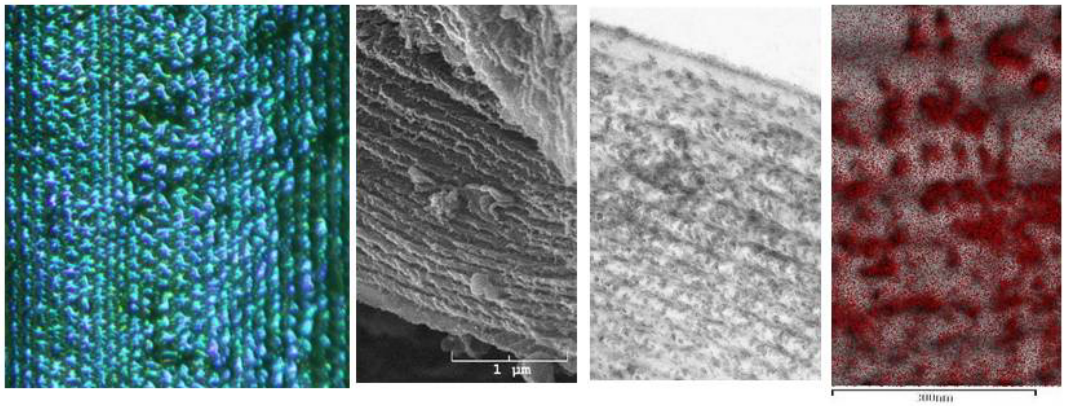

Figure 11. Blue iridescence in *Mapania caudata* (Cyperaceae). Left, surface of leaf with interlocking iridescent epidermal cells; left, SEM image of cell walls showing lamella, bar is 1 μm; right center, TEM image of wall, with some evidence of helicoidal microfibral arrangement, 1.3 μm top to bottom; right, energy dispersive x-ray diffractive image (EDS) superimposed on TEM image, showing granules of silica dioxide concentrated along lamellae, bar 300 nm. Photographs by Greg Strout of the Samuel Roberts Nobel Electron Microscopy Laboratory (SNRML) at the University of Oklahoma, Norman.

its thickness does not seem to account for the peak coloration of 480-490 nm. Electron dense bodies are produced at the adaxial margin of each helicoids and electron probe analysis indicates that these bodies are composed of silica (Fig. 11).

These particles are present at much lower concentrations in green leaves. From the ”choice” of materials it almost seems that the plant is the biomimic of some human invention.

3.4 Plant Diffraction Gratings.

A second mechanism for color production, rarely seen in animals, is diffraction, which produces a rainbow of colors, strongly dependent upon incident angle. I never thought that such a mechanism could work in plants, because plant surfaces, especially in their micro-topography, are uneven. McClenden[24] suggested that we might see diffraction patterns in a microscope, but not on a gross level; the variations of color would produce white light at a larger scale. However, a recent paper in Science[25] has made a believer of me. Heather Whitney, while working in Beverley Glover's laboratory at Cambridge University, showed that structures on the surface of petals of *Hibiscus trionum* function

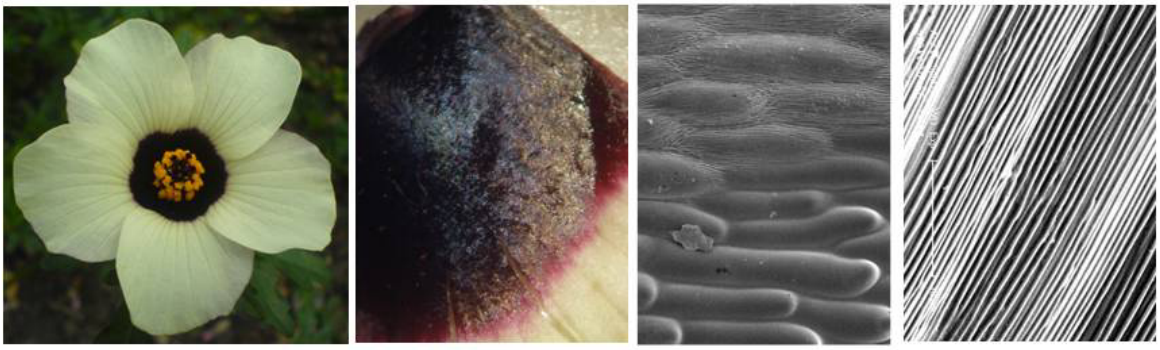

Figure 12. Diffraction gratings in flowers of Hibiscus trionum. Left, entire flower, ~4 cm across; left center, detail of red iridescent spot at base of petal, ~3 mm across; right center, SEM of petal showing smooth and striated cells, image 120 μm across; right, SEM of individual petal cells of *Adonis annua* with diffraction lines, image ~40 μm across.

as diffraction gratings and produce the iridescent pigmented patch at the base of each petal (Fig. 12). Whitney and colleagues duplicated the surface structures with epoxy casts, and reproduced the iridescent color. Furthermore, they demonstrated that bumble bees respond to these colors, and the shifts in hue depending upon approach angle, to successfully orientate themselves on the flowers. They also showed diffraction color produced in tulip petals (*Tulipa kolpakowskiana*). Since striations are relatively common in flowers, they speculate that diffraction structures may be quite common among flowering plants.

3.4 The Function of Structural Coloration in Plants.

In plants, structural coloration has three distinct features; each may relate to their functional significance in plants. This depends upon the plant organ with the color and the biological or physiological function that could be affected. It is also possible that coloration could have more than one function for a plant. First, structural coloration is relatively permanent. It persists in fruits long after they fall from the tree and the interior tissues are broken down. It is also persistent in leaves, perhaps particularly when it is produced within the cell walls. Such color persistence may be important if color is a signal to attract dispersal agents (fruits), or to disguise appearance to deter herbivores (leaves). Second, since structural color is produced by constructive interference, the structure will destructively interfere with electromagnetic radiation at longer wavelengths. Such destructive interference makes the structures less reflective at these longer wavelengths, meaning greater penetration of light into the structure. In *Selaginella*, the peak of constructive interference is at 405 nm, at the short end of the photosynthetic action spectrum. The filter is on the leaf surface and blue color is removed when the leaf is immersed in water. Thus, reflectance at a shorter wavelength is associated with greater transparency at longer wavelengths. Such a filter could then act as an anti-reflection coating (as it does in the coating of optical lenses) allowing more light penetration and more efficient photosynthesis at longer wavelengths. Thirdly, constructive interference alters the interior light environment of a plant organ in a highly specific way. In most blue leaves, constructive interference is at 480-490 nm. It is possible, that such changes in the interior light environments may be physiologically advantageous to the plant. Leaves, particularly those acclimated to deep shade, are vulnerable to photoinhibion of photosynthesis and even photodamage to, and destruction of, chloroplasts and whole segments of leaves. I have hypothesized that iridescent blue leaves may protect leaves from photoinhibition when they are exposed

to high light levels. I tested this hypothesis and found significant levels of photoprotection in leaves of *Begonia pavonina* and *Phyllagathis rotundifolia*, from field experiments in Malaysia (unpublished research). I found that fluorescence kinetics of blue leaves, as indicated by the ratio of variable to maximal fluorescence (Fv/Fm) changed less, indicative of less reduction in quantum efficiency and less photoinhibition, then leaves without structural blue color. These results are consistent with studies showing the value of accessory pigments in leaves, anthocyanins and carotenoids, in altering interior leaf light environments and protecting them against photoinhibition.

3. PROSPECTS FOR BIOMIMICRY FROM PLANTS

Much of the research described in this review is recent, having been published within the last decade. it is evident that there is much to be learned about structural properties of plant organs and their effects on optical properties. It is probably equally true that mechanical properties in leaves will provide a fertile field for research, and opportunities for biomimicry. I am reminded of plant movements, not just the closure of traps in carnivorous plants (as the venus fly trap and bladderworts), but also in the movements of floral parts in dispersing pollen and seeds. In jewel weed (*Impatiens* sp.) and many other plants, seeds are ejected from young capsules as they explode. In bunchberry (*Cornus Canadensis*), in the manner of a medieval trebuchet, pollen is ejected from anthers in 500 μ sec.[26] In the white mulberry (*Morus alba*), the motion of the springing stamens approaches half the speed of sound in dispersing its pollen, in a duration of 250 μ sec—now the world record holder.[27] What this requires is that plants not be ignored—but examined with a modicum of quantitative insight. Even better, collaboration between plant biologists, yes botanists, and materials scientists could lead to new insights about plant function, feeding our bioinspiration and leading to new biomimetic devices. The new kinds of interdisciplinary research will involve plant structure and physiology, biomechanics, biophysics, development and evolution, and molecular genetics. Good models for this type of research are seen in recent studies on the effects of petal shape[8] and petal diffraction[25].

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