The Mystery of Seasonal Color Change

David Lee

... the gods are growing old;
The stars are singing Golden hair to gray
Green leaf to yellow leaf,—or chlorophyll
To xanthophyll, to be more scientific ...

Edwin Arlington Robinson (Captain Craig)

Throughout New England each autumn—early October in some parts and as much as three weeks later in others—the pageant of color change in our forests unfolds. Though less noticed, in the springtime these forest canopies take on delicate pastel colors as buds swell and leaves expand. In the last 15 years, our understanding of the science behind color change has begun to emerge, with two different but not mutually exclusive hypotheses being formulated and defended. I have been involved in the research and debate on these color changes, and why that is so is a bit of a mystery in itself. After all, I grew up on the cold desert of the Columbia Plateau in Washington State, where the predominant colors were the grays of sagebrush and other pubescent shrubs. Occasionally I visited the forests of the Cascade Range to the west, witnessing the dark greens of conifers, occasional yellows of cottonwood, birch, and willow in the autumn, with just a few splashes of the reds of the Douglas maple (*Acer glabrum* var. *douglasii*). I did enjoy the autumn colors of the mid-Atlantic and Midwest forests as a graduate student and post-doctoral fellow, but was too busy in the laboratory to think much about that color.

Then I moved to tropical Asia—Malaysia specifically—and took notice of the differences in tropical rainforest vegetation, which I have been studying ever since. I was particularly struck by the red colors of leaves, both on the undersides of understory plants and the expanding leaves of giant trees (so colorful that from a distance they looked to be in flower). Yet, few of
the leaves turned red before falling from trees, and the canopies remained green because leaf fall was staggered. I began studying that red color—which led me back to the autumn reds of New England forests.

**A PALETTE OF PIGMENTS**

As poet Edwin Arlington Robinson partly described, the colors of leaves are the products of pigments produced in their internal tissues. Chlorophylls produce greens, xanthophylls produce yellows and oranges, and anthocyanins (left out by Robinson) produce reds. The leaf tissue is like the thick paper employed in watercolor painting. If you consider that most of the leaf consists of cellulose fibers, the similarities are particularly strong. The interior leaf volume, with its numerous air chambers facilitating the exchange of gases that supports photosynthesis, strongly scatters light, allowing some to reflect and some to be transmitted through the leaf. The leaf pigments are then like the soluble pigments in watercolors, and color is produced subtractively. Chlorophyll produces a green color because it absorbs light in the blue and red wavelengths. Xanthophylls produce yellow because they absorb blue into green, and anthocyanins red because they absorb even more green into blue. These pigments can combine to produce oranges (yellow and red), or even brown (green and red). The colors of spring and autumn are produced by these pigment combinations in leaves.

When I was a college student of botany in the 1960s, the textbooks taught us that autumn colors were produced by the loss of chlorophyll unmasking the yellows of xanthophyll and reds of anthocyanin pigments, and that the colors had no function. To me, this did not seem right for the reds of anthocyanins, because I knew that these pigments are quickly synthesized in leaves. When I began to work at Florida International University in Miami in 1980, I turned my attention to the young leaves of mango and

A red maple glows in autumn color at the edge of Connor Pond, between the towns of Petersham and Barre in central Massachusetts.
cacao, where anthocyanins are produced when developing leaves are rapidly expanding. We showed that the anthocyanins disappear when the leaves mature and that they do not effectively protect against ultraviolet (UV) damage [then the ruling hypothesis about anthocyanins' function in leaves]. However, the importance of the inhibition of photosynthesis by high levels of solar energy, in leaves not able to process this excess energy, was a newly appreciated facet of leaf physiology—and anthocyanins could function as a sunscreen to protect against this damage. Kevin Gould, now at Victoria University of Wellington, in New Zealand, came to Miami to work with me on this problem for a year. Kevin, along with FIU colleagues and me, pursued this hypothesis in understory plants with red undersurfaces (where shade-adapted plants are particularly vulnerable to damage from flecks of sunlight) and published a short paper in the journal Nature in 1995. Kevin went on to become the global expert on anthocyanin function in leaves.

RESEARCH AT HARVARD FOREST
I had thought that the Nature article would promote more interest and research in this phenomenon, but little happened. It was then that I turned my focus towards autumn colors. That was a phenomenon universally appreciated, and a powerful economic driver of tourist business in New England during the autumn months; I have observed Route 2, running west out of Cambridge, Massachusetts, turn into a parking lot of buses loaded with international tourists in the middle of October.

In 1997, during a conference on “Hinduism and Ecology” at the Harvard Divinity School, I had dinner with Missy Holbrook who was then a junior faculty member at Harvard (and an old friend) to discuss research on autumn foliage. At the time I thought that red leaf coloration during the autumn meant the synthesis of protective anthocyanin pigments during senescence. The riddle was that protection during leaf senescence made no sense; the leaves were about to die. The advantage had to go to the
entire tree for the following year, and we speculated that the advantage could be to protect the leaves during the process of the breakdown of chlorophyll. Leaves carefully disassemble the chlorophyll and associated proteins during senescence, and much of the nitrogen-containing compounds are resorbed in the woody tissues for use the following spring.

We discussed a plan of action, and Missy supported my application for a Bullard Fellowship at the Harvard Forest in Petersham, Massachusetts, which I used from late summer through early winter in 1998 and 2004. During those sojourns in central Massachusetts, with frequent cultural trips to Cambridge and Boston, I observed the changes in the forest pretty much every day, and made observations and physiological measurements of leaves during the process of leaf senescence and color change. When the snow started falling in early December, I high-tailed it back to balmy Miami.

Missy and I collaborated with her Ph.D. student Taylor Feild (now at the University of Tennessee) and Harvard Forest scientist John O’Keefe, who had been observing the phenology (when trees leaf out, when they flower and fruit, and when the leaves change color and fall from the trees) of common tree species at the forest starting in 1991. We found that most of the trees and shrubs (62 of 89, or 70%) produced anthocyanins during senescence, starting when leaves had already lost about half of their chlorophyll. Such leaves appeared red, red-orange, bronze, and even brown in color. The precise colors depended on the mixtures of anthocyanins, chlorophylls, and xanthophylls. We studied the changes in pigment composition and physiology in leaves of individuals of 16 species, 8 with anthocyanins and 8 whose leaves turned yellow (they had residual xanthophylls but no anthocyanins). We found that anthocyanin concentration during senescence was correlated with lower nitrogen content, consistent with the prediction that more nitrogen could be resorbed by the woody

Autumn leaf color in sugar maple (Acer saccharum) varies between (and even within) individual specimens.
tissue. We also reported that the timing of leaf fall varied between species, but was pretty consistent within species from year to year. However, with more data collected, John and other collaborators have been able to show that leaves are forming earlier and senescing a bit later—the early influence of climate change. We also conducted some shading experiments and showed that reduced solar radiation retarded leaf senescence (and anthocyanin production) in red leaves.

Following Taylor’s lead, we examined the physiology of leaves of red-osier dogwood (*Cornus sericea*) during senescence and obtained clear evidence of photoprotection by the anthocyanins accumulating in the vacuoles of the photosynthetic cells, additional support for this hypothesis. At about the same time that Taylor’s paper came out, William Hoch and colleagues published a review of this hypothesis in considerable detail, and then two years later published the best evidence of the photoprotection hypothesis, using green- and red-senescing varieties of three common shrubs, Elliott’s blueberry (*Vaccinium elliottii*), red-osier dogwood, and Sargent viburnum (*Viburnum sargentii*), showing that the anthocyanin-lacking mutants resorbed significantly less anthocyanin than the red anthocyanin-containing varieties.

About the time we were initially pursuing this research, William Hamilton, the famous evolutionary biologist known for his research on sexual selection, had proposed a radically different explanation. He argued that colorful leaves could serve as a warning to potential herbivores, specifically aphids, advertising the toxicity or low palatability of the leaves. Thus warned, the aphids would avoid those trees during the autumn and would lay their eggs on un-advertised (green) trees, thereby favoring the growth of the autumn-red or yellow trees the following year. Their initial evidence for this hypothesis was primarily for yellow leaves, and was based on existing literature. Hamilton, along with Sam Brown and Marco Archetti, began to test the hypothesis, but Hamilton tragically died in Africa from malaria in 2000. This hypothesis particularly stimulated Marco Archetti to tenaciously search for evidence supporting it.
DUETING HYPOTHESES
Publications supporting the two hypotheses stimulated additional research, along with a number of speculative reviews. A little animosity arose between proponents of these two views, even though the hypotheses were not mutually exclusive. To Marco’s credit, he convened a meeting at Oxford in March 2008, with researchers from both “camps” present. That created (1) some good will, (2) the understanding that we didn’t know much about either hypothesis (which is often the fuel for disagreement and animosity), (3) the most exhaustive review on the subject (see the citation at the end of this article), and (4) an exhortation that we should produce the missing data that would more critically test the hypotheses.

Because it involves animals, the co-evolution hypothesis has attracted the most research. When we observe color, we automatically think of signaling—as from attractive flowers to pollinators, and from colorful fruits to dispersers. Conversely, in the physiological hypothesis, color is merely the by-product of protective absorption at specific wavelengths we can’t see.

We now know that color, particularly yellow against a green background, repels visits by aphids, at least in the few trees that have been examined, especially European birch (*Betula pendula*). The evidence for red leaves is more controversial. Although there is some evidence of aphids avoiding red leaves, these insects seem not to have visual receptive cells sensitive in the red wavelengths. Limited evidence supports the contention that repelling aphids reduces egg laying, decreases activity of these sucking insects the following year, and increases seed production. Marco’s strongest supporting evidence is from wild apples, where autumn aphids lay more eggs on green rather than red leaves.

Another weakness is a lack of evidence of reduced palatability, greater toxicity, or less nutrition in yellow or red leaves, although such leaves would likely be more advanced in senescence and thus less nutritious than green leaves. A model of the kind of research needed was published in 2011 by Kevin Gould and colleagues in a New Zealand tree, horopito (*Pseudowintera colorata*), that has red leaf margins. They found a toxic plant molecule, polygodial, was associated with...
red edges, and the combination dramatically reduced attacks by insects feeding on the edges of the leaves.

The evidence for the physiological hypothesis has not increased appreciably since Hoch’s paper, although the photoprotective function of anthocyanins is now widely accepted. Reactive chlorophyll catabolite (RCC), a chlorophyll breakdown intermediate, may be especially important, and anthocyanins nicely intercept the wavelengths that activate this molecule. So, we’re pretty much in the dark about the mechanism of photoprotection by anthocyanins.

MORE QUESTIONS ABOUT COLOR

Much that we have recently learned about autumn coloration does not neatly fit with either of these hypotheses. For instance, Niky Hughes, now at High Point University in North Carolina, has shown the protective activity of anthocyanins in evergreen shrubs that turn reddish in the winter and return to green color the following spring. Examples of such shrubs in New England woods include cranberry (Vaccinium macrocarpon), swamp laurel (Kalmia polifolia) and wintergreen (Gaultheria procumbens).

Anthocyanins have additional physiological activity; they are extremely strong antioxidants. The consumption of blueberries (loaded with anthocyanins) is now seen as an anti-aging strategy, promoted by blueberry grower cooperatives and other marketeers. The importance of such activities in aging leaves is unclear, however. The reactive oxygen species (ROS) implicated in cell death and aging are produced in the chloroplasts, but during autumn color production anthocyanins are pumped into cell vacuoles, far from chloroplasts. In the vacuoles, they might react with hydrogen peroxide, but the physiological importance is unclear.

Paul Schaberg and colleagues at the United States Forest Research Laboratory in Burlington, Vermont, have been measuring changes in sugar maple (Acer saccharum) leaves during the autumn. Sugar maples display some of the brightest foliage in the forest during the autumn, but colors vary between green, yellow, orange, and red between—and even within—tree crowns. They have observed that leaves that will become red have lower nitrogen concentrations, that red leaves have higher sugar and starch concentrations, and that red leaves tend to be retained longer than other leaf colors.

In addition to woody plants, some herbaceous plants also change color during the autumn. I have been observing these changes, collaborating with John O’Keefe, at the Harvard Forest and nearby areas. There, the percentage of herbs with leaves turning red is much lower than for shrubs and trees.

The production of color by trees during the autumn is strongly influenced by their evolutionary histories. Trees have evolved different strategies for dealing with the stress of senes-
cence, or the pressures of herbivory. Many maples and oaks produce red colors during the autumn, and birches and beeches produce yellows. Hoch has shown that the birches resorb nitrogen as well as the species with red anthocyanins, so there are likely to be other protective mechanisms that have evolved. The color production in geographically distant forests also varies greatly. Among the most spectacular color displays are autumn forest scenes in New England, and also in the southern Appalachians (residents of the Great Smoky Mountains region think their colors are the most beautiful!). However, European forests produce little red, and a lot of yellow. Although red and yellow colors are produced in virtually all deciduous trees in New England, in other forests leaves may stay green. Israeli botanist Simca Lev Yadun has speculated that variation in color production may be the result of the different tree species in particular forests, and their evolutionary histories.

Past and future climates may affect color production by determining the distributions of different trees in forests. Diseases may also remove species and change the colors during autumn. For New England forests, I expect that a century ago there was much more yellow in the autumn color palette. The rapid decline of the American chestnut from chestnut blight...
and the loss of American elms from Dutch elm disease removed the autumn yellows of these large and often dominant trees from forest canopies. Oaks are now threatened by sudden oak death, maples by Asian longhorned beetle, and ashes by emerald ash borer; losses of these genera could remove many reds and purples from the autumn palette in the future. Finally, temperature increases, greater at higher latitudes, may remove trees essential to our autumn colors; the sugar maple (our single greatest source of oranges and reds) may not survive in a warmer southern New England, but will move farther north in eastern Canada. Then sassafras (Sassafras albidum), with its bright coral and red autumn leaves, may become more common farther north.

New England forests also produce colors in the springtime, pastel pinks and yellows as buds break open and delicate young leaves spread their blades. Although I suspect that young red leaves are common among trees of New England forests, I have not systematically collected such information. The majority of trees in forests of Israel, Finland, and Japan produce young red leaves, and a minority of these trees produce red autumnal foliage. Also, red leaves in the spring are not good predictors of red colors in the autumn, suggesting different functions by colors produced in spring and the autumn.

I hope that this discussion about the science behind seasonal colors heightens your appreciation of the autumn pageantry as you rake colorful leaves from your lawn or take a country drive. Maybe some of you would just as soon enjoy the autumn colors without knowing anything about chlorophylls, xanthophylls, and anthocyanins. Walt Whitman would have agreed, for he wrote:

> About birds and trees and flowers and water-craft; a certain free margin, and even vagueness—perhaps ignorance, credulity—helps your enjoyment of these things, and of the sentiment of feather’d, wooded, river, or marine Nature generally. I repeat it—don’t want to know too exactly, or the reasons why.

References


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