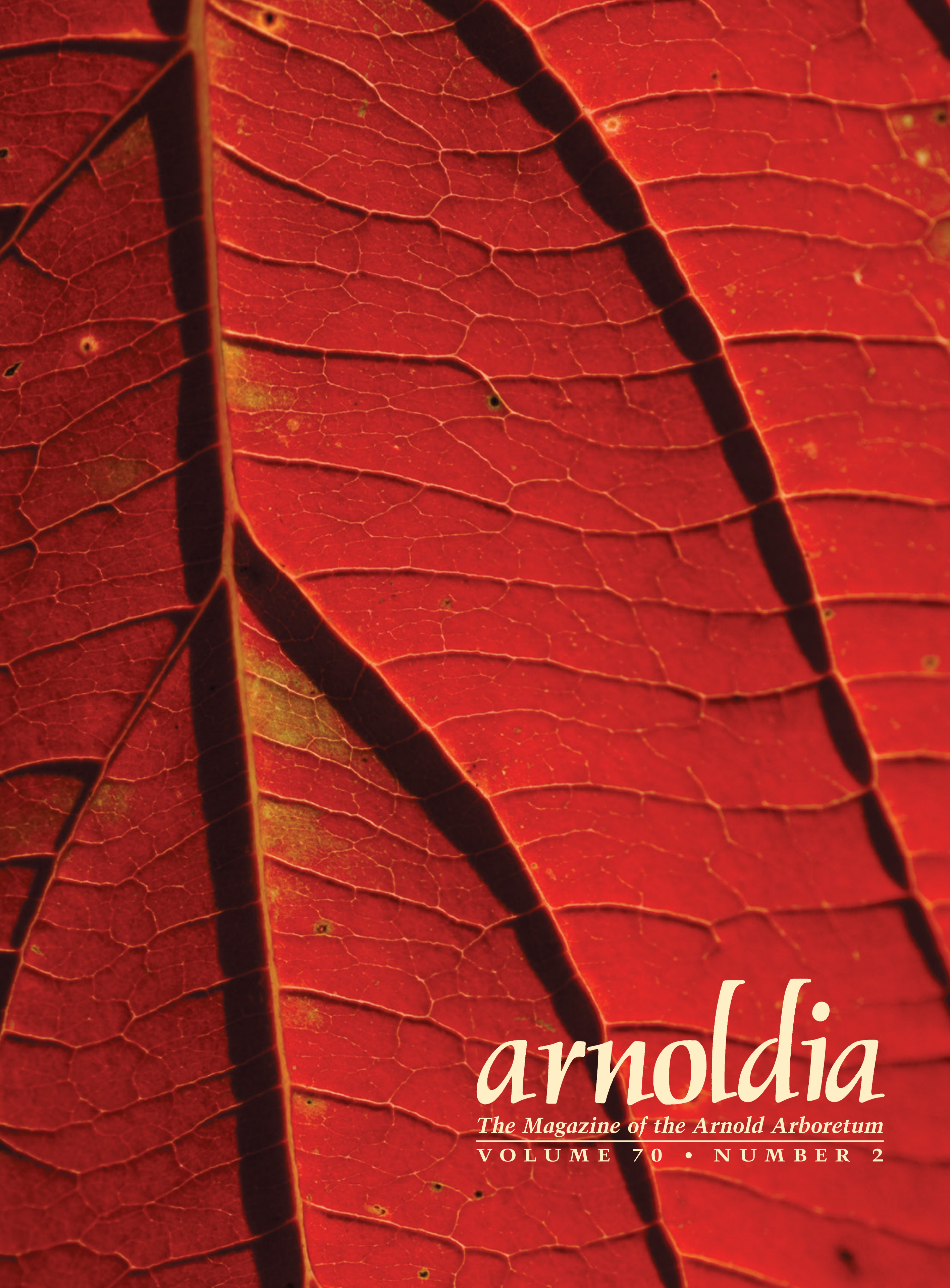

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The ARNOLD ARBORETUM of HARVARD UNIVERSITY

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Front cover: So, why *do* some leaves turn bright red in autumn? Learn more about this mystery, starting on page 2. Photo of *Cornus sericea* 'Ruby' by Nancy Rose.

Inside front cover: The flowers and fruits of over 170 plant species appear in sixteenth-century frescoes in Rome's Villa Farnesina, providing a treasure trove of information to present-day horticulturists. A number of the genera depicted in the Villa also grow at the Arnold Arboretum, including *Sorbus.* Photo of *Sorbus aucuparia* by Nancy Rose.

Inside back cover: The bumpy, softball-sized fruit of Osage orange (*Maclura pomifera*) matures in early autumn at the Arboretum. Photo by Nancy Rose.

Back cover: Autumn color under the microscope: this cross section of a sugar maple (*Acer saccharum*) leaf reveals red and yellow pigments. Photo by David Lee.

The Mystery of Seasonal Color Change

David Lee

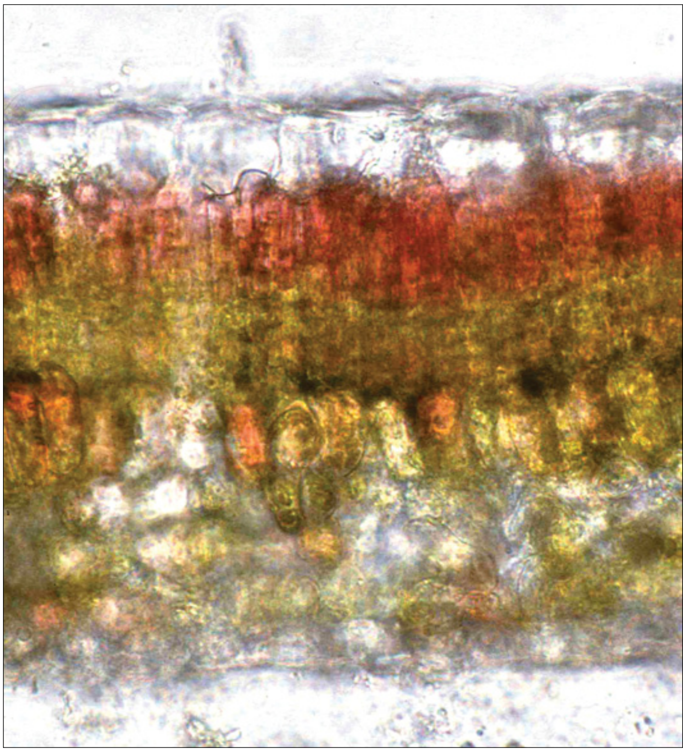
… the gods are growing old;
The stars are singing Golden hair to gray
Green leaf to yellow leaf,—or chlorophyll
To xanthophyll, to be more scientific …

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 undersurfaces 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

A red maple leaf shows developing red autumn color along with still-green sections.



This micrograph of a red maple (*Acer rubrum*) leaf shows that it contains both red anthocyanins and yellow xanthophylls.

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

ALL IMAGES BY THE AUTHOR

A red maple glows in autumn color at the edge of Connor Pond, between the towns of Petersham and Barre in central Massachusetts.

Autumn color in forests along the Deerfield River in the Berkshire Mountains of western 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.

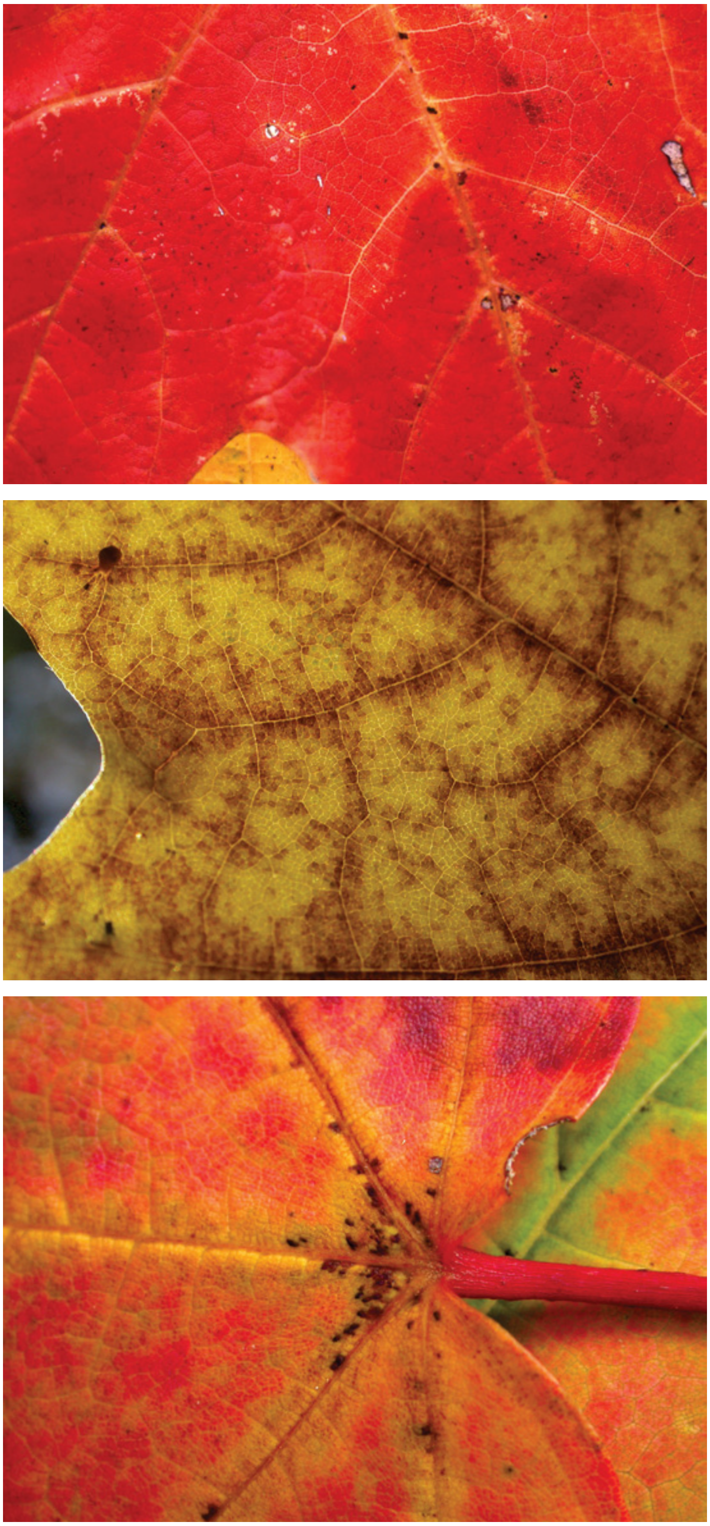
RESEARCH AT HARVARD FOREST

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

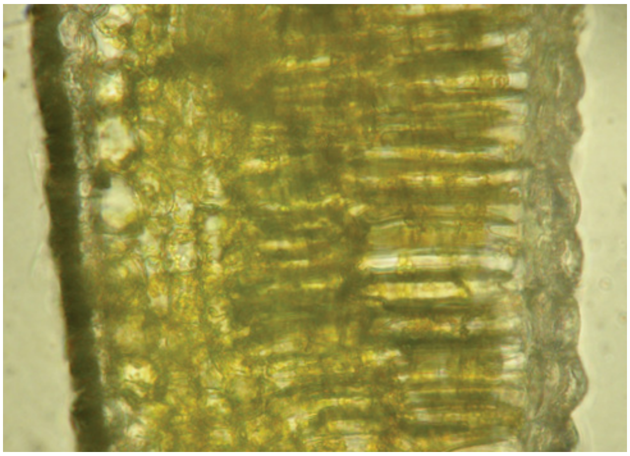


Autumn leaf color in sugar maple (*Acer saccharum*) varies between (and even within) individual specimens.

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.

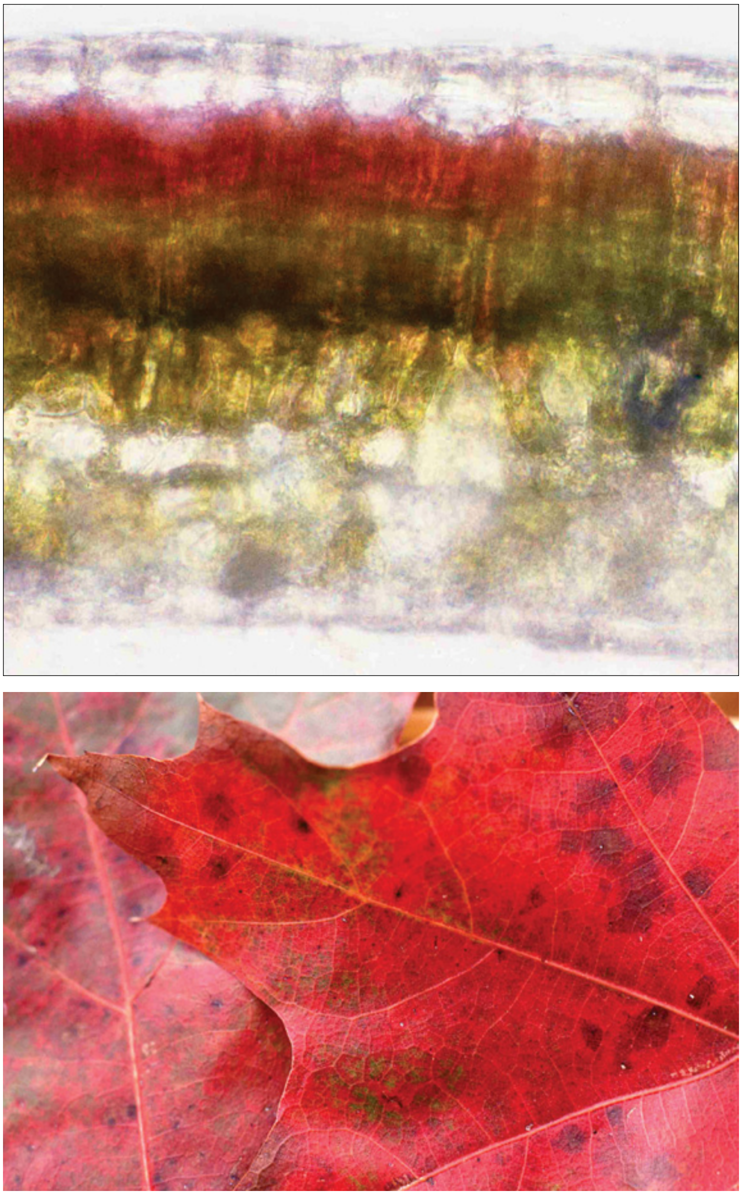
About the time we were initially pursuing this research, William Hamilton, the famous evolutionary biologist known for his research on sexual selection, had proposed a radically different explanation. He argued that colorful leaves could serve as a warning to potential herbivores, specifically aphids, 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.



A micrograph of an aspen (*Populus tremuloides*) leaf shows chloroplasts containing yellow xanthophylls.

Black gum, also known as sour gum or black tupelo (*Nyssa sylvatica*), is noted for developing bright red-orange to red-purple autumn leaf color.

Common witchhazel (*Hamamelis virginiana*) displays yellow autumn color, as do most birch (*Betula*) and beech (*Fagus*) species.



Inside and outside views of autumn leaf color in red oak (*Quercus rubra*).

DUELING 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-

Hobblebush (*Viburnum alnifolium*), a native woodland shrub, has autumn foliage color ranging from coral-pink to burgundy.

Though more subtle than in autumn, reddish color is also common in spring on expanding leaves, as seen here in woods near Beaverkill, New York.

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. Isreali 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.*

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Inside Plants: An Engineer's View of the Arnold Arboretum

Lorna J. Gibson

Gardeners tend their plants to produce a beautiful display in the garden or to harvest fruits and vegetables. Botanists study the anatomy, life cycles, and evolution of plants. Engineers, too, are interested in plants, although from a different perspective. Historically, engineers have been interested primarily in wood, because of its widespread use in everything from furniture to boats to buildings. But more recently, engineers have recognized that plants are very effective at resisting the loads they are subjected to (for instance, from the wind or from their own weight). Today, engineers study plants to learn what features make them so effective mechanically, with a view towards "bio-inspired design" of engineering materials and structures that exploit these features. In this article, I will take you for a walk through the Arboretum and describe a variety of plants and how they work from an engineering perspective.

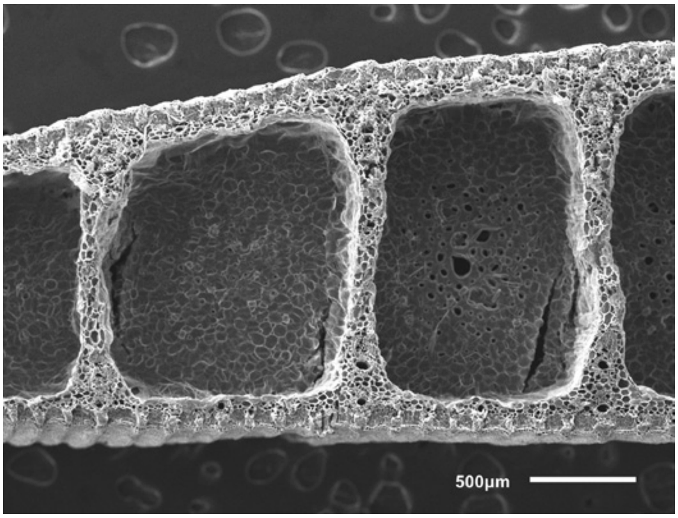
ROBERT MAYER

Cattails (*Typha* spp.) growing in the Meadow at the Arnold Arboretum.

THE TOUR BEGINS

Across from the Hunnewell Visitor Center, east of Meadow Road, lies the Meadow, a marshy area largely filled with cattails (*Typha* spp.). The leaves stand close to vertical and reach an impressive height, often over 6 feet tall. As you walk past, you can see the leaves bend in the wind; occasionally, a sparrow or red-winged black bird lands on the stem or its fuzzy, cylindrical seed head and bends that over, too. If you look at the leaves up close, you can see that they have fibers running along their length; if you draw your thumbnail across the width of the leaf you can feel the ridges of the fibers. How do the long, thin leaves stand up so tall?

A look at the cross section of a cattail leaf reveals the answer. The cross section shows two outer faces connected by a number of ribs. At the very outer top and bottom surfaces, you

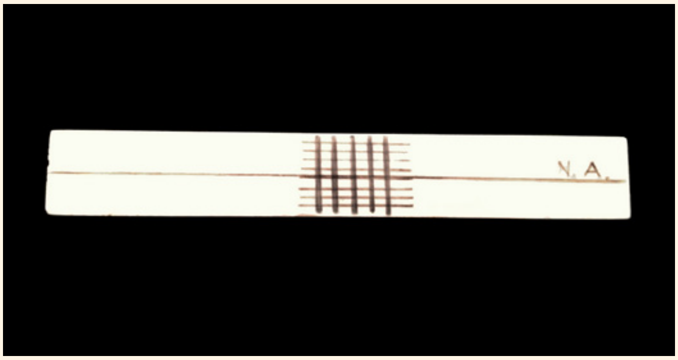


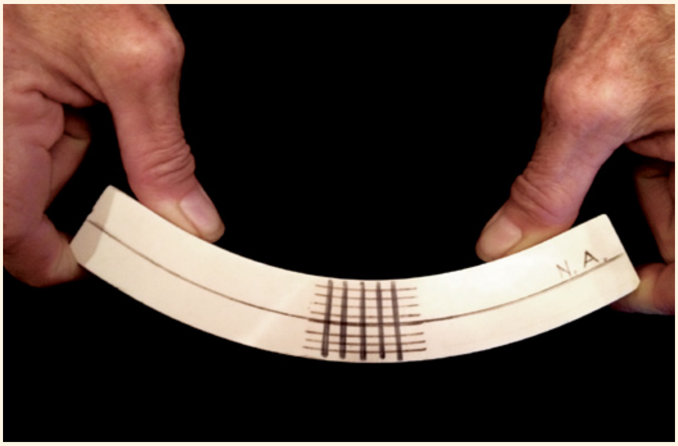
DON GALLER, MIT

In cross section, under a scanning electron microscope, this cattail leaf has a structure resembling I-beams.

can see small ridges that correspond to the fibers you can feel with your thumbnail. The ribs and outer surfaces of the leaf act mechanically in the same way as a steel I-beam in a building. The more material that one has away from the center of a beam, the more resistant it is to bending deflections and internal loads. Think of a 12-inch-long wooden ruler that is 1 inch across and 1/8 inch thick. It's much easier to bend the ruler if you are pressing on the 1-inch face than if you turn it and press on the 1/8-inch face. The separation of the outer surfaces of the leaf by the ribs increases the resistance to bending, in the same way as the separation of the flanges (outer plates) of a steel I-beam by the web (the inner vertical section).

Long, tapered leaves are typical of monocotyledonous plants such as cattails, irises,



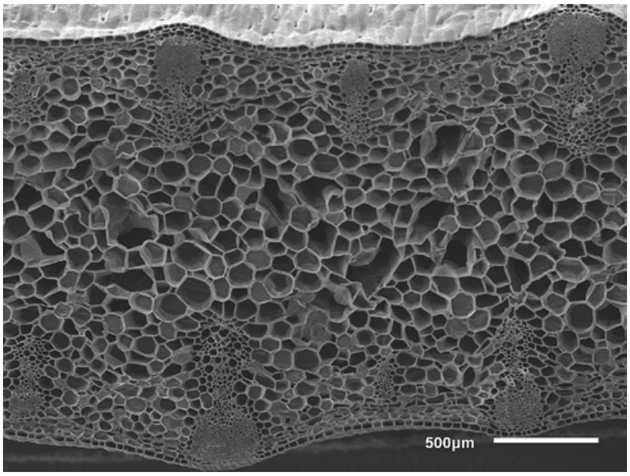


The Mechanics of Bending

PLANT LEAVES and stems, as well as tree trunks and branches, typically bend, either from the wind or from their own weight. If we look at a bent rubber beam on which we have marked a rectangular grid, we can see that the vertical lines rotate about the middle of the beam when it is bent. The horizontal lines on the top half of the beam get shorter and shorter the further they are away from the middle of the beam and, correspondingly, the horizontal lines on the bottom half of the beam get longer and longer the further they are away from the middle of the beam. The top half of the beam is in compression (pushing) while the bottom half is in tension (pulling) and the very middle sees no internal force at all. The material at the top and bottom surface of the beam is the most compressed or stretched, and sees the highest internal loads. The outer faces of the cattail leaves and the dense fibers at the top and bottom of the cross section of iris leaves resist the high internal loads at the outermost part of the leaves.

NANCY ROSE

The swordlike leaves of bearded iris have a "sandwich structure" that increases their resistance to bending.



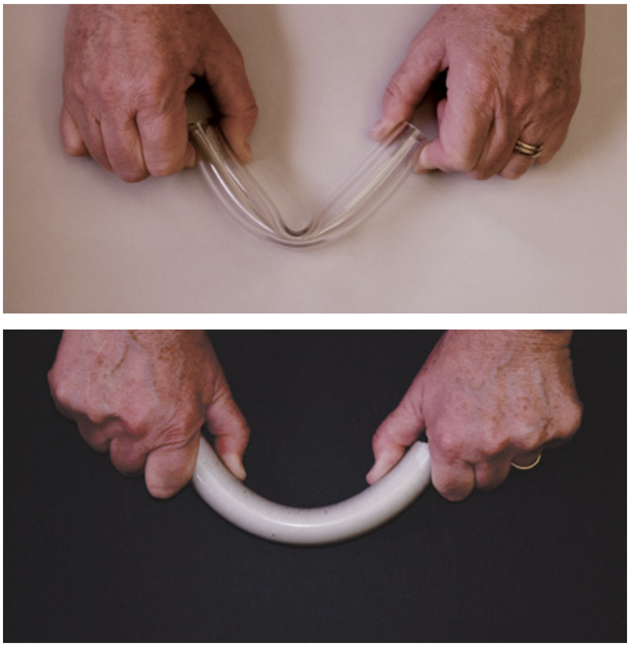
DON GALLER, MIT

Dense outer fibers (schlerenchyma) are separated by foamlike parenchyma in this iris leaf cross section.

and grasses. A cross sectional view of an iris leaf shows that it has large dense fibers (called sclerenchyma) at the outer surface and a thick inner layer of foamlike cells (called parenchyma). When the leaf is bent, the dense fibers carry most of the high internal loads at the outside of the leaf. The separation of the denser, stiffer fibers by the inner foamlike layer increases the resistance of the iris leaf to bending. Engineers make use of the same concept (a "sandwich structure") in the design of downhill skis, lightweight panels for aircraft, and the blades of windmills, which often have two outer skins of carbon-fiber-reinforced plastic separated by a foam (or sometimes an engineering honeycomb) core.

SUPPORTING ACT

If we walk back towards the Arborway Gate and look along Willow Path, we see the huge leaves of the butterbur (*Petasites japonicus*). How does the stem support such large leaves without falling over? The stem bends under the weight of the leaf and from wind acting on the leaf. The stem is roughly circular in cross sec-

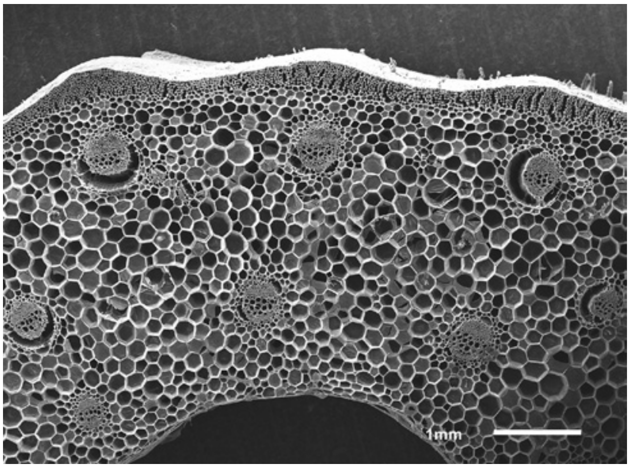


LORNA J. GIBSON

An empty tube kinks when bent, but the foam-filled tube resists kinking.


NANCY ROSE

Butterbur leafstalks must support very large leaves (often 2 feet or more in diameter).



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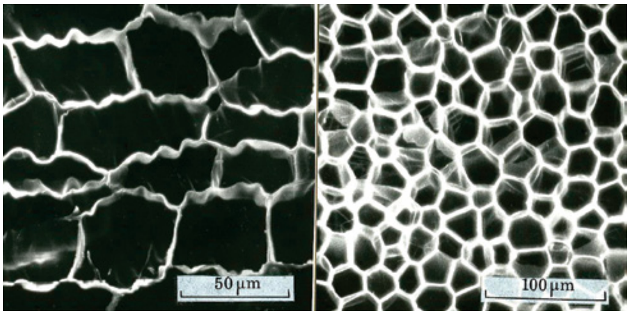
Cross section of a butterbur leafstalk.

tion, so that it can resist bending in any direction equally. If we look at a cross section of the stem in a scanning electron microscope, we see that it has a dense outer layer surrounding an inner foamlike layer of cells that are reinforced with bundles of fibers. At the center of the stem is a void. This combination of foamlike cells surrounded by a thin, denser outer layer is common in plant stems and is often called a "core–rind" structure. The dense outer layer resists most of the internal loads from bending on the stem, which are highest at the outer extremity of the stem. The inner foamlike core also plays a role: it helps resist kinking of the stem. The dense outer cylindrical shell of the stem is a little like a drinking straw. When a straw is sufficiently bent, it tends to fail by forming a crease or kink in the middle. If the drinking straw is filled with foam and then bent, the foam pushes back against the kinking, increasing the straw's resistance to this type of failure (see photos on page 13, lower right). The interior foamlike cells in the butterbur stem also help resist kinking by pushing back against the outer layer if it tends to kink inwards.

Slightly further along Meadow Road we pass by the cork trees (*Phellodendron* spp.) with their thick, deeply grooved bark. If you press your thumbnail into the bark you'll notice that it is quite soft and springy. Cork stoppers, such as those used in wine bottles, come from the bark of a different tree, however: the cork oak, *Quercus suber,* that grows in Mediterranean climates, particularly in Portugal and Spain. Remarkably, unlike most other trees, after the



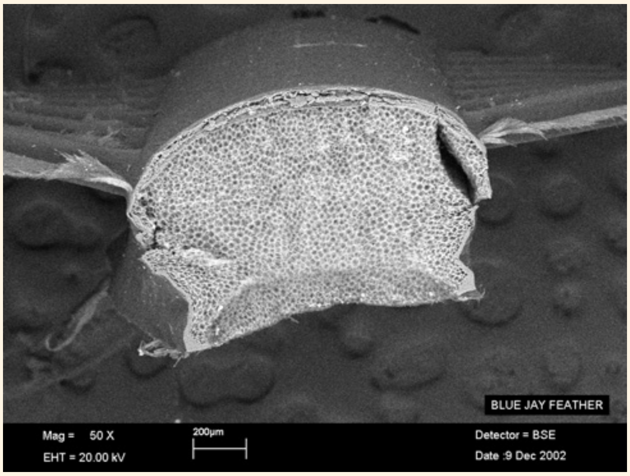
Scanning electron microscope images of cork oak (*Quercus suber*) cells.

Birds of a Feather

BIRD FEATHER quills have a similar structure to iris leaves. As the bird's wings beat in flight, the feather is bent up and down, so that the bending loads are highest on the top and bottom of the quill. A sandwich structure, with dense faces at the top and bottom of the quill, would seem to be an ideal option. But bird feathers also have to resist twisting, or torsion, and the foam-filled closed tubes are adept at this. (You can try this simple experiment: take a drinking straw and twist it. Now cut a slit along the length of the straw and twist it again. The straw is much better at resisting twisting when the cross section is closed and intact.) As with the butterbur, the foamlike core also helps resist kinking failure of the dense outer layer of material in the feather quill.

COURTESY OF AL REID

Blue jay (*Cyanocitta cristata*).



Cross section of a blue jay feather.

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bark of the cork oak is removed, it regrows, allowing harvesting of cork every 10 to 15 years. The cork cells are like little bellows: they are roughly box-shaped, but with corrugations running in one direction. When you compress the cork in the direction of the corrugations, they simply fold up, like a bellows, so that they do not expand in the lateral direction. This feature of cork is one reason cork works well at stoppering bottles. A rubber stopper, on the other hand, bulges out laterally when compressed, making it difficult to press into a bottle; for this reason, rubber bottle stoppers are always tapered.

TREES = WOOD

When we think of the Arnold Arboretum, we think of trees. And when engineers think of trees, they inevitably think of wood. Wood is one of the structural materials used for the longest time in human history and is still one of the most widely used. The oldest known wooden boat is Cheops's 4,600 year old barge, found dismantled in a pit next to the Great Pyramid in Egypt. In the late 1600s, eastern white pines (*Pinus strobus*) from New England were a strategic resource for the British Royal Navy. The tall, straight trunks of the pines were used as masts for ships; the taller the mast, the more sail area, the larger the ship, and the more cannons it could carry. And most houses in North America are still wood framed.

North American woods are divided into hardwoods (deciduous trees that drop their broad leaves annually) and softwoods (conifers with needles that are typically, but not always, evergreen). While hardwoods tend to be denser and harder than softwoods, that is not always the case: for example, Douglas fir, a softwood,

LORNA J. GIBSON

The tall, straight trunks of white pine were once used for ship masts.

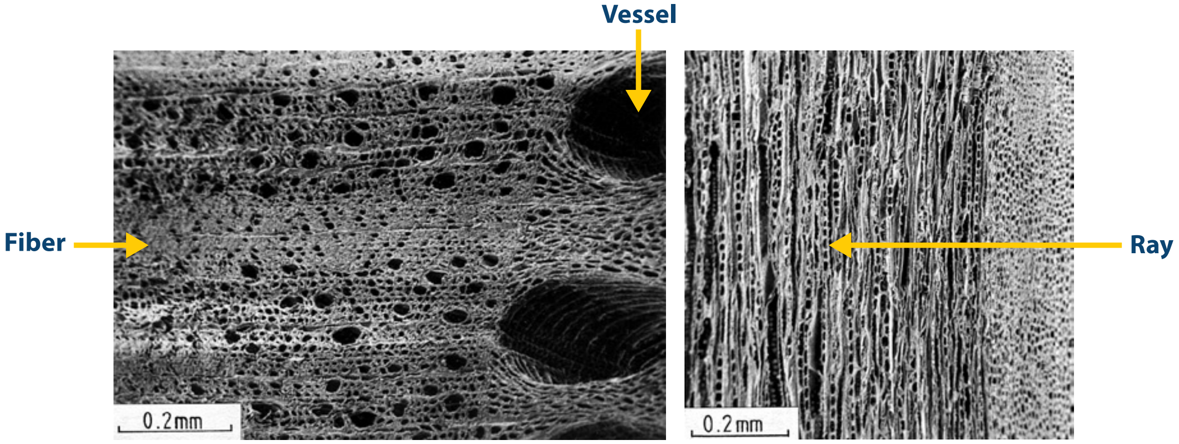
is denser and stronger than quaking aspen, a hardwood.

Up Bussey Hill Road, past the lilac collection, and past the turnoff to Bussey Hill, we come to the shady Oak Path, with its many species of magnificent oak trees (*Quercus* spp.). Oaks and other hardwoods have three types of cells: *fibers* that provide structural support, larger diameter *vessels* that conduct water and sap up and down the tree, and *rays* that store sugars: all three are visible in the images of the cross-section and longitudinal section of oak. The fibers and vessels, which make up the bulk of the cells, run longitudinally along the trunk and branches of the tree.

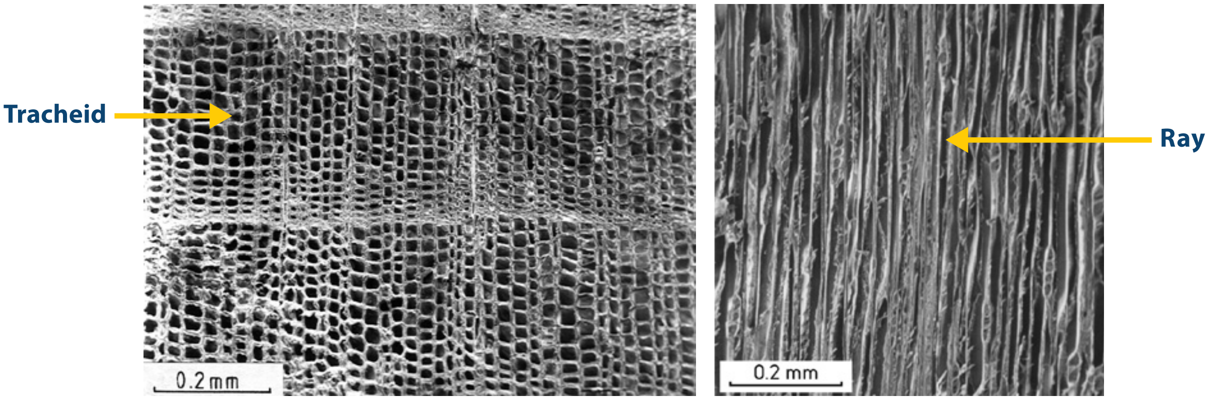
Walking across the grass towards Valley Road, we next come to the Conifer Path, with its hemlocks, pines, spruces, and firs. Softwoods have two types of cells: *tracheids,* which make up the bulk of the cells and provide structural support and conduct fluids (via small holes called pits along their sides), and *rays,* which again store sugars.

To a first approximation, the structure of both hardwoods and softwoods resembles a honeycomb, with roughly square, instead of hexagonal, prismatic cells. Forces applied to wood are largely carried by the fibers in hardwoods and by the tracheids in softwoods. Since these wood cells resemble an elongated honeycomb, the mechanical properties of woods can be modeled, to a first approximation, as a simple honeycomb with identical cells. It is well known that the stiffness and strength of woods are much higher along the grain than across the grain; the reason for this can be explained by modeling the wood cells as a honeycomb.

When a model honeycomb is loaded in compression (pushing) along the length of the cells (along the prism axis), the cell walls simply compress, and the stiffness and strength just depend on the amount of material in the cross section, or the fraction of the area that is solid. Wood cells loaded along the grain in compression also simply shorten axially, just like the honeycomb model. Using the honeycomb model, we see that the stiffness and strength of wood along the grain, too, depend on the fraction of the area of the cross section that is solid; for prismatic cells as in the honeycomb and



Oak wood, cross section and longitudinal section.

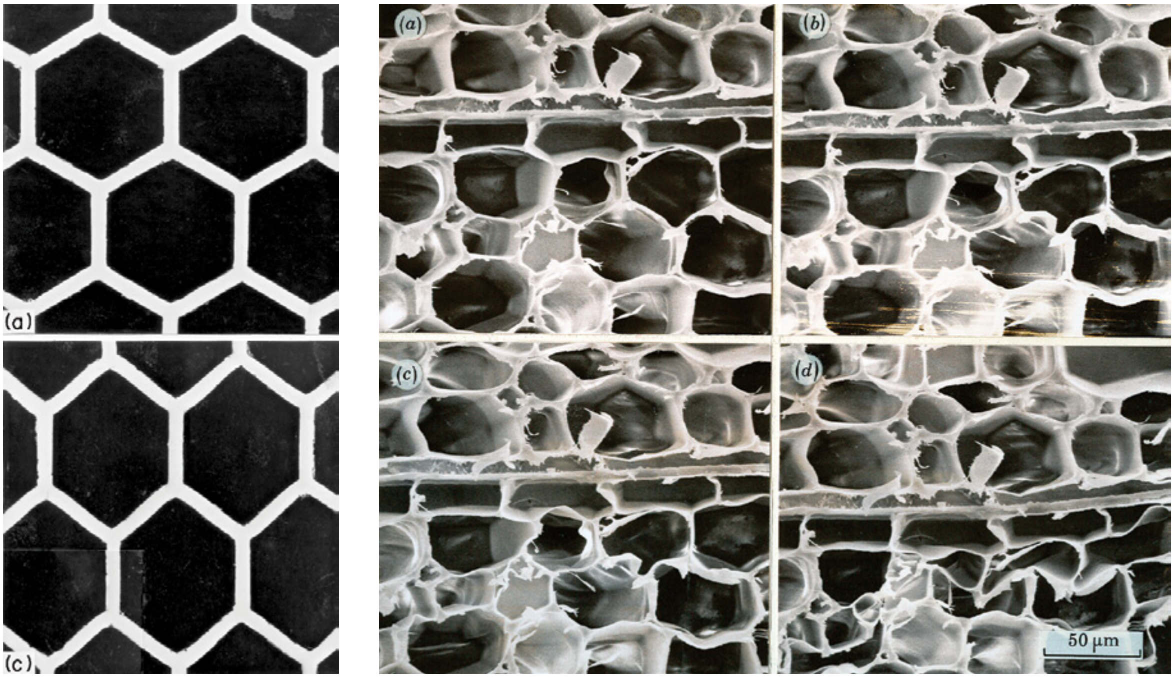


Cedar wood, cross section and longitudinal views.

wood, this is equivalent to the fraction of the volume that is solid.

In contrast, when a model honeycomb is loaded across the cells, it is much easier to deform the honeycomb, as the cell walls bend. Wood cells loaded across the grain also bend in a manner similar to the honeycomb; this can be seen most easily in a low density wood like balsa (*Ochroma pyramidale*) (see upper right images on page 18).

If you take a ruler and bend it, it deforms much more than if you rest one end on a table and compress it from the opposite end with the same load. It is also less strong when bent: it is much easier to break the ruler in bending than by compressing it on end. We have already seen how, in a bent beam, the amount that the material stretches or compresses increases as the distance up or down from the middle of the beam increases: the thickness of a beam plays a greater role in resisting deflection or internal loads than the width. When loaded across the grain, the wood cell walls bend, giving much lower stiffness and strength across the grain than along the grain. This effect can be analyzed in more detail to show that the stiffness of woods loaded across the grain depends on the cube of the volume fraction of solid, and the strength (loaded across the grain) depends on the square of the volume fraction of solid. This leads to the great difference in the stiffness and strength in woods when loaded along and across the grain, a difference that is greater in lower density woods, such as pine, than in high density woods, such as oak. For instance, in Eastern white pine the compressive strength



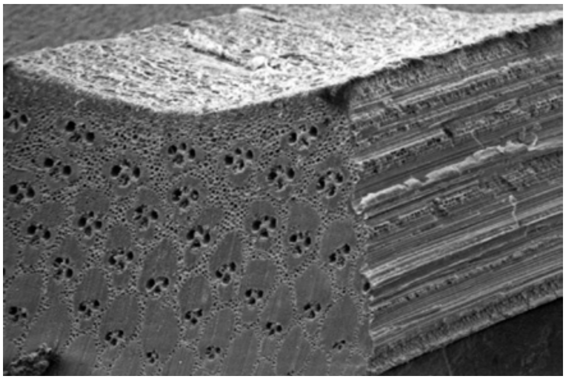
A rubber honeycomb model shown unloaded (top left) and, when loaded in compression from the left, with bent cell walls (bottom left). The set of four images (right) shows the same area in a piece of balsa wood under increasing load in a vice in a scanning electron microscope. The top left image (a) is unloaded, and images (b), (c), and (d) are at increasing compressive load.

along the grain is about 11 times that across the grain while in white oak the compressive strength along the grain is about 7 times that across the grain.

THE END OF THE TOUR

At the end of the Conifer Path, off to the right near Centre Street, is a group of bamboo accessions (mostly *Phyllostachys* spp.). Bamboo is a member of the grass family and is exceptionally fast-growing. Moso bamboo (*Phyllostachys edulis*), native to China, can grow 3 feet in a day and the stem, or culm, can have a 6-inch diameter. While the initial growth is remarkably fast, it takes several years for the stem to mature and fully densify and lignify. In countries where it is indigenous, it has been used traditionally for houses and other small structures.

A cross section through a bamboo culm shows vascular bundles surrounded by dense sclerenchyma tissue and separated from one another by ground tissue of low density parenchyma cells. There is a radial density gradient: towards the periphery of the culm there are more vascular bundles (and each one is denser) than at the inside surface of the culm. As we have already seen, placing dense material away from the center of a beam (where the deformation and internal loads are zero) increases the resistance of the beam to bending. Bamboo culms are



Cross section of bamboo stem.

typically loaded in bending from the wind—the increase in denser material towards the outside of the cross section increases the resistance of the culm to bending deflections and loads, compared with a section with the same amount of material evenly distributed across the section.

On our walk through the Arboretum, we have seen a variety of plants with different internal structures. Plants are often mechanically efficient, using material to resist internal loads where they are greatest. Engineers studying the mechanical behavior of plants take inspiration from them for the design of engineering materials and structures.


NANCY ROSE

Stems of a bamboo, *Phyllostachys makinoi*.

Acknowledgements

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Fruits and Nuts of the Villa Farnesina

Jules Janick

The loggia of Psyche in the Villa Farnesina. The paintings on the ceiling depict scenes from the love story of Cupid and Psyche.

In 1505, an extremely wealthy Sienese banker named Agostino Chigi (1466–1520) decided to build a new home for himself that was to be the most splendid in Rome. A banker to popes and kings, Chigi's modus operandi was to lend money and, in return, obtain monopolies for such things as importation of grain or production of alum from mines. He often accepted jewelry for "security." He was in a sense a pawnbroker and a wheeler-dealer who structured his deals so he couldn't lose. He became the richest man in Europe. Chigi was a courtier, very well connected, and truly a Renaissance man. Although not particularly well educated, he bought into humanism, a Renaissance movement that had rediscovered Latin and Greek writings and the mythical legends of the pagan world, was absorbed with nature, and was intensely concerned with the human condition.

Chigi built the most splendid residence in Rome to honor and glorify himself. Chigi's villa, now known as the Villa Farnesina (it was sold to Cardinal Farnesina by Chigi's heirs after they burned through their inheritance), is located on the West Bank of the Tiber in the district now known as the Trastevere, southeast of the Vatican and east of the Orto Botanico. Here Agostino Chigi, the Magnificent, received artists, poets, princes, cardinals, and the pope in opulence and pomp. At one famous dinner the silver and gold plates were thrown into the Tiber after use—but into nets. The building was an evocation of the classical world, with the rooms filled with paintings and statues, opulent furnishings, and a garden called the *viridiarium,* a repository of rare plants. Each room is decorated with a different theme, but this article will concentrate on the loggia, now known as the Loggia of Psyche, originally a veranda or gallery with one wall open to the outside.

The Loggia of Psyche was decorated under the management of Raphael Sanzio (1483–1520), the boy wonder of the high Renaissance and a rival to Michaelangelo Burotti. As judged by

Richly detailed festoons painted by Giovanni Martini da Udine contain thousands of botanical images.

the decorations of his home, Chigi was more interested in the sensuality of the pagan world than on the artistic representation of suffering, torture, and death of the medieval Christian tradition. The decorations—painted between 1515 and 1517—involve love and marriage, perhaps in anticipation of Chigi's marriage to his longtime mistress in 1519, one year before his death. The loggia is presented as a tentlike pergola with images of two large tapestries painted on the ceiling as a roof, depicting a scene of the Council and the Banquet of the Gods—the climax of the Cupid and Psyche story. The arches of the ceiling are divided into spandrels that contain scenes of the heavenly adventures of Venus, Cupid, and Psyche, alternating with severies that illustrate cherubs bearing trophies of the gods.

The Cupid and Psyche myth is based on the first novel that comes down to us from antiquity, known as the *Metamorphoses* (or *The Golden Ass*) of Apuleius, written in the second century but translated to Latin in 1469. The story, which was to become immensely popular, concerns the marriage of Cupid (mischievous God of Love) to the beautiful mortal Psyche ("soul") leading, after tribulations and trials, to the divinity of Psyche. The underlying theme of the story is that "love conquers all."

These Raphael frescoes illustrating the heavenly adventures of Cupid and Psyche are stunning, but for botanists and horticulturists an even greater treasure is found on the ribs enclosing the loggia's spandrels and severies. Here, the elaborate festoons and wreaths painted by Giovanni Martini da Udine (1487–1564) contain thousands of images of individual fruits, vegetables, and flowers, encompassing over 170 species (Caneva 1992a,b). The festoons have been deconstructed by scanning the images and collating each species, which makes it possible to examine genetic variability within species. For this article, I will concentrate on images within the festoons of selected horticultural crops, specifically maize, pome fruits, nuts, eggplant, cucurbits, and legumes. It is of particular historical interest that the festoons contain what may be the earliest known European images of maize, pumpkins, and squash from the New World, barely a quarter century after Columbus's encounter with the Americas, providing evidence of the rapid diffusion of these crops into Europe.

THE CROPS

Maize

There are a total of eight groups (28 ears) of maize (*Zea mays*) scattered throughout the festoons. A close examination of the maize ear images suggest that they are painted with some artistic license (Janick and Caneva 2005). Despite the presence of some atypical characteristics (as compared to United States cornbelt maize), the attribution is based on the combination of characters including kernel size and color, ear type (10 and 12 rows are depicted), the presence of white,

The strange tripartite extensions of the ear tips in image are suggestive of rudimentary tassels.

ARCHIVES OF THE ARNOLD ARBORETUM

Leonhard Fuchs 1542 woodcut of maize (*Zea mays*)was previously thought to be the first European depiction of the species.

yellow, and reddish silks, and the long, narrow leaves typical of maize. In addition, the historical evidence supports the conclusion that these images may be the earliest representation of maize in Europe, fully a quarter century earlier than the famous woodcut of Leonhard Fuchs labeled *Turcicum Frumentum* (Latin) and *Türckisch korn* (German), presumed to have been the first European image. The depiction of leaves suggests that maize was grown and seen by the artist, probably in the *viridarium,* a repository for rare plants at Chigi's villa, although the original drawings were probably made from detached ears. It seems obvious that most of the multiple ears within the same group are copies of a detached prototype ear. The shank depictions are probably invented since there appears to be an attempt to hide them in most images and those that are drawn are obviously botanically incorrect. Since maize ears have paired spikelets, the preponderance of interlocking kernels is disconcerting. One explanation is that a lack of synchrony of silk receptivity and pollen shed in these nonadapted exotics could cause pollination gaps leading to plump, round seed, and perhaps the artist filled in the voids in an attempt to portray perfection.

Maize has been cultivated in Spain, Portugal, and Italy for five centuries and selection and isolation have produced various races differing in maturity and phenotype. Characteristics of the maize ear phenotypes depicted in the images from the Farnesina can be found in races from Spain (Sanchez-Monge y Parellada 1962), Portugal (Costa-Rogrigues 1971), and Italy (Istituto sperimentale per la Cereali-

Though the ears don't look exactly like modern American cornbelt maize (note the irregular kernel orientation in these images), they are clearly identifiable as maize.

coltura 2002). The resemblance of the maize images painted in Italy between 1515 and 1519 to races of maize in Spain, Portugal, and Italy is confirmatory evidence for the early origin of some of these races. There is direct evidence that maize seeds reached Rome in 1594. A letter from Peter Martyr D'Anghiera, an Italian teacher connected with the Spanish court, to Cardinal Ascoanio Sforza, vice-chancellor of the papal court, describes news of the early returning ships from the second voyages of Columbus and encloses seed of maize (McNutt 1912; Janick and Caneva 2005).

Pome Fruits

Five types of pome fruits are illustrated in the festoons: apple (*Malus*: 97 fruits of cultivated apple and 21 fruits of wild apple); pear (*Pyrus*: 78 fruits of European cultivated pear and 21 of wild pear); quince (*Cydonia*: 31 fruits), medlar (*Mespilus*: 27 fruits), and hawthorn (*Crataegus*: 30 fruits in two clusters). The number of images are indicative of the relative popularity of these fruits in Renaissance Italy.

Of the apple fruits (*Malus* × *domestica*), 34 were solid red, 43 red–yellow bicolored, and 20 were yellow. A few show fungal spots. The cultivated apples all resemble modern types in shape and color. There were also three groups of small apples or crabapples (*Malus sylvestris*), each with multiple fruits (21 total) in clusters. One cluster consisted of 7 bicolored fruits, one had 5 red fruits, and the other had 7 dark purple fruits.

Apples (*Malus* spp.) appear throughout the paintings, including red, yellow, and bicolored specimens.

Examples of pears in the festoons.

Of the pears (*Pyrus communis*), 45 were red–yellow bicolored and 33 were yellowish. The preponderance of red fruits is much different from present day distribution of pear cultivars in Europe, where most are green, yellow, or russet. There were three cluster of small wild pears (*Pyrus pyraster*) totaling 21 fruits, all of varying degrees of red color.

There were 31 images of large quince (*Cydonia oblonga*) fruits, all lobed. Some were obviously mature, with an old gold color, a few were reddish, while others, obviously immature, were whitish or light yellow. All of the quince resemble the "golden apple" as described by Pliny: "cleft with incisions and has a color verging on gold" (Roach 1985).

The 6 groups of medlars (*Mespilus gemanica*) totaled 27 fruits, which were small and of the same type. They fit Pliny's description for the small and aromatic 'Anthedon', one of the three types of medlars in ancient Rome. Medlars are still found in Italian markets but are usually larger than the ones illustrated in the festoon.

There are two groups of hawthorn (*Crataegus oxyacantha*, a synonym for *C. laevigata*). They show sprays of fruits, one dark purple with about 22 fruits and the other bright red with 8 fruits.

Left to right. Quince, medlar, and hawthorn fruits.

Nuts

Acorns, chestnuts, hazelnuts (filberts), pinenuts, and walnuts, are illustrated on the ceiling. Acorns appear among the 8 groups of English oak (*Quercus robur*) and 4 groups of *Q. virgiliana.* European chestnuts are pictured in 3 groups of *Castanea sativa.* European hazelnuts appear in 4 groups of *Corylus avellana* and two groups of *C. maxima* (which some taxonomists lump in with *C. avellana*). Edible pinenuts are represented by 11 groups of Italian stone pine cones (*Pinus pinea*). There are also depictions of English (or Persian) walnuts (*Juglans regia*) in 6 separate groups.

Clockwise from upper left. Acorns, hazelnuts, chestnuts, and walnuts are depicted in the paintings.

The cones of Italian stone pine (*Pinus pinea*) hold large, edible nuts.

Eggplant

There are a total of 21 images (30 fruit) of eggplant (*Solanum melongena*). The fruits are very similar and are characterized by varying degrees of purple pigmentation and white undercolor.

Eggplant images include several yellow, fully mature specimens.

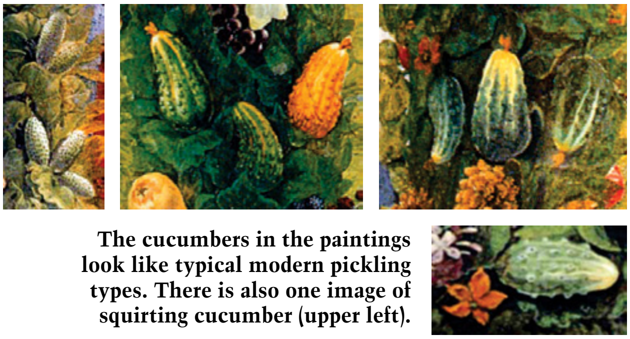
In some cases the eggplants are deep yellow, indicating maturity. Most of the fruits are club shaped.

Cucurbits (Old World Species)

Cucurbit fruits from Old World species are well represented (Janick and Paris 2006). Images include *Citrullus lanatus* (watermelon), *Cucumis melo* (melon), *Cucumis sativa* (cucumber), *Ecballium elaterium* (squirting cucumber), *Lagenaria siceraria* (bottle and serpentine gourd), and *Momoridica balsamina* (bitter gourd).

The four watermelon images, each with a single fruit, represent a single type with small, round, striped fruit similar to modern ice-box types. In contrast, the 16 melon fruits include three horticultural groups: Cantalupensis (12 fruits), Reticulatus (3 fruits of two types), and Flexuosus (single fruit). The Cantalupensis types represent four extant cultivars ('Cantalun', 'De Bellegarde', 'Noir des Carmes', and 'D'Alger'), indicating high genetic variability.

Old World cucurbits seen in the festoons include watermelon (upper left) and various melons within *Cucumis melo* horticultural groups.



The cucumbers in the paintings look like typical modern pickling types. There is also one image of squirting cucumber (upper left).

The cucumber images (13 groups, 25 fruit) all resemble the type known as "American Pickling." There is a single image of the so-called squirting cucumber.

Two types of *Lagenaria* fruit associated with white flowers are included: the inedible bottle gourd (var. *fiasco*) which is used largely for utensils, and the serpentine or club-shaped gourd (var. *longissima*), called cocuzza in Italy, that is edible when immature and still consumed in Sicily. There are 9 fruits of bottle gourds with slight variation in color and neck morphology. There are 19 groups (22 fruits) of cocuzza with subtle differences in shape based on the thickness of the calyx end suggesting that some might be hybrids of *fiasco* and *longissima* types. Cocuzza are widely displayed in Renaissance art, probably because of their phallic shape and association with the worship of Priapus, god of orchards and vineyards and the personification of the male generative organ (Morel 1984; Janick 2004).

Depictions of *Lagenaria siceraria* gourds include both the bottle type (with a broad, round base) and serpentine type (long, slender form).

Finally, there are 3 images (9 fruits) of bitter gourds, known also as balsam apple (*M. balsaminia*) and balsam pear (*M. charantis*). Fruits are reddish and slightly warty, with a pointed end.

Cucurbits (New World Species)

Of particular interest for the festoon images are representatives of two species of New World cucurbits: *Cucurbita maxima* (fall and winter squashes and pumpkins) and *Cucurbita pepo*

New World cucurbits seen in the paintings include large pumpkin or squash types of *Cucumis maxima* (upper left) and small gourd type examples of *C. pepo.*

(pumpkins, summer squash, and gourds). Some of these fruits were identified as *C. moschata* by Caneva (1992) but this may be a misattribution. There are 9 fruits of *C. maxima* of two types: brilliant orange, furrowed fruit with a protruding stylar end reminiscent of the turban gourds; and white, furrowed, round pumpkins, now called "show pumpkins" in the United States. The images of *C. pepo* are of two types: a large orange pumpkin type and 11 clusters (about 17 fruits) of striped, oviform to pyriform gourds.

Legumes

Six genera of legumes are represented in the festoons including: *Cassia* (1 image, 4 pods); *Ceratonia* (3 groups, 8 pods); *Trifolium* (1 image, flower only); *Phaseolus* (2 groups, 5 pods); *Pisum* (1 group, 3 pods); and *Vicia* (four groups, 15 pods). If *Phaseolus,* a New World species, is indeed represented, (the attribution is open to question) this is still not the first representation of *Phaseolus* in Europe. An image of *Phaseo-*

Legume genera include (clockwise from upper left) *Phaseolus, Pisum, Viscia, Cassia,* and *Ceratonia.*

Pictured Plants at the Arnold Arboretum

IT IS INTERESTING to note that many of the woody plant genera found in the ceiling of the Loggia are represented in the collections of the Arnold Arboretum, including the following:

Castanea
Cornus
Corylus
Crataegus
Cydonia
Hedera
Juglans
Mespilus
Morus
Pinus
Prunus
Pyrus
Quercus
Ribes
Rosa
Rubus
Sambucus
Sorbus
Vaccinium
Vitis

NANCY ROSE

Elderberry (*Sambucus* spp.) images from the Villa Farnesina (upper left: flowers and fruit; lower left: flowers mixed with flowers of *Anemone coronaria* and grapes) and the Arnold Arboretum (right).

lus is found in an illustrated manuscript, *Livre d'Heures d'Anne de Bretagne,* painted between 1503 and 1508 by Jean Bourdichon (ca. 1457–1521) (Camus 1894; Zevan 1997; Bilimoff 2001).

LEGACY OF THE VILLA FARNESINA

The images of the Cupid and Psyche legend and the botanical festoons found in Chigi's villa demonstrate the vigor of the Renaissance humanists in promoting art and science in the beginning of the sixteenth century. The beautiful art work is still admired after 500 years and accounts for a significant flow of tourist money into Italy. These images also contain significant scientific interest, especially within horticulture and agriculture, since they provide information on the genetic diversity of many horticultural plants as well as information about the dispersal of New World plants in Europe.

Chigi, in whose villa the images were displayed, may be a pivotal figure in the dissemination of New World plants in the Mediterranean Basin. He had a garden of rare plants (*viridiarium*), was well know to Cardinal Sforza and Pope Alexander VI, was influential in the affairs of the Vatican and the Republic of Venice, and was directly involved in the Mediterranean trade, especially between Venice and Turkey, through his monopolies concerning alum and cereals (Gilbert 1980). We owe a debt to Giovanni da Udine for his skill in illustrating what may be the first images of maize and New World cucurbits in Europe, and for leaving a breathtakingly beautiful visual record of crop diversity in the high Renaissance.

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Additional images can be seen at:
http://www.hort.purdue.edu/newcrop/udine/info.html

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Maclura pomifera: Neither Apple Nor Orange

Jon Hetman

Though I confess that plants held little sway among my childhood interests, a few specific trees stand out in my early recollections, all due to their memorable fruits. A seemingly ancient apple tree in a neighbor's front yard was a climbing favorite, and bore small, mottled green fruits that were a delight to eat as long as you didn't overindulge. Behind my grandparent's garage in central Florida, a moss-covered orange tree provided fragrant spring flowers and slightly sour fruits that remain indelible sensations of my youth. But the fruits that perhaps fascinated me most belonged to an Osage orange tree that grew near my elementary school—large, hard as baseballs, and looking to us like green brains, the bumpy orbs with their citrusy aroma were a delightful mystery that inspired a number of ingenious games of our own design.

In earlier days, Osage orange (*Maclura pomifera*) garnered significant interest among people of its native Oklahoma, Arkansas, Missouri, and Texas, though for very different reasons. Hunters in the Osage tribe fashioned war clubs and bows from the tree's bright yellow heartwood, which proved stronger than oak and as tough as hickory. Early settlers in the American frontier called it the hedge apple, planting it in thicket-like rows so that the thorny, interlacing branches sheltered fields from wind and provided an impenetrable animal barrier. As historian Paul Landacre famously described it, an Osage orange hedge was "horse-high, bull-strong, and pig-tight."

For me though, even as an adult, it's the fruits of these dioecious trees that really excite the imagination. If you cut one in half—and you may need a saw to do so—you'll discover a tough, pithy core surrounded by a couple hundred small seeds. Like other members of the Moraceae (mulberry family), *Maclura* bears a true multiple fruit composed of numerous separate ovaries, each developing from a separate female flower. In fact, the fruit's distinctive bumps—and their accompanying black, hairlike styles—rise from the fruit's numerous, tightly-packed ovaries. Though squirrels rip into fallen fruits to consume the seeds, nothing else seems to find these forbidding fruits the least bit appetizing. Nothing, that is, that still exists. In her book *The Ghosts of Evolution,* author Connie Barlow suggests that mammoths, mastodons, and other large herbivores of the North American plains ate *Maclura* fruits and were its dispersal agents before humans evolved their own interests in the plant.

Although the exact details of the original collection of this monotypic species remain murky, we know that *Maclura* was among the botanical specimens gathered by Lewis and Clark on their transcontinental expedition of the American West. By studying saplings subsequently cultivated in the Philadelphia garden of Bernard McMahon, Constantine Samuel Rafinesque produced the first botanical description of the tree in 1817, naming it *Ioxylon pomiferum,* or "poison apple." Perhaps unaware of Rafinesque's classification, Thomas Nuttall offered his own description the following year, honoring American geologist William Maclure with its generic epithet and proposing *aurantiaca* ("orange colored") as its specific epithet. Nearly a century later, Germany's Camillo Karl Schneider argued for the name that has stuck to this day, pairing Nutall's generic *Maclura* with a derivation of Rafinesque's specific, *pomifera.*

Coincidently, this Teutonic connection to *Maclura* is compounded in the Arboretum's most spectacular accession (471-36-B) of the plant, a female obtained in 1936 from the Hermann A. Hesse Nursery of Weener, Germany. Growing today on a steep bank near the Centre Street wall across from Faulkner Hospital, the tree exhibits the criss-crossing, nearly horizontal branching that once made the species so desirable as a hedging plant. It is 36 feet (11 meters) tall and its two trunks have diameters at breast height of 14 and 16 inches (36 and 40.5 centimeters). Visit it in autumn, when its limbs bend beneath the weight of its fruits and its glossy leaves turn yellow, and you'll likely acquire fond associations of your own with this most singular of American fruiting trees.

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