

Semprevirens

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Themes and Variations

Reproduction in *Cephalanthus occidentalis*

Article and illustrations by W. John Hayden, Botany Chair

The elements of how flowering plants reproduce by seed should be familiar to all native plant enthusiasts. Anthers make pollen; pollen, somehow, makes its way to a stigma from which the pollen grain grows a pollen tube to an ovule located inside the ovary; from the pollen tube, two sperm cells enter the ovule; one sperm cell fertilizes an egg cell contained in the ovule, initiating formation of the embryo, while the second sperm cell initiates the development of endosperm tissue that stores food used for growth of the embryo; culmination of the process is a seed from which the embryo emerges as a seedling plant upon germination. At its core, the reproductive process is monotonously uniform across the breadth of flowering plant diversity. But in detail, there is an extraordinary amount of diversity

in the reproductive processes of the 300,000 or so species of Angiosperms. The function of flowers is to make seeds, but flowers vary greatly in size, shape, numbers, presence/absence, and degree of fusion of their constituent organs (sepals, petals, stamens, and carpels/pistils). Often directly correlated with the particulars of floral structure, the ecology of pollination is, similarly, extraordinarily diverse. And at the microscopic level too, cellular details of how the basic elements of reproduction are carried out can differ markedly from plant to plant. This article explores highlights of the reproductive biology of *Cephalanthus occidentalis* (Buttonbush), the VNPS Wildflower of the Year for 2022 and attempts to provide perspective on how some of its reproductive details compare with those of other flowering plants. Much of the information about Buttonbush presented here is distilled from a study published by Imbert & Richards (1993).

First, let's consider the inflorescence and individual flower duration. Buttonbush flowers are grouped into spherical clusters containing, roughly, 120 to 200 flowers. **(Figure 1)** Individual flowers, isolated from the cluster, are illustrated in **Figure 2**. Within a given cluster, 90% of the flowers

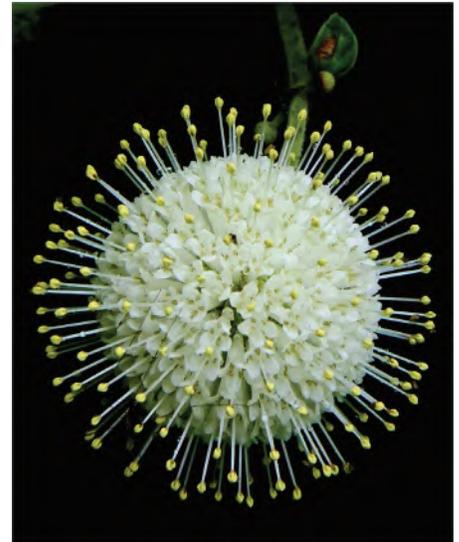


Figure 1. Head-like inflorescence of *Cephalanthus occidentalis* resembling a powder-puff or brush; pollen is first shed from anthers in closed flower buds and then presented to pollinators from stigma surfaces after flowers open. (W. John Hayden photo)

open within a two-day interval; the remaining few flowers open a little earlier or later. Each flower remains open and active in the pollination process for up to four days; the first day constitutes a male phase during which pollen may be dispersed to other flowers; the female phase, defined as the span of time during which stigmas are receptive to pollen, occurs during days two and three, and sometimes persists into the fourth day. Flowering plant reproductive systems in which pollen release precedes stigma receptivity are described as protandrous, literally, male-first. The opposite situation, stigmas

(See Buttonbush reproduction, page 10)

Download the
2022 WOY
Brochure
(PDF)
Buttonbush
(*Cephalanthus*
occidentalis)

Society continues to place conservation first



From the President, Nancy Vehrs

Great news! YOU, our members, set a record for our annual fundraiser for the Natural Area Preserves Fund in the Department of Conservation and Recreation (DCR). Thank You! Because of your generosity, we are sending a total of \$62,180.37 to Virginia's Natural Heritage Program to be used for the up-front costs such as title searches, surveys, appraisals, and environmental assessments, all necessary steps before actual purchase. These costs are generally reimbursed by the grants used to purchase the conservation properties, but they create a cash flow problem for the agency. This money will serve as a necessary revolving fund and includes the net \$6,250 we raised from our online silent auction. I am so proud that our organization was able to raise so much money for this important work. THANK YOU!

Unfortunately, we were not as successful in our fight against invasive plants. Despite the valiant efforts of Delegate David Bulova, the House Agriculture Subcommittee stopped HB491 in its tracks. A core group of interested parties worked with Delegate Bulova on the development of this bill that would have:

- Required signage about invasives to be posted at nurseries,
- Required landscape designers and contract planting services to inform landowners whenever using plants on the DCR invasive plants list,

•Directed DCR to update its invasives list regularly,

•Stipulated that no agency of the Commonwealth could plant, sell, or propagate plants on the DCR invasive plants list (with specific exceptions),

Delegate Bulova even brought a representative of the Agribusiness Council to testify that it did not object to the bill. Pat Calvert of the Virginia Conservation Network, Dan Holmes of the Piedmont Environmental Council, Tom Blackburn of the Audubon Society of Northern Virginia, and I all testified in favor of the bill, but it was "laid on the table," the parliamentary procedure's way of defeating it. Bills have to "report out" of the subcommittee to go before the full committee and then to the House floor for a full vote. Delegate Paul Krizek also patroned HB311

and HB 314. The first bill would have prioritized the use of native plant species on state properties, but this was also defeated in the House Ag Subcommittee. HB314 directed staff at the Virginia Department of Agriculture and Consumer Services to develop signs and labels for invasive plants. Even though the proposed legislation did not require the signs to be posted, the House Ag Subcommittee amended it to ask VDACS to develop a brochure that could be distributed to retail customers instead. As of February 14, that small action passed the house and crossed to the Senate. We thank both Delegates Bulova and Krizek for efforts on our behalf.

In other news, we welcome Barbara Ryan as our new Conservation Chair. She succeeds Alex Fisher who resigned in December. We thank Alex for his three years of service and wish him well as he pursues a master's degree in ecology while working full time at The Nature Conservancy and raising a family. ❖

WELCOME BARBARA RYAN

Barbara has been a resident of McLean for over 30 years. She currently serves as chair of the McLean Citizens Association's Environment, Parks, and Recreation Committee, on the Board of the McLean Trees Foundation, and as the Dranesville District representative on the Resilient Fairfax Community Advisory Group. She is the outgoing treasurer on the Board of the Chesapeake Conservation Landscaping Council and Governor and former president of the Potomac Boat Club (the oldest rowing club in Washington, D.C., located on the Potomac River in Georgetown).

Barbara's significant native plant credentials include a master's degree in



Sustainable Landscape Design from George Washington University, a Virginia Certified Horticulturist, a Level 2 Certified Chesapeake Bay Landscape Professional, and a Certified Fairfax Master Naturalist. She also serves

as the Invasive Management Area Site Leader for Pimmit Run Stream Valley Park, and is a Certified Interpretive Guide and currently pursuing coursework in herbal medicine, with a focus on native plants.

In addition to her horticultural background, Barbara spent her professional career as an economist focused on policy issues, teaching, and working with the Federal Deposit Insurance Corporation. ❖

Exploring ancient plants and new frontiers in Virginia

Over the past couple of years, we have been humbled by something at once very small but bigger than all of us. The pandemic has reminded me to think more often about small things, and I think that can be counted as a bonus in our time of virus vigilance. The work we do at Virginia Natural Heritage is often conducted on a grand scale, but thinking small is a good thing since conservation most often begins at the granular level.

Many of you have heard me talk about my foray into the world of mosses, liverworts, and hornworts, so some of this will be familiar. This plant group (collectively known as bryophytes) can be thought of as a green carpet, covering much of the earth and forming an understory below our well-known flowering plants; in some parts of the world, particularly farther north, bryophytes outstrip flowering plants in importance by every measure. In an agency tasked with the conservation of our natural landscape and the species in it, plants play a huge role in decision making, and until recently, this green carpet was missing as a piece of the decision-making puzzle.

This field season, one of my tasks was to examine a large block of steep mountain



Rock outcrop in Cove Creek, Scott County. (Johnny Townsend photo)

From Your Natural Heritage Program

By Johnny Townsend
Botanist



land near Big Stone Gap. The eastern slope of Powell Mountain is cut through by many deep topographic notches that grabbed my attention. Topographic maps of these areas show densely packed contour lines (indicating steep, sometimes inaccessible slopes), making the maps seem like brown shading had been added by an artist. Based on my experience with similar landscapes in Virginia and the Carolinas and due to the southern locale, my hopes were up for high diversity and some botanical oddities.

The most recent precedent for my high hopes came a few years back in the Dan River Gorge of Patrick County. My explorations of that wild and daunting area with bryologist Paul Davison, VPI herbarium curator Tom Wieboldt, and Natural Heritage ecologist Karen Patterson were driven entirely by Tom's hunch that such a deep southern Blue Ridge gorge must harbor some unusual bryophytes. And it certainly did. Two of the species we encountered on our first trip were new to Virginia and rare on a global scale. Another had been seen but once before, in another deep, mossy ravine in Giles County. The part of the story that was so gratifying is that we with the Virginia Natural Heritage Program, had not targeted this area for inventory before based on our usual botanical and ecological filters. It was a blank spot, now being filled by looking at the little things.

In subsequent months and years, we picked away at this area, a gorge over 1,000 feet deep that has been called the Grand Canyon of the East. Along with many bryophyte discoveries, we were able to document significant plant communities and one rare flowering plant. These developments are noteworthy: the

fact that we found any of them was because the green carpet brought us there. The grandeur of this place has always made it special to those with an appreciation for extremes, including those who passed along its rim on the old Appalachian Trail route. Now we know of many more reasons why it is a true Virginia treasure.

Coming back to 2021, working my way through those steamy gorges in Scott County has already paid off in a way that will take years to quantify. Rhododendron-lined streams, rock outcrops larger than houses, and steamy creek bottoms so humid that you can't see through your hand lens support a lush, green blanket over everything. Though slowed by the steep, rocky terrain, exploration has already netted two species of liverworts new to Virginia and two others very seldom seen in the state. All four are rare on a global scale. The two species new to Virginia (*Acrobolbus ciliatus* and *Plagiochila echinata*) are unfortunately among the many bryophytes that lack a common name, so I apologize on their behalf. Microscope work happens necessarily in the bryophyte world, so study of other specimens from 2021 could turn up additional significant species.

Like the Dan River Gorge, the gorges of Powell Mountain were a botanical black hole and are now becoming a little less dark. It is fun to be thinking of the land in a new way when exploring new terrain. Landforms, climate, meteorology, microclimate, and geology can point us in novel and interesting directions. Even a "cool rock" is now not just an attraction but a potential indicator of botanical diversity and rarity.

One feeling I can never get over in these places is a sense of great age. Maybe the gorges are particularly old, maybe not, but they certainly remind me of the eons passing across our ancient Appalachians. Here's hoping those mountains will continue to yield many new discoveries of some very old plants. ❖

Gary Fleming

Virginia's 'native plant' guru remembers his journey

For several years now, Society President Nancy Vehrs has been providing behind the scenes insight into the people whose lives are dedicated to telling the stories of Virginia's plants and habitats. This installment provides a look into the life of Vegetation Ecologist extraordinaire Gary Fleming who retired from Natural Heritage in December. Nancy recently caught up with him and asked him about his long career and his future plans.

Nancy: Please provide a little background on yourself.

I was born in Atlanta, Georgia, and grew up there and, later, in Washington, D.C. I attended St. Albans School in D.C., then the University of Pennsylvania for two years before transferring to the University of Texas at Austin. My wife Barbara and I have lived in rural Fluvanna County, between Richmond and Charlottesville, for the last 30 years. We have a 60-acre property with a variety of habitats that have served as a "laboratory" where I can step out the door and closely study and photograph a multitude of natural subjects. Barbara has a son, and he and his wife have given us three grandchildren. We are also animal lovers and over the years have shared our home and property with a number of them, including horses, guinea fowl, dogs, and cats. Currently, we have two dogs, a cat, and two adorable kittens that are basically running our lives!

Nancy: You are a native plant guru to those of us in the VNPS. How did you develop your interest in ecology and our native flora?

My interest in both plants and photography started while living in Austin. We rented an old farm on the outskirts of the city and I became intrigued with photographing the many wildflowers that popped up on the property. Soon, the flora



Gary Fleming took this self-portrait with one of the massive, old-growth Water Tupelo on the Blackwater River at Antioch Pines Natural Area Preserve.

of stream gorges and limestone hills in the Edwards Plateau caught my interest and I was taking undergraduate courses in botany. I also got to know many of the UT graduate botany students, all of whom were studying and technically describing new species from Mexico. Even back then, I was much less interested in taxonomy than in where plants grow and why; and for better or worse, seeing what those grad students were doing discouraged me from going down that road.

Nancy: Your photographs are exquisite. Is it true that you were originally a photographer? What was that career like, and why did you change?

After moving back to the D.C. area in 1975, I wasn't sure what I wanted to do and, despite lacking any qualifications, somehow landed a job as a public relations specialist with one of the area's prestigious architectural firms. I thought it was going to be a short-term endeavor, but it turned into a 16-year career, during which time I learned how to photograph architecture and landscape designs with a large-format view camera. At

first glance, architectural and nature photography may seem like inherently different art forms, but they have more in common than you might think!

During those years, however, I never lost interest in plants and natural history, and spent most of my free time hiking, botanizing, and photographing nature. My parents owned a farm on the Wildcat Mountain ridge in Fauquier County, and in the early 1980s, I met Jocelyn Sladen, whose family owned Wildcat Mountain Farm. Meeting Jocelyn really intensified my field activities, and we spent many days exploring and studying the Wildcat Mountain flora together. One day, she showed me the first-edition, hard-copy version of the *Atlas of the Virginia Flora*. The moment I laid eyes on that book and its county dot maps, I knew I would be getting much more serious about botany! Soon I met both Donna Ware (then curator of the College of William and Mary herbarium) and Ted Bradley (then curator of the George Mason University herbarium), both of whom became important mentors, encouraging me to collect plants, improve my skills,

and document county records. By the late 1980s, I was doing contract work for Chris Ludwig at the just-established Virginia Natural Heritage Program and for The Nature Conservancy studying the dwarf pine woodland on Panther Knob, West Virginia. Then, in 1992, a position opened at Natural Heritage and I was lucky enough to get the job.

Nancy: You have a brother who is a respected geologist. Do the two of you collaborate on any scientific research or papers? Are any other members of your family scientists?

My brother Tony is the only other scientist in the family. He is accomplished as both a bedrock geologist and hydrogeologist and is quite an all-around naturalist as well. We have spent a considerable amount of time hiking and exploring together, but our collaboration has been mostly informal. Nevertheless, Tony's expertise has helped me grow as a vegetation ecologist and greatly improve my ability to interpret the relationships between vegetation types, species distributions, geology, soils, and groundwater. He and USGS geologist Scott Southworth were instrumental in helping me with a study of the Potomac Gorge vegetation, which has correlations with an extremely complex set of Piedmont rocks. Tony also reviewed and edited the geology section of the *Flora of Virginia* introduction, which made it far more accurate and detailed than anything I could have written alone.

Nancy: Describe a typical day in the field. How much of your working time was spent in the field?

Over the 30 years I worked for Natural Heritage, I averaged between 80 and 100 days per year in the field, working in all parts of the state. The other roughly 150 days were devoted to documenting the field work, writing reports, analyzing data, studying maps and imagery to identify survey areas, and other administrative tasks that came

with the job. I would be remiss not to mention that all work at the Virginia Natural Heritage Program is strongly collaborative. My job was basically a 30-year learning experience made possible by being part of a group of very talented, dedicated colleagues with different and complementary skill sets.

The first five years I was with the program, I worked mostly on contract inventory projects at sites like military bases and national parks. In those early days, most field time was spent hiking to and within targeted sites to qualitatively document significant natural communities and rare plant populations. After that, I worked on both contracts and discretionary studies determined by data gaps we needed to fill. As the need for a statewide natural community classification became paramount in the late 1990s, many days were spent sampling vegetation plots, recording complete quantitative information on the composition of discrete areas. Overall, I was involved in sampling several thousand plots in all different types of vegetation, some of them (for example tidal swamps and talus slope woodlands) quite challenging! Although the process of plot sampling might seem tedious to some botanists, a real advantage is that it forces you to look very closely at things and often reveals plants that you might have otherwise walked right by without noticing. It also helps one learn how to identify plants in sterile and decadent conditions. Most importantly, working in so many different habitats gives one a good feel for the environmental and geographic affiliations that many of our species exhibit. In recent years, almost all of my work was discretionary and devoted to applying the community classification that we had developed, finding new conservation sites, and revisiting sites that needed updating.

A typical day could vary quite a bit depending on the location and tasks



Gary Fleming hard at work in the Natural Heritage herbarium. (Karen Patterson photo)

at hand, but generally started by 8 a.m. and finished up around 6 p.m. Although some work was done alone, more often I would work with one or more colleagues, especially my long-time partner-in-ecology Karen Patterson. Several miles or more of hiking and off-trail bushwhacking would often be involved. If we were looking for something in particular – say an historical rare plant population or rock outcrops seen on an aerial photo – we would navigate to the location using a GPS unit and often spend hours combing the targeted area. Other days might involve more general, “see-what-you-can-find” explorations along with sampling one or more vegetation plots. On some large wetland sites, we often worked from boats.

We carried quite a lot of equipment and supplies, including food and water; rain gear; GPS units and more recently iPads or tablets loaded with imagery and other data; and various sampling gear such as a laser rangefinder, clinometer, compass, DBH tape, surveyor's stakes, and tape measures. Snake gaiters and mosquito jackets would come out of the closet for special occasions!

I have to admit that being in the field is my passion. No matter how oppressive the weather or difficult the working conditions were, I loved every minute I was out doing Natural Heritage work. This was definitely the “dream job” for me, and I feel incredibly lucky that I could do it for so long.

(See Gary Fleming, page 12)

Confessions of a Poison Ivy Enthusiast

My passion for poison ivy scientific research began because I ignored some very sensible advice from my spouse. The 2012 derecho toppled an oak tree in our back yard and several days later we set out to reclaim it as firewood. I donned what I deemed appropriate personal protective equipment for the task of using a chain saw to cut up the limbs to stove-sized pieces: heavy work boots, long pants, eye goggles, and a short-sleeved cotton shirt to stay cool on a humid summer afternoon.

My wife suggested that a long-sleeved shirt might be more appropriate because “poison ivy is abundant in our yard.” In what I now ascribe to as a textbook case of clinical “chain saw -induced testosterone poisoning,” I responded “No Dear, I know what poison ivy looks like. I am a plant molecular biologist!”

The poison ivy skin rash symptoms quickly appeared on my forearms the next day (see photo). Having never experienced poison ivy rash before, I mockingly said “This is interesting. I will not treat the rash and see where this goes.”

Over the course of the next three weeks, my skin rash symptoms did not go well. The rash manifested as intensely red, swollen skin with skin blisters that ruptured, releasing copious amounts of pus. To my reckoning,



The second day of the poison ivy rash that began the Jeleško poison ivy research program. The cigar is included for scale.

the aforementioned symptoms were but a minor irritation compared to the dominant symptomatology.

Such symptoms were historically first described by Captain John Smith of the “James Town Colony” in “our faire Commonwealth of Virginia.” Captain Smith succinctly stated that poison ivy: “... doeth itcheth much.” The relentless itching sensation was particularly distracting, especially at bedtime. My insomnia was sustained by the cycling between two intrusive thoughts about how I would spend each night: “Shall I go to sleep, or shall I claw my itching flesh off?”

Near the end of the first week of this unproductive cogitation, another line of insomnia-associated inquiry emerged. It went along the lines of: “I am a plant molecular biologist who investigates plant defense chemicals (at the time, mostly nicotine biosynthesis). What are the poison ivy chemicals responsible for these skin rash symptoms? And what is the ecological context of this seemingly obvious plant chemical defense? The first question turned out to be an easy one to answer.

The chemical responsible for causing my skin rash symptoms is urushiol. Urushiol is derived from the Japanese word “urushi,” which loosely translates to “sap from the lacquer tree” in Japanese. Having lived and done plant research in Japan, I was familiar with urushi because it has special cultural significance in the production of



Emma Lear collecting mature poison ivy drupes at Virginia Tech’s McCormick Farm nature trail in Raphine.

highly prized lacquerware items such as cups and bowls.

The realization that urushiol is the same chemical responsible for both my skin rash misery and aesthetically pleasing lacquerware artistic expression was both shocking and transformative. Urushiol turns out to have a highly reactive chemistry in which individual urushiol molecules are allergenic (an immunological reaction, not a toxin), but when separate urushiol molecules combine/polymerize together into a lacquer varnish it results in harmless chemical bonds (and thus no allergenicity). Moreover, the exact chemistry used in the urushiol lacquer polymerization process is similar to the fascinating catechol-chemistry that aquatic mussels utilize to glue themselves to rocks under water (i.e., a glue that cures in water). In short, urushiol is a



Xiyuan Zhang collecting mature poison ivy drupes at Virginia Tech's Reynolds Homestead in Critz. She is wearing her orange vest on the second day of 2021 deer hunting season.

reckoning that there was a dearth of scientific knowledge about poison ivy biology and ecology. For example, the wildlife biology and veterinary medicine scientific literature did not indicate any extant wildlife or domesticated animals that show a comparable type of skin rash that humans manifest after contact with urushiol. Likewise, the medical scientific literature described lackluster results to develop a laboratory animal model for investigating poison ivy allergenic dermatitis. Oddly, only one strain of laboratory guinea pigs showed some urushiol-specific responses, but the guinea pigs entirely lost this allergenicity after six months of age, whereas humans show a lifetime of urushiol allergenicity.

It is worth noting that neither

guinea pigs nor humans co-evolved with poison ivy in North America (humans are an invasive species to North America), and therefore cannot be the co-evolved animal targets for a urushiol chemical defense.

By the end of three weeks of let's "see where this goes" self-imposed dermatological misery, I decided it was time to end the experiment. I sought medical intervention for my symptoms from my family physician. Within 24 hours of oral steroid treatment, the devastating "itch" sensation was completely gone, and my elephantine swollen pus-oozing arms were starting to turn a corner toward an eventual complete recovery.

In place of those dreaded clinical symptoms was now an intensely personal intellectual scientific curiosity (my children insist it is actually an obsession) about all aspects of poison ivy biology. Naturally, I realigned my scientific research program at Virginia Tech to singularly investigate poison ivy biology.



Bagged drupes reading for collecting on the McCormick Farm nature trail (Nancy Sorrells photo)

A former graduate student calls poison ivy "the familiar stranger" because it is a very common native plant, yet it is also largely a scientific enigma. By way of example, over 92 percent of nascently germinated poison ivy seedlings that we monitored in field plots were entirely browsed (disappeared) within the first several weeks of germination. We showed that poison ivy seedlings have very high urushiol levels, but this did not prevent intense herbivory.

Another example of an enigmatic finding was from a collaborative research project that showed poison ivy prefers human-disturbed habitats over nearby native forest environments. Looking to the future, my lab is performing experiments to investigate whether urushiol provides any measurable evolutionary benefit(s) to poison ivy plants (see photo of a Virginia Tech undergraduate student engaged in this research), and we are working to identify all the genes and enzymes responsible for urushiol biosynthesis.

There is still so much to discover about poison ivy (*Toxicodendron radicans* (L.) Kuntze), and I am itching to learn all we can!

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Janus-faced chemical. In one chemical form it is an allergen, yet in another chemical form it is a useful aesthetically pleasing bio-sustainable coating of wooden objects. Thus, urushiol chemistry is at the nexus of both skin allergenicity and cutting-edge material science.

I also queried the scientific literature about poison ivy plant biology. There was a lot of searching, but relatively few clear answers emerged. Despite the human misery that poison ivy produces each year, there were astonishingly few scientific studies solely focused on poison ivy plant biology or ecology. Unfortunately, two of the very few articles indicated that increasing atmospheric CO₂ levels result in faster poison ivy growth, more poison ivy biomass, and the accumulation of increasingly more allergenic chemical forms of urushiol chemistry. This is not good news for us humans into the Anthropocene.

By the third week, my allergenic dermatitis symptoms were not improving and there was an emerging

A ‘Just so’ story Is *Wisteria frutescens* an ecological anachronism?

Article by W. John Hayden, Botany Chair

“Just So Stories” is the title of a collection of fanciful tales published by Rudyard Kipling in 1902; the stories, evocative of far-away lands and exotic beasts, purport to explain such intriguing zoological questions as, “How the Camel got his Hump,” “How the Leopard got his Spots,” and so on. Modern day science has adopted Kipling’s title, just so stories, to characterize any elaborate hypothesis that weaves together disparate facts and observations into a single, coherent, logically satisfying narrative. There is nothing inherently wrong with just so stories in science, as long as one remembers that the story, i.e., the hypothesis, was constructed, intentionally, to connect known facts and that, consequently, fidelity of the story to individual facts is NOT proof of the story’s validity. A true test of a scientific just so story requires assessment of new evidence, i.e., evidence independent of the bits of information from which the story/hypothesis emerged. This article advances a just so story about *Wisteria frutescens*, the 2021 VNPS Wildflower of the Year. As such, readers are cautioned to remember that the core idea advanced herein is wholly speculative. It is a just so story.

The just so story that follows was inspired by the concept that certain plants are “anachronistic” in terms of their fruit predation and seed dispersal ecology, an idea first published by Janzen and Martin (1982). These ecologists had observed some three dozen or so large-fruited plants of Central America that presently have no obvious means of dispersal among the native animals found in the region. The fruits of these plants are too large to be consumed by any native modern-day animal found in Central America, so, in the wild; the fruits simply drop to the

ground below the trees that make them, which is not an advantageous location for their seedlings to develop. Janzen and Martin sought to address this paradoxical situation: Why would these plants make large fruits that neither disperse on their own nor support fruit-eaters that could disperse their seeds?

A resolution of the paradox emerged when Janzen and Martin had the insight to consider the ecology of these plants viewed through the lens of time. The world was a very different place about 12,000 years ago. This was the end of the Pleistocene, commonly referred to as Ice Ages. For nearly two million years, climate had oscillated between warm and cold intervals, each drastically different climate phase lasting tens of thousands of years. Throughout these Ice Ages, numerous large animals, dubbed “Pleistocene megafauna,” thrived. Citing paleontological data, Janzen and Martin (1982) identified more than a dozen species of large animals that once roamed Central America. Perhaps, hypothesized Janzen and Martin, these now-extinct beasts were the animals that ate the paradoxically large fruits and thereby dispersed the seeds contained therein. When their co-adapted seed dispersers became extinct, large fruits no longer functioned well in the altered post-megafaunal ecology of post-glacial times. In other words, these plants that make large fruits no longer fit the times in which they live, they have become “ecological anachronisms.”

Janzen and Martin’s hypothesis has been widely accepted as a reasonable inference to explain the seemingly mal-adapted characteristic of plants that produce fruits too large to be dispersed by contemporary fauna. In the

years since Janzen and Martin’s paper, additional examples from many parts of the world, including North America, have been proposed. In North America, one of the most prominent large fruited species without an obvious native animal disperser is Osage Orange, *Maclura pomifera*, the fleshy multiple fruits of which approach the size of a regulation softball. Another is the Kentucky Coffee Tree, *Gymnocladus dioica*, with tough seed pods that enclose hard seeds surrounded by sweetish gelatinous goo. Like the Central American large-fruited trees that inspired the idea of ecological anachronism, the fruits of Osage Orange and Kentucky Coffee Tree typically remain undispersed under their parent trees.

It was the Kentucky Coffee Tree that made me wonder if our Wildflower of the Year for 2021, *Wisteria frutescens*, might fit the profile of ecological/evolutionary anachronism, à la Janzen and Martin (1982). Multiple facts about the biology of *Wisteria frutescens* make it easy to weave dispersal anachronism themes into a just so story about this native vine.

First, let’s consider the actual natural range of *Wisteria frutescens* versus what plants in cultivation indicate about its potential range. In the narrow sense (i.e., as distinct from *W. macrostachys*), *W. frutescens* occurs no further north than southeast Virginia, which is USDA Hardiness Zone 7b (average annual winter low temperatures of 5° to 10° F). On the other hand, *W. frutescens* is known to escape cultivation as far north as southern New England and New York state in the vicinity of Albany (Biota of North America Program, 2021); in other words, this plant has sufficient cold hardiness to survive in USDA Plant Hardiness Zone 5b (annual average

winter lows of -10° to -15° F). Why does *W. frutescens*, in contemporary nature, occupy only a fraction of the range in which it could survive? Perhaps, because ever since the last glaciers melted, it no longer had fruit-eating megafauna to assist with its northward dispersal from its Gulf Coast glacial maximum refuge. Perhaps, *W. frutescens* is another ecological anachronism.

It matters not whether one opts to lump *Wisteria frutescens* with *W. macrostachys*. The latter entity grows naturally as far north as northern Illinois, which is USDA Hardiness Zone 5b, indicating a similar degree of cold hardiness for American Wisterias, regardless of how one partitions their taxonomy. Why, then, have the eastern elements of this complex fallen so short of their potential geographic range?

“But wait,” you might say, “*Wisteria* seed pods explode at maturity, ejecting seeds for distances of a few feet.” True, but this fact may not be sufficient to discount fully the missing herbivore-disperser story. *Wisteria frutescens* fruits mature by late summer (**Figure 1**) but remain on the plant for another few months before finally blowing apart in late fall, well after leaves have dropped. At the moment of dehiscence, there is little inside a *Wisteria* seed pod besides a few very hard seeds. However, I suggest that those very same fruits will have had more food value when the seeds first mature in late summer and I can cite an image of *Wisteria frutescens* fruits, published by Wang et al. (2006), showing a matrix of soft tissue between the fruit walls and tough seeds in support of this assertion. I am suggesting that fruit maturation in *Wisteria* may be similar to that of the common Green Bean, young pods of which offer food value before they dry and shrivel to the point of spontaneous dehiscence. Perhaps, I suggest, *Wisteria* fruits evolved to take advantage of megafaunal fruit eaters as a first mode of long-distance seed dispersal, but if



Figure 1 Late summer fruits of *Wisteria frutescens*, weeks prior to dehiscence. (Photo by Krzysztof Ziarek, Kenraiz; CC BY-SA 4.0.)

animal-based dispersal were to fail, if fruits remain intact on the plant, late-season explosive fruit dehiscence would provide dispersal for modest distances, just a few feet, from parent plants. Certainly, dispersal by megafauna would be much more advantageous in terms of efficient range expansion than the late-season explosive dehiscence alternative.

It is also noteworthy that *Wisteria* seeds contain toxic and bitter-tasting triterpene molecules called wisterins (North Carolina Extension 2021). Seed toxicity is another part of the syndrome of characteristics found among plants with fruit/seed dispersal by large mammals. Small mammals such as squirrels do indeed collect relatively large edible seeds—like acorns—some of which germinate after being dispersed, cached, and forgotten. But small mammals shun bitter and/or toxic seeds and fruits, a fact for which there is published evidence (Kistler et al. 2015). The same authors demonstrate that extant large mammals, however, have less sensitivity to bitter-tasting molecules. Moreover, hard legume seeds, like those of *Gymnocladus* and *Wisteria*, are likely to be swallowed whole by large animals, perhaps suffering some minor tooth

nicks that could function like scarification and hasten seed germination after the excretion of the digested meal. Further, small tooth scratches on the seed coat would likely result in only minor, if any, release of toxin molecules. The toxic, bitter, seeds of *Wisteria* may well be an adaptation that simultaneously discourages predation by small mammals but would be tolerated by much larger animals—were there any such beasts in contemporary North America to function as seed dispersers.

Is *Wisteria frutescens* an ecological anachronism? Several aspects of its biology seem to fit the hypothesis of a just so story. Perhaps *Wisteria frutescens* is an ecological anachronism. But do not forget that the anachronism hypothesis was built on those same aspects of its biology, so the fit of those facts to the hypothesis does not really test the hypothesis. An independent test of the idea is needed—something like discovery of a large, fossilized, Pleistocene beast with identifiable *Wisteria* seeds in its gut. Something like that would provide compelling affirmative evidence—but until or unless someone makes a remarkable discovery like that, we may never know. ❖

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Buttonbush reproduction

(Continued from page 1)

receptive before pollen release, is known as protogyny. There are still other flowers, of course, that activate their male and female functions simultaneously. For comparative perspective, *Cephalanthus* is considered a relatively advanced dicot, a group within which protandry is especially common; in contrast, among monocots and primitive angiosperms, protogyny is common. In terms of duration, some flowers last for much shorter time spans than those of Buttonbush—familiar examples include Morning Glories and Day Lilies. Other flowers, like those of tropical orchids, may persist for multiple weeks (unless or until pollinated).

In *Cephalanthus*, the male phase is further characterized by an unusual process known as secondary pollen presentation. In most plants, pollen is dispersed directly from the anthers in which the pollen was made. In secondary pollen presentation, however, pollen is transferred from anthers to some other floral organ from which the pollen is subsequently dispersed. Here is how secondary pollen presentation works in Buttonbush: As is commonly the case, its pollen grains are fully mature before flowers open. In Buttonbush, however, anthers open while still enclosed in the flower bud and deposit their pollen onto the surface of the stigma (**Figure 2**); this process happens early in the morning, well before the flowers open around sunset. For the next eight or so hours after flower opening, styles elongate greatly, in the dark, pushing the pollen-laden stigmas a little more than one cm beyond the petals. Thus, any pollinator approaching a Buttonbush flower cluster on its first day of opening will remove pollen

from stigmas, not directly from the anthers—thus meeting the criterion for secondary pollen presentation. As a reproductive strategy, secondary pollen presentation on stigmas occurs in only a few of the several hundred commonly recognized plant families. Further, in the usual pattern of secondary pollen presentation, pollen deposition does not occur directly on receptive surfaces of stigmas; rather, in most cases of secondary pollen presentation, pollen is deposited before branched stigmas separate from each other; later, after pollen dispersal, separation of stigma branches exposes their receptive surfaces. *Cephalanthus* appears to be the only case known in which pollen is deposited directly onto the receptive surface of the stigma.

In another aspect of pollen-presentation, flower clusters of *Cephalanthus* provide an example of the “powder-puff” or “brush” pollination syndrome—spatially, both the pollen-laden and receptive stigmas are situated in a three-dimensional cloud-like zone around the flower cluster. Across the diversity of flowering plants, students of pollination biology recognize several other floral configurations that control the details of pollinator access to, and behavior within, flowers; examples of these other general configurations include flowers that resemble bowls, or bells, or tubes, or closed cavities of various shapes, which the pollinator must enter to effect pollination. Another aspect of pollination biology addresses the different kinds of pollinators that a given flower attracts. In this respect, *Cephalanthus*, like many other plants, is relatively unspecialized; diverse

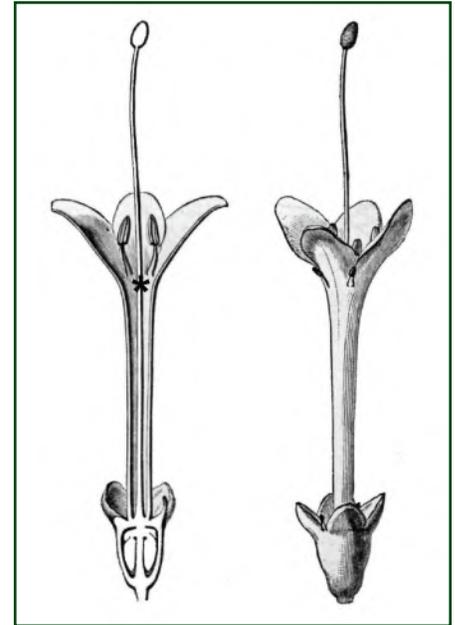


Figure 2. Flowers of *Cephalanthus occidentalis*. Left: longitudinally sectioned flower; asterisk indicates approximate position of stigma as it receives pollen from anthers shortly before flower bud opens. Right: intact flower; pollen disperses from stigmas on the first day of flowering; stigmas receive pollen on second and third day. (Image reproduced from H. Baillon, *Histoire des Plantes* (1866-1895).)

kinds of insects visit and pollinate its flowers. Other plants, however, are much more highly selective in terms of their pollinators; two examples include cactus flowers pollinated by bats and yuccas pollinated by yucca moths—the list of specialized, highly selective pollination systems goes on and on. *Cephalanthus occidentalis*, deservedly characterized as a pollinator magnet, represents just one of myriad combinations of ways that different angiosperms have found to accomplish pollination.

But, you might ask, why attract pollinators with nectar, which is metabolically expensive to produce, if *Cephalanthus* pollen is already deposited directly onto stigmas before the flowers actually open? The answer is, simultaneously, both simple and complex. The simple answer is that Buttonbush flowers are, to a large degree, self-

Buttonbush

(Continued from page 10)

incompatible—self pollen simply does not work very well. Pollen that might remain on stigmas after the first day of flowering (male phase), can germinate and begin to make pollen tubes on Buttonbush stigmas, but pollen tube growth from self-pollen is slow relative to that of pollen originating from different plants. Generally, proper growth of pollen tubes depends on cell-to-cell communication between pollen tubes and cells of stigmas. In self-incompatible plants, there needs to be some sort of genetically defined chemical difference between pollen tubes and cells of stigmas for effective pollen tube growth. The details of how self-incompatibility works at the cellular and molecular level is actually quite complex and details of the process differ from species to species. In the case of Buttonbush, microscope-level studies by Imbert

and Richards (1993) indicate that the self-incompatibility reactions operate only in the stigma because the few self-pollen grains that manage sufficient growth to enter the style then grow very much like non-selfed pollen tubes. Data indicate that there are few self-pollen tubes that reach ovules and, consequently, “selfed” offspring occur at relatively low frequencies in Buttonbush. It is widely acknowledged that self-incompatibility mechanisms promote genetic diversity at the population level and genetic diversity is viewed as beneficial because, over the long term, it permits greater adaptability to potential shifts in the environment. As a group, however, other angiosperms function differently. For some plants, self-pollination is the common pattern, and other plants are flexible—they will set seed whether self-pollinated or crossed with pollen from other plants.

This brief overview about the reproductive biology of flowering

plants illustrates a truism about evolution. Over the course of time, as organisms evolve, some characteristics remain the same while others morph into new character states. That is why we recognize a foundation of fundamental, general, structures and processes that determine how flowers bring about the next generation of their lineage, but when we look at the details of these structures and processes in different plants, we discover what constitutes a long series of variations on the grand, general, theme of how plants make new versions of themselves. ❖

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Workshop to feature plant-geology relationships

The intertwined relationships of plants and the geology underneath them will be the featured topic in the Society’s annual workshop to be held via zoom on two consecutive Tuesdays in March.

“Below the Surface: How Plants & Geology Interact” is the title of the workshop that runs from 6:30-9 p.m. on Tuesday March 8 and Tuesday March 15.

Each evening begins with a half-hour meet and greet at 6:30 and then sessions air at 7 p.m. and 8 p.m. The first session on March 8 will feature Bert Harris discussing “Land Management Lessons from Piedmont Prairies With Notes on Substrates and Soils.”

Chuck Bailey will follow at 8 p.m. with “Virginia Geology: A Journey from Deep Time to the Future.”

In the first session on March 15, Tom Wentworth will present “Geology & Soil Parent Materials as Determinants of Natural Communities in Virginia & the Carolinas: Overview from the Southern Appalachians to the Atlantic Coast.”

Wrapping up the workshop will be Tony Fleming’s “Beyond Substrates: Universal Geologic Principles For Interpreting Plant-Landscape Relationships.”

To register for the virtual Annual Workshop, visit www.vnps.org and click on the Annual Workshop button.



VIRGINIA NATIVE PLANT SOCIETY

Sempervirens (ISSN 1085-9632) is the quarterly newsletter of the Virginia Native Plant Society, Blandy Experimental Farm, 400 Blandy Farm Lane, Unit 2, Boyce, Va. 22620, 540-837-1600, info@vnps.org. Nancy Vehrs, President; Nancy Sorrells, Editor; Karen York, Office Manager. Original material in *Sempervirens* may be reprinted if credit is given to the Virginia Native Plant Society, to *Sempervirens*, and to the author of the material, if named. Readers are invited to send letters, news items, and queries for consideration. E-mail items to Nancy Sorrells at lotswife@comcast.net.

Next submission deadline:
March 15, 2022

Gary Fleming

(Continued from page 5)

Nancy: We heard rumors of your impending retirement for a number of years. What made you decide that this was the year?

Although I originally planned to retire at 65, when the time came, I kept putting it off because I loved the job so much. However, turning 70 last year was a wake-up call. At this age, life is definitely “too short,” and I knew it was time to dial it back and focus on a few, more personal goals. In addition, injuries, osteo-arthritis, and years of scrambling around steep slopes had really taken a toll on my joints, making it difficult to work in some of the rougher places where Natural Heritage biologists must go. So I made the very hard decision that 2021 would be my last.

Nancy: What do you plan to do now?

Well, I am looking forward to having more time for family, friends, and travel. I also plan to get one of my knees replaced, so that I can stay active in the field and hopefully stay engaged with Natural Heritage as an occasional volunteer and “emeritus” resource. I will certainly con-

tinue to be involved with the Virginia Botanical Associates and as an administrator of the Digital Atlas with Tom Wieboldt and Johnny Townsend.

There are a couple of specific projects I would like to finish up in retirement. The most ambitious one is to complete a scientific paper or perhaps a book on the vegetation and flora of the central Virginia Piedmont, which is historically one of the most under-documented regions of the state. I have been studying a 10-county area here for 30 years, and am still finding interesting habitats and significant new records. Knowing the patterns of species distribution in the Piedmont is critical to understanding how the overall Virginia flora has migrated into place during the last 12,000 years. Realistically, this is the type of project in which new discoveries keep fueling year after year of fieldwork, so it remains to be seen whether I can actually bring it to some kind of conclusion!

Nancy: Any advice about conserving wild flowers and wild places?

VNPS already does so much to directly promote conservation, from donating to the Natural Areas Preserves

Fund to managing a site registry program to funding research on native plants. But the educational outreach part of your mission is really an area that few other groups in Virginia can match. The native plant guides, speaker programs, symposiums, workshops, field trips, and online resources that VNPS offers are all critical tools for raising public awareness about the importance of our native ecosystems and flora. This in turn helps build political support for land conservation, natural area protection, and habitat restoration. The more VNPS can expand these programs and partner with other organizations, especially to engage children and young people, the better. Make no mistake: despite many successes in recent years, our collective attempt to build a truly viable network of protected natural areas is in a race against ongoing habitat degradation and destruction. Helping our younger generations experience the amazing diversity and value of the natural world will be key to winning the race, because it is going to take a sustained, multi-generational effort.

Nancy: Best wishes and thank you! ❖

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