Volume 34: Number 2 > 2017

The Quarterly Journal of the Florida Native Plant Society

Palmetto

Rosebud Continuum • *Canna flaccida* • Garden Revolution • *Nelumbo lutea*

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For most purposes, the phrase Florida native plant refers to those species occurring within the state boundaries prior to European contact, according to the best available scientific and historical documentation. More specifically, it includes those species understood as indigenous, occurring in natural associations in habitats that existed prior to significant human impacts and alterations of the landscape.

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Features

Palmetto

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Editorial Content
We welcome articles on native plant species and related conservation topics, as well as high-quality botanical illustrations and photographs. Contact the editor for guidelines, deadlines and other information.

ON THE COVER: American lotus (*Nelumbo lutea*). Photo by Shirley Denton.

Above: A great diversity of volunteers participate in projects at the Rosebud Continuum, such as planting portions of the wildflower meadow.

Native Plants, Sustainability and Rosebud Continuum

Craig N. Huegel, Ph.D. with Lisa Hoefler-Boing

For the past year, I have been intimately involved with designing the native plant landscape at the Rosebud Continuum in Land O'Lakes, Pasco County. It is a project near and dear to my heart as it encompasses all of the values I've espoused these past 30 years with the Florida Native Plant Society through my writing and lecturing about the value of native plants to a living landscape. As this project unfolds, I want to share its vision with you and encourage you to get involved on some level. This is a community project, and we can use everyone who wishes to be a part of our growing community.

As stated on the website, http://rosebudcontinuum.org: "The Rosebud Continuum is a dynamic, ever-evolving nexus between the best practices of our many pasts and traditional wisdoms, and the exciting synergies that are emerging as we apply our dedication to sustainability and education to the creation of a desirable future. At Rosebud, we seek to demonstrate and inspire so that visitors and volunteers can contribute to the widening solution space that can realistically tackle our individual and environmental health and

Above: Lisa Hoefler-Boing and one of the many loads of native plants purchased for the project. **Below:** Queen butterfly caterpillar feeding on a native milkweed planted in the wildflower meadow.

Above: Native wildflowers and grasses destined for the developing wildflower meadow.
Below: The south woodland with some of the newly installed native plants.

Above: The wildflower meadow nearest the lake edge becomes seasonally flooded. These are ideal conditions for many of the wildflowers we've chosen to add.
Below: A newly hatched white peacock butterfly in the wildflower meadow.

Above: Project owner Maryann Bishop with Lisa Hoefler-Boing at the trail entrance into the south woodland.

biodiversity conservation challenges. Rosebud is a place where ordinary folks and families can feel empowered to "try this at home." It serves as a resource for communities, neighborhoods and individual households seeking to wean themselves off dysfunctional systems and instead learn "systems thinking in the human food/energy/water nexus and wildlife preservation that resolve conflicts and lead to harmonious outcomes."

This honest mission began as the dream of Sonny and Maryann Bishop to transform their nearly 20-acre lakefront property into a model of how Floridians can live sustainably and to use it as a public educational center. It is not simply a native plant demonstration area – there are a great many other parts as well. My role is a piece of the overall puzzle; helping to transform a part of their property into a living landscape with native plants and then to showcase them in such a way as to encourage their use by others. Along the way, I have picked up the assistance of fellow Pinellas Chapter FNPS member Lisa Hoefler-Boing. She has provided a mind to bounce ideas off of, a yin to my yang, and more sweat equity than I can adequately measure. In all aspects, this has become our joint project.

The property that the Bishops purchased has a history of disturbance and was far from pristine. Once a citrus grove with a residence, part of the property was converted to improved pasture when the citrus failed and the remaining land was allowed to go fallow. The fallow land became dominated by invasive species. Right after the Bishops purchased the property, Maryann read that Pasco County officials were looking for a newly arrived invasive species that they were trying to track, so she invited one of their employees to look for it. Though she doesn't remember which species it was, she was told by the employee that much of their thriving vegetation was composed of invasive non-natives. Maryann decided to learn more about the problem and then do something to correct it.

Well before Lisa and I became involved, the Bishops had made significant progress in tackling the very significant problems they had from Brazilian pepper (*Schinus terebinthifolius*), and they had begun to clear some of the other major offenders. Since then, we have worked together to eradicate the major invasive species still present. The list is long and the battle is far from over, but we've reached the stage where we can begin replanting the fallow portions of their property with appropriate native species. There are other planned uses for the converted pasture areas and the residential portions of the overall Rosebud Continuum project.

The native plantings essentially occur in four major units of the property. Two are mesic woodlands with a relatively open canopy dominated by water oak (*Quercus nigra*). How water oak became the dominant canopy species still baffles me a bit, but many of these trees are decades old. Also naturally present in this canopy is sweet gum (*Liquidambar styraciflua*). The understory contains some native elements such as lyre-leaved sage (*Salvia lyrata*) and toothpetal false rein orchid (*Habenaria floribunda*), but we've had to battle a great many non-natives to get to the point we are today. Camphor tree (*Cinnamomum camphora*) was the worst offender remaining in the canopy, but we've also had to address areas of wedelia (*Sphagneticola trilobata*), caesarweed (*Urena lobata*), and skunkvine (*Paederia foetida*).

The southern woodlot occurs at the entrance to the property and lies on an east-west slope that ends at the edge of an undeveloped lake. This will serve perfectly as the trailhead to a self-guided nature trail and be one of the most visible aspects of Rosebud's many public programs. Here, we've maximized color in the palette of plants we've chosen. We want to demonstrate to the public both the beauty and utility of Florida native plants, and we've done this by adding a diversity of flowering subcanopy trees and shrubs to this area.

The nature trail leaves the canopy of the woodlot about 100 yards from the lake edge and enters a sunny open area of mowed "lawn" that continues sloping to the edge of the lake. This area is being planted as a wildflower meadow for the area's many pollinators. Before we could do this, the ubiquitous carpet of grasses, sedges, and invasive species had to be treated. We accomplished this over many weeks by using appropriate herbicides and then covering the area with thick plastic sheeting for more than a month. By our first planting day, most of the future meadow was bare soil. Our plant palette includes host plants for nearly every butterfly likely to occur in this region of Florida and it also includes a great many nectar plants for the area's diversity of pollinators.

From here, the trail will take visitors along the lake edge just upland of the wetland boundary. Over the past months, we've eradicated the many Chinese tallow (*Triadica sebifera*) that grew interspersed with bald cypress (*Taxodium distichum*), red maple (*Acer rubrum*) and Carolina willow (*Salix caroliniana*). We've also hand-pulled a thicket of submerged-rooted Peruvian primrose willow (*Ludwigia peruviana*) and persistent caesarweed along this edge in preparation for our native plantings. We hope to get aquatic natives installed by late spring of 2018, and they will include a wide variety of native wildflowers and woody species for pollinators and birds.

A second and larger woodland lies at the northern portion of the property. It, too, slopes upland of the lake edge, but it

rises to a higher elevation than the southern woodland and contains specimens of black cherry (*Prunus serotina*). We've had to eradicate the same invasive plants present in the southern woodland before we could start our replanting efforts. To provide a buffer between this project and the neighbor to the north, we've planted various species of woody shrubs that will provide habitat for birds and a screening hedge – Walter's and arrowwood viburnum (*Viburnum obovatum* and *V. dentatum*, respectively) and yaupon holly (*Ilex vomitoria*). We've also added more diversity to the canopy, planting less for aesthetics and more for wildlife habitat. The pignut hickories (*Carya glabra*), for example, should one day help feed the caterpillars of luna moths, and the sparkleberry (*Vaccinium arboreum*) will provide food for birds and nectar for pollinators.

Throughout the past year, Lisa and I have been blessed to work with a huge diversity of enthusiastic volunteers, Rosebud Continuum board members, and the Bishop family. Janice Puta of Ocala heard about this project and donated several hundred plants, including a great many Cooley's justicia (*Justicia pringlei*). Members of the Nature Coast Chapter of FNPS came out and supported our first public open house this past summer. Much more remains to be done before the Rosebud Continuum reaches its full mission goals, and we hope to be a part of it all throughout the years ahead. We could use your help in whatever form you have to give it. Over the next 12 months, we intend to complete the plantings and eradicate the remaining invasives. We will be managing the weeds, in some form or other, for the duration of the project. Please contact Lisa through the Pinellas Chapter FNPS or myself if you are interested.

End Note: The Rosebud Continuum is a public exhibition of sustainable living practices. It will serve as a classroom and a model for a wide variety of methods designed to reduce our footprint and make space for other living creatures. The following plant list was chosen to maximize habitat diversity, demonstrate to the public the best plants for aesthetics and wildlife value, and help the Bishops choose plants in harmony with site conditions. These plants will exist with no additional fertilizer and will not require supplemental irrigation.

About the Authors:

Craig N. Huegel, Ph.D. is a wildlife biologist, educator, consultant, and founding member of the Pinellas Chapter of the Florida Native Plant Society. He has written five books on landscaping with Florida's native plants. His sixth book, *A Plant Lover's Guide to How Plants Work*, will be published by the University Press of Florida in 2018.

Lisa Boing's love of plants, gardening and landscaping drew her to get certified through Pinellas County's Master Gardener program in 2012. She coordinates volunteer work at the Native Plant Demonstration Area at the Florida Botanical Gardens and serves on the Board of the Florida Botanical Gardens Foundation. Lisa also has a business maintaining native plant landscapes.

Rosebud Continuum – Plant List (To Date)

Woodlands

Callicarpa americana	American beautyberry
Carya glabra	Pignut hickory
Cercis canadensis	Redbud
Chionanthus virginicus	Fringetree
Cornus florida	Flowering dogwood
Halesia diptera	Two-winged silverbell
Ilex opaca	American holly
Ilex vomitoria	Yaupon holly
Justicia pringlei	Cooley's waterwillow
Liriodendron tulipifera	Tulip poplar
Lonicera sempervirens	Coral honeysuckle
Quercus alba	White oak
Quercus michauxii	Swamp chestnut oak
Quercus muehlenbergii	Chinkapin oak
Quercus shumardii	Shumard oak
Psychotria nervosa	Wild coffee (dwarf)
Sabal minor	Dwarf palm
Salvia lyrata	Lyre-leaved sage
Vaccinium arboreum	Sparkleberry
Verbesina virginica	Frostweed
Viburnum dentatum	Arrowwood vibunum
Viburnum obovatum	Walter's viburnum
Viola sororia	Common blue violet
Zamia integrifolia	Florida coontie
Zephyranthes atamasca	Rain lily

Wildflower Meadow

Aristida stricta	Wiregrass
Asclepias incarnata	Swamp pink milkweed
Asclepias perennis	Swamp white milkweed
Bacopa monnieri	Water hyssop
Boehmeria cylindrica	False nettle
Carphephorus corymbosus	Florida paintbrush
Carphephorus odoratissimus	Vanilla plant
Chamaecrista fasciculata	Partridge pea
Coreopsis floridana	Florida tickseed
Coreopsis lanceolata	Lance-leaved tickseed
Coreopsis leavenworthii	Leavenworth's tickseed
Eragrostis spectabliis	Purple lovegrass
Eryngium aquaticum	Blue-flowered rattlesnake master
Eryngium yuccifolium	Rattlesnake master
Helianthus angustifolius	Narrow-leaved sunflower
Liatris gracilis	Graceful blazing star
Liatris savannensis	Savanna blazing star
Liatris spicata	Dense blazing star
Muhlenbergia capillaris	Gulf muhly grass
Phyla nodiflora	Fogfruit
Rudbeckia hirta	Black-eyed Susan
Rudbeckia laciniata	Cutleaf coneflower (planned)
Ruellia caroliniensis	Wild petunia
Salvia coccinea	Red salvia
Scutellaria integrifolia	Skullcap
Silphium asteriscus	Starry rosinweed
Solidago fistulosa	Pinebarren goldenrod
Solidago odora var. *chapmanii*	Chapman's goldenrod
Solidago stricta	Wand goldenrod
Spartina bakeri	Sand cordgrass
Symphyotricum elliottii	Elliott's aster
Tiedemannia filiformis	Water dropwort
Vernonia angustifolia	Narrow-leaved ironweed

Above, top to bottom: The bright yellow flowers of golden canna; velvety seed pods appear after blooming; mature pods showing the nearly black seeds tucked inside. Photos by Sammy Tedder.

Plant Profile: Golden Canna (*Canna flaccida*)

Sammy Tedder

Golden canna, also called bandanna of the Everglades, can be found in most of Florida's 67 counties. These wetland plants live along the edges of rivers, ponds, swamps and in wet ditches. Their foliage provides hiding places for fish, amphibians, insects, and other aquatic life. It shades and cools the water, helping to preserve dissolved oxygen that might be lost to heating in small ponds. Some species of cannas have been shown to clean water by removing nitrogen (N) and phosphorus (P), making golden canna potentially useful in phytoremediation projects.

The flowers are a nectar source for the Brazilian skipper butterfly – also called the canna butterfly (*Calpodes ethlius*) and the leaves are a food source for the butterfly's larval stage. The canna's tall stems allow dragonfly larvae to climb above the water to find a place where they can metamorphose into adults.

Golden canna can grow up to 4 feet tall, and it has bright yellow flowers about 3 inches across. The broad vertical leaves are up to 2 feet tall and 6 inches wide with a wide base tapering to a point at the top.

Golden canna is pollinated by bees, bats, hummingbirds, and other small wildlife species. After blooming, green velvety seed pods form and then darken to a deep brown as they mature. The mature pods contain many buckshot-sized seeds that are hard and almost black in color.

In her book *Seminole Music*, ethnomusicologist Frances Densmore states that the Seminole made rattles from turtle shells, dried gourds or coconut shells partially filled with *Canna flaccida* seeds. The Creek and Miccosukee peoples also used the seeds in their rattles. According to Dan Austin in *Ethnobotany of Florida*, the Miccosukee word for golden canna is *sawakmalî:tî* and the Creek call golden canna *sáwko matihita* – both names mean "the contents of a rattle".

Above and right: The mature pods of golden canna contain many small seeds which have been used by indigenous people to make rattles. The example shown is a contemporary rattle made by the author. **Lower right:** A field of golden canna on the roadside. Photos by Sammy Tedder.

These wetland plants can be propagated by either piercing and soaking the hard seeds before planting, or dividing and planting the rhizomes from which the plants grow. Golden canna grows best in moist soil in full sun and it can be an attractive addition to moist areas of the home landscape in much of Florida.

This plant profile was adapted from The Trumpet*, the quarterly newsletter of the Sarracenia Chapter of the Florida Native Plant Society.*

Sources and Further Reading:

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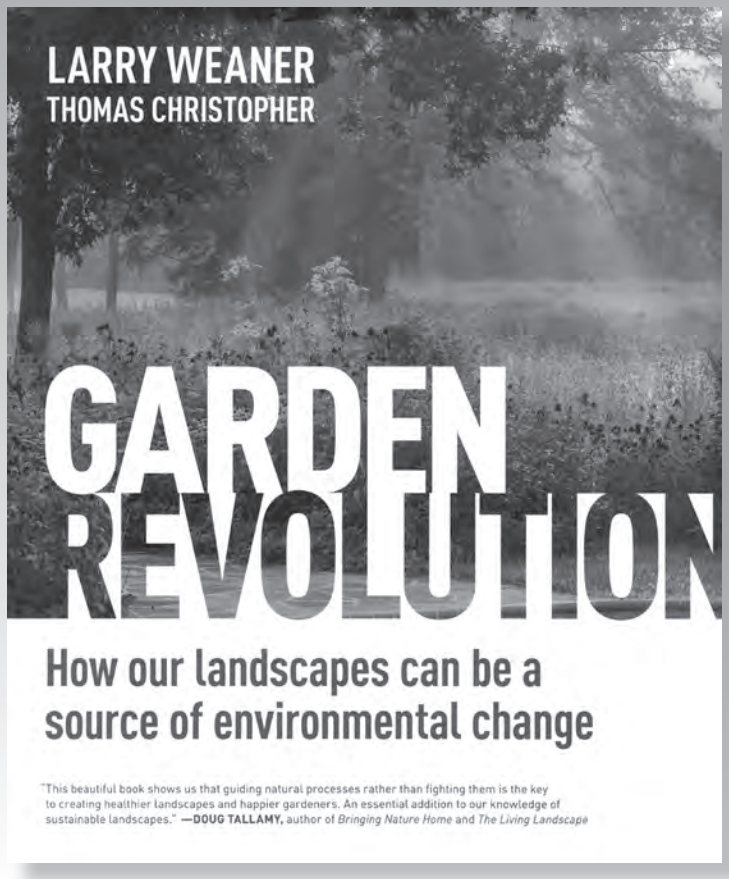
Florida Native Plant Society, online at www.fnps.org/plants/plant/canna-flaccida

University of Florida IFAS Extension, online at http://edis.ifas.ufl.edu/fp102



BOOKS of NOTE

Garden Revolution: How our landscapes can be a source of environmental change

Larry Weaner and Thomas Christopher
Hardcover: 328 pages
Published by Timber Press in 2016
ISBN-10: 1604696168

Review by Ginny Stibolt

I attended Larry Weaner's presentation at the 2017 FNPS conference and was so taken with his philosophy that I bought this beautiful book. While Thomas Christopher is listed as the coauthor, he explains that even though the point of view is Larry's, they both worked on the organization and the actual writing of the book. For this review, I continue their scheme and refer to the ideas as if they were Weaner's alone.

The book is filled with gorgeous color photos, the vast majority of which are of huge meadows – many 20 acres or more. There are studies of several meadows with photos in different years to illustrate the changes in plant populations. In fact, the best description of this book is that it's a meadow-building tutorial. While Weaner's plant palettes are for New England and the Mid-Atlantic states, there is much Floridians can learn here about how to design and maintain meadows, while reducing weeds – mostly without pulling them out of the ground.

This is accomplished in several ways, such as mowing and other cutting methods, done when it will most damage weeds, but minimize damage to desirable plants. Also key is paying attention to what the existing landscape has to offer instead of imposing an agenda on the landscape. This is characterized as a "brains over brawn" approach – spend time with a site, evaluate what is already present, and research and observe what the site was used for in the past. Then before planting a whole meadow, test your proposed plan in several ways to see what happens as you move forward. For instance, it's a good idea to test for what sprouts on its own from the seed bank and deal with those volunteers first, depending on whether they are desirable plants or not. By working with the site (including its soil), you create the meadow by working with nature. Weaner advocates not enriching the soil, but planting what will be happy in the existing soil and timing the planting so that weeds are at a disadvantage. This is a huge step beyond simply installing plants that are native to the general region.

The book is organized into three separate sections:

The Learning Process:

This section covers how important it is to really know the life cycles of plants, with special emphasis on timing, so meadow seeds can be planted at the best time for the desirable plants and the worst time for weeds. This section also includes The Garden Ecologist's Primer, which points out how landscaping strategies differ when the ecosystem is considered. It includes discussions on these topics: ecoregion, native, habitat, microhabitat, plant community, niche, novel ecosystems, generalist vs. specialist species, ecotypes, competition, succession, disturbance, r and K selected species (these relate to a plant's reaction to disturbance), colonization, senescence, and initial floristic composition. Yes, even though it's beautiful, this is a serious textbook.

Design:

The design section includes ideas for site analysis keeping the local ecology in mind, creating a master plan and a master plant list. Growth time is included in the plans and lists because Weaner suggests using vigorous annuals, biennials, and short-lived perennials that will keep out aggressive weeds for the first few years. These plants will eventually be replaced by long-lived perennials that need more time to become established.

The site analysis section includes six detailed diagrams and a number of photos of one relatively complex site. This illustrates what a thorough study really looks like and why it's important to do preliminary work so the project can be more successful in the long run.

In The Field:

This section provides specific examples of how to create prairies or meadows (and defines the difference between the two terms to be regional – meadows in the east, prairies elsewhere), creating shrublands, and even creating woodlands. The most interesting part of this section is "Setting the ecological processes in motion" because creating a relatively permanent landscape feature takes place over the years. One tactic covered in this section is locating mowed paths through the meadows so that they surround shrubby areas where sprouting or suckering is likely to occur. The mowing keeps the suckering to a minimum and contains the shrubs to a defined area.

Weaner's recommended strategy for meadows does not include pulling weeds because of the disturbance in the soil. He also claims you can cut four weeds by hand in the time it takes to uproot one plant. I love that he included the story of Rose, a client with a relatively small landscape who couldn't stop weeding. She dutifully pulled all the weeds up by the roots, which initially allowed more weeds to get a start. In looking at her landscape seven years later, Weaner realized that the plants coming up in the disturbed areas were native plants that had not been planted. So is disturbance good or bad? The answer, he admits, depends, "An ecologist would say that in a healthy landscape dominated by native plants, disturbance is good. It allows new individuals to enter the system and prevents what might be termed 'group senescence,' an overall aging of the plants within the garden. To avoid too much instability, however, disturbance events are most beneficial when small, scattered, and infrequent, like Rose pulling the occasional weed in her entry garden."

Another story called "A do-nothing attitude" related an initial meeting for a large meadow project to be installed near a new house in Connecticut. The contractors asked these questions: "Should we bring in topsoil?" Although the soil was bony and infertile, Weaner's answer was "No."
"Should we fertilize?" – "No."
"Some compost at least?" – "No."
"Do you want the field tilled?" – "No."
"What kind of irrigation do you need?" – "We don't need any irrigation."
"When do you want to plant this thing?" – "July."
After this exchange, Weaner imagined the contractors thinking – "Sure, you're the golden boy now, but if this becomes a weed field, you'll be out of here faster than a dandelion puffball in a hurricane." – so he explained his rationale. Despite their skepticism, the meadow project was a success.

I find this type of storytelling an engaging way to make a point and to make technical information more memorable.

Should Floridians buy this book? A definite maybe. I love the overall premise that landscapes should look natural and that there are ways to make this work, such as not enriching the soil, and really learning the life cycles of plants – both weeds and desirable plants. I recommend it for people who are designing native landscapes and working to install large meadows, but I think that some of his strategies might be more difficult to implement successfully in Florida. Our seasons are not as clearly defined and many of our weeds are more exuberant than those in the Mid-Atlantic states and New England. I gardened for many years in those regions, and Florida gardening was a total surprise to me when we moved here in 2004. It took all types of adjustments in my gardening methods to be successful. While I think there are many innovative ideas from this beautiful book that are worthwhile and good lessons to be learned, they will need to be adjusted for Florida. So take Weaner's advice with a grain of sugar sand to make it work for you and your Florida landscape.

About the reviewer: Ginny Stibolt is a lifelong gardener and she earned a M.S. degree in botany at the University of Maryland, but gardening is different in Florida. She's been writing about her adventures in Florida gardening since 2004. She wrote *Sustainable Gardening for Florida* (2009), *Organic Methods for Vegetable Gardening in Florida* with Melissa Contreras (2013), *The Art of Maintaining a Florida Native Landscape* (2015), and *Step by Step to a Florida Native Yard* with Marjorie Shropshire (2018) – all published by University Press of Florida. Also, she co-wrote *Climate-Wise Landscaping: Practical Actions for a Sustainable Future* with Sue Reed (2018), published by New Society Press. In addition, she manages a "Sustainable Gardening for Florida" Facebook page and writes the blog www.GreenGardeningMatters.com.

American Lotus and its Close Asian Counterpart

By Kristina Zakarkaite and Francis E. Putz, University of Florida

Fig 1. An American lotus (*Nelumbo lutea*) in full bloom. Photo by Shirley Denton.

While the word "lotus" evokes images of the Buddha, fast cars, painted porcelain, and Asian silkscreens, it also refers to a native plant that emerges from the muck on the bottom of ponds and marshes from Minnesota to Florida. The yellow-flowered American lotus (*Nelumbo lutea*) is closely related to the only other species in the genus, the pink-flowered Asian sacred lotus (*N. nucifera*). Throughout the Far East, the blossoms, fruits, and leaves of the sacred lotus have adorned porcelain and silkscreens for millennia, while its edible seeds and rhizomes figure prominently in local cuisines; dried, pickled, and other versions are also exported to markets all over the world. In contrast, most Americans only recognize our native lotus species as a wild plant and an ornamental, despite it once being a staple food for Amerindians (Swan, 2010). They ate its rhizomes fresh or dried them for winter consumption, unfurling leaves were cooked like spinach, young seeds (i.e., "alligator corn") were munched fresh, and mature seeds were dried, popped, or ground to make a high-protein flour. American wildlife such as ducks, beavers, and muskrats still relish lotus seeds and rhizomes.

Our interest in lotus was piqued when senior author Kristina Zakarkaite (KZ), who was then a first-semester freshman in a botany class taught by junior author Francis E. Putz (FEP), formulated what seemed to them to be an intriguing hypothesis about lotus evolution. After the second class of the semester, the senior professor asked the novice student about her major and her undergraduate research project. Asking such a young student about their research may seem outrageous, but efforts are being made at universities across the country to involve undergraduates in science early in their careers. KZ responded that she was a dual major in art and botany, but then admitted with chagrin that she did not yet have a research project. On a whim, FEP suggested that she contrast the cultural and ecological roles of lotus in Asia and America. When it became apparent her interest was not feigned, he went on to outline the little he knew about the subject and suggested she read up on the species.

Once KZ learned about the many uses for lotus in Asia,

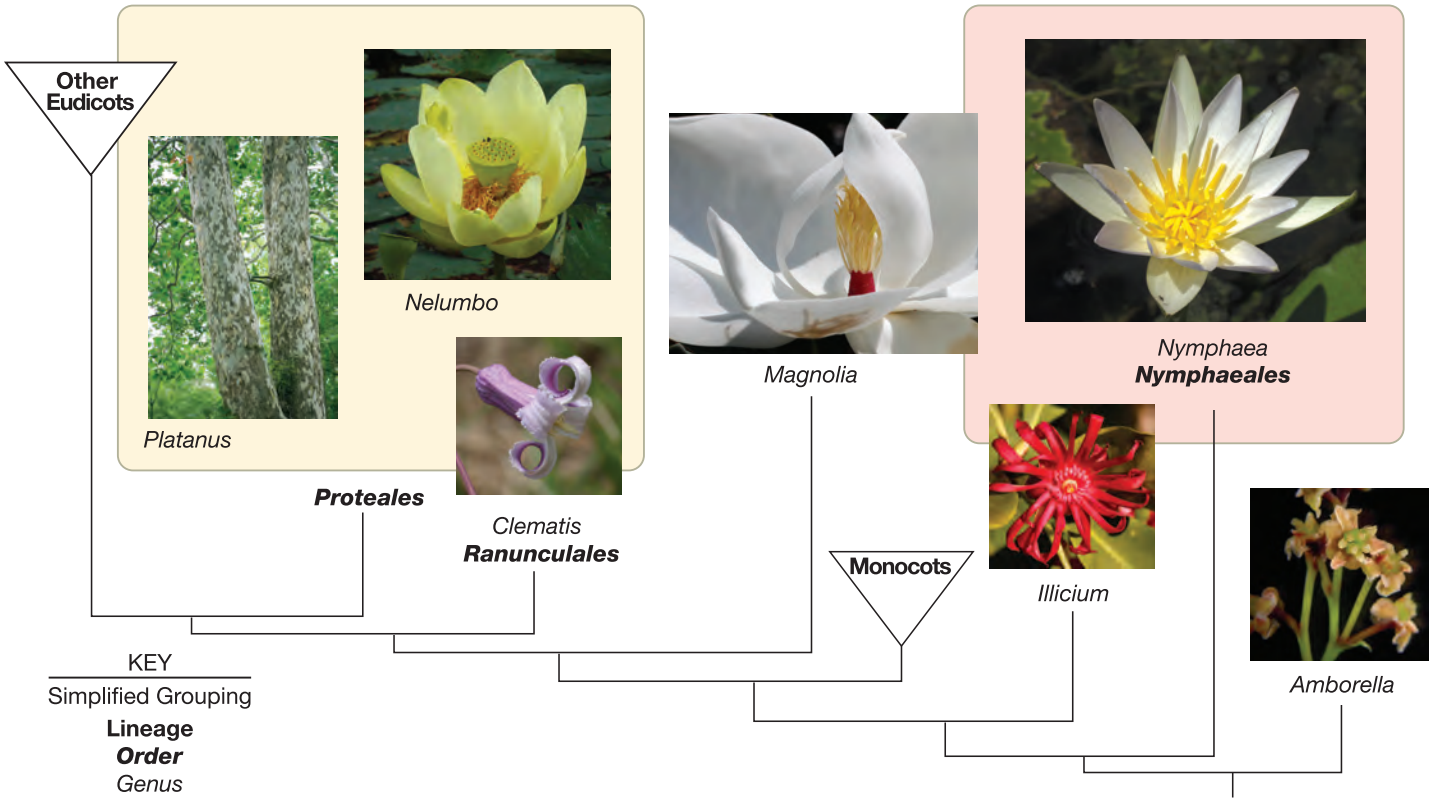


Fig 2. A simplified phylogeny consisting of indigenous Florida species. List of plant species pictured from left to right- *Platanus occidentalis*, *Nelumbo lutea*, *Clematis baldwinii*, *Magnolia grandiflora*, *Illicium floridanum*, *Nymphaea elegans*, and *Amborella trichopoda*. The latter is an understory shrub native to New Caledonia containing only a single species in the genus. Recently, phylogenetic analyses have placed it with or below other basal angiosperm groups, such as *Nymphaeales*. Photos by Shirley Denton. *Amborella trichopoda* photo by Sangtae Kim.

the capacity of its seeds to remain dormant for decades, and the ease with which the two species hybridize, she made an intellectual leap. She hypothesized that the American species was derived from seeds transported by people who colonized the Americans from Asia when they walked over the Bering Strait Land Bridge (Beringia) some 14,000 years ago. When she reported back to her professor that, instead of the project he envisioned, she wanted to pursue this novel hypothesis, FEP was stunned that such a young student would come up with such a bold idea. While he was only half convinced by the evidence she mustered in support of her hypothesis, he encouraged her to pursue the project. Here we describe the outcomes of that investigation.

First of all, it is important to clarify that although lotus shares with water lilies the emergent aquatic growth form, large round leaves, and huge flowers, the two groups are only distantly related evolutionarily and their similarities result from convergent evolution (Les et al. 1991). Plant taxonomists have long been uncomfortable about lumping lotus and water lilies into one family, but their suspicions were only recently confirmed with DNA evidence. By sequencing the hereditary code, it is now evident that the Nelumbonaceae, the family with two extant species of lotus, diverged from the rest of the flowering plants soon after flowers first appeared more than 100 million years ago (Xue et al. 2012). Remarkably, lotus counts among its closest living relatives sycamore trees in the genus *Platanus* and various Southern Hemisphere Proteaceae such as *Banksia* and *Macadamia*. In contrast, water lilies seem to have a purely aquatic ancestry that dates back to the first appearance of the flowering plants.

Similarities between the American and Asian species of lotus begin down where they root in the muck on the bottom of ponds. Both species produce fat rhizomes with huge air-filled channels (i.e., aerenchyma) arranged as elegant pinwheels. These channels facilitate the diffusion of oxygen down through the leaf stalks – which can be up to 7 feet long – through the rhizomes, and out into the roots that require oxygen to survive in the anaerobic soil. From an alimentary perspective, rhizomes of both species are packed with edible starch, vitamin C, calcium, and potassium.

Lotus propagates easily from rhizome fragments, and it is likely that Amerindians, like their Asian ancestors and contemporary Asian farmers, favored clones with tasty rhizomes, large seeds, or other preferred characteristics. The result of this type

Fig 3. Slices of lotus rhizomes showing their massive aerenchymatous canals. Photo by Kristina Zakarkaite.

of artificial selection in Asia has resulted in more than 400 named cultivars grown for their rhizomes, seeds, or flowers. If there was once similar subspecific differentiation in populations of the American lotus, those distinctions now seem lost. It is also likely that Amerindian farmers shaped the geographical distribution of lotus, a species that many tribal groups held sacred and to which they attributed magical properties (Swan, 2010).

It is easy to spot lotus from afar due to their parasol-size leaves. Both species produce round leaves with a leaf stalk emerging from the center. Lotus leaves are also remarkable insofar as they never get wet and always stay clean. The waxy cuticle that coats and protects all plant leaves is naturally hydrophobic, but lotus produces waxy dimples on which there are even smaller projections that cause water to bead up into nearly spherical droplets (Ensikat et al. 2011). These droplets are suspended on air pockets between the bumps, which makes them prone to bounce and roll; when they slide off the leaf, they take dirt and other small particles with them. Discovery of this arrangement of nano-bumps on micro-bumps,

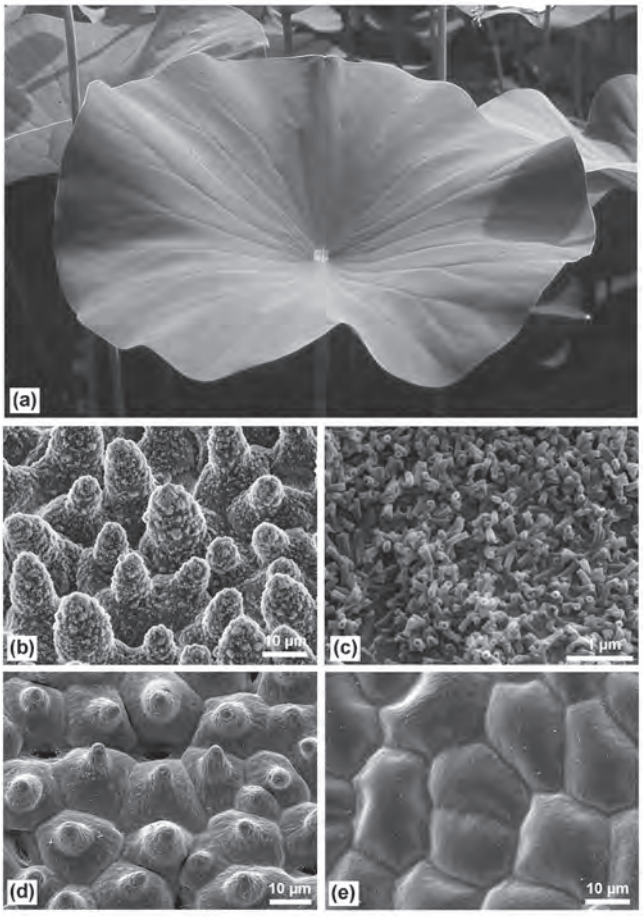


Fig 4. The upper surface of lotus leaves (a) show extraordinary microstructure (b,c). The underside (d,e), in contrast, does not and therefore exhibits little water repelling ability. Image courtesy of Hans-Jürgen Ensikat and used with permission. Copyright © 2011, Ensikat et al; licensee Beilstein-Institut. www.ncbi.nlm.nih.gov/pmc/articles/PMC3148040/

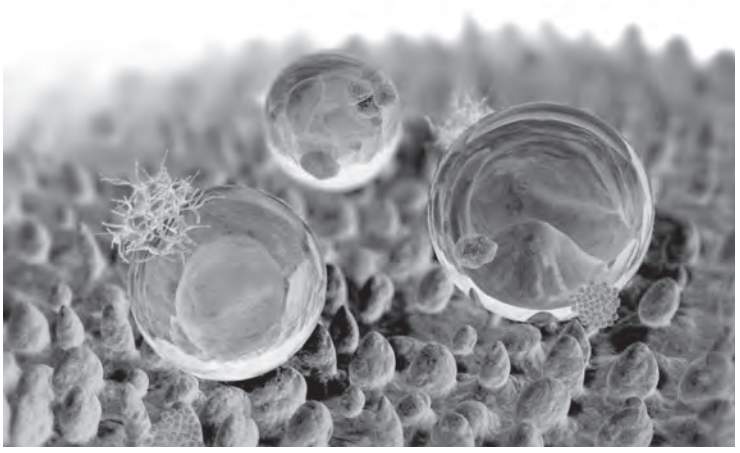


Fig 5. The "lotus effect" of superhydrophobicity – water beads up and the drops roll off, taking dirt and other particles with them. Image created by William Thielicke and used with permission of the author. http://william.thielicke.org/

which is referred to as the "lotus effect," spawned a technological revolution in engineered coatings that now serve to reduce drag on ship bottoms, prevent staining of textiles, and keep building materials dry and clean – imagine never having to wash or dry another dish, just tip sideways and re-shelve.

Both lotus species are recognizable by their plate-sized flowers, yellow in the American species and pink in the Asian. The flowers emerge during the summer months when, over their 3-4 day life spans, they change their sexual functions daily. First-day flowers are fully female with receptive stigmas that produce a sticky-sweet exudate enjoyed by many insect visitors including the chrysomelid beetles that are the syndrome pollinators (Li and Huang, 849). Second-day flowers are bisexual – the stigmas are still receptive but the anthers collectively release about a million pollen grains per flower (Li and Huang 2009). It is this abundant pollen that serves as the principal food reward for the many floral visitors. By the third day, the stigmas are dry and no longer receptive, but there is still pollen to be eaten and carried to other flowers (Dieringer, 358). But food alone is not the only benefit the pollinators derive from their nocturnal sojourns in lotus blossoms. They are also kept warm when the sun goes down, the petals close to form a chamber and the flowers continue to generate their own heat. Floral thermogenesis presumably benefits the lotus during the day by volatilizing the 1,4-dimethoxybenzene and 27 other compounds in the cocktail of fragrances that attracts pollinators (Dieringer et al. 2014). From the point of view of a cold-blooded beetle, on nights when ambient temperatures drop into the 60s, a biological thermostat set to the high 90s is likely attractive, not to mention the offer of protein-rich pollen.

Successfully pollinated lotus flowers produce large seeds

housed in tough, spongy fruits that adorn many dried flower arrangements. Young lotus seeds have a mild corn-like flavor whereas, to the authors' taste buds at least, mature seeds are quite bitter. Seeds of the Asian species are used in soups or pressed to produce a light oil. What is ecologically remarkable about lotus seeds is their longevity; seeds stored for hundreds of years can retain their viability. It is therefore easy to imagine people carrying dormant lotus seeds across Beringia when the Americas were first colonized by our species.

The final bit of evidence that KZ used to support her Amerindian-caused lotus divergence hypothesis is that the two lotus species differ little genetically. The first relevant article she discovered reported that, in a sequence of DNA that codes for proteins that participate in photosynthesis, the two species differ at only one locus. That report, coupled with the ready hybridization of the two very similar species, buttressed KZ's hypothesis until it crumbled under the weight of accumulated counter-evidence.

While the genetic evidence that KZ initially uncovered was compatible with a recent divergence of the two species (Les et al. 1991), she then found a study based on more extensive DNA sequencing that indicated that the two species have been separate for 1.5 million years, longer than humans have been a species (Xue et al. 2012). The two taxa remained similar in morphology and many other traits for all that time, despite the absence of gene flow. It was hard to doubt this DNA evidence, but KZ finally had to reject her "Amerindian introduction hypothesis" upon reading reports of lotus fossils from Montana and Wyoming that date back nearly 100 million years (Y. Li et al. 2014).

Considering the current spotty distribution of populations of the American lotus, it is hard to imagine that this species was once a staple food plant for Amerindians. To address the quandary of how lotus might have fed thousands of Amerindians, we have three suggestions. First of all, over the past 100 years, more than half of the wetlands in the range of American lotus were drained or otherwise destroyed. Second, we expect that if this species was as important as imputed from historical records, then Amerindians managed it carefully by planting, tending, selecting for clones with favorable properties, and eating the animals that might otherwise decimate their crops. Finally, in the course of our field investigation, we noticed that where water hyacinth (*Eichhornia crassipes*) or hydrilla (*Hydrilla verticillata*) are abundant, lotus is not. In the absence of these invasive exotic species, lotus may have flourished far more than it does today.

One seldom hears about rejected hypotheses, but such rejections are frequent and can be informative. Whether or not a hypothesis is finally falsified, much is learned in the process of collecting the necessary evidence. That was certainly the case for us in our venture into the historical biogeography and evolution of our lovely lotus.

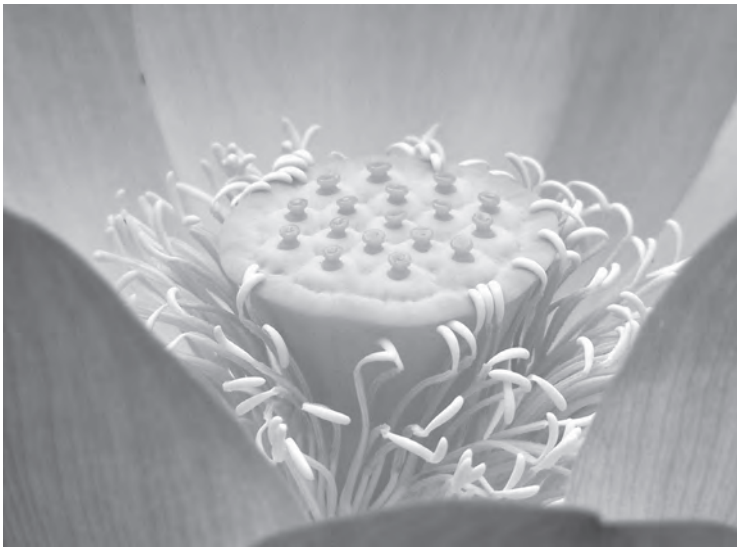


Fig 6. Bean of India (*Nelumbo nucifera*). Photo by Thomas Voekler (own work) [CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons. Used with permission of the author.

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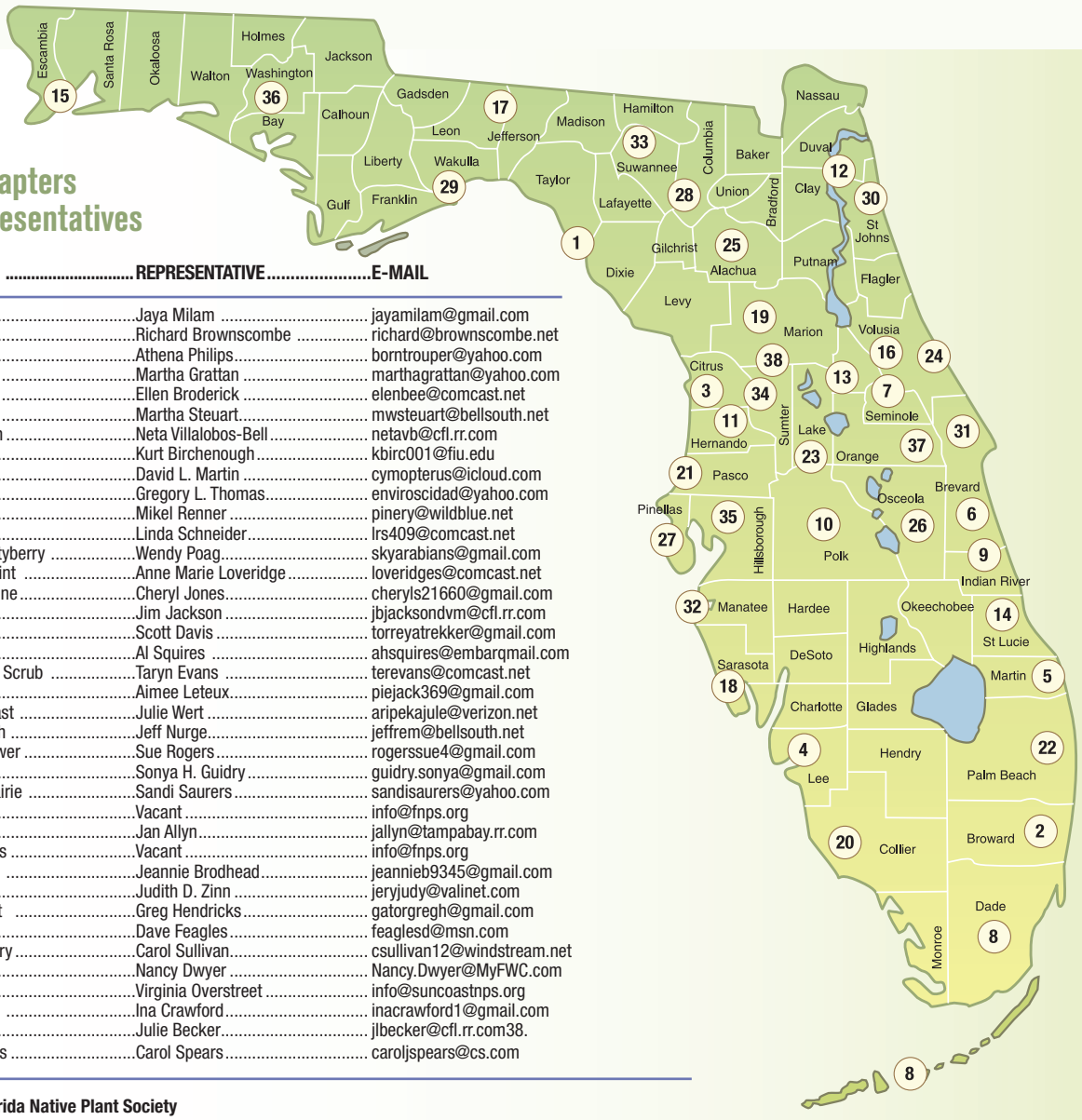

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