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CONTENTS

- 2 **Hill's Oak: The Taxonomy and Dynamics of a Western Great Lakes Endemic**
Andrew L. Hipp
- 15 **Tree Hormones and Why They Matter**
Joseph Murray
- 20 **2009 Weather at the Arboretum**
Bob Famiglietti
- 25 **An Essay on Naming Nature: The Clash Between Instinct and Science**
P. F. Stevens
- 28 **The Sand Pear—*Pyrus pyrifolia***
Peter Del Tredici

Front cover: The expanding leaves on this red oak (*Quercus rubra*) seedling exhibited a characteristic red blush on May 4, 2009, a warm, overcast, spring day. Read more about the 2009 weather conditions at the Arboretum starting on page 20. Photo by Nancy Rose.

Inside front and inside back covers: Peter Del Tredici profiles the Arboretum's majestic specimen of sand pear (*Pyrus pyrifolia*, accession 7272-C) on Bussey Hill, notable for its prolific spring bloom. Photos by Peter Del Tredici.

Back cover: Oaks (*Quercus* spp.) are notoriously challenging to taxonomists, thanks to the ready ability of oak species to interbreed. Andrew Hipp details his research distinguishing Hill's oak (*Q. ellipsoidalis*) from scarlet oak (*Q. coccinea*) and black oak (*Q. velutina*, pictured here). Photo by Andrew Hipp.

Hill's Oak: The Taxonomy and Dynamics of a Western Great Lakes Endemic

Andrew L. Hipp

Oaks afford a unique insight into the history of our landscape, flora, and vegetation. Oaks have been among the dominant trees of eastern North American forests and woodlands for approximately 10,000 years (Abrams 1992). Between 8,000 and 3,000 years ago, oaks spread to distributions close to those we observe today (Webb 1981). The landscape between the prairies of the Great Plains and the eastern deciduous forest had by that time settled into a broad transition zone in which prairie, woodland, and savanna shifted with the dynamics of climate and fire (Anderson and Bowles 1999). Some oak species in this region could persist below ground for decades as their shoots were regularly burned to the ground, growing to maturity only when a break in fire frequency allowed their stump sprouts to grow (Kline 1997). The oldest oaks still growing have borne witness to fires, changes in forest structure and composition, and substantial anthropogenic landscape changes. These old oaks sustain large numbers of mammals, birds, and insects. Blue jays, squirrels, and, previously, passenger pigeons have eaten, hoarded, and dispersed acorns in vast quantities (Johnson and Adkisson 1986; Keator and Bazell 1998; Price 1999, ch. 1), and civilization rests in part on the structural and nutritional properties of oaks (Logan 2005). It is hard for a North American



KRIS BACHTELL

The form and fall color of Hill's oak (also known as northern pin oak).

naturalist to imagine a landscape without oaks.

At the same time, oaks are remarkable for their ability to stump botanists. Even where there are only a few species to choose from, we often struggle to put a name on oaks in the field, and annotations on many herbarium specimens capture decades of disagreement. Oaks are noto-

riously promiscuous, with closely related species able to exchange genes seemingly at will. Pioneering work by James Hardin in the 1970s demonstrated hybridization among 14 of the 16 white oak group species of eastern North America, with hybridization occurring almost anywhere that different white oak species grow in sympatry (Hardin 1975). In the era of DNA-based taxonomy, hybridization has been demonstrated numerous times using chloroplast and nuclear data (Whittemore and Schaal 1991, Dumolin-Lapegue et al. 1997, Curtu et al. 2007, Cavender-Bares and Pahlisch 2009). For this reason, oaks have been described by two leaders in the field of speciation as a “worst case scenario for the biological species concept” (Coyne and Orr 2004, p. 43). Our understanding of the depth and orientation of genetic boundaries, our concepts of what constitutes a plant species, and our ability to differentiate morphologically similar species are tangled up in the oaks.

A worst case in a genus of worst cases

The Western Great Lakes endemic Hill's oak (also known as northern pin oak) (*Quercus ellipsoidalis*; Plate 1) is distinguished by the number of workers who have puzzled over its taxonomic status and proper identification (Trelease 1919; Jensen 1977, 1984; Overlease 1977, 1991; Maycock et al. 1980; Shepard 2009). Hill's oak is a member of the black oak group, *Quercus* section *Lobatae*, a New World lineage of more than 100 species, of which approximately 75 are found in Mexico and 35 in North America north of Mexico. The section is easily recognized in the field by the presence of bristles or awns on the tips of the lobes (in, for example, *Q. velutina*, *Q. rubra*, *Q. shumardii*, *Q. palustris*) or leaf apex if the leaf is unlobed (for example, *Q. imbricaria*, *Q. phellos*, *Q. pumila*). Most species in the group also mature acorns over two seasons.

In habitat, Hill's oak ranges from dry sandstone bluffs, oak barrens, and sand savannas to seasonally wet sandy soils and dry-mesic forests in clayey soils. The tree is particularly common in woodlands of northeastern Illinois. Typical Hill's oaks have deeply lobed leaves with more-or-less C-shaped sinuses; leaf undersides that



Plate 1. Hill's oak (*Quercus ellipsoidalis*), showing leaf and acorns. While the smaller leaf size and more ellipsoid acorn are typical of Hill's oak relative to scarlet oak (see Plate 2), leaf and acorn morphology are profoundly variable in Hill's oak. William Trelease (1919) wrote that the “extremes” of morphological variation in Hill's oak acorns range continuously from one to the other and have no obvious segregation on the landscape. This is a remarkable statement in light of the fact that the epithet “*ellipsoidalis*” references the acorn shape, which was instrumental in tipping Rev. Hill off to the species' distinctness. Vouchers of the illustrated specimens are deposited at the herbarium of The Morton Arboretum: A.Hipp #3096 (Hoosier Prairie, Lake Co., IN; leaf), A.Hipp & J.Schlimmann #2489 (Middlefork Savanna Forest Preserve, Lake Co., IL; acorn). Illustration by Rachel Davis.

are smooth or at most sparsely pubescent; terminal buds that are silky-pubescent on the distal (upper) third to two-thirds; and acorn caps that are smooth to sparsely pubescent on the inner surface, with scales on the upper surface that have tightly appressed tips. In these characters, Hill's oak is similar to the more widespread eastern North American scarlet oak (*Q. coccinea*; Plate 2), and in fact it was commonly



Terminal buds of Hill's oak, showing the silky pubescence on the distal (upper) half of the bud that is typical in this species. Hoosier Prairie, Lake County, Indiana.

identified as scarlet oak when first viewed by botanists in the late nineteenth century.

In 1891, Reverend Ernest J. Hill encountered a few populations in the area around Glenwood and Calumet Park, Cook County, Illinois that he identified as scarlet oak "with some misgivings." With further study, Hill judged that the leaf coloration in fall, bark texture, and acorn shape sufficiently distinguished the tree from scarlet oak to warrant its recognition as a separate species, and he published his description of the species in the *Botanical Gazette* in 1899. Subsequent to this work, many botanists accepted that Hill's oak was found throughout the upper Midwest to the exclusion of scarlet oak. However, the distinction between Hill's oak and scarlet oak is not always clear. At their morphological extremes, scarlet oak and Hill's oak are readily distinguishable. Typical scarlet oak has larger leaves and terminal buds; acorn cap scales with broad, glossy bodies and tips tending to be narrow and somewhat elongate/acuminate; and concentric rings of pits around the exposed (stylar) end of the acorn nut that appear as though they were scratched with an etching needle or burned into the acorn. Hill's oak has smaller leaves and terminal buds; acorn cap scales with dull or pubescent bodies and relatively short apices; and usually no rings around the tip of the acorn cap, occasionally one or two small rings. But these characters overlap in the greater Chicago region, espe-

cially northwestern Indiana, and as a consequence the taxonomy of these two species has remained in flux.

We began a study at The Morton Arboretum in 2005 to investigate whether Hill's oak, scarlet oak, and the widespread black oak (*Quercus velutina*; Plate 3) are genetically distinct from



Plate 2. Scarlet oak (*Quercus coccinea*), showing leaf and acorns; detail of the stylar end of the acorn illustrates the concentric rings typical of this species. While typical scarlet oak does possess these rings, and typical Hill's oak does not, we have found several specimens of Hill's oak that have one ring or, less commonly, two concentric rings of pits at the stylar end of the acorn. In Hill's oak, these rings are mostly solitary when present, 2.75–3.5 (–5) mm in diameter, but in scarlet oak, they are commonly 2 or more and greater than 3.5 mm in diameter. Vouchers of the illustrated specimens are deposited at the herbarium of The Morton Arboretum: A.Hipp & C.Kirschbaum #2627 (Wayne National Forest, Lawrence Co., OH; acorn largely enclosed in cupule, leaf and branch with immature acorns), A.Hipp #3107 (Tinley Creek Forest Preserve, Cook Co. IL; mature acorn, side view and stylar end detail). Illustration by Rachel Davis.



Acorns of Hill's oak, illustrating the tightly appressed acorn cap scales that distinguish the species from black oak. Striations on the acorn body are not uncommon in Hill's oak, but also not the rule. Acorn shape in Hill's oak is highly variable. Talltree Arboretum, Porter County, Indiana.

one another. My primary collaborator in this project, Jaime Weber, and I have sampled oaks from 58 sites (Figure 1) and genotyped nearly 700 Hill's and black oaks as well as populations of scarlet oak from Missouri, southern Illinois, southern Ohio, and upstate New York, and of the related species red oak (*Q. rubra*), Shumard's oak (*Q. shumardii*), and pin oak (*Q. palustris*).

We are currently investigating three basic questions. First, are Hill's oak and scarlet oak genetically distinct from one another? Do they show the genetic separation we expect of distinct species? Can we use genetic data to identify morphologically problematic populations

in northwestern Indiana and southern Michigan that confound our efforts to understand the natural distribution of Hill's oak and scarlet oak? Second, do local populations of Hill's oak and black oak exhibit gene flow, and does genetic intermediacy between these species correlate with morphological intermediacy? Finally, what is the evolutionary history of black oak section members, and what can this history tell us about the process of oak diversification?



Plate 3. Black oak (*Quercus velutina*), showing leaf and acorns. The loose apices of the acorn cap scales in typical black oak give the cap a fringed appearance clearly visible in the field. In both Hill's oak and scarlet oak, the acorn cap scale apices are more nearly appressed to the underlying scales, giving the cap a smooth appearance. An important but less recognized character for distinguishing black oak is the pubescence on the inner surface of the acorn cap, which is dense and matted in black oak only (illustrated in Hipp et al. in press). Vouchers of the illustrated specimens are deposited at the herbarium of The Morton Arboretum: A.Hipp #3087 (Hoosier Prairie, Lake Co., IN; leaf), J.Hitz & A.Hipp 100505-13 [TAL-013] (Taltree Arboretum, Porter Co., IN; acorns). Illustration by Rachel Davis.



Growing in a forest understory, this seedling of scarlet oak (left) shows relatively deep lobing of the leaves compared to those of a black oak seedling (right). Chemung County, New York.

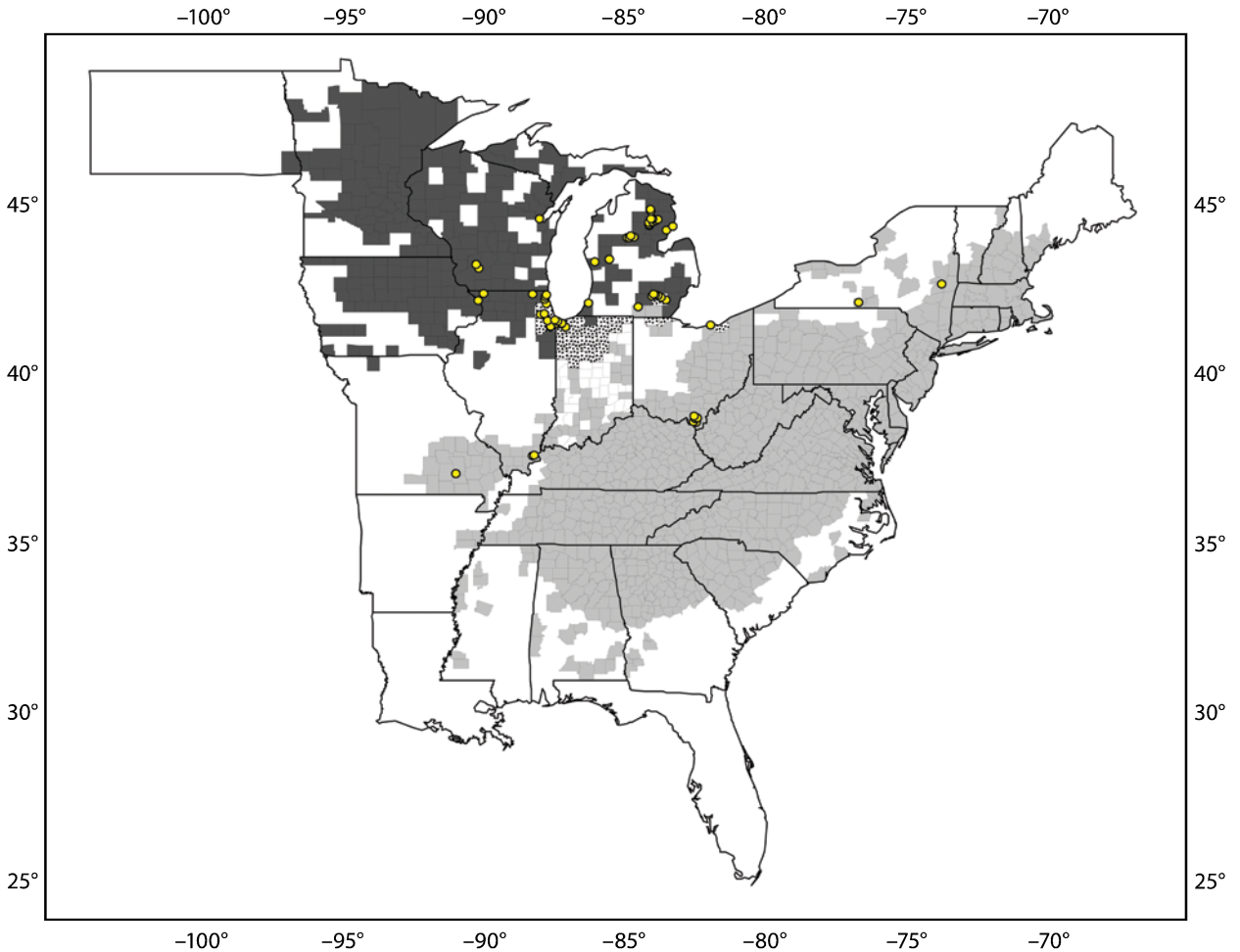


Figure 1. Map of species distributions, with sampling localities. The distribution of Hill's oak (*Quercus ellipsoidalis*) is mapped in dark grey, the distribution of scarlet oak (*Q. coccinea*) in light grey. Speckling indicates counties in which both species have been reported. Dots indicate sites where species were sampled for the current study. Note that only pin oak (*Q. palustris*) was sampled from the northern Ohio locality. Base map adapted from Hipp and Weber 2008, with Indiana distribution according to Biagi and Jensen 1995.

Hill's oak and scarlet oak: two different gene pools

We began our work uncertain as to whether Hill's oak and a genetically distinct scarlet oak were both present in the Chicago region. We also did not know whether we would be able to distinguish closely related species at all using genetic data. Previous workers in the region had found that microsatellite data, which is generated by surveying the genome for rapidly evolving repetitive DNA regions, is not consis-

tently able to distinguish such species as white oak and its relatives (Craft and Ashley 2006) or members of the black oak group (Aldrich et al. 2003). We decided to utilize the amplified fragment length polymorphism (AFLP) technique to genotype trees in this study. The AFLP approach is a shotgun-type approach used for DNA fingerprinting and genome scanning. The method entails cutting the genome of an organism into a large number of pieces at arbitrary points in the genome, then using the size dis-

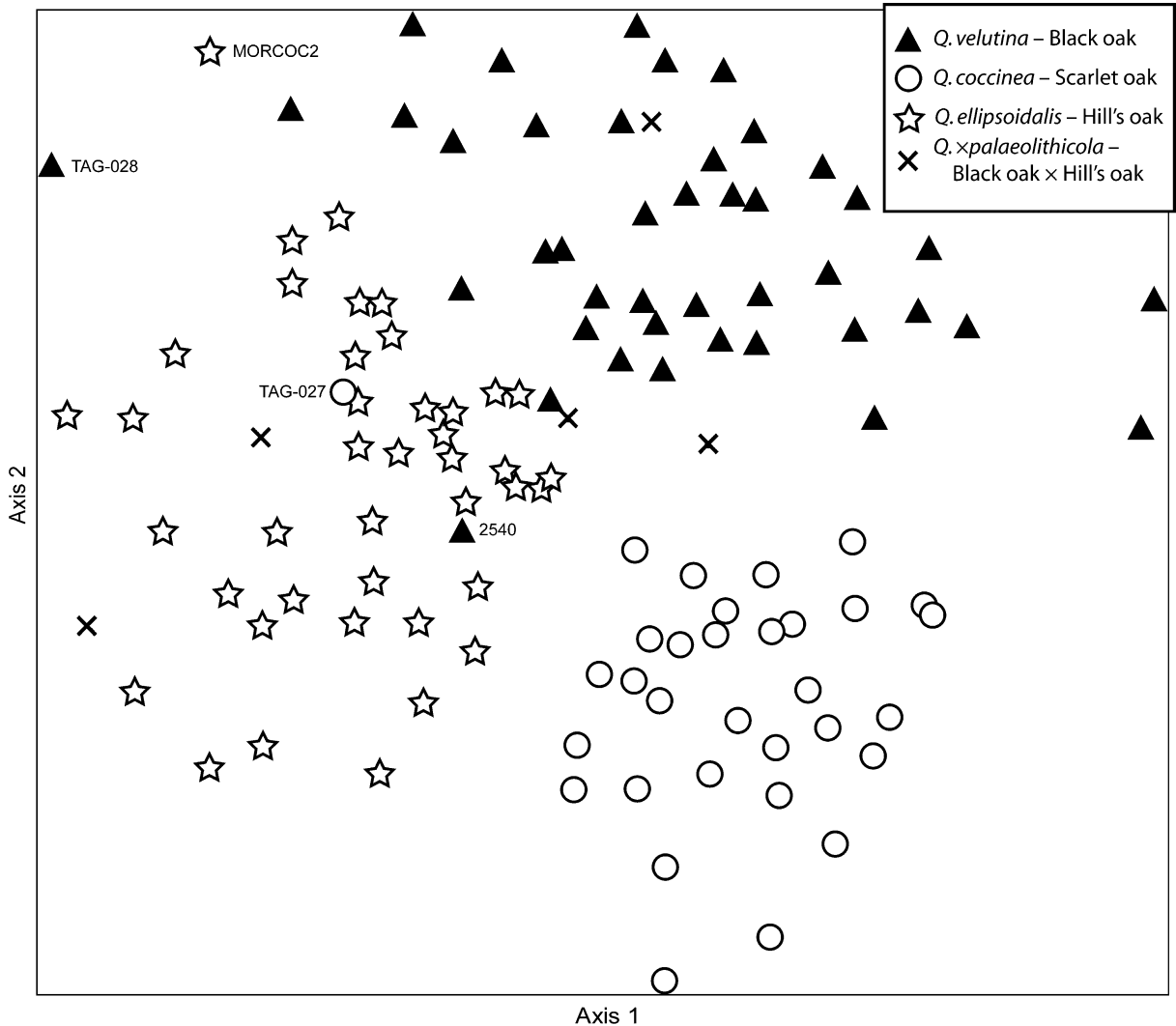


Figure 2. Two-dimensional ordination of 120 individuals representing *Quercus coccinea*, *Q. ellipsoidalis*, *Q. velutina*, and *Q. ellipsoidalis* x *Q. velutina* [*Q. x palaeolithicola*]. The ordination represents the best two-dimensional spatial representation of the genetic distances among individuals. Stated another way, each point on the figure represents a single genotyped oak tree, and the relative proximity between points represents the relative genetic similarity between trees. Ordination methods and voucher numbers are reported in Hipp and Weber 2008.

ANDREW HIPPE



Scarlet oak trunk, illustrating the planed-off appearance of the bark ridges, reminiscent of (though less pronounced than) red oak. Shawnee National Forest, Gallatin County, Illinois.

tribution of the DNA fragments to estimate genetic similarity between organisms. The disadvantages of AFLP data relative to microsatellite and DNA sequence data is that without directly sequencing AFLP markers, one generally has to assume that markers of a given length are identical by descent and that each marker represents a gene region independent of all others sampled, in which we can identify alleles that are present but not alleles that are absent. These facts render the data less useful for population genetic studies than microsatellite data, but the ability to sample large numbers of genes across the entire oak genome is desirable if we are to detect genetic differentiation even in the presence of interspecific gene flow.

All analyses we have conducted demonstrate a strong separation of scarlet oak from the other species investigated, stronger than the separation between Hill's oak and black oak (Figure 2). It is important to note that genetic divergence alone does not make a species. It has long been recognized that there can be strong genetic differentiation among populations within species (Ehrlich and Raven 1969). However, when genetic divergence between two putative species exceeds genetic differentiation between other closely related taxa recognized as being distinct at the species level, and when this differentiation is associated with geographic distance (allopatry; Figure 1), most biologists are inclined to recognize the taxa as distinct species. The divergence between scarlet oak and Hill's oak must be explained either as divergence between two species or as genetic divergence within a single, wide-ranging species. Although geographic distance may play a role in the strong separation between these two species, we have found in follow-up analyses (Hipp and Weber 2008; Hipp et al. unpubl.) that



Leaf of Hill's oak, illustrating the deep lobing typical of this species and scarlet oak. This specimen (TAG-027, housed at the Herbarium of The Morton Arboretum) genotypes decisively as Hill's oak, but morphologically it appears closer to scarlet oak (see discussion in text of article). Talltree Arboretum, Porter County, Indiana.



Foliage of a putative hybrid between Hill's oak and scarlet oak. This specimen (TAG-030, housed at the Herbarium of The Morton Arboretum) is one of the very rare specimens in our study that genotypes as a hybrid between Hill's oak and scarlet oak. These specimens bear further study. Talltree Arboretum, Porter County, Indiana.

there is little association between genetic differentiation and geographic distance in black oak across a similar geographic range. When we sample Hill's oaks of northwestern Indiana and southern Michigan that are morphologically similar to scarlet oak (e.g. Figure 2, individual TAG-027), for the most part they do not appear

to be genetically similar to scarlet oak, though the genotypes of a small number of samples we have collected in northwest Indiana suggest that scarlet oak may be present in that area. It is significant that we find very few individuals with genotypes intermediate between Hill's oak and scarlet oak. Naturally-occurring scarlet oak also appears to be rare in the range of Hill's oak, with a few exceptions. First, as indicated above, our data suggest that scarlet oak may be present in northwest Indiana, based on a few specimens that are genetically intermediate between Hill's oak and scarlet oak. However, the one specimen we sampled from northwest Indiana that appears morphologically to be unambiguous scarlet oak (TAG-027) genotypes as pure Hill's oak, and results at other sites where scarlet oak is not present (e.g., central Wisconsin) suggest that occasional genetic assignment discrepancies between Hill's oak and scarlet oak may be a consequence of genetic similarity between the two species. Our findings on this bear more detailed follow-up work. Second, we have genotyped a few trees from a stand of scarlet oaks and other southern Illinois trees previously reported from Tinley Creek Forest Preserve, Cook Co., IL (Shepard 2005). Scarlet oaks from this site are the only trees in our study to genotype as pure scarlet oak in the Great Lakes region, with no evidence of introgression from Hill's oak or black oak. However, they appear to have been planted in the twentieth century, as they occur on former oldfield habitat (pers. obs.). Moreover, smaller trees from an adjacent

forest margin genotype as scarlet oak as well, though with minimal evidence of introgression from Hill's oak, and may be natural offspring of these introduced trees. These facts notwithstanding, the strong genetic disjuncture we see between Hill's oak and scarlet oak gives us a great deal of confidence that the morphological intermediacy between them (Shepard 2009) has more to do with intraspecific morphological variation than with gene flow between them. Hill's oak and scarlet oak are distinct species.

Black oak and Hill's oak: gene flow, but not as much as you might think

Having determined that Hill's oak and scarlet oak are genetically distinct from one another, we were interested in understanding the source of genetic similarity between black oak and Hill's oak. In northern Illinois, Wisconsin, and Michigan, distinguishing these two species from each other is not always straightforward. As is the case with Hill's oak and scarlet oak, specimens that lie at morphological extremes are easy to identify: typical black oak has large, densely pubescent terminal buds; acorn caps with loose scales and dense, matted pubescence on the inner surface; and leaves that are often pubescent, even roughly so, tending to be less deeply lobed than those of Hill's oak. However, morphological intermediates are not uncommon (though with good material they are less common than people may suspect), and our first thought was that morphological intermediacy might be predicted well by genetic interme-



Inner surface of a black oak acorn cap (left) shows the matted pubescence typical of the species while the inner surface of a Hill's oak acorn cap (right) is typically hairless.

ANDREW HIPPI



Acorn of black oak, illustrating the loose acorn cap scale tips typical of this species. Talltree Arboretum, Porter County, Indiana.

diacy. Our attempt to place morphologically intermediate individuals on our ordinations suggests something different: specimens with mature winter buds and/or acorns as well as reasonably intact leaves and that nonetheless have characteristics of both Hill's oak and black oak genotype across a wide range of the two species rather than in a position intermediate between them (Figure 2). Other researchers have found similar discrepancy between morphological and molecular estimates of admixture (e.g., Craft et al. 2002, González-Rodríguez et al. 2004), which may be a product of the complex history of crosses and back-crosses expected in a group of outcrossing, readily hybridizing species like the oaks.

Subsequent analysis of our full set of sampled individuals demonstrates a few misclassifications between black oak and Hill's oak, i.e., incongruence between our identifications based on morphology and the population assignments based on genetic data: 14 black oak out of 286 sampled have > 0.20 assignment to Hill's oak in a commonly used Bayesian population genetic analysis approach. This mismatch between genetic and morphological species assignments is a hallmark of introgressive hybridization and has been reported previously in oaks (Cavender-Bares and Pahlisch 2009), and the presence of such individuals supports the hypothesis of gene flow between the two species. It is remarkable, however, that we find so little genuine misclassification or evidence of genetic admix-

ANDREW HIPPI



Branch of black oak, illustrating the densely pubescent buds typical of the species. Black oak has distinctive yellow petioles at some sites, as illustrated here, but that character is not reliable in much of the range of the species (though in *The Trees of Vermont* by Burns and Otis (1916), petioles of black oak are described as "stout, yellow, 3 to 6 inches long"). Talltree Arboretum, Porter County, Indiana.

ture between black oak and Hill's oak. Our findings build on those of a now-classic study of European oaks (Muir et al. 2000) in demonstrating that while oaks do hybridize, there are enough barriers to interspecific gene flow to make oak taxonomy a meaningful enterprise.

Phylogeny of the black oaks: a little information, a lot to learn

Our work going forward is aimed at understanding how these species and their relatives are related, and how contemporary gene flow and evolutionary history interact to define the limits of today's oak species. Utilizing a larger AFLP dataset and species sampling, we have found that Hill's oak and scarlet oak are sister



View from High Knob, overlooking a forest of white and scarlet oak. Shawnee National Forest, Gallatin County, Illinois.

species, meaning that they share a more recent common ancestor than either shares with black oak, red oak, pin oak, or any other species. The morphological overlap we see between Hill's oak and scarlet oak suggests that the two species may have inherited a similar pool of characteristics from a recent common ancestor, though these characteristics were inherited in differing proportions.

This finding is particularly interesting in light of the distribution of Hill's oak and scarlet oak. Hill's oak is the only oak species endemic to the Great Lakes region (Abrams 1992) and is distributed almost exclusively in glaciated terrain. It is tolerant of disturbance and has been characterized as the most drought-tolerant of the black oak species (Coladonato 1993), though it appears to be less common than black oak in the driest sand soils of northern Illinois. Its geographic range also overlaps closely with the distribution of dry soil oak savannas in the Great Lakes region (Will-Wolf and Stearns 1999). Scarlet oak, on the other hand, is distributed predominantly south of the edge of the ice sheet at the last glacial maximum. While also tolerant of disturbance and favoring dry sandy or gravelly soils, scarlet oak is not uncommon in mature forests in more mesic soils (Carey 1992). Given the broad geographic extent of scarlet oak and the compressed distribution of hardwood forests during the glacial maximum (Delcourt and Delcourt 1984), these two species likely co-occurred for at least a portion of the Pleistocene. Why, then, has Hill's oak migrated into postglacial environments while scarlet oak is largely confined to unglaciated terrain? It may be that differences in cold tolerance between the two species govern their relative distributions. Hill's oak may also be more tolerant of disturbance or of higher pH or finer soil texture. If so, it may have been more able to take advantage of newly opened territory as the vegetation of the savanna regions around the Great Lakes shuffled around rapidly following glacial retreat. This capacity to respond to relatively rapid environmental change may bode well for Hill's oak in the future. In the shorter term, our growing understanding of oak evolutionary relationships and ecology should allow us to address basic questions about oak

distribution and speciation, and guide predictions about how tree species will respond to future climatic and environmental changes.

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Tree Hormones and Why They Matter

Joseph Murray

Trees are the oldest, largest, and perhaps the most complex organisms on earth. Increasingly, society has moved beyond simply appreciating trees for the beauty and shade they offer, and now recognizes the significant societal, environmental, and economic benefits trees provide. These benefits can be especially important in urban areas, yet many urban sites present very difficult situations for growing trees. Most tree species should be able to live and provide benefits for several hundred years, but urban trees—often plagued by poor soil, restricted root zones, and limited care—rarely achieve even a fraction of their potential life spans. The more we (arborists, city foresters, growers, etc.) know about the biology of trees, the better we will be able to apply proper arboricultural practices to help trees help themselves.

Plant hormones and their effect on tree behavior is an often overlooked aspect of arboriculture. Plant hormones—generally defined as substances produced in very small amounts in the plant that influence the plant's physiological processes—play a crucial role in helping the plant to make adjustments in a changing environment. Knowing more about how plant hormones work in trees helps in understanding the implications of such common arboricultural practices as pruning, planting, fertilization, and irrigation.

What Do We Know About Plant Hormones?

Prior to 1950 in the United States, this article would only have addressed two hormones, auxin and ethylene, which were then considered responsible—by their presence, absence,



The hormone pathway runs from roots to branch tips in trees such as this *Stewartia pseudocamellia*.

concentration, or interaction—for everything happening in trees. Today, most plant science textbooks describe five major plant hormones: auxin, cytokinin, gibberellins, abscisic acid, and ethylene. However, there are more than five hormones in plants and research is ongoing.

Plant hormones present a number of challenges to the physiologists attempting to understand how they operate. Plant hormones are produced, and are active, in very small concentrations. At different times during the growing season, different parts of the plant produce specific hormones that influence dis-



NANCY ROSE

Hormones and Tropisms

An interesting example of a hormone causing a plant response is auxin's role in phototropism. A tropism in plants is any growth response resulting in the curvature of a plant organ toward or away from stimuli. Phototropism in plants typically consists of new growth in the shoot system growing toward light. Light striking the side of new growth at the end of branches stimulates the tissues to produce auxin, which then migrates to the opposite (dark) side of the stem where it triggers a physiological response loosening longitudinal cell walls, allowing those cells to expand in length, thus resulting in the curvature of the stem toward the light. Similarly, gravitropism also results in the curvature of the new growth in the root system downward to gravity in response to the unequal cell expansion in the tissue just behind the root tip. In addition to light and gravity, there are many other forms of stimuli that elicit a growth response.

This *Hippeastrum* exhibits phototropism—plant growth bending toward light. Charles Darwin was one of the first to research the mechanics of phototropism and, with his son Francis, published a summary of their observations in the book *The Power of Movement in Plants* in 1880. Later researchers identified auxin as the plant hormone involved in phototropism.

tant tissues that are receptive for brief periods of time. Furthermore, the same hormone may cause two different responses in the same receptive tissues, depending upon the concentration of the hormone.

Hormones are signal transducers, converting an environmental stimulus into a physiological or anatomical response. As an example, let's look at how sunlight makes roots grow in the spring, via a simple pathway using the plant hormone auxin. It makes sense for a tree to invest resources into the root system before the shoot system, so early in the spring sunlight on the shoot apical meristem (bud) and young leaves results in these tissues producing auxin, which travels down to the roots. Hormones in plants may travel throughout the plant but will only affect tissues composed of cells that have special receptors to receive that particular hormone. These target cells may perform a number of functions in response to the arrival of the plant hormone. In a physiological response

similar to that described for phototropism (see textbox), auxin stimulates cells at the root tips to release hydrogen ions into the surrounding cell walls. In response to the decreasing pH, enzymes become activated and begin loosening bonds between cellulose microfibrils, thus softening the cell walls. Inside the plant cell is an organelle, the central vacuole, full of water that is continually pressing against the cell wall resulting in turgor pressure. The collective action of softened cell walls expanding in response to the central vacuoles results in the elongation of the root tips. The signal transduction is complete. The hormone auxin allowed the tree to translate an environmental stimulus into a physiological and anatomical response. Simply put, sunlight made roots grow.

The Auxin-Cytokinin Pathway

Many gardeners are familiar with a common technique to produce bushier plants; by simply pinching off the end of a growing stem,



Removal of the branch tip (center of photo) disrupted the auxin-cytokinin pathway, allowing lateral shoots to develop just below the removal point.

there is a proliferation of branch development below the area that was removed. This growth response demonstrates what happens when the auxin-cytokinin pathway is disrupted.

The downward flow of auxin creates a pathway from the terminal buds to the root tips. As mentioned, the auxin acts as a signal transducer, notifying the roots that it's spring and it would be in the best interest of the tree to begin growing roots for the season. In addition to growth, the tissues in the root tips produce the hormone cytokinin. Cytokinin, like auxin, is going to stimulate growth as well, but in a different location—at the ends of the very branches that originally established the auxin pathway. Each spring, the auxin-cytokinin pathway promotes the timely growth of the root and shoot systems.

Like a male insect following a pheromone trail produced by a receptive female insect, cytokinin follows the increasingly stronger gradient of auxin directly to the shoot tips

responsible for the auxin's production. Left out of this pathway are the numerous lateral buds, especially those near the end of the branch. Without receiving the spring wake-up call from cytokinin, these lateral buds become dormant. Although they are no longer visible at the surface, each year the dormant buds move outward with the vascular cambium so that they remain close to the surface. Should something happen to disrupt the auxin-cytokinin pathway, then they may emerge and grow into branches, setting up their own auxin-cytokinin pathways with the root system.

It's also important to recognize that there are specific enzymes located at the shoot and root tips to destroy the arriving hormones after they have had their effect. These hormone-destroying enzymes are produced in the same tissue near the shoot and root tips. In the root tips, an enzyme is produced that will destroy auxin, just as in the shoot tips, an enzyme is made to destroy cytokinin. Should these enzymes not perform their tasks, the concentration of hormones will increase and cause a different response in the receptive tissues.

Common Tree Care Practices and the Impact of Hormone Pathways

Knowing that plants have internal mechanisms helping them with an ever-changing environment should make us pause and attempt to understand what is happening in the plant before beginning to actively “care” for the plant. Sometimes our efforts at achieving short term goals (e.g., darker green foliage, more growth, controlled shape) may be aggravating the tree's ability to achieve optimal health. Trees' hormone pathways are involved in the arboricultural practices described below:

Transplanting

Regardless of how carefully balled-and-burlapped or container-grown trees are transported and installed, some roots will be damaged and die. The roots that are particularly susceptible to damage are the very fine root tips. And it is these same roots that are to produce cytokinin and transport it up to the shoot tips to stimulate elongation of branches. This is why newly transplanted trees are so slow at developing significant shoot growth during

NANCY ROSE



Auxin accumulates at the base of stem cuttings, stimulating root initiation. Exogenous auxins, in the form of rooting powders or dips, are often applied to the bases of woody plant stem cuttings before sticking in propagation beds (rooted *Microbiota decussata* cuttings seen here).

the first year or two after transplanting. The loss of the root tips also means the loss of the ability to produce the auxin-destroying enzymes. As a result, the auxin concentration increases until the surrounding tissue responds by generating adventitious root growth. This kind of root proliferation can be observed when an African violet leaf stem is placed in water. Auxin moves down the base of the stem until it builds in concentration at the point the stem was severed from the plant, changing stem tissue into actively growing root tissue.

Fertilization

So long as there is adequate nitrogen available in the soil, tree roots will continue producing cytokinin at the appropriate times of the year in response to the establishment of the auxin pathway. However, when the nitrogen level is inadequate, the root system will suspend cytokinin production. Auxin will then

be the dominant hormone directing the majority of resources to continue root growth, and a larger root system enables a search through a greater soil volume for nutrients. In nutrient poor soil, it is in the tree's best interest to invest its limited resources in root growth and not shoot growth. But if a fertilizer is applied, the root system is fooled into thinking it is in a nutrient-rich environment and the production of cytokinin increases, resulting in a larger shoot system relative to the root system. If this nutrient subsidy ceases, the tree is caught with a shoot system that cannot be sustained with the current root system.

Irrigation

Cytokinin also functions in the opening of stomata on the underside of leaves, allowing the steady movement of water from the roots to the leaves. The arch-rival of cytokinin is another root-derived hormone called abscisic acid. Abscisic acid is responsible for the closure



COURTESY OF BOB MUGAAS

When trees receive environmental subsidies, such as supplemental water from lawn irrigation systems, their internal regulatory mechanisms can be disrupted resulting in imbalanced root-to-shoot growth.



Topping, an improper pruning practice in which tree trunks and major branches are drastically cut back, results in a proliferation of weakly attached lateral shoots at the pruning points.

of the stomata when there is not enough soil moisture to perform photosynthesis. As long as the fine roots are in contact with soil and able to absorb water, cytokinin is being produced and traveling to the leaves to keep the stomata open. Should the soil begin to dry and soil particles pull away from the roots, the root system will produce abscisic acid and send it to the foliage to shut the stomata. Periodic episodes of landscape irrigation disrupt this internal regulatory mechanism, possibly placing those irrigated trees at risk for more severe damage. If periodic irrigation stops (perhaps from failure of an irrigation system or institution of municipal watering bans) the trees are suddenly exposed to drought conditions made even more acute because the shoot system has developed at a faster pace than the root system.

Improper Pruning Cuts or Storm Damage

Similar to the response observed in trees following transplanting, the loss of shoot (branch) tips will also disrupt the auxin-cytokinin

pathway. Should the shoot tips be removed, the timely production of auxin and its transport to the roots will not occur in the spring. This means the cytokinin produced in the roots will not know where to travel to stimulate the growth at the end of the branch. The concentration of cytokinin will increase at the point where the branch broke or was cut because the tissue responsible for producing the cytokinin-destroying enzymes is gone. As a result, cytokinin will spread through this new truncated terminal end of the branch, finding and releasing the latent buds. This is why there is a proliferation of watersprouts emerging at the end of branches damaged by storms or by the ill-advised practice of topping trees.

Lessons Learned

Trees have existed for over 300 million years. The evolution of a hormone system allowed early plants to deal with a changing environment and to coordinate their parts in time and space. And for venerable trees, these hormone systems are particularly important. As caretakers of trees in urban areas, it is our duty to first understand these subtle internal mechanisms before blithely applying a treatment that we believe is in the tree's best interest.

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2009 Weather at the Arboretum

Bob Famiglietti

As in 2008, greater than normal rainfall occurred in 2009, resulting in optimum soil moisture conditions at the Arboretum. Excellent growth rates were recorded on a vast majority of our woody plants.

JANUARY was colder than normal. The minimum temperature dropped to at least 28°F on every night, a rare occurrence. Readings of -1°F were recorded on the 15th, 16th, and 17th, the low for the year. Three storms that each deposited about 6 inches of snow left a persistent snow cover on the ground. Snow total for the month was 21 inches.

FEBRUARY was mild and dry with only 7 inches of snow, six of that coming on the 3rd. The relative warmth reduced a foot of accumulated snow on the ground at the beginning of the month to all but a trace by the end of the month. February's high temperature of 60°F was reached on the 27th.

MARCH had average temperatures and produced only 10 inches of snow. A temperature of 61°F occurred twice, and the snow pack melted by mid month.

APRIL was a month of extremes. It began cool, as low temperatures dropped into the 30s for thirteen days. Our last freeze occurred on the 13th when it hit 32°F. Temperatures soared to the other extreme by the end of the month. Our first day over the 70°F mark arrived on the 24th, making it to 71°F. It reached 86°F on the 25th and 26th and then soared to 95°F on the 28th, an amazing leap from the freezing temperature barely two weeks earlier. This was the highest temperature since June 2008, and also turned out to be the high for the year. Rainfall was 4.13 inches for the month.

MAY was warm, cloudy, and dry. Even though rain was measured on fourteen days, it only totaled 2.76 inches for the month. Weather conditions for the Arboretum's annual Lilac Sunday event on May 10th were extremely windy, with gusts over 40 miles per hour. A high of 91°F was reached on the 21st, the only reading in the 90s for May.

JUNE had eighteen consecutive days with below normal temperatures (8th–25th) finishing almost 5°F below normal for the month. It was the third coldest June in 183 years of Boston weather-keeping records. Clouds were persistent and rain was measured on nineteen days with traces on four others. Precipitation was 3.99 inches for the month and there were only six days when no water was detected in our rain gauge. A frequent east wind kept us cloudy, cool, and damp. These cool, damp, early summer conditions made it an excellent year for post-transplanting establishment of new plants in the collection; little supplemental watering was needed. On the negative side, the cool, damp weather exacerbated a widespread outbreak of the late blight fungus (*Phytophthora infestans*) in the Northeast. Late blight attacks plants in the nightshade family (Solanaceae) and is the fungus that was a major factor in the Irish potato famine of the 1850s. Farmers and home gardeners in the region had to destroy tomato and potato crops to prevent the spread

Arnold Arboretum Weather Station Data • 2009

	Avg. Max. (°F)	Avg. Min. (°F)	Avg. Temp. (°F)	Max. Temp. (°F)	Min. Temp. (°F)	Precipi- tation (inches)	Snow- fall (inches)
JAN	29.8	13.9	21.8	40	-1	4.65	21.0
FEB	39.6	21.6	30.6	60	3	2.07	7.0
MAR	44.1	27.7	35.9	61	8	3.01	10.5
APR	60.1	40.1	50.1	95	30	4.13	
MAY	68.7	50.3	59.5	91	43	2.76	
JUN	71.5	55.5	63.5	83	43	3.99	
JUL	78.0	61.6	69.8	88	51	7.91	
AUG	82.2	65.2	73.7	93	55	3.40	
SEP	71.1	52.8	62.0	79	41	3.28	
OCT	58.2	41.2	49.7	73	32	5.62	
NOV	55.4	40.7	48.1	69	29	3.76	
DEC	39.4	23.7	31.6	69	9	5.27	10.5

Average Maximum Temperature 58.2°

Average Minimum Temperature 41.2°

Average Temperature 49.7°

Total Precipitation 49.85 inches

Total Snowfall 49.0 inches

Warmest Temperature 95° on April 28

Coldest Temperature -1° on January 15, 16, and 17

Last Frost Date 32° on April 13

First Frost Date 32° on October 19

Growing Season 189 days



SUE A. PEIFFER

A lightning strike at about 9 a.m. on July 2, 2009, destroyed this venerable Nikko fir (*Abies homolepis*) in the Arboretum's conifer collection. The explosive force threw pieces of the tree at least 180 feet away.

of late blight. The Arboretum has very limited holdings of woody plants in this family and no collections plants were affected. The damp conditions were also a factor in the appearance of fire blight (*Erwinia amylovora*), a bacterial disease, on some rose family (Rosaceae) plants in the collections. A high temperature of 83°F (lower than in April or May) was reached on the 26th.

JULY was also cloudy, cool, and wet, with 7.91 inches of rain, the sixth wettest July on record. There were fourteen days with measurable rainfall and traces on four others. Thunderstorms were frequent; on the 2nd, a lightning strike during a thunderstorm destroyed a notable 91-foot-tall, 110-year-old Nikko fir (*Abies homolepis*) in the Arboretum's conifer collection. 2.93 inches of rain fell on the 23rd, the highest one day total since December 11th, 2008. For five days it remained in the 60s and on eleven days it never made it out of the 70s. A high of 88°F was recorded on the 18th and 28th. We never reached 90°F, which is extremely rare for July. The combined June–July average temperature was the 4th coldest in Boston's recorded weather history.

AUGUST was very warm and, with only 3.4 inches of rain, our driest summer month. Measurable precipitation was recorded on only eight days. The high of 93°F was reached on the 18th. 90°F or greater was recorded on the 17th through the 19th, creating our only official heat wave of the summer.



NANCY ROSE

Visitors and Arboretum staff commented on the outstanding orange-russet fall color exhibited by the dawn redwoods (*Metasequoia glyptostroboides*) near the Hunnewell Visitor Center late in the autumn of 2009.

SEPTEMBER was cool, sunny, and a bit dry. A heavy rain occurred on the 11th and 12th, but rainfall was measured on only five days for a total of 3.28 inches. Long sunny breaks occurred between rain days. No temperatures of 80°F or higher were recorded during the month.

OCTOBER was cold and wet. Our growing season ended on the 19th with a low of 32°F. This was the 21st coldest October in 138 years of Boston weather history. Precipitation was measured on fifteen days for a total of 5.62 inches. Damp conditions notwithstanding, visitors to the Arboretum enjoyed another great fall foliage display this year.

KEVIN R. SCHOFIELD



A cool October followed by unusual warmth in November triggered an abundance of premature late-autumn blooms on this Fuji cherry (*Prunus incisa* f. *serrata*) in the Bradley Rosaceous Collection. An early December snow brought an end to the spring preview.

NOVEMBER was warm and somewhat dry, ranking as the 7th warmest November on record. It was only slightly cooler than October. A high of 69°F was recorded on the 9th. A low of 29°F was recorded on the 6th and 17th. This warm weather kept containerized nursery plants at the Arboretum's Dana Greenhouse from going completely dormant, the condition needed for winter root cellar storage. Many of our containerized plants had to wait for the cold of December to drop their leaves. Though they commonly open a few blossoms during late fall warm-ups, this year some of the mature cherry (*Prunus* spp.) trees in the Bradley Rosaceous Collection appeared to be in nearly full bloom.

DECEMBER started warm, reaching a high of 69°F on the 3rd. But it then turned cold, remaining below freezing for eight straight days from the 16th through the 23rd. This is just what our containerized woody plants needed to go into dormancy, and they could finally be put to bed for the winter. Almost a foot of snow fell over the weekend of the 19th and 20th.

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An Essay on Naming Nature: The Clash Between Instinct and Science

P. F. Stevens

Naming Nature: The Clash Between Instinct and Science
Carol Kaesuk Yoon. W.W. Norton & Company, 2009. 344 pages.
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Systematics, the science of the study of relationships between organisms, has seen remarkable developments over the last fifty years. Carol Kaesuk Yoon was a graduate student in Cornell in the late 1980s, trying to elucidate the relationships between some fruit flies using the then still fairly novel technique of DNA analysis. There she witnessed some of the vitriolic debates between cladists and evolutionary biologists, two warring groups of systematists who interpreted relationships in very different ways. In fact, analysis of the molecular data that she and others were then starting to use has had profound consequences for our understanding of the living world, and our knowledge of the genealogical relationships between organisms is increasing by leaps and bounds.

Taxonomists, those who classify, have in many cases redrawn the limits of groups to better reflect these genealogical relationships. Of course, systematists had long been interested in such relationships, but they used morphological differences to establish them. As Ernst Mayr (who figures in the book's pages) noted, everybody could tell a toucan, with its remarkable beak, from a barbet. Brightly colored though the latter bird might be, barbets had much more conventional bills, and nobody in his or her right mind would put toucans and barbets in the same family. But that is exactly what the genealogical evidence suggested to some.

The resolution of this particular story is that barbets are now in four separate families, toucans remaining in their own family. For some,



NAMING NATURE

THE CLASH BETWEEN INSTINCT AND SCIENCE

CAROL KAESUK YOON

this is a satisfactory solution; after all, this taxonomy does take into account genealogy. But situations like these seem to make no sense intuitively—are birds to be included in reptiles, are we humans really to be placed with fish, as genealogy would suggest? Such questions led Yoon to reflect on where taxonomists and systematists were going. They seemed to have taken leave of their everyday senses as they peered myopically at bands on gels that represented DNA. On the other hand, we have always classified the living world using our

ordinary senses, and these classifications make that world real to us in a way that the new classifications do not. It is this world—she calls it the *umwelt*, the world as it is apparent to our senses, the natural order that it discloses to us—that matters to us. In the world as we perceive it, objectivity, hypothesis testing, and evolutionary change are not relevant; the whale is a fish of sorts, as are clams and maybe even coots, and humans are not apes. This is folk taxonomy, not a scholarly endeavor but a hard-wired and ageless tradition that was co-opted by Linnaeus and hijacked by molecular systematists.

In the book, we then embark on a fascinating tour. Linnaeus's Herculean labors in classifying the world are explained in detail, "capturing," as he did, "the essential vision of the living world ... the vision of the human *umwelt*" (p. 50). A brief discussion on Darwin's barnacles ends with the conclusion that all his brilliant evolutionary inspirations would cripple taxonomy—a wall was being erected between the scientist and the living world. Indeed, despite the title of his book, *On the Origin of Species* ... , arguments about what a species really was were not settled by Darwin, nor later by Mayr, who thought that because he and New Guinea tribesmen could recognize the same species of birds this made species objectively real. This observation simply made James Watson wonder why Harvard faculty were needed to name things if they did no better than New Guineans.

The classifications of plants and animals all over the world show remarkable cross-cultural similarities, down to the numbers of different things that are included in any one classification—which turns out to be similar to the number of genera that some of Yoon's informants, professional taxonomists, could remember; around 600 is the upper limit. Similar numerical regularities apply to species; few genera have more than seven species. Indeed, there are general memory rules here, as George Miller noted in his classical paper, "The Magical Number Seven, Plus or Minus Two: Some Limits on Our Capacity for Processing Information." The great taxonomist George Bentham was aware of such limits as he wrote *Genera plantarum* with Joseph Dalton Hooker in the later nineteenth century. Yoon notes that it has been shown that

names of fish sound like names of, well, fish, rather than of birds or some other animal. This is the classificatory *umwelt* that we have left behind. She also describes some remarkable people with brains damaged in particular ways who could no longer classify organisms.

Returning to academia, the arguments between the three main group of systematists—cladists, pheneticists, and evolutionary systematists—are described very perceptively. Yoon sees that the cladistic approach—recognizing relationships because of shared unique characters—has allowed us to start assembling a tree of life that shows us surprising things about the world. However, this is not the world of our senses, since the living world has been excluded. What is the mere mortal to do?

Indeed, there is a tension here. Yoon suggests that classifications were developed specifically for communicating about organisms. However, classifications extend to every part of our world, living or not. We classify items in a supermarket just as effectively as we do organisms. We may have lost contact with life, but we have not lost the ability to classify. Indeed, classification is not so much part of an *umwelt* that has to do with life in particular but something we do to everything. The binomial, a noun-adjective combination that Linnaeus used, is simply two words we use to describe groups of things, whatever they may be. A red cart and a red oak have the same grammatical and cognitive structure, but one refers to things and the other to plants.

In the end, Yoon suggests that we name organisms as we please. There is no one classification, but each classification is a variation on a universal theme; we must reclaim our own *umwelts*. And herein is food for thought. What is our *umwelt*? She acknowledges that all individual classificatory systems may be different, but of course the great advance made almost inadvertently by Linnaeus was a way of communicating. A common language, a common classification, is always essential. And whether our *umwelt* tells us anything in particular or stable is debatable, certainly, our attitudes to the environment have changed dramatically over the last few hundreds of years, and our prelapsarian ideas might not seem very satisfactory to us now. Eyewitness accounts may well be decidedly less than accurate, as any trial



NANCY ROSE

Carolus Linnaeus, a larger-than-life bronze statue of the “father of modern taxonomy” by Robert Berks, in the Heritage Garden at the Chicago Botanic Garden.

lawyer or judge will know. Thus, to oppose the new classifications we are developing with an umwelt-based classification that reflects an understanding of the phenomenal (= real) world, seems a mistake.

I have been through the biological battles that Yoon describes, and am also a maker, user, and teacher of classifications. There is much more than just DNA sequencing and changing names going on. We are learning much more about the living world and in such a way that it makes us wonder and understand in a way that was impossible before. When I take beginning biology students around the campus and talk about bacteria in the nodules in the pea family, and the bacteria-that-were that pervade cells as mitochondria and chloroplasts (all features that also reflect the new classifications) students clearly understand the world in a very different way. A classification based on umwelt and instinct would be a sorry substitute.

The reader will learn a great deal from this book, which is well and clearly written (although the asparagus has never been included in the orchid family, p. 235). The issues that it raises are ongoing. Even aside from the “debate”

over global warming and evolution, scientists sometimes forget the limits of their world: their truth is not necessarily broadly self-evident. Readers of Yoon’s book will surely enjoy *Trying Leviathan: . . .* by D. Graham Burnett, which raises similar issues, but in a historical context, as the subtitle of that book explains: *The Nineteenth-Century New York Court Case That Put the Whale on Trial and Challenged the Order of Nature*. The ultimate question is surely why we need alternative classifications and what are the situations in which they help—and what are those in which they are a hindrance. Whether the umwelt, whatever it is (and the word is overused in this review as it is in the book itself), will help us as we think about this, I do not know, although I doubt it. And we do need to think about what is, not what seems—and I say this fully aware of the difficulties surrounding that most simple of words, “is”.

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The Sand Pear—*Pyrus pyrifolia*

Peter Del Tredici

In more than thirty years at the Arnold Arboretum, I have observed many trees in our collections. Some have not lived up to expectations, but others have proven themselves over time. One such tree is the specimen of sand pear (*Pyrus pyrifolia*, accession 7272-C) growing at the back edge of the open meadow below the summit of Bussey Hill, which I consider to be the most beautiful flowering tree in the Arboretum.

This tree comes into flower in late April or early May, depending on the weather, and at its peak bloom it shines like a beacon in the early spring landscape. When first glimpsed from Bussey Hill Road, against a backdrop of tall white pines, it looks like a giant white cloud—an effect that is intensified because no leaves compete with the floral display. The flowers are pure white with crimson anthers, 3 to 3.5 centimeters (1.2 to 1.4 inches) in diameter, and are borne in rounded clusters on slender stalks. In bloom, the tree can be easily spotted from the top of Peters Hill, some 800 meters (2,600 feet) away as the crow flies. It stays in flower for up to a full week, holding up well through all kinds of inclement early spring weather.

In fall, the tree's glossy, dark green leaves turn beautiful shades of orange and red. Its hard, round fruits are 3 to 4 centimeters (1.2 to 1.6 inches) in diameter, brown, and covered with pale dots. The fruit has an extremely gritty texture (hence its common name—sand pear) and a puckery aftertaste when bitten into. It's hard to imagine how the delectable Chinese and Japanese "apple-pears" in the supermarket were derived from this astringent ancestor.

The magnificent sand pear on Bussey Hill stands 16.9 meters (55.4 feet) tall with a spread of 25.7 meters (84.3 feet) and a trunk DBH (diameter at breast height) of 79 centimeters (31.1 inches). Remarkably, it seems never to have suffered any major snow, ice, or wind dam-

age—an unexpected observation given its age (101 years) and the exposure of the site where it is growing. Such structural integrity provides a striking contrast to the widely planted but notoriously weak 'Bradford' Callery pear (*Pyrus calleryana* 'Bradford'), which shows an all too predictable tendency to split apart in severe storms after about age 20. Were it not for its relatively large, messy fruits, our streets might well have been planted with sand pears instead of Callery pears.

The Arboretum's beacon tree was grown from seed collected by E. H. Wilson in the fall of 1907, somewhere in the mountains surrounding the city of Ichang in Hupeh (now Hubei) Province. When Wilson collected the seed he did not give the tree a species name, but noted that the Chinese called it "tang li tzu." At the time, sand pears were classified as *Pyrus sinensis*, a name which was used mainly to describe cultivated plants with large, edible fruits. Back at the Arboretum, Alfred Rehder decided that Wilson's tree was the wild ancestor of these cultivated trees and, in 1915, proposed the name *Pyrus serotina* for Wilson's specimens. Taxonomy is ever changeable, though, and in 1926 the Japanese botanist Nakai reduced Rehder's name to synonymy with *Pyrus pyrifolia*—the name the species now bears.

Wilson's sand pear seeds arrived at the Arboretum in April 1908 and germinated in the spring of 1909. Sometime prior to 1918, at least three of the seedlings were planted on the grounds. Remarkably, all three are still alive today—a testament to the toughness and tenacity of the species. Specimen 7272-C is the finest of the three, and it will, I hope, remain a shining spring beacon for Arboretum visitors for many years to come.

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