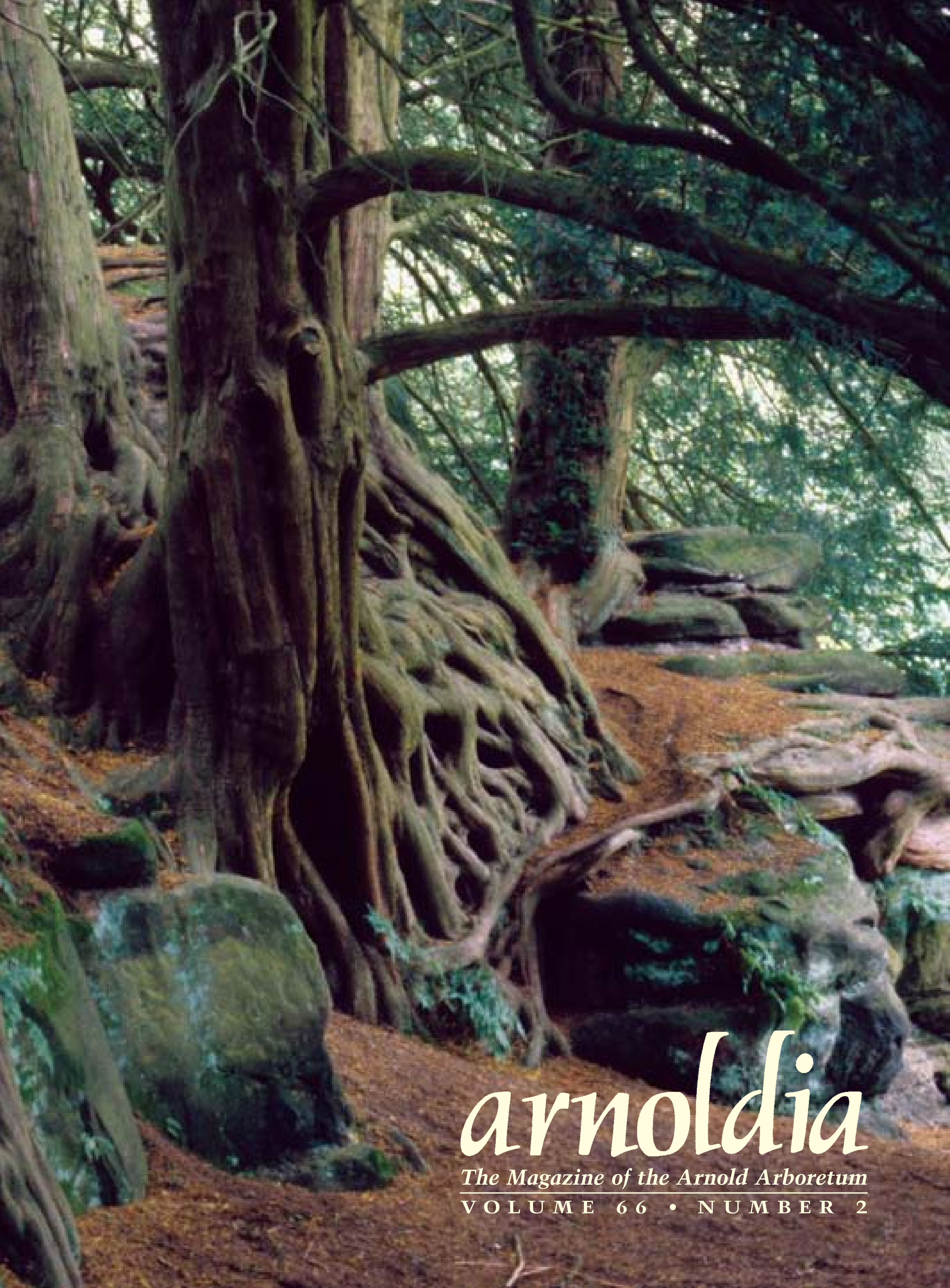

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Nancy Rose, *Editor*
Andy Winther, *Designer*

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Inside front cover: Tutti frutti: Autumn brings ripening fruit of all sorts, including the nannyberry (*Viburnum lentago*) drupes shown here changing color from yellow to pink to midnight blue. Photo by Nancy Rose.

Inside back cover: Plant collecting can be quite an adventure, as Arboretum plant propagator John H. Alexander III describes in his plant profile of this impressively corky-branched sweetgum (*Liquidambar styraciflua,* accession 1248-79-B). Photo by Nancy Rose.

Dysfunctional Root Systems and Brief Landscape Lives: Stem Girdling Roots and the Browning of Our Landscapes

Gary Johnson

Consider this comparison of potential life spans for trees (Burns and Honkola 1990; USDA 1998)

Quercus macrocarpa **(bur oak), in upland site**	**250+ years**
Acer saccharinum **(silver maple), in riparian site**	**125+ years**
Acer negundo **(boxelder), in lowland site**	**100+ years**
Pinus banksiana **(Jack pine), in field site**	**80+ years**
Betula papyrifera **(paper birch), in northern lowland forest**	**65+ years**
Tree planted in urban core street site	**less than 10 years**

That's a sobering thought—a tree with a normal life span of 65 to 250 years may live less than 10 years when planted in any American city's downtown landscape. Admittedly, that figure represents tree placement in the worst of our urban landscape sites: sidewalk cut-outs. These inhospitable planting sites are also known as tree coffins, tree burial mounds, or urban tree disposal units to frustrated urban foresters. When the mortality rate of downtown trees is compared to tree losses from Dutch elm disease, oak wilt, sudden oak death, and gypsy moth, it doesn't take too long to realize that there's an epidemic of urban tree loss going on and it's largely under the radar (Figure 1).

Another oft-quoted number is that the average urban residential tree lives for 30 to 35 years (Moll 1989). That life span is three times as long as a sidewalk tree, yet only half as long as a paper birch in its natural environment. Growing conditions in residential landscapes may not be quite as bad as sidewalk sites, but there are many natural and unnatural pressures on the trees that lead to briefer landscape lives. Residential landscape soils can be as stressful as downtown sites: poorly drained, outrageously alkaline, subjected to blends of every pesticide known to modern society, and compacted to such a degree that lawns may seem like nothing more than green concrete.

With few exceptions (perhaps tornadoes and a few diseases), there are no "angels of death" that descend and quickly kill trees in landscapes. More commonly, a multitude of predisposing stresses that occur in our highly altered urban landscapes combine to weaken trees over the years. Often, inciting events such as floods or hailstorms and/or contributing agents such as target cankers or wood boring insects complete the job for the majority of tree losses. Meanwhile, plant health care professionals attempt to determine the true causes of decline and death, and often the diagnoses are incomplete or incorrect because of the multiple offenders involved with the problem.

Predisposing Factors and Tree Decline

When trees are chronically stressed (long-term drought, repeated defoliation, etc.), their normal reserves of chemical energy—primarily as complex carbohydrates—are slowly depleted. Each year as stressed trees come out of dormancy, they emerge in a weakened state due to this energy depletion and find it increas-

PHOTO BY GARY JOHNSON

Figure 1. Trees in urban sidewalk sites are subjected to very unhealthy environments and live less than 10 years on average.

ingly difficult to releaf, grow, and deal with the harsh realities of urban landscapes on a normal basis. It takes a tremendous amount of chemical energy to push out new leaves and shoots, recover from accidental wounds on the stems, or produce flowers and fruit.

As the tree's energy reserves continue to decline—and thereby affect the tree's ability to capture and store new energy through photosynthesis—the entire system is affected and the decline spiral to premature death begins. So decline in a sense refers to the tree's ability to deal with life's normal stresses. A tree in decline may die suddenly because of an event such as a cold winter with no snow cover, a short-term summer drought, or a defoliation from insects or hail. The other trees in the landscape tolerate the damage and survive, but the predisposed trees—those in decline—are unable to recover from the damage.

Dysfunctional Root Systems as Predisposing Agents

Despite the fact that roots are seldom seen, dysfunctional root systems are too often the predisposing agents connected to tree health decline, and ultimately the reason why many urban landscape trees experience such brief lives. If the root system—approximately 50% of a tree's biomass—is not operating normally, the entire system will be abnormal. Abnormal is not always harmful, as seen in bonsai plants and trees growing on slopes. In bonsai plants, a restricted root system causes compacted growth in the rest of the plant system, but the system itself may be healthy and completely functional under most circumstances. In the case of a tree growing on a slope, the tree is anchored with a skewed and asymmetrical root system, but its overall health is not compromised even though the root system could certainly be considered abnormal.

PHOTO BY DAVE HANSON

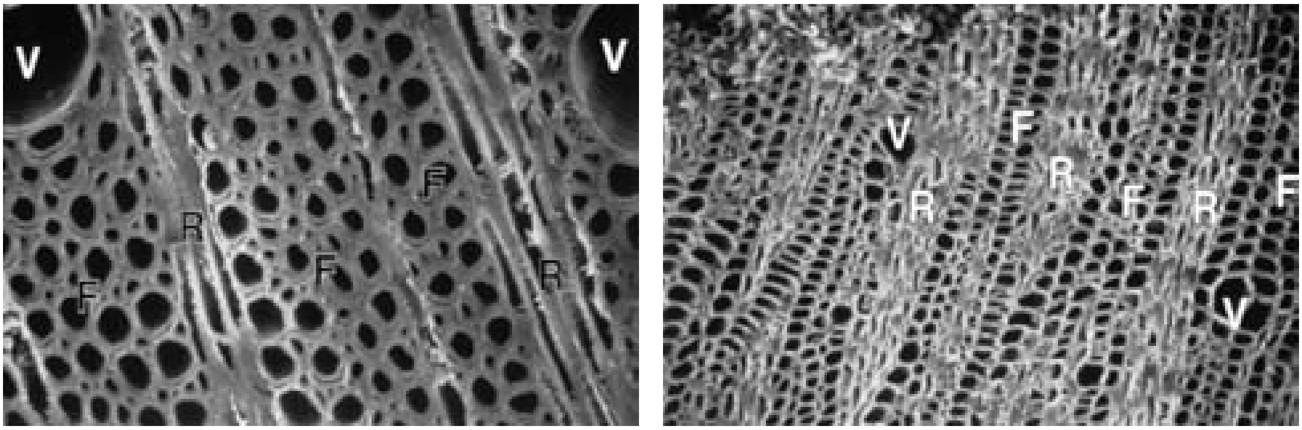
Figure 2. With part of a stem girdling root removed, the compression to the tree's trunk is evident.

But abnormal root systems that do affect the overall health or stability of the tree are considered dysfunctional. For example, when a container-grown tree with a severely pot-bound root system is planted, its rhizosphere does not occupy a large enough area to capture sufficient water and nutrients needed to support a normal sized tree without supplemental help. Dysfunctional root systems are also common on newly transplanted bare-root and balled-and-burlapped plants; these plants often lose 75% or more of their root systems during the harvest operation, resulting in transplant shock which may go on for several years until the root system regrows. And then there are stem girdling roots (SGRs), which create a root system so dysfunctional that it can end up killing the entire tree.

Stem Girdling Roots as Predisposing Agents

Stem girdling roots are those roots that grow either partially or completely against the tree's stem and compress (girdle) the stem tissues (Figure 2). Xylem and phloem tissues in the stem become much narrower at the point of compression, impeding normal water movement and sap flow (Figure 3). This restriction affects energy reserves by directly and indirectly affecting photosynthesis. Trees become stressed and more vulnerable to secondary problems. For this reason, SGRs are considered to be primary predisposing agents in landscape tree decline and death.

Some of the first symptoms of SGR-impacted tree health include leaf scorch or leaf wilting on a tree when no other plants in the area are showing the same symptoms. There may be adequate moisture in the soil, but the tree's ability to move water throughout the system is thwarted by the areas of compression, i.e. the greatly reduced diameter of vessel elements. Soon, this water stress evolves into early leaf coloration and leaf drop in the summer, late leaf-out in the spring, and chlorosis or other



G. W. HUDLER, CORNELL UNIVERSITY

Figure 3. Transverse views of normal Norway maple stem wood showing a healthy growth pattern (left), and malformed stem wood compressed by a stem girdling root (right). Water and nutrient transport in trees is negatively affected when tissue is malformed by compression. V = vessel element, R = ray, F = fiber tracheid. Both views are at the same scale.

nutrient deficiency symptoms. If the stem compression becomes more severe, affecting 50% or more of the stem circumference, so do the symptoms. Trees will tend to suffer more damage during the winter seasons, in particular true frost cracks, cambial death, and dieback. In the latter stages of decline due to SGRs, trees usually suffer from severe stunting (very small leaves, annual twig growth of 1 to 2 inches or less) and significant defensive dieback. With so little vascular capacity left, affected trees may succumb completely from even a short-term summer drought (Figure 4).

Though often a slow-acting cause of death, SGRs can also cause tree death that is a bit more sudden and dramatic. The compressed areas of tree stems are structurally weak points and far too often are the points of failure during windstorms (Figure 5). For example, in severe windstorms that occurred in Minnesota in 1998, 73% of the lindens (*Tilia* spp.) that were lost in urban landscapes failed at compression points from SGRs, and most broke several inches below ground. This is a different type of predisposition but equally damaging to a tree's ability to grow, survive, and add to the quality of life.

PHOTOS BY GARY JOHNSON

Figure 4. The middle littleleaf linden was in the last stages of decline from stem girdling roots at the time of this photograph. One year later it was dead.

Figure 5. Stem compression from SGRs located 4 or more inches below ground was the most common cause of urban tree failure in windstorms in Minnesota from 1995 to 2005.

More (Soil) is Not Always Better

Early SGR studies conducted by the University of Minnesota were in response to unexplained tree decline in urban areas. From 1994 through 1996, 220 declining and dying trees were diagnosed. In 81% of the cases, stem girdling roots were the only causal agents isolated. This figure closely paralleled data collected from a national survey of tree care professionals (Johnson and Hauer 2000). More specifically, these trees had been planted in the previous 12 to 20 years and had significant stem compression (greater than 50% of the stem circumference) from SGRs. In all cases, these SGRs were well below ground (from 4 to 14 inches)—out of sight, out of mind (Figure 6).

In landscape surveys conducted by the University of Minnesota Department of Forest Resources (1997 to 2004), five species of trees were investigated in three different communities. All trees were growing in public spaces: boulevards, schools, government centers, parks. Species surveyed included hackberry (*Celtis occidentalis*), littleleaf linden (*Tilia cordata*), sugar maple (*Acer saccharum*), 'Shademaster' honey locust (*Gleditsia triacanthos* 'Shademaster'), and green ash (*Fraxinus pennsylvanica*). Trees were randomly selected, evaluated for health and condition, and then examined for depth of soil over the main order roots and the presence of stem encircling roots (potentially conflicting roots within 6 inches of the stem) or stem girdling roots. The results were a bit depressing. Only 4% of the lindens, 8% of the ash, 10% of the maples, 15% of the honey locust, and 40% of the hackberries had their stems completely above ground. The rest of the sampled trees had from 1 to 12 inches of soil over the first main order roots and against the stems.

Non-destructive root collar examinations were performed on a total of 1,380 trees. The intent of these examinations was to determine the frequency of SERs (stem encircling roots—those potentially conflicting roots within six inches of the stem) and SGRs associated with different depths of soil (up to 12 inches) over the first main order roots. The excavations demonstrated that the deeper tree stems were buried in the soil or mulch, the more likely it was for them to have multiple layers of stem encircling and stem girdling roots. The increased presence of these problem roots showed up in trees beginning with as little as one inch of excess soil against the stem. In a nutshell, the more soil or pre-soil (organic mulches that will break down) that is piled over the root systems and against the stems, the more likely it is that trees will decline or fail due to multiple conflicts with SGRs (Figure 7).

PHOTOS BY GARY JOHNSON

Figure 6. This SGR, located approximately 4 inches below ground, runs tangential to the tree trunk and is compressing 30% of the stem circumference.

Figure 7. As shown on this littleleaf linden, more layers of SGRs develop as the stem is buried deeper. Greater than 40% of the stem circumference of this tree was compressed by several layers of SGRs.

How SGRs Form

Observations from the 1,380 root collar examinations conducted during the species surveys and a separate nine-year planting depth study have led to the conclusion that stem girdling roots form in one of two ways: first, new roots regenerating from deeply buried main order roots, and second, from stem adventitious roots. When main order roots are buried too deeply, new woody roots that originate from them or any part of the buried root system tend to grow closer to the surface. It is speculated that this action is in response to a more desirable soil oxygen and moisture balance. As the roots reach the soil surface, an unpredictable percentage of them grow tangential to the tree stem or in some cases encircle the stem. For the next number of years (12 to 20, from our observations), the roots and stems expand in diameter, resulting in the ultimate confrontation between roots and stems.

Stem adventitious roots are also sources of SGRs. When a buried stem begins forming adventitious roots, many or most of those roots grow away from the stem in a radial fashion. As with new roots growing from main order roots, an unpredictable percentage of these adventitious roots do not grow radially but instead grow tangential to the stem or encircling the stem. The interface area between soil and stem appears to be a highly desirable area for stem root growth, perhaps because it provides an ideal balance of soil oxygen and moisture and is also the path of least resistance for root proliferation. The exact reasons for these root growth responses are still speculative, but it is clear that when tree stems are buried by a media that supports root growth, SGRs are highly likely to occur.

It's worth noting that stem girdling roots are a problem primarily with younger trees. As trees mature, their growth slows down dramatically, including the growth of trunk diameter and encircling roots. Because of this reduced growth—and the fact that there is often a relatively thick outer bark—stems of mature trees that then become buried by soil or organic matter are much less likely to develop stem girdling root problems. SGRs can still develop, but if they do they are less likely to result in the decline and death of the tree.

How to Cause Stem Girdling Roots

If you want to cause the formation of SGRs, bury the tree stem with a medium that supports root growth. Here are some common ways SGRs occur:

- Excess soil is piled over the first main order roots during the growing and harvesting of balled-and-burlapped trees.
- Excess growing medium buries stems when container-grown trees are up-potted.
- Decayable organic mulch is piled high around tree stems in nurseries and landscape sites.
- Soil is piled against tree stems during construction regrading in landscapes.
- Trees are planted in a new landscape *before* final grading is completed.

There are so many different ways that stems can be buried—accidentally or with good intentions—that it is difficult to pinpoint the main source of the problem. One seemingly common cause is the act of burying trees rather than planting trees. Unfortunately, too many people still have the notion that trees are like fenceposts and need to be buried deep for stability. Not so.

In 2002, we conducted a planting depth study in collaboration with a large wholesale nursery. Bare-root birch (*Betula* spp.), ash (*Fraxinus* spp.), and crabapple (*Malus*) were potted up in number-ten containers at four different depths: 0, 2, 4, or 6 inches of soil over the first main order roots. On a weekly basis, each of the 240 trees was inspected for lean or windthrow from the containers. At the end of the four month study, all trees were well-rooted in the containers and the results of the study showed that all trees, regardless of depth, leaned at the same frequency and to the same degree. Planting tree stems deeper had absolutely no positive effect on tree stability. If newly planted trees are unstable, they may need temporary support from a guying or staking system, not entombment.

Nine Years of Burial

In 2000, a long-term planting depth study was installed at the University of Minnesota's Urban Forestry and Horticulture Institute's research fields. Three hundred and sixty trees equally represented by two species (sugar maple [*Acer saccharum*] and littleleaf linden [*Tilia cordata*]) were planted at three depths: 0, 5, or 10 inches of soil over the first main order roots. All trees were planted in a complete, randomized block design in a .75 acre plot as unbranched, 2 to 3 feet tall liners. At three year intervals, one-third of the trees were harvested and had their root systems excavated with a supersonic air tool. Each year, mortality rates, growth rates (stem caliper), number of suckers produced, and percentage of dieback was recorded. In 2009, the final third of the original experiment will be harvested, but some interesting trends and

PHOTO BY GARY JOHNSON

PHOTO BY NANCY ROSE

Figure 8. Bury the stem of littleleaf linden just 5 inches deep and a profusion of suckers will develop. These suckers eventually become SGSs (stem girdling suckers) as they grow in caliper and compress the tree's stem.

significant data have already been revealed from the first two harvests, including:

- Planting sugar maples 5 to 10 inches too deep is an effective way to kill them. The mortality rates for the 0, 5, and 10 inch depths as of 2006 were 30, 40, and 65%, respectively.
- There was a significant positive relationship between placing 5 to 10 inches of soil against the stems and the frequency of SGRs on *Tilia cordata* in both the 2003 and 2006 harvests. *Acer saccharum* showed a trend in the same direction.
- *Tilia cordata* with stems buried in 5 inches of soil will produce masses of stem suckers, making the tree look more like a shrub.

Sucker formation on *Tilia cordata* doesn't just ruin the tree's appearance, it can also cause premature failure. Stem girdling suckers (SGSs) are suckers that form prolifically and, when they enlarge in diameter, can girdle the stem vertically and horizontally (Figure 8).

How Often do Trees Die from SGRs?

This question is likely unanswerable. When trees suddenly fail and die during a windstorm, diagnosing the problem below ground is not often considered. Weather alone is often blamed for the deaths, and the trees are hastily removed and replaced.

Research we conducted from 1995 through 2005 on tree failure in windstorms exposed a broader picture of the effects SGRs have on landscape trees. During this period over 1,500 "tree autopsies" were conducted on trees that had failed during wind-loading events in Minnesota. These trees were not those from the centers of severe wind-loading events such as straight-line winds or tornados. Rather, they were victims of thunderstorms or those at the edges of severe wind events.

From that data, the destruction and economic losses from premature tree failures due to SGRs were determined, and it was startling. The most common tree size category for boulevard tree failures was the 6 to 10 inch DBH (diameter at breast height, 4.5 feet above ground) range. Of those trees, 50% snapped off at compression points from SGRs at a depth of 4 or more inches below ground. The Achilles' heel was a compression root that couldn't even be seen because the stem was buried so deeply. The data also indicated that littleleaf lindens (*Tilia cordata*) were grossly affected by SGRs. Littleleaf linden ranked as the third most common species for total failure (the tree went down completely) during those years, and 73% of those trees snapped off at below-ground SGRs, almost the exact percentage of littleleaf linden that failed during the previously mentioned 1998 storms. After 11 years of data collection, the presence of SGRs and, more specifically, stem compression from SGRs that amounted to 50% or more of the stem circumference, emerged as the number one reason why urban trees failed in windstorms.

What to Do, What to Do?

Prevention is the easiest and most effective way to eliminate the SGR problem in landscapes. Whether you are an urban forester, commercial landscaper, or home gardener, follow these steps to prevent or manage stem girdling roots:

- Don't plant container or balled-and-burlapped trees that are already buried too deeply. Assume there is too much soil over the first main order roots and remove that excess soil before planting a newly purchased tree (Figure 9).
- Plant trees, don't bury them. If stems aren't buried, it's not likely that SGRs will become a problem. They can still occur on correctly planted trees, but much less frequently than on buried trees.

PHOTO BY GARY JOHNSON

Figure 9. Most containerized trees will have 2 to 6 inches of excess soil over the first main order roots and against the stem. Use a pruning saw to remove this excess soil before planting. Of 500 trees subjected to this treatment at the University of Minnesota's research nursery, there has been a 0.7% mortality rate in 2.5 years.

- Don't pile mulch against stems. Organic mulch is basically pre-soil. Piling on mulch will result in a buried stem and a wonderful environment for SGRs to develop.
- When suspicious, investigate. Root collar exams are not all that difficult to perform (Figure 10). If you have a trowel and a wet-dry vacuum, you can perform a non-destructive root collar exam. If you find offending roots during the exam, remove them. Also, remove all that extra soil. If you do nothing, it will only get worse.
- If greater than 50% of the stem's circumference is severely compressed, it is probably best and safest to remove the tree and start over.


PHOTO BY DAVE HANSON

Figure 10. The fastest and most non-destructive method for conducting a root collar exam is with a supersonic air tool that blows the soil away without harming the roots. This root collar exam was accomplished in approximately fifteen minutes.

Treatments for affected trees are uncertain. If SERs (stem encircling roots) can be removed before compression begins, that's an excellent and effective treatment. If the SERs have become SGRs and if, during the course of removing SGRs, the stem is wounded, the long-term potential for recovery is uncertain. The study of stem girdling roots is a relatively young science and long-term data on treatment options and efficacy are not there. If 50% or more of the tree's trunk is severely compressed by the SGRs, and if the symptoms included dieback and severe stunt, the tree is probably beyond salvation. If that same tree is ten feet from a house or utility line, then the risk of leaving the tree is unacceptable. Buy a new tree. Remove the excess soil over the root system. Plant it with the trunk fully exposed. Mulch the roots, not the trunk. These steps will put your new tree well on the way to a long, healthy life.

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Gary Johnson is a professor in the Department of Forest Resources at the University of Minnesota.

Wake Up and Smell the Ginkgos

Peter Del Tredici

Ginkgo biloba is one tree that most Americans—even those with little knowledge of botany—can recognize. There are two reasons for this: first, its fan-shaped leaves are highly distinctive and impossible to confuse with any other tree; and second, it is widely cultivated as a street tree in many urban areas throughout much of the United States. Because of its environmental adaptability, its resistance to pests and diseases, and its general tolerance of inhospitable growing conditions, ginkgo is experiencing a spike in popularity as evidenced by the long rows of them that are showing up in commercial and municipal landscape projects across the country. In this regard, Americans are following the pattern set in Japan where ginkgo accounts for 11.5% of all the street trees growing in that country—more than any other single species (Handa et al. 1997).

As well as gaining in popularity, ginkgo has also been experiencing a surge in attention from the scientific community, particularly from the Chinese, for whom the tree has become a national symbol of their botanical heritage. The pur-

ALL PHOTOS BY THE AUTHOR EXCEPT AS INDICATED

An allée of ginkgos, about 100 years old, on the campus of Tokyo University.

Ginkgo has unmistakable fan-shaped leaves.

One of the old ginkgos at Bai Yuan village in Wuchuan County, Guizhou Province. Note the epiphytic ferns growing on its trunk.

pose of this article is to acquaint the reader with some of this new information about the plant's unique evolutionary history as well as its ecological role as a plant teetering on the brink of extinction in the wild.

Ginkgo's Homeland

Questions about the extent of *Ginkgo biloba*'s native range in China—or if native populations even exist at all—have been the subject of debate among botanists for well over a hundred years (Del Tredici et al. 1992, Li et al. 1999). The conflict has only recently been resolved with the help of DNA analyses (Fan et al. 2004, Shen et al. 2005, Wei et al. 2008) which have demonstrated that isolated ginkgo populations located in southwest China, especially around the southern slopes of Jinfo (or Golden Buddha) Mountain in Chongqing Province (28°53' N; 107°27' E), possess a significantly higher degree of genetic diversity than populations in other parts of the country, indicating native status. The area has a mesic, warm-temperate climate with a mean annual temperature of 16.6°C (62°F), and a mean annual precipitation of 1,185 millimeters (47 inches), with ginkgos growing mainly between 800 and 1,300 meters (2,625 and 4,265 feet) elevation (Li et al. 1999).

In addition to the genetic evidence, there is ecological and cultural evidence which suggests that these populations are wild. Ecological work in Chongqing Province, as well as in adjacent parts of Guizhou Province (Xiang et al. 2006), has identified dozens of small populations of ginkgos which can be considered either to be wild trees growing in the midst of native forest or the remnants of wild populations that have lost their forest context. These ginkgo populations occupy land that usually measures a few hectares at most, and they are surrounded by small villages whose residents practice subsistence agriculture. In areas where livestock has been excluded, spontaneous ginkgo seedlings and saplings are common in the forest understory.

In the cultural realm, much of northern Guizhou Province has been settled over the past three hundred years or so by people of Miao descent who, unlike the Chinese of Han descent, have no tradition of consuming ginkgo nuts and therefore have no history of cultivating the tree. While this situation began to change around 1980, cultivation by humans cannot explain the many large ginkgos scattered throughout the area that are *not* growing near temples. (Ginkgos found near temples are usually human cultivated.) From the ecological/botanical perspective, wild populations of ginkgo tend to show a number of characteristics which distinguish them from populations of cultivated trees. These differences are summarized in Table 1 (page 14).

In addition to the populations around Jinfo Shan, a second area of high genetic diversity for ginkgo occurs in eastern China, in Zhejiang Province, primarily on the slopes of Tian Mu Shan, a sacred mountain with many Buddhist shrines and temples, located about 100 kilo-

The agricultural terraces in the vicinity of Shan Jiang village in Wuchuan County, Guizhou Province. Over the past several hundred years, these have replaced the mixed conifer–broadleaf evergreen–deciduous forest that originally grew there.

meters (62 miles) west of the city of Hangzhou. This area, which was the site of one of the first nature reserves in modern China, has long been considered by botanists to be one of ginkgo's wild locations, but only recently—through the work of Wei Gong and her colleagues (2008) at Zhejiang University—has the distinct genetic ancestry of this population been established.

In contrast to its very limited distribution as a wild plant in China, ginkgo is widely cultivated throughout the temperate world, across a broad range of moisture, temperature, and topographic gradients. In China, the tree can be cultivated between 25° and 42° N latitude where minimum winter temperatures can reach -32°C (-26°F) and maximum summer temperatures 42°C (108°F) (He et al. 1997). Detailed phenological studies in Japan over a fifty year period by Matsumoto and his colleagues (2003) have determined that spring bud break in ginkgo occurs 40 days earlier in the extreme south of the country (30° N latitude) than it does in the far north (43° N latitude) and that autumnal leaf drop happens about 40 days later, making for an effective vegetative growing season range of 170 to 260 days across 13° of latitude. It's no wonder that ginkgo is touted as a paragon of environmental adaptability.

Ginkgo Sexuality

Ginkgo biloba is a dioecious species, with separate male and female trees occurring at roughly a 1:1 ratio. Ginkgo shows a long juvenile period, typically not reaching sexual maturity until approximately 20 years of age. Male (microsporangeate) and female (ovulate) sex organs are produced on short shoots in the axils of bud scales and leaves. The male catkins emerge before the leaves and fall off immediately after shedding their pollen to the wind. Pollination

(Left) A portion of the stand of wild ginkgos at Bai Yuan village in Wuchuan County, Guizhou Province. Note the tall, straight form of the trees indicting that they grew from seed. (Below) Cultivated ginkgos in this orchard show the typical shorter, wide-spreading form.

Table 1. The botanical and ecological characteristics of remnant natural ginkgo populations versus cultivated ginkgo populations in China

Remnant natural ginkgo populations	Cultivated ginkgo populations
Sex ratio should be more or less balanced with males at a 1:1 or greater ratio than females.	Skewed sex ratio—overwhelmingly female.
Trees are growing mixed in with numerous other species that are native to the surrounding forest.	Few other species growing with ginkgo; if other trees are present, they are typically cultivated for some specific purpose.
The growth form of most of the trees is single stemmed with relatively few lower branches (indicative of having grown up from seed).	Low-branched growth form of female trees (indicative of vegetative propagation by cuttings or grafts).

typically occurs anywhere from mid-March in areas with mild winters to late May in areas with severe winters.

The ovules on female trees are 2 to 3 millimeters (about .1 inch) long at the time of pollination, and are produced mostly in pairs at the ends of long stalks. When the ovule is receptive, it secretes a small droplet of mucilaginous fluid from its apical tip which functions to capture airborne pollen. Retraction of this droplet at the end of the day brings the pollen into the pollen chamber. Once inside the ovule, the pollen grain germinates to release the male gametophyte which attaches itself to the inside wall of the ovule. Here it undergoes a four- to five-month-long period of growth and development which is supported by the tissues of the expanding ovule (Friedman and Gifford 1997).

Ginkgo ovule with pollination drop at tip.

Sometime in September or October, depending on the latitude, the development of the male gametophyte culminates with the production of a pair of multiflagellated spermatozoids. In one of nature's most dramatic moments—first described by the Japanese botanist Hirase in 1896—the two microscopic sperm cells must swim, propelled by about one thousand tiny flagella, a full millimeter across a fluid-filled channel to reach the waiting egg cell, where only one can claim the prize. Contrary to what has often been written, fertilization takes place while the ovules are still on the tree and embryo development begins posthaste. The embryo length may range from less than 1 millimeter to 5 millimeters (.04 to .2 inch) at the time of seed drop, which can occur anywhere between September and November, depending on local weather conditions. Once the seeds fall to the ground, the embryo continues to develop until the arrival of cold temperatures (below 10°C [50°F]), at which point elongation stops. With the onset of warm weather in the spring, the embryo resumes its growth, which culminates in germination in late spring or early summer.

Ginkgo Nuts

It is now generally accepted that ginkgo was first cultivated by the Chinese not for religious purposes but rather for its edible seeds, which at maturity are relatively large and nutritious. The seed, as it falls from the tree, consists of an embryo embedded in the tissue of the female gametophyte surrounded by a thick seed coat. The intact seed coat consists of a soft, fleshy outer layer (the sarcotesta), a hard, stony middle layer (the sclerotesta), and a thin, membranous inner layer (the endotesta).

The seed, devoid of the famously smelly sarcotesta, is generally referred to as the "nut" with dimensions that range from 19 to 30 millimeters by 11 to 14 mm (approximately 1 by .5 inch). Over the past several hundred years, Chinese horticulturists have selected scores of cultivars which produce large and/or distinctively shaped nuts. Large plantations of these select ginkgo cultivars are common throughout eastern and central China.

The putrid odor often associated with ginkgo seeds typically develops only after they have lain on the ground for several days and have begun to rot. The smell is due to the presence of two volatile compounds in the sarcotesta—butanoic and hexanoic acids (Parliament 1995). The sarcotesta also contains numerous fatty acids and phenolics, one of which, ginkgoic acid, is known to cause allergic contact dermatitis in some people (Kochibe 1997).

A Common-Garden Experiment

The timing of pollination, fertilization, seed abscission, and germination in ginkgo are strongly affected by the latitude of cultivation as well as by local climate conditions. In the

Mature ginkgo seeds on a tree at Forest Hills in Boston, Massachusetts.

fall of 2002, I undertook a series of common-garden experiments to explore the relationship between the timing of pollination and the timing of germination in ginkgo by cultivating in a common location seeds produced by trees from two different latitudes. One lot consisted of about 500 cleaned seeds from trees that were being cultivated for nut production, which I purchased on September 22, 2002 at Tuo Le Village, Panxian, in southern Guizhou Province, China, (25°36' N). For comparative purposes, I collected ginkgo seeds on October 31, 2002 from beneath a number of trees growing at the Forest Hills Cemetery in Boston, Massachusetts (42°17' N).

When sown in the Arnold Arboretum's heated greenhouse (20°C [68°F]), the Guizhou seed began germinating on November 12—approximately 58 days after abscission—while the Boston seed did not begin germinating until January 6—some 67 days after abscission. Assuming approximate pollination dates of March 24 for the Guizhou seed and May 17 for the Boston seed, the total time elapsed from pollination to germination under continuously warm greenhouse conditions was 233 days and 234 days respectively, a remarkably confluent result given their different latitudinal origins.

A second striking result of the experiment was that only 15% of the uncleaned, outdoor-sown Boston seed germinated versus 72% germination for a replicate lot of one hundred seeds washed clean of their smelly sarcotesta. The fact that cleaned ginkgo seeds germinated at statistically significantly higher percentages than those with their sarcotesta intact suggests that animals which consume the seeds—provided they do not crush the thin-shelled nut—might play a role in promoting successful seedling germination (Rothwell and Holt 1997, Del Tredici 2000). The specific mechanism whereby the sarcotesta reduces the germination capacity of ginkgo seed is currently unknown, but the exclusion of light is probably not an explanation given that William Friedman (1986) has shown that female gametophytes with all their seed coats intact are capable of photosynthesis.

Ecological Implications

The results of my experiment indicate that aspects of ginkgo's sexual reproduction cycle are strongly influenced by temperature (Del Tredici 2007). For seeds left outdoors immediately following seed drop, the timing of their pollination influences the timing of their germination the following spring which, in turn, influences their chances of surviving the following winter. In warm-temperate climates—such as Guizhou Province—ginkgo seeds are shed in late summer or early fall, and the embryo is able to make considerable growth during the mild weather that follows. In cold-temperate climates—such as Massachusetts—seeds are shed much later in the season and the cooler temperatures of mid to late fall delay embryo development until warm weather arrives the following spring. This differential timing of embryo maturation means that seeds produced by trees growing in warm-temperate climates will be ready to germinate during the favorable conditions of

Table 2. A comparison of the phenology of the sexual reproduction cycle of *Ginkgo biloba* growing in Guizhou Province, China versus Massachusetts, USA.

Location	Pollination	Seed Abscission	Outdoor Germination
Guizhou, China (25° North latitude)	mid-March to early April	mid-September	mid-March
Massachusetts, USA (42° North latitude)	mid-May	late October to early November	mid- to late June

mid to late spring (March through early June), while those in cold climates will not germinate until later in the summer (late June through early August), when conditions for establishment are less favorable and the seedlings have less time to accumulate carbohydrates before going into winter dormancy.

In this regard, it is worth noting that in Tuo Le Village in Guizhou Province, ginkgo seeds sown outdoors would typically germinate in March, while the same seed sown outdoors in Boston did not germinate until May 29, approximately two months later. From an ecological perspective, the complex phenology of ginkgo's sexual reproduction cycle may well have constrained the species' ability to migrate, independently of humans, into cold-temperate regions with short growing seasons, and probably accounts for its limited warm-temperate distribution as a wild or semi-wild tree in the mountains of central and eastern China (Li et al. 1999, Xiang et al. 2006, Wei et al. 2008). Table 2 presents a comparison of the phenology of *Ginkgo biloba*'s sexual reproduction cycle in Guizhou Province, China versus Massachusetts, USA.


NANCY ROSE

A fossilized leaf of *Ginkgo yimaensis*.

Evolutionary Implications

The fossil species *Ginkgo adiantoides* existed in the northern hemisphere from the Upper Cretaceous through the Middle Miocene (roughly 70 to 12 million years ago) and is considered by paleobotanists to be morphologically indistinguishable from the modern *G. biloba* (Tralau 1968). Most of the ginkgo fossils from this time period in Europe and North America come from sites above 40° N latitude that were originally disturbed stream margins and levee environments, and typically occurred in association with a consistent set of riparian plants, including *Cercidiphyllum, Metasequoia, Platanus,* and *Glyptostrobus* (Royer et al. 2003).

Fossils of a new *Ginkgo* species (*G. yimaensis*) from Liaoning Province, China, recently described by Chinese paleobotanists Zhou and Zheng (2003), have pushed the lineage of *G. biloba*-type ovules back to the Lower Cretaceous, about 120 million years ago. This suggests the possibility that the seeds of *G. yimaensis* could have possessed a temperature-sensitive, developmental-delay mechanism similar to that of *G. biloba.* Such a trait would have allowed this species to reproduce successfully in regions of the northern hemisphere that were undergoing dramatic cooling after a long period of warm conditions. Indeed, Zheng and Zhou (2004) have proposed that "the drastic climatic changes during the Upper Jurassic and Lower Cretaceous, around 140 to 150 million years ago, were responsible for the transformation of the ovulate organs of the *G. yimaensis* type into the modern *G. biloba* type," including the development of short shoots, the reduction and protection of ovulate organs, and the production of larger seeds. *Ginkgo biloba*'s temperature-sensitive, embryo-development-delay mechanism could well have been another climate-induced Cretaceous innovation—an evolutionarily primitive but ecologically functional form of seed dormancy.

Ginkgo Seed Dispersal

Researchers studying various ginkgo populations in Asia have reported a number of animals feeding on, and presumably dispersing, the malodorous, nutrient-rich seeds. In China, dispersal agents include two members of the order Carnivora: the leopard cat (*Felis bengalensis,* family Felidae) in Hubei Province and the masked palm civet (*Paguma larvata,* family Viveridae) in Zhejiang Province (Del Tredici et al. 1992). In Japan, where ginkgo was introduced from China some 1,200 years ago, another member of the order Carnivora, the raccoon dog (*Nyctereutes procyonoides,* family Canidae), has been documented feeding on ginkgo seeds, and its droppings have been found to contain intact seeds which germinated the following spring (Rothwell and Holt 1997).

The existence of three reports of omnivorous members of the Carnivora consuming whole ginkgo seeds suggests that the rancid smelling sarcotesta may be attracting primarily nocturnal scavengers by mimicking the smell of rotting flesh—in essence acting as a carrion-mimic (Del Tredici et al. 1992). The fact that ginkgo seed germination percentage is enhanced by removal of the sarcotesta lends further credence to this theory.

Ancient Dispersal Agents

In 2002, Zhou and Zhang reported the discovery in China of a long-tailed bird (*Jeholornis* sp.) from the Early Cretaceous with a large number of ginkgo-like seeds in its crop. This provides direct evidence that early birds potentially *could* have been involved in seed dispersal activities, although the seeds' intact nature suggests they were destined for digestion in the gizzard. In general, *Ginkgo biloba* seeds do not fit the typical profile of a fruit dispersed by modern birds (van der Pijl 1982).

Prior to the discovery of *Jeholornis,* most of the speculation about Cretaceous ginkgo dispersal agents centered on dinosaurs, based primarily on their temporal overlap. If dinosaurs were involved with the dispersal of ginkgo seeds, it probably would have been carrion feeding scavengers, with teeth adapted to tearing and swallowing flesh, rather than herbivores with grinding dentition that would have crushed the thin-shelled seeds. At any rate, any connection between dinosaurs and ginkgo seed dispersal is, at best, conjecture based on circumstantial evidence.

A spontaneous ginkgo sapling growing out of a karst rock formation at Niu Tang village in Wuchuan County, Guizhou Province.

Ginkgo's Future

By rights, *Ginkgo biloba* should have gone extinct long ago along with all of its close relatives. The fact that it did not provides botanists with a unique window on the past—sort of like having a living dinosaur available to study. As remarkable as ginkgo's evolutionary survival is, the fact that it grows vigorously in the modern urban environment is no less dramatic. Having survived the climatic vicissitudes of the past 120 million years, ginkgo is clearly well prepared—or, more precisely, preadapted—to handle the climatic uncertainties that seem to be looming in the not too distant future. Indeed, should the human race succeed in wiping itself out over the course of the next few centuries, we can take some comfort in the knowledge that the ginkgo tree will survive.

This ginkgo, growing as a street tree in New Brunswick, New Jersey, shows the species' outstanding yellow fall color.

True survivors, these severely pruned ginkgos on a Tokyo street are growing in spite of cramped planting spaces and air pollution.

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Peter Del Tredici is a Senior Research Scientist at the Arnold Arboretum. A more extensive discussion of this topic can be found in the author's article "The Phenology of Sexual Reproduction in *Ginkgo biloba:* Ecological and Evolutionary Implications", 2007, *The Botanical Review* 73(4): 267–278.

The Fruits of Autumn

Nancy Rose

Autumn is prime time for observing a great array of maturing fruits on woody plants. Fleshy types like pomes, drupes, and berries are often brightly colored and highly noticeable at this time of the year. Fall-fruiting trees and shrubs—viburnums (*Viburnum* spp.), crabapples (*Malus* spp.), mountain ash (*Sorbus* spp.), beautyberries (*Callicarpa* spp.), and hollies (*Ilex* spp.), to name a few—provide a showy display, especially as deciduous leaves begin to fall. In addition to adding color to the landscape, fall-fruiting plants also serve as an important food source for birds.

Other fruiting structures seen in autumn are less showy but still interesting. Pods, samaras, and inflated capsules are some of the diverse forms to be seen. As anyone who has ever tried to learn woody plants knows, fruits often provide the key for correct identification.

Here are some examples of fruits to look for this fall:

ALL PHOTOS BY THE AUTHOR EXCEPT AS INDICATED

Grape honeysuckle, (*Lonicera reticulata*)

ROBERT MAYER

Common persimmon (*Diospyros virginiana*)

The word "berry" is often used to describe just about any rounded, juicy-looking fruit, but botanically speaking a ***berry*** is a fleshy, indehiscent (not splitting open at maturity) fruit that develops from a single pistil and contains one or multiple seeds. A number of woody plants bear berries including vines like *Vitis* (grape), *Actinidia* (kiwi), and *Parthenocissus* (Virginia creeper, Boston ivy). Both vine and shrub species of *Lonicera* (honeysuckle) have berries, often attractive bright red ones. Common persimmon (*Diospyros virginiana*) is one of few large trees that produces true berries; look for the golden orange, globe-shaped fruits persisting on branches through late autumn.

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Clockwise from upper left:
Donald Wyman crabapple (*Malus* 'Donald Wyman')
Korean mountain ash (*Sorbus alnifolia*)
Chinese sand pear (*Pyrus pyrifolia*)
Black chokeberry (*Aronia melanocarpa*)

A ***pome*** is a fleshy, indehiscent fruit that develops from a compound ovary set within a fleshy floral cup or tube. Multiple seeds are found in the core of the fruit. Pomes are the fruits of a number of well-known genera in the rose family (Rosaceae), including *Malus* (apple, crabapple), *Sorbus* (mountain ash), *Pyrus* (pear), *Crataegus* (hawthorn), *Aronia* (chokeberry), *Cotoneaster,* and *Pyracantha* (firethorn).

Clockwise from upper left:
Sapphireberry (*Symplocos paniculata*)
American cranberrybush (*Viburnum trilobum*)
Purple beautyberry (*Callicarpa dichotoma*)
Winter Red winterberry (*Ilex verticillata* 'Winter Red')

Another common berrylike fruit found on woody plants is the ***drupe.*** A drupe is a fleshy, indehiscent fruit containing a single seed which is surrounded by a stony endocarp. Many of the showiest fall-fruiting shrubs and small trees bear drupes, including viburnums (*Viburnum* spp.), beautyberries (*Callicarpa* spp.), dogwoods (*Cornus* spp.), and hollies (*Ilex* spp.). Many delicious drupes are found in the genus *Prunus* including cherries, plums, and peaches.

A ***hip*** is a pomelike structure formed by a fleshy hypanthium (a cup-shaped structure formed from fused floral parts at the flower's base) which surrounds multiple achenes (small, dry fruits containing single seeds). The term hip is used specifically for roses (*Rosa* spp.). The large, scarlet hips of *Rosa rugosa* (left) give it one of its common names: beach tomato.

Aggregate fruits are composed of numerous small fruits that develop from multiple pistils in a single flower. Raspberry fruits, for example, are aggregates of drupelets. Magnolias produce conelike aggregates of follicles; at maturity, each follicle opens to reveal a seed covered by a brightly colored aril (fleshy seed coat) and attached by a stretchy thread. The fruit of a hybrid sweetbay magnolia (*Magnolia virginiana*) is seen here (right).

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Multiple fruits develop when the fruits derived from numerous individual flowers in an inflorescence fuse together to form what appears to be a single fruit. Pineapple (*Ananas* spp.) and mulberry (*Morus* spp.) are examples of multiple fruits. The unique, baseball-sized green fruits of osage orange (*Maclura pomifera*), shown at left, are also multiple fruits.

Built to be carried by the wind, ***samaras*** are winged achenes. The papery wing part of the structure takes variable forms; for example, in elms (*Ulmus* spp.) the wing encircles the achene, in ash (*Fraxinus* spp.) the wing extends like a paddle from a single achene, and maples (*Acer* spp.) bear paired (two-winged) samaras that usually split apart when they mature and fall. The size and wing angle of maple samaras provide a good identification key among species.

Three-flowered maple (*Acer triflorum*) bears triplets of two-winged samaras. Another samara variation—a single achene dotted in the middle of the wing—is seen in this red-fruited form of the notoriously seedy tree-of-heaven (*Ailanthus altissima* f. *erythrocarpa*).

Exclusive to oaks (*Quercus* spp.), ***acorns*** are hard-shelled seeds (nuts) nested in cup-shaped involucres. Acorn size and degree of involucre extension on the nut provide a good clue when trying to identify oak species. Noted for their extensively fringed involucres, the acorns of bur oak (*Quercus macrocarpa*) are seen in this image.

Many plants bear seed-holding ***capsules*** but the forms of these dry, dehiscent (splitting open at maturity) fruits vary widely. The inflated, paper-lantern-like capsules found on golden rain tree (*Koelreuteria paniculata,* left) turn from green to tan—sometimes with a blush of pink—and often persist well into the winter. Also shown (right) are the small, rounded capsules of summersweet (*Clethra alnifolia*), filled with numerous tiny seeds.

Pods are dry, dehiscent or indehiscent fruits that contain seeds. The legume family (Fabaceae) is well-known for producing pods as its fruiting structure. Woody plants in this family include honey locust (*Gleditsia* spp.; pods of *G. triacanthos* pictured), Kentucky coffee tree (*Gymnocladus dioicus*), wisteria (*Wisteria* spp.), and silk-tree (*Albizia julibrissin*).

Book Review: *Fruits and Plains: The Horticultural Transformation of America*

Thomas J. Schlereth

Fruits and Plains: The Horticultural
Transformation of America
Philip J. Pauly. Harvard University Press,
Cambridge, Massachusetts,
2007. 336 pages.
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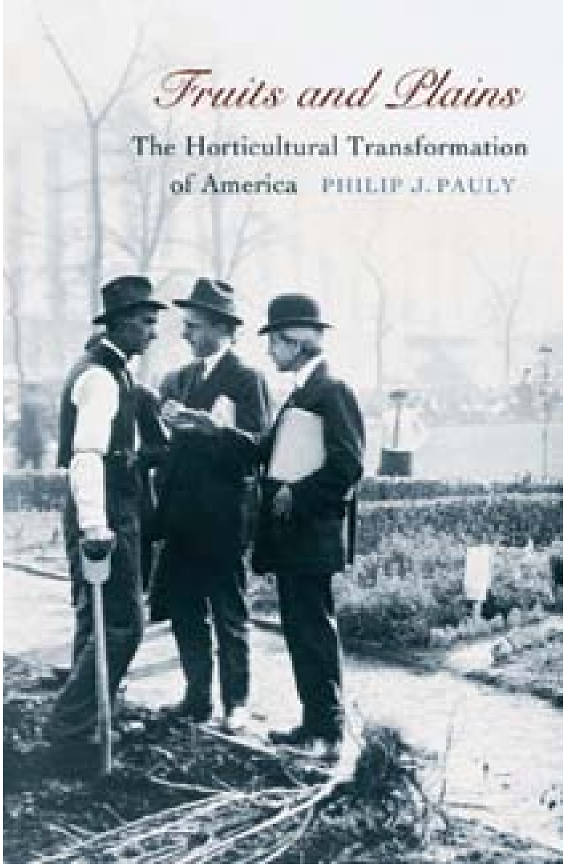

Many readers, at first glance, may find this book's main title a bit puzzling. What do pomology and plains have in common? The author intends this minor mystery but he does provide several clues in his introduction and the nine chapters that follow. I must admit I had not completely grasped his full meaning until reaching his closing chapter where a complete explanation is found. Out of respect for the author's book-craft, I too will leave this resolution for the end.

Long before arriving at the book's conclusion, I knew that what I was reading was a provocative and persuasive re-interpretation of several interrelated research fields; namely American plant pathology, biogeography, and cultural history. Moreover, it was a brilliant and novel re-interpretation of nineteenth-century American history using American cultivated plants as a primary resource.

Beginning with the introduction ("Taking the History of Horticulture Seriously"), Philip J. Pauly launches his methodology of interconnecting American horticultural history with American cultural history. This fruitful hybrid yields many useful insights, one of which is how our perpetual indulgence in claiming to be exceptional in our nationhood can also be found, repeatedly, in our horticultural history.

As one might expect of a cultural historian, Pauly frequently reminds us of a more universal issue evident in all of our interactions with the natural word: that is, whether we are home gardeners or plant scientists, landscape architects or arboretum directors, USDA bureaucrats or environmental historians, we all *culture* nature. When we *horti*-culture nature, its plants become, to various degrees, natural artifacts subject to various forms of human artifice.

Hence there are two general perspectives that characterize Pauly's achievement. First, one can see it as a revisionist interpretation in American Character historiography, a subfield in interdisciplinary American Studies scholarship since the 1950s. Second, the book is also a carefully documented survey of how Americans, despite their professed objectivity (scientific and otherwise), historically brought various types of cultural baggage (political and economic; regional and religious; professional and personal) to their several centuries of interactions with other living organisms and particularly with plants and plant pests.

To document this dual approach—explaining both American history and the history of American horticulture—Pauly analyzes the motives and actions of a cadre of Americans who cultured nature in diverse ways and often for divergent purposes. Many will be familiar to *Arnoldia* readers: for instance, Thomas Jefferson, Frederick Law Olmsted (Senior and Junior), Charles Hovey, Charles S. Sargent, Horace J. McFarland, Jens Jensen, and Liberty Hyde Bailey. Also studied are less well-known but influential plant culturists such as David Hosack, Beverly T. Galloway, William Saunders, Ephraim Bull, Charles T. Simpson, Daniel Simberloft, Charles L. Marlatt, and Katherine Bates.

With these *dramatis personae,* Pauly explores several additional subthemes. In chapter one, for example, he stages Thomas Jefferson as an early exemplar of American horticultural chauvinism, particularly in his *Notes on the State of Virginia* (1785, 1787) written, in part, to answer Guillame Raynal's *Historie de deux Indes* (1770), a European best seller that claimed the New World's flora, fauna, climate, as well as its native peoples and even its recent emigrant Europeans were all in a state of continual anthropological and biological degeneracy.

In chapter one, he also provides early definitions for terms readers will find throughout the book: first, a vocabulary of " N-words": nature, natural, naturalism, nationalism, and nativism; second, a litany of "C-words" that no cultural historian can do without: culture, cultural, and culturalism, plus related "culture" nomenclature that Pauly uses frequently.

Chapter two initiates another important book topic—the tensions and controversies (diplomatic, military, economic, political, and scientific) that have been factors in the history of plant introductions and plant pests all arriving in increasing numbers to a supposedly virgin land. The first culprit is the Hessian fly (*Mayetiola destructor*) which Pauly discusses as "America's first invasive" as well as "the nation's first postcolonial public scientific issue."

This initial late eighteenth-century debate over invasives and introductions resurfaces in several places throughout the book in its survey of nineteenth- and early twentieth-century arguments over exotic vs. native species as well as the horticultural practices (organic vs. chemical) in solving plant pathologies. Chapters five and six, cleverly named by Pauly as "Immigrant Aid: Naturalizing Plants in the Nineteenth Century" and "Mixed Borders: A Political History of Plant Quarantine," document the local, regional, and national aspects of these prolonged conflicts, many of which are still contested issues in present-day horticulture.

Massachusetts Gypsy Moth Commission employees scraping gypsy moth egg masses off of a notable elm in Malden, Massachusetts in the early 1890s. From *The Gypsy Moth* (1896), Edward H. Forbush and Charles H. Fernald.

STEREOPTICAN IMAGE COURTESY OF WELLESLEY COLLEGE ARCHIVES

5544 Wellesley College from Hunnewell's Gardens.
Copyright 1901 by C. H. Graves.

In chapter six's subtitle, another Pauly interpretive emphasis appears. He recognizes that plants have politics in the sense that people culture plants with political (and other) motives. For some readers, however, his extremely detailed accounts of the political infighting among plant importers and breeders, university science faculty and nursery growers, government officials and departments as well as plant collection administrators may prove too tedious a tale to stay with until the chapter's conclusion.

Turning back to chapters three and four, respectively titled "The Development of American Culture, with Special Reference to Fruit" and "Fixing the Accidents of American Natural History: Tree Culture and the Problem of the Prairie," we find major clues to the book's main title as well as nineteenth-century America's fascination with pomology. It also introduces us to Midwestern horticultural biogeography, one of the book's three such foci—the other two being the country's northeastern corridor and the anomaly of the "horticultural construction" of Florida. The latter history turns out also to have interesting ties to northeastern plant culturists, as diverse as diplomat Henry Perrine, proprietary town builder and citrus magnate Henry Stanford, railroad and luxury hotel entrepreneur Henry Flagler, plus the USDA's David Fairchild (after whom the Fairchild Tropical Botanic Garden in Coral Gables is named), and America's most famous nineteenth-century woman abolitionist and author, Harriet Beecher Stowe. (Interestingly, author Pauly grew up in Ohio, one gateway to—as well as an important part of—the Midwest's horticultural hearth.)

Pauly's chapter nine (titled "Culturing Nature in the Twentieth Century") is unfortunately only a 28-page introduction to what might have been a larger *Fruits and Plains* or a second volume as its sequel. Here we find important developments such as the founding, at long last, of a National Arboretum in 1927, and the influential Midwestern prairie restoration by James Curtis and Aldo Leopold at the University of Wisconsin Arboretum in 1936. Also treated are the importance of the American Society for Horticultural Science and the enormous multiplication of garden clubs nationwide, plus a brief survey of "How Pests Became Invasive Species." Given its brevity, the chapter is a tantalizing but selective overview of an extremely complicated and conflicted century in American horticultural history.

In beginning his final chapter, Pauly references the poetry, travels, and academic career of Katherine (Kitty) Bates, an undergraduate and later a lifelong English professor at Wellesley College. Pauly muses that Bates, both as student and teacher on the Wellesley campus, could gaze across Lake Waban and see the highly cultured conifer topiary garden and arboretum at the estate of H. H. Hunnewell, one of New England's most well-known horticulturists and a generous benefactor of the Arnold Arboretum. In 1893, Professor Bates took a combined pleasure/professional trip to teach a summer-school course at Colorado College. En route she visited Chicago's World's Columbian Exposition designed in part by Frederick Law Olmsted, Sr., travelled through Kansas prairies and wheat fields, and climbed Pikes Peak for a majestic view of the seemingly never-ending Great Plains. Atop that mountaintop, she reflected on all that she had seen on her westerning odyssey. On the peak, the beginning words of a poem also came to her. It was published in 1895 by *The Congregationalist* as its Fourth of July number. New Yorker Samuel A. Ward set the poem to music and we have sung it ever since, a geographical and horticultural counter point to Francis Scott Key's militant navel ode whose melody Key borrowed from a British drinking song.

Professor Pauly deploys Professor Bates's verses (obviously "the fruited plain") to announce his final chapter titled "America, The Beautiful." More an epilogue than a chapter, it serves as his own anthem to his subject's meaning in both American horticultural history and American cultural history. He concludes by noting that the Bates metaphor provided him with "a kind of professional and personal perspective" by which to summarize and to reflect on his book's methodology (the transformation of horticulture by American culture, culturing, and culturists) and its ambitious scope and synoptic brilliance (to offer an answer, in my judgement, to the question: "What's American about American nature?").

In his moving, intimate acknowledgements—placed significantly but uncharacteristically at the end of his conclusion—he alludes to his personal battle with lymphoma cancer. Phillip J. Pauly died of the disease in April, 2008, at age 57, and American historical scholarship lost one of its most insightful culturists.

Thomas J. Schlereth is Professor of American Studies and History at the University of Notre Dame.

An Excerpt From *Fruits and Plains: The Horticultural Transformation of America*

Philip J. Pauly

Prairie Spirit

Northeasterners' struggles to garden landscape were recapitulated, in a shorter time span and with greater seriousness, in Illinois and Wisconsin. Interest in replicating familiar Anglo-Hudson scenery competed with desires to evoke the regionally distinctive prairie. Landscape historians have focused on the pre-World War I innovations of the Danish German immigrant Chicago park designer Jens Jensen and the American horticulturist Wilhelm Miller. I suggest, however, that Jensen's and Miller's "prairie style of landscape gardening" drew so much from German and Olmstedian naturalism, and placed so much emphasis on shrubs and trees, that it contained little that was distinctive. The truly important development occurred, not on Chicago parklands or North Shore estates in the 1910s, but in southern Wisconsin in the 1930s, where Aldo Leopold planted a vast wildflower garden. [p. 187]

Original Wisconsin

Aldo Leopold, Norman Fassett, and Theodore Sperry were the developers of a real prairie style of landscape gardening. Between 1935 and 1940, they transformed about twenty-seven acres of old pasture in Dane County, Wisconsin, a few miles southwest of Madison, into a naturalistic garden of grasses and wildflowers that they called a prairie. This act of historical naming enabled them to resolve the problem faced by landscape gardeners from Downing to Miller. They planted a landscape that was distinguishable from, and an improvement upon, the common vegetation around it, but which was plausibly naturalistic.

The University of Wisconsin Arboretum began as a provincial Olmstedian park project. In 1911 the private Madison Park and Pleasure Drive Association hired the young Massachusetts landscape architect John Nolen to prepare a comprehensive plan for the improvement of their city. Among Nolen's recommendations was the idea that the city and the university should emulate Boston and Harvard's partnership of the 1870s by establishing an arboretum-park on the shore of Lake Mendota, west of the city and the university campus. That suggestion went nowhere. The arboretum idea was revived in the late 1920s, however, by local boosters seeking to transform a failed suburban development on the small and marshy Lake Wingra, a few miles southwest of the city. They argued that the state and the university should fund a park, arboretum, and wildlife refuge as part of the ongoing initiative to establish a conservation professorship for Madison-based forester and game manager Aldo Leopold. The university approved this plan in 1932, appointed landscape architect William Longenecker to the position of executive

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MOLLY FIFIELD MURRAY, UNIVERSITY OF WISCONSIN

The Curtis Prairie at the University of Wisconsin Arboretum as it appears today.

director, and asked Leopold to take on the arboretum's research directorship as one of his professorial duties.

Disagreements arose immediately over issues of plant choice. Longenecker envisioned a landscape park containing systematically and ecologically ordered displays of all the perennials, shrubs, and forest trees that might prove hardy in Wisconsin. Visitors to the arboretum would be inspired to beautify their own properties, and would learn what different ornamentals and woodland trees looked like and which were worthwhile. Leopold wanted to send the visiting public a different message. He was uninterested in what he considered merely "a 'collection' of imported trees." Instead he wanted to show how much the state's vegetational quality had declined since the 1830s, and to provide a vision for improvement in the future. Advised by botany professor Norman Fassett, he proposed that the arboretum should be "a reconstruction of original Wisconsin." It would be "a bench mark, a datum point, in the long and laborious job of building a permanent and mutually beneficial relationship between civilized men and a civilized landscape." This disagreement was resolved by dividing the arboretum into areas controlled by either Longenecker or Leopold.

For Leopold and Fassett, original Wisconsin was an essentially steady state, consisting of forest, wetland, and prairie, that had existed prior to Anglo-American settlement. (They passed over the major presence of Indians in Dane County during the Woodland Period, evident in the number of mounds—over one thousand, more than anywhere else in the United States.) Creating replicas of these plant communities on a few hundred acres would require a number of different kinds of effort. Sections with trees could redevelop on their own if there were fire suppression and culling of undesirable species. The right mix of wetland vegetation depended largely on steam dredges that could change the monotonous marsh into a more varied landscape of islands and lagoons. Shoreline areas with different slopes and soil compositions could then be planted with cattails and pondweeds that would attract wildfowl.

The real gardening challenge, however, was to create a "Wisconsin prairie" (the present-day Curtis Prairie). The basic prerequisite was labor. In 1934 the arboretum received a windfall when the state established a work relief camp for transients on its grounds. Then, when complaints arose about the behavior of these migrants and hoboes, the university persuaded the National Park Service to take over the camp and use it for the Civilian Conservation Corps (CCC) (see Figure 7.9). The CCC recruited a more tractable pool of young local men, and its involvement enabled the university to hire the young National Park Service plant ecologist Theodore Sperry as foreman. "Camp Madison" averaged about two hundred residents during the second half of the 1930s, at a cost to the federal government of more than two million dollars.

This photograph from the 1930s shows University of Wisconsin horticultural director William Longenecker directing Civilian Conservation Corps workers planting prairie sod.

COURTESY UNIVERSITY OF WISCONSIN-MADISON ARCHIVES

The first step in the creation of a Wisconsin prairie park was to clear existing old-field growth. Tree control was a straightforward matter of destroying saplings, but was complicated by Fassett and Sperry's interest in leaving one large tree standing to evoke early settler accounts of "oak openings"; each year laborers had to pull up a crop of squirrel- and bird-distributed oak seedlings. The major problem was quack grass. Sperry and his workers sought to eliminate this Old World pasture mainstay and agricultural weed by plowing deeply, harrowing to dry out the rhizomes, and then replanting with clover to smother remaining growth. Irritating plants such as nettles and thistles were also a concern, without regard to their geographic origin. Finally, Leopold sought to suppress high-density populations ("thickets") of plants that were too common, such as goldenrods and asters.

Once the ground was cleared, the major issues involved plant choice. In principle, Fassett and Sperry's palette could include any of the species

A Civilian Conservation Corps worker displays a massive *Silphium* taproot.

UNIVERSITY OF WISCONSIN-MADISON ARBORETUM ARCHIVES

associated with prairies in or near Wisconsin during the previous century. A present-day list of such plants totals between 340 and 550. But prairie gardeners in the 1930s were neither capable of nor interested in cultivating such a diverse flora. Sperry's planting list from 1935 to 1939 consisted of about fifty species. In both his exclusions and featured species, his goal was to plant an assemblage that would not be confused with common or despised pasture.

The largest category of excluded species consisted of the dozens of plants that were small, had inconspicuous flowers, or were visually generic. There was minimal interest in devoting labor and space to vegetation that added little to the field's visual composition. More straightforwardly, Sperry did not replant the nettles and thistles that had been removed when the land was cleared, nor did he introduce additional species with similar properties. While some of the more memorable native species that people encountered on Wisconsin prairies were greenbrier (*Smilax lasioneura*), prickly pear (*Opuntia macrorhiza*), and poison ivy (*Toxicodendron radicans*), they were not part of the arboretum plantings. The most interesting group of exclusions was of species poisonous to livestock. Prairie larkspur (*Delphinium carolinianum* subsp. *virescens*), sundial lupine (*Lupinus perennis*), and death camas (*Zigadenus elegans*) were all visually impressive Wisconsin natives. But the prosperous rural citizens whose sensibilities Leopold wanted to touch would not have appreciated a field filled with seed-bearing specimens of the weeds they had worked for a century to eradicate.

NANCY ROSE

Compass plant (*Silphium laciniatum*) was one of the forbs selected by plant ecologist Theodore Sperry for the Wisconsin prairie park.

Sperry wisely emphasized familiar species that would, under proper cultivation, provide a spectacular mass display. His most frequently planted species was turkeyfoot grass (*Andropogon gerardii,* now commonly called big bluestem). The most-planted forbs were stiff sunflower (*Helianthus rigidus*) and three species of *Silphium* (including compass plant and rosinweed). Others included blazing star (*Liatris*), prairie goldenrod (*Solidago rigida*), prairie rose (*Rosa carolina*), prairie bush clover (*Lespedeza capitata*), prairie coneflower (*Lepachys pinnata*), and prairie painted cup (*Castilleja sessiliflora*). They were either large (big bluestem, compass plant, and stiff sunflower could all grow ten feet high in a good summer), had conspicuous flowers (blazing star, rose, coneflower), or unusual characteristics (indicated in names such as compass plant and painted cup). While Wisconsinites might know these plants, they would have seen them only in small populations or in fields browsed by livestock. At the arboretum, by contrast, they were able to display their capabilities and to reinforce each other visually as elements of a multiacre garden. People who visited this landscape, especially in the peak summer vacation months of July and August, would experience a wonderful wildflower garden in the style of a prairie. It was both easy and pleasant to imagine that this was original Wisconsin. [pp. 190 to 194]

Collecting Sweetgum in the Wilds of Missouri

John H. Alexander III

On a sunny day in December, 1979, in the countryside near Zalma, Missouri, a tractor dutifully worked the upper end of a 40-acre field. In search of native tree seeds, Arboretum horticulturist Gary Koller and I were about half way across the lower end of the field when the tractor turned toward us. The farmer, clearly silhouetted against the skyline, picked up a rifle.

It suddenly became clear that we were trespassing. Gary turned to me and said "Do you have a business card?" I don't recall the expletives or the suggestions I proffered, but I handed him a card. He ran toward the tractor, waving the card like a tiny white flag. Dumbfounded, I stood and watched, then followed.

As it turned out, the farmer's brother had been shot (not fatally) by errant hunters while working in these fields a week or two earlier. The farmer was friendly, apologized for the rifle, and welcomed us to collect seeds in an uncultivated area by the river. It was there in the floodplain of the Castor River that Gary and I collected the seed from which the sweetgum (*Liquidambar styraciflua,* accession 1248-79-B) pictured at right was grown.

At 28 years old, this sweetgum is 36 feet (11 meters) tall with a DBH (diameter at breast height) of 16 inches (40 centimeters). Typical mature height for sweetgum is around 60 to 80 feet (18 to 24 meters). Sweetgum has a pyramidal habit when young; older trees often have a rounded canopy. Its star-shaped leaves can develop striking fall color in shades of yellow, red, orange, and purple. The spiky, 1 to 1 ½ inch (25 to 38 millimeters) diameter fruits may be dried and used in decorations, but in large numbers can be an inconvenience when they fall on lawns and walkways. Sweetgum's branch texture is variable from tree to tree; branches may be fairly smooth or have corky wings. The latter trait is impressively displayed on specimen 1248-79-B; its eye-catching abundance of large, corky, winged protrusions gives the tree great textural interest, especially in the winter.

Native Ground

The Arnold Arboretum is well-known for its international plant explorations, especially in China. Woody plants from around the world fill the Arboretum's collections. But collecting from wild populations of native North American plants is also important to the Arboretum's mission. Gary and I were in Missouri to attend a plant propagators' conference in St. Louis, but we had also scheduled a couple of extra days for collecting in the area.

Our goal in southeast Missouri was to find species that were native to southern regions of the United States but were growing wild in a climate that was similar to our own in Boston. Sweetgum's principal native range extends from New Jersey to southern Illinois, south to eastern Texas and northern Florida. It is usually listed as hardy to USDA Zone 5, but specimens grown from seed sources in the southern part of its range may suffer significant damage in northern winters. We must have succeeded in collecting from an appropriate location—all three specimens of accession 1248-79 are in good condition. Currently, these are the only sweetgum trees in the Arboretum that are from a known wild source.

In addition to sweetgum, we collected a number of other species in Missouri and neighboring Illinois, including Ohio buckeye (*Aesculus glabra*), pawpaw (*Asimina triloba*), sycamore (*Platanus occidentalis*), possumhaw (*Ilex decidua*), buttonbush (*Cephalanthus occidentalis*), American hornbeam (*Carpinus caroliniana*), and river birch (*Betula nigra*). These species are all fairly common, but what's important is that our collections provide a genetic representation of each of these species as it exists in the wild. When one of these plants, like sweetgum specimen 1248-79-B, turns out to have ornamental characteristics that appeal to us as gardeners, that's icing on the cake.

John H. Alexander III is Plant Propagator at the Arnold Arboretum.