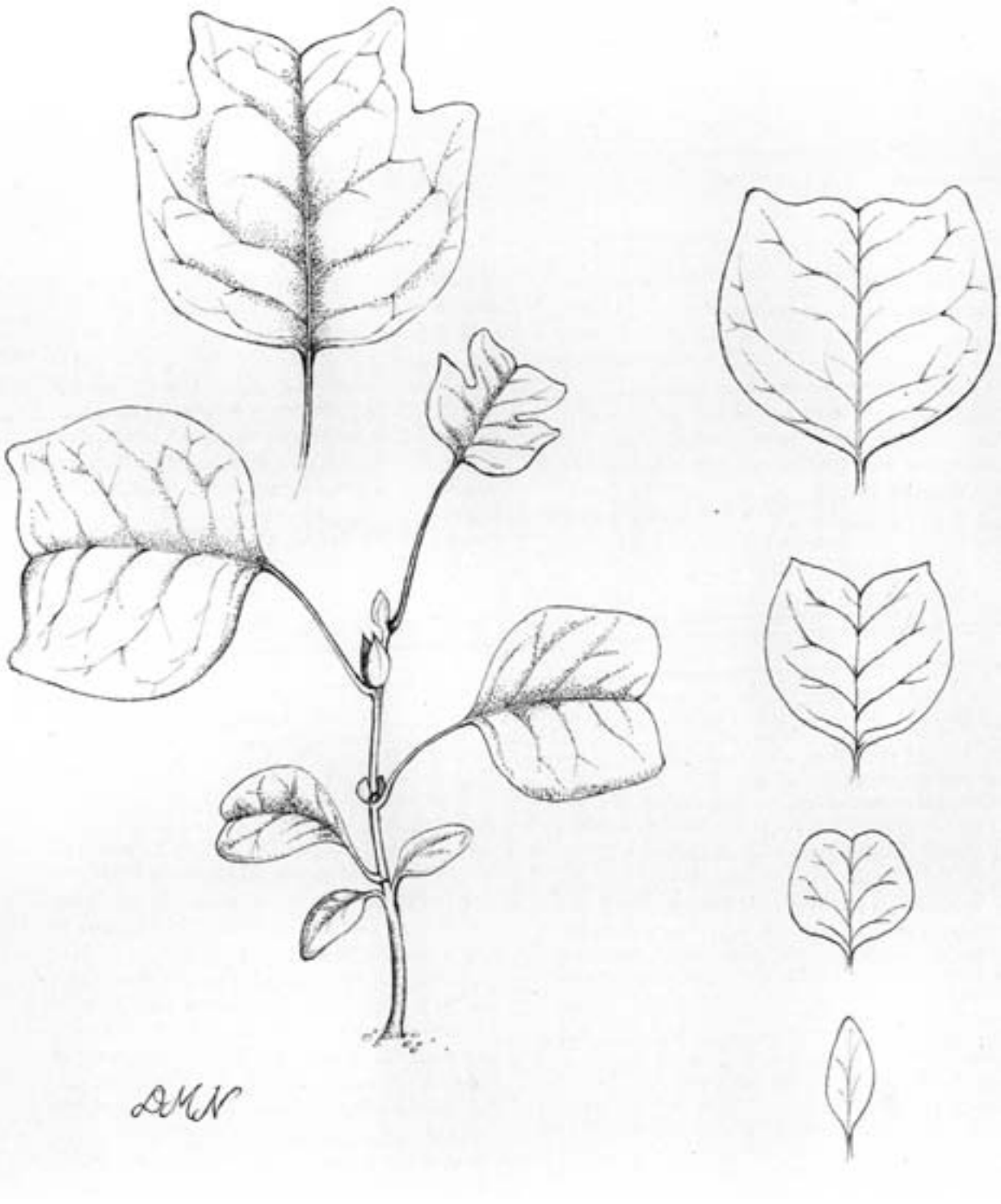


The shape of the mature leaf of the tulip tree is the result of a process that began with the seed leaves, or cotyledons

What's in a Leaf?

Peter Del Tredici

The tulip tree, *Liriodendron tulipifera*, is unusual among the trees growing in the forests of eastern North America in combining stately massiveness with delicate beauty. Its unbranched trunk, often as much as six feet in diameter, rises straight up out of the ground like a pillar and seems to hold up the sky above the forest in which it grows. I have never seen another tree, save the redwoods of California, that can evoke such an impression. These magnificent trees have managed to escape destruction by growing on the hard-to-reach slopes of mountain ravines throughout the eastern half of our continent. In the moist coves of the Great Smoky Mountains of Tennessee and North Carolina, they can reach 150 to 200 feet in height.

It is the absolutely straight, unbranched bole of the tulip tree that makes it instantly recognizable in the forest. Many other trees are equally straight when they are young, but few maintain such straightness into maturity the way *Liriodendron* does. The lower branches seldom get thick enough to produce forked trunks, even those of specimens growing in full sun. In the dense shade of the forest, the tree usually sloughs off its lateral branches before they get much more than an inch thick, and the columnar trunk extends far up into the crown. This habit of self-pruning, as it is called, makes the tulip tree particularly desirable to the forester, who wants good, straight lumber, and a bit bothersome to the homeowner, who wants a neat front yard.

In contrast to the great size of the tulip tree is the delicateness of its flowers, which come out in May or June, depending on the latitude in which the tree grows. They are quite large as tree flowers go—about two inches long and equally wide when fully opened—and very beautiful. The petals are of an unusual light, bright green and have a conspicuous orange splash at their bases. The central core of the flower—the anthers and the gynoecium—is a clear yellow. Unfortunately, the petals and the leaves are so nearly the same color that you have to look closely to tell whether a tree is in bloom. Indeed, not until you actually have removed a flower from the background of leaves can you fully appreciate its beauty. The blossoms are faintly fragrant and, like those of other members of the magnolia family, are pollinated by flies, beetles, and bees.

As if its trunk and flower weren't enough to recommend the tulip tree, its leaf is noteworthy for its graceful, elegant shape. While normally there is a high degree of variability in form from one leaf to the next on the same tree, all leaves share a feature that makes them unmistakable—notched, rather than pointed, tips. So fixed in most people's minds is the idea that leaves should taper to a point, that many nineteenth-century botanists described the *Liriodendron* leaf as having three lobes, with the tip of the middle lobe cut off. Even those botanists who correctly described the leaf as having four lobes noted that the leaf's apex was "missing" or "chopped off." Evidently they had a preconceived notion about what a leaf should look like—some sort of archetype, from which modern forms are de-

Figure 1. Progressive variation in the shape of the tulip tree leaf, beginning with the simple, lance-shaped cotyledon (lower right) and culminating in a miniature version of a mature, four-lobed leaf (upper left). A seedling (lower left) bears all five variations Drawing by Dawn M. Nunes.

rived—and tried to make *Liriodendron* fit the mold.

A better way to view the shape of the *Liriodendron* leaf is to follow its development in the germinating seedling. My own research in this regard suggests that the shape of the mature leaf is the result of a progressive, not a degenerative, process. The first structures the germinating tulip tree seedling produces are the seed leaves, or cotyledons, which are simple, lance-shaped structures that taper to blunt points. After the cotyledons, the next leaf is much simpler than those that the mature tree will produce. Almost round in its shape, it has a shallow notch at its tip. On the third leaf, two lobes begin to take shape on either side of this notch; on the fourth leaf, two lower lobes make their debuts. In healthy greenhouse-grown plants the next leaf, the fifth, has fully developed lower lobes and is a miniature version of the mature leaf. In effect, the plant is performing a kind of developmental dance in its progressive movement from one leaf to the next (Figure 1).

There is nothing unique about *Liriodendron* in its progressive leaf development. Botanists have recorded similar patterns in many other species. No one did it as early or as well as the great German poet–naturalist, Johann Wolfgang von Goethe, however. In 1790, Goethe published a little book entitled *Essay on the Metamorphosis of Plants*, in which he describes the life of a plant from the seed stage to the seed-producing stage as a series of internally regulated contractions and expansions. In his book, the leaf is considered the basic building block of the plant, and all other structures (except for the stem and the root, which he does not discuss) can be seen as modifications of the leaf. The key idea in *The Metamorphosis* is that plants are not static in their growth patterns but that, as they develop and grow, they change. Development, according to Goethe, is by its very nature dynamic, and the structures that a plant produces—the leaves and flowers—take on different forms depending upon whether they are produced during a phase of contraction or a phase of expansion. Regardless of what one feels about the correctness or accuracy of Goethe's ideas, his conception of growth as a dynamic process that results in a great deal of variation in leaf and flower structure would not be denied by anyone who works with plants. Goethe viewed the progressive development of the leaves of seedlings as part of the very first expansion phase in plant development:

> At each successive node the form of the [seedling] leaf attains greater perfection; the midrib lengthens, and the side ribs, which arise from it, extend more or less towards the margin. The different relations of the ribs to each other are the principal cause of the various shapes we observe in leaves which are notched, deeply incised, or formed of many leaflets, looking like little branches The Date Palm is a striking instance of the most simple form of leaf becoming gradually but deeply divided As the leaves succeed each other, the midrib lengthens, till at last it tears asunder the numerous compartments of the simple leaf, and an extremely compound, branch-like leaf is formed.

While the date palm shows increasing dissection of its leaves with each new leaf produced, the seedling leaves of the tulip tree show a dramatic change in their shape from one to the next. This can be seen most clearly by laying out the *Liriodendron* leaves in sequence. When I did this for the first time, I was reminded of Ernst Haeckel's famous nineteenth-century adage, "Ontogeny recapitulates phylogeny." In plain English, this means that the embryonic development of an individual organism encapsulates, summarizes, or repeats the whole evolutionary history of the species. While Haeckel's conception is not accepted as biological fact, it can help a person grasp the basic principles of growth and development. And so it is with the tulip tree. In arriving at the mature form of the leaf, the seedling must undergo a stepwise developmental process that may actually reflect the historical evolution of the leaf's shape. While this hypothesis is unprovable, it points out the dynamic nature of plant growth and evolution, much as Goethe's expansion–contraction theory does.

The pattern of change in the development of

the *Liriodendron* leaf does not stop at seedling leaf number five, but continues throughout the life of the tree. As the plant matures, it produces larger and larger leaves. These reach their maximum size during the plant's juvenile stage—roughly between five and ten years of age. During this period, the tree can, and does, produce perfectly shaped four-lobed leaves up to twelve inches long and ten inches wide (Figure 2). (Why some trees produce larger than normal leaves during their adolescence is not certain, but enough different species do so to suggest that these larger than normal juvenile leaves serve some function.)

As the tree approaches sexual maturity in ten to twenty years, the leaf size shrinks to six inches by six inches. And in fully mature trees, the leaves are usually only about five inches by five inches. Curiously, these mature leaves often have one or two extra pairs of lobes at their bases (Figure 3).

The developing bud in *Liriodendron* is no less fascinating than the developing leaf. The careful anatomical work of W. F. Millington and J. E. Gunckel, in 1950, showed that the intriguing stipules that grow together to form the outermost bud covering should be considered lobes of the leaf, or more precisely, as "products of leaf base rather than of stem" (Figure 4). We thus have the rather unusual situation (found also in the genus *Magnolia*) where the lower lobes of one leaf are modified during development to protect the next leaf in line. Interestingly, these leaf-protecting stipules do not make their appearance until the second seedling node, those at the first node being little more than rudimentary flaps of tissue incapable of surrounding anything. This fact suggests that the stipules, like the other lobes of the leaf, develop in a stepwise fashion.

In addition to being of botanical interest, *Liriodendron* buds are aesthetically fascinating, particularly in the spring when they burst apart to reveal their contents. The great French naturalist, François Michaux, described this process better than anyone in his classic, *The North American Silva*, published in 1818:

> On the Tulip Tree, the terminal bud of each shoot swells considerably before it gives birth to the leaf: it forms an oval sack which contains the young leaf, and which produces it to the light only when it appears to have acquired sufficient force to endure the influences of the atmosphere. Within this sack is found another, which, after the first leaf is put forth, swells, bursts, and gives birth to a second. On young and vigorous trees, five or six leaves issue successively in this manner from one sack Till the leaf has acquired half its growth, it retains the two lobes which composed its sack, and which are now called stipulae.

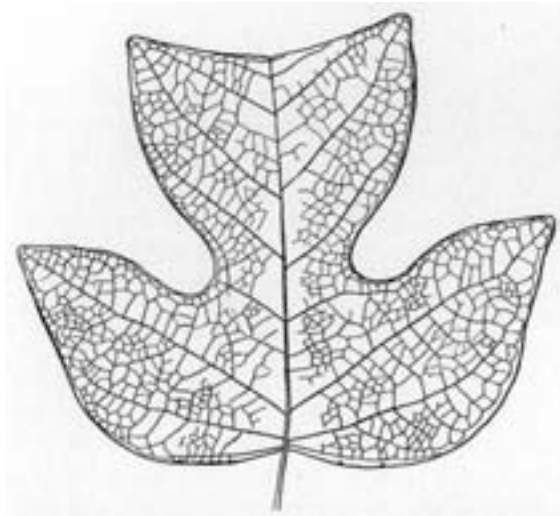
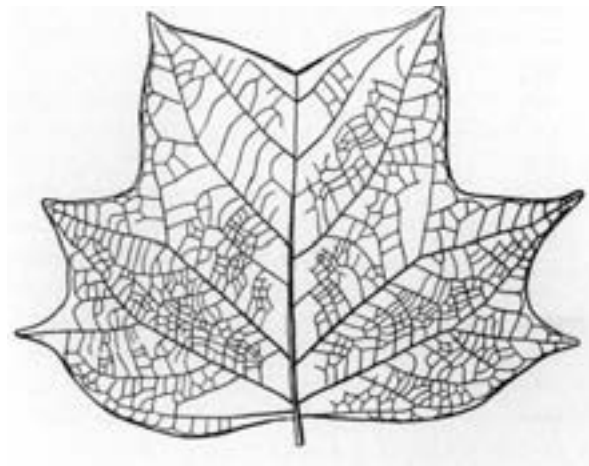


Figure 2. A four-lobed tulip tree leaf. This figure (and Figure 3) from *Proceedings of the U S National Museum*, Vol 13 (1890) Both figures courtesy of the Museum of Comparative Zoology, Harvard University.

Figure 3. The leaf of a fully mature tulip tree.



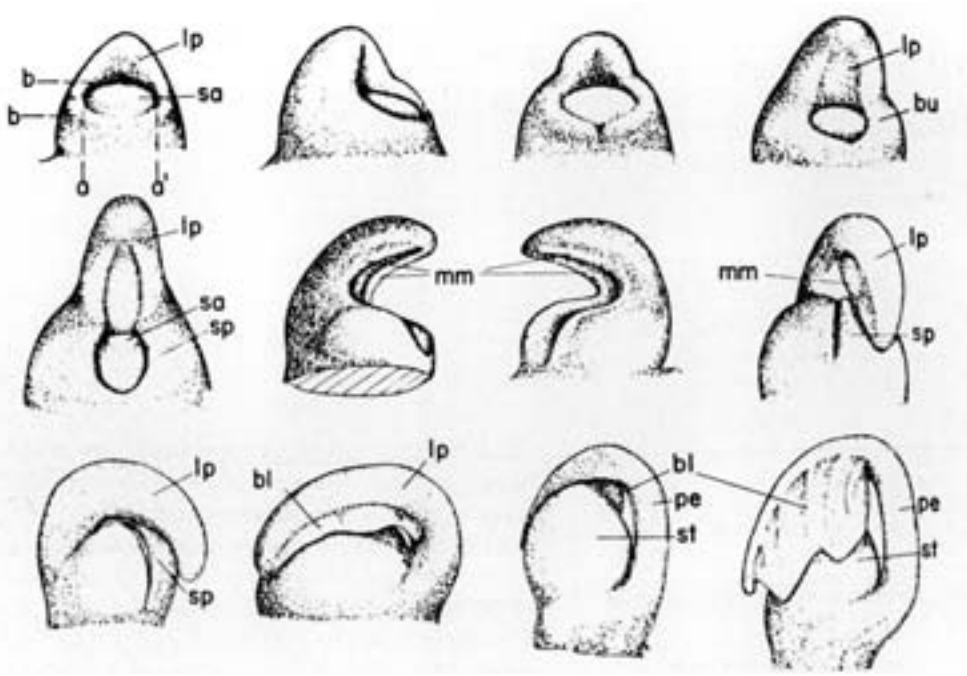


Figure 4 Development of leaf primordia and stipules of the tulip tree. From the research of W. F. Millington and James E Gunckel, reported in the *American Journal of Botany* Used with permission

The *Liriodendron* bud is like a series of boxes within boxes—Russian dolls, if you will—that nest together perfectly. Unfolding one by one, the leaves seem to have no limit to their numbers. Although Michaux doesn't describe it, the buds usually stop producing leaves in June with the beautiful green, yellow, and orange flowers. The whole process is a bit like a symphony, slowly building up through a crescendo of larger and larger leaves to a floral fortissimo.

After all of this, are we close to describing the leaf of the tulip tree? The answer depends on when one chooses to look at its leaves: seedling leaves differ from adolescent leaves, which differ from the leaves on mature trees. The simplistic drawings found in most field guides do not do justice to the variation shown by an individual tree, let alone that shown by the species as a whole. While such variation may be difficult for the taxonomist to reckon with, it can be a source of delight and inspiration for the poet and the curious naturalist.

Related Readings

A. Arber. Goethe's botany. *Chronica Botanica 10,* No. 2, pages 67–124 (1946).

J. W. von Goethe. *Essay on the Metamorphosis of Plants*. Translated by Emily M. Cox. *Journal of Botany 1,* pages 327–345 and 360–74 (1863).

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