The most remarkable thing about trees is how they develop and change over time. Every year they add height and girth in a flush of new growth. They are forever expanding, from the bottom to the top and from the inside to the outside—a tree that is not expanding is a tree that is dying. The growth of trees is totally different from that of vertebrate animals, which tend to reach their full developmental potential relatively early in life, and then maintain themselves in the mature stage for as long as possible. To put it another way, animals are closed and entire in their development while trees are open and expansive.

The easiest way to visualize what is meant by open development versus closed is to look at the different approaches to dealing with bodily injury. In trees, if a limb is broken off, then so be it; the trunk will grow around the break and attempt to cover over the dead branch by producing callus tissue that grows inward from the outer edges of the wound. In many cases, the tree will also produce a new branch just below the location of the old one. Some people call this response wound-healing, but in reality the tree is simply walling off the damaged or dead tissue—compartamentalizing it—in an effort to protect the undamaged portions of the trunk. Dead tissue embedded within the trunk is of little consequence so long as rot does not spread into the living wood (Shigo 1986). Mammals, of course, cannot tolerate the presence of dead tissue within their bodies. If they are to survive, they must repair the injured body part; growing a new one is not an option.

Understanding what trees are and how they grow is central to the discipline known as tree architecture, which was developed during the 1970s by a Frenchman, Francis Hallé, a Dutchman, Roulof Oldeman, and an Englishman (and Harvard professor), Barry Tomlinson. As these three scientists have defined the field, tree architecture describes the processes that regulate the growth and development of trees. Contrary to the meaning of the term architecture when applied to buildings, tree architecture is about dynamic change in tree form over time, it is not about the static, geometrical shapes of mature trees.
trees seen in field guides. To put it another way, tree architecture describes how trees develop their shapes, not what shapes they display. The discipline is particularly exciting because it deals with trees holistically, as intact, well-integrated organisms that are greater than the sum of their parts. Compared to most modern biology with its fixation on DNA sequencing, tree architecture takes a refreshingly nonreductionist approach to development.

The Meristem

Meristem is the term used for the specialized tissue that allows trees to continue expanding throughout their entire life span. This meristematic tissue produces the leaves, the stems, the flowers, the bark, and the roots—the differentiated tissues of the plant—while remaining undifferentiated itself. What makes meristematic tissue unique is that it exists in a perpetually embryonic state that allows the tree to be reborn every spring throughout its entire life.

Four different types of meristems are produced by trees. The most obvious one is the shoot meristem, or growing point, which is located at the heart of every bud on every tree. On a mature specimen oak, for example, there can be thousands, if not tens of thousands of buds, each with a tiny dome of embryonic tissue that is the meristem. Shoot meristems produce leaves, flowers, and primary twigs. Located at the tip of

Tree growth is continuously embryonic, with meristematic centers localized in the shoot and root tips and in the vascular and cork cambiums. Clockwise from top left:
- Expanding buds of Fraser's magnolia, Magnolia fraseri, showing prominent, foliaceous stipules that protect the expanding leaves. All leaf tissue, as well as floral, is produced by the shoot meristem.
- The primary and lateral roots of the red mangrove, Rhizophora mangle. The brackish water the tree grows in makes it easy to observe the branching of the root system.
- The cambium layer of the Japanese maple, Acer palmatum, made visible by the growth of wound-induced callus following a botched attempt at grafting.
- The dramatic, exfoliating bark of the paperbark maple, Acer griseum. The more extensive the cambium growth, the more extensive the exfoliation.
every root—and again, there are thousands of root tips on a mature tree—is a root meristem that, over time, produces the tree’s massive, underground root system.

The third type of meristem is the *vascular cambium*, a column of tissue that sheaths the trunk, the branches, and the roots of the tree, and is responsible for the secondary increase in girth in all these parts. The vascular cambium is basically a gigantic cylindrical meristem that outlines the periphery of the entire tree and produces the wood that forms the bulk of the tree. When injury—such as that broken branch mentioned earlier—exposes the cambium layer to the elements, it is the vascular cambium that produces the callus tissue that overgrows the wood. The last type of meristem found in trees is the *cork cambium*, which produces the bark that protects and insulates the tree. In general, the growth of the cork cambium keeps pace with the growth of the vascular cambium, sloughing off the old layers of bark as it produces new ones.

Whereas the specialized cells that compose meristems retain their full developmental capacity throughout the life of the tree, cells in mammals can express their full developmental potential only in very young embryos. As the mammalian embryo ages, a liver cell can only produce a liver cell and a brain cell a brain cell. This closed system of development, which limits the potential of any given cell early in its life span, stands in contrast to the open system of plants, in which cells located at the periphery of the plant body retain their full developmental potential throughout the life of the tree. Theoretically speaking, a tree’s life span is limited only by environmental disaster or predation by other organisms (Kaplan and Hagemann 1991).

A direct consequence of the meristematic structure of trees is that everything that has ever happened to them over the course of their long lives is embedded in the very fiber of their being, which is to say, the structure of their wood. The growth rings in nontropical trees are the footprints of vascular cambium activity, with each ring accurately recording the amount of growth a tree makes in any given year. Because tree growth is mostly a function of rainfall, the width of an annual growth ring provides an indirect measure of the moisture available to the tree that year. Scientists have used the information embedded in the width of growth rings to recreate past rainfall patterns that go back, quite literally, thousands of years (Cohen 1998). Similarly, for trees that shed portions of their bark in discrete plates, such as londons planes, stewartias, and ponderosa pines, the size of the plates that are sloughed off each year serve as an indirect measure of the trunk’s expansion: the greater the cambium expansion the larger the plates. Bark patterns are distinctive for each species.

**Growth Rings and Goethe**

Growth rings and bark plates are just some of the more obvious indicators of the principle that everything that happens to a tree over the course of its life is embedded in its form. To put it another way, both the external and internal structure of trees are manifestations of basic physiological processes. It was the German poet, philosopher, scientist Johann Wolfgang von Goethe who developed this concept and pioneered its use in science. The word he coined for this type of analysis—morphology—is still
in use today. Morphology, literally, is the study of the development of form. Indeed, it was Goethe who, in 1790, first published the revolutionary idea that the various components of flowers are actually modified leaves—an idea that modern genetic analysis has come around to supporting some two hundred years later (Arber 1950; Kaplan 2001).

Goethe’s ideas about morphology have mostly been forgotten by modern science, but they can be powerful analytical tools for anyone who takes the time to learn how about them. Indeed, within the field of mechanical engineering Goethe’s concept of “reading nature” is making a comeback thanks to the development of sophisticated computer programs that can accurately model the dynamic growth processes of living organisms.

What these models demonstrate is that the growth of a tree is responsive to external stimuli, especially light, water, gravity, and wind, and that these responses are embedded in the tree’s external form. For trees, the problem is balancing the need to expand its surface area as it searches for light and water with the need to remain stable in relation to the force of gravity. In the real world, where destabilizing forces abound, the necessity for expansion is often in conflict with the necessity to remain upright. Trees have resolved this dilemma by employing a process known as adaptive growth, which allows trees to add extra tissue (i.e., wood) to reinforce those parts of the trunk that are overloaded, while ignoring those parts that are underloaded. To put it another way, adaptive growth allows trees to structurally optimize their trunks, branches, and roots in order to reduce the chances of mechanical failure under conditions of extreme loading such as wind, snow, and ice.

By carefully studying the growth of trees, Claus Mattheck, a professor of biomechanics at
the University of Karlsruhe, and his colleagues have developed a sophisticated computer program—known as Computer-Aided Optimization, or CAO—that accurately describes the growth of real trees in real situations. By adapting this program to industrial design problems, engineers are now able to analyze the stresses experienced by various machine parts that tend to break frequently and to "grow" new parts that add extra material only to locations where it can have the greatest impact in terms of reducing mechanical stress. In other words, they reinforce only those sections of the part that typically fail as opposed to making the entire part heavier. It is a remarkable and important engineering breakthrough that specifically mimics the adaptive growth processes that trees use to minimize the stresses they experience in their natural habitats.

From Meristems to Modules

Another consequence of the meristematic nature of trees is their modular growth, a concept that refers to the construction of a tree through the repetition of uniform structural units. For every tree, these basic modular units remain consistent through its life and are composed of a segment of stem that produces leaves, branches, and—when sexually mature—flowers. When trees are young, the modular units that they produce are relatively large in size and few in number. As trees age, however, the modular units become smaller and more numerous, resulting in an increasingly finer and more ramified network of branches, as seen on the cover of this issue. Every tree species has its own characteristic module that helps to define its architecture. Halle, Oldeman, and Tomlinson have identified twenty-three models that describe the architecture of all known trees—both tropical and temperate—based on the branching pattern of their twigs and on the position of their flowers. While somewhat theoretical in concept, these architectural models are useful in categorizing the known array of growth forms displayed by trees. Relatively few of the twenty-three models are required in order to describe the vast majority of temperate trees.

One corollary of the modular nature of tree growth is that most trees have the capacity to repeat their basic architectural model during the course of their lives. Such repetition of the basic model can happen either because of traumatic injury to the tree's framework, or because the tree is experiencing conditions that are particularly favorable to its growth. Regardless of the cause, such reiteration, as it is called, is an important part of tree growth in a world fraught with diseases, insects, snow, ice, drought, and hurricanes that threaten the health and stability of trees.

A striking example of reiteration in tulip poplar, Liriodendron tulipifera, growing at the Arnold Arboretum. It was probably induced by a dramatic increase in light following the death of a nearby specimen of the same species.
At the risk of sounding anthropomorphic, one might say that the shape of an individual tree is analogous to the personality of a human, being the product of the complex interaction between genetic endowment (nature) and environmental pressures (nurture). Quite literally, everything that ever happens to a tree in the course of its long life is embedded in its form, even the little things that might have happened to the tree when it was just a sapling. The body language of trees speaks not only to the influence of the past in the present, but also to the promise of the future.

Bibliography


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