The Shapes of Trees: A Matter of Compromise

Peter Thomas

The whole point of a tree's woody skeleton is to ensure that the leaves get as much light as possible. At the same time, the tree must attend to its needs for pollination and seed dispersal and cope with environmental challenges like high winds and poor soil—all the while investing as efficiently as possible in its woody structure. The enormous range of tree shapes that we see—from the unbranched stems of palms and tree ferns to the tall spires of conifers, the oaks' broad, spreading crowns, and the multiple stems of old yews—all represent compromises among these often conflicting goals.

The nature of the compromise can be hard to pinpoint, but some gross generalizations are possible. Tree shapes can be divided simplistically into two categories: the conical outline of conifers and the rounded dome of hardwoods. Conifers of high latitude and altitude are typically steeply pyramidal with short branches that slope downwards to help shed snow and to intercept the maximum amount of light from a sun that is low on the horizon. The very similar shape found on conifers in dry regions, by contrast, appears to be an adaptation for intercepting the least amount of light (and therefore the least heat) when the sun is at its noonday hottest, thereby reducing the amount of water loss needed for cooling.

Pines farther south in savanna-type climates, such as the Mediterranean stone pine (*Pinus pinea*), develop a flat-topped, umbrella shape that helps resist drying winds by allowing leaves to hide behind one another and at the same time maximizes heat loss by allowing free passage of air up through the canopy.

The broad crowns of most hardwoods, on the other hand, are associated with cloudy climates, where the light is diffused and in effect comes from over the whole sky—the environment of most of Great Britain and the Pacific coast of North America, where most trees take on the same roughly spherical shape.

The Biomechanics of Shapes

The principles of biomechanics play a large part in determining the sorts of compromises that trees must make. The longer a branch, the more
Stone pine (Pinus pinea) growing in Tuscany, Italy, showing the aerodynamic shape of the canopy, which helps in conserving water.

Branches of two English oaks (Quercus robur) grafted together. Just as roots pressing against each other will weld together, so will branches. This is often claimed to be impossible because the constant movement by wind prevents the tissues joining, but with enough pressure the union is possible, as demonstrated by the photograph. Cheshire, England.

The distinctive shape of European linden (Tilia x europaea). At left, note the typical arch of the main branches. Because the end buds tend to die, new growth comes from near the branch end, resulting in another arch, creating the effect of multiple rainbows joined together at their ends.

The tree at right has the characteristic congested growth of small twigs in the center of the canopy. What you can’t see are the mass of shoots that normally spring from the base of the tree. Staffordshire, England.
After the loss of the top part of the tree, a single branch acts like a lever, bending the stem where the twisting force exerted (M) is the weight of the branch (F) multiplied by the length of the lever (I, branch base to the branch’s center of gravity). The tree reacts by bending the branch to reduce the length of the lever (the twisting force becomes zero), thus bringing the center of gravity of the branch over the base of the trunk. This is analogous to the ease with which we can carry a bucket of water.

likely it is to break under the pull of gravity, in the same way that a longer wrench puts more turning force on a stiff nut. The tree must therefore compromise between displaying as many leaves as possible and limiting the growth of the branch to a manageable length. There are ways of cheating, of course. If branches graft together, the additional support can allow them to become abnormally long without breaking. But trees also try to balance their weight on all sides, with no net force acting to bend the trunk. The drawing above shows a tree that has lost its top, leaving one branch sticking out sideways. To reduce the strain on the trunk imposed by this lopsidedness, the branch will soon begin to bend upright even if the tree is in the open and gets no additional light by doing so.

The same principle applies when entire trees lean. The leaning tree shown in the drawing below will gradually bend to bring its center of gravity above its base, thereby reducing the danger of falling over. We do the same thing when carrying a heavy load on our backs, bending forward to get the center of gravity above our feet. Here again, however, the tree may need to compromise between conflicting goals: in order to reach extra light, it may undergo the strain of unbalanced weight by leaning out into the center of a gap in the forest.

Buds, Branches, and Tree Shapes
How do trees manage to grow into their characteristic shapes? The question is best answered by examining the building blocks used. While animals basically have a fixed shape that simply gets bigger as they grow to adulthood, plants grow by repeatedly adding small modules.

The basic module of a tree is the portion of a twig that it grows each year from the terminal bud at the end of the previous year’s growth.
It is obvious, of course, that the shape of an individual tree will vary with conditions. Light, wind, snow, herbivory, fire, root health, and many other factors can influence shape. For example, in an effort to reach more light, species that form a bushy crown when grown in the open may take a taller and narrower form with fewer side branches when grown in the shade. Mountains provide ample evidence of the effect the environment has on the shapes of individual trees. Because of increased wind, conifers become shorter and squatter the higher they grow on a mountain. Quite literally, shaking, or even rubbing, a tree stunts its growth: a greenhouse study showed that shaking sweetgum trees (*Liquidambar styraciflua*) for just thirty seconds a day reduced their vertical growth to less than a third that of the unshaken trees.* This makes good mechanical sense: the stronger the wind the more leverage is exerted on the tree so its optimum design will be squatter.

Higher up on a mountain, trees survive only in tight, isolated clumps usually called Krummholz (German for “crooked wood”). In winter, harsh winds carrying ice particles wear away the waxy coating on needles, leaving them open to death by dehydration. This often produces “banner” trees that look like flags blowing in the wind, with branches surviving only in the lee of the prevailing wind. Flagging can also be seen on cliffs by the sea, where the effect of wind is exacerbated not by ice but by salt spray.

But trees are not passive in the face of the environment: they react. If branches are lost, new ones can be grown from stored buds or from new adventitious buds. Or an existing branch can fill the gap, perhaps by bending or taking on a different role. This is seen to perfection when a tree falls over but remains at least partly rooted. What were minor side branches become the new leaders, eventually producing a row of what appear to be individual trees.

* Neel and Harris 1971

*Subalpine fir (Abies lasiocarpa) in the Canadian Rocky Mountains demonstrating the effect of hostile conditions at high altitude. Above, a “flagged” specimen, bare on the side facing prevailing winds. Below, a larger clump of Krummholz with the prevailing winds moving into the picture. Note the skirt of healthy foliage around the bottom, showing where snow protects against winter winds.*
A branch in winter  The successive sets of bud scale scars mark how much of the branch grew each year. The leaf scars mark the positions of the previous year's leaves and the bud associated with each leaf can be seen clearly.

The young twig bears a number of leaves that leave behind a scar to mark the year's growth when they fall off, as well as a lateral (or axillary) bud that contains next year's growth—a new twig complete with leaves and new buds. New leaves can only be grown on new twigs, although the twig is sometimes inconspicuous. Each new module, or new addition to a twig, is the fingerlike projection of the new coat of wood that is added every year over the entire tree, so last year's twig will be fatter this year and will have two rings. The twig from the year before will be fatter still and will have three rings, and so on, the branch getting thicker as you trace back to the trunk.

But if every bud on a tree grew into a branch, the canopy would soon become a hopeless tangle, and a hundred-year-old oak would have ninety-nine orders of branching, whereas in reality temperate trees rarely show more than five to eight orders and tropical trees have at most four. [Tropical trees generally have bigger leaves, requiring a less dense network of branches to hold them.] A tree has three major strategies for limiting the number of branches: getting rid of its excess buds, shedding branches, and altering the length of branches.

Environmental conditions sometimes help the tree get rid of excess buds. Spring frosts may kill them, or neighboring trees or branches may rub against them in the wind, causing them to fall off. But trees have methods for solving the problem of excess buds themselves. European white birch (Betula pendula)—and undoubtedly other trees—develops fewer buds in parts of the crown that are already dense, or where the crowns of different trees meet. In shaded parts of trees many buds die, which explains the tendency of trees in close proximity to grow more on the sides that face away from neighbors. In some species, such as oaks, surplus buds are deliberately aborted. In fact, there is a steady rain of aborted buds from oak canopies throughout the growing season, representing as much as 45 to 70 percent of all buds produced. Or the buds may be “stored” unopened for future years.

In addition, some buds simply fail to develop as a normal part of the tree's lifecycle. The spines of hawthorn and honey locust and the bundles of needles on pines are all modified branches that eventually lose the ability to produce new buds. Conifers with many small, needlelike leaves, like spruces and firs, concentrate resources in relatively few buds at the end of each year's branches; if they produced a bud in the axil of every leaf, they would end up with an impossible number of buds and potential branches.

Trees can also avoid clogged canopies by getting rid of branches once they have achieved their purpose. As a tree gets bigger, it continues to grow new layers of foliage. If you look up through the canopy of a large tree, you will see that its center is made up of large branches (the “scaffold branches”), with small branches only at the edge of the canopy; those that once occupied the shaded center (the “dysphotic zone”) are long gone. In many trees, branch shedding is a regular, seasonal act, just like leaf
A shoot of purging buckthorn (Rhamnus catharticus) made up of long shoots and short shoots

shedding in autumn. Some species regularly shed small twigs complete with leaves toward the end of summer; others shed only the twigs that do not produce enough carbohydrate to cover their own running costs, perhaps because of inadequate light.

A less drastic way for trees to avoid congestion in the canopy is to regulate branch length. In many trees there is a clear distinction between “long” and “short” branches, or shoots. This is true of apple, birch, beech, hornbeam, katsura, ginkgo, pines, larches, and cedars, and to a lesser extent of elm, poplar, and linden. The long branches form the framework of the tree, making it bigger. The job of the short branches (called “spur shoots”) is to produce leaves, and often flowers, at more or less the same position every year. They can be distinguished by the proximity of their annual bud scales, since they grow in length each year only enough to produce closely packed leaves and the next set of buds. The bundles of needles on pines, cedars, and larches are also borne on short shoots.

**Flowers and Tree Shapes**

Flowering is an important determinant of tree shape because the shoot that produces a flower dies when flowering and fruiting end and consequently does not produce a new bud. In magnolias, dogwoods, maples, and horse chestnuts, the flowering tip is replaced in the next year by two side buds, leaving a fork to mark where the flowers were. In elms and cherries, on the other hand, the terminal bud of each twig, and perhaps of one or more farther back, produces only leaves, while the buds still farther back on the twig produce only flowers. More complicated patterns exist in which trees produce mixed buds containing both flowers and leaves (plums, pears, blackcurrant). In all cases, however, it is clear that different patterns of flowering produce different patterns of branching, thereby affecting the overall shape of the tree.

**How Does the Tree Control Shape?**

We have seen that the shape of a tree is governed by the way buds and branches grow and die. How does the tree control this? In the simplest terms, the end, or apex, of each branch governs what happens farther back along the branch, or lower down in the tree, in a process influenced by the amount of available light: the more light it gets, the more power an apex has. The topmost growing tip—the leader—has the most power of all. In turn, the strongly growing ends of side branches have great influence over the buds and smaller branches near them, but they themselves are still influenced by the leader. In effect, every growing tip from the very top apex to the most insignificant branch end exerts some control, albeit greatly varying in importance. The more minor the bud, the more likely it is to be suppressed or to result in a small, slow-growing branch. Complete removal of the leader or of another powerful branch by pruning
or by accidental damage means that one or more lesser branches—or a completely new branch from a previously suppressed bud—will bend upwards and compete to be the new leader. This is the reason that clipping young Christmas trees results in bushier trees.

Two terms are used to describe this hierarchical control. *Apical dominance* refers to the ability to prevent buds from developing in the first place and is the force leading to the rounded ovals of hardwoods. *Apical control* refers to the ability to govern the growth from nonsuppressed buds and is responsible for the spire shapes of conifers. In rounded trees with high apical dominance, like the oak, lateral buds are often suppressed until they are left so far behind the terminal end of the branch that they are finally able to develop into branches themselves, and the spire shape of the young tree gradually disappears into a rounded mass of strong branches.

Conversely, in conifers with weak apical dominance, most of the buds are allowed to grow, but because of strong apical control, the leader keeps the new branches shorter and more horizontal. Because the older branches lower down continue to grow, the conifer’s spire shape is maintained throughout the life of the tree.

The mechanism by which bud growth is regulated is not perfectly understood. It is known that the hormone auxin, and perhaps other hormones such as cytokinins, play a fundamental role. Auxin is produced at the apices and is transported through the phloem. Internal competition for minerals and sugars no doubt also plays a part. A number of studies have shown that “shoot inversion”—bending the upper shoot over to point downwards—can weaken apical regulation. This undoubtedly explains the old country custom in Great Britain of snapping over the top branches of hazel trees to improve fruiting: hazelnuts are borne on short shoots, which will grow and fruit more prolifically once apical regulation is partly removed. It also explains how true weeping trees grow taller: as the leader gets longer and flops over, it loses apical dominance and releases lateral buds to produce new branches that grow upwards and eventually flop over in turn.
Changes with Age

Because of the modular growth patterns of trees, a mature tree is not just a seedling writ large; its shape changes with age. The branching in young trees is usually much less dense than in older trees, especially in species with compound leaves (which in effect are cheap, throwaway branches, as in horse chestnut), or that self-prune (as do tulip trees [Liriodendron tulipifera], easily identified by their long straight, unbranched trunks). Tropical trees, which can sometimes be aged purely by their shape, may reach 25 feet in height before branching. The speed with which the shape changes depends on the species (early in horse chestnuts, late in poplars, never in many conifers) and on the soil (earlier on drier, poor soils).

Branch angles also change with age. Over the short term, branches have a set angle to which they try to return if bent, by the weight of snow, for instance. But over the long term, branches tend to sag as they get longer and heavier, a change that intensifies as more new wood is added to the crotch—just as putting on more and more coats forces a person’s arms to be more and more horizontal. Thus younger branches at the top of the tree are the most upright, while the increasingly older branches farther down become more and more horizontal.

One may think of the sagging of old branches as one of the disadvantages of age, like wrinkles and an expanding waistline, but in fact trees may benefit from these changes. The erect shape of a young tree encourages rainfall to run down the trunk, concentrating it on the developing roots at the base. In an older tree, however, the sagging branches and weeping tips encourage most of the water to drip off the edge of the canopy onto the area where it is most needed—above the absorbent ends of the tree’s growing roots.

Further Reading


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