

# Why Are Bonsai Leaves Small?

Robert E. Cook

**The Japanese term *bonsai* translates literally as “planted in a container,” but in popular usage it also denotes any ornamental plant that is dwarfed by means of pruning.**

It seems obvious that plants, unlike most animals, do not have a brain. But it is not so clear where they make those critical decisions that govern their lives. You who garden certainly know that plants have a mind of their own. Given that humans, and the majority of animals, solve many of their stressful problems (say, hunger) with a change in behavior (foraging for food), where are these decisions made in plants?

An intriguing, and visually pleasing, example of such decision-making can be seen in bonsai. These dwarfed trees, which have suffered severe pruning, bondage by wire, and permanent confinement in a small ceramic pot, respond by forming a canopy of miniature leaves that are essential to the aesthetic of this Asian art.

It need not be this way. One could imagine a tiny tree, rooted in shallow soil, with its slender limbs sprouting foliage of normal or nearly normal size, as though someone had planted a well-shaped branch. It would hardly qualify as the elegant and delicate creation characteristic of a refined horticultural sensibility.

In fact, the bonsai leaves of deciduous species may be thirty to fifty times smaller, while conifer leaves or needles are one-fifth or one-eighth the size of those on trees growing unconstrained in the ground. So why are the leaves of bonsai plants so small?



*The compact Hinoki cypress, Chamaecyparis obtusa ‘Chabo-hiba’, in the “octopus” shape, started in Japan in 1787, part of the Larz Anderson Bonsai Collection at the Arnold Arboretum. Often grown in containers and intensively pruned, this cultivar responds by producing congested, planar foliage and contorted, horizontal branches. Photo by Rácz and Debreczy.*

## **The Modular Organism**

The answer can be sought in an understanding of how leaf size in general is determined. Like most living organisms, the body of a plant consists of different kinds of very small cells

arrayed in combinations of types to form organs such as roots or leaves. Plants, however, grow and develop in a way fundamentally different from animals, especially higher vertebrates. In a population of rabbits, for instance, one can determine the size of the population by counting the total number of ears and dividing by two. In general each individual has a very predictable number of any kind of organ: one liver, two eyes, ten toes. That number is determined in the embryo and remains the same throughout growth and maturation.

Plants, on the other hand, are modular organisms. The basic unit of construction, so to speak, is the leaf, with an associated bud capable of growing as a branch and a section of stem connecting the leaf and bud to the other units of the plant. Similarly the root is really an interconnected network of branched, growing root tips. New modules are continually produced by growing shoot tips where decisions about size and shape are made at the time of module construction.

Unlike many animals, plants have no fixed adult size and can continue increasing their stature throughout life through the generation of more modules, each of which is more or less the same size whether produced at the age of twelve or one hundred and twelve. The number of such organs, however, depends upon the history of growing conditions experienced by the individual. It can potentially increase throughout the life of the plant.

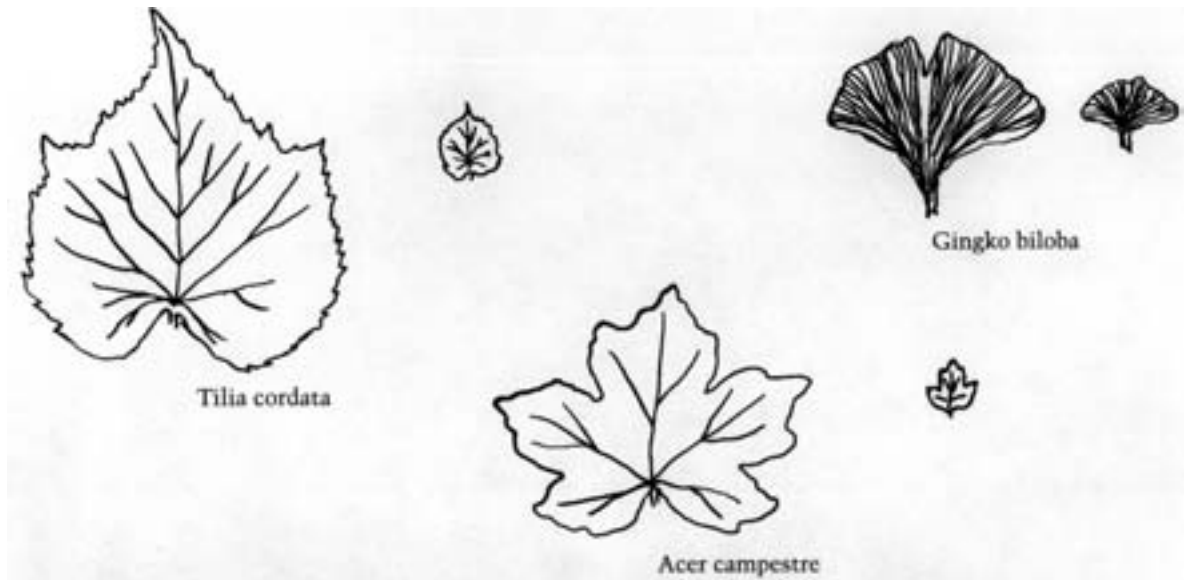
Given that individual leaves live only for a year or two, the ability to continue leaf production must also be retained throughout life. How do plants do this? The answer lies in the behavior of the growing tip at the end of each twig or branch. Here, where all the decisions regarding the number, size, and shape of organs are made, the annual production of leaves, stems, and buds (new modules) will, when repeated by multiple growing tips each season, give trees the shapes so distinctive of different species. The growing shoot tip, called the *meristem*, is the most intriguing plant organ of all.

### The Growing Shoot

When I lecture students in introductory biology about plant development, I bring in a loose-leaf head of lettuce with which to search for its meristem. A head of lettuce is really just a growing shoot with lots of green leaves, compact in some varieties and loose in others. With a good deal of dramatic flourish, I hold up the head and proceed to strip away the largest leaves, one by one. Try this sometime. It quickly demonstrates that successively younger leaves toward the center of the head are smaller and smaller, that this sequence of leaves is arrayed in a spiralling geometrical pattern around the center, and that the last identifiable leaf, now sitting atop a tapered stem base, is exceedingly small to the unaided eye. There at its tip, too small to see without a microscope, lies the shoot meristem. It is less than one one-hundredth of an inch across.

This meristem, from which all the lettuce leaves have been formed, consists of a small population of proliferating cells that retain the ability to form daughter cells through cell division. Both parent and daughter cells may continue dividing for several generations until a subset of the descendants stop dividing, begin to expand, and subsequently specialize as a form of functioning tissue for photosynthesis or the transport of nutrients. Newly formed descendent cells remain unspecialized as part of the meristem for a number of division cycles before making the decision to specialize. Thus plant cells in the growing meristem cannot continue dividing and specialize at the same time.

The meristem as a whole has a distinctive dome shape, sometimes broad or narrow, depending upon the species; and the cell divisions occur in such a way that this overall shape is maintained through the life of the shoot. In a sense, the meristem functions like the principal of an endowment in the bank: it generates income (specialized cells in plant organs) to support the whole while remaining more or less the same size over time.



Leaf size differences between normal and bonsai individuals of the same plant species. Redrawn from Körner 1989 by Susan Hardy Brown.

### Leaf Formation

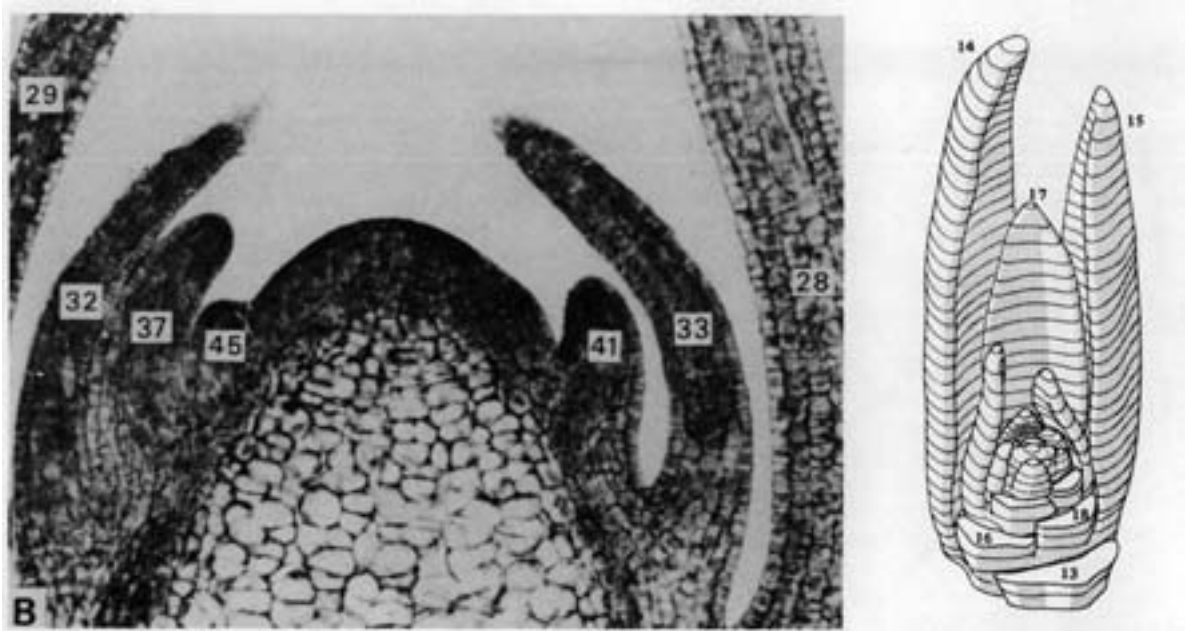
Leaves are formed from the meristem when a clump of cells on the side of the dome divide in a different direction such that a bump begins to emerge from the surface. This bump continues growing away from the meristem tip and gradually takes on the shape of a leaf. Within a short time, another bump appears on the opposite side of the meristem, followed by another to form the characteristic spiral sequence of leaves around the stem. Each of these young leaves also develops a small bud at its base. Initially this bud will remain dormant and later it may begin growing away from the stem to form a new branch with its own shoot tip generating new leaves.

While it still lies wrapped within the protection of older leaves, a newly formed leaf will increase in size very slowly because growth consists primarily of continuous cell divisions; each cell appears to divide a certain number of times before specializing and individual cells remain relatively small. After multiple gener-

ations this period of cell division gradually declines and the leaf enters a phase of cell expansion, coincident with tissue specialization, which greatly increases its size until the mature leaf size is reached. For many species that are dormant during the winter season, the overwintering bud contains a number of small leaves that have formed most of their cells but have yet to enter the expansion phase. With the coming of warm temperatures and rising sap, these leaves quickly begin expanding to rapidly approach maturity.

Thus the size of a leaf is determined by the average size of its mature plant cells and the number of such cells that are produced in the cell division phase early in the life of the leaf. Returning to our bonsai plant, we can ask whether its miniature leaves are smaller because the average leaf cell is smaller or because there are fewer cells in each leaf.

To answer this question, Professor Ch. Körner, a European botanist working at the University of Innsbruck in Austria, selected six



The photomicrograph on the left shows a slice through the middle of the shoot tip of an 18-day-old flax plant. The developing leaves are shown numbered on each side of the domed meristem. The 45th leaf has just emerged from the side of the dome. Leaves not shown (44, 43, and 42, for instance) are on parts of the dome not captured in the slice. The drawing on the right of a 15-day-old flax shoot tip was reconstructed from a sequence of slices starting at the tip of the longest leaf (#14) and slicing across at very small intervals. Using a microscope, each slice in sequence is drawn to create the 3-dimensional form. Leaves #13, 16, and 18 have been omitted to permit the shoot tip to be seen. Note the spiral arrangement of successively smaller leaves around the shoot tip. Reprinted from *The Shoot Apex and Leaf Growth*, R. F. Williams, by permission of Cambridge University Press.

species of trees—*Carambola*, *Averrhoa carambola*; Japanese zelkova, *Zelkova serrata*; hedge maple, *Acer campestre*; European linden, *Tilia cordata*; ginkgo, *Ginkgo biloba*; and European larch, *Larix decidua*—to conduct a comparative study of leaves in samples from normal trees and trees that had been grown as bonsai for six to seventeen years. Five individual leaves per plant were cut and examined with a light microscope to measure the length and width of individual cells, and the thickness of the leaf as a whole. Any differences found between the normal plants and the bonsai were statistically tested for significance.

In four out of the six species, the average size of the cells in the bonsai were *larger* than normally grown plants; cells of the remaining two species appeared to be the same size in normal

and bonsai leaves. However Körner did find that bonsai leaves are about twenty percent thinner than normal leaves because there are only four cell layers instead of the usual five. Still, this difference cannot account for the much smaller overall size of the leaves in bonsai; clearly each layer has many fewer cells, each of which is normal in size or even somewhat enlarged. Körner concluded that the dwarfed leaves of bonsai result from reduction in the production of cells, not from any shrinkage in average cell size.

Based on evidence from studies of other plants that produce dwarf or miniature leaves under stressful conditions, Körner also concluded that the greatly reduced number of cells in bonsai leaves is not due to a reduction in the rate of cell division; during development such

cells divide as frequently in normal and dwarfed leaves. The decision to form a miniature leaf appears to be made at the time a leaf is first initiated on the surface of the meristem. Körner believes that the bump itself starts smaller (that is, many fewer cells decide to alter the direction of division to form the bump). Consequently, although the future leaf grows at the normal rate and specializes on schedule, its size at maturation is greatly reduced because it commenced growth with a smaller starting capital of cells.

I should mention one note of caution with Körner's interpretation. It is a practice of some bonsai growers to strip off the first set of leaves produced in spring to stimulate the production of a second set. Körner's paper gives no indication that the bonsai he examined were so treated, but such spring pruning might have contributed to the very small sizes seen by Körner.

### The Magic of the Meristem

What remains unclear is how the conditions of growth characteristic of a bonsai cause the many meristems at branch tips to make these decisions for each new leaf. The stressful environment surrounding a bonsai plant is due to the constrained nature of root growth in a very small pot, coupled with occasional, but severe, root pruning. In some way the roots of the plant, restricted in their ability to absorb water and minerals, communicate this stress to the arborescent parts of the plant growing above the soil. At the level of individual growing shoots, each tiny meristem responds by allocating many fewer cells to the initiation of a new leaf and this leads to leaves which, when fully mature, are in a decidedly dwarfed size appropriate for a miniature tree.

At one level, therefore, the bonsai plant responds to stressful growing conditions by reducing the size of its modular building blocks (leaves); but at a second level, each

meristem responds to the same conditions by maintaining, or even increasing, the size of the building blocks (cells) and producing fewer of them to form a leaf. Cell size, unlike leaf size, is highly conserved under stress.

Perhaps the larger lesson for the botanist and gardener lies in the magic of the meristem itself. This organ, which sits hidden amidst the packed layers of expanding leaves in the growing shoot, is never seen by the naked human eye. Yet it is here that the critical decisions are made each season that will come to form the final size and shape of the leaves and stems of each individual. Such sequential decisions, made by the entire network of connected branch tips can, carried over the lifetime of the plant, create the characteristic architecture of trees that is so pleasing to our human sense of nature.

How all of this is coordinated, and how such coordination reaches from the deepest root tips to the tallest growing shoots on the tree, is unknown. But it is remarkable that, despite the harsh treatment we humans sometimes impose on bonsai, such coordination survives this mutilation intact, leading to the elegantly miniaturized leaves so essential to the beauty of these plants.

### References

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