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PHOTOSYNTHESIS

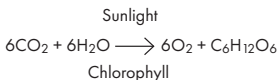
In 1634, Belgian scientist Jan van Helmont initiated a project, often considered the first biological experiment, to test the then-common idea that plants grew by assimilating soil. He weighed a willow stem, planted it in potted soil that he had also weighed, and added water when needed. After five years, he reweighed the willow and soil. The willow had gained 164 lb (74 kg), while the soil had lost only 2 oz (57 g)! Van Helmont rejected the idea that the soil provided for the weight gain. However, he concluded (wrongly) that the weight gain had come from water.

In retrospect, the experiment had several flaws (for example, van Helmont did not weigh the water inputs nor account for evaporation). He also failed to consider the possibility of an atmospheric source for the weight gain: carbon dioxide. Van Helmont's work paved the way, but the discovery of photosynthesis, the process by which plants use sunlight, carbon dioxide, and water to produce energy-rich compounds (in the form of sugars) and oxygen had to await the work of Jan Ingenhousz in 1779.

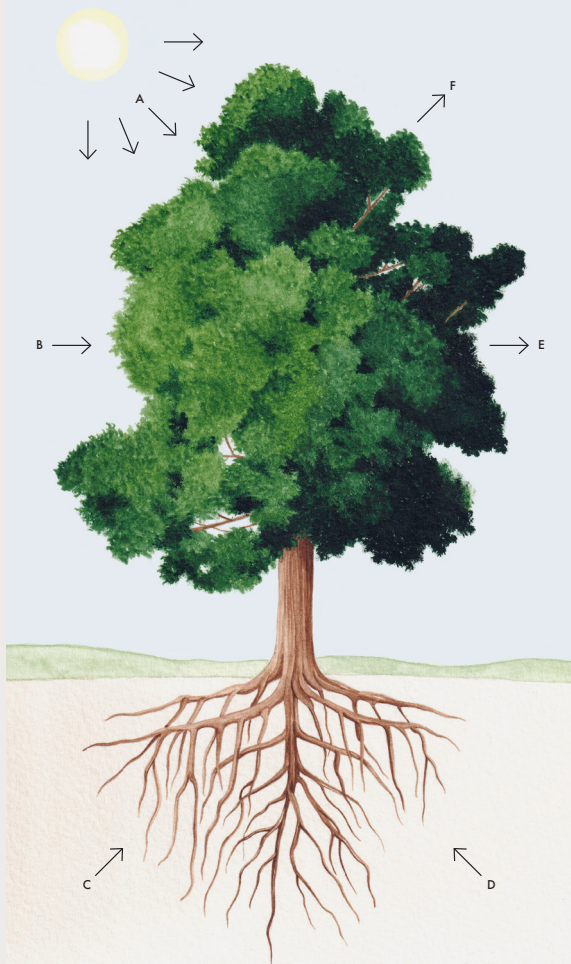


↙ In willows (*Salix*), male catkins (upper left) are produced on different individuals than female flowers (lower right). Willow leaves (lower left) are typically long and narrow.

→ (A) Sunlight supplies energy for photosynthesis in which (B) carbon dioxide (CO_2) is absorbed from the atmosphere and (C) minerals and (D) water (H_2O) are taken up from the soil. The source of soil moisture is precipitation. (F) oxygen (O_2) is released as a by-product. Water vapor leaves the tree through (E) evapotranspiration.



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PHOTOSYNTHESIS, CO₂, AND H₂O

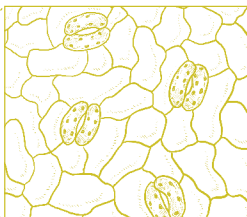
Photosynthesis transforms carbon dioxide (hereafter CO₂) and water to sugars and oxygen. The sugars provide the energy source for plant growth and reproduction. Photosynthesis takes place in chloroplasts, organelles that contain the energy-capturing compounds, chlorophyll a, chlorophyll b, and accessory pigments (carotenoids). Leaves are green because chlorophylls use less of, and therefore reflect, the green part of the solar spectrum.

Water and inorganic nutrients from the soil are transported to the leaves via the thin tubes of the xylem, one of two types of vascular tissue in higher plants (the other is phloem). The evaporation of water from leaf surfaces, called “transpiration,” creates tension within the

THE ROLE OF STOMATA

To regulate water and CO₂, leaves have surface pores called stomata. These are bordered by guard cells that can widen or shrink the size of the opening. The stomata are an important crossroads, with water vapor leaving and CO₂ entering the leaf through these pores. This creates a potential conflict, however: opening the stomata to absorb CO₂ necessarily increases water loss, while closing the stomata to conserve water decreases CO₂ uptake.

→ Stomata are leaf pores that serve as the crossroads of water vapor loss and carbon dioxide gain by leaves.



xylem, pulling water upward. Maintaining water flow is critical; severe droughts can cause a permanent interruption of the water column when bubbles of water vapor form (known as “cavitation”).

THE BOUNDARY LAYER

Leaf characteristic can also affect the thin layer of air (the boundary layer) next to the leaf surface. This layer determines the rate of movement of CO_2 and water vapor close to the surface, as the concentrations of these substances are different within the boundary layer compared with the external atmosphere. While the thickness of the boundary layer is influenced by temperature and wind, it can also be affected by leaf morphology. Leaves that are undivided or unlobed have thicker boundary layers. Some plants have hairy leaf surfaces, which increases the thickness of the boundary layer. Boundary layers can be more humid than the external environment, thereby slowing water vapor loss from the leaves.

THE ROLE OF PHLOEM AND XYLEM

Sugars produced in the leaves are transported throughout the tree in the vascular tissue. Annual increments of phloem and xylem are produced in the tree stem by the cambium, a ring of undifferentiated tissue. The phloem is produced to the outward side of the cambium and the xylem to the inward side. The increasing diameter of the tree trunk reflects the concentric rings of xylem that are produced—the phloem is regenerated, but older cells do not persist. The xylem becomes a non-living tissue with only a one-directional (upward) movement of water, which is governed by physical forces (the tension created by transpiration). The phloem is a living tissue that moves sugars, amino acids, and other organic substances from the leaves to other parts of the tree.

While vascular tissue is hidden in the trunk, it is likely that all of us have had at least one direct experience of its function. Many trees in seasonal climates mobilize sugars rapidly at the beginning of the growing season to fuel the production of new leaves. This “sap” run in sugar maple trees is collected and boiled, becoming maple syrup in the process. Indigenous populations also made sugary syrups from other trees.

PHOTOSYNTHESIS AND CLIMATE CHANGE

Climate warming impacts natural systems in diverse ways, from rising sea levels to catastrophic fires and extreme weather events such as floods and droughts. Here, we address only the effects on photosynthesis, which occur through two interconnected pathways:

Firstly, warming increases the rates of transpiration and respiration. Closing stomata can conserve water, but this restricts CO_2 uptake, potentially reducing productivity. Warming increases leaf respiration, resulting in the release of CO_2 . There is also a possible positive effect: warming can result in longer growing seasons (unless other factors become limiting). Warming effects depend on water supply, though future changes in precipitation are harder to predict than temperature changes. Secondly, CO_2 is a raw material for photosynthesis, so added CO_2 increases productivity (again, unless other factors become limiting) and carbon storage.



PHENOLOGY

Phenology is the study of the timing of biological events such as flowering, fruiting, and leafing. Trees sense stimuli such as light, temperature, and the time of day and, in essence, predict when favorable conditions may occur. Thus, an area of climate research is whether events like flowering are occurring earlier in the year. Beyond shifts in timing, however, a deeper concern is that a tree's calibration of the relationship between day length (a function of latitude and season) and temperature (which has considerable variation) will become incorrect and their responses non-optimal. Mismatches between the responses of trees and their pollinators or seed dispersers may also occur if organisms shift in different ways due to climate warming.

The balance of negative and positive effects on photosynthesis varies geographically and over time. A study by Martin Venturas of the University of Utah and colleagues concluded that the amount of warming and CO₂ increase was less important than the ratio between them. In other words, if temperature rises faster than CO₂, respiration losses will outpace photosynthetic gains. It is concerning that respiration increases with temperature, but photosynthesis reaches a plateau, suggesting warming effects will become increasingly negative.

The leaves themselves can play a role in how much climate change affects photosynthesis through acclimation, in this case a shift in size and shape, as well as the density of leaf stomata. At present, this is one of the uncertainties in predicting the effects on photosynthesis.

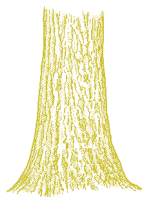
← Towers such as this one in a European beech forest monitor concentrations of CO₂ and other greenhouse

gases to gauge effects on tree productivity. In some experiments, towers release CO₂ to test effects of future increases.

GLOBAL PATTERNS OF HEIGHT

In 2010, Professor Michael Lefsky, of Colorado State University, analyzed satellite-based measurements from an instrument originally designed to measure the growth and melting of glaciers by observing changes in the height of the Earth's surface. The measurements were taken using a laser from the satellite bounced from the Earth's surface, through the forest canopy, and back up to the satellite. Lefsky cleverly realized that this data could also provide a space-based reconnaissance of the heights of the world's trees.

Forests composed primarily of tall trees were found in hot, moist locations with plenty of sunlight—the tropical wet forests of South America, Africa, Indomalaya, and New Guinea. Tall forests were also found in the Pacific Coastal region of Canada and the United States and the Appalachian Mountains of the eastern United States. Forest clearing has reduced the presence of tall trees in agricultural zones in Europe, North America, and Asia except for a few remnant forests, which are mostly in mountainous terrain.



← Large trees such as this red oak (*Quercus rubra*) expand at the base, a phenomenon known as “butt-swell.” In the USA, a tree’s diameter is taken at a height of $4\frac{1}{2}$ ft (1.37 m) to avoid errors due to butt-swell.

→ Shown here in Borneo, dipterocarp trees (in the family Dipterocarpaceae) are found across the tropics in tropical lowland rainforests. Dipterocarp trees in Southeast Asia are among the tallest trees on Earth. They emerge from the subcanopy and tower over the other trees.



← The tallest wooden structure is Poland’s Gleiwitz Radio Tower. Completed in 1934, and built with Siberian larch (*Larix siberica*) with brass connectors, it stands 364 ft (111 m) tall.

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MECHANICS OF GROWING TALL TREES

At the time of the American Revolutionary War, a first-rate English ship of the line had a mainmast with a base diameter of 40 in (1 m). The mast height of a tall ship was a yard of mast length per inch of diameter. Ship masts have a perverse tendency to break at the most inopportune times—in battle or during heavy storms. The danger of installing massive masts on a rolling ship in wind and heaving waves created a keen interest in engineering light but strong ship's timbers.

WITHSTANDING STRUCTURAL DAMAGE

In 1973, the late Professor Thomas McMahon, of Harvard University, argued on mechanical grounds that a tall, self-supporting, tapering column (like a tree trunk) should have a height proportional to its diameter raised to the power of $2/3$. When one looks up from the base of a large tree, the taper of the trunk implied by this relationship is



WHAT RESTRICTS TREE HEIGHT?

Beyond the mechanical limits of the heights of wooden structures, Professor F. Ian Woodward (formerly of Sheffield University) noted that trees are limited in height by four physiological constraints:

1. There is a limit on how high transpiration can lift a column of water in the transporting xylem tissues against gravity and friction before undergoing embolism and the formation of air bubbles.

2. The upward flow of water decreases with height, which decreases growth capacity.

3. The increase in investment in non-photosynthetic, structural leaf tissue with height decreases photosynthetic efficiency.

4. The rate of diffusion of CO_2 needed for photosynthesis into the leaf decreases with height.

These constraints imply a maximum tree height of 400–427 ft (122–130 m).

obvious. When McMahon considered over 700 record trees of different species, he found that trunk heights and diameters were typically about four times stronger than necessary to prevent buckling under their own weight. This “over-engineering” is to be expected. A trunk should have additional strength beyond that needed to stand under its weight if the tree is to survive stronger winds. In forests, tree saplings are often bent or buckled, implying that they are closer to the edge of buckling. One also sees buckled trunks and other damage in forests after strong winds, hurricanes, or tornados.

← General Sherman is a giant sequoia located 6,919 ft (2,109 m) above sea level in the Giant Forest of Sequoia National Park in Tulare

County, California. By volume, it is the largest known living single-stem tree on Earth. It is thought to be around 2,200 to 2,700 years old.

TRUNK STRENGTH TRADE-OFFS

In 2009, Professor Jérôme Chave and colleagues, of the University of Toulouse, examined the functional attributes of the woody tissue of 8,412 tree species, including density, biochemistry, anatomy, and the mechanical strength of their wood.

WOOD DENSITY

Wood density is determined as the weight of wood relative to wood volume after prolonged drying in an oven. Wood density is positively related to the amount of stress needed to break wood, the elasticity of wood, the resistance to splitting along wood fibers, and the work needed to break a piece of wood. Wood density across thousands of tree species worldwide accounts for 43 to 77 percent of the variation in these mechanical features. The density of wood indexes the allocation of a tree's photosynthetic production to trunk volume and suggests "economic" trade-offs in the growth of trunks. Is it a better strategy to allocate more photosynthate to building strong, elastic, hard-to-break trunks, or to invest less in dense wood but grow taller and faster and capture a greater portion of sunlight?

WOOD DENSITY VARIATION

Wood density varies within individual trees. As a tree grows, for both the trunks of conifers and angiosperms, interior sapwood layers are converted into heartwood by filling water conduits and pores with polymerized organic biochemicals. As a result, heartwood densities are significantly higher than sapwood densities. The proportion of heartwood to softwood in a tree is larger at the base and grows systematically smaller with height. For this reason, larger trees have proportionally higher wood densities than smaller trees of the same species.

VARYING WATER FLOW VELOCITIES

The water conduits in ring-porous angiosperms are arranged in rings, often annual rings. They are scattered in diffuse-porous angiosperms. These water transport systems differ in the speed that the sapwood can transport water. Maximum flow velocities range from 0.3 to 0.8 mm per second in conifers, 0.2 to 1.7 mm per second in ring-porous hardwoods (poplars, maples), and 1.1 to 12.1 mm per second in ring-porous hardwoods (ash, elms).

WATER HIGHWAYS

Not only do trunks require mechanical strength, but they must also conduct water from the tree's roots to the leaves. The use of water by the leaves is generated by intermeshed needs:

- 1 To supply the tree with water (H_2O) for photosynthesis. When energized by the energy of incoming light, the photosynthesis process combines carbon dioxide (CO_2) and water to produce sugars and oxygen (O_2).
- 2 To supply the water that evaporates from and cools the leaves, bringing leaf temperatures into a livable range.
- 3 To provide water to prevent leaf wilting.

In both conifers and angiosperms, the sapwood conducts water. In conifers, sapwood xylem cells are hollow, tubelike structures called tracheids. Thin-walled tracheids move water and thick-walled tracheids supply mechanical strength. In angiosperms, the sapwood xylem cells are differentiated into structures called pit vessels, which are specialized to move water, and wood fibers that provide strength.

Higher flow speeds mean different trees need less sapwood "plumbing" to move water upward. In ring-porous angiosperms, water may move through sapwood rings laid down over the past one to three years. This allows them to rapidly reconfigure their water transport systems when conditions change.

APICAL DOMINANCE

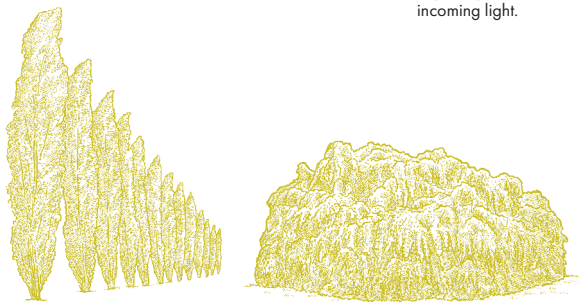
As a tree grows from a seedling, the main stem develops more strongly than the side stems. This phenomenon is known as apical dominance and is attributed to the effect of a plant hormone called auxin, which, when it is produced by the apex bud of a stem, inhibits the outgrowth of other auxiliary buds.

Auxin, produced by the main bud, moves down the shoot and suppresses the outgrowth of auxiliary buds. The high demand for sugars by the growing tip could augment this suppression by heavily using plant sugars and suppressing lateral growth. Trimming or herbivores grazing on central buds removes this apical control and can result in bushier plants. One result of this is that small tree seedlings often have a pleasing, crystalline regularity. This regularity is also seen at the tops of trees where the apical dominance allows for tree-determined geometry.

↓ Horticultural varieties of tree variation in apical dominance were used in landscaping, as seen in the apically dominant black poplar (*Populus nigra*) alleys in France.

↘ Horticultural cultivars that lack apical dominance take on a spreading form, as seen in this Sargent's weeping hemlock (*Tsuga canadensis* 'Pendula').

→ Engelmann spruce (*Picea engelmannii*) as well as other spruces (*Picea*) show strong apical dominance and a resultant conical form. This form makes the tree more efficient at capturing horizontal incoming light.



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HOW TO BE A HYPER-TALL TREE

The degree of apical dominance influences the ratio of tree height versus the width of the tree's crown. We discuss how trees develop extraordinary widths on page 57. Here, we consider how two of the tallest trees, the mountain ash (*Eucalyptus regnans*) and coast redwood (*Sequoia sempervirens*), resemble each other ecologically.

The world's tallest tree is a coast redwood called Hyperion, which stands at 380.3 ft (115.92 m), and the second tallest is a mountain ash named Centurion, which is 329.7 ft (100.5 m) tall. The redwood is a conifer and the eucalypt an angiosperm. Although separated by thousands of miles, they grow in relatively similar climates, according to Professor Elgene Box of the University of North Carolina: "both occurring in the transition from Mediterranean to marine west-coast Climate." These winter-wet, summer-dry, and often foggy forests can suffer horrific wildfires with devastating fire-tornadoes and other firestorm effects.

WILDFIRES: A TALE OF TWO TREES

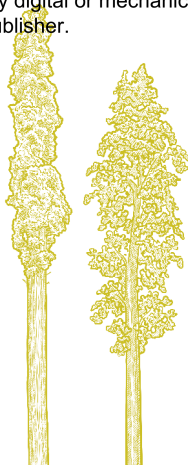
Mountain ash has a restricted range and is found in the Australian states of Victoria and Tasmania. It is a valuable timber tree used for furniture construction, trims, and general construction. A member of the *Eucalyptus* sub-genus *Monocalyptus*, like other monocalypts (and unlike most other eucalyptus species), mountain ash does not sprout when damaged by wildfires. Instead, its regeneration requires large wildfires so hot that they leave a sterile soil covered with a fine white ash.

Coast redwoods are restricted to small areas in California and are the state's most valuable timber species. The trees have thick bark, an adaptation to help them resist wildfires. The species can be regenerated from seeds or cuttings from saplings and has been successfully used in forest reclamation projects. The trees are considered resilient to wildfire and can sprout after fires from the roots and dormant buds in the trunks.

These very tall trees differ in several ways. The coast redwood is one of a species with 1,000-year-plus ages. It can resist fires and is, in general, adapted to regenerate well after a wildfire. The mountain ash is shorter lived (only 400 years). It is sensitive to the powerful wildfires typical of its habitat and requires recovery time to recruit new seed trees before the arrival of a second fire. Over geological time scales, *Sequoia* was widespread and successful. Hopefully, it will remain so, even if the fire climate is changing. The same should be said of *Eucalyptus regnans*.

→ Hyperion, the tallest tree, is a coast redwood from California, and Centurion is a *Eucalyptus regnans* from Australia. Both are found in similar

climates with wet winters and dry, fire-prone summers. But they differ in their ecological adaptations to similar climatic settings.



Hyperion Centurion

MOUNTAIN ASH FIRE VULNERABILITY

Wildfires hot enough to provide the sterile ash beds and an optimal seeding site also destroy mountain ash parent trees. It then takes years for mature, seed-producing trees to grow. A young mountain ash forest may regenerate and grow from the ashes of hot wildfires, but it takes 20 to 30 years before any of this generation of trees becomes large enough to resist light surface fires. The fire-generated new forest is thus fire-vulnerable during this time. When fires are too frequent, the forests burn a second time before the young trees can produce seed, and this too-rapid return of wildfire eliminates mountain ash from the site. Since only hot fire produces the necessary sterile soil, if wildfire does not burn the site in a tree's lifetime, then mountain ash is lost from the site. These unburned forests are likely to become temperate rainforest.

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NON-MONOPODIAL LARGE “TREES”

The biggest trees are not the tallest. Instead, they reach their immense mass in two ways: either dropping trunks down from their canopies or growing trunks up from their roots. Both approaches produce prodigiously large trees, assuming your definition of a “tree” includes multi-stemmed plants.

BANYANS AND CLONES

The “down from the canopy” method is common in figs (*Ficus*) like the banyan (*Ficus benghalensis*), the national tree of India. A striking specimen is the Great Banyan in the Acharya Jagadish Chandra Bose Indian Botanic Garden in Howrah, India, which has 2,880 prop roots and covers 3.71 acres (1.5 hectares).



ROOT-GRAFTED TREES

Below ground, roots from a single tree can join or graft together—as can those from different trees of the same species—to form connected trees, which, like clones, have an extended shared root system. This can also occur among trees of different species. Usually, the less related the species of individual trees, the less likely their roots are to graft. Root-grafted trees are able to share resources, which can mutually promote the overall vigor of a stand of adjacent trees, but there are potential downsides to this mutual sharing of root resources. For example, plant diseases can spread rapidly across shared root systems. In a bizarre case from New Zealand, a single, large, living stump of an ancient kauri (*Agathis australis*) tree survives as a “vampire tree”—drawing water and nutrition from root systems shared with its neighbors.

Clonal trees, in contrast, sprout what will become trunks from an extended root system. Pando is the name of a clonal colony of an individual male quaking aspen (*Populus tremuloides*) growing from a common rootstock in the Fishlake National Forest, in Utah, in the United States. It is a gigantic, single, individual organism with identical genetic markers throughout. It occupies 108 acres (43.7 hectares) and weighs an estimated 6,600 US tons (6,000,000 kg). Pando is a consequence of the ability of quaking aspen, as well as other tree species, to throw out lateral roots that then send up erect stems. Repeat the process for several thousand years and one ends up with a super-clone such as Pando. Pando is thought to be over 10,000 years old.

← Quaking aspens sprout from their roots to produce multiple trunks over large areas. Some

of these clonal trees are among the Earth's largest organisms, living for thousands of years.

CROWN SHYNESS

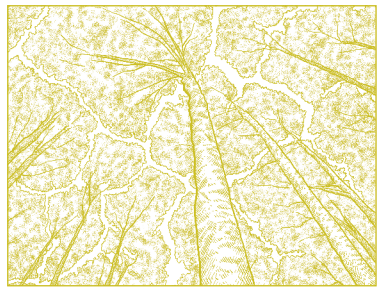
When one looks straight up through a forest canopy, the tree crowns typically do not touch, a phenomenon called “crown shyness.” This is emphasized in images taken with a “fish-eye” camera lens, which allows views of canopies as if they were displayed on the inside of a hemisphere.

There are multiple explanations of crown shyness. For example, winds can whip twigs on the branches of adjoining trees together, knocking off buds and blocking the growth of the crowns into each other. This “crown-pruning” mechanism also affects tree spacing in forest plantations. Crown shyness can also arise as a result of shade avoidance in plant growth. A proportional increase in far-red light indicates the presence of a nearby plant and plants tend to grow away from elevated far-red light. Plants also grow away from increased blue light to avoid shade. Crown shyness among trees in a forest hint at a mechanism for ecosystem self-organization—a theme we will explore further in this chapter.

↓ Crown shyness in a *Dryobalanops aromatica* tree canopy, Forest Research Institute of

Malaysia (FRIM), Kepong, Malaysia. Note the spaces outlining individual tree canopies.

→ If one walks through a relatively dense forest of trees of similar heights and sizes, the regularity of the canopy crown shyness can be striking. Once one learns to look for such geometry, it becomes clear that this pattern is widespread.



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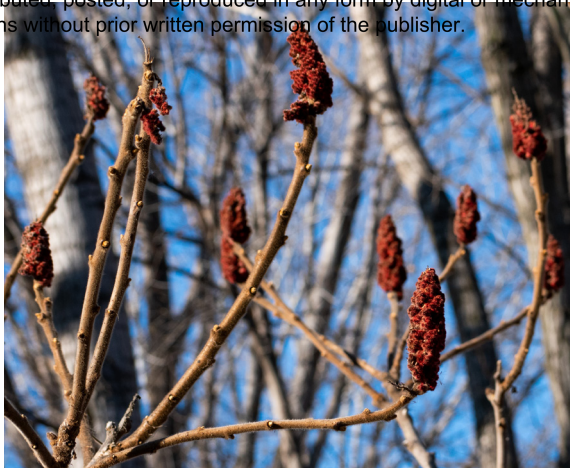
HALLÉ/OLDEMAN MODELS

Tropical ecologists Francis Hallé and Roelof A. A. Oldeman, subsequently joined by Philip B. Tomlinson, proposed the concept of architectural tree models based on the production, activation, and growth of meristematic tissues. Meristematic cells, which can be programmed to develop into flowers, shoots, leaves, or bark, and so on, reside in buds (protective protuberances, or “bumps,” on the stems of vascular plants) and elsewhere in the tree. Buds can be triggered to grow or can be suppressed by biochemical signals from other tree tissues. These interactions work in concert to selectively enhance or suppress the growth of meristematic tissues from other buds in tree crowns. This programming can produce almost crystalline forest geometries.

DIFFERENT TREE MODELS

For the trees themselves, other simple “rules” involving temporal changes in buds can produce an astonishing range of tree shapes. In the Hallé/Oldeman models, the timing and patterns of bud-break and flower production, as well as the rate and patterns of stem growth, produce a tree’s geometry. There are 23 such architectural models, each named after a prominent botanist.

The simplest of the Hallé/Oldeman models is Corner’s model, in which the meristem tissue in a bud at the top of a single, unbranched trunk grows to trunk height and then the trunk produces a flower. Afterward, the entire plant dies and seeds produced by the flower repeat the cycle. In the more complex Nozeran’s model, a bud at the apex of the plant produces a tier of horizontally oriented branches; a new vertical stem then arises from below this tier. The bud at the top of this new stem repeats the process to form additional horizontal tiers.



↑ Found across the eastern United States, staghorn sumac (*Rhus typhina*) grows according to

Leeuwenberg's model. Twigs will grow from a pair of buds below each seed cluster the following spring.

LEEUWENBERG'S MODEL

Leeuwenberg's model is slightly more complex. Here, the tree grows in modules. A primary shoot called a sympodium lengthens to produce a growth unit. The apical meristem at the end of this shoot dies, often because it is irreversibly programmed to produce flowers or leaves. Further growth is then initiated, often from two activated lateral buds. The tree is formed of a collection of "Y-shaped" units. The stem elongation, flowering, and activation of growth from the lateral meristems often occur simultaneously and in sequence in the growing tree.

CROWN GEOMETRY: MONO- AND MULTI-LAYERED TREES

There are trade-offs in a tree's ability to survive under relatively low light conditions versus high light conditions, which consistently emerge at multiple scales from leaf to forest canopy. These trade-offs are sometimes posed as economic questions: How much of an essential nutrient (or of photosynthetically produced sugars or of water) should be invested in growing more leaves? . . . in growing taller trunks? . . . in developing more roots and root surfaces? . . . in making more seeds?

SUN-LEAVES AND SHADE-LEAVES

At the level of a single leaf, one can see similar patterns in trade-offs operating at different levels through the canopy. The leaves in the top of a tree's canopy are smaller but thicker because they contain more cells with chloroplasts full of chlorophyll. They are richer in nitrogen and other nutrients. If the leaves have lobes, they are more deeply incised. In the fall, look at fallen leaves beneath a deciduous tree. The "sun-leaves" from the top of a tree are strikingly different from the "shade-leaves" from the lower canopy. So much so that the leaves seem as though they could be from different species.

MONO- AND MULTI-LAYERED TREES

The same trade-offs are seen in sun-leaf/shade-leaf morphologies. Imagine the differences between sun-leaves and shade-leaves did not exist and that a tree had the same kinds of leaves. What might be the best way to arrange these leaves? The late Princeton Professor Henry Horn considered this question and investigated the theoretical consequences of two extreme cases: mono- and multi-layered trees.

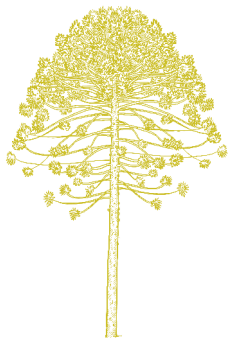
At high light levels, a multi-layered tree can capture the available incoming light and undergo maximum photosynthesis. Under lower light levels, the amount of light absorbed to drive photosynthesis is reduced and some of the shade-leaves become net losers. Mono-layered canopies underperform multi-layered canopies when there

FUNCTIONAL DIFFERENCES

Differences in leaf appearance between sun-leaves and shade-leaves are paralleled by differences in function. In low light, shade-leaves have more net photosynthesis—because they bear lower “costs” from spending photosynthetic capital on maintaining non-productive tissue. Sun-leaves in low light use more energy to maintain their capacity for high rates of photosynthesis, a capacity that cannot be used in lower light. At high light levels, shade-leaves cannot take advantage of the extra light. Relative to shade-leaves, sun-leaves have higher productivity in full light but lower, even negative productivity in low light.

is ample light. At low light levels, mono-layered canopies can survive a shade so deep that multi-layered canopies are in a negative balance and perish.

Multi-layered trees are likely to survive in young forests or those that have been destroyed by fire, clearing, and similar events. In this scenario, rapid growth with high rates of photosynthesis would favor the multi-layered tree. But mono-layered trees are destined to play a long game—surviving on the shady forest floor, waiting for an overhead tree to die, and taking opportunities to grow a little larger.



→ The bunya pine (*Araucaria bidwillii*) is a native tree in Queensland (Australia) rainforests. The tree has an open but functionally

multi-layered canopy, meaning that a beam of light from any point above strikes upon more than one group of leaves.

ADAPTIVE GEOMETRY OF TREE CROWNS

The overall geometry of tree canopies changes with the environment. In the northern boreal forests of Eurasia and North America, spruces (*Picea*) and firs (*Abies*) show a remarkable capacity to capture light due to the arrangements of their leaves and are often referred to as “dark conifers” for this reason.

Black spruce (*Picea mariana*), for example, which covers vast areas of Canada and Alaska, has light-capturing arrangements of needles. As NASA’s Dr. Kenneth Jon Ranson explains, this is to ensure that “photons go in but they don’t come out.” There is clearly a good reason for the common name, black spruce. At the whole tree level, black spruce presents as a tall, narrow spire of needles that go all the way down to the ground. They capture the flat sunlight that is associated with the near-horizon location of the sun at high latitudes.

↓ The multi-angled orientations of black spruce (*Picea mariana*) leaves are very effective at capturing light from different angles.



↓ Vertical leaves of alpine ash (*Eucalyptus delegatensis*) capture morning and sunset light, when conditions in the Australian Alps are more favorable for photosynthesis.



→ The vertical canopies of black spruce trees serve to increase the capture of direct sunlight found under the light conditions in the high-altitude boreal and Arctic regions. A boreal tree can shade or be shaded by a surrounding tree, depending on the time of day.

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SHINOZAKI PIPE MODEL THEORY

One of Leonardo da Vinci's most famous drawings is his *Vitruvian Man*, which depicts a nude male figure with two positions for the arms and legs, one inscribed on a circle and the other on a square. The drawing depicts the "perfect" proportions of the human body as described by the Roman architect Vitruvius between 30 and 15 BC.

TREE PROPORTIONALITY

A less well-known drawing by Leonardo depicts regular proportions in tree branching. His mathematical rule for tree proportionality was that the summation of the cross-sectional area of all the tree branches above a branching point at any height equals the cross-sectional area of the trunk or branch immediately below that branching point. Puzzling over and testing this rule—"Is it correct? How is it caused?"—has continued to the present day.

For example, Kichiro Shinozaki and an interdisciplinary group of colleagues (K. Yoda, K. Hozumi, and T. Kira) at Osaka City University, in Japan, launched investigations in 1964 that have continued for over 50 years in pursuit of a basis for Leonardo's rule. Shinozaki's Pipe Model represented a tree as a collection of "pipes" carrying water from the roots to the leafy canopy. The resultant plumbing would have a constant cross-sectional area of sapwood from the bottom to the top of the tree. With the pipe model, if the cross-sectional areas of pipes in a tree implies the mass of leaves in a tree, then the number of pipes in a forest would imply the mass of leaves in the forest. The expectation is that the cross-sectional area of sapwood summed over an area of a forest should have a strong relation with the mass (or area) of leaves over the same area.

→ An aerial view of
rainforest canopy in
Bellenden Ker, North

Queensland, Australia.
Photograph taken in
November, 1989.

FOREST REGULARITY

The connection between leaves and sapwood cross section encoded in the Shinozaki Pipe Model, and the leap to enlarge this to the forest scale, implies rules for a constancy in the formation of a forest's geometry. There are many regularities in forests. For forest plantations and in natural forest ecosystems, the cross-sectional area of "pipes" supplying water to leaves show consistent ratios, as do other measurements of tree geometry.



FOREST PLANTATIONS

One of Shinozaki's colleagues, Kyoji Yoda, developed a mathematical model of a phenomenon called self-thinning, the tendency for the logarithm of the numbers of trees comprising a forest versus the logarithm of the average size of the trees in the forest to lie on a line with a slope of 1.5 (an "allometric function").

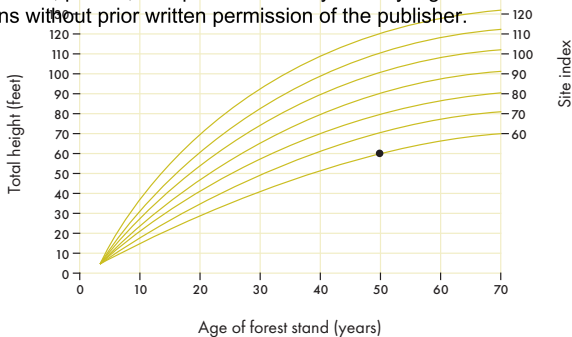
Called Yoda's self-thinning law, this is another of the interwoven regularities in forests. It is a "packing rule" involving how many trees of a similar size and shape can be packed into a box of a given size. All sorts of natural systems roughly conform to such allometric packing, with the number of things adjusted to fit the size of container. For example: How many corals can grow in a reef? How many oysters can be found in an oyster bed? How many radishes can grow in a pot? And so on . . .

MANAGED FORESTS AND THE SITE INDEX

In practical forestry, there is the analogous case that involves using forest data compilations to determine when to thin (partially harvest) or harvest trees. Modern scientific forestry had its origins in the virtual clearing of the European forests for houses, great wooden ships,

SELF-THINNING RULES

Yoda's self-thinning rule has the additional consideration that if the average number of trees predicted for a forest with trees of a given size is too large, then some of the trees would be expected to die, or, in forestry parlance, the forest should thin itself of the extras. Which trees die? Often it is the smaller trees, or those too close to other tree crowns, or tall trees exposed to chilling winds. Whatever the reason, the forest becomes an automaton, thinning itself to agree to a fundamental rule of forest stand geometry as the trees grow larger.



↑ A site index is the height of trees in a stand growing in a plantation at an index age (in this

case, 50 years). From this, one can predict future height, growth, increase in wood, etc.

construction timbers for mines and railway ties, and fuel for houses and industry. The proper stewardship of natural resources, particularly forests, was an integrated set of practices called *Nachhaltigkeit* by its mostly German-speaking developers. Sustainability was first used in English as a direct translation of *Nachhaltigkeit*. Central to this practice was the regular compilation of data on the growth, size, height, and mass of merchantable timber for millions of individual trees on thousands of forest survey plots. It was found that the tree height in a forest of a given age (the “site index”) allowed the data to be organized to predict forests over time, which is the preamble to forestry decisions of when to harvest, when to thin, and so on.

The site index also draws on the quasi-regularity of the descriptors of forests. These geometric rules may fascinate quantitative ecologists, as well as provide them with ample opportunities to sharpen their understandings of the nature of nature. But for many of us, forests are simply beautiful environments to contemplate—much as crystals, the rhythm of waves, and the colors of a sunset are beautiful in their spontaneously generated regularity.

BARK VARIATION

Bark plays a critical role in protecting tree stems from fungi, insects, mammalian herbivores, desiccation, fire, mechanical injury, and temperature fluctuation. Although bark comes in many colors, textures, and designs, it tends to be overlooked in tree identification compared to the leaves, flowers, and fruits. While some species have unmistakable bark, one problem is that the appearance can change with age and diameter. In some trees, there are three or more bark stages: unbroken bark when young, ridged bark in middle age, and smoother and plated bark in old age. Bark is also overlooked because bark traits can be difficult to describe or measure.

TEXTURE AND COLOR

In most trees (dicots and gymnosperms), stems increase in circumference over time through secondary growth. In some species, the bark can remain smooth if its growth keeps pace with this growth (for example, in beech trees). However, for most trees, the stem surface changes from smooth to rough, with the timing of this change varying among species from a few years to a few decades.

The bark surface then takes many forms in different species: vertical ridges with furrows in between, plates, scales, and papery sheets. Some bark is regularly shed and replaced by new layers

A PROTECTIVE SHIELD

The outer bark is a mechanical barrier but also a chemical one in that it is low in nutrients and high in lignin, and therefore unattractive to herbivores compared to the living tissues it protects. Bark can also be protected by toxic or repellent compounds, thorns, and warty outgrowths. When injured, bark can exude resins or latex that seal wounds and repel herbivores.

(continued...)

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