Leaves: when should they fall?

A chapter in: *Trees of the People*, by Alan R. Walker

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About three hundred million years ago, on land south of the equator as far as the drifting continent Antarctica, there were plants called *Glossopteris*. Now fossils of their leaves have been discovered in many places. Their patterns reveal *Glossopteris* as a seed-bearing plant, classified amongst the seed-ferns. Their leaves were up to thirty centimetres long, with surface texture, pattern of veins and simple oval shape they resemble the expansive leaves of trees in modern tropical forests, although it is not known if *Glossopteris* ever grew as trees with tall trunks.

Fossilized leaves of *Glossopteris* plant.
Credit: Wikimedia, James StJohn.

Earlier than plants like *Glossopteris* there were massive trees such as *Lepidodendron*, the scale tree. They grew thirty metres tall and after they fell down dead they slowly became the coal seams of the Carboniferous geological period. Scale trees achieved their massive growth with meagre leaves in comparison with those of *Glossopteris*, but the leaf scales emerged from the entire surface of trunk and branches. Plant life on land, starting from simple algae then mosses and ferns, evolved the ability to grow tree-like by the time of the Carboniferous period.

Sometime between the flourishing of scale trees to the times of *Glossopteris* the cone-bearing plants evolved. The earliest of these looked like the cycad, ginko, and *Araucaria* (monkey-puzzle) trees that remain with us today. These bore foliage variously as: broad-leaves, scale-leaves, deciduous or evergreen leaves. They arose in the later years of the Carboniferous through to the Permian period, which lasted from about three hundred to two hundred and fifty million years ago. Earlier plants of tree form reproduced by exchange of minute spores. The male spores needed to swim through films of water on both the ground and plant to reach the female spores. But here was opportunity to flourish on lands too dry for such a wet method of reproduction. Cone-bearing plants exploited this through the evolution of the female spores as eggs, also known as ovules, in the form of unfertilized seeds. Seeds remained on the parent plant. Male spores evolved as minute pollen grains spread by wind. Within female cones were simple seeds, without a full protective layer that could develop as a fruit in other types of plant.

Type of tree that evolved during Permian period, *Araucaria araucana*, in Chile. Credit: Wikimedia, Delohimalya Alosandes.

These plants with cones and seeds came be defined as *gymnosperms*, meaning naked seeds. Seeds were a great leap of evolutionary invention, allowing developing embryos to remain on their parent plants whilst growing to a robust size, better able to survive once dispersed away from their parent tree. When shed by the tree these seeds were able to delay development until season or environment was suitable for growth into a seedling. Thus gymnosperms and similar seed bearing plants (collectively the Spermatophyta) gained the crucial advantage of being able to reproduce without needing a film of water on the plant for exchange of genetic materials. Cone-bearers, the gymnosperms, flourished through the Triassic period and into the Jurassic period that started two hundred million years ago. They dominated the land flora in terms of bulk despite being browsed by huge dinosaurs. Pollen blew away from their male cones like dense smoke. Tough or spiny tipped leaves containing noxious tasting tannins and resins developed to deter these herbivores. In those times the atmosphere was rich with the carbon dioxide that trees need for growth, and the greenhouse effect of that gas warmed the climate and drew up moisture from the seas and lakes.

TIMELINE for origin of gymnosperms and angiosperms

Era: **Cenozoic**, from 66M years ago.
Period: **Quaternary**: modern humans and agriculture.
Neogene: mixed forests widespread; grasses worldwide.
Paleogene: diversification of angiosperms (flowering plants); first grasses evolve.

Era: **Mesozoic**, from 252M years ago.
Period: **Cretaceous**: angiosperms spread from tropical regions; pollinating insects co-evolve with flowering plants.
Jurassic: gymnosperms common and widespread, angiosperms diversifying; dinosaurs and small mammals common.
Triassic: coniferous gymnosperms dominate tree flora; possible time of origin of angiosperms.

Era: **Paleozoic**, from 540M years ago.
Period: **Permian**: gymnosperms diversify into cycads, ginkos and conifers.
Carboniferous: possible times of origin of seed bearing plants as early gymnosperms toward end of times of the coal-forest flora.

Leaf shedding.

Leaves work mostly to convert carbon dioxide, water and mineral nutrients into the simple materials that the rest of the plant will use as building blocks for construction of cells, tissues, stem, roots, and apparatus for reproduction. Leaves make this material, this photosynthate, by the deeply complex process of photosynthesis. Complex and also wearing where it occurs within the delicate chemical structures of those leaf cells. Trapping energy of photons from the sun whilst risking the dangers of oxygen and its radicals, as reactive oxygen species, cannot be done without damaging cells. So leaves age, they become senescent, some types more rapidly than others. Before their death the remaining healthy plant has either to draw back as much nutritious material from each leaf into the central plant as possible, or alternatively keep the leaves working for years to make best use from their ageing photosynthetic apparatus.

Maple leaf during fall in New Hampshire, USA. These beautiful colours are due to carotenoid and anthocyanin pigments that remain after the chlorophyll and other molecules are resorbed. This is a typical broad-leaf of an angiosperm tree, with complex venation. Thanks to Carol Morely for the leaf.

Various strategies evolved as solutions to the problem of leaf ageing. Early in evolution of the leaf, the parent plants gained a specific mechanism to shed leaves. Abscission it is called, working at a zone of tissue of that name, located in the narrow petiole that connects the leaf to the branch. The abscission zone has a region of cells with weak connections between adjacent walls and also a region of cells that can either expand or become suberized, hardened, to start a split between leaf and branch.

The enzyme cellulase dissolves cellulose of cell walls in the abscission zone. The plant hormones auxin and ethylene control the timing of this enzyme activity, they work together in synergistic fashion. When auxin levels are seasonally high in the leaves the abscission zone is insensitive to ethylene, so it remains inactive. When auxin levels decrease in the leaf there is less to influence the abscission zone, which then becomes sensitive to ethylene. The enzymic and differential separation of abscission zone cells causes the connection between leaf and branch to break under pull of gravity or wind.

General categories of leaf shedding by trees

Broad-leaf deciduous (common, eg. beeches, *Fagus*)
Broad-leaf evergreen (rare, eg. holm oak, *Quercus ilex*)

Needle-leaf deciduous (rare, eg. larches, *Larix*)
Needle-leaf evergreen (common, eg. spruces, *Picea*)

For the tree this is an expensive loss: thousands and millions of leaves growing from their buds each had taken energy and material from the rest of the plant. Most trees, with either broad-leaves or needle-leaves, can extract from senescent leaves about half of the nutrients they had contributed to leaf construction. This extraction has its own cost of respiratory energy of the tree to sustain the enzymic reactions and transports of these nutrients. The harder structural materials of the leaf cannot be extracted and recycled before abscission but at least they will eventually decompose into humus in the soil, providing some nutrients that the tree can recycle.

Another type of seed-plant.

Sometime between about two hundred and fifty to two hundred million years ago there evolved a different type of seed-plant. Seemingly they arose not directly from the gymnosperm plants, but alongside those early plants like cycads, ginkos and other cone-bearers. These new plants bore their ovules as seeds within a full protective layer that grows into a fruit. Botanists named these plants with enclosed seeds *angiosperms*.

Together with this new type of seed there evolved flowers as aids to reproduction. Flowering plants flourished and diversified during the Jurassic, through the Cretaceous, and into the Paleogene period that lasted to thirty four million years ago. They became the smallest herbs, massive trees, and the powerfully fast growing grasses (see 'Reproduction').

Left: Needle-leaf tree: production of seeds from cones, (spruce, *Picea sitchensis*)

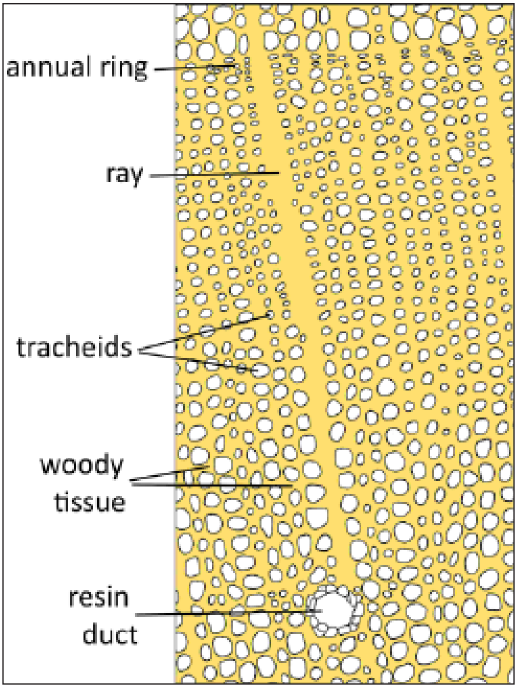
Right: Broad-leaf tree: production of seeds from flowers (apple, *Malus floribunda*)

Flowering plants out-competed the cone-bearing plants in various ways. Flowers evolved alongside insects and other animals, particularly those with wings: bees, beetles, bats and birds. The birds had evolved from dinosaurs and flew together with winged insects during the Jurassic period from two hundred million years ago. Flowers and animal pollinators evolved together, converging to the intricacy of mutual benefit shown in the deep nectaries of an orchid, the long proboscis of a moth, and the precise positioning of the pollen bearing anthers in the visually attractive flower. Cone-bearers remain as a thousand species, more or less, grouped in twelve families. Flowering plants diversified into about three hundred thousand species in four hundred and five families. Nevertheless, the conifers amongst the gymnosperms dominate vast areas of Earth, particularly in the boreal climatic biome of the high latitude regions of North America and Eurasia. Here vast forests of spruces, firs and pines spread from ocean to ocean. But life, as always, has many anomalies and amongst wide regions of cone-bearing trees most of them evergreen, there grow populations of flowering trees. Birches and poplars flourish here, all with leaves that they shed before the onset of each winter season. The business of how long trees should keep their leaves, according to what the regional climate and seasons are doing appears contradictory. What is going on?

Broad-leaf deciduous aspens (*Populus tremula*) and needle-leaf evergreen Englemann spruce (*Picea engelmanni*) at 3000m altitude in a forested region of western USA during mid-winter.

Structure of wood and leaves.

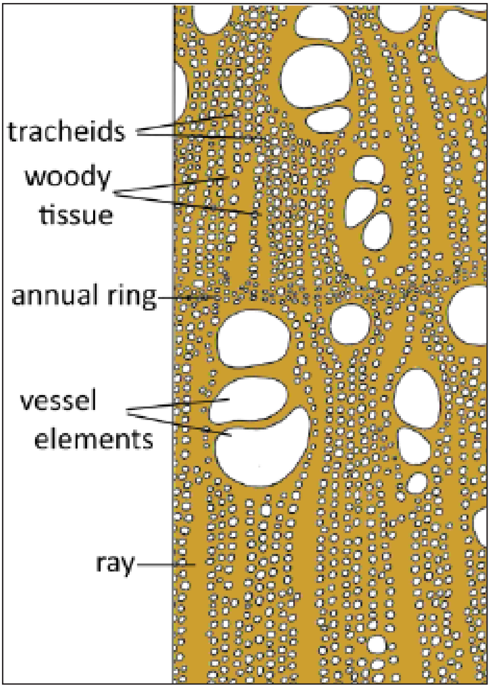
Tree has no strict botanical definition, it can include banana plants and bamboo. Here it means a perennial plant with a thick strong stem or trunk that raises branches bearing leaves high into the sunlight. This plant form depends on the evolutionary engineering feat called xylem, with its attendant cambium and phloem: wood it is called. Gymnosperm trees have xylem constructed of tubes to carry water up from roots and these tubes form as vertical arrays of cells called tracheids. The outer walls of these tubes are tightly packed together so that in cross-cut, against the grain, view they are roughly rectangular, packed like biscuits in a box (see 'Buildings'). Tracheids are connected to each other at their sloping ends through interconnecting pores. The inner bore of these cells varies from wider early season wood at about 80 micrometres diameter to narrower in late season wood. This bore is fine enough to exert strong capillary force on the xylem sap they contain. Against this force xylem sap is pulled up the trunk as the water it contains evaporates from the leaves in the process of transpiration.



Pattern of xylem tubes in a gymnosperm, Sitka spruce, repesented as a cross section through the grain of the stem in this drawing. Empty holes are the lumens of tracheid cells and the packed walls of these cells form the woody tissue, in yellow.

Although this chapter is about leaves of trees it is necessary to think of leaves as part of a suite of traits or adaptations of the tree at the level of root plus stem plus leaves. This is most obvious in how trees cope with the stress of drought conditions. Drought is not just a lack of rainwater, it is also caused by freezing conditions, even in the tropics for trees growing high on mountains.

In regions far from the equator, with long winters and temperatures dropping far below freezing point of water, sap in tracheid elements is liable to freeze. After it eventually thaws then vapour bubbles are likely to form – a cavitation as a type of embolism. Drought conditions may also cause similar damage, and frozen soil around roots is as much a risk to a tree as lack of rain. The greater the tendency for cavitation can be reduced the better a species of conifer is able to live in these freezing lands towards the poles. It pays conifers keep their tracheid elements with narrow diameters despite the disadvantage of pulling up the sap against strong capillary force during the summer growing season.



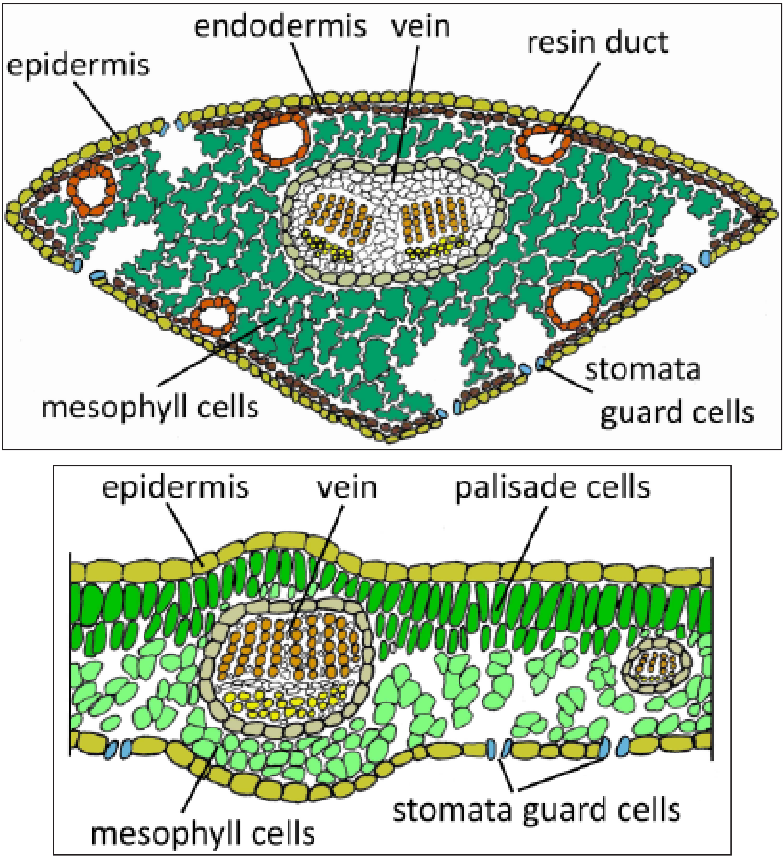
Pattern of xylem tubes in an angiosperm, common ash, repesented as a cross section similar to drawing on pg 8. Empty holes are the lumens of tracheid cells but in addition this broad-leaf tree has large-bore vessel elements as part of its vascular system.

A cross-cut through the grain of the stem of an angiosperm tree reveals fine-bore tubes similar to those seen in conifers. Depending on tree species some of these tubular cells are classed as fibres, others as tracheids and both types have thick walls and narrow bores. In addition there nestle cells of conspicuously wider bore and thinner walls – the vessel elements. These permit rapid rise of xylem sap from roots up to the broad-leaves of these trees. As soon as there is enough light and warmth growth accelerates as the flat wide leaves expand in spring to absorb as much of photons and carbon dioxide as possible. But these wide vessel elements, up to 500 micrometres in diameter, are susceptible to cavitation blockages. Only a few types of angiosperm trees can survive in regions close to the poles. In contrast, vessel elements are advantageous to trees growing in regions that are warmer but prone to seasonal drought. During rainy periods they draw up rapidly sufficient xylem sap of water and nutrients to support continued lower levels of growth, or just basic maintenance during the drought. In the same environment where both deciduous and evergreen species of angiosperm trees grow the evergreens will be more likely to have narrower vessel elements than the deciduous species.

Left: Twig of Scots pine showing a new cohort of needle-leaves at tip with cohorts from previous years lower. Right: Leaves of a deciduous gymnosperm ginko tree (*Ginko biloba*), showing pattern of veins that developed in early times of evolution of trees. Credit: Wikimedia, Julio Reis.

Conifers grow a new batch of leaves at the tips of their twigs (sprig or branchlet) each spring, advancing beyond cohorts of leaves remaining from previous seasons. As a seedling a conifer manages during its first year with a single cohort of adult form needle-leaves. Little leaf area is available for photosynthesis to support substantial growth of the stem and roots. Fast growing flowering grasses and herbs, also mosses, often overgrow conifer seedlings during summer, preventing the seedlings from establishing. But once a conifer seedling can raise its crown above the competing layer of grass and herbs, then it will be able to rise rapidly above seedlings of flowering trees. This is more likely to happen if the soils are too poor in nutrients, or waterlogged, or winter is severe, for many of the flowering plants.

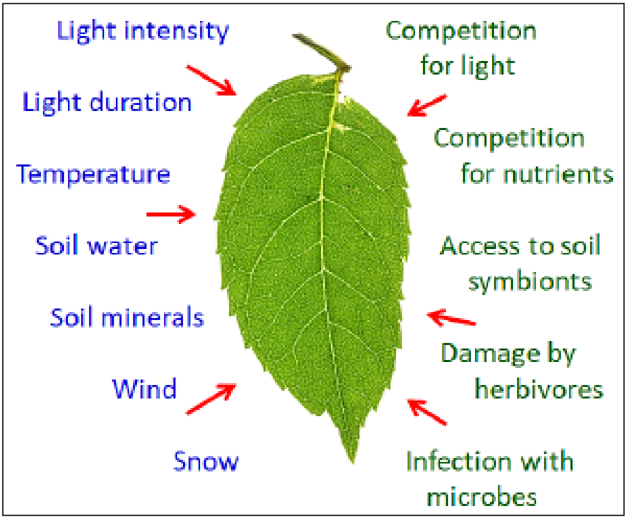
Broad-leaved precursor plants were flourishing early in the history of plants and later on flowering plants retained this leaf habit without any of them arising as needle-leaf species. The earliest fossils of flowering plants show leaves that have well developed vascular supply as networks of veins, and a wide flat surface as a thin lamina or sheet of tissue.



Top: Cross section of a gymnosperm needle-leaf (angular shape is formed in the tight leaf bud.) Bottom: Cross section of central part of an angiosperm broad-leaf.

Leaves of flowering plants evolved for a fast rate of photosynthesis and delivery of photosynthate for growth of the whole plant. Their embryos often grew large on the parent plant providing an ample food store, a resistant coat and often a fruit attractive to animals to disperse the seeds.

Germinating angiosperm seeds come equipped with wide spreading seed-leaves, cotyledons, to photosynthesize rapidly in support of early production of ordinary leaves able to soak up energy and carbon. Special pores for entry into the leaf of carbon dioxide, and exit of oxygen and water vapour, evolved early in land plants. Now they remain the same structure in both conifers and flowering plants but their number per area of leaf surface varies greatly. A species of flowering tree, black oak, *Quercus velutina*, for example, has no stomata on the upper surface of its broad-leaves but fifty thousand of them per square centimetre of the leaf's lower surface. A conifer species, Scots pine, *Pinus sylvestris*, has twelve thousand stomata per square centimetre on both its upper and lower surfaces of its needle-leaves. The vascular supply of broad-leaves is densely fine as a network of xylem and phloem vessels with the ability for each of the finest veins to service any layer of cells that are just two or three cells deep, up to one tenth of a millimetre away. Needle-leaves make do with a central vein that services more cells at a slower rate of photosynthesis and growth.



Examples of physical and biological factors that constrain the physiology of leaves.

Physical and biological constraints on leaves.
Leaves are the crucial organs for life on land. All animals included. Most forms of land life, other than some microbes, depend on the materials and nutrients provided from photosynthesis of aerial leaves.

Important yes, but not easy – being a leaf is highly demanding and options to achieve their singular task are limited. All leaves, broad or needle, small and intricate or large and simple, must operate within a tight range of constraints.

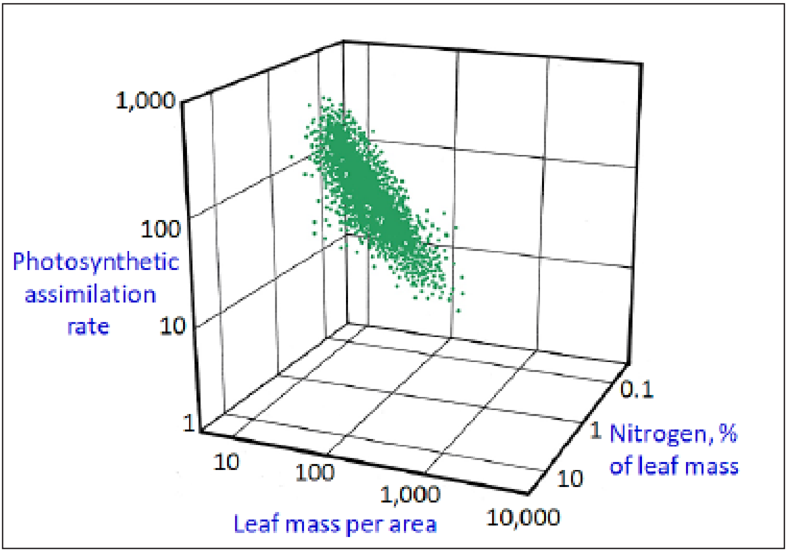
There are biological constraints of varying severity. Other plants compete for access to nutrients and light. Herbivores eat leaves whilst fungi and viruses invade leaves and whole plants. The rate of photosynthesis is dependent on the degree of warmth, and the power of light available, its irradiance as watts per square metre of leaf. Supply of water and the nutrients that rise from the roots to the leaves exert tight control over a plant's ability to maintain photosynthesis. Rains fail, or soils are full of water but as ice during winter. Snow and wind bear down and tear at leaves and branches of trees. Crystals of ice blasted in gales erode the outermost protective layer of needle-leaves, the waxy cuticle, which becomes less waterproof. Living is tough, even for trees.

Evolution of organisms arises from natural selection of genetic variants for their ability to reproduce well. Variants likely to prosper are however an infinitesimally small subset of all genetically possible variants. There is what researchers think of as a genetic landscape of evolutionary design. The variants that reproduce well and expand their populations come to occupy higher parts of this landscape. In this graphic metaphor the unsuccessful variants lie at the bottom and die out in the valleys. This mental image can be extended to the design of an organ as well as a self-reproducing organism. The limb design of four legged vertebrate animals could have evolved as, say, three fingers and one thumb, like all cartoon characters. But ten digits per limb would probably not have been twice as effective as the universal five-digit limbs. Once the early precursors of vertebrates survived and reproduced well with five-digit limbs then that design became fixed in genetic space. Digits can appear to be lost during evolution: horses stand on legs with only one effective toe, but the evolutionary history of horses shows when the other four digits were reduced. Similarly leaves work within a combination of many constraints and what evolution has provided in the distant past as available options.

All leaves, from scale-leaves of sequoia trees to the enormous leaves of banana plants, must operate within these constraints. Furthermore, leaves are constrained by what bears them, the whole seedling, or herb or tree. The leaves are constrained by roots adapted to low levels of nutrients, specially nitrogen and phosphorus, or roots adapted to live in waterlogged soils. The trunk of the tree will be adapted to resist freezing cavitation, or in contrast adapted for rapid translocation of xylem sap in spring and summer. Or the trunk of a species of tree may be adapted for rapid gain of height to reach into the sunlight and the branches will be adapted for a steep or a flat canopy to intercept the most light according to distribution of the species far from, or close to, the equator.

An early student of leaves was Charles Darwin, who commenting on the ways of evolution, wrote of 'The multifarious means of achieving the same end . . .' Now students of seasonality, phenologists, who ask why some types of leaves are shed at the end of the summer season whilst others are shed throughout the year, call these 'multifarious means' by names such as *universal trade-off surface,* or *leaf economics spectrum*. For simplicity, and only here, I will use *leaf compromise* to mean the same thing. The universality of these evolved adaptations seems to enable close coexistence of many species of trees within the same environment.

The anatomy and physiology of all leaves studied from this perspective, many hundreds of species (conifers, herbs, bushes, flowering trees) are all constrained in various ways, but all fitting within an overall pattern. The anatomy of the leaf must be adapted to diffusion rates of carbon dioxide, oxygen and water vapour, and also to the density of the vascular network of veins. The ratio of the mass of the leaf to its surface area must conform either to the needs of rapid summertime or rainy season growth of broad-leaves, or to resist the harsh winter endured by needle-leaves. The material that comprises the walls of leaf cells is the predominant part, up to 70% of leaf mass, particularly in leaves with a high mass per unit area such as needle-leaves. In contrast leaves with low mass per unit area such as broad-leaves can intercept more light for a more active, seasonal photosynthesis.



The *leaf compromise* concept as a cluster of data points from many species of plants. This example has two horizontal axes for: mass of leaf per unit area; and % of leaf mass that is nitrogen. Similar graphs represent: % of leaf that is phosphorus; respiration rate in the dark; leaf life span. (Simplified representation of data from several research papers. See: References and notes.)

Simple generalizations in the use of this concept of leaf compromise do not work. The trees of northern Australia for example are predominantly evergreen, despite an intensely seasonal climate of drought or rain. What seems important in this example is the balance between rate of photosynthesis leading to growth and the balance of advantage between evergreen or deciduous habit.

The net rate of photosynthesis must be favourable to the plant after the losses of nutrients consumed by respiration for the maintenance of the plant. The leaves must have access to sufficient watery sap containing sufficient nitrogen for the construction of proteinaceous enzymes, and phosphorus for the construction of nucleic acids and energy carrier molecules such as adenosine triphosphate. Then there is the matter of how leaves are adapted to their life spans and times of shedding in response to various combinations of climate and soil condition.

These combinations of data from observations and experimental measurements of leaf traits from several thousands of species of gymnosperm trees and angiosperm plants of varied forms, at over one hundred sites in various biomes, can be analysed statistically. The simplest representation of such analysis is on three dimensioned graphs: one axis going vertically and two axes projecting horizontally at separate angles. In all cases there arise from the analysis a cluster of data points, each at the intersection of three of these variable leaf traits. These distinct clusters represent the leaf compromise. This suite of leaf traits seems universal: consistent across a spectrum of rapid or slow return on growth relative to investment of carbon and nutrients in the leaves. The analogy with financial economics is central to these analyses. The leaf compromise has been found to operate with substantial independence through the variations of needle-leaf or broad-leaf, from leaf shedding seasonality, and from location of plants in any of the major climatic biomes of plant distribution.

Scale leaves and tree of giant sequoia, *Sequoiadendron giganteum*.

There is more to how leaves do their work for the whole plant. How many leaves are there relative to the mass of the trunk and branches for example? Some of the largest living organisms on earth are the awe inspiring giant sequoias, *Sequoiadendron giganteum*. This tree of over a thousand tonnes rises seventy or more metres. But look closely for its tiny leaves: mere scales, although vast numbers of them on a single tree. They remain producing photosynthate for an extra month or more at the start and end of the warm growing season compared to any deciduous broad-leaf tree in the same region.

So the outcome for overall growth and productivity of a typical broad-leaf species, leafless in winter, compared to a needle-leaf species with leaves all year, can be counter intuitive. The broad-leaf example of European beech, *Fagus sylvatica*, has been compared in detail to the needle-leaved Norway spruce, *Picea abies*, growing close to each other in their natural habitat in northern Europe. The photosynthetic capacity of the beech was measured at 13.3 milligrams of CO_2 per gram-hour whilst the spruce was measured at 4.4 milligrams of CO_2 per gram-hour. However, in a typical year in this region plantation stands of the spruce gain 14.9 tonnes of carbon per hectare per year, whilst stands of beech gain 8.6 tonnes.

A hypothetical comparison of the spruce trees with their same photosynthetic capacity, but the same total mass of leaves and the same leaf seasonality as the beech, showed the spruce trees would gain only 4.9 tonnes of carbon per hectare per year. The higher productivity of the spruce lies in having multiple cohorts of many densely packed leaves active for a longer photosynthetic season. That is despite their lower rate of photosynthesis per unit area of leaf. A further general adaptation of conifers to northern boreal regions is their greater mass of roots relative to the above ground mass of shoot: the trunk, branches of leaves. This varies from 0.19 tonnes of *roots* to every tonne of *biomass above ground* for tropical broad-leaf trees; to 0.23 tonnes of roots for temperate forests; to 0.32 tonnes of roots for boreal forests.

Types of leaf shedding.

The leaves of all gymnosperms and angiosperm trees fit into wide categories of seasonal leaf shedding and other adaptations to their environment. Most of these categories are occupied by species of both conifer and flowering type and within families and genera of these types. These categories within the leaf compromise are the result of convergent evolution. This is the type of evolutionary trend that produces the same 'means of gaining the same end' seen in reptiles, birds and mammals that have evolved the ability to make a living by swimming.

There are trees that retain their needle-leaves or scale-leaves through summer and winter such as spruce (*Picea*), pines (*Pinus*), and firs (*Abies*). These avoid cavitation in their xylem during severe frosts and utilize poor soils by means of a relatively large mass of roots. Such roots are well able to recycle nutrients from the slowly decaying litter of needle-leaves. The tall narrow tree form utilizes well the low angle of light at high latitudes. The tannins and phenols and thick outer layers of the leaves repel many herbivores but at the cost of extra energy and carbon for their construction.

Baobab tree, *Adansonia digitata*, on East African savanna with highly seasonal rainfall pattern, coming into leaf during wet season.

Some conifers bear their needle-leaves in summer only, such as larch (*Larix* species), swamp cypress (*Taxodium distichum*) and dawn redwood, originally of China (*Metasequoia glyptostroboides*). Like other conifers their xylem is adapted to avoid cavitation during freezes. They can exploit waterlogged soils because their loss of leaves during winter avoids the danger of frost-drought in the case of larch species in boreal regions. Also swamp cypress seems adapted for habitats that are seasonally flooded in the sub-tropical rainforest in south eastern regions of the USA where this species is indigenous.

Swamp cypress, a deciduous conifer in wintertime. This species is adapted to waterlogged soils, and other deciduous conifers such as larches also flourish in boreal regions on poor and wet soils. Leaf seasonality of these gymnosperms may be causally related to these soil conditions.

Dawn redwood, a deciduous conifer, coming into leaf at spring time.

NOTE: both these well developed trees were photographed in a botanic garden in northern Europe.

Broad-leaved trees may shed all their leaves at end of the summer growing season, such as species of elm (*Ulmus*) and most species of beech

(*Fagus*). Trees with this type of leaf compromise are able to photosynthesize rapidly from spring to end of summer as long as they are on fertile and moist but well drained soils. They avoid destruction by freezing of their delicate leaves but bear each year the high cost of withdrawing only about fifty percent of the nutrients from their senescent leaves. Other broad-leaved trees retain their leaves through summer and winter season, or in tropical regions through wet and dry seasons, such as the rosy trumpet tree (*Tabebuia rosea*), and the Tasmanian oak (*Eucalyptus regnans*) which is the tallest flowering plant. Their leaves are shed by normal abscission but only when they individually decline with age, not by a seasonal timing. The form of many of these types of tree is adapted for light from the sun high in the sky. They raise a towering canopy when growing where there is sufficient water in the soil to cope with high losses of water through transpiration under hot sunlight. Their root systems may be a compromise for soils leached of nutrients by heavy rainfall but with rapid recycling of nutrients from a continuous fall of leaves onto warm and moist soils. It is in the sub-tropical and tropical regions that the all season broad-leaved gymnosperm trees live, such as totara (*Podocarpus totara*) and kauri (*Agathis australis*).

A category occupied by fewer tree species is called leaf exchanger. Such trees lose rapidly their complete set of leaves then straight away start to replace them with a fresh set. The southern magnolia (*Magnolia grandiflora*) and the Californian live oak (*Quercus agrifolia*) are examples. They typically occur in regions with infertile soils and distinct dry seasons, or in the Mediterranean type of climate as with the cork oak (*Quercus suber*).

Climate influences where particular species of trees can establish, but if trees are categorized by their seasonal patterns of leaf shedding, then these categories do not correspond neatly to the six wide categories of climatic biomes in which trees grow throughout the world. That is six out of the nine global biomes defined by rainfall and temperature. Those six that support trees range from boreal forests, through treed savanna, to tropical rainforest. This lack of close relationship between climate and distribution can be compared to the experience of foresters and tree collectors working for botanic gardens and private estates. Exotic trees often do not merely grow well in climatic regions substantially different from their native origin – some species will adapt to their new homes sufficiently to reproduce naturally, then expand their populations.

Montery pine, *Pinus radiata*, in its indigenous habitat on south west coast of USA. Credit: Wikimedia.

The Sitka spruce (*Picea sitchensis*) is indigenous to a thin coastal strip from southern Alaska to northern California. Now it is one of the commonest species in commercial plantations in many parts of the world. The Monterey pine has the status of *endangered* in its indigenous region of small coastal areas of south western USA, with warm dry temperate climate. Now it is the dominant plantation tree in New Zealand and common elsewhere from South Africa to Chile.

The Tasmanian blue gum (*Eucalyptus globulus*) is a splendid tall tree that for centuries has provided excellent timber and pulp-wood. Indigenous populations inhabit parts of the Australian states of Victoria and

Tasmania and small islands in between. Wherever this species originated it was likely from one population and that new species must have spread over these scattered areas of southern Australia.

Tasmanian blue gum growing in Hawaii, but its indigenous habitat is in Tasmania and Victoria states of Australia. Credit: Wikimedia, Forest & Kim Starr.

This tree in its natural indigenous state has a small range in an area of the world characterized by two biomes: sub-tropical rain forest, and tropical rain forest. Now this species is a timber plantation tree of very wide distribution from New Zealand to California, from Europe to Africa. This new range includes five vegetation zones, all in addition to those two of the tree's indigenous region, ranging from temperate broadleaf forest to dry steppe. In some countries and states where this gum tree has been introduced, California for example, they spontaneously reproduce and disperse so well that they are treated as an invasive species, a weed to be eradicated locally. This species of tree has leaves that work well in many of the world's climates where trees grow, but where the tree lived thousands of years ago was due to chance of evolutionary history. Where such species of plantation trees have been introduced was originally a matter of trial and error experimentation by estate owners and foresters. The successful introductions, in terms of how well the new forests flourished and produced profitable timber, owed much to the fundamental versatility of leaves. The evolutionary invention the leaf, with is core suite of adaptive compromises, was the key to a universal means of vigorous plant life on land, supporting nearly all other life. Now foresters exploit this versatility by planting non-indigenous species selected for their ability to flourish as timber trees in many new environments.

References and notes.

(Many articles are accessible as abstract or full text using search engines such as Google Scholar, institutional log-in, or a pay-wall.)

Evolution.

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