How trees in forests behave

A chapter in: *Trees of the people*, by Alan R. Walker www.alanrwalker.com

Trees behave in the sense that a beech tree growing in a natural forest will behave differently from a beech tree of the same age that happens to be growing in isolation, out on farmland for example. Beech trees growing in a plantation for production of timber, lumber, are forced by how the foresters planted them. Packed close together the trees behave differently from those in a natural forest. When that timber is used by a carpenter to make furniture of seasoned beech wood, he will work with the knowledge of how that species of wood behaves under the carving and bending forces applied.







Broafleaf: Ash, Fraxinus excelsior

The carpenter behaves toward this woody construction material through remembered experience of what works best and the plan he has thought of for an attractive new design of furniture. The carpenter has a brain connected to nerves throughout his body, enabling his intelligence. Plants have no brains to do any thinking with, so they are not intelligent. However they have much ability to respond to the situation they find themselves in: that is, the place where the seed happened to land and rooted into the ground. Trees respond by growth, as do most other forms of plant life, but their growth is so slow that this is often not apparent to us busy people.



Umbrella thorn, *Vachellia tortilis:* a common shape of a broadleaf species in hot savanna climate, with form responding to sunlight directly overhead, and to dry soil.

A beech tree will grow into a different form than an oak tree in the same stand of trees, and a spruce tree more distinctly different. Trees of tropical savannas often grow spaced well apart and shaped like a parasol. Each species has its separate inherited pattern of growth but all of them respond fundamentally to their common source of energy: sunlight. Trees feed, as do all plants, on the energy from sunlight. Enormous quantities of this radiation energy shine down on forests but the complex process of capturing it and turning it into the material of a tree loses most of the energy. So, paradoxically, in a forest bathed in overhead sunlight from a clear sky, there is for each tree, a potential shortage of energy. Each tree responds to this shortage by behaving to gather as much energy to itself as possible. In this way, and imperceptibly slowly to us, the trees behave in relation to their surrounding trees, creating a slow moving dynamic of the forest.

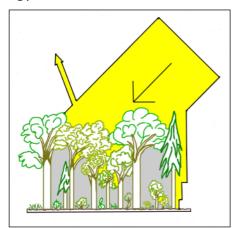
Trees have a trunk, a tall stiff stem. Usually central, with a few exceptions, hazel for example, *Corylus avellana*, with multiple stems growing ten to fifteen metres. The trunk of an ordinary tree, conifer or broadleaf, softwood or hardwood type, is an invention of evolution that arose long ago and has been extraordinarily successful ever since. The earliest major group of trees to evolve are the conifers, about 630 species distributed worldwide. Apart from a few species adapted to live high on mountains or in deserts, these conifers are mostly conspicuous by their single central trunk growing straight and tall toward the sunlight.



Single layer of branches and leaves of a beech tree, Fagus sylvatica.

The broadleaf trees evolved much later than the conifers but with a form of growth with many options, more flexibility of shape and general form of the mature tree. There are about 950,000 species of them named: a successful group. All of these different ways of being a tree enables this form of plant life to be as widespread and varied as the grasses are. One quarter of all species of plants are trees, as a general estimate. But that is just a count of species. The sheer mass of trees on Earth, their biomass measured by the million of tonnes, and the space they all occupy, vastly exceeds all other forms of plant life, with the possible exception of plant plankton in the oceans. Trees grow with stout tall trunks to reach up into the top layer of the forest, there to harvest with their leaves as much energy as possible from sunlight. Trees with their leaves behave like some kind of self-propelled solar panel, equipped with a feed-back mechanism that instructs the trunk to grow taller and the branches of the tree's crown to spread wider than that of the surrounding trees.

Energy.



Photosynthesis can capture 2% of energy in sunlight. Some sunlight is reflected back up to space and the leafy canopy captures most, with little left for plants at lower levels.

Life on Earth depends almost completely on the energy of sunlight. A few life-forms as microorganisms have other direct sources of chemical energy. Animals in the depth of oceans or caves survive on the organic materials that sink into the depths, but these sources were originally powered by sunlight, measured technically as watts (joules per second). Despite night-time and cloudy days the amount of sunlight energy available to plants greatly exceeds what their green leaves can use. The process of turning sunlight into the material needed to make a plant is called photosynthesis. This is a greatly complex chain of chemical reactions working within special cells of each leaf (see: 'Photosynthesis.').

Furthermore, each tree in a forest has to spread its leaves in a pattern to intercept as much sunlight as possible. Some of the light that does impact the leaves is just reflected off the surface of the leaf. Leaves have on their upper surface a waxy waterproofing and defensive layer that is often shiny (see: section here "Stress"). Information illustrated here about the amount of energy captured and used by trees of a forest comes from many sources.

Patterns of growth of trees and how trees interacts with close neighbours, are influenced by sunlight that penetrated between the trees and is captured by their leaves. Behaviour of each tree, revealed decade by

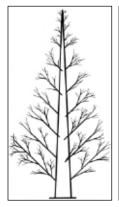
decade of growth pattern, give rise to a particular distribution of species, sizes and forms within any stand in the forest. Each tree grows up against gravity and in general the straighter the trunk the more efficient will be the tree's use of its resources of materials from photosynthesis. Early growth of a tree needs to be rapid: there is a race between neighbouring trees to reach the sunlit upper region the canopy. So young trees gain height on relatively thin trunks. This can be seen in young plantation of conifer trees, before any thinning has been done by foresters.



Canopy of a tropical rain forest: most light is captured at this level. Credit: P. Jeganathan, Wikimedia.

The laws of the physics of light and of chemistry of photosynthesis apply equally to both conifer and broadleaf trees. There is a concept of forest botany called leaf economics spectrum (see "Leaves: when should they fall"). Needle-leaves and broadleaves are equally efficient at gathering sunlight and using that to capture the carbon from the carbon dioxide of air then convert that into the material of a tree. Some species of conifers thrive in warm sunny climates but most of the World's conifer forests are in temperate to boreal regions of climate. There the typical narrow cone architecture is best adapted to harvesting light from the Sun when it shines low in the sky.

Trunk, branch and wood.





Conifer tree form is dominated by growth point at apex of trunk, and regular distribution of branches.

Broadleaf trees have multiple growth points of branches and irregular distribution of them.

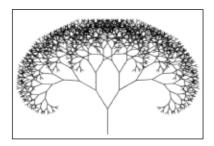
Conifer:
Swamp
cypress,
Taxodium
distichum is
leafless in
winter





Broadleaf: Common Ash, Fraxinus excelsior.

A tree is: "... a large woody perennial plant with a distinct trunk giving rise to branches or leaves at some distance from the ground." A clear enough definition from a dictionary – unfortunately missing any mention of the roots. Be assured that roots and their intimate connection with leaves to make the whole thing work is covered in the next section. Tall trunks define most trees. Another type of tree can be constructed mathematically as a fractal design with short thin trunk and ever increasing iterations of branching. Wooden trees have thick trunks to support their need to grow tall toward sunlight but the taller the trunk the greater the problem for this design.

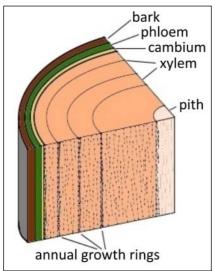


A mathematical tree, made with a fractal equation but too spindly to work.



English Oak, *Quercus robur*: thick trunk, massive branches.

The roots are a long distance from the leaves. From the outermost roots water must by drawn up to the outermost leaves. The taller the tree grows the greater the cost of materials for growth of its plumbing system. Water is drawn up through roots and trunk by suction from the leaves as water evaporates from pores in the leaves; a process called evapotranspiration. The passages for this transfer are special cells called xylem. These need to be narrow enough that the surface tension of water in them is great enough to maintain a column of water that will not break. Any break causes an embolism, an air-lock, in the plumbing that deprives some part of the foliage of water.



Section of a 3 year old tree.

Transport tubes of trees are of two types. Both are generated from a growth layer, the cambium. Wood is xylem tubes that transport water upwards. Nutrients from leaves are transported in the phloem tubes.

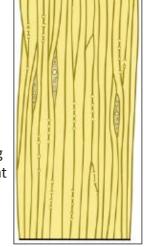
Only the outermost layer of transport tubes are active. Inner layers die and form the woody skeleton of trunk and branches.

Thus evolution of trees has produced an extraordinary material: wood. This is best seen under a microscope for the multiple layered complexity of how it grows. This topic is covered in more detail in chapter: "Wooden buildings". The plumbing tubes of the trunk, the xylem cells, are tightly bound together. So an oak tree might, in response to what other neighbouring trees were doing long ago, have a branch or two that has grown out sideways from the trunk at angle and for a length that would leave a building engineer wondering when to start using beams made of wood. Tree trunks simultaneously grow thicker and taller by adding layers of new woody tissue to both trunk and branches. This addition comes from the cambium layer at the outer layer of the woody tissue. The cambium is a meristem tissue; its cells keep dividing for the life of the tree. Each additional layer adds to both width and height of the tree as a whole. Xylem cells are narrow and greatly elongated vertically. As they are produced by the cambium the tree grows taller. Simultaneously the trunk grows thicker. Eventually upward growth ceases, but the trunk thickens gradually throughout life of the tree..



Cross cut through trunk of Sitka spruce, Picea sitchensis, with 60 growth rings.

Lengthwise drawing of softwood trunk at high magnification showing individual xylem tube cells.



Tree trunks are similar to flag poles, both become narrower with height, and for trees that saves on amount of woody tissue needed to reach the canopy whilst distributing the bending force of a gale onto the tree further down the trunk. Here the overall bending force, the leverage, will be greatest. Bending in the face of a storm wind saves the tree

The diagram on page 6 compares the architecture of a conifer with a broadleaf tree. The regular pattern of the conifer trunk and branches contrasts with the irregular branching pattern of the broadleaf tree. These patterns are caused by structures within the trunk and repeated along every branch. They are growth buds: similar to the easily seen leaf-buds and flower buds on broadleaf trees. The growth buds in trunks and branches are potent sites for their role because they contain a special type of cell. These have the normal capacity to divide into two cells but one of these remains where it is without developing into any specialized type. It retains this sole ability to keep on dividing whilst remaining in the bud. The other cell has different work to do, growing as part of wood, leaf, flower . . . These growth buds, known to biologists and medical researchers as meristems, have potent capacity for repeated division of cells. This starts from a fertilized egg cell, through to providing all the functional types of cell of the fully grown plant or animal.



Pollarded broadleaf tree with vigorous new branching from growth buds in bark of trunk.

Top of a conifer tree where the meristem at the apex dominates typical growth as an elongate cone shape.



Meristems of trees form just below the inner surface of the bark. They are spaced apart by small distances and this can be seen on any broadleaf tree with a broken, or coppiced trunk. New branches sprout from the bark. Also the apex of the trunk of a conifer has a particular growth

bud, the apical meristem that defines the distinctly conical and repeated simple branching pattern of this type of tree. Going up the trunk of a conifer, in order of age, the branches directly from the trunk have each started from a growth bud in the trunk. Branch upon branch upon branch is a reiterating pattern of growth. However, not a pattern imitated by fractal trees: conical not domed.



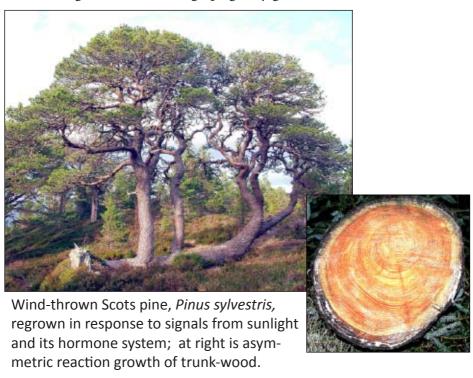
Birch. *Betula pendula,* branching pattern.

Rowan, *Sorbus aucuparia*, branching pattern.

This reiteration forms a regular pattern of the growth of many species of conifer because the process is under the control of a hormone system. These hormones do the same job, but with different types of bodily chemicals, as do the hormones of animals such as us. For plants in general these hormones are called auxins. How they work for body of a plant is as complex as it is for the hormones of humans, and beyond the scope of this chapter. Broadleaf trees grow tall and branched following the control of an auxin system that is distributed throughout the branches. So, soon during the growth of a broadleaf tree there forms a varied pattern of branching between neighbouring trees of the same species.

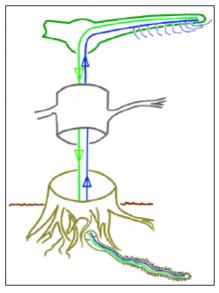
Trees behave by growing in response to stimuli, to signals, such as access to sunlight or to patches of soil rich in mineral nutrients. Once grown a trunk retains ability to adapt to a large change in its circumstances. So a

wind-blown tree lying on the ground but with its root plate sufficiently intact to function may reorient itself by differential rate of growth of the trunk to produce reaction wood. In cross section of a trunk seen as asymmetric pattern of annual growth rings. The photograph here of a reorganized tree shows a side branch growing as a substitute main trunk, and the original trunk turning upright by growth of reaction wood.



A young tree in a forest forages for its source of energy. Once in the canopy it will need to compete with surrounding trees for the same resource. Information about strength and duration of sunlight penetrating the canopy travels to the growth buds of the branches through the tree's hormone based signalling system. The signals start in the leaves of the foraging tree. Stimuli for growth to those branches best placed to gain most energy will increase the reiteration growth of the affected branches and on the finest of these branches more leaves will grow.

Roots seeking water and nutrients.



Roots and leaves work together through plumbing systems of phloem (green arrows) taking carbohydrate from leaves to roots, and xylem (blue arrows) taking water and nutrients to leaves. Water is pulled up by transpiration from the leaves.

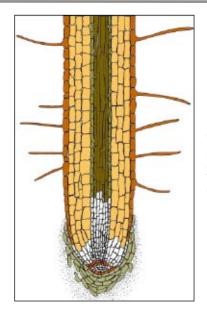




Main and fine roots of a wind-thrown beech tree.

Root hairs on a fine root within soil. Credit: Wikimedia.

A tree can only keep searching for the energy of sunlight if it supplies its leaves and branches with sufficient water and dissolved nutrient minerals. Furthermore, water as the chemical compound dihydrogen oxide, is part of the chemical reactions of photosynthesis, not just a solvent and carrier of nutrients. Like the water we use in a kitchen for cooking, not just for washing the dishes.

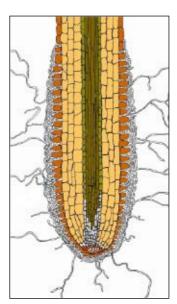


Structure of tip of fine root showing root hairs, phloem, xylem, root meristem, and cap of mucilage.

The work of a root starts at its furthest branchings, its final reiteration of structure. However, the activity of roots is far more active than above-ground branches. As one patch in the soil is found by a root then depleted of its resources, another patch is needed. Soil is a harsh environment for roots at their finest size. Here a root is equipped with many root hairs. These are microscopically fine and need to be replaced at short intervals. The delicate structure of root hairs provides the easiest passage of the water in soil into the tree. Entry is active, under a slight force of negative pressure that is transmitted from the leaves, through trunk, to roots out furthest into soil.

An equally vital flow of liquid goes in the opposite direction: leaves to branches, to the trunk and then out to the finest roots. This transport network carries the phloem liquid containing the building materials, mainly carbohydrates that the tree uses to grow, and when mature enough, to produce cones or flowers, and seeds. Responses of roots to their dark, wet, abrasive environment is another world from the branches and leaves of the tree. For a root foraging for water and nutrients a behaviour of trial and error seems most likely to succeed.

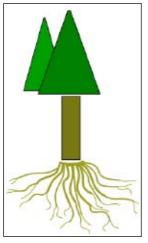
Tip of fine root with hyphae of ecto-mycorrhizal fungus at surface of the root.



Mycorrhizal fungi are likely to be useful to the tree, enhancing the transfer of nutrients from soil to tree, in exchange for carbohydrates from the tree. However, it is the tree and its roots that forcefully spread through the obstructions of sand and rocks, rotting roots and stems of plants, and past the fauna of soil dwelling animals – many of them herbivores.

Branches with their leaves, so responsive to the direction of sunlight are able to extend themselves into spaces in the crown of the tree that will be best for further growth. Which direction should a root grow toward? What distant and diffuse signal can the root respond to? Trial and error is likely to be the most rewarding behaviour, despite the cost of errors, of fruitless foragings. Making mistakes is an unfortunate part of staying alive for all of us, and for a root of any tree there will be many and frequent mistakes.

Balance between leaves, branches, trunk and roots.



When a tree gets its crown into the canopy then resources are adjusted toward the needs of many years of seed production. Branches form into a crown that occupies as much space as possible within the forest canopy. Apical dominance of the trunk reduces so that little more height is gained whilst width of the trunk continues to expand. Roots increase their activity and range of foraging for more resources of minerals and water to support yearly production of male and female cones.

Once a tree, conifer or broadleaf, has pushed its crown up into the canopy of the forest, then it needs to adjust how its resources for growth are allocated. By the time the tree has grown for that long and reached that far it will be mature enough to start producing seed. For many plants, and specially trees, reproduction is an enormous yearly production of vast numbers of seeds. Nearly all of that seed will die, without issue, decade after decade. The need for a tree is to adjust growth from a race to the canopy toward a maintenance of that physical position in competition with surrounding dominant trees.



Mature and dense canopy of a beech wood.

Fine roots of a fallen Douglas fir, *Pseudotsuga menziesii*.

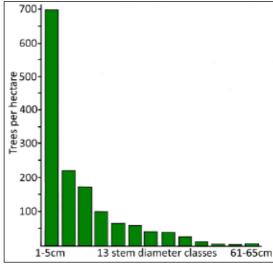


The growth of a tree, or of a plantation of the same trees, is often measured as Net Primary Productivity, that is how much increase in biomass as leafy and woody material there is left after subtracting the mass of material consumed by that tree's own metabolism of respiration. So there comes about a decline in the Leaf Area Index of a tree. That is: fewer leaves per unit of ground area, per square metre, covered by the crown of the tree.



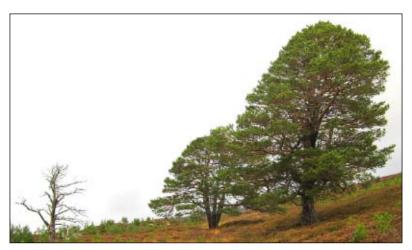
Natural Stand of young Scots pines, *Pinus sylvestris*, many of them with narrow trunks. Their growth form is adapted to competition from surrounding trees.

Typical distribution of trees of one species ranked by diameter of trunk, from 5cm to 65cm.



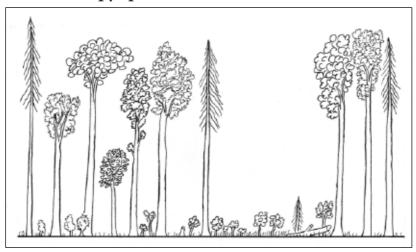
The diameter at breast height of trees measured in a plantation can be measured as slowly increasing over time. Simultaneously risk to the tree of blockage of xylem tubes, causing air embolism, is likely to be reduced by larger allocation of building materials to the roots.

These re-allocations of resources by a tree that has reached a place in the canopy enable a dynamic balancing of its metabolism. Such balance is often described as a state of homeostasis This is an active process, not some rigidly fixed state. If the outside environment of the tree, or the forest in which it lives, changes then the individual trees retain ability to change in response. Their total leaf area can change rapidly. Unproductive branches can be actively shed by the tree. Exploratory grow by the roots can increase by both number of roots or can change gradually what volume of soil they grow into to forage for water and minerals. The balancing act of homeostasis is active.



Scots pines isolated from main forest. Ample sunlight from many directions enables extensive retention of branches at lower levels. The growth form of these trees has not needed to adapt to competition from surrounding trees in a forest.

Growth to occupy space in a forest.



A section one tree wide through a mixed forest of central Europe. Canopy trees dominate access to light energy. Sub-dominant tree species can manage with less light. A gap created by wind-storm allows enough sunlight to start a full regeneration in this space.

Each individual tree in a wood, a forest, or plantation competes with all its near neighbours for space in which to thrust its crown into the canopy and for its roots to spread in soil already occupied by many other root systems. Compare an oak or beech or pine tree that has matured to full reproductive size out in the open ground of a park or agricultural ground. They all grow into a shape that a child will recognize as how to draw a tree in a classroom lesson about nature: like a lollipop.



Dominant and subdominant trees of a moist temperate climate. Trees do not grow in natural forests all crammed together for companionship or some other driver of mutual assistance. Individual trees grow close to each other as mixes of species in a forest because that small place in the forest is where a seed of their parent pair of trees landed. Some species of trees, birches for example have small lightweight seeds that may be blown far on the wind. The acorns of oaks travel no further than forgetful squirrels and birds bury them. A forest may migrate, slowly by the decade and century, as its various species of seed disperse in direction of the prevailing wind. Otherwise, seed within a forest will only grow into a mature tree when a space appears. Seed that lands below a thickly developed canopy of beech trees is doomed to grow no larger than a spindly sapling, starved of sufficient light. The natural forest becomes thinned in a way similar to the active thinning procedure of foresters managing early stages of a plantation.

Growth form of a mature oak tree that grew isolated within farmland. No need to grow any taller



Some species of tree have evolved to occupy space available below the canopy of a forest. Here there is substantially less light energy available to them. Nevertheless the evolved traits of these species for survival and growth to reproductive maturity enables these trees to occupy this unpromising seeming habitat. Botanists and foresters call these species of tree sub-dominants. Typical species of them in northern temperate forests include hawthorn (*Crataegus monoygyna*) and holly (*Ilex aquifolium*).



Little sunlight penetrating canopy of a mature stand of beech trees.



First year seedling of beech beneath the canopy of these trees shown on left.





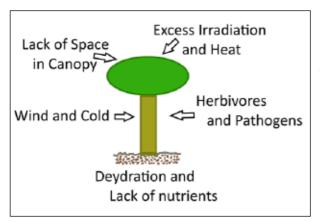
Wind storm, fire, and massive infestation of insects or microbes create distinct gaps in a forest, defined by their sharp edges against the intact forest. Soon after formation of the gap each individual tree still standing at this boundary will respond to the new space. This sunlit place contains no mature trees as competition for space. So the standing trees at the edge expand by sideways growth of branches to spread their leaves

into the sunshine. The same trees disperse their seed onto the ground of the gap and those seeds will have more sunlight and space available than seed of the same tree dispersed out past the forest canopy. These gaps range in size from that formed by a single tree wind-blown onto the ground, maybe 30 x 30 metres. Or a forest fire, after a long drought and aided by strong wind, might create in a forest a gap of hundreds of hectares. Over the time-scale of a forest, by the century, a large scale mosaic develops of stages of growth, maturation, destruction or natural death of the forest. These are difficult to see from **within** the forest, but increasingly images of forest structure from above reveal these large scale dynamics of behaviour of entire forests.



Response of a beech tree at the edge of a gap in the forest: branches next to the gap grow out into the sun-lit space.

Avoidance of stress: heat, cold, irradiation, herbivores.



Plants are eaten by many types of animals and microbes.
Tree trunks are at risk of wind-storm. Leaves suffer from excess radiation and wind damage. Roots die during droughts.

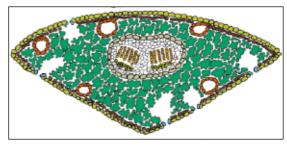
Plants cannot run away and hide from predatory herbivores. They have few natural shelters from wind and cold. Too much sunlight, specially when not filtered of far ultra-violet irradiation by humid and dusty air, is a direct threat to health of plants. The radiation can be directly fatal to plant cells, specially the active cells of growth buds. Sunlight originates from an ongoing, at astronomic scale of time, hydrogen bomb. This is not a simile, it is the reality of nuclear physics. The chloroplasts of leaves, the active centres of photosynthesis may migrate deeper into the mesophyll for protection. In tropical climate, with overhead sunshine, excess irradiation can be avoided by some species of trees being seasonally deciduous. We people protect ourselves from excess irradiation by ultraviolet light using hats and sun-screen.

Coldness as a stressor is easiest for us to understand, as we feel it directly. Trees slow down to a minimal growth rate, a metabolism for simply maintaining life. A winter storm can batter the leaves of conifers with crystals of ice that abrade the outer waxy waterproofing layer of needle-leaves. Hot or cold weather causes stress to the metabolism of photosynthesis. These complex chemical reactions can work at a wide range of temperature, with 25°C good for efficiency. At higher temperatures trees that are both in leaf and on well-watered ground gain some relief to their leaves by passive cooling effect of evaporation of water from stomata.





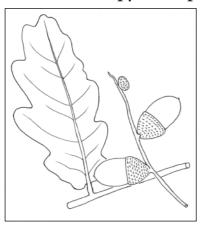




Examples of stressors, threats and defences for the health of trees. Roe deer, *Capreolus capreolus*. Larva of spruce budworm moths *Choristoneura fumiferana*. Scots pine at the tree line, reproductively active but distorted by wind. Cross section through a conifer needle-leaf with red coloured ducts containing resin that is repellent to herbivores. (Credit Wikipedia for deer and caterpillar.)

Overall for the health of a tree the more reserves of carbohydrate molecules it can store in its branches, trunk and roots, the better it will resist various causes of stress. The ability of the tree's hormone mechanisms to sense stress and to behave by allocation of resources is important to tree survival, but it is a field of botany currently best studied in small convenient herb species grown in greenhouses.

Trees in the canopy can reproduce.



A forest will persist for as long as its trees reproduce themselves sufficiently. As trees reproduce at the margin of the forest then the forest can migrate. Production of massive amounts of seed most years is needed because the chance for a seed to grow into another mature tree is very low.

Trees of a particular species growing as a large population over a wide area of land will retain the characteristic form and dynamics of growth of that species as long as they reproduce themselves vigorously. So, from perspective of evolutionary genetics, the purpose of a tree is to reproduce itself. The same applies to all forms of life on Earth, us humans included. But this stark statement, a reduction to the absolute basics of life, needs more context, more about the drives of the organism and the place that it lives in.



Young oak tree at early stage of its long reproduction phase of life.

Old and decrepit oak tree at end of growing season. It was heavily laden with acorns possibly during a mast year.



An oak tree, a beech or a pine growing slowly in a mixed species woodland is likely to grow its crown up into the canopy. There the tree will re-adjust how it operates so that maximum resources can be directed at production of seed. Acorns full of reserves to make a seedling; beechnuts with smaller reserves. Pine and spruce seeds, adapted for dispersal on the wind, have by comparison a meagre supply of nutrients for the earliest days of a new tree. Tree seeds use their reserves of materials to make their first shoot and root. Rapidly after that first claim on a patch of land, the seedling produces its own first type of leaf, seed-leaves (or cotyledons). A successful seedling will have established enough reserves from its first true leaves before winter or dry season prevent further growth. The fate of that seedling then depends on chance. If the seed landed not only in a gap in the forest well sunlit for growth, and not already occupied by dense growth of grasses and herbs, it may grow into a sapling. Then many years later it will mature into another tree with its crown up in the canopy.

Meanwhile, this pair of trees, these oaks, beeches, pines, spruces, all continuing as reproductive units, will continue to produce a large crop of seeds for dispersal by gravity or by wind, for another hundred years or more. To maintain a stable population of their species in that forest region requires each pair of trees to give rise to more than just another pair of trees, but three of four offspring will probably be sufficient, per parent

pair, to maintain the population. All that effort for so little to show for it – from our perspective that is – but we people live fast, behave economically, then die young. Trees live by the century: reproductively active for most of all of those years. This vast and prolonged extravagance of seed production works as an evolved strategy of conspicuous success to judge from how the approximately one million species of tree on Earth live this way in their vast and enduring forests.



Mature Sitka spuce, *Picea sitchensis*, part of one of many branches laden with maturing female cones that will produce huge numbers of light, wind-borne seeds.

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