# *Tree reproduction*

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

During the times when the land surface of Earth was barren dusty sands, rocks and lava flows, plant life was thriving in open seas and along shore-lines. These were plants as algae, microscopic to sea-weed sized. As some of those early plants evolved to live on the inter-tidal zones of about five hundred million years ago they had to adapt to the new problems of life on land. Problems that included desiccation, rapidly changing temperature, and ultra-violet radiation. Those that survived best on land found many new opportunities, new ways of living in an environment that despite its hazards provided both ample space to attach to solid ground and ample energy from sunlight. As plant life colonized new resources of varied nutrients and climates, and grew large as they fed on carbon dioxide by photosynthesis, their decomposing bodies formed soils for the first time. In turn microorganisms, small animals and fungi colonized and enriched the soils.

Rowan (*Sorbus aucuparia*) inflorescence, and crop of mature berries:

A crucial problem remained for plants on land. Their marine ancestors had evolved a method of reproduction by a sexual process: an individual of one sex needed to combine with an individual of another sex. To combine and ensure that offspring had a functioning genetic constitution required special cells: eggs to be fertilized by sperm. For marine algae the sperm swam across to immobile eggs. On land free water is available to plants most of the time through their roots in soil but on the above-ground parts of the plant free water is only present intermittently, unless the plants confine their range to damp habitats. Hence the success of mosses and ferns during the warm wet times of the Carboniferous period. Some species of these early plants grew to size and form similar to modern trees. Other successors of these early mosses and ferns remain with us now, well adapted to their damp habitats and in the case of some mosses continuing to create massive beds of peat.

DEVONIAN period, 420-360mya: arthropods started; earliest insects.
CARBONIFEROUS period, 360-300mya: gymnosperms started; winged insects started.
PERMIAN period, 300-250mya: modern gymnosperms; winged insects spreading.
TRIASSIC period, 250-200mya: conifers dominant; angiosperms started.
JURASSIC period, 200-155mya: modern winged insects; evolution of birds started.
CRETACEOUS period, 155-65mya: gymnosperms declining; angiosperms spreading; insects co-evolving with angiosperms.
PALEOGENE period (start of Cenozoic era): gymnosperms reducing; angiosperms dominating; pollinating animals proliferating with diverse flower forms.

Time line: evolution of plants and potential pollinator animals.

Now life on land, as sheer biomass, is dominated by grasses, herbs, needle-leaf trees and broad-leaf trees. All these plants evolved as members of two broad groups. First came those that reproduce using some type of cone structure in which seeds develop as the life cycle stage for dispersal. Later, along a separate evolutionary path from some ancient common ancestor, came plants that reproduce using flowers develop into fruits containing seeds as their dispersal stage. Amongst trees, these two groups are, broadly, the needle-leafs and the broad-leafs respectively. All of these land plants, from grasses to giant sequoias or oaks have adapted their sexual reproduction by two similar methods where the sperm actively migrate to the eggs whilst avoiding desiccation. Now various species of these plants can live on lands as lush as tropical monsoon areas or as harsh as tundra, deserts or mountains.

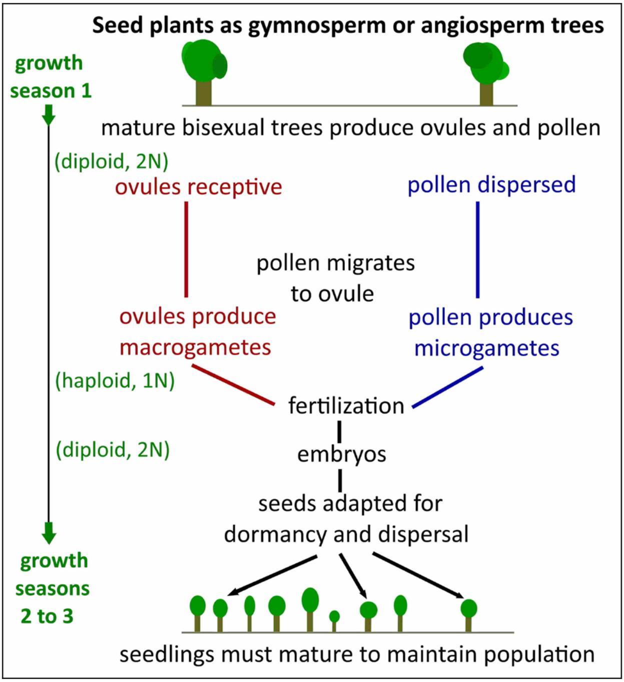
> To describe the reproduction of trees I need examples of both needle-leaf and broad-leaf types, and of botanical terminology. The term *gymnosperm* is general for a group that has about 1000 living species in 12 families. These include the cycads and ginkgos, and the large group known as *conifers*, in the division *Pinophyta*, with 11 living

> genera including cedars, pines, firs, larches, spruces and others. They all reproduce using a botanical structure known as *cone*. Also they are all needle-leaf trees, soft-woods. The term *angiosperm* is general for a group of about 300,000 living species in 443 families. They all reproduce using a botanical structure known as *flower*. Here the term *flowering plant* or tree is used in preference to angiosperm. These are typical broad-leaf trees, hard-woods. Cones and flowers are different structurally but both produce *seeds* using a mechanism of the same basic type. All these seed producing plants are collectively known by the informal term *spermatophyte*.

**Reproduction during first colonisation of land.**
The seemingly minor matter of actively migrating sperm cells is a good start to explain how cones and flowers work: minor but crucial. First though, the way mosses and ferns reproduce clarifies the problem for plants newly colonising dry land. They modified the method of their marine ancestors involving two separate life cycle stages of different form and genetic content.

Prothallus of a fern (*Onoclea sensibilis*) growing on bare soil as the gametophyte stage of life cycle, lower; and sporophyte, upper, developing as the first part of the mature fern. Credit: Wikimedia Commons.

A typical fern, male fern of *Dryopteris* species, is familiar with its group of large and intricate leaves supported by central stems. On the lower surface of these leaves many small bodies develop to produce spores in vast number. This spore producing stage of the fern's life cycle is called sporophyte. The process of cell division and replication that gives rise to the single celled spores halves the number of chromosomes in the nucleus of each spore. This reducing type of cell division (termed meiosis) is needed for sexual reproduction. Two cells must fuse, male with female, to create the next stage in the life cycle. The nucleus of every cell produced by meiosis has only a half set of chromosomes (the haploid state, or 1N for short). These fern spores scatter far on the wind. Each is capable of developing into a whole plant consisting of a flat sheet of tissue several millimetres wide (called a prothallus). This makes close contact with moist ground using short extensions from its lower surface to act as roots. As the prothallus obtains nutrients and grows by photosynthesis it produces two groups of cells that will separately provide sperm and eggs. The technical name for these sexual cells is gamete, so the prothallus form of the fern is termed gametophyte. (All plants cycle through sporophyte and gametophyte phases in a process termed *alternation of generations*.)




Generalized life cycle representing both conifer trees and flowering trees, in which the gametophyte phase is minute and borne within cones or flowers of the sporophyte tree.

Sperms of ferns have hair like extensions, flagellae, that work like the tail of a fish. The sperm swim through a film of water on the prothallus to reach the ovule structures which each contain an egg cell. Once that egg cell is fertilized by nuclear fusion with a sperm cell it becomes a normal cell with a full set of chromosomes and is called zygote (now diploid, or 2N). The zygote soon starts to divide repeatedly to form an embryo.

The cell divisions now work without any reduction of the number of chromosomes per cell because the chromosomes themselves replicate. This ordinary type of cell division, essential for growth, is called mitosis. Growth of the embryo from the tissues of the prothallus produces a new individual fern of mature form, as the sporophyte phase of its life cycle. The small delicate prothallus withers and dies.

Sitka spruce (*Picea sitchenis*) branches in spring.

Top left: upright green female cones. Bottom right: red male cones.

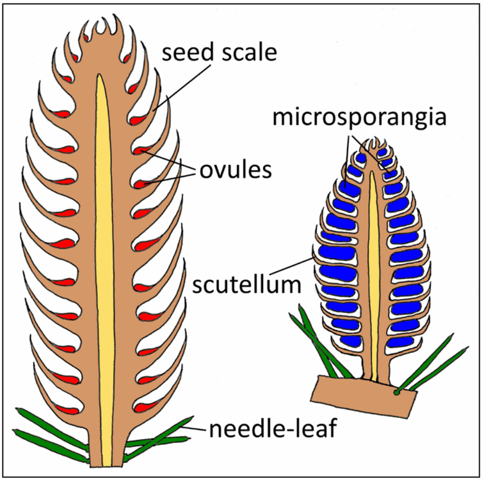
Plus some old female cones, central.

This chromosomal and genetic process of formation of haploid sexual cells, then fusion of them to form a single diploid cell that then grows into a new organism works the same for plants and animals. This sexual reproduction evolved a long time ago and serves us all well, but it is complicated, specially as varieties of plant reproduction. Plants reproduce in more flexible ways than animals because they have no chromosomes specialized for determining the sex of new individuals. These new individuals can be of one sex, or both sexes together, on the same plant. Some plants can reproduce without any sexual mechanism and have no need of seeds to spread their offspring or colonies. Trees are so obviously rooted to the ground that it is easy for us to ignore the huge influence this reproductive flexibility has for sexual combination followed by dispersing their seeds onto new ground to mature into reproductive new individuals.

**Seeds: their origin and significance.**

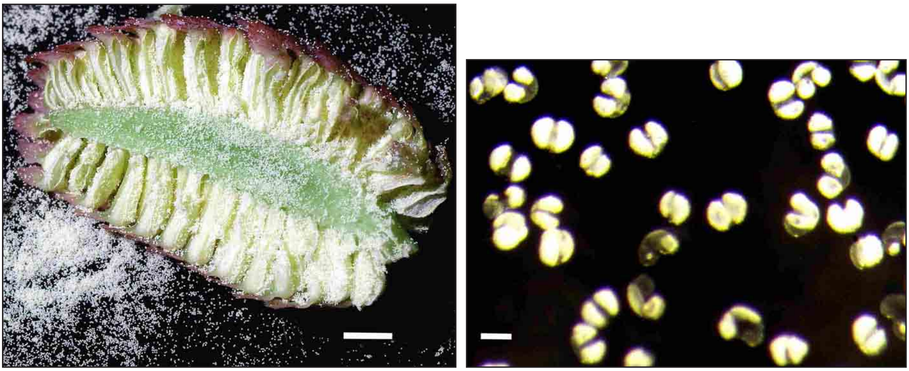
As plants on land evolved, the tree form thrived with the new opportunities for growth of individuals and expansion of populations. Mineral nutrients, oxygen, and carbon dioxide became so ample at any place with sufficient water that for trees reaching their canopy of leaves into the sunlight a tall stem was also efficient for dispersing their seeds. The first true trees included *Lepidodendron*, described in 'History' chapter. Many fossil forms of this type of tree exist but of uncertain lineage. Also a few species remain that are sometimes called living fossils, and can be grouped with the gymnosperm type of cone-bearing trees. You may be able to see examples in botanic gardens: dawn redwood from China, and Wollemi pine discovered in 1994 in remote canyon of Australia.

Basic structural features of female cone, left, and male cone, right, of a spruce tree. Female ovules in red, male pollen sacs or microsporangia in blue. Both in their natural upright position for reception and dispersal of pollen.




On a conifer tree the reproductive units, male and female, develop as buds emerging from a small shoot as a branch or at its tip. The bud grows scales in a way similar to needle-leaves as they spiral around a growing shoot. As the buds grow larger their scales broaden and overlap and the overall shape becomes conical. The technical name for this growth form is strobilus. This is a design found in many plants from mosses such as *Lycopodium* to flowering trees such as birches and willows. These reproductive cones do two jobs: to produce and to protect seeds as they develop hidden at the bases of the scales.

Male cones usually start to develop earlier than female cones. As the spiral of scales grow from a central core they form a series of flat plates and the outer margin of each scale grows into the visible outer scale as a thick protective form called scutellum. On the underside of each plate grows a large thin walled sac. (A technical name for this structure for producing small spores is microsporangium.) Inside the sacs repeated cell divisions produce grains of pollen. A pollen grain comprises a protective coat around around a group of cells that will mature as sperm cells and accessory cells. Pollen grains are about one tenth of a millimetre across, just visible to unaided vision if well lit against a dark background. Each pollen sac produces great numbers of these grains and when fully ripe release pollen so prolifically that a stand of conifers can seem to be on fire as sunshine strikes clouds of pollen. Try this yourself if you find a convenient low branch with ripe male cones: shake it to release the pollen.



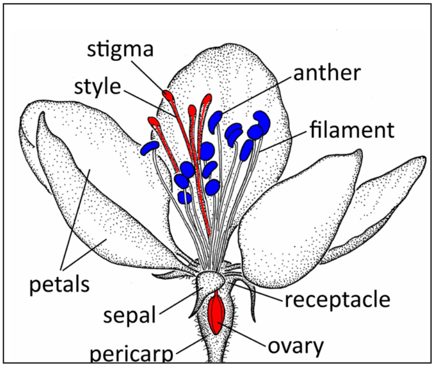
Left: spruce male cone bisected, and pollen; see drawing for labels; scale bar: 2mm. Right: spruce pollen grains showing two air sacs, white, attached to each semi-transparent pollen grain, scale bar: 0.1mm.

Pollen grains are dry and the male cells within them that will develop as sperm have no need or means to swim anywhere. The only liquid in their journey toward the egg cells will be a pollination drop at the entrance to the ovule, at the base of a scale of a female cone. (Pollination drops are typical of the examples here but not all gymnosperms.) Pollen was the other crucial evolutionary advance for seed plants to predominate. A female cone develops by growing scales from its central core, spiralling upward so that each scale overlaps several others. The spaces between these large scales have room for a supportive bract to one side and for the ovule to grow on the other side. Female scales are called seed scales because the ovule develops there into a seed. (A technical name for ovule is megasporangium, a producer of big spores, as seeds.) Each seed scale of conifers produces two ovules and the outer layer of each ovule expands over the surface of the scale as a membranous wing.

The term gymnosperm derives from *naked seed* but these ovules and seeds are only exposed to the outside world in comparison to those of flowering plants. A female cone continues to develop after its ovules have been fertilized. The scales expand and thicken to form tough barriers against herbivores and microbial pathogens. Thus protected the seeds mature.

Sitka spruce branch at mid-summer showing: down hanging pale green/brown female cones of that year; large brown woody female cones of previous years; smaller brown remnants of male cones of that year.

Looking at a conifer tree whilst wondering how it reproduces can be confusing! Different stages and forms of both sexes of cone vary and the seasonal sequences vary between groups of conifers. Most of them bear cones of both sexes on the same tree (the monoecious character) but the two types are never combined together as a single hermaphrodite form. Conifers of the genus *Pinus* have female cones that start in spring as small, red, spikey conelets at the tip of young shoots. When these are fertilized by the end of that year's growth they mature as medium size green cones, tightly closed up. These green first year cones mature the next year as typical woody brown cones that will eventually open up to release their seeds. Pines as well as spruces also confuse us because the prominent upstanding female cones, green or red, turn upside down once fertilized fully. When the apex of the cone points skyward pollen can drift onto the ovules. After fertilization the supportive core of each cone grows to arch over and turn the cone's apex downwards, well placed for seeds to shake out from brown woody cones during windy days at the end of their season. Exhausted cones, male and female, often remain on the tree for a year or so.



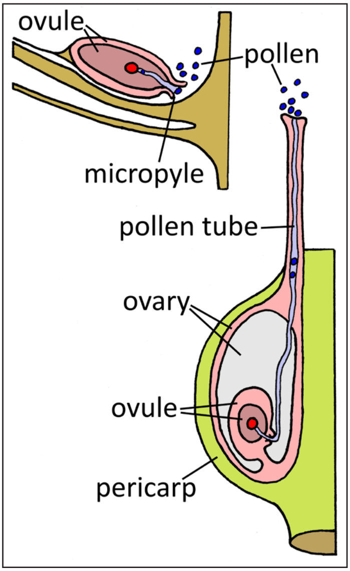

Japanese crab-apple flower (*Malus floribunda*) in spring; scale bar: 5mm. Female parts in red, male parts in blue.

**Evolution of modern trees.**

Conifer plants are widely distributed on Earth and cover vast areas of northern North America, northern Europe and Asia, also with populations in the southern hemisphere. Their diversity however is limited compared to flowering plants, one thousand species compared to three hundred thousand. The earliest type of gymnosperm evolved about 300 million years ago, as typical trees similar to those described in 'History'. The crucial evolutionary advances mostly concern wood for central stems that raise the canopy of branches and needle-leaves up into the sunlight whilst resisting both gravity and gales. This woody skeleton remained alive at its growing margins and was able to thicken the shoots and roots from layers of generative cells that lasted the life of the tree. These generative layers are in the thin cambium layer that forms xylem inwards and phloem outwards (see 'Photosynthesis'). These woody cells types transport, respectively, water upwards from the roots and sap downwards from the leaves.

Domestic bee (*Apis mellifera*) seeking nectar at an apple tree (*Malus domestica*). Note yellow pollen basket on bee's leg.

This ancient form of life, as sequoias, spruces, firs, pines and others growing naturally are amongst the worlds most elegant and magnificent forms of life, reaching over eighty metres high and living for hundreds, even thousands of years. Conifers are also of huge economic importance to people as species that grow well in plantations to provide timber, lumber, and whilst doing so to store carbon as both trees and later in buildings (see 'Buildings'). As a branch of plant life conifers however have been greatly exceeded in diversity by flowering plants, from minute herbs to oak trees, and to the grasses of prairies and savannas. Here the evolution of animals becomes important for this story. Animals coming out from the seas to colonize land faced a problem with water as severe as did plants. To breath the earliest land animals had to avoid loss of water from their respiratory membranes. A molecule of water is smaller than a molecule of oxygen. So these membranes are wet because $H_2O$ diffuses out through gaps wide enough to allow $O_2$ to diffuse in. This was not a problem for marine crustaceans but when similar animals, early arthropods with an external skeleton and jointed limbs, started to colonize land they first had to adapt to the desiccation problem. They evolved a system of tubes, called tracheae which funnel air deep and direct to internal organs.



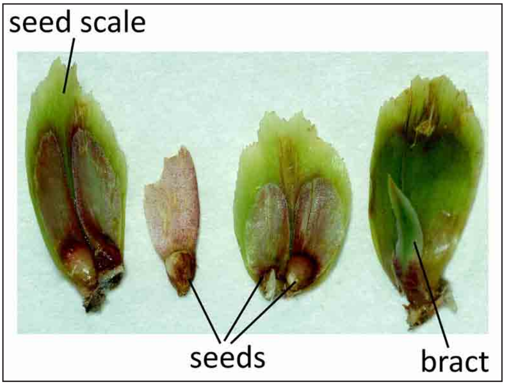

Comparison of basic structures of a conifer seed scale and seed, with a flowering plant stigma, style, ovary and pericarp. Blue/black pollen grains represent the microgametophyte phase of life cycle, red egg and associated tissue represent the megagametophyte phase.

Insects, these most diverse forms of arthropod life, later invented wings to fly with and search for food and mates. Food came first and insects soon discovered that some plants provided it better than others. So an evolutionary duet, a dance, of two radically different life forms started. Insects evolved in tandem with plants, and vice versa: they co-evolved. Life of two different forms interlinked like this is called symbiosis in general, and when of clear benefit to both partners it is called mutualism. (Symbiosis is discussed in 'Roots' chapter, in relation to mycorrhizal fungi. Symbiosis also includes parasitism and commensalism.)

Flowering plants provided nectar whilst insects adapted with their sensory systems and mouthparts to feed on this rich food. The adaptive advantage for the plants was that the insects carried away pollen from one plant to another. Dispersal of pollen this way, rather than on wind as the gymnosperm trees do almost exclusively, was better for cross pollination and thus avoiding the genetic problems of inbreeding.


Sitka spruce ripe female cones, entire and bisected, with seeds, scale bar: 10mm. Drawing shows a growing cone.

About two hundred million years ago, during the Triassic period, plants evolved that bore their reproductive structures within flowers. These assemble in a way basically similar to strobili as cones but flower structure is looser and enables an amazing proliferation of form and function. As flowering trees diversified and their flowers co-evolved with animal pollinators it seems from evidence of fossil trees that flowering plants out-competed cone-bearing trees in many regions. Researchers also have evidence that the genetic content of the earliest flowering plants doubled at some particular time. The new plants were no longer alternating simply between haploid and diploid chromosomal phases of their life cycles. The number of chromosomes of the diploid phase doubled or tripled or more. These plants became polyploid and now there are many species of flowering plants with three to twelve sets of chromosomes. (A few species of conifers are polyploid.) Polyploidy as a genetic character gave to these plants the power of increased genetic flexibility and opportunity for new forms and abilities to live in new environments.



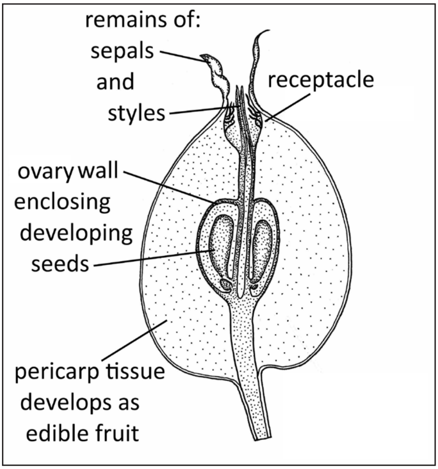

Sitka spruce seed scales and developing seeds from a green mid-summer cone. Pair of seeds on each seed scale.

Polyploidy is also a characteristic outcome of breeding flowering plants to grow as food crops. Hybridization between species of such plants is readily achieved both naturally and in nurseries and laboratories as long as the two species are closely related and able to form fertile new populations. The meaning of the term species dissolves amongst this vigour of flowering plants to reproduce. The genus *Sorbus*, with rowan or mountain ash as one example here, exasperates taxonomists through their ability to hybridize naturally and continue as fertile offspring. Possibly a taxonomy of plants based entirely on molecular analysis of their nuclei will resolve these problems, but the plants may speciate faster than researchers can chase after them. Researchers predict there are many more species of flowering plant to be discovered out there in remote forests and mountain valleys, let alone be given a formal name.

**Flower structure and workings.**

Flowering plants have more variable arrangements of their flowers than most coniferous plants with their cones. Several gymnosperm genera, such as junipers and yews have the mature plant bearing only male cones or only female cones. This is the dioecious character. Flowering plants can be similarly dioecious with only male flowers on one plant and female flowers on another. They can be monoecious as described above for conifers, with both sexes on one plant. Or flowering plants often have hermaphrodite, bisexual, flowers with the male and female components combined together in all flowers of every plant. The apple tree flowers illustrated here are hermaphrodite.

Another common arrangement of flowers is as a dense cluster of many flowers, called an inflorescence. Rowans are one example of an inflorescence of hermaphrodite flowers illustrated here. On trees this arrangement may also permit the reduction of some parts of the flower, sepals and petals for example, as adaptation to pollination by wind rather than by attracting animal pollinators. Birch flowers, as separate male and female catkins (or aments) on the same tree are a common example of inflorescences of monoecious flowers.




Wild crab-apple fruit (*Malus sylvestris*) cut in late summer; scale bar: 5mm. Fruit formed by expanded tissues of the pericarp that attracts herbivores to ingest toughly coated seeds, later to be excreted.

The example of flower structure has an open simplicity typical of the rose family, Rosaceae. *Malus floribunda* is derived from wild apple trees for its beautiful display of pink spring time blossom. The early bud is protected by a whorl of sepals which fold back at bud burst. The petals of similar form and same number as sepals provide the visual stimulus for insects to go first to the tree. In the centre is whorl of stamens consisting of anthers on long filaments. Anthers are sacs that produce pollen to be be released when the sacs split open. Innermost is a whorl of styles, each with a stigma surface at their tips. The styles are connected directly to the ovaries, one style to each ovary. In this family the ovaries are situated in a flower part called receptacle, below the whorls of sepals and petals. Within the ovaries lie the ovules, usually two of them although only one of them is likely to develop into a seed. The entire composite of each stigma, style, ovary and ovule is termed carpel, or pistil. There are usually five carpels in these flowers. A composite of carpels is called gynoecium and for an apple that we eat this is the core with its leathery protective layers. In the genus *Malus* it is the receptacle that will form the bulk of the fruit containing the seeds. (As with conifers, so for flowering plants: anthers producing pollen are termed microsporangia and ovules with their egg cells are megasporangia.).

**Seeds of conifers and flowering trees.**

All of these plants, using cones and flowers, have another fundamental key to their success: the seed. Although there is no agreed formal taxonomic group for such plants they are called spermatophyta, or seed plants in plain language. All these plants evolved ways of protecting the earliest stages of their offspring against external hazards and to provide the minute embryo at the centre of the seed with a store of nutrients surrounded by a protective coat, and in the case of seeds dispersed by animals another layer of some nourishing material. The process of forming the sexual cells, sperm and eggs, is closely similar in both flowering plants and conifers. When an egg cell (also called ovum) is fertilized a zygote is formed, complete now with a double set of chromosomes, one set each from their sources in sperm and egg.

Coniferous and flowering trees have differences in how closely they protect their ovules from the outside environment. Where a seed scale is attached to the core of the female cone two ovules nestle. They have a small opening, a micropyle, that faces inwards. Here the tissues of the ovule secrete a drop of liquid, the pollination drop. Grains of pollen stick to the drop and will be drawn onto the inner surface of the ovule as the droplet evaporates and shrinks. Then the pollen grain can release its two sperm cells and a pair of cell nuclei that produce a tube. The tube grows toward the egg cell, carrying the sperm cells with it. This passage from micropyle to egg cell is through a scrap of tissue that is technically the female gametophyte. This remnant has the same evolutionary lineage as the gametophyte stage of the life cycle of mosses and ferns.

Flowering plants evolved to have a mechanism for reproduction with even greater protection of the ovule and its egg cell. Here pollen arrives at the centre of the flower where it may be caught by the adhesive surface of the stigmas. Grains of pollen hatch to release two sperm cells and a tube cell. The task for the tube cell is to create a passage for the sperm cells from the stigma all the way down through the style, into the tissue of the ovary, then finally out and across to one of the ovules within the cavity of the ovary. The two sperms act by a double fertilization to produce two new diploid cells. One of these cells is the zygote that will grow into the embryonic plant. The other new cell will divide repeatedly to create a reserve of food for the embryo. The advantage to flowering plants of this complex fertilization is that the parent does not commit resources to a potential seed unless a zygote is created and grows as an embryo.

However, in both conifers and flowering plants sexual reproduction by these similar mechanisms provides mature trees in general with abilities to flourish in habitats from tundra to savanna, to wet tropics or sandy desert. The keys to this are fertilization without need water for sperm to swim in, protection of the ovum, and versatility of seeds. An embryo of a seed plant that starts as a single cell, the zygote, is surrounded by layers of cells loaded with nutrients and an outer coat that is protective and adapted for dispersal.

**Dispersal: a problem for pollen and seeds.**
It is difficult for us to understand how a forest works as an assemblage or community of individual trees. We can hunt large animals by running them down, we can migrate hundreds of kilometres by walking if our

lives depend on it. Plants on land are rooted there and so tend to grow together in patches or broad clusters: peat bogs, prairies, heathlands, and forests. Within a forest each tree grows where its seed fell by chance. Other chances followed when as a seedling it found sufficient light, space and lack of herbivores to grow and mature. A seed has to take its chances of how strong the wind was or how far the bird with the seed in its gut flew before voiding the remains of its last meal. The seed may grow to maturity but with poor chance of being able to reproduce because the chance of fertilization by pollen is lower than close to its source forest. Out beyond the margins of a forest the tree may grow on poor soils or be exposed to harsh weather or higher risk from herbivores. Despite these multiple risks for seeds and seedlings, mature trees continually invest large proportions of their resources to producing huge mass and number of pollen and seed. There must be some long term balance between the costs and benefits of this method of reproduction.

Birch (*Betula pendula*) in spring; ripe male catkins at left; undeveloped female catkins upright at top, and a receptive female catkin in photograph at right.

Pollen adapted for dispersal by wind is produced in nearly all conifers, also flowering trees such as birches, poplars, willows, and oaks. The pollen is usually released from the male cones before the female cones of the same tree are receptive. The same applies for the male and the female parts of flowers. This greatly reduces the risk of self-pollination. Such pollen needs to be produced in huge quantities relative to the size of the tree's flower. Male catkins of a birch tree are illustrated here, larger than the female catkins even when these are loaded with mature seed.
Many species of flowering trees reproduce within a mutualistic symbiosis with some species of animal for dispersal of pollen and separately of seed. Pollination as a topic needs an entire book to describe the fantastic relationships that have evolved between plants and their animal pollinators. Just one example of the intimacy of this relationship will suffice. Some species of orchid attract bee pollinators by mimicking the shape and colour of a bee — pollination occurs when a bee attempts to copulate with the orchid.

Birch in late summer; ripe female catkins and seed; scale bar: 10mm.

To return to the main example here, apple trees in blossom provide an overall display attractive from a distance to flies, bumble bees, honey bees, and other insects. Such ability has been exploited to breed decorative trees such as the Japanese crab apple, *Malus floribunda*. A fly or a bee is attracted closer to individual flowers by the colours of the petals, although what they see with their compound eyes is different from our vision. There may be pollinator guides on the petals as patterns that insects see as ultra-violet rays but are invisible to us. Closer to the flower the scent of nectar will attract many insects. Nectar is a sugary liquid secreted by glands near the base of the styles. The insect pushes past the anthers to reach this food below. If the anthers are ripe and have split open much pollen will adhere to the setae and bristles on the insect. A bumblebee at a flower seen in bright sunlight may reveal a heavy dusting of yellowish pollen that adheres in clumps over the body, only its wings remaining clear. As the bee travels from tree to tree the chances of effective cross pollination for the plant are increased. This was, in evolutionary perspective, the bargain that early seed plants made with animal pollinators: outbreeding for the plant in exchange for nectar for the animal.

Conifers and flowering trees protect their ovules, egg cells and seeds well against herbivores and pathogens whilst on the tree. They provide the seeds with a means of dispersal away from the parent and various protections against destruction whilst the seeds are dispersing or lying dormant.

Each seed scale of a cone bears a pair of seeds and as winds shake the branches at the end of reproductive season when the ripe cones have opened up the seeds drop. How far the seeds are blown away from the parent is studied by researchers using seed traps. These are placed radiating away from a stand of one species of tree. Aleppo pine, *Pinus halepensis* is a favourite to study for its convenient short stature and location around the Mediterranean. A graph plotted to show number of seeds over distance from the stand will typically show a steep decline with distance from the tree followed by a long tail of very few seeds that are blown kilometres away. Most seeds fall to the ground close to their parent tree.

Some species of pine tree produce large seeds without wings. They have evolved a relationship with birds of the crow family for their dispersal. The birds are able to extract seeds from ripe cones and bury them in numerous caches as wintertime reserves. Clark's nutcracker of western North America is a conspicuous example that feeds substantially on pine seeds and is similar in form to the jay of Europe. These birds have good memories but are not infallible, so trees such as pinyon pine in North America and Arolla pine in Europe become dispersed as forgotten buried seeds.

Flowering trees have more varied methods of dispersing their seed. Trees with catkins have minute seeds. Those of birches have a pair of small wings and these seeds may disperse far from their original stand on strong winds. Many tree species have large seeds with one large wing that are sufficient to disperse away out from the shade of the parent tree. Maples are a conspicuous example – they produce a joined pair of seeds each with its own wing expanded sideways and these can be seen slowly descending to the ground like helicopters.

Seed varieties of flowering plants have many technical names, such as samara for the winged seeds as from maple, ash and birch trees but their form follows a common pattern. The wings grow as extensions of the ovary wall, the pericarp. This whole structure is a fruit and that is a technical term for the entire fully developed ovary in which the seeds are housed. The variety of fruits of flowering plants is as great as that of their flowers. More about this follows in the next section.

This all appears to be a precarious way to reproduce for conifer and flowering trees, until that is, the number of seeds per tree each year is multiplied by the number of years a reproductively mature tree will live. This will be an enormous number. For a single tree, a spruce or oak, to reproduce itself as another mature tree all it needs is just one of those trillions of seeds to survive and thrive. For the genetically necessary pair of trees as parents, egg from one fertilized by sperm from another, all that pair need to produce during their entire lifetimes to maintain and spread their genetic character is three mature trees as descendants. From the perspective of how we reproduce this method appears as colossal wastefulness. For trees this method works. Economy is not the driving force here, nature is often extravagant for a purpose. What drives this form of reproduction is what works through the genes of the tree. The information contained in their genes determined how these types of plant evolved by natural selection to have sexual methods of reproduction, with its advantages for survival of these plants that outweigh the costs.

**Fruits of flowering plants.**

Fruits of flowering trees come in great variety and the terminology is similarly diverse and also confused by vernacular language. A pine nut is a nut to a shopkeeper but to a botanist it is the seed of a conifer tree of genus *Pinus* and by definition these trees have only naked ovules, unprotected by the additional layer of an ovary that flowering plants have. The ovary alone or in combination with the receptacle tissue of a flowering plant forms the fruit as a combination structure for protection and dispersal. One of the many types of fruit of flowering plants is termed nut. (Pine nuts are harvested as a nutritious food for people from ten or more species: stone pine, Korean pine, Colorado pine . . .)

Mature fruits of wild crab-apple becoming red to attract herbivores and with expanded pericarp tissue that is edible. The withered sepals and styles remain.

Here apples provide an example of the mechanics of fruits. The ovules that formed in an apple tree flower are in a toughly walled part of the ovary that provides space and protection for the developing ovule. In this example of the genus *Malus* the ovaries are situated below the whorls of sepals and petals, at the level where the receptacle meets the flower stem. The ovules start as a pair in each of five ovaries but usually only one is fertilized whilst the other aborts. The ovaries fit closely together and an apple cut through its equator reveals the leathery walls of all ovaries. A cut from top to bottom reveals: withered sepals and styles; tissue that connected each style to the chamber of its ovary; sections of two ovaries. An apple flower has five units consisting of ovary, style and stigma. Each unit is a carpel, or pistil, and this provides the term pericarp for the tissue surrounding the ovaries. This tissue will develop into the attractively edible part of this particular type of fruit from a domesticated fruit tree. For a wild apple tree the seeds, pips, will mature fully with a leathery brown outer layer and contain a food reserve for the central embryo. The pericarp expands as its middle layer grows as a pulp of cells containing much water but also carbohydrates including sugars. A wild crab apple fruit (*Malus sylvestris* or similar species) contains insufficient sugar to attract us, but a hungry animal will eat it and later void the seeds out onto the ground. If the conditions are right each seed will germinate into a potential new tree.

The botanical name for apples and pears is pome. In the same family, Rosaceae, the plums, peaches, cherries, rowan berries and almonds are all drupes. These comprise the fleshy fruit that we usually eat. However, with almonds we discard the fleshy part and keep the woody part that we call a stone and is formed from the inner layer of the ovary and then we crack open that stone to extract the edible seed (which we are likely to but incorrectly call a nut). Clearly, our feeding habits do not match needs of almond trees to disperse their seeds, but wild herbivores feed naturally and robustly.

Hazel trees can clarify the definition of nut. These small trees produce large crops of pleasantly edible seeds for human consumption. Hazel nuts were an important staple food for some of our ancestors, produced prolifically from hazel trees managed as coppice for both food and structural wood. The seed grows within the woody outer case of the fruit formed from the pericarp. The seed and its woody case is the botanical nut. Hazel trees evolved to disperse their seeds by wild herbivores, squirrels and others, as winter reserves to be buried. As long as the squirrels are a little forgetful then sufficient nuts will remain buried and dormant ready to germinate as potential new trees. Similarly the acorns of oak trees, these are nuts that birds such as jays bury as winter reserves, as do those birds of the same crow family that disperse seeds of some species of pine. Jays also are forgetful, but they do have large numbers of acorns on their mind.

Almonds, plums, peaches, also damsons, greengages and even sloes from blackthorn bushes are all in the genus *Prunus*, family Rosaceae. They were the first flowering trees to be domesticated for their edible fruits, or simply the wild plants are harvested for flavouring agents such as the bitter sloes.

Domestic apples of James Grieve variety, bred for eating/cooking apples suitable for cultivation as espalier form in cool climates, here fan-trained on a dwarfing root stock against a south facing wall.

Once a seed or seed within its fruit lands on the ground its next task is to either germinate and continue developing or to become dormant until the season or physical conditions are best for successful germination. There can be a substantial seed bank in soil, holding many species of plant with natural lengths of dormancy from a few months to many years. Dormancy protects the seed over winter, or over one or more dry seasons, and will be broken by environmental or internal signals. There is also a type of seasonality for production of seed that is termed mast or masting. A particular species of tree, oaks and beeches are typical, in a particular region will produce approximately every three to five years, a crop of seeds much larger than in the intervening years. There are various explanations for the advantage this may have for individual trees, mostly beyond the scope of this chapter. An explanation relevant here is that masting contributes to balancing demands on the whole tree for growth or for reproduction.

Oak (*Quercus robur*) upper, and beech (Fa*gus sylvatica*) lower, seedlings showing cotyledons. The oak has underground cotyledons as food stores and here the root develops before the shoot. The beech has a long root and a shoot bearing above ground a pair of cotyledon leaves and the first two ordinary leaves. The seeds, acorn and beech-nut respectively, of both these trees are true nuts.

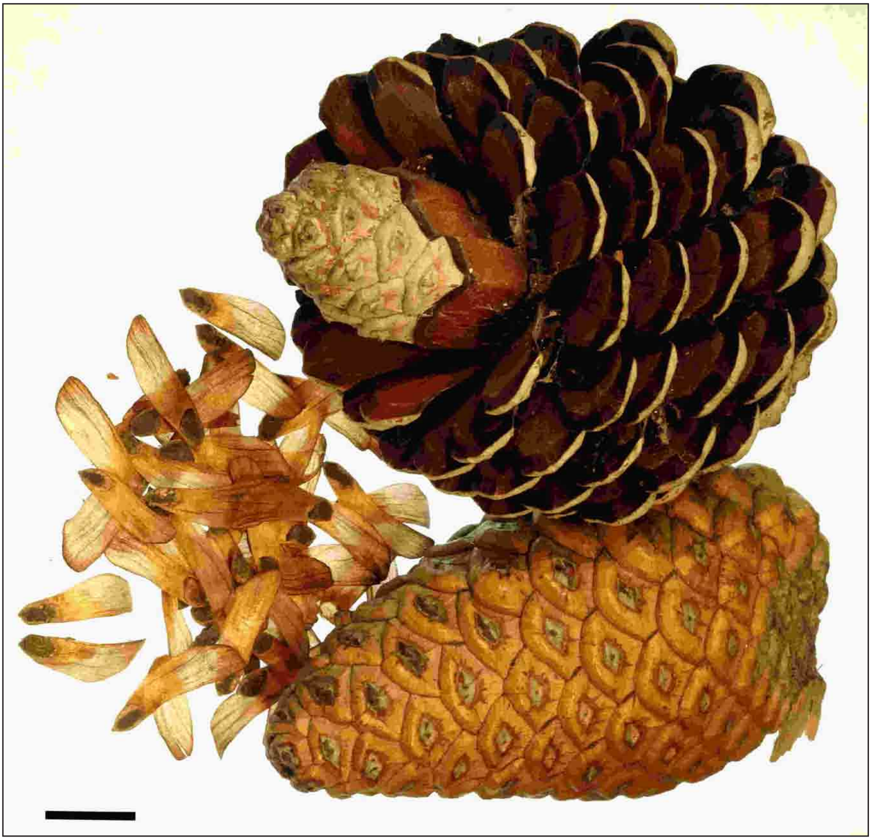
For seeds of both conifers and flowering plants the transition from an embryo within the seed to a plant no longer dependent on food reserves from its parent is crucial but fraught with risks of dehydration, poor soil, herbivores and pathogens. Fresh supply of water and the nutrients it carries will come from the root radicle that rapidly grows downward. The nutrients will come from structures called cotyledons. For conifers the cotyledons look like a whorl of small green needle leaves. As long as cotyledons are sufficiently well lit they will photosynthesize carbohydrate to provide energy for the cellular metabolism of new growth.

Seeds of flowering plants either produce from their shoots a pair of broad green structures as leaf like cotyledons. Then soon after the first true leaves appear near the top of the shoot. Alternatively, as with oak trees, their acorns consist largely of two thick cotyledons that remain where the nut was buried in the ground by an animal. The root radicle soon obtains water and soil nutrients and the food reserves in these non-photosynthetic cotyledons support growth of roots then shoot with the seedling's first true leaves. Again for these seeds of flowering plants sufficient light is usually the critical factor for successful growth to at least seedling stage.

> There is a terminology of seed dispersal based on the suffix -chory. Thus: zoochory = dispersal by animals; anemochory = by wind; endozoochory = by animals eating then excreting seed; epizoochory = on surface of animals; and so on.

**Costs and benefits of sexual reproduction.**
For a mature tree to produce each crop of seeds it uses a large proportion of nutrients and water from its roots plus newly synthesized carbohydrates, proteins and fats within its stem and branches. This cost of reproduction is additional to its annual maintenance cost of new leaves, replacement of lost branches, resisting herbivores and pathogenic microbes. This cost continues until the tree has accumulated so much genetic, cellular and large scale damage that it dies.

Some species of tree are minimalists for costs of reproduction whilst others are prolific. Birches compared to rowans, although both these types of tree thrive on the same ground and often predominate whilst living on the poor soils and harsh weather of uplands. A broad environmental relationship for both these tree types is not evident – at least for their reproductive methods. Instead it seems that long ago in their evolutionary history they diverged into two methods for reproducing under the same conditions: small light winged fruits onto the wind or heavy fleshy fruits attractive to birds.



Female cones and seeds of radiata pine (*Pinus radiata*). A cone fills an open hand and weighs about 150 grams. An example of the energy and material costs of reproduction; scale bar: 20mm.

A researcher might compare these costs and benefits from a different perspective. The question would be: how much does the effort of a reproductively active tree that is still growing reduce its potential rate of reproduction, or rate of growth? That is: if we remove all female seed cones from these pine trees will they grow better compared to those without this experimental intervention? Again, *Pinus halepensis* is suitable to study this because as a pine its cones take two years to produce seeds. In one study all developing female cones were removed from test trees at a specific time whilst control trees were left intact. Trees of the test group retained sufficient nutritive reserves in their stems and branches to produce in the next year 70% more new green cones than the control trees. However, the relationship between growth and reproduction can be complex and differ between the effect of male cones compared to female cones. The second year female cones are green and can contribute photosynthate to the tree. A study of lodgepole pine, *Pinus contorta*, found that branches with two year old female cones provided between 17-45% of the current year's increase in dry weight to those cones.

Another example of this cost to benefit relationship shows how stress on the growth productivity of trees can affect their reproductive capacity. The resin used to manufacture the perfume ingredient frankincense is tapped from a flowering tree of north eastern Africa, *Boswellia papyrifera*, and others of the same genus. If a stand of these trees is not tapped the trees are likely to produce three times as many fully mature and healthy seeds than the tapped trees. Furthermore, seeds from these untapped trees will have a germination rate of about 80% compared to 16% for the tapped trees.

The whistling thorn tree of eastern Africa, *Vacchellia drepanolobium*, an acacia tree, bears formidably dense arrays of long sharp thorns to deter browsing herbivores: elephants, giraffe, gerenuk . . . Researchers enclosed stands within tall fences and compared the trees with controls still being eaten. The protected trees responded over several years by switching their photosynthesized resources to flowers and seeds. Removing the cost of growing large thorns and replacing browsed leaves and flowers enabled a doubled increase in seed production.

**Avoiding the cost of sexual reproduction.**

Reproduction by sexual means is inefficient in the economic context of allocation of resources within a tree or a population of them. So there must be some reason why this costly, complex and chancy method of reproduction prevails in trees and any other type of life that reproduces sexually, from single celled protozoans such the *Plasmodium* parasites that cause malaria, through to organism such as humans or oak trees. Genetic recombination during sexual reproduction provides the diversity of individuals that in turn enables the growth of populations of animals or plants that survive better than their ancestors. The ability to survive better the invasions and depredations of pathogens, parasites, herbivores and predators is essential for life. *Homo sapiens* has been in genetic combat with *Plasmodium* for millennia as our immune defences find new ways of counteracting fresh adaptations of the parasite. There are all sorts of wild organisms out there that want to live off us, or to live at the expense of pines or oaks. The ability of plants to survive the threats from viruses, bacteria, fungi, insects, and voles through to elephants, derives mostly from the genetics of sexual reproduction.

Despite these advantages of sexual reproduction there are species of flowering trees that are able to reproduce and maintain their populations without sexual methods. They are asexual, or clonal, or can spread vegetatively, but they might also be capable of reproduction by normal sexual means as well, depending on their distribution and history. This is not, however, a method of reproduction found in conifers.

A distinction between how conifers and flowering tree grow lies in their cellular workings. Growth of shoots and roots, leaf and flower buds, starts at specialized tissues called meristems. These are made up of cells of a type, in both plants and animals, called stem cells. One stem cell will divide into two by ordinary mitosis, then one of the cells moves out into new tissue whilst the other remains in the core of the meristem to continue as a stem cell. That cell is ready to divide again and again throughout the life of the organism. Trees have meristems at the tips of shoots, and specially tips of roots which need to constantly replace themselves whilst seeking out fresh sources of water and nutrient minerals. Also along the length of shoots and the main stem there are clumps of lateral meristematic tissue that lie dormant until needed to produce new branches. This type of meristem within shoots and roots is called an adventitious bud.

Willow tree, wind-thrown but main stem rooted, with epicormic shoots and adventitious roots growing from a large branch resting on soil.

If a mature flowering tree in a dense stand finds itself without close neighbours after a storm it will respond with activation of its lateral meristems to produced more branches that will spread to capture the increased light. If a storm snaps the stem of an ash tree, or a lime or an oak, near its base then lateral meristems will soon grow many new shoots out through the bark and up into the air. This type of meristem tissue is termed epicormic and can produce sprouts as new stems and branches. Similarly roots can produce suckers, described as adventitious, that may grow into new stems and an uprooted and fallen stem may be able to regenerate by the activity of these types of dormant meristematic tissues. Natural coppice formation is produced by these meristems, the broken tree first survives the massive damage then it thrives as several ordinary main stems. This is the biological basis of the arboricultural methods of coppice and pollard. Also a strange form of activity of lateral meristems is probably the cause of the burls or burrs that grotesquely bulge from the stems of some flowering trees in their old age.

In comparison to flowering trees conifer trees have poorer ability to respond to damage. Their apical meristem at the tip of the single central shoot dominates by hormonal mechanisms the growth pattern of the entire tree, leaving poor ability to recover from being snapped off at mid stem by a storm.

Similar to the coppice method for producing timber the development of the root stock method for combining the advantages of two strains of domesticated trees depends on vigorous ability of flowering plants to heal and regrow. The root stock part of the new tree has meristematic activity at its roots so that these grow well to supply the new stem, the scion, that is grafted to it. The scion will have a cultivated character of flowering and fruiting. This is particularly useful for developing types of fruit trees or decorative trees that have a dwarf form and are convenient for commercial horticulture or private gardens.

Flowering plants of many families and species have considerable ability to grow as individuals or clonal colonies to proliferate as large patches, or stands of trees. No sexual reproduction or genetic mixing and recombination is involved. Aspen trees of North America, *Populus tremuloides*, demonstrate this clearly. Stands of these beautiful flowering trees thrive right up to the tree line alongside large conifer trees. Under conditions where they reproduce asexually they proliferate by lateral spread of their roots. From these roots adventitious buds produce suckers that grow upwards as normal shoots and mature into fully grown trees. These trees are not only widespread and successful in various habitats, they are also a challenge to the concept we humans have of what is an individual organism. In the state of Utah there is a colony of *P. tremuloides*. This distinct colony has been named 'Pando'. Genetic analysis of Pando reveals that its trees are all males, all derived from a single tree that lived several thousand years ago. Now the progeny of this tree occupy forty four hectares of land. This clone of trees also challenges the claim that the humongous fungus, described in 'Roots', is the largest organism on Earth. Although this parasitic fungus, as mycelia in soil, covers a much larger area than the Pando clone of aspens, it weighs a mere six hundred tonnes compared to the six thousand tonnes of Pando!

Trees are a highly successful form of life because they follow so variedly and effectively the primal imperative of all living things: to reproduce.

## References and notes.

(Many articles are accessible as abstract or full text using a search engine such as Google Scholar, an institutional login, or a paywall.)

**Origins of modern trees.**

Anonymous., 2021. Evolutionary history of plants; also Timeline of plant evolution, Wikipedia.

Bond, W.J., 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biological Journal of the Linnean Society, 36: 227-249.

Burger, W.C., 1981. Why are there so many kinds of flowering plants? BioScience, 31: 572-581. [Paired with this article is: Stebbins, G.L., 1981. Why are there so many species of flowering plants? BioScience, 31: 573-577.]

Coomes, D.A., *et al.*, 2005. The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. Journal of Ecology, 93: 918-935.

Hickey, L.J. & Doyle, J.A., 1977. Early Cretaceous fossil evidence for angiosperm evolution. Botanical Review, 43: 3-104.

Melville, R., 1983. Glossopteridae, Angiospermidae and the evidence for angiosperm evolution. Botanical Journal of the Linnean Society, 86: 297-323. [Argues that flowering plants evolved from plants like *Glossopteris* on the supercontinent Gondwanaland during late Carboniferous period.]

Moore, R., *et al*., 1995. *Botany*. Wm. C. Brown Publishers, Dubuque, USA. ISBN: 0697037754. [Chs. 27-30.]

Mora, M. *et al*., 2011. How many species are there on earth and in the ocean? PLoS Biology, 9: e1001127. [These are species of eukaryote organisms: ~ 8.7million is this estimate, but the number of plants is greatly underestimated probably because of problems encountered by plant taxonomists, as in Stace 2019, below. Prokaryote bacteria and archaea types greatly outnumber the eukaryotes but the concept of species works poorly for these organisms.]

Stace, C., 2019. *New Flora of the British Isles.* C & M Floristics, England. ISBN: 9781527226302. [4th edition of this definitive flora; see pg. 213 for an example of taxonomic difficulty generated by the ability of flowering plants to diversify and hybridize.]

Stewart, W.N. & Rothwell, G.W., 1993. *Paleobotany and the evolution of plants*. Cambridge University Press, England. ISBN: 0521382947.

**Cone and flower structure and function.**

Pell, S.K. & Angell, B., 2016. *A Botanist's Vocabulary: 1300 terms explained and illustrated*. Timber Press, Portland, USA. ISBN: 9781604695632. [With line art illustrations of great clarity.]

Taiz, L., *et al*., 2018. *Plant Physiology and Development*. Oxford University Press, New York. ISBN: 9781605357454 [Chapter 21: Gametophytes, pollination, seeds and fruits.]

Thomas, P.A., & Packham., J.R., 2007. *Ecology of Woodlands and Forests: Descriptions, Dynamics and Diversity*. Cambridge University Press, England. ISBN: 978-0-521-54231-9. [Chapter 4. Reproductive strategies of forest plants.]

Walker, T., 2020. *Pollination: the enduring relationship between plant and pollinator*. Princeton University Press, Princeton. ISBN: 9780691203751. [Popular science style, superbly illustrated.]

**Seeds of conifers and flowering trees.**

Bowes, B.G., 1996. *A Colour Atlas of Plant Structure*. Manson Publishing, London. ISBN: 1874545200 [Chapter 8. Sexual Reproduction.]

Dorken, V.M., 2020. *Cones of Conifers: morphology, anatomy and functional aspects of coniferous reproductive structures*. Kessel Publishing House, Remagen-Oberwinter. ISBN; 9783945941607. [Covers wide range of gymnosperm cones with numerous photographs.]

Moreira, X., *et al*., 2014. Masting promotes individual and population-level reproduction by increasing pollination efficiency. Ecology, 95: 801-807.

**Dispersal of pollen and seeds.**

Aschero, V. & Vazquez, D.P., 2009. Habitat protection, cattle grazing and density-dependent reproduction in a desert tree. Austral Ecology, 34: 901-907.

Bollen, A. & Gamzhorn, J.U., 2004. Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). Oecologia, 139: 604-616. [Review of animal dispersal of seeds.]

Hewitt, N. & Kellman. M., 2002. Tree seed dispersal among forest fragments: II. Dispersal abilities and biogeographical controls. Journal of Biogeography, 29: 351-363.

Horn, H.S., Nathan, R. & Kapland, S.R., 2001. Long distance dispersal of tree seeds by wind. Ecological Research, 16: 877-885.

Howe, H.F., 1993. Specialized and generalized dispersal systems: where does 'the paradigm' stand? Vegetatio, 107/108: 3-13.

Kremer, A., *et al*., 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. Ecology Letters, 15: 378-392.

Khurana, E. & Singh, J.S., 2001. Ecology of tree seed and seedlings: Implications for tropical forest conservation and restoration. Current Science, 80: 748-757.

Montoya, D., *et al*. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. Science, 320: 1502-1504. [Survey of 34 tree species using 89,365 plots in Spain.]

Nathan, R., Safriel, U.N. & Noy-Meir, I., 2001. Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. Ecology, 82: 374-388.

**Costs and benefits of sexual reproduction.**

Coley, P.D., 1988. Effects of plant growth rate and leaf life-time on the amount and type of anti-herbivore defense. Oecologia, 74: 531-536. [On 41 tree species in rainforest in Panama.]

Dick, J.M., Leakey, R.R.B. & Jarvis, P.G., 1990. Influence of female cones on the vegetative growth of *Pinus contorta*. Tree Physiology, 6: 151-163. [A study demonstrating complexity of relationship between growth and reproduction.]

Goheen, J.R., *et al.*, 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. Journal of Ecology, 95: 129-138. [Study of acacia whistling thorn trees in East Africa.]

Goubitz, S., 2001. Reproductive ecology of *Pinus halepensis*, a monoecious, wind-pollinated and partially serotinous Mediterranean pine tree.

Lively, C.M. & Morran, L.T., 2014. The ecology of sexual reproduction. Journal of Evolutionary Biology, 27: 1292-1303. [Discussion of sexual reproduction as "... one of the major unexplained phenomena in biology".]

Mable, B.K. & Otto, S.P., 1998. The evolution of life cycles with haploid and diploid phases. BioEssays, 20: 453-462.

McDonough, W.T., 1985. Sexual reproduction, seeds, and seedlings in Aspen: Ecology and Management in the Western United States. General Technical Report RM-119. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 25-28, Fort Collins, Colorado.

Rijkers, T., *et al.*, 2006. The effect of tapping for frankincense on sexual reproduction in *Boswellia papyrifera*. Journal of Applied Ecology, 43: 1188-1195.]

Santos-del-Blanco, L. & Climent, J., 2014. Costs of female reproduction in a conifer tree: a whole-tree level assessment. Journal of Ecology, 103: 1310-1317. [Experimental study on *Pinus halepensis*.]

Wheelwright, N.T. & Logan, B.A., 2004. Previous-year reproduction reduces photosynthetic capacity and slows lifetime growth in females of a neotropical tree. Proceedings of the National Academy of Science of the United States of America, 101: 8051-8055.

**Reproduction in relation to silviculture.**

Hemery, G. & Simblett, S., 2021. *The New Sylva: a discourse of forest and orchard trees for the twenty-first century*. Bloomsbury Publishing, London. ISBN: 978-1-5266-4010-9. [Inspired by the original *Sylva* discourse by John Evelyn, published in 1664, this completely new, modern and beautifully illustrated book contains detailed information on silviculture in Ch 4.]

Hirons, A. & Thomas, P.A., 2018. *Applied Tree Biology*. Wiley-Blackwell, Oxford. ISBN: 9781118296400. [Chapters 2 and 5 for many varied practical details of arboriculture.]

Sedgley, M. & Griffin, A.R., 1989. Sexual reproduction of tree crops. Academic Press Ltd, London. ISBN: 0126344701. [Densely detailed account aimed at horticultural aspects.]

Thomas, P.A., 2014. *Trees: their Natural History*. Cambridge University Press, England. ISBN: 9780521133586. [Chapter 5. ‘Towards the next generation: flowers, fruits and seeds’.]

Tudge, C., 2005. *The Secret Life of Trees: how they live and why they matter*. Penguin Books, London. ISBN: 9780141012933. [Popular science style, packed with fascinating facts.]