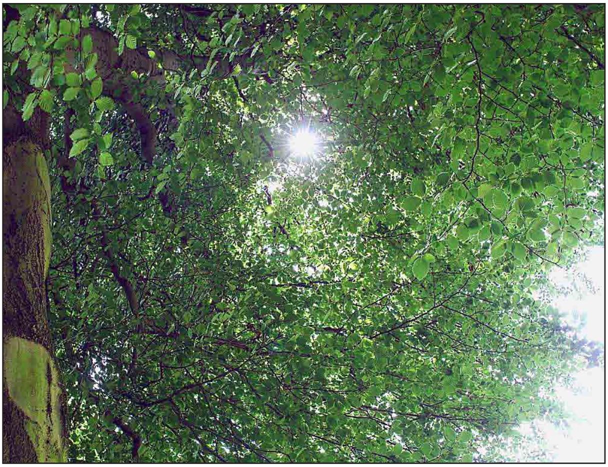
Energy of sunlight harvested as wood

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

www.alanrwalker.com

Sunlight poured through a gap in the canopy of beech trees and down onto a patch of bare ground. There lay the remains of fruits of the trees – small woody bristly pyramids. Within each fruit lay a pair of seeds, angular and leathery coated, but each seed hid a rich store of food. Small mammals and even a few boar ate most of the seeds but thousands upon thousands had fallen that season so by next spring a few germinated in the newly warmed soil.



Beech tree (*Fagus sylvatica*) canopy of leaves.

An embryonic tree.

One of these embryonic trees drew on its food reserve, its endosperm, and started to grow. Cell after cell divided within the embryo. First the embryo grew a root, a radicle. Close to the radicle's tip was a clump of stem cells, an apical meristem. The meristem cells were capable of endless division whilst retaining their embryonic character, but the cells they gave rise to soon specialized for different characters and functions. New cells stacked up behind the meristem, they elongated as they absorbed water and so pushed the radicle further into the soil. The outer tip of the meristem continually produced cells to form a cap. Cells that soon were shorn off as their loosely lubricated nature protected the meristem against rough soil. As the radicle grew it detected the direction of gravity. Some of its root cap cells contained small organelles, amyloplasts, denser than their surrounding cellular liquid. As the amyloplasts sank downward to press on skeletal components of the radicle's cells they activated a hormone called auxin. The hormone increased the growth rate of the radicle differentially, forcing the growth earthward. The radicle penetrated further into the soil.


Beech seedling: radicle, stem, 2 cotyledons, 2 leaves.

The radicle, as the root of the potential tree, needed to return water loaded with nutrients up to the rest of the embryo. The outermost layer of radicle cells, forming the epidermis, grew fine extensions as root hairs. The hairs penetrated between mineral grains, rotting leaves, microbes, fungi, mites, and worms that formed the soil. The water passed through the root hairs and into the transport system of the root, its vascular bundle of tube-like cells. That water had to be sucked up later by the leaves, carrying nutrient minerals to support the seedling's growth.

The shoot was next to grow. At last the seedling cast off its thick coat and opened itself out to the sun. Upwards it pushed, guided by the direction of light and with growth of its cells stimulated by auxin hormone. The apical meristem, at top of the shoot, needed to produce leaves rapidly, so whilst reaching tall it also expanded sideways as a pair of flaps. These grew into the seed-leaves of the young plant, its cotyledons that had already started to develop within the seed, pressed tight between the tissues of the endosperm. Once out into the warm air and bright light they expanded like wings of a butterfly freshly emerged from its chrysalis.

The cotyledons were simple half circles, broadly gathering sunshine. Their early pale green soon intensified as the cells containing the pigment chlorophyll responded to the sunlight. These special cells started to capture carbon – they photosynthesized. Not just carbon was gained by the seedling: along with carbon came hydrogen and oxygen as other products of photosynthesis, whilst up from the roots came nitrogen and minerals. Simple organic compounds, as photosynthates, were manufactured in the cotyledons then distributed along the vascular system to its stem cells in shoot and root, and to diffuse as far as the epidermal cells with their root hairs.

Left: Develping beech tree fruits and mature seeds. Right: Beech seedlings emerging with cotyledons and first true leaves. Credit: Wikimedia, Steffen Heinz.

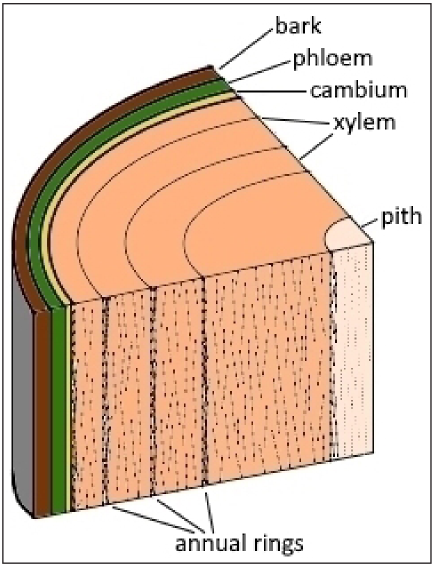
When the shoot grew a centimetre tall it produced its first true leaf-buds. Just two of them, expanded: translucent, softly wrinkled and fringed with pale wispy hairs. Photosynthesis accelerated now as the sun rose higher and longer in the sky, illuminating these first leaves. More emerged as the seedling became a fully functioning plant, a miniature tree called European or common beech, *Fagus sylvatica*. This all seemed simple enough except for the tree's singular task: for it would become an improbable structure in the form of a tree specialized eventually to reproduce itself. That would take much good luck of not being eaten as a seedling by animals small and large, or being ring barked by starving deer, or toppled during a gale. That final reproductive task would take much longer: this species of plant had evolved a means of maintaining its populations that required it to grow into one of nature's giants – thirty five metres tall standing on a trunk one and a half metres wide and topped with a intricate network of branches forming a broad canopy.

Growth of wood.

The young tree needed to expand. From season to season of warmth and ample light it pushed its leaves above the surrounding grass and herbs into its place under the sun. The apical meristem of that first season's growth had replicated as the meristems of multiple branches. To outgrow grassy and herbaceous competitors the sapling had to grow strong – it needed a woody stem. The apical meristems spread sideways to form a cylinder near the outer margin of the shoot and branches. This part of the meristem specialized into the cambium region of cells, capable of continual division pushing out sideways. Thus the main trunk and branches thickened as they grew longer. The cambium operated separately from two layers: with the innermost layer growing toward the centre of the stem.

From its inner region the cambium produced layer upon layer of tubular cells, compacting into a structure called xylem, the basic material of wood. Cambium cells continued to divide until the tree fell down dying. Every year the inner cambium reactivated in the warmth of spring and produced big wide xylem cells, but the cambium never stopped. So later in the season regions of narrower xylem cells were produced. This yearly pulsation produced rings of varying diameter, ring after ring, tens of them, hundreds of them. Cells of the xylem were of two main types, both grew to about one millimetre long. When their cell walls were sufficiently thickened they died but remained in place and intact. Tracheid cells grew thinly elongated with many patches of pores along their length. Tracheids aligned up the stem, densely packed with their angular ends mingling in close alignment with others. Together they all formed into tubular connections, cell to cell to cell from the finest roots to the pointed tips of the leaves. Similarly, and amongst the bulk of the tracheids there grew cells called vessel elements. Also tubular, but wider than tracheids, these vascular cells formed more distinctly interconnected tubular systems for transport of water upwards, roots to branches.

This tree belonged to a hardwood species, toughened with fibrous cells that ran radially through the elongating bulk of conducting cells of the xylem. All these three types of xylem cells had their individual walls strongly reinforced with lignin – a large and complex polymer molecule made of various and repeated groups of carbon, hydrogen and oxygen atoms. Lignin is not just strong, it contains many groups of atoms as aromatic rings. These, together with resins and waxes that penetrate the xylem, make wood resistant to wetting.

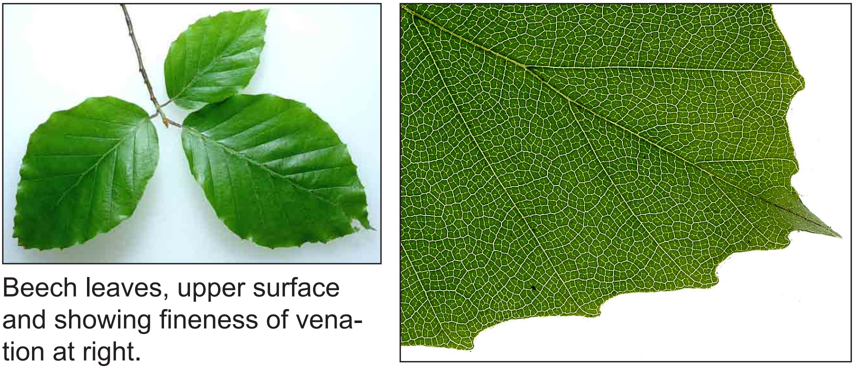


Left: Section of 40 year beech tree. Right: Basic structure of wood in a 4 year tree. Thickness of *cambium*, in yellow, is exaggerated for clarity.

The cambium produced from its outer region a thin layer of tubular cells forming the phloem: a vascular system to transport nutrients. Within the phloem tubes watery sap flowed down from leafy chemical factories, bearing carbohydrates, lipids and proteins. This food, this photosynthate, flowed inwards from branches toward the trunk, and on down to the furthest reaches of the roots. The phloem grew like the xylem but always to remain a narrow soft and living outer layer around the accumulating bulk of xylem. Long thin cells called sieve elements formed most of phloem. Along their lengths they bore large pores so that arrays of sieve elements aligned to act as tubes. Moreover, the cambium produced vascular cells called sieve tube members. These had large pores at their end walls and the cells grew with these pores directly aligned to create wide bore tubes. Special companion cells, one for each sieve tube member provided physiological support. Life for individual phloem cells was short and they were not destined to remain in skeletal form, so this layer never accumulated as a bulk of woody material.

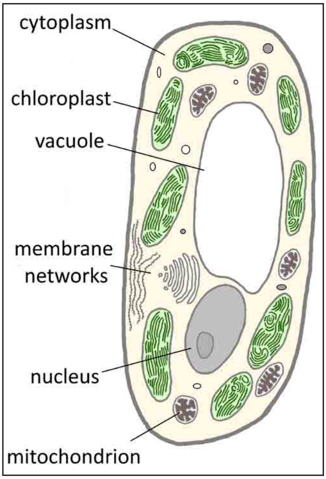
Leaves and chloroplasts.

Leaves burst out from their shiny brown buds each spring. For this *Fagus sylvatica* a simple leaf: one blade with its petiole stem to attach to a minor branch. They expanded into a classic simple oval with a wavy edge; one leaf smaller than the palm of your hand. As each leaf grew the side that would face the sun developed a single layer of cubical cells uppermost as its epidermis. This layer was protected from abrasion and water by a thin layer of wax that later would turn the pale green leaves of spring into the denser shiny leaves of mid-summer. Below the epidermis developed a closely packed row of elongate cells, palisade cells forming one or two layers. (chapter 'Leaf-fall' for drawings of leaves.)



Beech leaves, upper surface and showing fineness of venation at right.

Each palisade cell was coloured by densely packed bean shaped particles. Green particles, chloroplasts, were filled with chlorophyll and numerous potent enzymes, co-factors, energy transporting molecules, and so on. This biochemical factory was packed into arrays of membranes called thylakoids within the chloroplasts. The palisade cells were also packed with the ordinary components of cells: the nucleus with its DNA; a network of membranes spreading throughout the cytoplasm that had many biochemical functions; the mitochondrion particles in which the energy-consuming reactions of the cell were directed; and typically with a vacuole containing watery fluid.



Representation of a palisade cell of a leaf to show in simple form the main structures and organelles. In living cells chloroplasts are densely packed throughout. The green colour of leaves derives from the chlorophyll pigment within the chloroplast organelles.

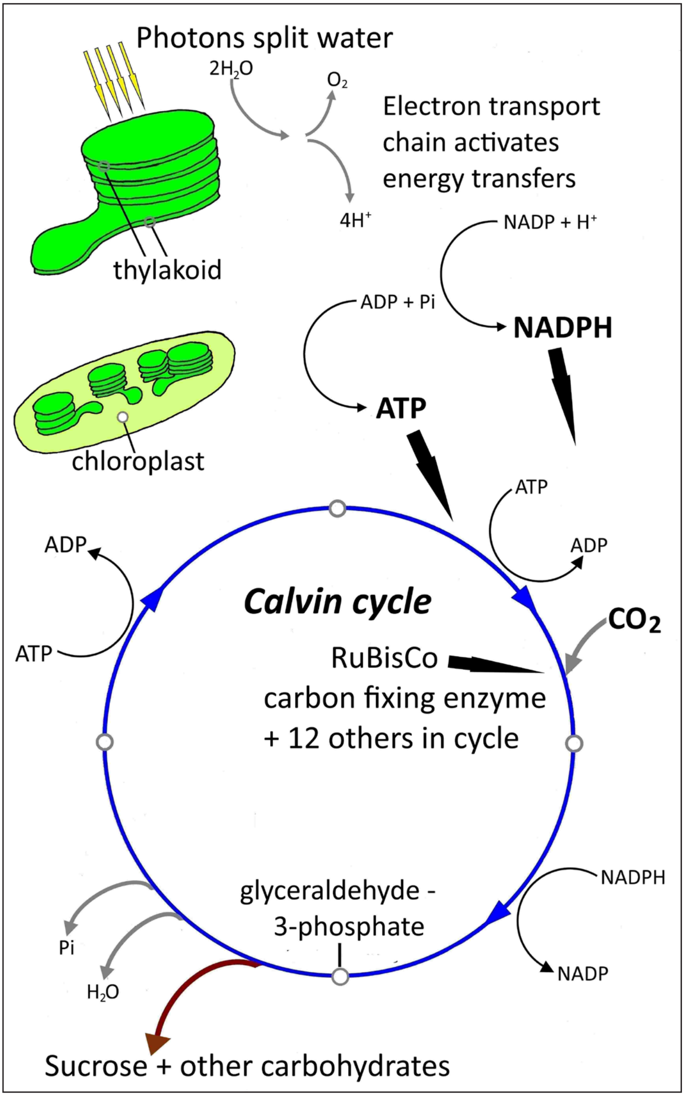
Below the palisade cells was a loose spongy layer of cells, the mesophyll. Here, as each new leaf expanded, grew leaf-veins as minute vascular bundles complete with xylem and phloem. At their finest these veins would never be more than fifty to one hundred micrometres from the energy gathering palisade cells. At the lower surface of the leaf was another and more specialized epidermis. This contained pores, stomata, made of a pair of guard cells able to change shape. These cells would open or close the pore according to physiological condition of the leaf as that varied with availability of sunlight, water, and warmth. Each leaf grew many stomata: fifty thousand on each square centimetre. Together with the aerated open structure of mesophyll this multitude of pores would control a delicate balance. The leaf needed to provide air to chloroplasts, to allow evaporation of water from the leaf so that water was sucked up from roots through the xylem, and all without wilting. One tonne of water would be sucked up, passively, from roots to leaves each summer day – the feat of biological hydraulics called transpiration.

About the origin of photosynthesis.

Researchers use circumstantial evidence to propose that chloroplasts originated about one billion years ago as bacteria. A microbe similar to the cyanobacteria so common today that live by independent photosynthesis. How some of them came to live with cells of early plant-like organisms is uncertain. Possibly they were engulfed as potential food but lived on, having avoided digestion. Or they might have been parasitic, then with continued adaptation became able to destroy membranes of the host plant that would otherwise have surrounded them as digestive vacuoles. Rather than being harmful these cyanobacteria became useful – a mutually beneficial relationship developed. They needed the host cell whilst the host cell came to benefit from the cyanobacteria. These microbes became symbiotic with their early multicellular hosts, they became endosymbionts. For green plants this mutualistic type of symbiosis, beneficial to both, became fundamental.

Likewise the mitochondria of plants, fungi, and animals are proposed to have started their evolution as free-living bacteria that became mutualistic endosymbionts. So green plants contain two types of organelles generically called plastids. Chloroplast plastids feed on sunlight and fresh air to make simple carbohydrates. Mitochondria plastids burn some of these carbohydrates to provide the same cells with energy, but the rest of the material from the chloroplasts assemble into the bulk of the plant.

> The greenness of plants is due chloroplasts soaking up sunlight. This light is a stream of photons, or a beam of rays within a narrow band of wavelengths (photon or ray depends on how light is measured). So far, this is simple but weird for us humans. For this account the essence is that photons/rays are highly energetic and travel fast and far. What happens between photons penetrating molecules of chlorophyll and molecules of carbohydrate diffusing out of chloroplasts into phloem cells is so complicated that modern textbook accounts of photosynthesis contain much that is tentative and provisional. This is not a textbook, so the diagram on page 9 is a basic outline of photosynthesis as the series of reactions from which carbon can be incorporated into the structure of a plant. The key point is that starting from light interacting with chlorophyll through to one atom of carbon fixed into the material of the tree requires the energy gained from eight photons as in the equation on page 10.



H+ = hydrogen ion; NADP+ = nicotinamide adenine dinucleotide phosphate; NADPH = reduced form of NADP+; ADP = adenosine diphosphate; ATP = adenosine triphosphate; Pi = phosphate group.

Photons and energy transfer molecules.
Photons penetrated the outer membrane of chloroplasts and then into layered membranous structures. These were thylakoids, arranged as

wide interconnected discs. Within thylakoids photons were channelled through a series of pigment molecules acting as a light guide until they hit a molecule of chlorophyll. This molecule, a pigment made of protein, was adapted for absorbing light of certain wavelengths whilst letting others pass by. Photons of red and blue wavelengths were absorbed, photons of green wavelengths carried on past the molecule. At the centre of this molecule the intense energy of an absorbed photon jolted an electron to a higher energy level. The energized electron sped along a series of intermediate reactions with other molecules in an electron transport chain. As it progressed it split molecules of water into hydrogen ions, electrons, and oxygen. Some of the oxygen diffused into the cytoplasm of the palisade cell to be used for the separate energy releasing reactions of respiration; the rest was a waste gas that leaked away into the atmosphere. Electrons cleaved off the water molecules passed along the chain, from complex molecule to molecule within the thylakoid membrane.

Reactions to capture light energy:

$$2H_2O \quad \overset{\text{4 photons}}{>} \quad 4e^- + 4H^+ + O_2$$

[photons strip electrons e^- from water]

and energy transferred to form **NADPH** and **ATP**

$$2H_2O + 2NADP^+ + 3ADP + 3Pi \quad \overset{\text{photons}}{>} \quad 2NADPH + 2H^+ + 3ATP + O_2$$

[reaction dependent on light]

Reactions to fix carbon:

$$3CO_2 + 9ATP + 6NADPH + 6H^+ \quad >>$$
$$G3P + 9ADP = 8Pi + 6NADP^+ + 3H_2O$$

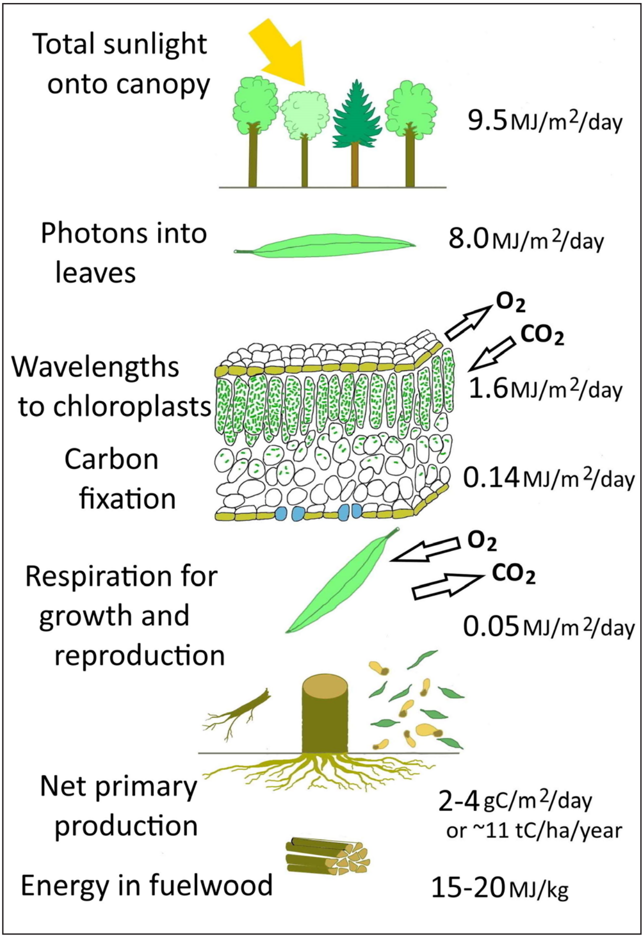
[reaction of Calvin cycle fixing carbon into G3P,
glyceraldehyde-3-phosphate]

Within the membrane were two types of energy transfer molecules which became readily energized by the electron transport chain and hydrogen ions. Adenosine diphosphate became adenosine triphosphate, ATP, whilst nicotinamide adenine dinucleotide phosphate converted into its reduced form, NADPH. These energized molecules are unstable and would transfer their energy to promote a great range of enzymic conversions of reactants through the sequence of photosynthesis. The cells of the leaf with their chloroplasts and mitochondria were continuously recycling these two types of energy transfer molecules – a ceaselessly rapid biochemical churning.

Light powered the first part of photosynthesis but once the energy transfer molecules were energized then the reactions continued without need of light. A cyclic pathway of reactions now captured the carbon from atmospheric carbon dioxide, added more oxygen and some hydrogen atoms plus a phosphorus containing group. So halfway round the cycle a more complex molecule was produced with that carbon fixed into it. That molecule was the intermediate called glyceraldehyde 3-phosphate. Most of that G3P continued around the cycle, but one in six molecules of it were diverted away and transformed enzymatically into simple carbohydrate molecules, sugars. These reactions (the Calvin-Benson-Bassham cycle after three discoverers) continued round, guided by thirteen enzymes. The key enzyme, called RuBisCo, coordinated the link between reactions energized by light and those energized by ATP that fixed atmospheric carbon.

Respiration.

About half of the carbohydrate generated in this cycle was burnt up. It was oxidized in the biological fires of respiration to supply energy to reactions needed to synthesize the materials for the tree to construct itself: complex carbohydrates, proteins, fats and other lipids . . . These construction materials were rapidly incorporated into the soft tissues of leaves and root hairs, and the hard xylem that became the bulk of the tree. As a mature tree of 60 years the weight of its trunk, as useable but wet unseasoned timber, would be about 6 tonnes. As dry seasoned wood the weight would reduce by about 50 percent and the carbon content of this dry wood would be another 50 percent less. Thus the mature trunk would have accumulated about 1.7 tonnes of carbon over its lifetime so far. During the peak of its growth the tree added yearly 10 to 20 kilogrammes of carbon to its trunk. Its trunk gradually grew thicker and taller, xylem cell by xylem cell added from the cambium. Trees grow slowly, specially hardwood species, but they grow big. That same mature tree, the whole thing from fine roots to leafy crown would weigh about 40 tonnes. Beech trees have magnificent trunks, smooth and straight when grown close together, corrugated and broad if growing alone.



Energy flow in a forest (megajoules per square metre per day). Composite data from 4 sources in References, for softwoods or hardwoods, in temperate climate on fertile soils. Datum for net primary production is for entire biomass of a tree (grams of carbon per square metre per day).

Energy and carbon flow in a forest: some technical details.

The data in the energy flow diagram are given in joules, also in mass of carbon because researchers often express energy flow through forests in the standard units of grams of carbon per square metre per day (charcoal, a form of the pure carbon of wood, has a specific energy of 30,000 joules per gram). One joule is the energy used to lift a mass of 100 grams (a tomato) through one metre against the gravity of the earth. Or similarly the energy released if that same mass falls back to earth. A joule is a minute amount of energy, but one megajoule is one million joules, and equal to about 0.28 kilowatt-hours, or the energy required to run a small domestic cooling fan for one hour.

Beech logs from a thinning harvest in a commercial plantation.

During daylight hours energy as photons radiates onto the canopy at a rate far greater than the trees can use fully: 9.5 MJ per square metre each day. The chloroplasts cannot catch all this fraction of useful light. Much green light streams on through the translucent cytoplasm of leaf cells in the canopy of a beech tree. Of the light that penetrates leaves only a minor fraction is used by the mechanisms of photosynthesis: the photosynthetically active radiation, blue light and red light of approximately 0.4 nanometres and of 0.7 nanometres wavelength respectively. Both parts of photosynthesis, needing light and independent of light, consume approximately 50% of the energy available to the tree to keep the reactions going. This consumption is known as autotrophic respiration. So the overall thermodynamic efficiency of photosynthesis is about 33%.

All the while the tree is growing, and even when fully mature it continues slowly to grow whilst shedding its leaves each year, producing millions of fruits, and losing branches to gales or disease. What accumulates in the trunks of the trees as harvestable timber has an energy value of about 0.05 MJ per square metre each day, depending on local conditions of nutrients, temperature and rainfall. From sunlight onto the canopy into biomass of the tree there is a loss of 99.5 percent of available energy. When expressed as quantity of carbon accumulated in trunks, a measure known as net primary production, this captured energy is the equivalent of 2 to 4 grams of carbon per square metre each day. Expressed as trunks of trees this is about 10 tonnes of fresh hard-wood per hectare per year as the crop of timber from a plantation. The time taken for a new plantation on good soils in a suitable climate to reach this level of productivity varies greatly for different species: about 40 years for softwoods, 80 years for hardwoods. The energy value of fully dry seasoned wood, either softwood or hardwood, is approximately 20 megajoules per kilogram.

> 10 tonnes of dry fully seasoned wood, used as fuel, could provide 200,000 megajoules. This wood could be burnt in an electricity generator or a furnace for hot water. To appreciate more directly what 200,000 megajoules of energy means, imagine a row of 6 electric heaters, each rated at 1 kilowatt, glowing continuously for 1 year. The basis of this comparison is that 1 watt is equal to 1 joule per second, thus 200,000 megajoules is equivalent to 55, 556 kilowatt-hours.

Reproduction.

The seedling matured into a tree able to fulfil its function: to reproduce itself. Thirty years has passed whilst the trunk grew tall and the branches wide. The task of reproduction could have continued for another one hundred years or more if by chance the tree avoided felling by storm or chain-saw. At eighty years or so when it was most vulnerable to both fates, the tree was a massive wide leafy canopy borne on its straight long column of a trunk. The great mass of its high branches had spread up and outwards as each apical meristem of each twig responded to sunlight. Each spring its aerial framework again burst out from its leaf-buds as millions of energy capturing fresh green ovals. On a clear summer day the energy beaming down onto the tree seemed vast but the task of harvesting this energy was hard for the tree’s biochemical factories. The mechanisms had been borrowed from tiny bacteria aeons ago. In those times life on earth consisted of single celled organisms – individually microscopic but often forming collective films, mats and even the large mounds called stromatolites. These organisms had various means of extracting vital energy from their environment, several purely chemical mechanisms, and photosynthesis. Then a sequence of combinations gave rise to plants standing tall in the sunshine: endosymbiosis by chloroplasts and mitochondria, then multicellular organisms with specialized parts like roots and leaves. The possibilities for life burst upwards: mosses, ferns, herbs, bushes and trees. Their photosynthesis also pumped oxygen into the atmosphere. Then when animals eventually crawled from the sea onto the land to breathe they found there large plants to eat.

Stand of young beech trees shading the ground.

The taller the trunk stretched and the wider the canopy spread the more energy the tree gathered and transformed into wood and into flowers, fruits and seeds. The higher and wider it went so the more seeds it shed and the darker became its shadow on the ground below. Within this stand of beech trees little else could establish itself below – starved of the sun's energy. The roots spread as wide as the canopy, finding the upper layers of soil an ample source of water and mineral nutrients. These beeches were adapted to the fertile soils and atmosphere of a moist temperate climate with mild winters and summers. The soil, that gritty substance compounded with humus and its microcosm of organisms, provided all the tree's needs except photons and freely available carbon.

The root hairs imbibed water, and with that compounds containing nitrogen, phosphorus, calcium, potassium, sodium, iron, magnesium, and so on in a list of essential elements for the tree to incorporate into the vast biochemical factory of its construction.

Flowers of beech tree; 2 males at lower left; 1 female at lower right. Credit: Wikimedia.

At thirty years the tree grew its first effective flowers. Dull coloured and diminutive things, nevertheless entirely suitable for the male flowers to release pollen grains and the female flowers to capture pollen dispersed on the wind to other trees. The male flowers were tassels of bare stamens, pale green and stretching out into the breezes amongst the high branches. The female flowers hid their pistils within small dull bracts and when pollen from another tree was caught on the sticky stigma at the apex of the pistil then fertilization could lead to development of the embryo. The fruit grew from the wall of the ovary that was the base of the pistil, it expanded slowly and hardened into a protective case. The heavy fruits fell in their many thousands, littering the ground. Most of the seeds within the fruits would be eaten and digested by animals and the woody walls of the fruits would rot and give up their nutrients to the soil and the roots of the same tree. But if just two or three of the many millions that a mature tree produced would germinate, survive the threats of hungry animals, grow to produce more seed, then that population of beeches would continue. This vast reproductive extravagance of that style of living we call tree is what incidentally provides us people with the timber that we turn into furniture, tools, or fuel. And more: trees give us the joy of walking underneath a woodland canopy glowing green in the summer sunshine.

References and notes.

(Many articles are accessible as abstracts or full text using search engines such as Google Scholar, or institutional login, or a pay-wall.
Conversions: 1 kilocalorie = 4184 joules, and 1 watt-hour = 3600 joules.)

Photosynthesis.

Anonymous, 2017. Photosynthesis. Wikipedia. [A comprehensive account, including many leads to related aspects of plant physiology.]

Bolton, J.R. & Hall, D.O., 1991. The maximum efficiency of photosynthesis. Photochemistry and Photobiology. 53: 545-548.]

Moore, R., *et al*., 1995. *Botany*. Wm.C. Brown Publishers, Dubuque, USA. ISBN: 0697037754 [See Ch.7. Photosynthesis.]

Taiz, L. *et al*., 2018. *Plant Physiology and Development*. Oxford University Press, New York. ISBN: 9781605357454 [See Ch.7. Photosynthesis: the light reactions; and Ch. 8. Photosynthesis: carbon reactions.]

Physiology.

Hari, P., Heliovaara, K. & Kulmala, L., 2013. *Physical and Physiological Forest Ecology*. Springer, Dordrecht. ISBN: 9789400756021.

Larcher, W., 1995. *Physiological Plant Ecology: ecophysiology and stress physiology of functional groups.* Springer, Berlin. ISBN: 0387581162.

Ryan, M.G., Lavigne, M.B. & Gower, S.T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. Journal of Geophysical Research (Atmospheres), 102: 28871-28883.

Growth and primary production.

Andersson, G., *et al*., 2001. Production of Forest Energy. Ch. 3 in: *Bioenergy from Sustainable Forestry: guiding principles and practice*. Editors: Richardson, J., *et al*., Kluwer Academic Publishers, Netherlands. ISBN: 0306475197.

Asikainen, A., *et al*., 2008. Forest energy potential in Europe (EU27). In: *Working Papers of the Finnish Forest Research Institute*.

Cannell, M.G.R., 1982. *World Forest Biomass and Primary Production Data*. Academic Press, London. ISBN: 0121587800.

Cannell, M.G.R., 1984. Woody biomass of forest stands. Forest Ecology and Management 8: 299-312. [Analysis of Cannell's data in his 1982 book above.]

Cannell, M.G.R., 1988. The Scientific Background. Ch. 2 in: *Biomass Forestry in Europe: a strategy for the future*. Editors: Hummel, F.C., Palz, W. & Grassi, G., Elsevier Applied Science Publishers Ltd, London. ISBN: 1851662553.

Cannell, M.G.R., 1989. Physiological basis of wood production: a review. Scandinavian Journal of Forest Research, 4: 459-490. [This review of many sources of information summarizes the more comprehensive account by Cannell in the 1988 book chapter above.]

Christersson, L., Sennerby-Forsse, L. & Zsuffa, L., 1993. The role and significance of woody biomass plantations in Swedish agriculture. The Forestry Chronicle, 69: 687-693.

Cleveland, C.C., *et al*. 2015. A comparison of plot-based satellite and Earth system model estimates of tropical forest net primary production Global Biogeochemical Cycles, 29: 626-644. [Demonstration of use of satellite data to survey tropical forest of S.America, Africa, S.E.Asia, in relation to their productivity.]

Edwards, N.T., *et al*., 1981. Carbon Metabolism in Terrestrial Ecosystems. Chapter 9 in: *Dynamic Properties of Forest Ecosystems*. Editor: Reichle, D.E., Cambridge University Press, UK. ISBN: 0521225086.

Gower, S.T., *et al*., 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecological Applications, 11: 1395-1411.

Hardiman, B.S., *et al.*, 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology, 92: 1818-1827. [Demonstration of how overall physical structure of a forest is important to its productivity.]

Kira, T., 1975. Primary production of forests. Ch. 1 in: *Photosynthesis and Productivity in different Environments*. Editor: Cooper, J.P., Cambridge University Press, UK. ISBN: 0521205735. [Dated but still provides a comprehensive survey of global data on primary production and nutrient flows in forests.]

Kloeppel, B.D., Harman, M.E. & Fahey, T.J., 2007. Estimating above ground net primary productivity in forest-dominated ecosystems. In: Fahey, T.J., *et al.*, *Principles and Standards for Measuring Primary Production*. Oxford University Press, ISBN: 9780195168662.

Lagergren, F., *et al.* 2005. Net primary production and light use efficiency in a mixed coniferous forest in Sweden. Plant, Cell & Environment, 28: 412-423. [Detailed account of how light availability and use by trees is studied.]

Landsberg, J.J., 2011. The Carbon Balance of Trees and Stands. Ch. 5 in: *Physiological Ecology of Forest Production: principles, processes and models*. Editors: Landsberg, J.J. & Sands, P., Academic Press, London, ISBN: 9780123744609. [Mostly methods for mathematical models, and contains parameter values for energy and carbon flows.]

Newman, G.S., Arthur, M.A. & Muller, R.N., 2006. Above- and below-ground net primary production in a temperate mixed deciduous forest. Ecosystems, 9: 317-329. [Relates various production characteristics to soil moisture and nitrogen availability.]

Waring, R.H., Landsberg, J.J. & Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiology, 18: 129-134.

continued

Sylva Foundation, 2017. *OneOak Project*. [Data used here to estimate increment of tree trunk is based on data at 2017 from *Sylva* website, for different densities and sizes. An English oak tree that had grown within woodland for 222 years was felled then entirely weighed and measured. Tree height 23.9m; stem diameter 89.8cm; crown diameter 17.8m; stem height 12.9m; stem volume 4.96m^3; leaf area index 1.7; tree weight 14.38 tonnes; tree volume 11.58 m^3; dry mass 7.86 tonnes; carbon content 3.93 tonnes.]

van Tuyl, S., *et al*. 2005. Variability in net primary production and carbon storage in biomass across Oregon forests - an assessment integrating data from forest inventories, intensive studies, and remote sensing. Forest Ecology and Management, 209: 273-291. [Comparative forest inventories for study area of 120,000 km^2 for biomass and production.]

Xiao, C.-W., *et al*. 2003. Above-and below-ground biomass and net primary production in a 73-year-old Scots pine forest. Tree Physiology 23: 505-516. [Detailed information on whole tree biomass of *Pinus sylvestris* forest.]

Zheng, D., Prince, S. & Wright, R., 2003. Terrestrial net primary production estimates for 0.5° grid cells from field observations - a contribution to global biogeochemical modeling. Global Change Biology, 9: 46-64.

Ecology of energy flow.

Golley, F.B., 1961. Energy values of ecological materials. Ecology, 42: 581-584.

Gates, D.M., 1971. The flow of energy in the biosphere. In: *Energy and Power* (a Scientific American book) Chapter 4, pgs 43-52.,W.H. Freeman and Company, San Francisco, ISBN: 0716709384

Gosz, J.R., *et al*., 1978. The flow of energy in a forest ecosystem. Scientific American, 238: 92-102. [Comprehensive account of a study in 1970s of energetics of deciduous forest stands in north east USA, including effects of many species of herbivores.]

Kimmins, J.P., 2004. *Forest Ecology: a foundation for sustainable forest management and environmental ethics in forestry.* Prentice Hall / Pearson Education Ltd, London. ISBN: 0130662585 [See Ch 4. Production ecology.]

Korhonen, J., Wihersaari, M. & Savolainen,I., 2001. Industrial ecosystem in the Finnish forest industry: using the material and energy flow model of a forest ecosystem in a forest industry system. Ecological Economics, 39: 145-161. [Mostly about industrial forestry but with detailed flow-diagrams of biomass and energy within plantations.]

Krebs, C.J. 2014. *Ecology: the experimental analysis of distribution and abundance*. Pearson Education Ltd., Harlow, England. ISBN: 9781292026275 [See Ch. 22. Ecosystem metabolism: primary production.]

Morton, O. 2009. *Eating the Sun: the everyday miracle of how plants power the planet*. Fourth Estate, London. ISBN: 9780007171804. [Fascinating popular science about history of research on photosynthesis and significance of plants for life on Earth.]

Ovington, J.D. & Heitkamp, D., 1960. The accumulation of energy in forest plantations in Britain. Journal of Ecology, 48: 639-646. [Information on mass and energy flows through forest stands that remains useful.]

Reichle, D.E. 1975. Advances in ecosystem analysis. Bioscience, 25, 257-264. [See Figure 3 for pictorial presentation of the carbon cycle in a hardwood forest. Table 7 for metabolic parameters of a deciduous forest.]

Smil,V. 2009. *Energy, a beginner's guide*. One World Publications, Oxford. ISBN: 9781851684526 [See Ch. 2 Energy in the biosphere: how nature works. This explains, in simple language, the physics and chemistry of energy to the workings of living organisms.]

Thomas, P.A. & Packham, J.R. 2007. *Ecology of Woodlands and Forests: description, dynamics and diversity*. Cambridge University Press, England. ISBN: 9780521542319. [See Ch.8, Energy and Nutrients.]