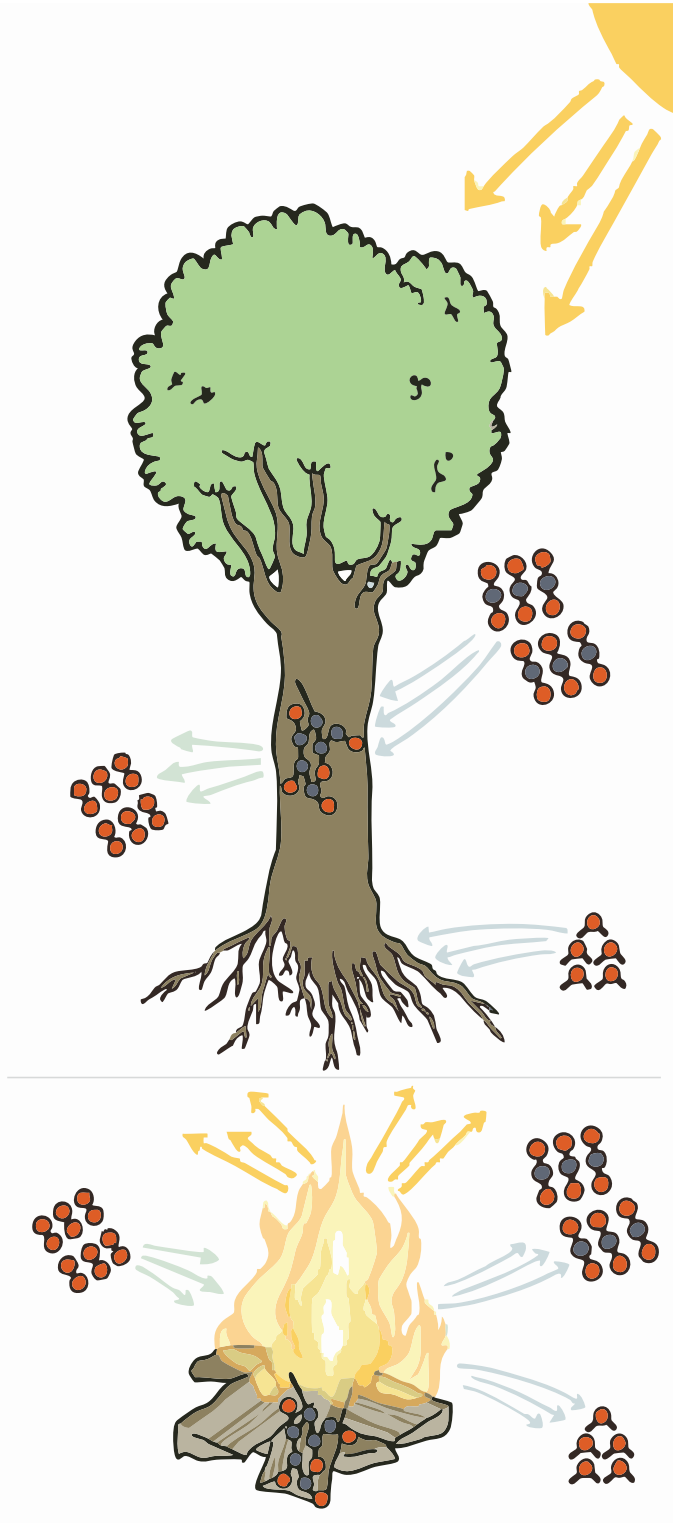
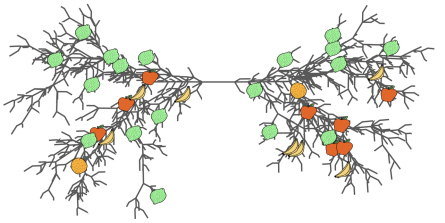
From Air to Arbor



Photosynthesis and Carbon Fixation: This diagram illustrates the process by which trees build their mass from atmospheric CO_2 rather than soil nutrients. The top section shows the molecular mechanism of photosynthesis: light energy driving the conversion of carbon dioxide and water into glucose through the Calvin-Benson cycle. Chloroplasts in leaf cells capture photons to power the fixation of atmospheric carbon into organic compounds. The bottom section demonstrates the carbon flow: from diffuse CO_2 in the atmosphere, through stomatal uptake, into the structural polymers (cellulose, lignin, hemicellulose) that comprise wood. Each ring of tree growth represents a year's accumulation of atmospheric carbon, transformed by solar energy into solid biomass. As Feynman noted, trees are literally "made of air" — their dry weight consists primarily of carbon atoms that were once distributed throughout the atmosphere.

From Air to Arbor

Ask where a tree's mass comes from and intuition points downward: soil, water, nutrients drawn up through roots. This is almost entirely wrong. Trees are made of air — ∼95% of their dry mass comes from atmospheric CO_2. Through photosynthesis, plants build themselves from carbon dioxide, converting invisible gas into solid wood, cellulose, and lignin using sunlight. Van Helmont's 1640s willow experiment demonstrated this: a tree gained 164 pounds (∼74 kg) while the soil lost only two ounces (∼60 g). Isotope labeling confirms the molecular accounting — carbon in wood comes from air, not earth or water. When trees burn, they simply return their borrowed carbon and sunlight to the atmosphere, completing a chemical cycle that temporarily crystallizes air into living architecture.



Trees Made of Air ∘ Atmospheric CO_2 Fixation ∘ Photosynthesis Energy Capture ∘ Water Splitting & O_2 Release ∘ Calvin-Benson Cycle ∘ Cellulose & Lignin ∘ Stored Solar Energy ∘ Great Oxygenation Event ∘ ^{18}O Isotope Experiments ∘ Feynman's Air Quote ∘ Combustion Symmetry

"I am the Lorax and I speak for the trees."
— The Lorax

"It is not the deer that is crossing the road,
rather it is the road that is crossing the forest."
— Muhammad Ali *(probably misattributed)*

From Air to Arbor

In the early seventeenth century, Jan Baptist van Helmont conducted an experiment that would later become emblematic of early quantitative biology. He planted a willow sapling in a weighed quantity of dry soil, supplied it only with water, and allowed it to grow for five years. At the end of the experiment, he found that the tree had gained over 70 kilograms in mass, while the soil had decreased by less than 60 grams. From this, he concluded — correctly in direction though not in mechanism — that the tree's substance did not come from the soil.

Van Helmont identified water as the key source of mass, unaware of the role of atmospheric gases. His result was significant for shifting scientific attention away from Aristotelian elemental explanations and toward empirical measurement. The idea that a tree might be built from intangible substances posed a conceptual challenge to early chemistry, which had yet to recognize air as chemically active.

In the late eighteenth century, Joseph Priestley and Jan Ingenhousz discovered that plants could "restore" air that had been "damaged" by combustion or respiration. Ingenhousz, in particular, demonstrated that this process required light and occurred only in green parts of plants. The observations hinted at a connection between sunlight, plant matter, and atmospheric gases.

By the mid-nineteenth century, Julius von Sachs and others had established that plants produce starch in the presence of light and that carbon dioxide is the source of carbon in organic compounds. Quantitative combustion analysis allowed chemists to determine the proportions of carbon — hydrogen — and oxygen in plant tissues, confirming that nearly all plant biomass derived from these three elements.

In the twentieth century, isotopic labeling techniques enabled direct tracing of carbon atoms from CO_2 into plant tissues, definitively establishing air as the origin of most biomass. Experiments using ^{14}C-labeled carbon dioxide showed its incorporation into sugars, cellulose, and lignin. By the mid-twentieth century, the principal pathways of photosynthesis — including the light reactions and the Calvin–Benson cycle — had been elucidated.

A breakthrough came in the 1940s when Samuel Ruben and Martin Kamen used oxygen-18 isotope labeling to resolve a question about photosynthesis. Earlier researchers knew that oxygen gas was released, but its source remained unclear — did it come from carbon dioxide or water? By supplying plants with ^{18}O-enriched water while keeping CO_2 normal, they found that the heavy oxygen appeared exclusively in the released O_2 gas, not in the organic products. Atmospheric oxygen originates from water splitting, while the oxygen atoms in biomolecules derive from CO_2 fixation. The experiment established the precise molecular accounting of photosynthesis and confirmed that plants literally separate air from water at the atomic level.

A tree's material body, the wood, leaves, and branches it accumulates year by year, is not extracted from the ground in the way stones or metals are quarried. Its dry mass derives from elements that were once distributed in dilute form throughout the atmosphere and

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hydrosphere. The key components of this mass, carbon, oxygen, and hydrogen, enter through invisible flows: air, water, and sunlight. A tree is built from what passes through it.

Although visually and mechanically tied to the soil, a tree records processes that unfold mostly above ground. The mass that persists after all water is removed, the dry matter, is composed primarily of carbon atoms originally fixed from atmospheric CO_2. The atoms were drawn down through the stomata of leaves, diffused through mesophyll tissue, and incorporated into sugar molecules via light-powered biochemical cycles.

The notion that trees "grow out of the earth" conflates anchorage with origin. The soil does provide essential ions and mechanical stability, but its contribution to the actual mass is minor. Most of what endures in a dried trunk, cellulose, lignin, hemicellulose, was once part of the air surrounding it. The verticality of a tree, its rise toward the sky, is materially made possible by the intake of that sky's gaseous contents.

The central process enabling this conversion is photosynthesis. It is a layered sequence of energy transduction and molecular reconfiguration. The first phase occurs in the chloroplasts of leaf cells, where chlorophyll pigments absorb incoming photons. The photons excite electrons to higher energy states, dislodging them from their atomic orbitals and initiating a cascade of electron transfers through the thylakoid membrane.

Oxygen-producing photosynthesis altered Earth's atmosphere and biosphere. When it first evolved in cyanobacteria around 2.5 billion years ago, it triggered the Great Oxygenation Event — a transformation that poisoned most existing anaerobic life but enabled the eventual emergence of complex organisms. The oxygen released by water-splitting is a byproduct that reshaped planetary chemistry. Every breath taken by an animal, every flame that burns, every rusting of iron depends on this ancient process continuing in plant chloroplasts. Trees are participants in a planetary-scale atmospheric engine that has operated continuously for billions of years.

The chain of transfers generates two critical energy carriers: ATP (adenosine triphosphate) (Lohmann, 1929) and NADPH (nicotinamide adenine dinucleotide phosphate). The molecules store the electromagnetic energy harvested from light and shuttle it into the chemical domain. In the aqueous interior of the chloroplast, the stroma, the stored energy is used to convert inorganic carbon into organic intermediates.

Isotopes are versions of an element with the same number of protons (Soddy, 1913) but different numbers of neutrons. For example, oxygen has 8 protons and can have 8, 9, or 10 neutrons. This gives rise to the isotopes ^{16}O, ^{17}O, and ^{18}O. Carbon has 6 protons and can have 6, 7, or 8 neutrons. This gives rise to the isotopes ^{12}C, ^{13}C, and ^{14}C. Isotopes are a way to label atoms and track them in chemical reactions. This is how we know that the oxygen in wood comes from atmospheric CO_2, not from the soil.

When water molecules are split in photosystem II (oxygenic photosynthesis), their oxygen atoms are released directly to the atmosphere as O_2 gas. Isotope labeling experiments using ^{18}O-enriched water demonstrated (Ruben et al., 1941) that the heavy oxygen appeared in the released gas, not in the organic products. The oxygen atoms incorporated into cellulose and other biomolecules originate from CO_2. Every molecule of atmospheric

oxygen released by plants represents a water molecule that was split to extract electrons, while the oxygen in wood records the atmospheric carbon that was fixed.

The fixation of carbon takes place in the Calvin–Benson cycle (Bassham, Benson & Calvin, 1950). Atmospheric CO_2 diffuses into leaf tissue and reacts with ribulose bisphosphate, a five-carbon sugar, under the catalytic action of the enzyme rubisco. The resulting six-carbon intermediate is promptly split into three-carbon molecules, triose phosphates, that serve as building blocks for carbohydrates. The triose units are reassembled into glucose and other hexoses, which in turn feed biosynthetic pathways across the plant.

Sunlight delivers approximately 1,000 watts per square meter on a clear day — plants capture 1–3% of this energy in chemical bonds. What is captured becomes concentrated: each kilogram of dry wood stores about 16–20 megajoules of energy, roughly equivalent to the combustion energy of natural gas. A single mature tree may contain 50–100 gigajoules of stored solar energy, accumulated over decades of photosynthetic capture. Millions of individual photons contribute quantum energy to the construction of molecular architecture that can persist for centuries.

Once synthesized, the sugars are exported from the site of fixation. Through the phloem, a network of conductive tissues, they are distributed to growing regions: root tips, shoot apices, developing leaves, and the vascular cambium. At the cambium, a cylindrical layer of dividing cells just beneath the bark, the imported carbohydrates are used to construct macromolecules.

Cellulose, hemicellulose, and lignin form the principal constituents of wood. Cellulose $(C_6H_{10}O_5)_n$ assembles into long, unbranched chains that crystallize into fibrils, giving tensile strength to cell walls. Hemicellulose $(C_5H_8O_4)_n$ binds the fibrils into a cohesive matrix, while lignin, a complex phenolic polymer, fills the spaces between them, adding compressive strength and water resistance. The polymers are laid down in geometric arrangements within the expanding walls of growing cells.

At the vascular cambium, cell division proceeds laterally, producing xylem cells toward the center and phloem cells outward. The radial expansion creates the familiar pattern of growth rings. Each ring corresponds to a cycle of photosynthetic capture and biosynthetic deposition.

Elongation occurs at the apical meristems, where undifferentiated cells divide and specialize into tissue types. The regions at the tips of roots and shoots coordinate patterning, orientation, and organogenesis. As cells expand and walls thicken, the imported sugars are converted into permanent form.

Hydrogen atoms in the biomass originate from water. Water is absorbed by roots and pulled upward through the xylem under tension. Though over 99% of it eventually evaporates through stomatal pores, a small fraction is chemically incorporated into organic molecules. The hydrogen forms part of the fixed material, bound into carbohydrates and lipids.

Water's functional role extends beyond hydrogen donation. It serves as a solvent for ions, a medium for transport, and a buffer against temperature fluctuations. It enables the tree's biochemical metabolism and what remains after desiccation is not water but the elements it helped mobilize and bind.

Oxygen atoms in biomass come from CO_2. During photosynthesis, water molecules are split to provide electrons, but their oxygen atoms are released directly to the atmosphere as O_2 gas. The oxygen atoms incorporated into cellulose, forming hydroxyl, carboxyl, and ether linkages, originate from the atmospheric carbon dioxide that was fixed. The high oxygen content of wood, about 40 to 45 percent by weight, is a direct record of atmospheric CO_2 that was captured and converted into solid form.

Mineral ions absorbed from the soil are essential but contribute little to the total mass. Nitrogen, phosphorus, potassium, calcium, magnesium, and micronutrients serve catalytic and regulatory roles. They enable enzymatic function, membrane potential maintenance, and nucleic acid stability. Their aggregate proportion in dry matter is often less than 5 percent. They are mainly facilitators rather than substrates.

When all water is removed from a tree, what remains is a carbon-rich composite of organic polymers. Cellulose, lignin, and related molecules form a lattice of energy-stored mass, chemically stabilized and mechanically resilient.

The transformation exhibits chemical symmetry. Photosynthesis builds sugar units from atmospheric inputs, $6CO_2 + 6H_2O + \odot\,\text{light} \longrightarrow C_6H_{12}O_6 + 6O_2$, which are then polymerized into cellulose by removing water: $n(C_6H_{12}O_6) \longrightarrow (C_6H_{10}O_5)_n + nH_2O$. When wood burns, the process reverses exactly: $(C_6H_{10}O_5)_n + 6nO_2 \longrightarrow 6nCO_2 + 5nH_2O +$ heat. The stored solar energy is released, and every atom returns to its original atmospheric or aqueous state. The carbon dioxide and water vapor that rise from the flame are identical to the molecules that entered the tree decades earlier. A tree is a temporary configuration of atmospheric components, held together by captured light. As Richard Feynman remarked, trees are “made of air”. When a tree burns, the carbon returns to the atmosphere, and the stored sunlight is released as heat.

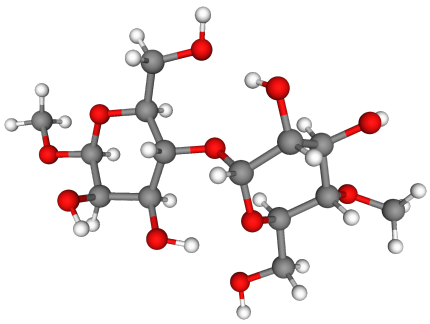


Figure by author. Molecular structure of cellobiose, the repeating β-1,4-linked D-glucose disaccharide unit of cellulose.

The Growing Tree

(NOT by Shel Silverstein)

Once there was a tree,
and she loved a little boy.

Every day the boy would come —
gather her leaves to make crowns,
climb her trunk,
swing from her branches,
eat apples,
and rest in her shade.

And the boy loved the tree.
And the tree was happy.

But time passed,
and the boy grew older.
The tree often stood alone.

One day the boy came back.
The tree said,
"Come, climb my trunk, swing, eat, and be happy."

"I'm too big to play," said the boy.
"I want money, to buy things and have fun."
"I don't have money," said the tree,
"but you can take some apples —
sell a few, share a few, and plant one or two."

And the boy did.
And the tree was happy.

Years passed. The boy returned.
"I want a house," he said,
"for warmth, for family."

"I don't have a house," said the tree,
"but take my fallen branches.
Leave enough for me to grow."

And the boy did.
And the tree was happy.

More time went by.
The boy returned, older.
"I want a boat to go far away."

"Some of my thicker branches grew wild," said the tree.
"You can use them."

And the boy did.
And the tree was happy.
After many years, the boy returned, tired.

"I don't need much now," he said,
"just a place to rest."
The tree said,

"Come sit.
There is shade again.
And I'm glad you're here."
And the boy did.

and the boy was happy.

And the tree was happy,

Carbon Fixation and Mass Accumulation in Trees

Trees accumulate mass through atmospheric CO_2 fixation powered by sunlight. This section quantifies the chemical and energetic processes converting gaseous carbon into solid biomass.

Light-Driven Reactions

Photosystems I and II generate ATP and NADPH from light energy (680 nm photons ≈ 176 kJ/mol):

$$2\,H_2O + 2\,NADP^+ + 3\,ADP + 3\,P_i + h\nu \rightarrow 2\,NADPH + 3\,ATP + O_2.$$

Quantum requirement: 8–10 photons per CO_2 molecule fixed.

Carbon Fixation and Biomass Synthesis

In the Calvin–Benson cycle, carbon dioxide is enzymatically fixed into triose phosphates using the energy carriers from the light reactions. The overall reaction for one glucose unit is:

$$6\,CO_2 + 18\,ATP + 12\,NADPH \rightarrow C_6H_{12}O_6 + 18\,ADP + 18\,P_i + 12\,NADP^+.$$

Glucose is polymerized into cellulose by dehydration:

$$n\,C_6H_{12}O_6 \rightarrow (C_6H_{10}O_5)_n + n\,H_2O.$$

These polymers form the primary structure of wood (secondary xylem), alongside lignin and hemicellulose.

Oxygen Source Identification via Isotope Labeling

The ^{18}O labeling experiments by Ruben and Kamen (1941) definitively established oxygen source separation:

Water source test:

$$CO_2 + H_2^{18}O + h\nu \rightarrow [CH_2O] + {}^{18}O_2.$$

Result: Heavy oxygen (^{18}O) appeared exclusively in released O_2, not in organic products.

CO_2 *source test:*

$$C^{18}O_2 + H_2O + h\nu \rightarrow [CH_2^{18}O] + O_2$$

Energy Storage Density

Wood represents highly concentrated solar energy storage. **Energy density:** 16–20 MJ/kg (dry wood); **Solar capture efficiency:** 1–3% of incident radiation; **Mature tree storage:** 50–100 GJ total (accumulated over decades); **Photon requirement:** ∼8–10 photons per CO_2 molecule fixed.

This energy density approaches that of fossil fuels, demonstrating that photosynthesis creates a highly efficient biological battery.

Quantitative Mass Accumulation

For annual NPP of 10^4 kg/ha dry biomass (50% carbon):

$$CO_2 \text{ fixed} = 18.4 \text{ tonnes } CO_2/\text{ha/year}$$

$$\text{Per tree (100/ha)} = 184 \text{ kg } CO_2/\text{year}.$$

Over 50 years, each tree accumulates ∼2.5 tonnes carbon, corresponding to ∼5 tonnes total dry biomass — consistent with mature forest measurements.

Elemental Mass Contribution

Typical dry mass composition:

Carbon: 45–50% (from atmospheric CO_2)

Oxygen: 40–45% (primarily from CO_2)

Hydrogen: ∼6% (from water)

Minerals: 1–5% (from soil: N, P, K, Ca, etc.)

References:

Farquhar, G. D., von Caemmerer, S., Berry, J. A. (1980). A biochemical model of photosynthetic CO_2 assimilation in C_3 leaves. *Planta*, **149**, 78–90.
Taiz, L., Zeiger, E. (2010). *Plant Physiology*.