Photosynthesis

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Part 1 Photosynthesis, energy and food chains

Photosynthesis is the process by which plants and algae use energy from sunlight to synthesize carbohydrates from carbon dioxide and water. All plants and animals as well as most microbes are dependent on the products of photosynthesis for their existence.

Photosynthesis is represented by the reaction:

carbon dioxide + water = carbohydrate + oxygen

$$CO_2 + H_2O = CH_2O + O_2$$

Photosynthesis takes place in very small particles in the plant cells called chloroplasts. The process consists of two distinct phases: a light phase and a dark phase.

In the light phase sunlight is absorbed by chlorophyll and converted into chemical energy and results in the formation of two energy carrier molecules which play an essential role in the dark phase. They are nicotinamide adenine dinucleotide phosphate (NADPH) and adenosine triphosphate (ATP).

Thus, the energy requirement of the reaction (480 kilojoules per mole of CO_2) is provided by sunlight.

In the second, dark phase NADPH and ATP provide the energy which is used for the synthesis of carbohydrate. Chlorophyll is not involved in this phase.

Energy Flow in Ecosystems

Energy rich solar radiation that would otherwise be transformed to low energy heat is diverted into the ‘steam of life’ by the process of photosynthesis. Energy flows through ecosystems from the green plants and algae, called *autotrophs* or producer organisms to *herbivores*, the primary consumers that use the autotrophs as their food source and then to *carnivores*, secondary consumers, as they eat the herbivores. Some organisms such as huans are *omnivores,* eating both plant products and animal products.

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Dr. Boardman was Chief Executive of CSIRO from 1985 until his retirement in 1990.
He is interested in the potential for renewable solar energy to provide a reasonable fraction of world energy usage. Other current interests include the impact of increased atmospheric carbon dioxide on plant production and the effect of climate change on ecosystems.

There is loss of energy and biomass as the energy passes from one organism to another. The energy stored in carbohydrate and other organic material consumed as food by an organism is used in respiration for growth or maintenance with the release of some low-grade heat to the environment. Organic matter is lost as excretory material or upon the death of an organism when there is decomposition by microorganisms, the *decomposers* of the ecosystem. Energy does not recycle and ultimately the fate of energy in the ecosystems is to be lost as heat. The flow of energy in an ecosystem is often portrayed as a food chain or food web.

Compared with trees and many other terrestrial plants, the autotrophs of the ocean, the phytoplankton, contain a very small amount of the total biomass of the ocean food chain because they are rapidly consumed by predators.

Primary Production

Trees and other terrestrial forms of vegetation with large surface areas of leaves are well designed for the collection of solar energy. About 45% of sunlight is at wavelengths that are absorbed by the photosynthetic pigments and under ideal greenhouse conditions about 9-10% of the solar radiation is fixed in carbohydrates and other plant organic compounds. Nearly 50% of the fixed carbon is lost by dark respiration at night and by photorespiration. The net maximum efficiency of photosynthesis under these ideal conditions is 5%-6 %, equivalent to a net primary production (NPP) of 5-6 x 10^{12} tonne of dry organic material.

A peak efficiency of solar energy conversion of 4.5% has been measured for sugar beet (a C3 plant) and maize (a C4 plant - see Part 2 below) grown for short periods in the field under optimal conditions. However, maximum growth rates of high yielding crops averaged over the usual period of growth represent an efficiency of solar energy conversion of 1%-2%. On a global scale, terrestrial photosynthesis is severely limited by availability of water and nutrients or by low temperature. Marine photosynthesis is limited by ocean nutrients. The oceans, in general, have very low levels of some of the minerals needed for plant growth, since the mineral-rich waters sink to the bottom of the ocean. Only where deep water currents rise as upwellings to the surface or where major rivers disgorge their contents into neighbouring seas do the vital nutrients reach a level sufficient to allow for high marine primary production. A satellite-based study of marine phytoplankton showed a decrease in global production of phytoplankton in years of higher ocean surface temperature. The reduction is attributed to a reduction in upwelling. Net primary production (NPP) overall in the marine environment is slightly less than NPP in the terrestrial environment.

The average photosynthetic efficiency on a global scale is approximately 0.2 %. This is equivalent to an annual global NPP of 250 Pg of organic material or 250 x 10^9 tonne. (one Pg equals 10^{15}g or 10^9t).

Food Chain

A food chain indicates the flow of energy from the producer autotrophs through the series of consumer organisms that feed on each other. Only a fraction of the energy in plants and algae is transferred to herbivores and only a fraction of the energy in herbivores is transferred to carnivores. As a rough estimate approximately ten percent of the biomass of one trophic level is transferred to the next higher trophic level. In agricultural systems there are large inputs of fertiliser and large outputs as agricultural produce is harvested. In terms of energy, agricultural systems increase the efficiency of solar energy conversion and increase the NPP for human consumption.

Appropriation of Net Primary Production (NPP) by Humans

The fraction of the Earth's NPP appropriated by humans is a measure of human impact on the biosphere.

In 1986, Vitousek *et al.* published estimates of the fraction of NPP appropriated by humans. Their estimates were the outcome of an extensive analysis of the data of many previous studies of land use and NPP. In their paper they provide three calculations of the human appropriation of NPP; a low calculation, an intermediate one and a high one.

The low calculation was simply the amount of organic material consumed by humans. Assuming an average calorific intake of 2500 kcal/person/day and a world population of 5 billion, the annual consumption of organic material by humans was calculated as 0.91 Pg. Plant products accounted for 0.76 Pg and animal products 0.15 Pg. The amount of agricultural plant products harvested for human consumption was 1.15 Pg indicating a loss of 0.39 Pg or 34% to pests or post-harvest spoilage. An estimate of consumption of plant products by livestock was equivalent to 2.2 Pg of dry organic material. This indicated an efficiency of 6.8% for conversion of plant material to human food. Total annual fish catch was 0.02 Pg. Although the consumption of fish by humans is a very small fraction of marine NPP some fisheries are under threat due to overfishing. It was estimated that humans use 2.2 Pg of wood (dry weight) from forests. In developed countries most of the wood is used for construction and as fibre for paper manufacture, whereas in developing countries firewood is the principle use.

Vitousek *et al.* estimated that humans use approximately 7.2Pg of organic material each year or about 3% of the annual global NPP.

For their intermediate calculation Vitousek *et al.* included the NPP of the Earth's croplands, estimated as15 Pg/yr and the NPP of land that had been converted during human history to human-controlled pastures and forest plantations. The NPP of the derived grazing land (9.8 Pg/yr) was estimated from the average productivity of the converted woodlands and grasslands. Plantation forests were estimated to add 1.6 Pg/yr to the NPP appropriated by humans. Yitousek *et al.* considered that all cropland NPP, derived grazing land NPP and plantation forest NPP was unavailable to the natural community and therefore co-opted by humans. The NPP consumed by livestock on natural grazing land (0.8Pg/yr) also represents NPP appropriated by humans. Fires caused by humans on natural grazing lands consume biomass estimated as 1.0 Pg/yr. The waste from the harvesting of forests for construction and fibre was estimated as 1.3 Pg/yr. A significant component of the intermediate calculation was the biomass (8.5 Pg/yr) that is destroyed by the clearing of forests, either for shifting cultivation or permanent forest clearing. Land under cities and highways represents an appropriation of 2.6 Pg of NPP.

From these calculations Yitousek *ei al.* estimated that humans co-opt 42.6 Pg of NPP each year, equivalent to approximately 19% of global NPP or 31% of terrestrial NPP.

The high calculation included both the NPP co-opted by humans and an estimate of the potential NPP that is lost as a consequence of the presence of humans on Earth. The high calculation suggests that humans appropriate nearly 40% of potential terrestrial NPP or 25% of global NPP.

The calculations of Vitousek *et al.* were based on data from small field studies made prior to 1986. In 2001, Rojstaczer *el al.* calculated human appropriation of the NPP from contemporary data, many of which were satellite based and collected at global and continental scales. Their mean estimate showed that humans appropriate 39 Pg/yr of organic material or 32% of their estimate of terrestrial NPP. This agrees remarkably well with the intermediate calculation of Vitousek *et al.*

Ecology of photosynthesis in sun and shade

Plants growing under a very low light intensity on the floor of a dense rain forest synthesise more antenna chlorophyll to improve the capture of available light quanta. They have less Rubisco (an essential enzyme involved in the synthesis of carbohydrate – see Part 2 below) than plants growing at high light intensity. Many plants have the ability to change their photosynthetic capacity (termed acclimation) depending on the light intensity under which they are growing. At high light intensity the plant invests more of its synthetic capacity to increase the amounts of Rubisco and the photosynthetic electron carriers in proportion to the amount of chlorophyll. The leaf morphology can change with an increase in the frequency of stomates for improved uptake of atmospheric CO_2. Plant species, however, differ markedly in the acclimation of their photosynthetic response to light intensity. Marine phytoplanton also have the ability to acclimate to light intensity.

Plants grown under high CO_2 concentrations show higher growth rates (termed CO_2 fertilisation). The increasing atmospheric concentration of CO_2 due to fossil fuel burning should have a beneficial effect on plant growth but the long term consequences of increased CO_2, coupled to rising temperatures on ecological plant communities are unknown. It is possible that some species of plants will acclimate to long term growth in high CO_2 by reducing the amount of Rubisco and the rate of plant growth.

Environmental factors such as temperature, light intensity, CO_2 concentration and water and nutrient availability will affect the photosynthetic process differently in different species to the advantage of some and the disadvantage of others with impacts on the ecology of plant communities.

Part 2 The process of photosynthesis in more detail

Light Phase

Higher plants and green algae contain two green pigments, chlorophyll a and chlorophyll b and yellow pigments, the carotenoids. The red and blue-green algae do not have chlorophyll b but they contain red and blue pigments called phycobilins.

The secret of the conversion of light energy to chemical energy in photosynthesis lies in the way the chlorophyll molecules are combined with proteins within small structures in the plant cell called chloroplasts.

Light and electron microscopy of higher plants show chloroplasts as saucer shaped bodies 5 to 10 um in diameter. Each chloroplast has an outer membrane or envelope and internally it contains a system of flattened membranes (thylakoids) arranged in stacks, known as grana. The grana are interconnected by a system of loosely arranged thylakoids. The chlorophyll molecules and the other components of the light phase of photosynthesis are combined with proteins within the thylakoid membranes.

Most of the chlorophyll a molecules as well as all of the chlorophyll b and the carotenoids are not involved directly in the photochemical reaction where light energy is converted to chemical energy. They function as an ‘antenna’ of light-harvesting pigments to absorb light quanta and transfer the energy to special chlorophyll a molecules where the light energy is converted to chemical energy. These light-harvesting chlorophylls are organised into units of about 200 molecules. Each unit, known as a photosynthetic unit, has one reaction centre chlorophyll a molecule which, on excitation, promotes an electron transfer and charge separation.

Two Photosystems

The light phase of photosynthesis requires the cooperation of two different chlorophyll assemblies and photochemical reactions, known as photosystem 1 (PS-1) and photosystem 2 (PS-2).

Photosystem 2 catalyses the photochemical splitting of water and the evolution of molecular oxygen to the atmosphere. Recent structure studies by Xray crystallography have illustrated a very complex structure for the organisation of the chlorophyll molecules and proteins in PS-2. The site for water splitting involves a cluster of four manganese ions and a calcium ion surrounded by the side chains of proteins. The details of the chemistry of the manganese cluster in water splitting has not been elucidated although it has been known for 30 years that there is an accumulation of four positive charges on the manganese cluster before a molecule on O_2 is produced. Excitation of chlorophyll a in the reaction centre of PS-2 by transfer of energy from the antenna chlorophylls of PS-2 produces a charge separation leading to the oxidation of water and the reduction of a quinone (plastoquinone) within the thyakoid membrane.

The production of NADPH and ATP that are needed for the conversion of carbon dioxide to carbohydrate requires additional energy from sunlight absorbed by PS-1.Photosystem 1 also has an antenna of chlorophyll molecules and its own special chlorophyll a in a reaction centre. Excitation of the reaction centre of PS-1 by energy transfer from antenna pigments produces a charge separation which results in the reoxidation of the plastoquinone that had been reduced by PS-2 and the reduction of nicotinamide adenine dinucleotide phosphate (NADP) to NADPH. Electron transfer between reduced plastoquinone and the reaction centre of PS-1 occurs via a chain of electron carriers within the thylakoid membrane. Electron flow through the carriers produces a hydrogen ion gradient (pH gradient) across the membrane resulting in the production of ATP from adenosine diphosphate (ADP) and inorganic phosphate.

Dark Phase

In the dark phase of photosynthesis NADPH and ATP are used for the production of carbohydrate and other carbon compounds from carbon dioxide. NADP and ADP are regenerated for activation again in the light phase. The pathway by which carbon dioxide is converted to glucose in the dark phase of photosynthesis was elucidated by Calvin and Benson in the 1950’s. The key enzyme in carbon dioxide fixation is Rubisco which catalyses the addition of carbon dioxide to a 5-carbon sugar, ribulose 1,5 bisphosphate. Rubisco is a large water soluble protein in the chloroplast that accounts for about 50% of the soluble proteins of the chloroplast and about 20% of all plant protein. It is the most important protein to life on earth..

Conversion of CO_2 to glucose in the Calvin-Benson pathway also involves a reduction phase that requires NADPH and a regeneration phase, requiring ATP, where ribulose 1,5 bisphosphate is regenerated to continue the fixation of CO_2. The Calvin- Benson cycle runs 6 times for the reduction of six molecules of carbon dioxide to glucose. Thirteen different enzymes are used to operate the Calvin-Benson cycle. For each molecule of carbon dioxide that is reduced to CH_2O, 3 molecules of ATP and 2 molecules of NADPH are required.

Carbon dioxide fixation into carbohydrate by the Calvin-Benson pathway is compromised by the competition between carbon dioxide and oxygen for the same reactive site on Rubisco. Competition with oxygen not only reduces the efficiency of Rubisco for fixing carbon dioxide but reaction of Rubisco with oxygen causes the breakdown of carbon compounds by ‘photorespiration’ and a loss of carbon dioxide. The relative rates of reaction of Rubisco with CO_2 and O_2 depends on the relative concentrations of CO_2 and O_2 at the site of the reaction in the chloroplast. Rubisco much prefers CO_2 but the concentration of CO_2 is much lower than the oxygen concentration.

Atmospheric carbon dioxide enters the leaf of a higher plant through small pores, called stomates on the leaf surface. Each stomate is surrounded by two guard cells and can be opened or closed by movements of the guard cells. On a hot dry day the stomates are closed to inhibit the loss of water vapour from the leaf and in so doing the entry of CO_2 to the leaf is inhibited. The concentration of CO_2 at the site of Rubisco declines, thus reducing the rate of photosynthesis but increasing the rate of photorespiration.

C4 Plants

Many tropical plants such as sugar cane and maize have evolved variations of the Calvin-Benson pathway for CO_2 fixation that gives them an advantage in hot dry conditions. They are known as C4 Plants because CO_2 is initially fixed into 4-carbon compounds. Most plants only have the Calvin-Benson pathway and are known as C3 plants. The worst weeds are C4 plants.

C4 plants have developed a different leaf anatomy. The vascular tissue is surrounded by two concentric layers of cells, an inner layer of bundle sheath cells and an outer layer of mesophyll cells. C4 plants have two types of chloroplasts located in the mesophyll and bundle sheath cells. The mesophyll cells which are close to the leaf surfaces fix carbon dioxide into 4- carbon compounds. For example, one of the 4-carbon compounds formed in the mesophyll cells is malate which then is transported to the chloroplasts of the bundle sheath cells. An enzyme in the bundle sheath cells releases CO_2 from malate for re-fixation into carbohydrate by Rubisco and the Calvin-Benson cycle enzymes which are located in the bundle sheath chloroplasts. Release of CO_2 from malate produces a higher concentration of CO_2 in the bundle sheath cells of C4 plants than the concentration found in the mesophyll cells of C3 plants. The C4 pathway of photosynthesis was elucidated by Hatch and Slack at the laboratories of CSR in Brisbane, Australia.

C4 plants have higher rates of photosynthesis than C3 plants at high light intensities and high temperatures and lower rates of photorespiration, due to the higher concentration of CO_2 relative to oxygen in bundle sheath cells. C4 plants have better water efficiency because their stomates are less open than for C3 plants.

A variant of the C4 pathway is found in several desert plant families such as the Cactaceae. It is called crassulacean acid metabolism (CAM) because it was first studied in the family Crassulaceae. The leaf stomates are closed during the day and open at night when water transporation rates are lower. CO_2 is taken in at night and fixed into malate and other C4 compounds. During the day CO_2 is released from malate within the plant and refixed by Rubisco by the Calvin-Benson pathway. Unlike C4 plants, CAM plants do not segregate the C4 and C3 pathways in different parts of the leaf.

Peter Vitousek, Paul R. Ehrlich, Anne H. Ehrlich and Pamela Matson (1986)

BioScience, Vol. 36, No. 6, pp. 368-373. *Human appropriation of the products of photosynthesis*

Stuart Rojstaczer, Shannon M. Sterling and Nathan J. Moore (2001)

Science Vol. 294, No. 5551, pp. 2549-2552. *Human appropriation of photosynthetic products*

Glossary

autotroph – an organism that makes its own food.

ADP – a diphosphate of adenosine.

ATP – the triphosphate of adenosine that stores chemical energy in cells.

bundle sheath cells – a layer of cells that surround the vascular bundle in C4 plants.

Calvin-Benson cycle – a sequence of 13 proteins that convert CO_2 to sugar.

CAM – crassulation acid metabolism – a variant of C4 in some desert plants.

carotenoids – yellow carotene-related compounds.

chlorophyll a – the principal green pigment in leaves.

chlorophyll b – a green pigment slightly different chemically from chlorophyll a.

chloroplast – a small particle within a leaf cell and the site of photosynthesis.

C3 plant – a plant that has the Calvin-Benson cycle to convert CO_2 to sugar.

C4 plant – a plant that first converts CO_2 to compounds with 4 carbon atoms.

electron carriers – organic molecules containing iron or copper that transfer electrons.

guard cells – cells that cause the opening and closing of stomates.

mesophyll cells – a layer of cells close to the surface of a leaf.

Pg – pegagram equal to 10^{15}gram or 10^{9}metric tonne.

photorespiration – oxidation of organic molecules driven by light in photosynthesis.

photosystem 1(PS-1) – chlorophyll-protein complex that reduces NADP.

photosystem 2(PS-2) – chlorophyll-protein complex that splits water molecules.

phycobilin – a pigment in red and blue algae.

phytoplankton – marine algae(microscopic plants).

plastoquinone – a lipid-like quinone molecule.

rubisco – ribulose bisphosphate carboxylase, the catalyst for the fixation of CO_2.

stomata – a small opening in the surface of a leaf.

thylakoid – an internal membrane of the chloroplast.