REVIEW

Oxygenic photosynthesis—a photon driven hydrogen generator—the energetic/entropic basis of life

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Abstract

Photosynthesis, as a fundamental element in the life process, is integrated in the evolution of living systems on the basis of hydrogen cycles on various hierarchic levels. Conversion of radiant energy enables the oxidation of water, whereby free oxygen accumulates in the atmosphere. Hydrogen is (reversibly) stored in organic materials formed under reductive CO_2-fixation and by the incorporation of the other elements, which are necessary for living systems. All endergonic processes in living cells are finally driven by the energy released through the clean recombination of protons and electrons with oxygen to water. Duration of the stored energy and the complexity of the systems thus produced is correlated negatively with the conversion efficiency of the radiation energy. Entropy is a unifying principle in the evolution of living systems, inclusive human societies.

Additional key words: evolution; hydrogen; life; photosynthesis; radiant energy.

Basic forces and laws in nature

The current physical state of our galaxy in the universe is determined by the "evolution" of hydrogen. Calculations tell us that roughly 75-84 % of atoms in the cosmos are hydrogen. Only about 16-25 % are converted to helium and about 1 % amounts to heavier elements (Ditfurth 1972, Ebeling and Feistel 1994, Vaas 1994, Holzmüller 1995). In our galaxy, these nuclear fusions take place in the sun where (according to the Einstein law, $E = m c^2$) 4.3×10^9 kg hydrogen per s are transformed

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to helium while the mass difference is radiated in the form of 5 800 K photons. This radiation reaches our planet with an energy of 1 353 kW m^{-2} (290-4000 nm; solar constant). In comparison with the other cosmic forces (Fig. 1) this electromagnetic radiation is characterized by what may be called a dialectical unity of energy and information (Rompe and Treder 1988). This has led to attempts to construct a unified field theory on the basis of electromagnetic radiation. The dual aspects of light, that

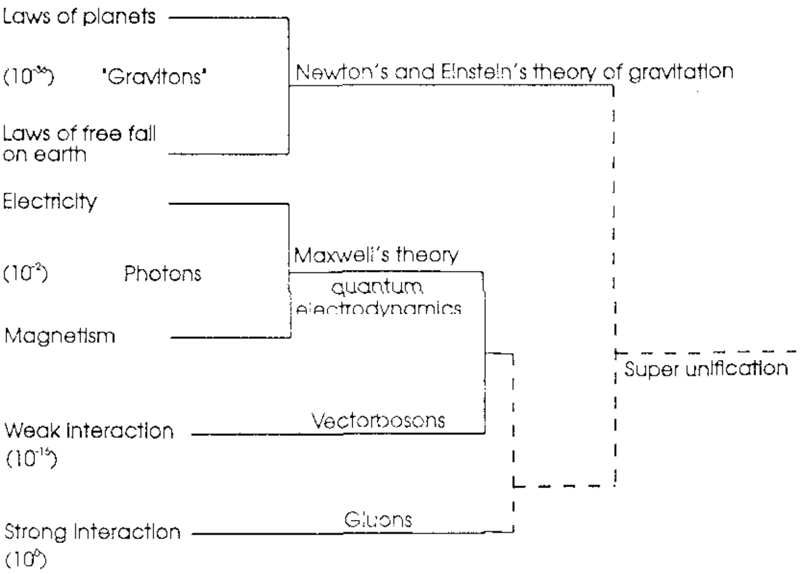

Fig. 1. Scheme of cosmic forces and their interrelations (according to Mainzer 1994).

is, energy and information (the complementary principle, Bohr 1933, Ebeling and Feistel 1994)—which is valid under the condition that there are receptors capable of recognizing this information and of transmitting it to the whole system so that the system may respond adequately—provides a basis for the evolution of living systems on the Earth (Stahl 1993). Given, however, that life is a potential of matter throughout the universe, it may be that in other galaxies living systems had developed on the basis of other elementary particles or may do so in the future (Stöltzner and Thirring 1994, Holzmüller 1995). The transformation of this cosmic radiation flow to drive matter cycles enabling the formation of structures with increasing complexity and negentropy is primarily realized through processes organized in the photosynthetic apparatus. This machinery, hierarchically and symbiogenetically integrated (in both time and structure; Schwemmler 1991, Tiezzi and Marchettini 1991) in the bioenergetics of the whole biosphere, realizes the following principles:

Harvest and accumulation of sufficient energy amount for conversion into biologically meaningful forms of different lifetimes.

Ensurance of cooperation between reversible and highly irreversible reactions (like photosynthetic water oxidation and reductive CO_2 fixation), and thus supplying evolution with a directional component.
Dissipative mechanisms of hierarchic levels (among others, from fluorescence quenching mechanisms in the chloroplast thylakoids to substance excretion *via* leaves or roots and different apoptotic phenomena) to avoid overreductions of the primary electron acceptors by the high natural photon pressure (thus underlining the general sink limitation of physiological processes due to the huge solar photon source).
Development of adaptive and defence systems to maintain the homeostasis/homeorhesis of the whole system as long as possible (bioenergetic coupling of biogenesis, development, senescence, and death with reproduction ensuring the continuity of life; ontogeny and phylogeny), including mechanisms for evolutionary progress.
Last but not least, life acts in two directions: it develops different strategies adapting to the changing exogenous conditions (like C_4 and CAM, symbiotic relations, morphological changes of hygro-, meso-, and xerophytes, *etc.*), but it also changes the environment (producing soil, mineral content in the ocean, oxygen containing atmosphere, *etc.*: cf. also Lovelock 1992, Holzmüller 1995).

This concept is supported, against the background of hydrogen priority, by the fact that the proton-electron system enables the stability of matter (Lieb 1991, Stöltzner and Thirring 1994). The structure of all beings obey the fundamental natural law of harmony, realized in the galaxy as well as in organisms or parts of them (Francé 1926, Ebeling and Feistel 1994).

Photosynthesis—a photon driven hydrogen generator

The primary reactions of photosynthetic energy absorption occur in the light-harvesting antenna systems (Kühlbrandt *et al.* 1994) including cooperative, non-linear mechanisms, as is the case with all fundamental processes (Ebeling and Feistel 1986, 1994, Hoffmann and Leupold 1991, Hess 1994, Mainzer 1994, Kelso and Haken 1995). Already on this level, multiple paths are possible for adapting the incoming photon amount to the need determined by the endergonic and exergonic conditions. So besides the channeling towards reaction centres (Deisenhofer and Norris 1993) leading to charge separation, more and more possibilities are discovered for dissipating the photon excess (different fluorescence quenching processes, including xanthophyll cycle, and induction of defense systems that eliminate the resulting reactive oxygen species - Foyer and Mullineaux 1994, Angerhofer and Bittl 1996, Horton *et al.* 1996). After charge separation in the reaction centres, water oxidation occurs and photosynthetic electron transport over the thylakoid membrane creates an electrical potential, combined with a proton gradient (Witt 1987, 1996, van Voorthuysen 1997). The energy stored on this level is consumed in manyfold ways, predominantly, however, used for ATP production, directly by photophosphorylation. The protons and electrons resulting from the photosynthetic water oxidation are bound by the universal hydrogen carrier $NADP^+$. In contrast to these anabolic sequences, in catabolic metabolism unphosphorylated pyridine nucleotides are used, thus reaching a high independence of energy accumulation from RNA turnover (Kaufman 1993). Due to conversion reactions and shuttle mechanisms, the reduced pyridine nucleotides reach into the nonplastidic part of the cell, and are available there for many purposes. Predominantly they are used in mitochondria for respiratory ATP production (for references see Hoffmann 1987, Kitzmann 1996). In any case, the "universal fuel", hydrogen, is cleanly recombined with the photosynthetically evolved oxygen to the "molecule of life", to water [hydrogen cycle between chloroplasts and mitochondria; (1) in Fig. 3].

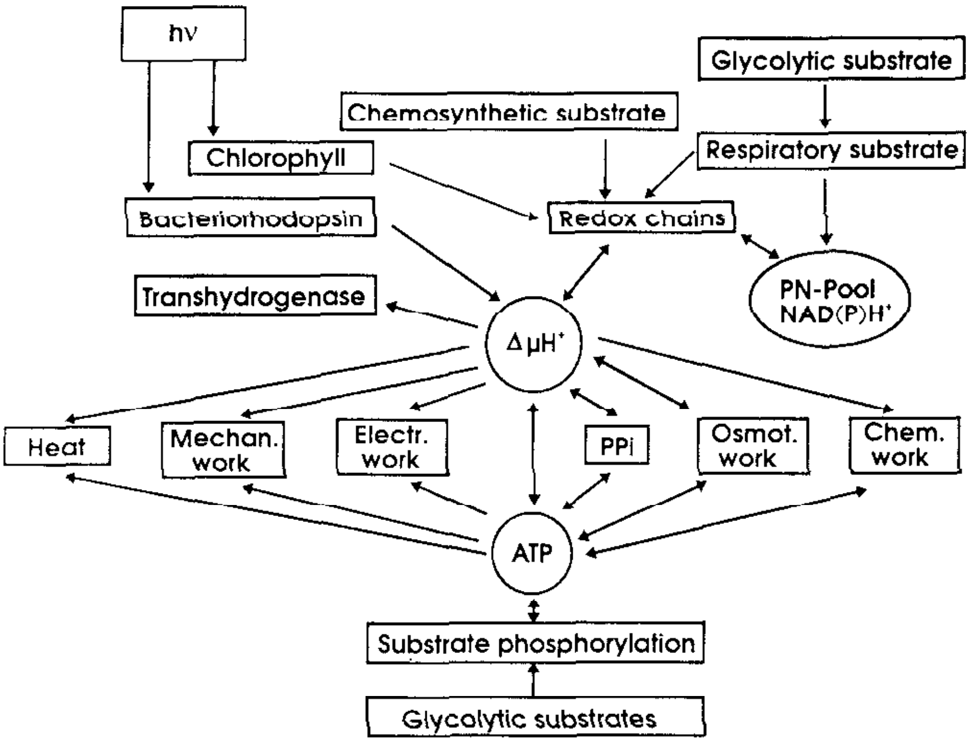

Fig. 2. The complex network of bioenergetics in living cells, unified by the membrane bound proton gradient. The scheme underlines the basic role of radiant energy in creating this gradient. All other sources depend on substrates produced by photosynthesis (modified according to Skulachev 1977, Ernster 1992, Kitzmann 1996).

The replacement of the early archebacteria photosynthesis (due to conformation changes of rhodopsin; Danon and Caplan 1977, Caplan and Ginzburg 1978, Mohr and Schopfer 1992) by light driven redox processes in the more complex (two photosystems) oxygenic photosynthesis (Goldworthy 1987) made the unlimited amounts of hydrogen in the water accessible by making use of the redox-couple H_2O/O_2. The onsetting oxygen accumulation in the atmosphere—noteworthy stabilizing at about 21 %—created the oxidant for extensive supply of free energy from metabolizable substances as another precondition for the evolution of highly organized complex biological systems (Riedl 1973, Kuhn and Waser 1982, Renger 1987, Grassmann 1988, Haken 1988, Rensch 1988, Holzmüller 1995).

The central function of proton pumps in both ATP-producing systems (photosynthesis and respiration, Fig. 2) is a convincing example for unity in the diversity of phenomena in nature (Hoffmann 1978, 1990, 1991, Stryer 1995).

Hydrogen not immediately needed to maintain cell homeostasis (Langley 1973, Atkinson and Bourke 1995) is reversible, and for a longer time-period stored on carbon dioxide *via* the Calvin cycle. The unique property of carbon (something similar is valid also for nitrogen) to form long branched chains (which provides, besides the reversible hydrogen/energy storage, also the means for storing information) explains the employment of these elements as material basis of living systems (Laskowski and Pohlit 1974, Holzmüller 1995). Continuing compartmentations of the hydrogen cycle in cormophytes are *via* assimilates [distributed morphologically between shoot and root, and temporally between day and night; (2) in Fig. 3]. Besides the fairly high reversibility of enzymatic reactions, the key enzymes of this hydrogen generator (water oxidizing enzyme, ribulose 1,5-bisphosphate carboxylase/oxygenase, cytochrome *c* oxidase) are characterized by a high irreversibility. So a trend-setting in the evolutionary dimension is favoured also by this behaviour.

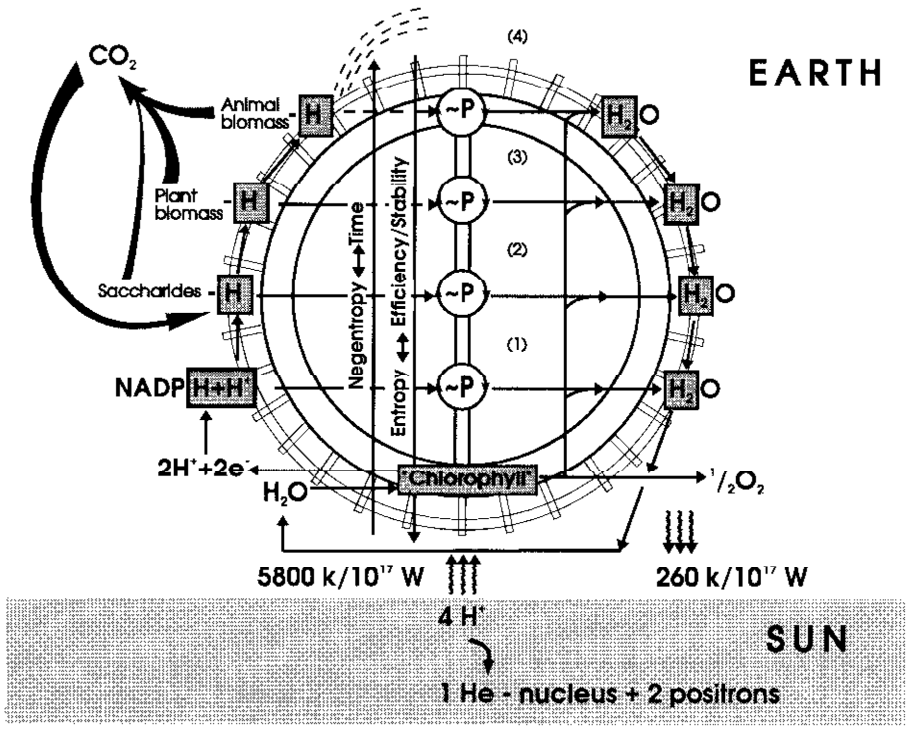

Fig. 3. Integration of photosynthesis as photon driven hydrogen generator on increasing system levels in ontogeny as well as phylogeny of living systems. Explanation in the text.

The spectrum of dissipative mechanisms on the cellular level includes ways of wasteful ATP- and $NADPH_2$-degradation (Heldt 1996), Mehler reaction (Polle 1996), and photorespiration (Heber *et al.* 1996). In the complex system of whole plant, there exist, in addition to the mechanisms noted already, various further regulatory principles (like root-shoot ratio, root excudates, Reining *et al.* 1995; secondary metabolism and isopren or allelopatica emissions, Hansen and Seufert 1997, Hansen *et al.* 1997; apoptotic mechanisms, Havel and Durzan 1996).

The following hierarchic level of the hydrogen cycle is realized with respect to biomass of plants and animals, and to their decomposition [(3/4) in Fig. 3]. While the time constants of absorption of radiant energy in the photosynthetic antenna are around ps, the stepwise charge separation needs ps to ns, and the electron transfer occurs in the ns to ms range (Dau 1994, Ebeling *et al.* 1994, van Grondelle *et al.* 1994). Enzymatic reactions last up to a few seconds, the biomass production requires minutes, and growth lasts (depending on species) up to years. This underlines, among other things, the importance of time constants in the regulation of hierarchic structures (Schuster and Heinrich 1987, Tiezzi and Marchettini 1991, 1992, Heinrich and Schuster 1996).

With increasing duration of storage of the radiation energy fixed by photosynthetic charge separation on different hierarchic levels in the photosynthetic system (Fig. 3), the efficiency of energy conversion decreases. The complexity and negentropy, however, increase. While the conversion yield in the reaction centre is nearly 100 %*, we find in saccharides only 5-10 % of the energy absorbed. The efficiency of biomass production in cultural plants is around 3 %, and calculated on the planetary basis, the annually formed plant biomass contains only about 0.11 % of the incoming radiation energy (for references see Wiedenroth 1981, Hoffmann 1987). Nevertheless, the energetic potential annually captured in biomass is 10-40 times higher than the primary energy used in human society per year (Hoffmann 1977, Ebeling and Feistel 1994). In this basic process, high efficiency in sensitive structures (like reaction centres) correlates with a decreasing yield in more stable systems (saccharides, biomass, organisms, populations). In living nature, mechanisms were evolved to reduce this decrease of efficiency (loss terms). Conversely, these loss terms compete in a sophisticated way with the processes enabling loss terms as "price" for the system maintenance under varying exogenous and endogenous conditions.

The elimination of loss terms (for example by breeding) increases the sensitivity of a cultivar, which requires special assistance (irrigation, fertilizers, pesticides, *etc.*; *e.g.*, compare growth of *Triticum aestivum* L. with that of *Agropyron repens* L.) and is, in a long time scale, ecologically as well as economically mistaken. In other words: the accumulation of endogenous reserves according to the overflow concept (Lambers 1983) or the redundance hypothesis (Lawton and Brown 1993) or to apoptotic capacity (from cells to tissues and organs, like leaf or early fruitfall, Havel and Durzan 1996) is an important factor for the system maintainance.

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*Radiation energy is always accompanied by entropy, thus it cannot be completely converted into other forms of energy (Kabelac and Drake 1992).

Light and life

The summarizing scheme (Fig. 3) shows the integration of photosynthesis in the cosmic energy/entropy flow. Entropy is also a measure of complexity (Chapman 1988, Peliti and Vulpani 1988, Ebeling and Feistel 1986, 1994, Leuschner 1989, Prigogine 1989, Stahl 1993, Schneider and Kay 1995), and the continuous decrease of entropy (accumulation of negentropy) by the irreversible conversion of free energy provides the thermodynamic basis of life (Harold 1986, Leuschner 1989, Tiezzi and Marchettini 1992, Ebeling and Feistel 1994). Contrary, Klippel and Müller (1997) and Klippel (1997) argue that photosynthesis and transpiration must proceed in the presence of excess air, more than is needed for bringing the necessary CO_2 to the plant. In this manner the transpired water finds enough air to create a sufficiently big entropy of mixing to offset the entropy decrease of the reaction [$CO_2 + H_2O = {}^1/_6\ C_6H_{12}O_6 + O_2$]. According to this idea, light ensures only the energetic part. In this hypothesis, however, photosynthesis is exclusively identified with glucose synthesis, and all other energetically important cumulative and dissipative basic mechanisms are neglected.

As Fig. 3 also makes clear, the CO_2 and O_2-cycles are in the final analysis attributes of the "hydrogen evolution". Over a long-time scale, however, these cycles were not always closed. So the retardation of degradation of organic carbon compounds gave rise to coal, oil, and gas accumulation in the earth as well as to the oxygen enrichment in the atmosphere (Lovelock 1992, Holzmüller 1995). More or less the same is valid for the nitrogen cycle. The energy loss terms on the different system levels as well as the combustion heat leave the earth in form of 360 K radiation (photons). Because of the expansion of the universe in the present phase, the entropy dust is diluted (Ebeling and Feistel 1986, 1994, Stahl 1993). So by the photon driven photosynthetic hydrogen generator (confined to the earth) the evolution of living structures (increase of negentropy) at the expense of increasing entropy in the earth's surrounding is thermodynamically in balance—according to Schrödinger's premise of order from disorder (Schneider and Kay 1995). The causal connection between photosynthetic radiation conversion and life-enabeling negentropy-accumulation was characterized already by Boltzmann 1905 (p. 40) by the following (translated):

"The general struggle for existence among living beings is therefore not a struggle for elementaly resources—these elementary resources are superabundantly present in the atmosphere, water, and soil—neither for energy which is abundantly present, though unfortunately inconvertible, in every body, but is a struggle for entropy which becomes available as a result of the transference of energy from the hot sun to cold earth. To make best use of this transference, the plants unfold their immense wealth of leaves and enforce the sun's energy in as yet unknown ways, before deteriorating to the earth's temperature level, to carry out chemical syntheses, of which our laboratories are as yet ignorant. The products of this chemical brewery form the object of struggle for the animal world."

Under the aspect of the unity of the world, also the evolution of mind and even of humanities (animal-man-brain-thinking-*etc.*) may be integrated in the course of hydrogen evolution, in our connection basically mediated by the apparatus enabling oxygenic photosynthesis [(4) in Fig. 3; Riedl 1973, Broda 1975, Bresch 1977, Unsöld 1983, Gierer 1986, Mlikovsky and Novák 1987, Grassmann 1988, Haken 1988, Hoffmann 1990, 1991, Stahl 1993, Ebeling and Feistel 1994, Mainzer 1994, Kelso and Haken 1995). These developments take place non-linearly, and are in possession of the capacity for oscillatoric and chaotic behaviour, including all the consequences connected with it (Pool 1989, Hastings *et al.* 1993, Hess 1994, Heinrich and Schuster 1996).

From the energetic point of view, oxygenic photosynthesis effects a decrease of the velocity in cosmic energy flow thus producing stable structures at the expense of efficiency. The photosynthetic apparatus, spread over our planet, is to be understood like a "water mill", scooping hydrogen from the water by means of radiation energy, lifting it on increasing levels of complexity, driven by the solar photon flow in ways in which the atmosphere and biosphere begin representing a self-regulating system which finally comprises the whole earth (acting like a superorganism: Gaia-Hypothesis, Lovelock 1992).

Human society during the industrial revolution, starting with the invention of the steam engine, has practically connected an electric motor with this "water mill", thereby increasing the velocity of energy flow in order to enlarge efficiency, with the consequences of increasing destabilization of the biosphere in all its parts. By the development of worldwide gigabyte multimedia networks whole mankind acts nearly synchronously like a "superman", thus increasing the velocity of the so-called progress in orders of magnitude (Markl 1996). But the discussion of these antagonisms between the evolution in nature and the development of societies (Riedl 1973, Hoffmann 1990, 1991, Stahl 1993, Ebeling and Feistel 1994, Markl 1996) cannot be the topic of this review.

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