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Photosynthetic Reaction Centres – from Basic Research to Application Possibilities

László NAGY[1)], Kata HAJDU[1)], Béla FISHER[1)], Klára HERNÁDI[2)]
Krisztina NAGY[3)], János VINCZE[4)]

[1)] *University of Szeged, Department of Medical Physics and Biophysics, Szeged, Rerrich B. tér 1., Hungary; lnagy@sol.cc.u-szeged.hu (corresponding author)*

[2)] *University of Szeged, Department of Applied and Environmental Chemistry, Szeged, Rerrich B. tér 1., Hungary*

[3)] *Institute of Biophysics, Biological Research Centre, Hungarian Academy of Sciences, Szeged, Temesvári krt. 62, Hungary*

[4)] *Human Health Environment International Foundation, 1476 Budapest Pf. 240, Hungary*

Abstract

There is no doubt that studying the photosynthetic conversion of light into chemical energy is extremely important in many points of view: 1) technical-in order to improve the utilization of the solar energy; 2) food production – to improve the photosynthetic production of plants in agriculture; 3) ecology – keeping the primer production in ecosystems in the biosphere balanced, etc. In the photosynthetic reaction centre protein, RC, light energy is converted by a quantum yield of almost unity. There is no such a system designed by human which is able to do that. The RC purified from purple bacteria provides an extremely unique system for studying the requirements for high efficiency conversion of light into electrochemical energy. Thanks to the recent structural (e.g. crystallography (Nobel prize to Michel, Deisenhofer, Huber) and functional (Nobel prize to Marcus)) results together with the works of molecular biology, computer- and electro-techniques, a wealth of information made a relatively clear picture about the kinetics, energetics and stabilization of electron transport within this protein that opens possibilities for new generation practical applications. In this paper we provide a short summary of fields in which the reaction centre protein can be important from practical points of view.

Keywords: photosynthesis, reaction centres, solar energy, charge separation

Abbreviations:
AFM, Atomic Force Microscopy; Blc., Blastochloris; BPh, bacteriopheophytin; DEAE, Diethylaminoethyl; LDAO, N,N-dimethyldodecylamine-N-oxide; MQ, menaquinone; P, primary donor; Q_A, primary quinone; Q_B, secondary quinone; Rb., *Rhodobacter*; RC, photosynthetic reaction centre; Tc., Thermochromatium; T., Thiocapsa; UQ-10, ubiquinone-10.

Introduction

It would be hard to confute that the photosynthetic conversion of solar energy into chemical energy is one of the most important processes on Earth. The evolution of present form of life and even the huge (but not inexhaustible) amount of the fossil fuels are thanks to the solar energy. There are more and more evidences for scientists, outsiders can feel more and more that the exhaustion of the energy sources can really change our life, perhaps in the very close future. Any use of the solar energy can be very important.

The photosynthetic reaction centre (RC) is one of the most important proteins, if not the most important one, as during the harness of the light energy the first steps take place in it. In the conversion of light into chemical energy in the RC the first step is the formation of chemical potential of charge pair, which is the condition of creating transmembrane chemical potential of the hydrogen ions. This state ensures the free energy for the energy consuming processes on every level of living beings – from the cell organelles to the biosphere (Mitchell – chemiosmotic theory, Mitchell, 1961).

It is thought-provoking that even though the reaction centre protein – called the „nature's solar power stations" or „nature's solar comb" too – ensures the energy for the whole earthly life, including the fossil fuels, its size represents only nanometers in the cells (about 10 nm, Fig. 1, Dorogi *et al.,* 2006) and it works only in nano-efficiency (one photon initiates one charge separation, Wraight and Clayton, 1974).

On Fig. 2 the reaction centre is signed with the ellipsoidal scheme pillowing into a lipid bilayer, to picture its most important functions. After the excitation by light, electrons are pumped across the membrane, making a very

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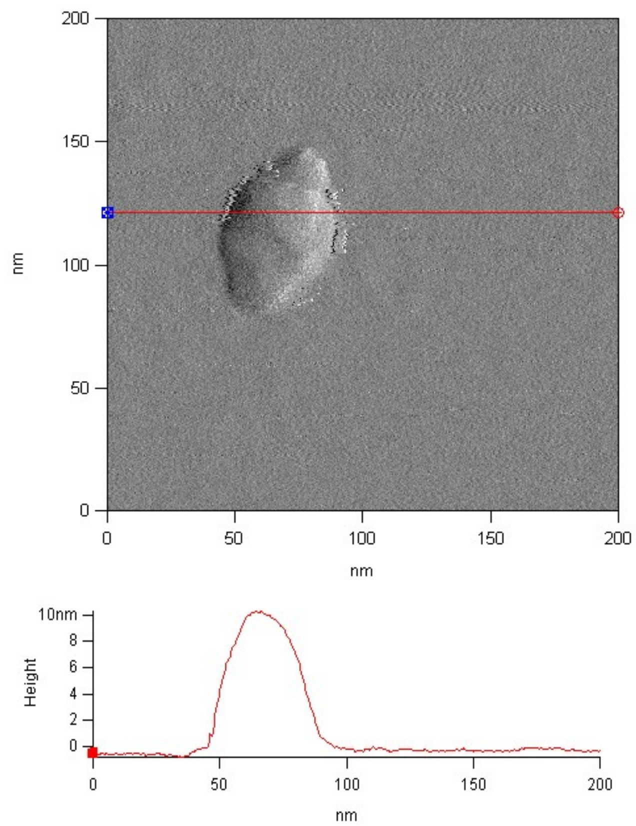


Fig. 1. AFM amplitude image and height section (along the line) of photosynthetic reaction centres purified from *Rb. sphaeroides* R-26. The average height of the RC is 10±2 nm

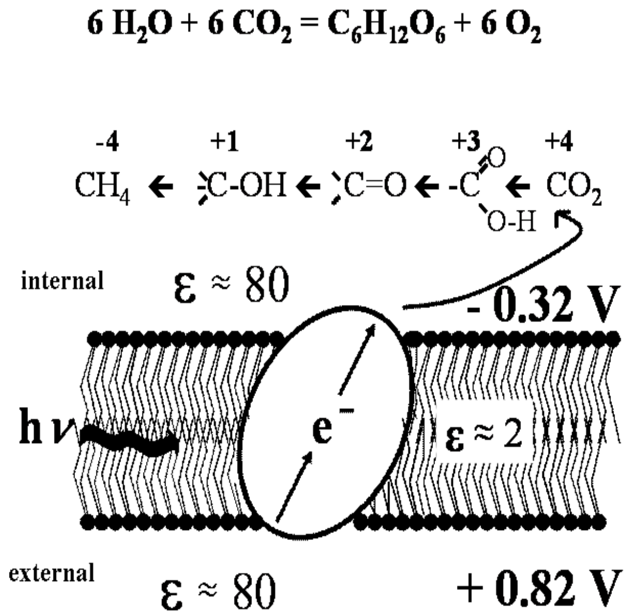


Fig. 2. The role of the reaction centre protein in the charge separation and stabilization processes in the photosynthetic membrane. The free energy of light is used to drive an electron across the membrane in order to create a high reducing power for carbon reduction

strong reducing power what is necessary to reduce the carbon.

The free energy of light ensures:

1. on one hand, the electron transport to a lower potential place where the redox potential is more negative. This process does not work spontaneously, it needs free energy that is provided by the light.

2. on the other hand, the electron transport over the lipid bilayer. Both sides of the membrane have aqueous phase where the dielectric constant is about $\varepsilon \approx 80$. Within the membrane the commonly used value is about $\varepsilon \approx 2$. It is a considerable amount of energy gap for the charged particles, even for the electrons. It can be calculated that these conditions mean a very high, about 170 kJ/mol energy claim for the electron transport over the membrane. For comparison, about 2.5 kJ/mol energy of the thermal motion would not be enough for the electron to get over the membrane. So living beings are really concerned about reducing the free energy needs of the process. It can be solved with the help of the reaction centre's proteins.

During the evolution several proteins have been evolved, that attend basically the functions mentioned above, so they move the electrons from the higher potential place to the lower one over a membrane that has small dielectric constant. The distribution of these proteins is very characteristic to the photosynthetic organisms (like plants, cyanobacteria, photosynthetic bacteria). The detailed characterization of the RCs can not be our aim in this paper, just we would like to show that although there are significant differences between the structure and the function of these proteins, the following processes are performed in all cases.

- *Electron excitation:* light excites a chlorine type pigment that is specially connected to the protein. An electron is excited from the highest occupied molecular orbital (HOMO) to one of the unoccupied orbitals (usually to the lowest unoccupied molecular orbital, LUMO).

- After the excitation the next step is the charge separation inside the protein.

- The primer charge-pair is stabilized by consecutive redox processes, still inside the protein.

- The charge separation and stabilization is connected to protonation and deprotonation of specific amino acids.

- The charge movements are accompanied by conformation changes of the amino acids and the realignment of the hydrogen bonding network.

The importance of the research on the reaction centre protein

While these basic processes take place in every type of reaction centre, the entity of the differences lies in the way of how the energetic and structural requirements are insured. The researches are focusing at only these differences and analogies. It is very important to consider the undermentioned viewpoints (Nagy *et al.,* 2009):

1) *Academic importance:* even now the photosynthetic reaction centre is one of the most studied proteins. As its structure can be described by atomic resolution, it is the best model of several processes, as the protein dynamics, the kinetics and thermodynamics of the primary photochemistry, and the electron transport inside the protein.

2) *Technical importance:* the most significant that we should emphasize is, of course, the exploitation of solar energy, but nowadays researchers turn to other possibilities as well. A promising way is to use RCs in nanosystems for example as circuit part in integrated optoelectronical devices or in imaging technologies.

3) *Importance in agriculture*: the elemental task of the agriculture is to appease the comestible demand of humanity. For this the primary production of plants is a special importance. Every intention, willing to increase harnessing the solar energy and to raise the primary production, deserves attention.

4) *Ecological importance:* It is enough to think of the fact that this protein ensures the energy input for the entire planetary ecosystem. More and more attention is paid also to the research about the use of photosynthetic microorganisms (bacteria) during the removal of dangerous substrates-like heavy metals-from the environment.

Thereinafter these emphasized points will be detailed even though there is no chance for us to exhaust this theme here.

Rc is an excellent model protein

What do we need to explore the structure, the working and the biological function of a protein? Of course, the first is to be able to purify the protein retaining its biological activity, than to be able to monitor its structure and working with the most appropriate and up-to-date methods. In the case of the photosynthetic reaction centre these expectations are largely realized. We have to admit that this statement does not hold for RCs prepared from every photosynthetic organism until now. For example the authors of this article are also trying to purify protein from special organisms and the task looks not so easy. The basic model organisms of the reaction centre researches are the *Rhodobacter sphaeroides* and the *Blastochloris* (formerly *Rhodopseudomonas*) *viridis* purple bacteria. First time-in the 60's-the reaction centres could only be retrieved from these organisms. Nowadays the number of the used photosynthetic bacterial species for RC purification increased, moreover even the plant and cyanobacterial first (PS-I) and second (PS-II) photochemical system have been available for a long time. So it is visible that there are methods to isolate and purify membrane protein keeping its function.

This exercise is not so easy in the case of the membrane protein, as the membrane protein has to be crystallized what means an extra challenge. For the first crystallization of *Blastochloris viridis* RCs and its crystallographic description by atomic resolution a Nobel-price was given to Michel, Huber and Deisenhofer in 1988. The first crystal structure was followed by more and more ones, and there are more than 150 RC crystal structures deposited in the Brookhaven protein data bank. However, the accessible atomic resolution of structures is available only from three bacterial species (*Rhodobacter sphaeroides*, *Blastochloris viridis*, and *Thermochromatium tepidum)* up to now (e.g. Allen *et al.,* 1988; Deisenhofer *et al.,* 1985; Fathir *et al.,* 2001). Though it is not always public, the authors have the information that there are experiments with other species (popular like the *Rhodobacter capsulatus*) but this scheme seems to be as a big and hard exercise as there have been no successful results for a long time. However, it is interesting that there is a well resolved crystal structure from the plant's first (Kruip *et al.*, 1993) and second photochemical system (Ferreira *et al.,* 2004).

The knowledge of the atomic coordinations means that the distances between certain atoms and groups are countable. As an example, we present here the model of RCs of *Rhodobacter sphaeroides* (Fig. 3). Not only the positions of different atoms, but the motions inside the protein can be determined and they are more or less foreseeable, within obvious limitations of course. This fact deserved a new Nobel-price for the development of the model of high distance electron transfer inside the proteins (Marcus, 1993).

In the case of the reaction centre protein the fortunate encounter of a lot of features insure that the sophisticated methods can be used and the given results can be united. Apart from the crystallography (even in big time-resolution; Baxter *et al.,* 2004) a wide array of the FTIR spectroscopy (e.g. Breton, 2007) is available to analyze the protein conformation. The non-protein cofactors are redox active pigments, so that a number of absorption and resonance spectroscopy was applied. As there are charge-movements inside the protein, electrical methods can be used as well. The electron transport is accompanied by conformational movements, i.e. rearrangements of the amino acid side chains and the hydrogen bonding network inside the protein. The conformation movements allow us to use photo thermal phenomena, like photacoustic (Edens *et al.,* 1999; Nagy *et al.,* 2001), or transient grating (Nagy *et al.,* 2008; Ohmori *et al.,* 2008) measurements. Computer science develops faster and faster providing more and more memory and speed and in this way the presentation of these big proteins is also more widespread and precise (Grafton and Wheeler, 1999; Rabenstein, 1998).

Subsequently, it is hard to decide if there is a method that has not been used during the observation of the reaction centre protein, taking part in the information bomb around this field in the last 1-2 decades.

Technical importance

In this respect the conversion of solar energy into other energy types-to store and use for human seems to be obvious. Without the work of the only few nanometers sized

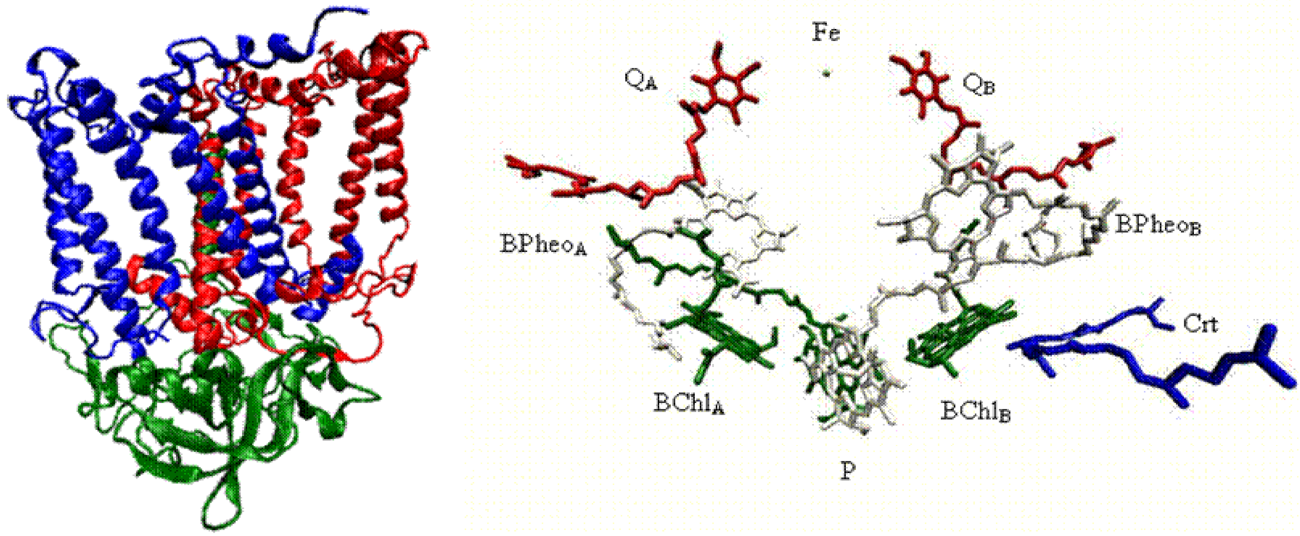


Fig. 3. The molecular model of photosynthetic reaction centre of *Rb. sphaeroides* calculated from data of crystal structure downloaded from the Brookhawen Protein Data Bank (www.rcsb.org, code name: 1pst). Picture was drawn by VMD program. Left: the protein frame with three subunits (H-green, L-blue and M-red, as indicated). Right: redox acive cofactors carrying the electron transfer. P: primary donor bacteriochlorophyll dimer. BChl: monomer bacteriochlorophylls. BPheo: bakteriopheophytine. Q_A and Q_B are the primary and secondary quinone type electron acceptors, respectively

reaction centre proteins we would not have enough energy e.g. to build tunnels or to actuate the jet planes and plasma televisions or to build skyscrapers. These natural solar stations transform the energy of every photon into chemical potential with almost 100% efficiency (Wraight and Clayton, 1974).

The research of the proteins to harness the solar energy is a real challenge today. On one hand nature made a system during milliards of years, that can work with such efficiency that could not have been imitated by human so far. On the other hand it is necessary to explore every subject that can help to appease the energy esurience.

The protein owns such technical properties that other applications are also possible for example its use in the nano-structures or in the optoelectronic systems. Some of them will be mentioned as follows.

a) This protein has characteristic light absorption in the near infra red range (700-1000nm) of the spectrum. It offers applications in equipments using this wavelength range (for example in security devices or to investigate pigment absorbing light out of the visible region).

b) After the excitation by light there are components with different lifetimes inside the protein. We can find different kind of processes from the few femtoseconds of the excitation to the picoseconds of the primary charge separation or to the seconds of the charge recombination. On the whole, such protein can be made that we need, so that it is able to generate a redox process in any kind of time interval what we are interested on.

c) As stated above, every absorbed photon is able to generate a charge pair in the reaction centre and the quantum efficiency is almost 100%. This extreme characteristics of the RCs is very useful for designing systems for harnessing solar energy.

d) The redox centres arisen inside the protein after excitation by light can be in interaction with their environment (either in the donor or in the acceptor side). The created redox systems ideally can be made to work, offering numerous chance of application (Giardi and Pace, 2005; Lu *et al.,* 2007). There are successful essays in nano systems as well, for example RC can be bound to carbon nano tubes (Dorogi *et al.,* 2006), to transition metal-oxides (Lu *et al.,* 2005) or other electrode surfaces (Das *et al.,* 2004; Lebedev *et al.,* 2006). In these systems the electron-excited by the light-is trapped in the redox system around the RC and, among other things, it can be part of circuit segments. This redox system might be used to produce alternative fuel or to reduce CO_2 by using sunshine. Possible arrangement of solar battery created by using carbon nanotubes and RCs is shown in Fig. 4.

Agricultural importance

The primer production is the biomass that arises first during the ecological auxiliary chain, after the conversion of the light energy. Its function is incontestable in the biosphere but it will be detailed later. In this chapter the agricultural importance is highlighted, emphasizing, that the primer production of the agriculture is a necessary and important part of the biosphere.

The function of the agriculture is, of course, to assure the stores for the humanity. Though there are differences between areas on the Earth, it seems that the demand of the temporal population cannot be supplied by the present food production. People are definitely interested in raising the primer (i.e. food) production of the agriculture. One

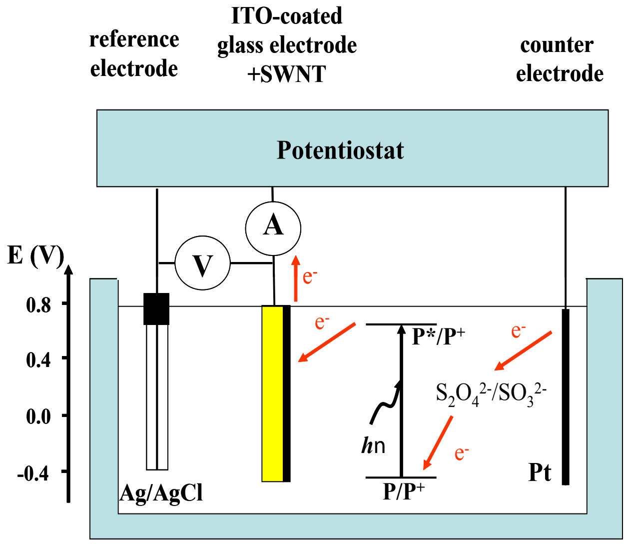


Fig. 4. Possible arrangement of solar battery created by using carbon nanotubes and RCs. RCs are bound to single walled carbon nanotubes attached to ITO electrode. Light excitation generates charge separation in the RCs and the excited electron is pumped in the SWNT/ITO electrode. The electrical circuit is closed by mediating the electron flow between the Pt-electrode and the RC by dithionate. The redox potential is indicated versus standard hydrogen electrode (SHE)

of the availabilities is to extend the bearing surface, what means that we make the absorption cross section for sunshine bigger. Lately scientists pay more and more attention to the stress factors that reduce the efficiency of the photosynthesis, reducing the biomass production as well. Among others the salt stress, desiccation, UV-stress and surprisingly the light as well (photo inhibition) are good examples for these kinds of stress factors (Barber, 1992). Herbicides-that are widely used in the agriculture-also have interesting effect on photosynthesis.

The photosynthetic production of the plants is very sensitive for the UV radiation even on more score (Nagy *et al.,* 1995). The photosystem two (PS-II) is especially sensitive to UV light, mostly the D1 protein of the reaction centre and the water-splitting Mn-complex. The activation of the Rubisco (ribuloz-1,5-biphosphate-carboxilase) enzyme-that is responsible for holding the CO_2-decreases significantly. Surprisingly the first photochemical system (PS-I) has high resistance with the UV radiation.

It is important that too much light can be also detrimental for the photosynthesis (Barber, 1992). The increasing light intensity goes hand in hand with more intensive photosynthesis but only until a flooding point. After the saturation level, the efficiency increases with increasing light intensity. This period is due to photoinhibition. During the photoinhibition not only the intensity of the photosynthesis decreases but the photosynthetic apparatus is also impaired. The strong reducing and oxidizing substances-that arise up during the charge-separation -cause the autocatalytic enzymatic degradation of the PS-II-reaction centre. The photosynthetic plants try to compensate this process so the D1-protein of the PS-II is one of the proteins that are able to be resynthesized very quickly. If we think on the fact that the light intensity can be very high at noontime (even more than 1000 mol/m^2s) it is visibly that the lock in the production, caused by the photoinhibition, can be very big.

The effect of certain-photosynthetic- herbicides is very interesting. These herbicides, attaching to the Q_B site (see Fig. 3) of the reaction centre protein, retard the photosynthetic activity of the plant by arresting of the electron

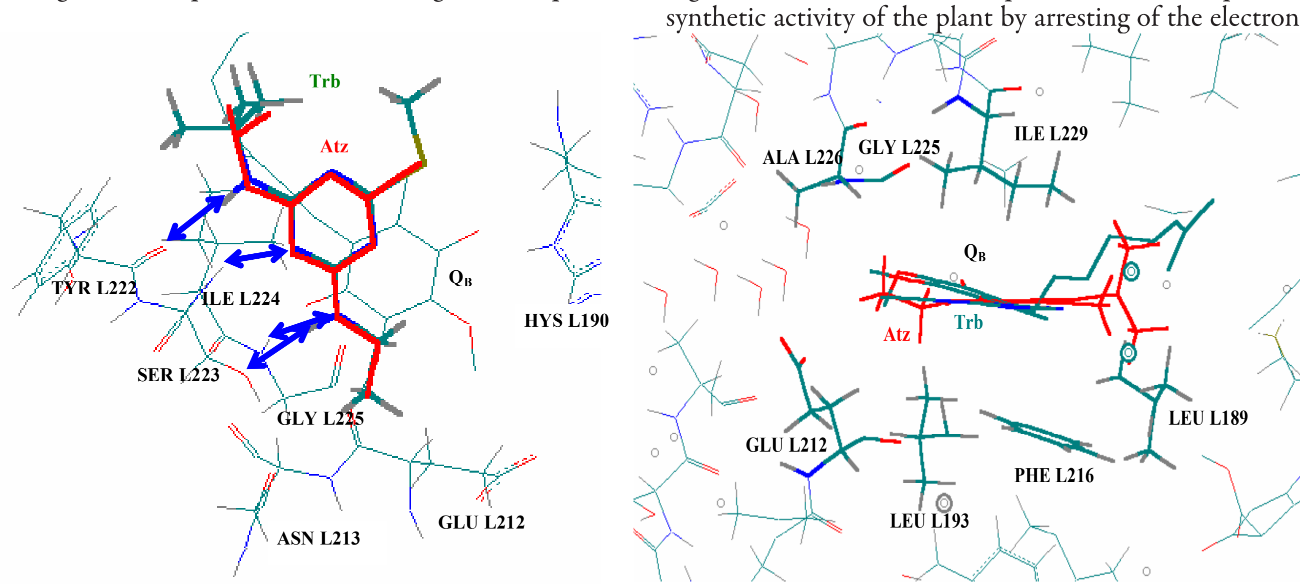


Fig. 5. The binding of atrazine (thick red line) and terbutryne (thick green line) to the reaction centre of *Blastochloris* (formerly *Rhodopseudomonas*) *viridis* according to the crystal structure. Figure was completed by using the files downloaded from the Brookhaven Protein Data Bank: 2prc (RC/ubiquinone), 1dxr (RC/terbutryne), 5prc (RC/atrazine) complexes. The arrows show the possible hydrogen bonds (the distances shorter than 3 Å) and neighbouring amino acid groups. Graph was completed by HyperChem 7.0

transport inside. Using this effect it is possible to obliterate the weeds in culture populations. As these compounds bind to reaction centre protein, resistance can be evolved arresting the bonds, especially if they are used badly-for too long time or in too big dose (Halmschlager, 2002; Wright, 1981). By the way exactly it happened in the 60' (in Hungary as well) until the nature of the herbicide resistance was not clarified. Today it is known that only one change of amino acid in the right place of the RC causes, that the herbicide cannot bind. In this way the herbicide loses the efficiency and there is no effect sprinkling them on the land. As they are resolved slowly and with difficulty, they accumulate in the land and groundwater over years. Though the attachment to the RC protein is very specific, there are results that certain herbicides (for example the triazin-progenies like the atrazine) thought to have human pathogen or oncogen effect (Marchini et al., 1988; Tchounwou *et al.,* 2000). Because of this, their use is stopped in the European Union. The experiments about the photosynthetic reaction centres helped (and help) a lot to see the mode of action during the herbicide's bonding. This way it is easier to understand the nature of the mode of action of herbicide and to engineer new type of herbicides. Fig. 5 shows the relative orientation of the terbutryne and atrazine (triazine type herbicides) at the RC crystal of *B. viridis* modeled into the Q_B site excerting a strong competitive inhibition toward the quinone at this position.

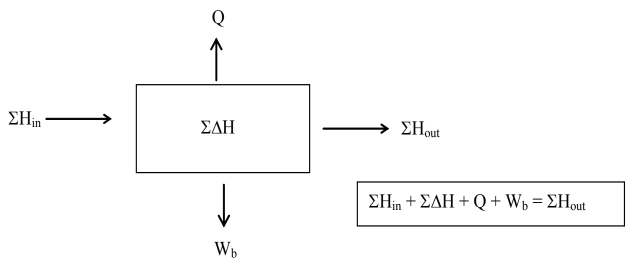
Ecological importance

Maybe that is the most obvious, if we think of the ecological system, for example of the biosphere, as a thermodynamic system. This way we can observe how the main thermodynamic laws prevail in the living system.

The first thermodynamic law is about the conservation of energy. So the whole energy of the ecological system-on every level (producers, consumers and decomposers)-has to be equal with the energy of the biomass ($E_{biomass}$) with the beneficial work (W_b) and with the amount of the reaction heat (Q):

$$E_{total} = E_{biomass} + W_b + Q$$

As the ecological systems are open systems, Q means the heat-change between the system and the environment, ΣHin is the entering energy, ΣHout is the outgoing energy and ΣΔH is the enthalpy changes in the system, accordingly the following flowsheet can be made:



All the energy incoming from the biosphere (except for the slight but not negligible ones) is derived from the sun. As we said, in the RC the quantum efficiency of the primer charge separation is almost 100%. It means that if there is a photon of 600 nm wavelength on the flowsheet above, ΣH_{in} is 180kJ/mol. As the energy difference between the basic and excited state in the RC protein is practically equal with this value (177.6 kJ/mol), the energy of the photon is transformed completely into chemical energy. During the following processes there is a big energy loss and naturally just a small part of it will appear in the biomass of the producters. For example the formation heat of the glucose is 2810kJ/mol:

$$6\,CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$
$$\Delta H=2810 kJ/mol \text{ glucose.}$$

We have to talk about the material balance too. It is well known that the photosynthetic organisms get the molecular oxygen into the air and bind the carbon-dioxide from the atmosphere and oceans. It is true that oxygen is derived from the photosynthesis in the atmosphere but now there is so big amount of this gas (about 20%) that a small change in its concentration does not induce important changes in life, i.e. it is not a limiting factor for it. The case of the carbon-dioxide is different, its amount is only 0.03%. Its change influences the intensity of the photosynthesis and as a greenhouse gas, it has a complex effect on the estate of the air and the biosphere. According to certain ideas the isolated RC-in convenient systems-could be applied to reduce CO_2 from the atmosphere, subserving our fight against the greenhouse effect.

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References

Allen, J. P., J. Feher, T. O. Yeates, H. Komiya and D. C. Rees (1988). Structure of the reaction centre from *Rhodobacter sphaeroides* R-26 and 2.4.1. In: The photosynthetic bacterial reaction centre, Breton and Vermeglio (Eds.). Plenum Publishing Co.

Barber, J. and B. Andersson (1992). Too much of a good thing - light can be bad for photosynthesis. Trends in Biochemical Sciences. 17:61-66.

Baxter, R. H. G., N. Ponomarenko, V. Strajer, R. Pahl, K. Moffat and J. R. Norris (2004). Time-resolved crystallographic studies of light-induced structural changes in the photosynthetic reaction centre. Proc. Natl. Acad. Sci. USA

101:5982-5987.

Breton, J. (2007). Steady state FTIR spectra of the photoreduction of QA and QB in *Rhodobacter sphaeroides* reaction centres provide evidence against the presence of a proposed transient electron acceptor X between the two quinones. Biochemistry 46:4459-4465.

Das, R., P. J. Kiley, M. Segal, J. Norville, A. Yu, L. Wang, S. A. Trammell, L. E. Reddick, R. Kumar, F. Stellacci, N. Lebedev, J. Schnur, B. D. Bruce, S. Zhang and M. Baldo (2004). Integration of Photosynthetic Protein Molecular Complexes in Solid-State Electronic Devices. Nano Letters 4:1079-1083.

Deisenhofer, J., O. Epp, K. Miki, R. Huber and H. Michel (1985). Structure of the protein subunits in the photosynthetic reaction centre from *Rps. viridis* at 3 A resolution. Nature 318:618-624.

Dorogi, M., Z. Bálint, Cs. Mikó, B. Vileno, M. Milas, K. Hernádi, L. Forró, Gy. Váró and L. Nagy (2006). Stabilization effect of single walled carbon nanotubes on the functioning of photosynthetic reaction centres. J. Phys. Chem. B. 110:21473-21479.

Edens, G. J., M. R. Gunner, Q. Xu and D. C. Mauzerall (2000). The enthalpy and entropy of reaction for formation of $P^+Q_A^-$ from excited reaction centres of *Rhodobacter sphaeroides*. J. Am. Chem. Soc. 122:1479-1485.

Fathir, I., T. Mori, T. Nogi, M. Kobayashi, K. Miki and T. Nozawa. (2001). Structure of the H subunit of the photosynthetic reaction centre from the thermophilic purple sulfur bacterium, *Thermochromatium tepidum*. Implications for the specific binding of the lipid molecule to the membrane protein complex. European Journal of Biochemistry 268:2652-2657.

Ferreira, K. N., T. M. Iverson, K. Maghlaoui, J. Barber and S. Iwata (2004). Architecture of the photosynthetic oxygenevolving centre. Science 303:1831-1838.

Giardi, M. T. and E. Pace (2005). Photosynthetic proteins for technological applications, TIBS 23:257-263.

Grafton, A. K. and R. A. Wheeler (1999). Amino acid protonation states determine binding sites ofthe secondary ubiquinone and its anion in the *Rhodobacter sphaeroides* photosynthetic reaction centre. The Journal of Physical Chemistry B 103:5380-5387.

Halmschlager, A., J. Tandori, M. Trotta, L. Rinyu, I. Pfeiffer and L. Nagy (2002). A mathematical model for the quinone-herbicide competition in the reaction centres of *Rhodobacter sphaeroides*. Functional Plant Biology 29:1-7.

Kruip, J., E. J. Boekema, D. Bald, A. F. Boonstra and M. Rogner (1993). Isolation and structural characterization of monomeric and trimeric Photosystem-I complexes (P700-centre-dot-fa/fb and P700-centre-dot-fx) from the cyanobacterium synechocystis pcc-6803. Journal of Biological Chemistry 268:23353-23360.

Lebedev, N., S. A. Trammell, A. Spano, E. Lukashev, I. Griva and J. Schnur (2006). Conductive wiring of immobilized photosynthetic reaction centre to electrode by cytochrome c. J. Am. Chem. Soc. 128:12044-12045.

Lu, Y., Y. Yuan Liu, J. Xu., C. Chunhe Xu, B. Liu and J. Kong (2005). Bio-nanocomposite Photoelectrode Composed of the Bacteria Photosynthetic Reaction Centre Entrapped on a Nanocrystalline TiO_2 Matrix. Sensors 5:258-265.

Lu, Y., Y. Xu, B. Liu and J. Kong (2007). Photosynthetic reaction centre functionalized nano-composite films: Effective strategies for probing and exploiting the photo-induced electron transfer of photosensitive membrane protein. Biosensors and Bioelectronics 22:1173-1185.

Marchini, S., L. Passerini, D. Cesareo and M. L. Tosato (1988). Herbicidal triazines: Acute toxicity on Daphnia, fish, and plants and analysis of its relationships with structural factors. Ecotoxicology and Environmental Safety 16:148-157.

Mitchell, P. (1961). Coupling of Phosphorylation to Electron and Hydrogen Transfer by a Chemi-Osmotic type of Mechanism. Nature 191:144-148.

Nagy, L., E. Bálint, J. Barber, A. Ringler, K. M. Cook and P. Maróti (1995). Photoinhibition and law of reciprocity in photosynthesis. J. Plant Physiol. 145:410-415.

Nagy, L., V. Kiss, V. Brumfeld and S. Malkin (2001). Thermal and structural changes of photosynthetic reaction centres characterized by photoacoustic detection with a broad frequency band hydrophone. Photochem. Photobiol. 74:81-87.

Nagy, L, P. Maróti and M. Terazima (2008). Spectrally silent light induced conformation change in photosynthetic reaction centres. Febs Letters 582:3657-3662.

Nagy, L., K. Hajdu, B. Fisher and K. Hernádi (2009). Photosynthetic reaction centres-from theoretical considerations to possible applications, p.65-84. In Vincze, J. (Eds.). Biophysics, NDP, Budapest.

Ohmori, H., L. Nagy, M. Dorogi and M. Terazima (2008). Charge stabilization in reaction centre protein investigated by optical heterodyne detected transient grating spectroscopy. Eur. Biophys. J. with Biophys. Lett. 37:1167-1174.

Rabenstein, B., G. M. Ullmann and E. W. Knapp (1998). Energetics of electron-transfer and protonation reactions of the quinones in the photosynthetic reaction centre of Rhodopseudomonas viridis. Biochemistry 37:2488-2495.

Tchounwou, P. B., B. Wilson, A. Ishaque, R. Ransome, M. J. Huang and J. Leszcynski (2000). Toxicity assessment of atrazine and related triazine compounds in the Microtox assay, and computational modeling for their structure-activity relationship. Int. J. Mol. Sci. 1:63-74.

Wraight, C. A. and R. Clayton (1974). The absolute quantum efficiency of bacteriochlorofill photooxidation in reaction centres of *Rhodopseudomonas sphaeroides*. Biochem. Biophys. Acta 333:246-260.

Wraight, C. A. (1981). Oxidation-reduction physical chemistry of the acceptor quinone complex in bacterial reaction centres: evidence for a new model of herbicide activity. Isr. J. Chem. 21:348-354.