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REVIEW

What are quantasomes ? The background of a nearly forgotten term

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Abstract

After the formulation of the photosynthetic unit (PSU) concerning the cooperation of 2400 chlorophyll molecules in the reduction of one molecule of CO_2 by Emerson and Arnold in 1932, the search for a morphological expression of the functional unit began. The quantasome hypothesis is an attempt to relate the structure visible in the electron microscope, the quantasome, and the PSU. The term 'quantasome' was introduced by Park and Calvin as a name for grana subunits. The quantasomes were regarded as the main integral parts of the grana lamellae in the protein lipid layers. Yet it soon became clear that a morphological unit such as the quantasomes did not exist. Nevertheless, the term was still used in various applications till the eighties.

The starting conditions

In the years 1862 and 1864 Julius Sachs showed that starch is the final product of CO_2 assimilation produced by the work of chlorophyll under the influence of light. We are indebted to him for the classical equation of photosynthesis:

$$6\ CO_2 + 6\ H_2O + \text{solar energy} \rightarrow C_6H_{12}O_6 + 6\ O_2$$

Engelmann (1881) pointed out that oxygen evolution is restricted to chloroplasts only. Further on, Meyer (1883) and Schimper (1885) discovered grana in chloroplasts. So it had become natural to admit that the chloroplasts were playing an eminent role in the photosynthetic process. Yet the knowledge of the grana structure within the chloroplast got lost during the following decades because of the emerging protein chemistry and colloid science and their influence on the interpretation of biological structures. Thus the inside of the chloroplast was accepted as being homogeneous. A thready, fluid-gelatinous aggregate state was attributed to the chloroplast (Menke 1938). Those structures, which had been found within the

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chloroplasts were seen as the products of coagulation of protein molecules or as artefacts (Frey-Wyssling 1937).

Only in 1936 the grana were discovered once again by Heitz, and the old grana theory of Schimper and Meyer became evident again. Heitz (1936) described the regular granulation in chloroplasts of 180 plant species and differentiated between three elements within the chloroplast: (*1*) the colourless stroma, (*2*) the grana, and (*3*) the pigments, existing only within the grana. The form of the grana was thought as separated little disks. Also Frey-Wyssling (1936) with prudent forecast suspected that the period of structureless and homogeneous hydrogels is over.

The rediscovery of the grana structure brought up a fact important from a methodological point of view. Frey-Wyssling (1937) pointed out that the morphological method with its specific way of observation has always been a precursor and a pioneer of the physiology. Only if the detailed organization of an object is known, one can generally understand how it works. The opposite was true concerning the investigation of the chloroplasts: One had a rather deep understanding of their function without any knowledge of their exact organization.

Since the twenties the physiological investigation of mechanisms of photosynthesis has been very intensive (*e.g.* Warburg 1919, 1920, Warburg and Negelein 1922). Yet the postulation of the cooperation of many chlorophyll molecules in the reduction of one molecule CO_2 by Emerson and Arnold (1932a,b) was decisive for the relation between structure and function of photosynthesis. The term 'photosynthetic unit' (PSU) meant the number of chlorophyll molecules, which were coupled and cooperated in reduction of one carbon dioxide molecule. In a modern interpretation Wild and Egle (1968) named the PSU as a collective of chlorophyll molecules, which collaborate in collecting radiant quanta and in transferring the energy to a photochemical reaction centre. Emerson and Arnold calculated a total number of 2400 chlorophyll molecules in one PSU; other authors, *e.g.* Gaffron and Wohl (1936), attributed only about 1000 chlorophyll molecules. What would be more obvious than to attribute a structural unit to the functional cooperation of many hundred chlorophyll molecules? Frey-Wyssling (1937) pointed out that, if assimilation units were existing, one would expect them also at a morphological level. Because the investigation on the structure of the chloroplast was far behind the investigation of its functions, it was impossible to attribute to the PSU an adequate structure within the chloroplast at this early time. After the calculation of the space dimensions of a unit of 2000 chlorophyll molecules of about 0.03 μm, it became obvious that such a structure could not be visible in a light microscope: "This assimilation unit is amicroscopical" (Frey-Wyssling 1937, p. 296).

Only the progressing investigation of the chloroplast with the help of the electron microscope enabled the resolution of more and more accurate structures and this made conceivable and visible coordinations to the PSU possible. The composition of the grana out of membranes, in which the pigments worked, became apparent first. Yet at that time, there were no definite theories about their molecular and structural composition. One of the approaches is the so-called hypothesis of quantasomes.

The establishment of the quantasome hypothesis

The quantasome hypothesis was the attempt to coordinate a structure, visible in the electron microscope - the quantasome - and the PSU.

In the literature the term 'quantasome' was first used in 1962. Calvin (1962) and Park (1962) introduced this term to name grana subunits. Yet one year before, Park and Pon (1961) had reported on the isolation of various grana subparticles (not identical with thylakoids), which they had got from ultrasonic treatment of isolated spinach chloroplasts. These particles were of various sizes and different chemical qualities, and "small fragments of the lamellar structure are capable of Hill reaction though not capable of rapid light-dependent CO_2 fixation without addition of stroma protein" (Park and Pon 1961, p. 10). These little subunits of 10 nm thickness and 20 nm diameter, which together with protein lamellae were thought of as integral parts of the grana lamellae and which were described a few years before in a similar way by Smith and Kupke (1956), were termed 'quantasomes' by Park (1962). In 1961 Park and Pon had shown similar particles - particles *b* in Fig. 1 - which he now called quantasomes. In a general view Park reported a possible differentiation of isolated chloroplasts into different fractions, which were able to do either light or dark reactions. After centrifugation it became clear, that "the green precipitate is composed of double layered structures made up of small particles. This fraction carried out the light reactions of photosynthesis, oxygen evolution and photosynthetic phosphorylation...The granular subunits are oblate spheres 200 Å in diameter, are 100 Å thick, and are osmiophilic over one surface. We have chosen the term *quantasome* to describe this particle" (Park 1962, p. 428).

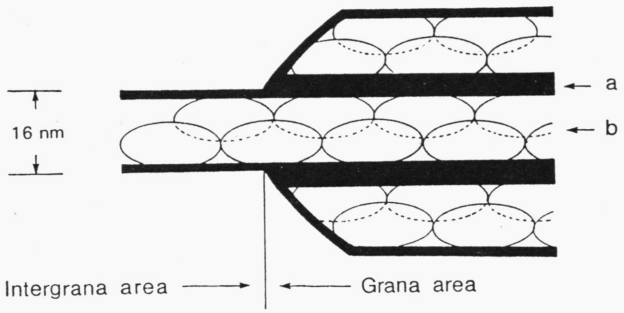

Fig. 1. Model of the lamellar structure within a spinach chloroplast (Park and Pon 1961, p. 5). *a*: Osmium-staining layer of the lamellar structure; *b*: particles forming the granular inner surface of the two layers (called quantasomes).

One year later Park and Pon speculated about the possible role of these particles: "The possibility exists that the single quantasomes are the smallest units which will perform the light reactions of photosynthesis and thus are a morphological expression of the photosynthetic unit as formulated by Emerson and Arnold (1932)..." (Park and Pon 1963, pp. 105-106).

After applying various colouring methods, micrographs by electron microscope lead to the conclusion that chlorophyll existed only in the lamellar structures of the chloroplast, namely in the quantasomes. At a rough guess - with the help of the molecule size - the number of chlorophyll molecules per quantasome was estimated to a few hundred. After Emerson and Arnold had calculated the number of 2400 chlorophyll molecules per PSU, which was corrected among others by Kok (1956) to 200, nothing stood in the way of the interpretation that with the quantasomes the long sought structural part of the PSU had been found: "It is appealing to think that the 200 Å quantasome is perhaps a morphological expression of the photosynthetic unit of Emerson and Arnold" (Park 1962, p. 429).

This discovery seemed to be the key for further investigation of the photosynthetic mechanism: "This small particle holds the answers to much of what we do not know about photosynthesis" (Park 1962, p. 429). Park could not know at that time that his newly created term even would almost be forgotten ten years later.

The authors did not explain the etymology of the term 'quantasome'. It can only be speculated that this term of Latin-Greek derivation (quantum, ta soma) was introduced with the intention to attribute a definite number of chlorophyll molecules (quantum = how much) to a single body (ta soma). One might also use the term 'quantum' as it is done in physics although. Thus the quantasomes would be bodies collecting radiant energy and able to perform the light reaction ("Park named the granules quantasomes - membrane units that transduce light" - Anon. 1969, p. 14).

Although the physiological investigation of chloroplasts was ahead of its structural investigation till the 30ies and even the 40ies, this advantage was seemingly made up for by the electron-microscopic discovery of the quantasomes. The gradual elucidation of chloroplast structure, of the grana and above all its membrane structure, and the following discovery of the quantasome itself, recovered the discommoded equilibrium of physiological and morphological investigation of photosynthesis. There was hope again now to find the structural-morphological fundaments of the physiological-biochemical discoveries.

The quantasome model was accepted very fast, and it started a series of various investigations and experiments on photosynthesis, which now used quantasomes instead of the hitherto experiments with isolated chloroplasts. Thus, Sauer and Calvin (1962a) measured the absorption spectrum and the bleaching of pigments in spinach quantasomes, and they saw that the absorption spectrum of quantasomes did not differ from an *in-vivo* spectrum within wavelengths from 230-900 nm. They also investigated the molecular orientation of chlorophyll in quantasomes (Sauer and Calvin 1962b). Measurements of dichroism and electric birefringence gave not only evidence for the existence of parallelly oriented membrane structures within the quantasomes, but the dependence of birefringence from wavelength provided to the idea, "based on a model which assumes the existence in the quantasome of a small fraction of the chlorophyll *a* molecules which are relatively highly oriented..." (Sauer and Calvin 1962b, p. 461).

This would affect about 10 molecules in a PSU of 200 chlorophyll molecules. Their maximum absorption spectrum is in relation to the 'normal' chlorophyll *a* shifted by 15 nm to 695 nm. All these molecules serve as a special 'trap' for the

radiant energy and can be found at a place of the quantasomes where a cytochrome molecule and one or several acceptor molecules are situated as well. Sauer and Calvin named this spot 'quantatrop'. Because of the possible energy uptake of the ten highly orientated chlorophyll molecules at -150 °C, the quantatrop has to be the primary site of the light reaction in the quantasomes. In contrast, the reduction of the oxidized cytochrome is a temperature dependent enzymatic reaction, which proceeds at 20 °C with a time constant of 2×10^{-2} s. This is exactly the time period used by Emerson and Arnold (1932) in flashing light experiments for the respective dark phases. This interpretation tried to localize the mechanism of the light reactions within the quantasomes and even attributed separate reaction steps to corresponding sites of the quantasome (*e.g.* quantatrop = primary excitation trap).

In the laboratory of Calvin one always tried to separate the light reactions into individual reaction steps within the scope of quantasome investigation. In further publications on the molecular orientation within quantasomes, for example, the Hill reaction and the absorption of quantasomes were measured (Sauer and Park 1964). Dichroism measurements of quantasomes resulted in the photochemical activity of the pigment P700 (Sauer 1965). The pigment P700 was identified and characterized as the trapping centre of photosystem (PS) 1 a few years before by Kok (1961).

With the use of the new term 'quantasome' a certain inexactness was introduced. Now all lamellar chloroplast subunits of various sizes, originated by ultrasonic treatment, were called quantasomes (Sauer and Park 1964, p. 476). It was neglected that in 1962 Park used this term only for those particles which fill out the interlamellar zones (cf. Fig. 1). This wide interpretation of the term did not allow for a strict interpretation of the experiments in relation to the most of the smaller subunits.

Park and Pon (1963) and Park and Biggins (1964) aimed at the description of the composition and organisation of the quantasomes. Assuming that the analysis of quantasomes has to precede new statements on them ("However, before an adequate molecular model of quantasome structure can be constructed, chemical analysis and localizations of substances within the quantasome must be performed" - Park and Pon 1963, p. 106), Park and Pon calculated the molecular mass of a 20 nm quantasome on the basis of manganese content at 960 kDa. Thereby 55 % of the mass were lipid compounds, whereas only 25 % were carotenoids and chlorophylls. However, Park and Biggins calculated a molecular mass of 2000 kDa, a length of 18 nm, a width of 15.5 nm and a thickness of 10 nm from the measurements of volume and density. This was twice as much as Park and Pon had calculated. Shibuya and Maruo (1965) found that all sulpholipids of the chloroplast were located in the quantasomes.

As concerns the effects of growth conditions, chloroplast membranes of long-day spinach showed only a weak structure and few quantasomes in contrast to quantasomes that had grown under short day. This corresponded with a much weaker photosynthetic activity of the long-day chloroplasts (Park and Drury 1967).

Lichtenthaler and Calvin (1964) confirmed the *in-vivo* character of quantasomes. The analysis of pigment and quinone contents as well as of further photosynthetically significant elements of spinach quantasomes and whole chloroplasts showed

practically the same results. This lead to the following conclusion: "The observation that quantasome aggregates contain the same pigment and quinone composition as do chloroplasts, as well as the fact that they are fully active in quantum conversion and electron transport as assayed by the Hill reaction, suggests that quantasomes, the subunits of chloroplast lamellae, represent the actual functional unit, responsible for photosynthetic quantum conversion" (Lichtenthaler and Calvin 1964, p. 39). However, these experiments were done with aggregates of 7-8 quantasomes.

In next years, Gross *et al.* (1964) and Becker *et al.* (1965) questioned the model of quantasome with 20 nm units as the analogue of the PSU. Their physiological tests were done with chloroplast fractions (CF) of different sizes, which they got by centrifugation at various speeds of ultrasonic treated spinach chloroplasts. The unexpected result was that the relatively big fragment $CF_{20\text{-}50}$, which the authors got by centrifugation at 20 000 - 50 000 × *g*, showed the highest Hill activity and was very stable. The Hill activity was many times higher than that of the $CF_{70\text{-}140}$, which was described by Park as the quantasome fraction. The size of this $CF_{20\text{-}50}$ particle (150 nm diameter, 36 nm height) was calculated from the sedimentation coefficient as well as from electron micrographs: "Certainly, $CF_{20\text{-}50}$ particles are too large to be considered fundamental photosynthetic units themselves" (Becker *et al.* 1965, p. 249), especially since at the surface of such a particle 16 000 chlorophyll molecules could be sited. 88 of the 'normal' quantasomes would fit into such a subunit, if one $CF_{20\text{-}50}$ would have a molecular mass of 144 MDa. These stable units, however, are composed of subunits of 38 S particles. They proposed, that these 38 S subunits will be termed 'polyquantasomes' (Becker *et al.* 1965, p. 250). Yet a connection to the quantasomes was not questioned. The polyquantasomes could be an aggregate of 2-3 quantasomes.

We thus find a gradual hierarchy in the discussion about the structural equivalent of the PSU. At its lowest level the quantasome is situated. It does not contradict the quantasome model that the Hill activity depends on the fragment size. It only shows that through the cooperation of many subunits, synergistic effects are possible, which in biological systems have to be expected. Also the restrictions by working with aggregates instead of individual quantasomes which were done by many authors, agree with the interpretation of Gross, Becker and Shefner. The isolation of PS1 and 2 in the middle of the 60ies also supports the interpretation of the cited authors. Fractions which contain PS2 are composed of parts larger than 150 nm, whereas fractions containing PS1 are composed of parts of about 60-70 nm. "The size of all these particles is immense in comparison with quantasomes or polyquantasomes" (Gross *et al.* 1966, p. 615).

Kreutz (1965) and Kreutz and Weber (1966) reported on experiments to determine the substructure of quantasomes by means of small-angle X-ray measurements. A quantasome seemed to be composed of 4 subunits, and each of them contained 4 centres of protein mass. Thus, the authors had reached a further step of reduction of the PSU, and they tried to investigate "the proteinaceous part of a quantasome" (Kreuz and Weber 1966, p. 12). But the interpretation of the quantasome as a functional unit as in the first definition was completely ignored here.

The last comprehensive model of the arrangement of photosynthetic pigments in spinach quantasomes was constructed by Thomas *et al.* (1967) by means of dichroism measurements. Only in flat 'summer chloroplasts' one could see dichroism effects. 80 % of them are supposedly due to structural causes, 20 % are due to special orientation of chlorophyll molecules especially situated at the surface of the lamellae. Thus, these would only be 2 % of the chlorophyll *a* content. Yet first it had to be explained where the pigment molecules are really situated: "(*1*) in the spherical quantasome subunits, (*2*) in the underlying part of the lamellae, or (*3*) of both of these sites"? (Thomas *et al.* 1967, p. 215). After estimation of the surface size of one quantasome, the authors came to the conclusion that "in such a sphere, quite close packing occurs... We shall therefore consider the situation where the pigments occur on the surface of the subunits" (Thomas *et al.* 1967, p. 216). A model which considers the PS1 and PS2 (discovered 5 years before) as well as further compounds of photosynthetic mechanism is shown in this publication (Thomas *et al.* 1967, p. 217-218). Accordingly, a quantasome is supposedly composed of 4 subunits. In its centre one P700, one cytochrome *f* and b_6 are situated which serve the subunits. Yet the idea of the 4 subunits was originated by Mühlethaler *et al.* (1965) and Mühlethaler (1967) who named groups of 4 protein particles of the surface of the thylakoid membrane as multienzyme complexes and related them to quantasomes. With this model the hypothesis of quantasomes had reached a culmination point: The functional PSU of Emerson and Arnold was thus completed by a structural model. The beginning investigation of photosynthesis at a molecular level invited new questions and the quantasome model was able to answer them.

The ideas of Park, the originator of the quantasome hypothesis, are once more summarized: "In summary, the conversion of light energy to chemical energy takes place in the lamellar system of the chloroplast. The lamellar system appears to be made from 200 Å diameter oblate spheres attached to a membrane. These spheres with the attached membrane are called quantasomes" (Park 1963, p. 360).

The end of an idea: the quantasome hypothesis in the cross-fire of critique

Only a few years had passed since the introduction of the term 'quantasome' in 1962, when the first critical arguments against the quantasome hypothesis were uttered. The methodical improvement of electron microscopy and the technique of isolating the thylakoid subunits together with various physiological tests managed to elucidate the physiological capacity, the arrangement, and the role of quantasomes in photosynthesis. The concepts of the composition of the thylakoid membrane and the contradictory opinions about the site of the quantasomes (at the inner or outer side of the membrane, or between the membranes) provoked doubts that were first uttered by Heslop-Harrison (1966, p. 534).

In 1965, Izawa and Good reported on experiments concerning the inhibition of the Hill reaction in isolated chloroplasts by DCMU and atrazine (Izawa and Good 1965). They calculated from the concentration of the applied inhibitory substances and the present number of chlorophyll molecules a 50 % inhibition of Hill activity and under

consideration of the still free inhibitory substances the number of chlorophyll molecules per catalytical centre and got a total of 2500. This result contradicted the number of 200-400 chlorophyll molecules per quantasome, which was accepted till then. So Izawa and Good doubted the hitherto existing interpretation of quantasomes: "Certainly the quantasome cannot be an autonomous unit in the overall Hill reaction if we are interpreting our data correctly" (Izawa and Good 1965, p. 35). Park and Pon had perhaps experimented with enriched quantasomes, *i.e.* with the enrichment of active centers. Izawa and Good therefore maintained their interpretation of an oxygen evolving unit of 2500 chlorophyll molecules in the photosynthetic apparatus, and fully agreed with the primary calculation of the size of the PSU by Emerson and Arnold.

The doubts became stronger when Howell and Moudrianakis discovered that the Hill reaction did not take place in the quantasomes, which meant that they did not participate in the photoreduction. Chloroplast preparations, free of any quantasome particles, showed a relatively high DCPIP Hill activity. Yet the addition of quantasome populations did not increase the activity rate (Howell and Moudrianakis 1967a). With this publication the quantasome model was still not refuted, but doubts about the central role of the described particles in the photosynthesis were increased. (Experiments by Becker *et al.* and Gross *et al.* already showed maximal Hill activity only for particles larger than quantasomes - Becker *et al.* 1965, Gross *et al.* 1966.) Park and Pfeifhofer (1968) repeated the experiments of Howell and Moudrianakis and doubted the methodical correctness of the investigations. The used method of negative staining was supposedly not suitable for identification of quantasomes, and therefore their preparations were not really free of quantasomes.

The beginning of the end of the quantasome model was also announced by Howell and Moudrianakis (1967b). Purified quantasome preparations of spinach chloroplasts were tested for a possible ATPase activity and for their capacity of a reconstitution of photophosphorylation of uncoupled membrane subunits. The results were positive and the quantasomes enabled the uncoupled subunits to photophosphorylation. According to the authors this showed that quantasomes were identical with the coupling factor of phosphorylation ("13s photophosphorylase") and had nothing in common with the light-collecting function of the PSUs.

In next publication the authors produced further arguments against the quantasome hypothesis (Moudrianakis *et al.* 1968). Formazan reduced by the Hill reaction was spread over the entire membrane and was not situated in distinct granules. By means of the electron microscopical negative staining method, particles up to a size of 10 nm could be differentiated. Thus, either the photoreduction was a process continuously distributed over the membrane or the particles were smaller than 10 nm. Both contradicted the quantasome model. The authors also pointed out the uncertainity that still existed concerning structural organization of the quantasomes. The quantasomes were often interpreted as independent structural units, which are associated with the chloroplast lamellae but are not a part of them, though in the original interpretation they had to be part of the membrane.

To sum up: (*1*) Neither the quantasomes themselves, nor the instead introduced 13s photophosphorylase could be the morphological expression of the PSU of

Emerson and Arnold. (*2*) The Hill reaction is not restricted to distinct areas of a size of 10 nm. (*3*) This interpretation does not exclude a detailed structuring of the membranes; the elements only have to be smaller than 10 nm.

In the middle of the 70ies there was no longer any doubt about the confusion between quantasomes and other membrane associated complexes: "It may be recalled that several workers...considered ATPase knobs observed on the outer surface of the chloroplast membrane to be identical with the quantasome....It is sufficient to say that quantasome has now been identified with the big B face particles.." (Sane 1977, p. 528). Thus the idea of the quantasome as the structural part of the PSU of Emerson and Arnold was eventually overcome, and the model of arrangement of the pigments in quantasomes of Thomas *et al.* (1967) was refuted.

The idea and the term of quantasomes as the central PSU in photosynthesis were maintained for such a long time because the investigation of membrane composition even toward the end of the 60ies had not provided final results: "There is as yet no generally agreed interpretation, and even so fundamental a question as the location of the chlorophyll in the lamellae remains unsettled" (Heslop-Harrison 1966, p. 522). First of all the spatial relation of the chlorophyll, and thus the site of the primary reaction, were still unclear so that, for a long time, the idea of quantasomes seemed to be the solution of this problem.

Even the creator of the term 'quantasomes', Park, expressed his doubts concerning the correctness of the interpretation of the membrane surface at the 30th congress of biologists in 1969. He, of course, kept the term, but he admitted that not all particles which were seen under the electron microscope were quantasomes: "The largest of these particles are probably ribosomes and the enzyme carboxydismutase" (Park 1971, p. 36). Nevertheless, particles of the B-surface of a size of 17.5 × 9 nm, fractured by freeze-etching-technique, were called the quantasome core; but now they did not represent entire PSUs any more but only their centres. Branton (1967), who investigated the same subject, supported this view.

The further investigation of photosystems, of their function und distribution on the membrane, threw a new light on the quantasome hypothesis. Especially the idea that PS 1 and PS 2 do not have to be situated together confronted the quantasome concept with unsurmountable difficulties (Arntzen and Briantais 1975). Thus the idea of the structural expression of the PSU eventually failed: "It is necessary to suggest at this time that a PSU may be only a statistical unit which is not always accompanied by a structural counterpart" (Arntzen and Briantais 1975, p.106).

Nevertheless, the relation of the idea of a structural PSU with the understanding of the cooperation of photosystems at photosynthesis is the result of this hypothesis. The functional - and first of all structural - investigation of the photosystems replaced the investigation of quantasomes: "...it is possible that quantasomes are simply an identification of coupled PS 2 and PS 1 activity and in themselves have no functional significance" (Branton 1967, p. 406).

Beginning with the preparation of oxygen evolving PS2-particles by Berthold *et al.* (1981) new techniques for the isolation of defined thylakoid substructures became available. Considering these advances there was no need for the further use of the term quantasome in photosynthesis research.

The quantasomes are dead; long live the quantasomes! (Aftermath of a term)

Though the interpretation of quantasomes as the structural expression of the PSU was refuted at the end of the 60ies, the once originated and established term survived in scientific publications beyond the 60ies and 70ies. Yet in contrast to textbooks it was used in two new ways: Firstly, the quantasomes were related to other structural models, secondly, this term was used at the investigation of bacterial photosynthesis at last in 1985.

Let us now look at the first interpretation: Kutyurin (1970) reported on the water-splitting system of quantasomes of a size of 200-300 chlorophyll molecules and related them to a row of other structural units of the photosynthetic apparatus. One quantasome or an association of two represent a minimum unit for an oxygen evolution. For the electron transport it has to be a chlorophyll-protein complex. For both functions, however, a bigger chloroplast fragment is necessary. Thus Kutyurin distanced himself from the originally defined possibility of the quantasomes to carry out the entire light reactions on their own (compare Park and Pon 1961, chapter 2).

Stillwell and Tien (1977) used lipid microvesicles as a model for the composition of the thylakoid membrane. With these particles - like others with quantasomes - they carried out various photosynthetic tests and created a gradual model of the thylakoid organisation: At the lowest level there is a chlorophyll solution, then follow the lipid microvesicles, whereas the quantasomes are characterized by the extra content of lipoproteins. The most stable part in this sequence is the thylakoid membrane itself. Yet, in this article the term quantasome does not have the meaning of a PSU.

Already in 1974, Giller and Yukhananova had reported about similar experiments with synthetic pigment-lipoprotein complexes to study the pigment-protein and pigment-pigment relations, and put their results in analogy to quantasome investigations.

The second use of the term quantasome is related to the area of bacterial photosynthesis. Garcia *et al.* (1968) during fractioning of the photosynthetic membrane of *Rhodopseudomonas* by Triton X-100 had detected membrane-bound particles of a unit size of 13.5 nm. These particles contained the reaction centre of bacteriochlorophyll and showed a quinone reduction. "This, then, is the usual photochemical small particle which is liberated from all of the photosynthetic bacteria by the action of this detergent" (Garcia *et al.* 1968, p. 332).

The term 'quantasome' was used in the investigation of the photosynthetic apparatus of bacteria till 1985 (Breton *et al.* 1985, Nabedryk *et al.* 1985): "A quantasome consists of a reaction center surrounded by six antenna complexes,.." (Breton *et al.* 1985, p. 421). These structural units, which covered in regular arrangement the photosynthetic membrane of bacteria, contained the most important polypeptides (cytochrome, H-, L-, M-chain) and could be removed from the membrane by adequate treatment (Jay *et al.* 1984).

Because of the advance in preparation and characterization techniques (which was still not available in the period of quantasome discovery) it was possible to elucidate the supramolecular membrane structure. So in 1985 Deisenhofer *et al.* were able to

determine the structure of the photosynthetic reaction centre of *Rhodopseudomonas viridis* at 0.3 nm resolution by the use of x-ray analysis.

The quantasome concept by Park might get a certain satisfaction from the above mentioned definition, but it is surprising that in further literature on investigation of the bacterial photosynthesis the term quantasome is not used any more after 1985. This could be evidence for the unsuitability of the term in this context. Yet, nevertheless, the quantasome hypothesis contributed a decisive share to the discussion of the function-structure relation of the photosynthesis: "The quantasome concept has been of fundamental importance in stimulating and influencing numerous structure-function studies in recent years" (Arntzen and Briantais 1975, p. 101).

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Vorst, J.J. (ed.): **Experiments in Crop Science.** - Crop Science Society of America, Madison, Wisconsin 1990. 62 pp.

A series of eight experiments is intended for junior high or high school biology, or science classes. Individual experiments concern plant tissue culture and cell culture, plant genetics, germination and seedling growth under a water stress, nutrient deficiencies in plants, nitrogen fixation and legume inoculation, germination and vigour of seeds, seed viability and plant growth regulation.

In the "students guide" the main objective of the experiment and the procedure are shortly described and questions stimulating a better understanding of the problem are asked. In the "teachers guide" experiments are presented in more detail including necessary material and equipment, procedure, evaluation and discussion. In some cases important references are added.

It seems to me that the main purpose of the publication, *i.e.* "to help teachers relate basic plant biology to the world outside the classroom *via* demonstrations and laboratory experiments" is fulfilled very well in a cheap and sophisticated way, using well-known and easily available plants. Maybe not in all countries one can get *e.g.* hormone kits - therefore it is necessary to give their composition.

Nevertheless, the booklet is a good way how to get acquainted with basic biological experimentation.

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Fahey, G.C., Jr., Collins, M., Mertens, D.R., Moser, L.E. (ed.): **Forage Quality, Evaluation, and Utilization.** - American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison 1994. 988 pp.,U.S.$ 44.00.

The publication is based on the National Conference on Forage Quality, Evaluation, and Utilization held at the University of Nebraska in Lincoln on 13-15 April 1994. It reviews twenty-five years of development of forage science. It describes interaction of forage quality and animal production, plant and environmental factors affecting forage quality, identification and quantitative measurement of forage quality components, modern methods of analysis of forage intake, the role of digestion and metabolism in determining forage quality, the factors influencing digestion of forage-based diets by ruminants, and methods of estimation of digestibility of forages. Some chapters are devoted to modelling of forage quality changes and forage intake and digestion by ruminants. One section analyzes plant-animal interactions during grazing and changes in forage quality during harvest and storage. Harvest and storage losses are mentioned there too. The last section describes the possibilities of improving forage quality. The book will be useful for the researchers and the students who are interested in forage production, conservation and animal alimentation. The authors attempt to define where more information is needed and where new research efforts need to be focused.

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