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What role does sulpholipid play within the thylakoid membrane?

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Abstract. Sulphoquinovosyldiacylglycerol is a negatively charged lipid which exists in the thylakoid membrane. It is proposed that a large proportion of this acidic lipid does not form a part of the bulk lipid matrix but is closely associated with protein complexes where it is tightly bound and participates in either optimising catalytic activities, or maintaining the complexes in a functional conformation. Experimental evidence for this proposal is emerging from studies with isolated photosystem 2, and coupling factor complexes.

Introduction

Sensitive fluorescence and absorption spectroscopy are the major experimental approaches for investigating the primary processes of photosynthesis. Classical studies using these techniques by Professor Duysens and his colleagues on a wide range of prokaryotic and eukaryotic photosynthetic organisms established: (i) a firm basis for our understanding of energy transfer mechanisms between light harvesting pigments [23, 27], (ii) knowledge of the photochemical trapping and primary charge separation processes [25, 29] and (iii) evidence for electron transfer pathways [24, 26]. These outstanding contributions were made in the absence of a detailed understanding of the structure of the proteins which harbour the chromophores and redox centres involved, and indeed did not take into account the fact that the primary processes of photosynthesis take place within a complex membrane system. The relationship between primary photosynthetic processes and membrane structure did not emerge until the realization that the redox reactions of electron transport could act as a proton pump able to create an electrochemical potential gradient for driving ATP synthesis [50]. Even at this stage the main challenge was to arrange the various redox components vectorially across the membrane and there was no need to consider the nature of the proteins and lipids which constituted the reaction matrix [70]. Today we are rectifying this latter deficiency. We now know that the redox reactions take place in supermolecular multipeptide complexes and that the light harvesting pigments are specifically interacting

Dedicated to Prof. L.N.M. Duysens on the occasion of his retirement.

with proteins. Some of these protein complexes are strikingly comparable, both in structure and function, within a wide range of photosynthetic organisms while others are not. In the case of higher plants and green algae five different major complexes have been identified [4, 6]: photosystem 1 (PS1), photosystem 2 (PS2), light harvesting chlorophyll *a*/*b* complex (LHC), cytochrome *b*-*f* complex (cyt *b*-*f*) and coupling factor complex (CF_0-CF_1). It is generally agreed that these complexes are segregated into the two different domains of the thylakoid membrane [2, 6]; PS2 and LHC are preferentially localized in the appressed regions of the grana while PS1 and CF_0-CF_1 are restricted to the unappressed regions. The distribution of cyt *b*-*f* is not so certain but the complex seems to occur in both membrane regions [1]. The identification of different functional protein complexes and their asymmetric distribution in the membrane has a number of important consequences and has focussed attention on the roles of plastoquinone, plastocyanin and ferredoxin as long-range diffusible redox carriers able to communicate between various complexes so as to facilitate electron flow [37, 49, 72]. In the past few years many of the polypeptides which constitute each complex have been identified and are now being further characterised by the techniques of molecular genetics [17]. Crystallization of isolated complexes suitable for high resolution X-ray studies is also possible as demonstrated by the success with reaction centres isolated from *Phodopseudomonas viridis* [20].

Clearly, as the level of understanding of the structure of the photosynthetic apparatus grows, spectroscopic studies of the type pioneered by Duysens find a new dimension for interpretation. For example, Duysens and Talens [28] identified a process occurring in intact tissue which has been termed State transitions. This work, together with that of Bonaventura and Myers [13] and Murata [53] established that the State transitions are a regulatory mechanism which exists within oxygen evolving organisms to optimise the delivery of quanta to PS2 and PS1 under limiting light conditions. Because of our present day appreciation of thylakoid organisation we can now describe the State transitions in structural terms by which LHC diffuses laterally between appressed and non-appressed regions in response to surface phosphorylation [3, 5, 8].

The relationship between structure and function will continue to be an important facet of photosynthesis research for some years to come. An area of consideration which has yet to develop is the role of the polar lipids which, together with the intrinsic protein complexes, make up the photosynthetic membrane. In the case of higher plant thylakoids the major polar lipid components are the electroneutral galactolipids, monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG) having levels of about 50% and 25% of the total lipids, respectively [14]. A special property of MGDG which has been discussed in considerable detail in terms of its possible function in the intact membrane [30, 63] is that on isolation

it forms non-bilayer structures [34]. Another important feature is that both lipids have mainly 18 carbon long acyl chains which are extremely unsaturated, a property which makes the thylakoid membrane highly fluid at normal temperatures [7]. The remaining polar lipids are phosphatidylglycerol (PG) and sulphoquinovosyldiacylglycerol (SQDG) which typically have concentrations in higher plant thylakoids of 10 and 12%, respectively, while phosphatidylcholine (PC) makes up most of the remaining 3%. Although the values given represent an average percentage composition, the relative amounts of the thylakoid polar lipids can vary with species or environmental conditions. PG and SQDG are the only lipids having a net negative charge and are characteristic of the membranes of photosynthetic organisms. Although PG is found in many different types of biological membranes, in the thylakoid a proportion of this lipid contains trans-Δ3-hexadecenoic acid [22]. This form of PG is unique to fully mature thylakoids and there have been speculations about the involvement of this particular molecular species in maintaining the organisation of pigment protein complexes within the membrane [65]. SQDG is an intriguing lipid class since it is an unusual molecule found in high concentrations only in photosynthetic membranes. Recent considerations of surface electrical properties of thylakoids and isolation of specific protein complexes are giving hints as to the localization and function of this sulpholipid and it is the implications of these new developments which we wish to discuss here.

Sulphoquinovosyldiacylglycerol: Structure, occurrence and biosynthesis

Sulphoquinovosyldiacylglycerol, commonly referred to as the "plant sulpholipid", was first discovered by Benson and co-workers in 1959 [10]. It was the availability and use of [^{35}S]-sulphate that led to its identification and allowed for its subsequent analysis. Studies on its degradation products [18] revealed that deacylation yielded sulphoquinovosylglycerol which exhibited a molecular rotation $[M]^{25}D$ of $+31\,000°$, characteristic of alkyl α-D-glucopyranosides. In addition, its rotational shift in cupra B of $-370°$ indicated three adjacent equatorial hydroxyl groups as in glucosides [46]. SQDG resulting from either deacylation of the lipid or from chemical synthesis [51] has been shown to have similar infra-red spectra [38] and the structure has also been confirmed by X-ray crystallography of its rubidium salt [58]. Complete degradative analysis of SQDG has now been carried out and it is described as: 1,2-diacyl-[6-sulpho-α-D-quinovopyranosyl-(1′→3)]-sn-glycerol. D-quinovose is 6-deoxy-D-glucose and the prefix sulpho- denotes a sulphonic acid group. The chemical structure of the headgroup of the lipid is shown in Figure 1. It is important to note that, in contrast to most naturally occurring organosulphur compounds, including sulphur containing lipids, where sulphur occurs in an ester ($C-O-SO_3^-$) linkage, SQDG contains a sulphonic acid group in which carbon

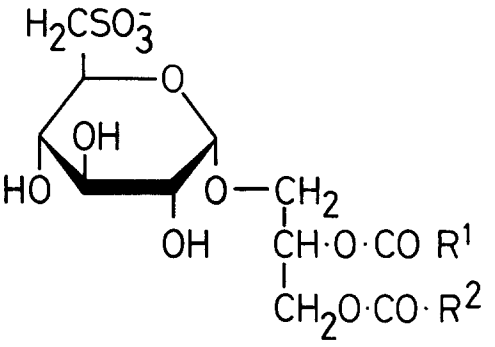

Figure 1. The chemical structure of the plant sulpholipid, SQDG (1,2-diacyl-[6-sulpho-α-D-quinovopyranosyl-(1′→3)]-sn-glycerol).

is directly bonded to sulphur as $C-SO_3^-$. Sulphonic acids of this type are chemically very stable and strongly acidic in a wide pH range.

SQDG has been reported to occur in a variety of organisms although some characterisations are only preliminary. It has thus been found to occur in phytoflagellates, cyanobacteria, green, red and brown algae, purple sulphur and non-sulphur bacteria [43] and in higher plants [41]. In higher plants it occurs in very low amounts in non-photosynthetic tissue but in higher amounts in photosynthetic tissue. In the latter it is only found in the chloroplasts [19] and in particular in the thylakoid membranes [21].

The apparent lack of a lipase specific for sulpholipid [41] has prevented the unequivocal characterization of its distribution within the thylakoids. Examination of thylakoid fragments shows SQDG to be present in both appressed and non-appressed regions, the actual amounts varying with the type of procedure involved for the preparation of the membranes [16, 35, 54]. Results obtained with detergent derived particles also point to an association of SQDG with protein complexes found in both regions of the membrane (see later section). The use of lipid antibodies [64] has indicated that polar lipids are in general most abundant at the internal rather than the outer surface. Nevertheless, the same techniques suggest that SQDG may be preferentially located at the external surface although most of it is not accessible to antibodies from either side of the membrane. In addition, hydrolase treatment of membranes (Harwood JL, personal communication) has confirmed that the majority of sulpholipid molecules are inaccessible from the aqueous media. Recently, it has been argued that the acidic lipids are located in the inner leaflet of the bilayer [69] supporting the proposal that the charged head groups could act as a proton conducting pathway [39]. Other evidence, however, tends to indicate that at least two thirds of the phosphatidylglycerol molecules are in the outer leaflet of the bilayer [30].

The positional distribution of fatty acids in the molecular species subfractions obtained from SQDG has not been unequivocally determined. It appears that linolenic (C18:3) and palmitic (C16:0) acids are the major constituents while linoleic (C18:2) and oleic (C18:1) acids occur in lesser amounts. It has been shown that the proportion of palmitic acid at the C-1 or C-2 position of the glycerol backbone varies with the plant type [40]. In most plants examined, however, SQDG is mainly composed of the palmitoyl/linolenoyl and palmitoyl/linoleoyl species [42, 57].

The metabolism of SQDG has attracted a considerable amount of research, but the actual biosynthetic pathway remains unclear and it is not yet established whether the chloroplast is autonomous in SQDG biosynthesis or not. The biosynthetic routes suggested have been summarized [41]. Briefly, a pathway analogous to glycolysis has been proposed and called the 'sulphoglycolytic pathway'. This results in the formation of a nucleotide diphosphate sulphoquinovose. The precursor(s) of the pathway remain a matter of controversy and more recently [52] the very existence of the sulphoglycolytic pathway has been questioned. The catabolism of SQDG in plant tissues also remains obscure mainly through the lack of identification of a sulpholipid specifc enzyme.

Correlations between the appearance of chlorophyll and the presence and concentration of sulpholipid in photosynthetic tissues have been found. Thus, although the initial levels of this lipid are significant, it has been shown that the amounts increase on greening of etiolated tissue or on maturation of protoplasts [45, 12, 48]. It has been suggested that SQDG may assist the orientation of chlorophyll molecules in the membrane [9] and model systems have indicated the possibility of interactions between these two types of molecules [71]. In contrast, however, it has been shown that *Chorella pyrenoidosa* [68] can be grown heterotrophically so as to completely lack sulpholipid and have normal levels of chlorophyll, but such cultures could not photosynthesise.

Most interestingly, in a series of labelling experiments on leaf sulpholipid [42] it was found that certain molecular species of the lipid were labelled faster than others. It was thus suggested that besides a structural role the sulpholipid may have a metabolic role within the membrane.

Surface electrical charge on the thylakoid membrane

Free flow particle electrophoresis measurements on isolated thylakoid membranes made by Mercer et al. [48] and more recently by Nakatani et al. [55] and Nakatani and Barber [56] suggest that the electrical charge on the outer surface is due to acidic and basic residues of exposed segments of intrinsic proteins. Variations of pH and experiments involving the use of chemical modifiers suggest that the negative charges are derived from carboxyl groups of aspartic and glutamic acid residues. At about pH 4.3

the surface is isoelectric and below this pH value it becomes positively charged. The use of 1,2-cyclohexanedione treatment indicated that most of this charge is due to the guanidino group of arginine. These conclusions gain support from other studies including treatments with carbodiimides [11] and calcium binding [62].

Thus there is no evidence to suggest that acidic lipids contribute to the electrical charge on the outer surface. Far less is known about the nature of the electrical charge on the inner lumenal surface. Using inside-out vesicles derived from the appressed lamellae of the grana, Mansfield et al. [47] concluded that the inner surface is more negatively charged than the outer but no chemical modification studies were conducted to investigate the nature of the ionisable groups involved. However, the isoelectric point of the inner surface was found to be at pH 4.0, a value higher than expected even if the acidic lipids were preferentially located in the inner leaflet of the bilayer.

For the sake of argument, if it is assumed that PG and SQDG are located entirely in either the outer or inner leaflet then they would be expected to contribute significantly to the electrical charge density on either surface. As can be seen in Figure 2 a surface pressure-area isotherm of SQDG indicates that the area occupied by its head group, prior to the collapse point of the monolayer, is about 0.48 nm^2. A slightly smaller headgroup size has been obtained for PG of 0.40 to 0.42 nm^2 [31]. Taking the combined level of SQDG and PG as 22% of the total lipid and assuming a random distribution, then each negative charge due to the acidic lipids would occupy 200 nm^2 corresponding to a charge density of about -8×10^{-2} C m^{-2}. This calculation has assumed an average head group area for the total lipids of about 0.60 nm^2 (MGDG and DGDG have larger head groups than SL and PG) but no allowance has been made for the presence of protein. If we assume the thylakoid membrane has a lipid to protein weight ratio of 1:1 then there will be about 500 lipid molecules of molecular weight 1 KDa to each protein complex of 500 KDa. Assuming that the protein complexes carry no net charge and can be taken as cylinders having an exposed end surface area of 200 nm^2 then the area per negatively charged lipid increases to approximately 360 nm^2 so that the surface charge due to the acidic lipids reduces to -4.4×10^{-2} C m^{-2}. This minimal value is only slightly higher than the values for the outer and inner surfaces measured using a range of techniques [3]. However, as already stated above, in the case of the outer surface it seems that the net negative charge is due entirely to carboxyl groups of amino acids. Therefore it can be concluded that for the outer surface SQDG or PG must be closely associated with protein in such a way that their charges are inaccessible to the external aqueous phase. It is possible, however, that the majority of the acidic lipids are located almost entirely at the inner surface although direct experimental evidence tends not to support this [30]. In fact, as stated earlier, both antibody and

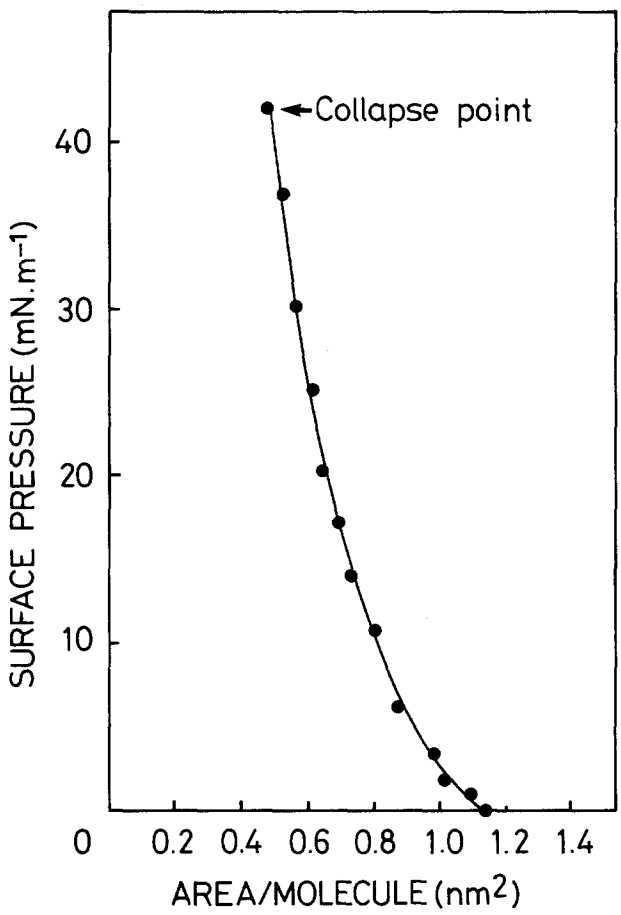

Figure 2. Force-area isotherm obtained from SQDG at 20° on a distilled water subphase [31].

lipase treatments, as well as the isoelectric point measurements argue against this possibility.

Alternatively, the electrical characteristics of the inner surface may, like the outer surface, also be due to amino acid residues so that the majority of SQDG and PG in the thylakoid membrane would be closely associated with proteins.

Location and function of SQDG

What evidence is there for the suggestion that acidic lipids are closely associated with proteins? For some years now Remy and his colleagues [65] have argued that PG plays an important role in the formation of oligomeric forms of LHC. However, although there have been speculations there has been no

evidence concerning the specific location and function of SQDG. Nevertheless experimental data is now emerging which suggests that SQDG may play a very important role in the structure and function of at least two important protein complexes. In collaboration with Pick and Weiss we have found that SQDG is tightly bound to CF_0-CF_1 complex isolated either from spinach chloroplasts or the halotolerant alga *Dunaliella salina* [60]. The estimated level of SQDG ranged from 5 (in spinach) to 20 (in *D. salina*) lipid molecules per CF_0-CF_1 complex and the lipid could not be exchanged with phosphatidylcholine, phosphatidylserine or with glycolipids. Moreover, removal of some of this tightly bound SQDG (10 to 30%) with extensive detergent treatment was accompanied by an inhibition of ATPase activity which could not be restored by the addition of glycolipids. Clearly these results suggest that the association of SQDG with CF_0-CF_1 is very strong and is essential for the integrity of the enzyme. Interestingly the addition of excess SQDG and other acidic lipid, to isolated CF_0-CF_1 causes an inhibition of its activity [59]. SQDG is important, however, at low concentrations for reconstituting the ATP-Pi exchange of this enzyme but this is due to the ability of SQDG to decrease the proton permeability of membrane vesicles composed of thylakoid galactolipids [61]. Although less well studied than CF_0-CF_1 we also have evidence that SQDG is firmly bound to the PS2 protein complex [33]. Using Triton X-100 and sucrose density centrifugation we have isolated a PS2 complex from spinach chloroplasts which contains a small number of polypeptides and redox components. Associated with this complex are SQDG and MGDG possessing unusually saturated fatty acids. Taking 40 chlorophyll-*a* molecules per PS2 reaction centre indicates that there are about 12 molecules of SQDG associated with each isolated complex. As in the case of CF_0-CF_1, it has been shown that excess acidic lipids result in an inhibition of PS2 activity when monitored as oxygen evolution from PS2 enriched membrane fragments [36].

These interesting findings raise the question about how much of the total SQDG is closely associated with protein complexes. Above we crudely estimated that there are about 500 polar lipid molecules per complex, a number also derived by considering chlorophyll-lipid ratios [15]. Since SQDG makes up about 12% of the lipid composition then 50 sulpholipid molecules are available for interacting with each complex assuming that they are all about the same size. As yet there is no experimental evidence to suggest that there is specific association of sulpholipid with other main intrinsic complexes; the calculated pool of 50 molecules per complex would increase if this acidic lipid is preferentially associated only with PS2 and CF_0-CF_1.

Although it is now accepted that there is a lateral separation of protein complexes between the appressed and non-appressed regions of the thylakoids and that there is transmembrane asymmetry of polypeptides, a similar distribution of SQDG along or across the membrane is not established. On

balance it seems that this lipid occurs in both membrane regions consistent with its interaction with PS2 (normally in the appressed region) and CF_0-CF_1 (localized exclusively in the non-appressed region).

Conclusion

Experimental evidence is emerging to support the idea that SQDG is closely associated with intrinsic complexes of the thylakoid membrane. This association is probably partly stabilized by electrostatic interactions between its negatively charged sulphonate group and positive charges within the proteins. In some cases the interactions may be very strong as suggested by the resistance of some SQDG molecules bound to CF_0-CF_1 to exchange with other acidic lipids. It is possible that SQDG has a function similar to cardiolipin in the inner mitochondrial membrane. Cardiolipin is a negatively charged lipid which is required for the catalytic activity of cytochrome oxidase [66] and CF_0-CF_1 ATP synthetase [44] and has been shown to be firmly bound to the former [67]. We suggest that SQDG probably does not form a significant part of the general lipid matrix or is involved in "protein packaging" as postulated from MGDG [32, 63]. Rather we suggest that this acidic lipid plays a more specific and intimate role in the catalytic activity of proteins and therefore does not readily exchange with other lipids in the membrane. Consistent with this proposal is that the lipid class contains a high degree of saturated acyl fatty acid chains indicative of a "boundary" rather than a "bulk" lipid. Indeed, ratio labelling experiments indicate that saturated forms of sulpholipid are important for the functional activity of the thylakoid during their illumination [41, 42]. The close association of this lipid with proteins functioning in photosynthesis is further emphasised by the fact that a wide range of photosynthetic bacteria have membranes containing lipids quite different to those of the higher plant thylakoids but still retaining a significant level of sulpholipid [43].

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