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Membrane in chloroplasts. A topological approach to grana and frets

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Abstract

The membrane system of chloroplasts, where photosynthesis takes place, presents a remarkable organization of flat thykaloïds in grana and frets which contributes to the efficiency of the photochemical and biochemical steps of the process. A topological analysis of this organization is proposed, which develops a relationship with screw dislocation walls in lamellar liquid crystals. This analysis makes possible a rather simple geometrical description of the organization depending upon two parameters only: the stacking distances of thykaloïds in grana and frets. This suggests that the formation of grana and frets, and their overall structure, might be viewed as a separation between two lamellar stackings of thykaloïds whose different spacings are associated with a distribution along the membrane of the molecules intervening in the photochemical process.

Keywords: Chloroplasts; Membranes; Lamellar liquid crystals; Screw dislocations

The organization of the membrane system of chloroplasts in grana and frets is shown in fig. 1. This figure, drawn from serial sections of chloroplasts observed by electron microscopy [1,2], is an over-symmetrical representation of a biological organization and the reader is invited to consult the references in order to appreciate it within the context of the original micrographs. The basic elements of this organization are flattened bags of lipid membranes, called thylakoïds, with a thickness of about 150 Å, which are distributed in appressed regions, the grana, and non-appressed regions, the frets. In the appressed regions the thylakoïds have a disk-like shape and are piled up in close contact to build a cylindrical granum with a diameter of about $1–3 \times 10^3$ Å; in the non-appressed region they form extended lamella, the frets, which are separated by a distance which can be estimated from the micrographs to be 2–3 times larger than their thickness. The frets connect together the discs within a granum and those belonging to different grana. One of the major achievements of the studies described in refs. [1,2] was the recognition that grana and frets are indeed "tailored" out of a unique membrane folded upon itself in a rather complex manner. Finally, grana and frets are embedded in the plasmatic non-differentiated part of the chloroplast called the stroma. Photosynthesis occurs within this membrane system along two sequential processes: a photochemical one taking place in the membrane followed by a biochemical one taking place in the stroma. The grana and frets organization most likely favors optimal yields for

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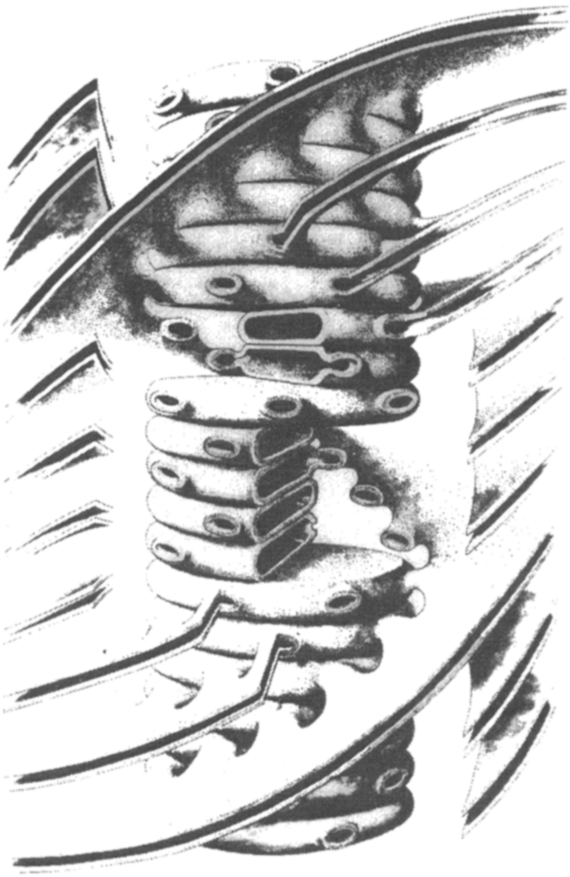

Fig. 1. Representation of a granum showing the multiple fret connection to each disc. Only one fret is shown in full, the rest being cut away, along with parts of some of the discs. The thickness of one disc is about 150 Å (from ref. [1] with authorization).

these two steps: the stacking of disks in the grana increases the probability of photon capture while the large area of contract between the frets and the stroma makes the diffusion of the products of the photochemical reactions in the stroma more favorable. It should be noted also that molecules intervening in the photochemical process, forming the so-called photosystems I and II, have different relative concentrations in grana and frets.

The scope of this paper is to propose a description of this organization in the simplest topological terms possible and to suggest a physical mechanism for its formation from the rather regular stacking of flat thylakoïds which is presented as the precursor state [1]. We were encouraged in such a project by the consideration that the topology and symmetry of the organization are the same whatever the plant studied [1] and that the stacking/unstacking of the discs in the grana can be observed in vitro by changing the ionic strength of the surrounding medium [3]. These two facts strongly suggest that this complex organization is governed by genetic factors common to most green plants which express themselves through a limited number of physico-chemical parameters. For this reason we thought that an analysis of this organization using purely physical chemical terms, and inspired from liquid crystal studies, might be of interest.

For the sake of simplicity we represent the thylakoïds by their middle surface. In fig. 1 it appears that two adjacent parallel surfaces of discs within a granum are connected on the boundary of the granum by the parallel surfaces of the frets surrounding this granum, and vice versa. The two families of surfaces, discs and frets, are therefore tilted relative to each other, as shown in fig. 2, and their connections can be organized along helicoïdal trajectories with parallel axes which define the wall ensuring the junction between the two families of parallel surfaces. If these two families had equal spacings they would be tilted by opposite angles relative to the direction of the axes of the helices, the helices would be regular and this corresponds well to the description of a wall of screw dislocations in smectic or lamellar liquid crystals [4,5]. If the two families of surfaces have different spacings, and this is the case here, they have different tilt angles relative to the axes of the helices and the helices are distorted. Following this, we propose to describe a granum as a domain of one lamellar phase with small spacing (≈ 150 Å) delimited by a wall of distorted screw dislocations ensuring the junction with a surrounding domain of another lamellar phase with larger spacing (from 300 to 450 Å), this wall being wrapped as a cylinder around an axis normal to the lamellar phase of small spacing so that the axes of the screw dislocations draw helices on this cylinder. A geometrical description can be deduced from this topological description which provides information about the structure of the wall on the basis of rather simple arguments.

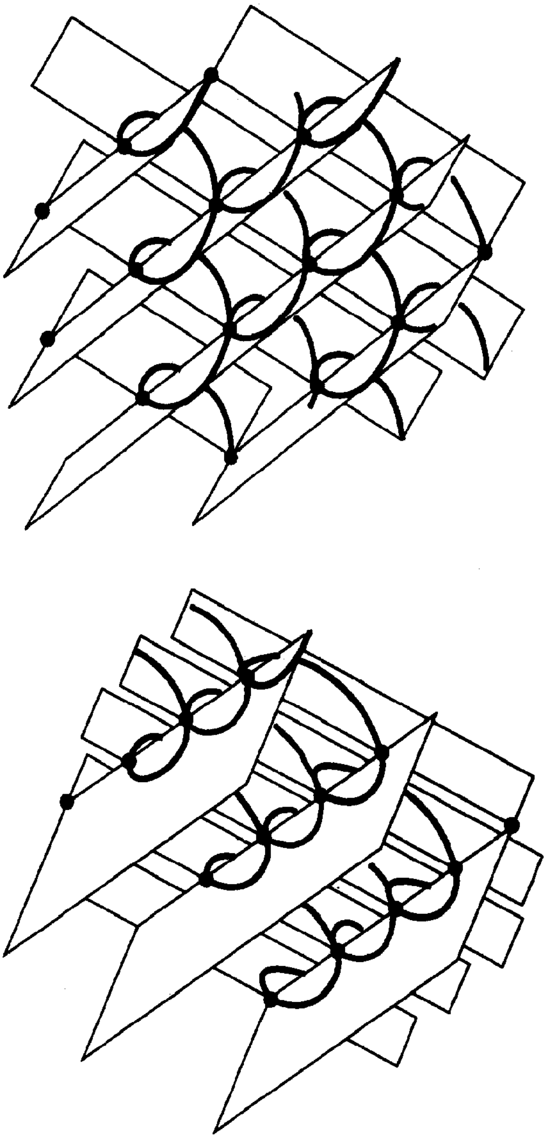

Fig. 2. The trajectories linking the connecting points between two families of parallel surfaces with equal spacings (above) and different spacings (below). In the first case they are regular helices analogous to screw dislocations in lamellar liquid crystals, in the second case the helices are distorted. The surface containing the axes of the helices is the wall separating the domains of the two families.

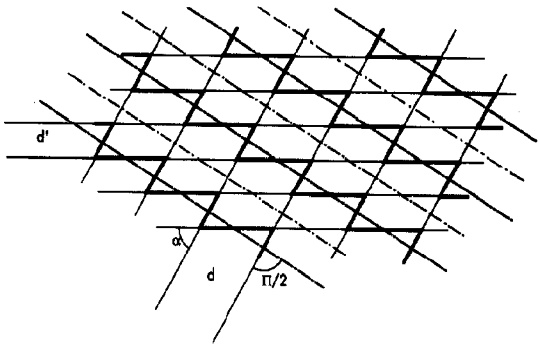

Fig. 3. The wall separating two domains with spacings d and d' (thin lines) with the projection of the distorted helices (heavy and thin zig-zag lines) and their axes (dotted lines).

First, screw dislocations are defect lines with a tension and they have a minimal length when their axes are close to normal to the lamellar phase with large spacing. Second, these lines must cross as many surfaces of small spacing as surfaces of large spacing (as the grana and frets organization is formed from a unique stacking of thylakoïds). It results from these arguments that the two lamellar systems must be at an angle a such that $d' = d \cos \alpha$, d' and d being the small and large spacings, respectively. The organization of the dislocation lines in the wall is thus totally determined by the values of the two spacings, as shown in fig. 3, and their separation δ measured along the surface of small spacing is such that $\delta = d/\sin \alpha$. Finally, the wrapping of the wall on a cylinder must respect the periodicity of the wall and the cylinder with smaller diameter will be that built from the translation cell of the wall as shown on fig. 4. If the side of the cell perpendicular to the cylinder axis contains m surfaces with d spacing at a distance $d/\sin \alpha$ measured along this side, hence m dislocation lines, and the side parallel to the axis contains n surfaces with d' spacing at a distance d' then m and n are related by $m/n = \sin^2\alpha$. Thus it appears that the structure of the wall and that of the granum are directly related as the radius of the latter is $r = md/2\pi \sin \alpha$, and its pitch $p = nd'$ and their ratios $r/p = (\tan \alpha)/2\pi$.

With $d'/d = \frac{1}{3}$, one obtains $\alpha = 70{,}53°$, $m/n = 0.88$ and $r/p = 0.45$. These ratios have the

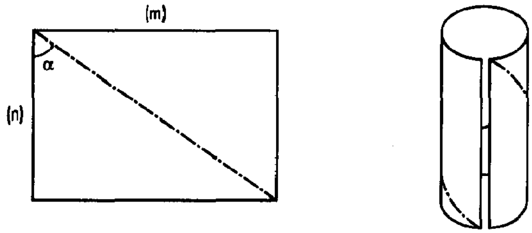

Fig. 4. One pitch length of a cylindrical granum is obtained identifying two opposite sides of the translation cell of the flat wall admitting one axis of a helix as a diagonal (the $m-1$ other axes are not represented).

same orders of magnitude as those which can be deduced from fig. 1 or the equivalent representations and micrographs of ref. [2]: the number of dislocation lines around the granum is close to the number of discs in the pitch and the length of the pitch is close to the diameter of the granum.

Thus, one of the main geometrical features of the organization of the internal membranes of chloroplasts as grana and frets, the relation between the diameter of the granum and the pitch, can be approached from the knowledge of the spacings of the thylakoïds in grana and frets. It is also interesting to notice that the ratio of two integers m/n closest to 0.888 is $\frac{8}{9}$ which corresponds coarsely to the topology (number of dislocations) and the size (radius) of the structure presented in fig. 1. This leads us to propose that the formation of such a particular organization might result from the appearance, within a uniform lamellar stacking of thylakoïds with only one spacing, of two types of lamellar stackings with different spacings. This might be looked at as formally similar to the phase separation process between lamellar phases with different spacings observed in liquid crystals [6]. Such a process might be induced by the appearance, at a certain stage of the chloroplast development, of molecules associated with the photochemical process whose lateral distribution along the membrane would be coupled to the thykaloïd stacking. Also, the interface between two coexisting domains with different lamellar spacings is ensured by a wall of distorted screw dislocations which might find their origin in the non-distorted ones which are most likely naturally present in the precursor system of thylakoïds, as in any lamellar liquid crystal [5]. Such a wall costs energy and this cost might be decreased in two ways: on one hand that associated with the line tension of the dislocations is minimized by having their axes normal to the thylakoïds of the frets with the largest spacing, on the other hand that associated with the distortion of the helices of the screw dislocation (which has a path in the appressed region of the granum larger than that in the non-appressed region of the frets as shown in fig. 3) can be decreased curving the wall around an axis normal to the thylakoïds of the appressed region so that the core of the dislocation becomes closer to a minimal surface [7]. Following this approach the overall structure might be seen as the result of the competition between the interaction of the thykaloïds and the distorsion of the dislocations and taking those terms in account should help to improve the rather simple approach proposed in this paper.

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