Molecular Crystals and Liquid Crystals Incorporating Nonlinear Optics

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/gmcl17

Cholesteric-Like Pattern in Plant Cell Walls: Different Expressions

Daniele Reis [a]

[a] Laboratoire des Biomembranes et Surfaces Cellulaires Végétales, ENS, 46 rue d'Ulm-75230, Paris, Cedex, 05, France

Version of record first published: 13 Dec 2006.

To cite this article: Daniele Reis (1987): Cholesteric-Like Pattern in Plant Cell Walls: Different Expressions, Molecular Crystals and Liquid Crystals Incorporating Nonlinear Optics, 153:1, 43-53

To link to this article: http://dx.doi.org/10.1080/00268948708074523

Mol. Cryst. Liq. Cryst., 1987, Vol. 153, pp. 43-53
Photocopying permitted by license only

Printed in the United States of America

CHOLESTERIC-LIKE PATTERN IN PLANT CELL WALLS: DIFFERENT EXPRESSIONS

DANIELE REIS
Laboratoire des Biomembranes et Surfaces Cellulaires Végétales, ENS, 46 rue d'Ulm, 75230 Paris Cedex 05, France.

Abstract A striking similarity exists between helicoidal cell walls and cholesteric liquid crystals. The generality and the versatility of the system are illustrated. The question of the respective role of cell directed and self assembly mechanisms is discussed. In particular the importance of the heteromolecular assembly (grafting of matrix subunits on cellulose) is emphasized.

INTRODUCTION

Analogies can be drawn between liquid crystals and numerous living structures. The cholesteric-like structures provide the most remarkable examples. They can be found in several biological materials, particularly those made of fibrils arranged according to defined three-dimensional patterns: chitin in cuticles of Arthropods, DNA in chromosomes of Dinoflagellates, collagen in the matrix of bone structures (1, 2). Such examples are generally interpreted as consolidated cholesteric systems (1).

Recent data indicate that cell walls often present a helicoidal internal geometry similar to cholesteric liquid crystals. They correspond to a complex heteromolecular construction, built from both cellulose microfibrils, i.e long and regular molecules, and numerous matrix elements, i.e short and branched polysaccharide and glycoprotein molecules.

The construction provides a highly ordered envelope

around the cell, allowing several functions (resistance to tension or compression strain, capacity for growth). Recent data have focussed on the generality of the helicoidal system (for review, see 3). At present, the question is to understand how the cell can build the helicoid and adapt it to differentiation and environmental signals. According to the majority of plant cytologists, the construction of the wall seems mainly directed by membrane movements and energy consuming structures (4). Self-assembly mechanisms of actual liquid crystal type could also intervene (5, 6).

The present paper is an attempt to draw the attention on the cholesteric-like characteristics of cell walls, by taking into account the versatility of their structure and the diversity of their behaviour.

MATERIAL AND METHODS

The wall of plant cells is highly massive and chemically complex. The exposure of the framework as well as its visualization raise particular problems. The basis of the techniques of sequential extractions have been previously provided (7). Results were obtained by transmission electron microscopy. Stereoscopy was by using a goniometric stage.

Attempts of *in vitro* reassembly were performed from polysaccharide fractions extracted from cell walls (elongating mung bean hypocotyls, wood cells, tamarind seeds). Their behaviour was followed by means of the polarizing microscope according to Livolant (8).

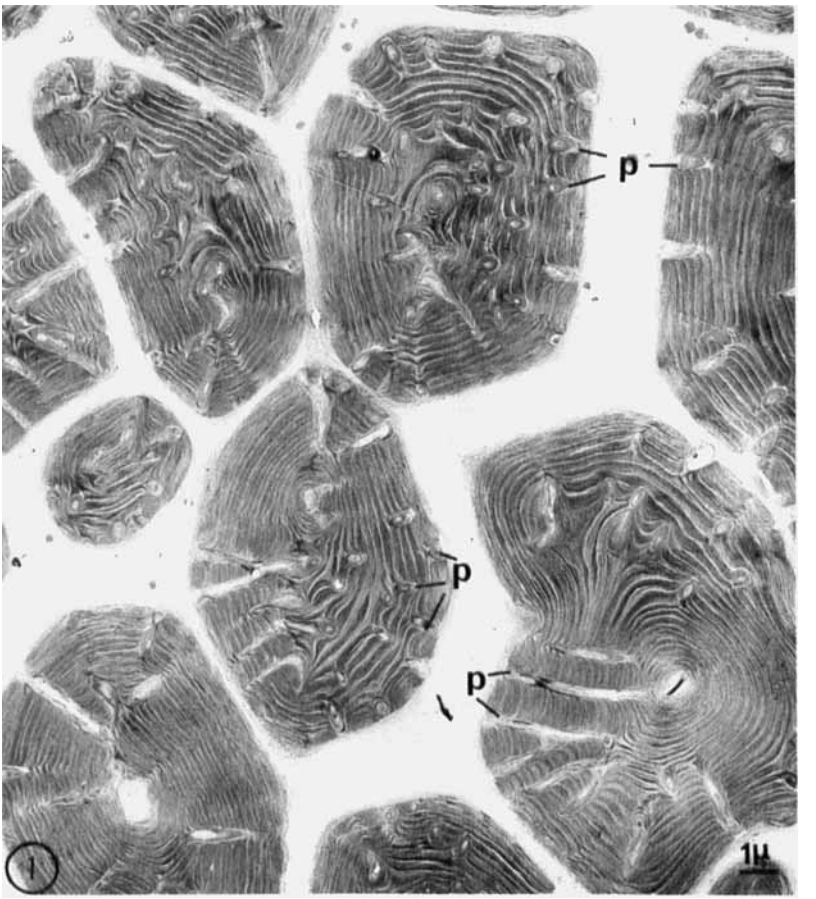

FIGURE 1. General view of plant cell wall. Hazelnut shell. Thick and strongly consolidated cholesteric-like system; p, pit field.

HELICOIDAL GEOMETRY OF PLANT CELL WALLS

Once a routine technique had been developed which allowed to expose the wall framework, it became possible to study cell types left aside for long because of technical reasons. It appeared that walls showing a helicoidal pattern are en-

countered in numerous types of cells, the young ones as well as the highly differentiated and thick walled ones (fig. 1).

The basic texture shows a geometry similar to the geometry of cholesteric structures: the cellulose microfibrils are organized in parallel planes and their orientation regularly varies from one plane to the following. On oblique sections one obtains characteristic series of successive arcs (fig. 2). The arcs are cancelled or inverted when the section is tilted. They constitute a monotonous system which can remain self-maintained for a long time (from 5 to some tens nested arcs). Such structures present a very high resistance (as expressed in the so called "stone cells").

A detailed examination of many examples reveals that many variations occur in helicoids. Some are directly depending on technical reasons such as microtomy artefacts (9) or differences in accessibility of the reactive sites (10). These variations can be easily taken into account. From a biological viewpoint, two types of variations exist which occur either at the moment of the assembly of the wall subunits or after the assembly.

During the assembly of cell walls specific variations can be dependent on the cell differentiation. They can be also responses to external treatments: hormones (ethylene), inhibitors, signals targetting the cytoskeleton (colchicine). Beside the monotonous cholesteric-like structures, destabilized systems occur which are more or less difficult to interpret (3). For example, in many supporting cells (sclerenchyma, fibres, wood cells) the helicoid appears only temporarily. Large areas are seen in which the microfibrils keep a constant orientation (blocked zones). The

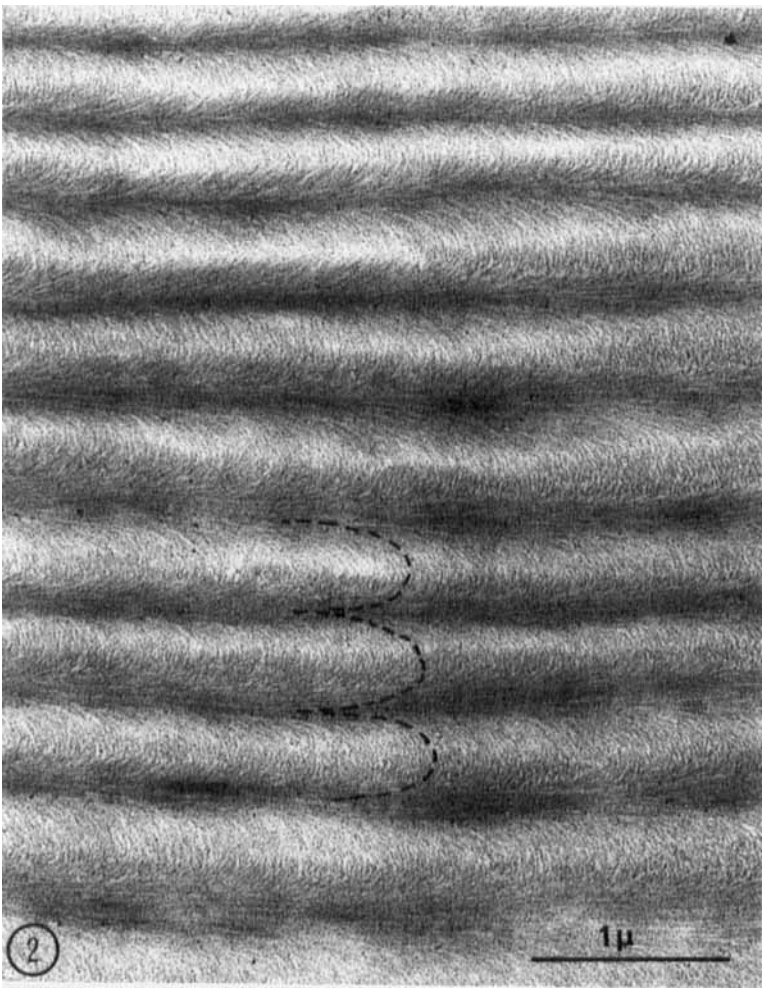

FIGURE 2. Detail of figure 1. Monotony of the arced pattern. Classical alternation of clear and dark bands. The series of nested arcs are built during cellular differentiation.

helicoid occurs only episodically as bursts (single or double semi-helicoids) inserted between these blocked areas (fig. 3).

Once assembled, the wall construction can be consoli-

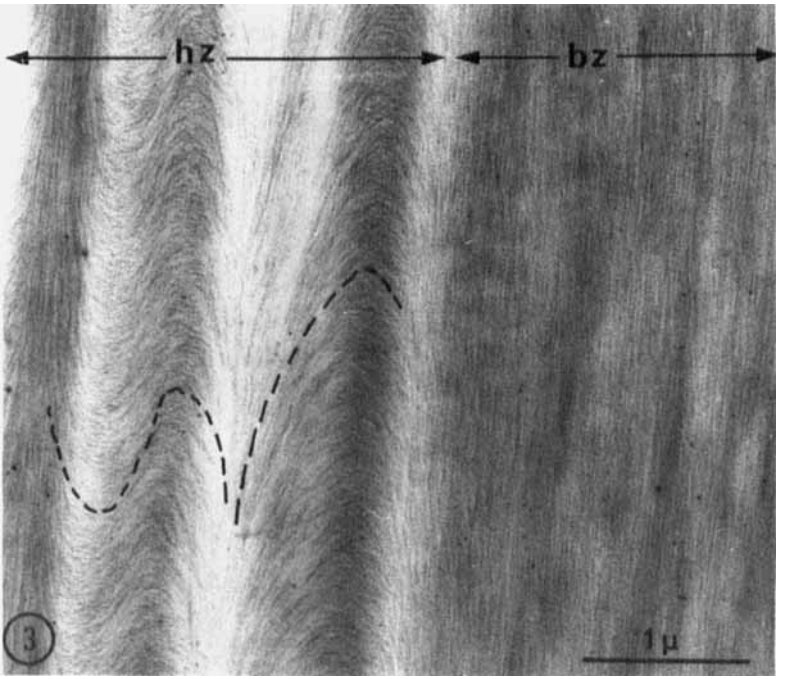

FIGURE 3. Destabilized texture of cell wall. Fibre of birthwort stem. Helicoidal pattern expressed only temporarily (helicoidal zone, hz). In the blocked zone (bz) cellulose microfibrils keep a constant orientation.

dated (locking by chemical bonds) or can remain fluid. In the cell walls of some young cells, the elements which are assembled as typical helicoids show a fluidity which allows their surface growth (fig. 4). The helicoidal geometry becomes dispersed. The arcs and the layering are destroyed and the texture progressively becomes random (11). The process, which is characteristic of growth, is irreversible and its regulation is determinant for the cell physiology. In such case, the consolidation occurs when the construction appears no more cholesteric-like but is dispersed.

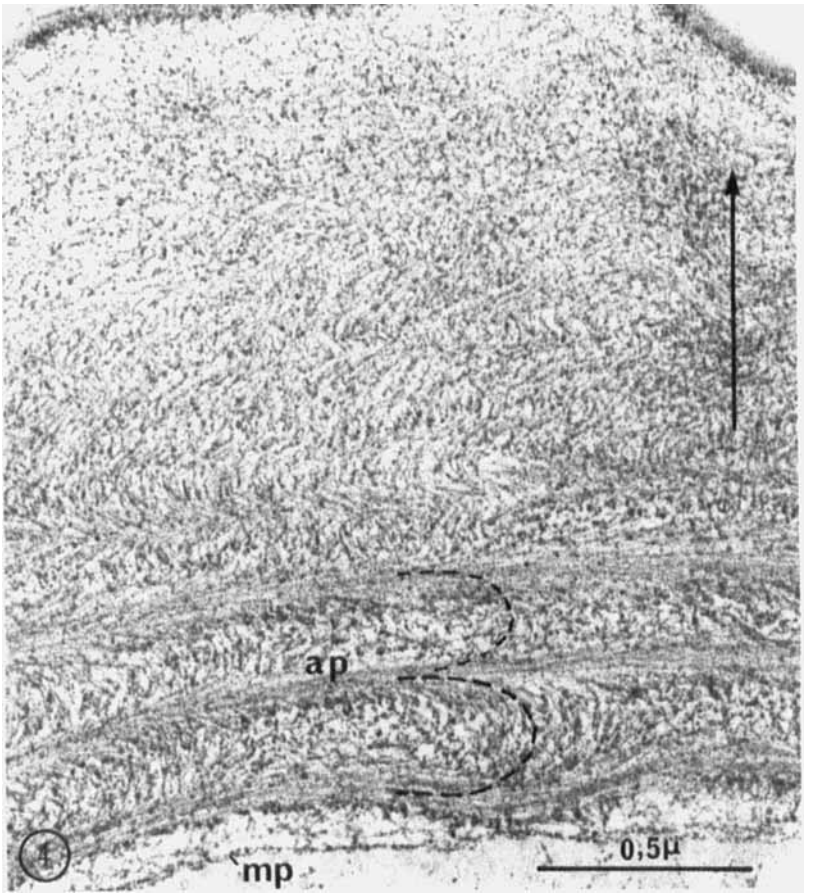

FIGURE 4. Texture of the wall in a growing cell. Mung bean hypocotyl. Cell wall deposited near the plasmalemma, mp, with a typical helicoidal texture (arced pattern, ap). Note the progressive dispersion of the helicoidal construction (arrow).

CHOLESTERIC ASSEMBLY AND/OR DIRECTED ASSEMBLY

All studies indicate that a mosaic of different and sequential events occur in order to construct the wall. Figure 5 is a hypothetical scheme of the assembly of a helicoid wall.

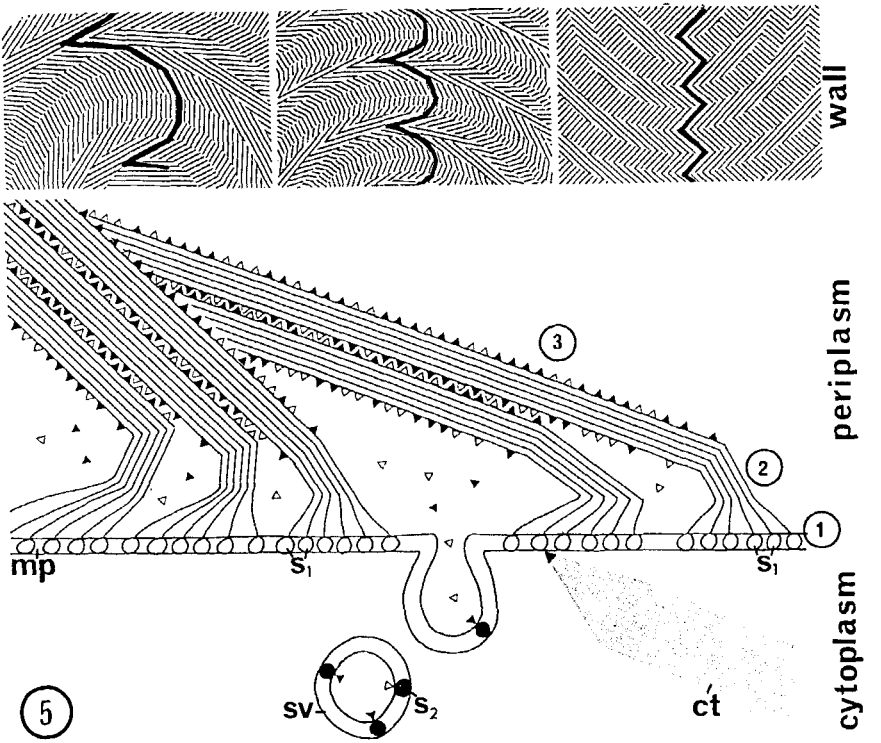

FIGURE 5. Three successive steps in the assembly of cellulose microfibrils of helicoidal cell wall.
1. polymerization; 2. fibrillogenesis; 3. helicoidal assembly.
△ ▲ Pool of matrix subunits; S_1, cellulose synthetases localized in the plasmalemma, mp; S_2, matrix synthetases localized in the membrane of cytoplasmic secretory vesicles, sv. The matrix subunits, excreted into the periplasm via membrane flow, coat the cellulose microfibrils allowing a helicoidal construction. The bulk of the wall hypothesizes that different aspects of helicoidal pattern are due to varying heteromolecular ratios (cellulose/matrix), which can be quantitatively or qualitatively modified.

A causal chain of at least three explicite levels can be distinguished. They link up very rapidly in the periplasm, i.e. the interface plasmalemma-cell wall.

- The first step is the polymerization (formation of covalent bonds) of glucose chains from glucan-synthetases located within the plasmalemma.

- The second step is the microfibrillogenesis which implies self-assembly mechanisms with formation of H-bonds and crystallization. This assembly level is homomolecular (aggregation of glucans).

- The third step is the positioning of the microfibrils into 3-dimensional structures with occurrence of cholesteric-like assemblies. It corresponds to a superior degree of order and is heteromolecular (association of cellulose microfibrils and matrix molecules).

At present the main question is to know how the directed and the self assembly factors are balanced in the helicoidal construction. An important bibliography indicates how the membrane fluidity can orientate the terminal complexes (glucan-synthetases associated to the membrane) in cooperation with the cytoskeleton (12, 13, 14). It does not need to be developed in this paper. Conversely the comparison between helicoidal walls and liquid crystals shows that an evident analogy exists between both systems. The analogy is not sufficient to prove that their ontogenesis is similar . Evidence remains incomplete as long as these systems have not been reconstituted in vitro without cell mediation. In that domain the results are still partial (15). At the present time we focus on purified fractions of matrix (xylans, xyloglucans) extracted from helicoidal cell walls. In certain conditions of concentration, birefringent figures have been observed in vitro in homomolecular fractions (fig. 7). Though no typical cholesteric figure has been until now definitely obtained, they express that a rough

draft of ordered assembly occurs.

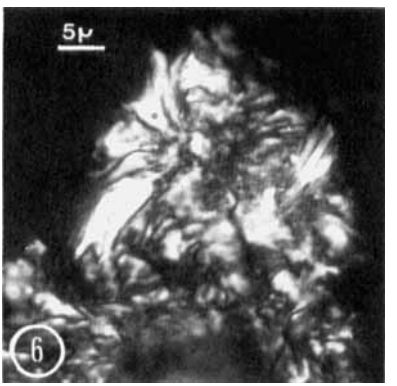

FIGURE 6. Anisotropic solution of concentrated glucuronoxylans in 24% KOH . Extraction from linden tree wood. Polarizing microscope. Birefringent domains and dark areas denoting a certain liquid crystalline order.

Moreover, in some walls in which the helicoidal expression is only temporary, recent data indicate a strong correspondence between the accumulation of glucuronoxylans, the major matrix component of these walls, and the resuming of the cellulose motion in a transitory helicoid (4). It seems that these molecules play a role in the helicoidal assembly of cellulose. One hypothesis is that by lateral grafting on the cellulose chains, they can serve as twisting agent and lead to a heteromolecular assembly. The hypothesis is supported by the results obtained with hydroxypropylcellulose in which the grafted lateral chains of hydroxypropyl serve as an internal plasticizer and provide the cellulose backbone with the capability to arrange in cholesteric mesophases (16, 17).

In order to improve the in vitro experiments, the question is now to reconstitute the conditions of concentration, pressure, charges as close as possible of conditions occurring in the periplam, which is still badly

known. Due to these reasons attempts are still empirical. Further studies will have to take into account the heteromolecular balance and try to target the sequences of matrix elements, both plastifying or locking, along the biosynthetic pathway.

REFERENCES

1. Y. Bouligand. Tissue and Cell, 4, 189 (1972).
2. A.C. Neville. in Biology of the Arthropod cuticle (Springer Verlag, 1975).
3. J.C. Roland, D. Reis, B. Satiat-Jeunemaitre and M. Mosiniak. Protoplasma, in press.
4. S. Bartnicki-Garcia. in Structure, function and biosynthesis of plant cell walls, edited by W.M. Drugger and S. Bartnicki-Garcia (Amer. Soc. Plant Physiol. 1984).
5. B. Vian, D. Reis, M. Mosiniak and J.C. Roland. Protoplasma, 131, 185 (1986).
6. A.C. Neville. Phys. Bull., 37, 74 (1986).
7. D. Reis. Ann. Sc. Nat. Paris, 2-3, 121 (1980-1981).
8. F. Livolant. Thèse, Paris (1984).
9. M.M. Giraud-Guillé. Tissue and Cell, 18, 603 (1986).
10. P. Bonfante-Fasolo, B. Vian and B. Testa. Biol. of the Cell, 57, 265 (1986).
11. J.C. Roland, D. Reis, M. Mosiniak and B. Vian. J. Cell Sci., 56, 303 (1982).
12. W. Herth. in Botanical Microscopy 1985 edited by A.W. Robards (Oxford University Press, 1985).
13. R. M. Brown, C.M. Haigler, J. Suttie, A.R. White, E. Roberts, C. Smith, T. Itoh, K. Cooper. J. Appl. Polymer. Sc., 37, 33 (1983).
14. I.N. Roberts, C.W. Lloyd, K. Roberts. Planta, 164, 439 (1985).
15. D. Reis. Ann. Sc. Nat. Paris, 19, 163 (1978).
16. R. Werbowyj, D.G. Gray. Macromol., 13, 69 (1980).
17. D.G. Gray. J. Appl. Polymer Sc., 37, 179 (1983).