THE CELLULAR STRUCTURE OF CORK FROM QUERCUS SUBER L.

by

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Summary

The main characteristics of the cellular structure of cork from *Quercus suber* L. are reviewed and complemented with new observations of virgin and reproduction cork by scanning electron microscopy. Particular emphasis is given to cell geometry and topology and to the corrugations that are observed in the cell walls. The effect of the growth season in these features is described. Large variations in cell size, wall thickness and corrugations are reported.

Key words: Quercus suber, cork, cell geometry, topology, cell wall corrugations.

Introduction

The cork tissue in the outer bark of *Quercus suber* L., the cork oak, has retained a special place in the history of plant anatomy, ever since Hooke examined thin cuttings of cork under the microscope and revealed for the first time the cellular structure in plants (Hooke, 1664). Cork was used as a case material by early microtomists and made its contribution to the origins of plant and wood anatomy. Original hand-cut sections of cork made by Leeuwenhoek in 1674 were found recently and could still be examined with the light and scanning electron microscope (Ford, 1982).

The description of the structure of cork as made by these researchers was basically confirmed by later studies, mostly by Natividade (1938, 1950), in Portugal. Cork has been described as a homogeneous tissue of thin-walled cells, regularly arranged without intercellular spaces. There is no communication between contiguous cells, which are therefore closed units. Cork cells are figured as rectangular prisms, mostly pentagonal and hexagonal, with their axes along the tree's radial direction, stacked in columns. Accounting for the staggered arrangement of the columns, cork cells have also been described as tetrakaidecahedrons (i.e. polyhedra with 14 faces).

A recent study on the mechanical properties of cork (Gibson et al., 1981) uses the hexagonal prism as a model for cork cells, but further indicates that cell walls are corrugated as shown by scanning microscopy. Defects of different origin which affect the utilisation of cork have also been examined in recent years (Liese et al., 1983). Among these, the lenticular channels are certainly very important and their density and size define the porosity of cork, which is closely related to its quality.

Suberin is the main chemical component of cork cell walls (Pereira, 1982), which were reported as being made up of a lignin and cellulose rich middle lamella and a thicker secondary wall of alternating lamellae of suberin and waxes (Sitte, 1962).

The structure and chemical composition of cork impart remarkable properties: cork is a light weight material, impervious to liquids, a very good thermal insulator, chemically stable and mostly unaffected by microbial activity. It has a high damping capacity and a high coefficient of friction. This special combination of properties long ago found application. Today, one of the best known uses of cork is as stoppers for wine bottles. This is also the most important economical outlet for cork, which is produced only in the Mediterranean and Mediterranean-influenced Atlantic basin, with Portugal having more than half of the total world production.

The first cork layers produced by the original phellogen of the cork oak are removed from the tree at an age of approximately 20–30 years. This cork, named 'virgin cork', is of poor quality; it is used in granulated form for the production of corkboards for insulation or decorative purposes. The new cork layers, produced by a regenerated phellogen after the removal of the virgin cork, are grown for 9 years. This is the 'second cork' and still of relatively

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poor quality. The successive cork layers, grown after the removal of the second cork, are called 'reproduction cork'. They are harvested from the tree at 9-year intervals, with a thickness from 2 to 5 cm. Stoppers are made from reproduction cork.

In spite of the early studies on the anatomy of cork from *Quercus suber*, many aspects relating to its structure and properties are still largely unknown. This paper reviews the previously reported characteristics of the cellular structure of cork and includes new information on its anatomy, particularly related to cell topology, corrugation of the cell walls and variation in cell aspect and size.

Material and Methods

Cork samples were obtained from *Quercus suber* trees growing in Portugal (Serra de Grândola). Two types of cork were sampled and examined: virgin cork and reproduction cork. Cork specimens were cut with razor blades and prepared for scanning electron microscopy (SEM) by surface coating with gold (~ 200 Å thickness).

Results and Discussion

The observations of cork with SEM are summarised in Figure 1, which shows typical shapes and arrangements of reproduction cork cells in tangential, transverse and radial sections. In the tangential section (Fig. 1a), cork cells are seen as polygons in a honeycomb-like arrangement. Three cell walls meet at each vertex of the network. The number of sides in the polygons was found to vary between 4 and 9. Table 1 indicates in the first column the distribution function of cell sides (i.e. the fraction f_i of cells with i sides) observed in the tangential section of reproduction cork. Heptagonal, hexagonal and pentagonal cells are the most frequent, accounting for approximately 95% of the total. Triangular forms are very rare and probably result from a section cut close to the cell base and not parallel to it. They are not sections of triangular prisms, and therefore f_3 is recorded as zero in Table 1. An example of a triangular form is shown in Figure 1a.

Table 1. Distribution function of the number of sides of cork cells in the tangential, transverse and radial sections.* μ_2 = second moment of distribution. For explanation of f_{3-9}, see text.

	Tangential section	Transverse section	Radial section
f_3	0	0	0
f_4	0.021	0.026	0.024
f_5	0.249	0.226	0.203
f_6	0.478	0.526	0.562
f_7	0.216	0.178	0.172
f_8	0.034	0.041	0.038
f_9	0.002	0.004	0
μ_2	0.71	0.70	0.62

* These results correspond to measurements of 900 cells in the tangential section and of 100 cells each in the transverse and radial sections.

It should be noted that as a consequence of Euler's law for two-dimensional networks, the average number of sides in a network with three edges at each node must be 6. The dispersion around the average 6 is indicated by the second moment of the distribution:

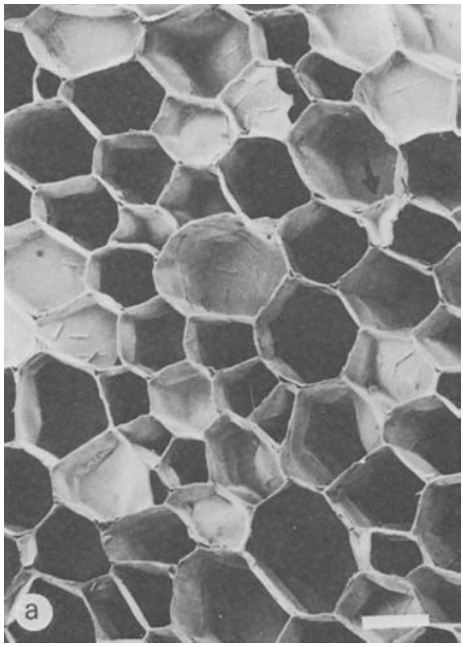
$$\mu_2 = \Sigma (i-6)^2 f_i,$$

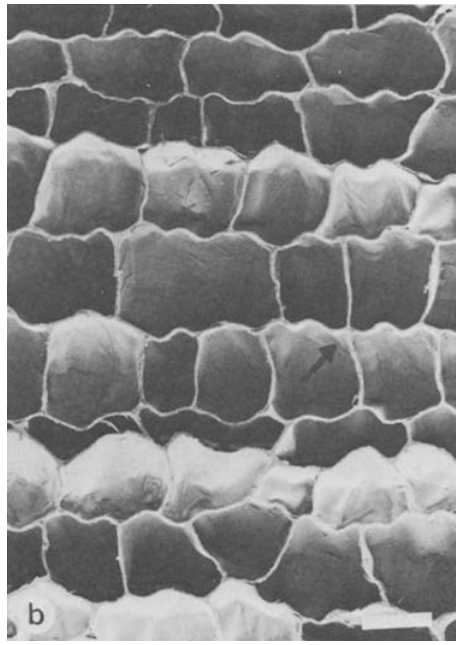
where f_i is the fraction of i-sided polygons. The value of μ_2 for the tangential section of cork is 0.71 (Table 1). Finally, there is a tendency for cells with more sides to have larger areas.

In contrast with the tangential section, transverse and radial sections show a structure that resembles a brick wall (Figs. 1b & c). Again, three edges meet at each vertex, although occasionally it may happen that four edges meet at a vertex, as in Figure 1b. The cells are arranged in rows parallel to the tree's radial direction. Although the aspect of the cells is rectangular, topologically they contain a number of sides (and vertices) which is not always four. In fact, the average number of sides is again 6. The distribution function of the number of sides in each of these sections (Table 1) is not significantly different and the two sections are therefore almost identical. In fact, topologically the three sections are nearly equivalent, as can be concluded from the data in Table 1.

The three-dimensional structure of cork is usually described as formed by prismatic cells, arranged in columns parallel to the tree's radial direction and connected base to base. Since the rows are staggered, with the bases in different planes, the lateral faces of the prisms contact the bases of adjacent cells and are therefore divided into additional faces (Fig. 2a).

These features of the cork structure, as observed previously by optical microscopy, led to the description of ideal cork cells as space filling polyhedra with 14 faces, topologically equivalent to Kelvin's polyhedron with 8 hexagonal and 6 quadrangular faces (Natividade, 1950). In this ideal structure, the bases of cells adjacent to a given cell are at levels 1/3, 2/3,





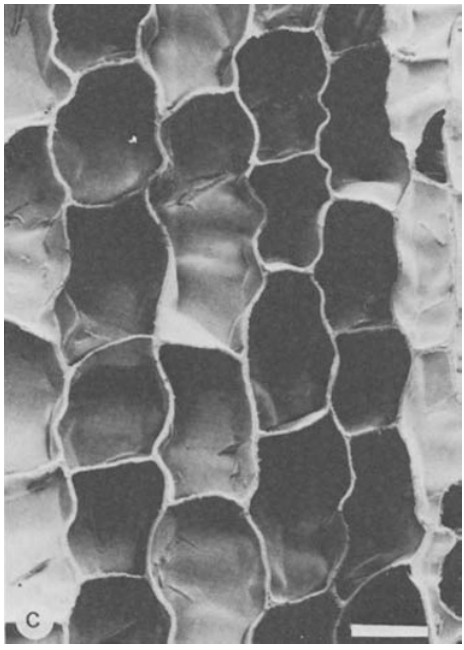


Fig. 1. Scanning electron micrographs of reproduction cork from *Quercus suber*. – a: Tangential section (arrow shows a triangular form). – b: Transverse section (arrow shows four edges meeting in one vertex of the network. – c: Radial section. – Bar is 20 μm.

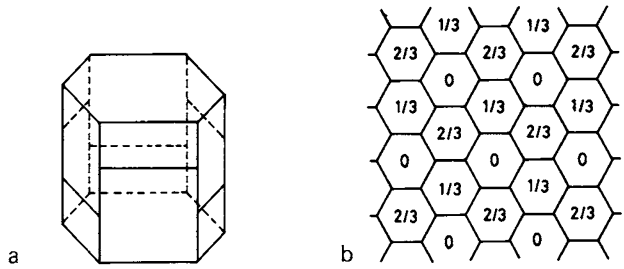


Fig. 2. Schematic representation of (a) a prismatic cork cell and (b) rhombohedral lattice of the cork structure.

1/3, 2/3, 1/3, 2/3, in successive lateral faces, the figures denoting the distance between a base of the reference cell and the adjacent bases of the surrounding cells, expressed in terms of the height of the prism (Fig. 2b). Such a structure of identical prisms is in fact periodic and has a rhombohedral lattice.

The actual structure of cork deviates from this ideal structure of Kelvin's polyhedra for two main reasons: the number of lateral faces is not six for all cells (cf. tangential section) and the heights of the prisms are not the same for all of them (cf. radial and transverse sections). If the heights were uniform, the average number of faces per cell would be 14, i.e., each cell would have, on average, 14 adjacent cells, even if the prisms are not all hexagonal. The number 14 will subsist if there is no correlation between the number of lateral faces and the heights of the cells. This is unlikely to happen. If, as expected, the aspect ratio of the cells is nearly constant and the height is larger for cells with more sides (and therefore bases of larger areas), the coordination number will be smaller than 14 (Fortes, 1986).

In each section, it is possible to determine m_i, the average number of sides of cells adjacent to a cell with i sides. In a space filling planar structure, it is expected that m_i decreases as i increases and, if the arrangement is random, m_i should be nearly linear with 1/i (Aboav, 1980). Figure 3 shows a plot of m_i versus 1/i for each section, indicating a nearly linear relation, which suggests a random arrangement of the cork cells.

The average dimensions of cork cells depend appreciably on the season in which they were formed. Cells formed in the early growing season ('early cork') are larger and have thinner walls than the cells formed in the late growing season ('late cork'). Dimensions of early cork cells were: prism height 30–40 μm, prism base edge 13–15 μm, average base area 4–6 × 10^{-6} cm^2, cell wall thickness 1–1.5 μm. In 'late cork', the prism height is reduced, in some cases to as much as 10 μm, and the cell wall thickness nearly doubles. The number of cells per cm^3 varies from 4–7 × 10^7 for early cork and 10–20 × 10^7 for late cork.

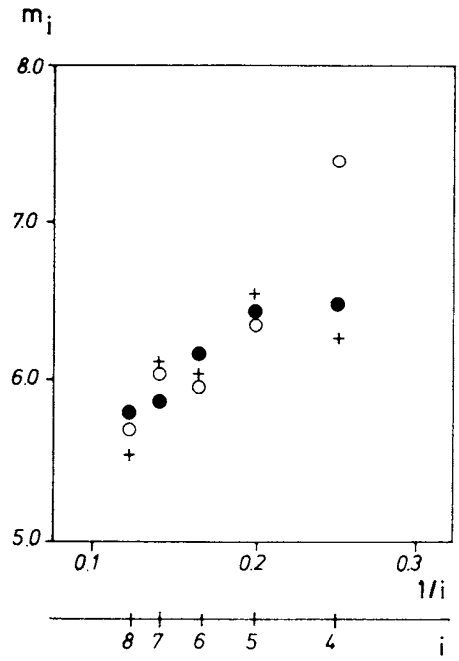


Fig. 3. Average number of sides, m_i, in cells adjacent to a cell with i sides, as a function of 1/i, in each of the three sections of cork: ● = tangential; + = transverse; o = radial.

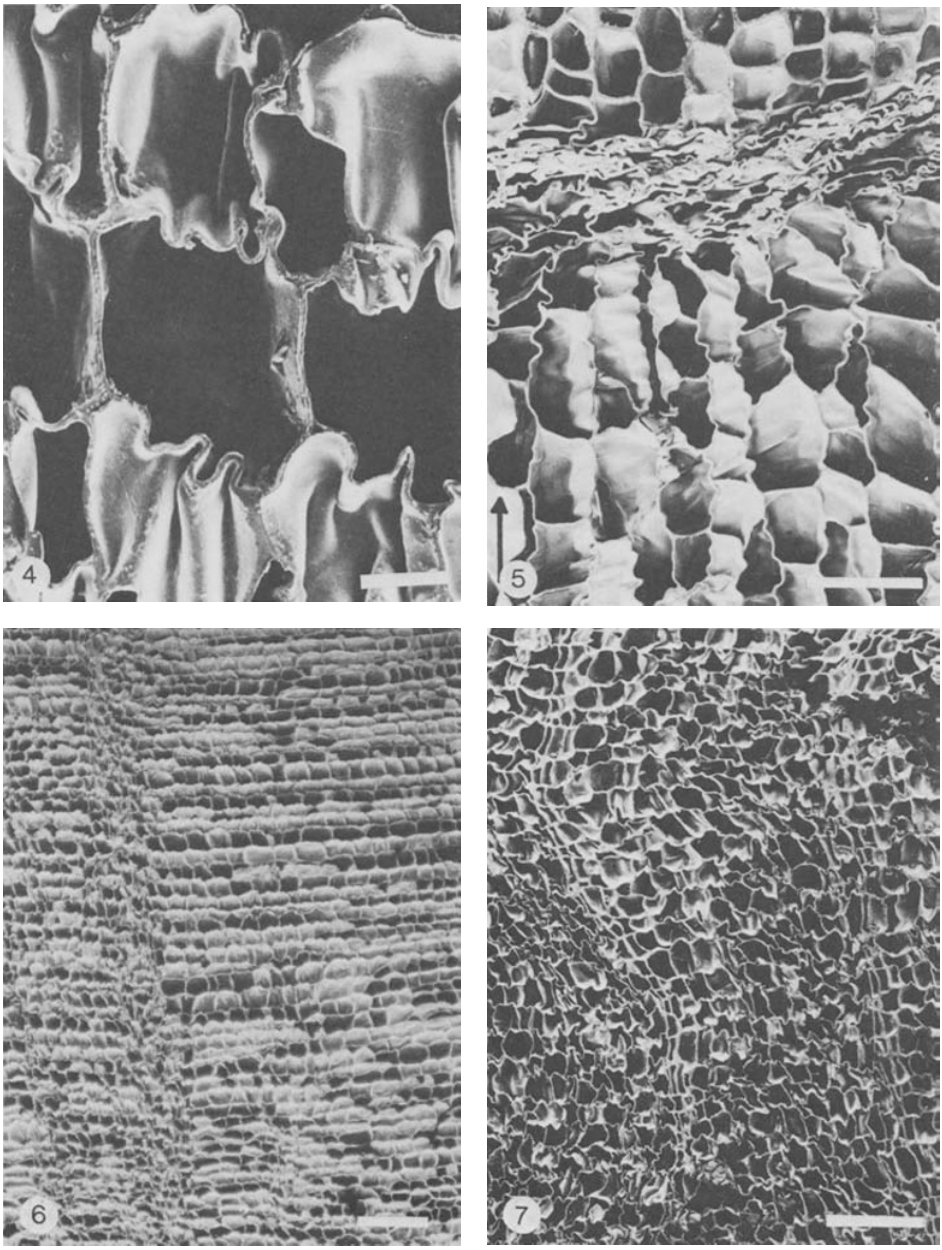


Fig. 4. Heavy corrugation of cork cells. Transverse section of reproduction cork. Bar is 10 μm. – Fig. 5. Heavy corrugation and collapsing of thin-walled early cork cells against previously formed late cork cells. Transverse section of reproduction cork. The arrow is in the outward radial direction. Bar is 50 μm. – Fig. 6. Bands of corrugated cells within one growth ring. Transverse section of reproduction cork. Bar is 100 μm. – Fig. 7. Radial section of virgin cork, showing growth rings. Bar is 100 μm.

An important characteristic of prismatic cork cells is that their lateral faces are corrugated. These corrugations have been previously described as consisting of 2 to 3 complete corrugations per cell (Gibson et al., 1981). However, we found the corrugation of cork cells to be far from regular; cells ranging from almost straight to heavily corrugated, and some even collapsed (Figs. 1, 4, 5). The bases of the cork cells were also undulated or somewhat wrinkled, but complete corrugations were not generally observed.

The corrugation of the lateral cell walls probably results from compression during cell and bark growth. In fact, heavily corrugated and collapsed cells are most frequent in the beginning of the growth layer against the last cells produced in the previous growing season. These late cork cells, with their thicker cell walls and reduced prism height, show much less or no corrugation of the lateral walls and are likely to be more rigid and resistant to the mechanical stresses that are generated during cell and bark growth. In extreme cases, the thin-walled early cork cells collapse completely against the previously formed layers of late cork cells, as shown in Figure 5. These collapsed layers probably contribute to a better visual definition of the growth rings, which in some cases are very sharply outlined.

Corrugation bands were also observed in the radial and transverse sections within the same annual growth ring. They consist of groups of cells which are more corrugated and may extend to form a corrugated ring within the annual growth ring (Fig. 6). These corrugated bands probably account for the darker stripes which can often be observed macroscopically in cork growth rings.

In virgin cork, the structure is more irregular and the growth increments are narrower. Within one growth ring, the proportion of late cork cells is larger than in reproduction cork and the thin-walled cells are heavily corrugated, as shown in Figure 7.

Heavily corrugated cork cells do not appear to have cell wall fractures, as observed in compression of wood fibres by Côté and Hanna (1983). This is likely due to the specific chemical composition and topochemistry of cork cell walls. The presence of a high amount of waxes and suberin (Pereira, 1982), as well as the cell wall structure of alternating lamellae of suberin and waxes (Sitte, 1962) favours cell wall flexibility and plane slipping during corrugation.

Although few studies have been made, some results reported for cork cells in the bark of other species, e.g. Douglas fir and other *Quercus* species, show that cell form and arrangement are similar to those of *Quercus suber* (Krahmer & Wellons, 1973; Howard, 1977). In *Melaleuca quinquenervia*, the wrinkling of the cell walls was also observed in the tangential section (Chiang & Wang, 1984).

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