



UNIVERSITY OF CALIFORNIA PRESS  
JOURNALS + DIGITAL PUBLISHING



---

Cellulose and the Evolution of Plant Life

Author(s): Luc C. Duchesne and D. W. Larson

Reviewed work(s):

Source: *BioScience*, Vol. 39, No. 4 (Apr., 1989), pp. 238-241

Published by: [University of California Press](#) on behalf of the [American Institute of Biological Sciences](#)

Stable URL: <http://www.jstor.org/stable/1311160>

Accessed: 04/03/2013 11:58

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*University of California Press* and *American Institute of Biological Sciences* are collaborating with JSTOR to digitize, preserve and extend access to *BioScience*.

<http://www.jstor.org>

# Cellulose and the Evolution of Plant Life

*The physical and biological properties of cellulose have made it the most abundant molecule in the biosphere*

Luc C. Duchesne and D. W. Larson

The biosphere is dominated by land-plant biomass. An estimated 99.9% of the global standing crop, the total quantity of biomass present in the biosphere, is classified as vegetation (Lieth and Whittaker 1975). Primary production, the yearly contribution of plant life to the standing crop, represents 97.7% of the total annual global production. Although marine plant life (including phytoplankton) makes up 32% of the total annual primary production, it represents only 0.2% of the global standing crop (Woodwell et al. 1978). Therefore, terrestrial vegetation constitutes almost all of the biomass on earth.

Plant biomass is primarily comprised of cell wall materials, which therefore represent the vast majority of the dry weight of living tissues (Figure 1a). Between 40% and 60% of the total mass of the cell wall is comprised of cellulose, a polymer of 100–15,000 units of  $\beta$ -1,4 glucose (Figure 1b) (Cote 1977, Delmer 1987, Stamm 1964), depending on the plant tissue and species. The remainder of the cell wall includes hemicelluloses, lignin polymers, and pectic substances deposited differentially in the several cell wall layers (Cote 1977,

---

## The presence of cellulose microfibrils in cell walls may be one of the most critical factors in the evolution of modern plant life

---

Panshin and de Zeeuw 1980). If one accepts Lieth and Whittaker's (1975) estimate of the total standing crop to be  $1.841 \times 10^{12}$  tons produced at the rate of  $1.7 \times 10^{11}$  tons per year, and if roughly 50% of this weight is cellulose, then the existing global standing crop contains approximately  $9.2 \times 10^{11}$  tons of cellulose, produced at the annual rate of  $0.85 \times 10^{11}$  tons per year. In view of the enormous biochemical and phylogenetic diversity of living systems, it seems remarkable that one compound, cellulose, should contribute so significantly to the bulk of the biomass on earth.

Cell walls of modern terrestrial multicellular plants are cemented together with lamellar structures containing cellulose microfibrils, which are bundles of approximately 80 molecules of cellulose (Jensen and Salisbury 1982). These cellulose microfibrils, embedded in the cell walls in a matrix of amorphous polysaccharides, lignin polymers, polyphenolic materials, and proteins (Preston 1974), appear to be a critical factor in the evolution of modern plant life.

A number of authors have speculated about the role of the cell wall in the evolution of life (Bartnicki-Garcia 1984, Preston 1974, Swain 1971) and the mechanisms of cellulose and cell-wall biosynthesis (Colvin 1982, Delmer 1987). In this paper, we analyze the functional characteristics of cellulose to explain its widespread occurrence in the biosphere. We explore the evolution of cellulose and other aquatic plant wall materials and examine why cellulose has been universally selected as a major wall component of terrestrial plants.

## The appearance of cellulose

The first cells on earth were heterotrophic microbes. They inhabited reducing aquatic environments containing organic molecules that could be used directly in metabolism (Horowitz 1945). Unlike most modern unicellular organisms, ancestral cells probably resembled protoplasts, bounded by only a primitive selectively permeable envelope (Bartnicki-Garcia 1984). Because protoplasts lack the mechanical support provided by the cell wall, they must maintain low turgor pressure and remain in osmotic equilibrium with the substrate.

Two features of the ancestral cells can be deduced from their lack of cell walls. First, because low environmental concentrations of solutes are associated with slow metabolism and solute-rich environments favor greater metabolic activities (Bartnicki-Garcia 1984), ancestral cells' low turgor must have limited their metabolic

---

Luc C. Duchesne is a postdoctoral fellow in the Department of Botany, Erindale Campus, University of Toronto in Mississauga, Mississauga, Ontario L5L 1C6, Canada. D. W. Larson is an associate professor in the Department of Botany, University of Guelph, Guelph, Ontario N1G 2W1, Canada. © 1989 American Institute of Biological Sciences.

rate. Second, the cells must have competed among themselves for the reducing power contained in the environment. Most of them must have eventually died out as resources in the medium were depleted. Under these conditions, strong selection pressures would have favored autotrophism to reduce competition. Autotrophism requires higher internal solute concentrations than does primitive heterotrophism because of a more complex cellular machinery, and would have favored the evolution of cell walls.

Present evidence indicates that primitive cell walls appeared by 3.5 billion years ago (Bartnicki-Garcia 1984). Evolution of a cell wall would have resulted in increased survival because the wall protects the cell from changes in osmolarity. Cell wall evolution could also have permitted higher concentration of cellular solutes that led to greater metabolic rates and, ultimately, capacity for faster growth and colonization of hypotonic environments.

The mechanical function of cell walls in the regulation of turgor pressure must have given a tremendous advantage to the ancestral walled organisms compared with their non-walled competitors. The random mutations responsible for cell-wall evolution probably resulted in an initial diversity in the chemical nature of these walls. Some of this variation was retained provided that turgor regulation was not impeded; the variation can be observed today in the variety of materials—including silica, amorphous polysaccharides, and microfibrillar polysaccharides such as chitin and cellulose—that give modern plants their mechanical strength. Modern land plants, however, all have cellulose microfibrils as a wall component. We speculate that cellulose, as compared with other kinds of wall materials, originally did little to directly enhance the mechanical strength of primitive aquatic plants, but the passage of plant life to terrestrial environments selected for the universal presence of cellulose in land plants.

### Cellulose and terrestrial plants

Selection pressures encountered on land—in the form of gravity, wind, and desiccation—differ dramatically

from those in aquatic environments. The mechanical support afforded by cellulose, which was of little use in aquatic ecosystems, was favored under these conditions. The appearance of structures such as stems and leaves (Percival and McDowell 1981) allowed for the extension of plant life above the earth's surface, but it is difficult to appreciate from the outward appearance of these organs how their growth, form, and behavior are influenced by the characteristics of their cell walls.

The mature cell wall, which is composed of primary and secondary layers (Figure 1a), is a rigid structure responsible for the shape and mechanical support of the cell and for regulating turgor pressure (Preston 1979). The significance of mechanical support is particularly evident for tall trees such as redwoods, whose tremendous structures are supported primarily by the physical properties of strongly interconnected cell walls (Figure 2). On the other hand, the wall must be plastic and extensible so that changes in shape and size are accommodated by the primary wall at least during early plant growth (Vian 1982). For instance, it is not unusual for leaf cortical palisade or parenchyma cells to show a 500-fold increase in volume as compared to meristematic cells, from which they are derived (Greulach 1973). Growth and survival is a direct result of the interaction of these two cell-wall properties.

### Physical properties of cellulose

One of the roles of cellulose in plants is in cytomorphogenesis. In plants, the polarity of cell division and cell shape have long been known to be associated with the orientation of the cellulose microfibrils in the primary wall (Colvin 1982, Green 1980, 1984, Taiz 1984), whose deposition is the result of polar exocytosis of wall materials (Schnepf 1986). In turn, cell shape and the spatial arrangement of cells as defined by the polarity of cell division provide plants with the ability to form the basic architecture of various tissues required for light and nutrient acquisition. Clearly, a microfibrillar cell wall capable of cytomorphogenesis must be favored by natural selection in

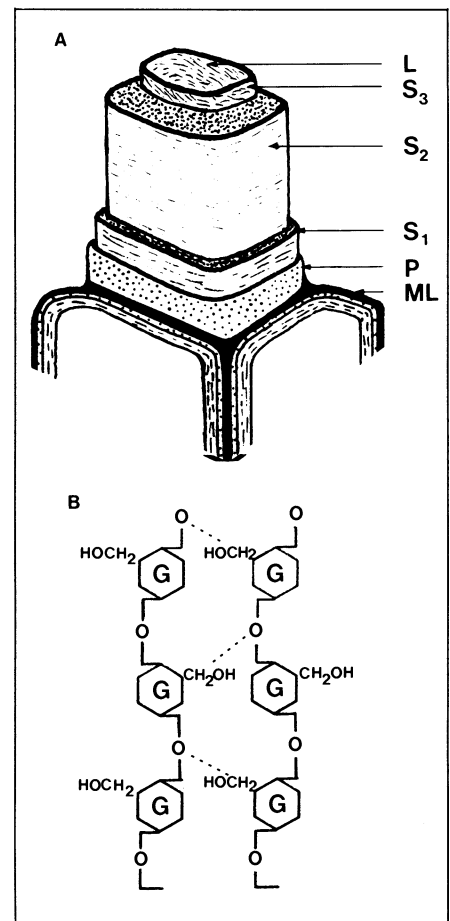


Figure 1. a. Typical cell-wall structure of woody cells of vascular plants. ML, middle lamellae; P, primary wall; S, secondary cell wall; S<sub>1</sub>, S<sub>2</sub>, and S<sub>3</sub>, different layers of the secondary cell wall; L, lumen of the cell. b. The cellulose molecule. 100–15,000 units of β-1,4 glucose are linked together in long chains that are included in cellulose microfibrils. Dashed lines indicate hydrogen bonding.

those instances where survival is closely linked to competition for light and nutrients.

In the plant cell wall, the bundles of cellulose molecules in the microfibrils provide the wall with tensile strength. The tensile strength of cellulose microfibrils is as high as 110 kg/mm<sup>2</sup>, or approximately 2.5 times that of the strongest steel in laboratory conditions (Stamm 1964). When cellulose is wetted, as in the cell walls, its tensile strength declines rapidly, significantly reducing its ability to provide mechanical support. But in biological systems, the cellulose skeleton is embedded in a matrix of pectin, hemicellulose, and lignin that act as waterproofing and strengthening ma-



Woodland area in Duval County, FL. Photo: K. Cunningham.

terials (Stamm 1964). Lignin also plays an important role in protecting plants against pests and in rendering inert phytotoxic phenolic compounds, from which lignin is formed.

Three other cell wall constituents are also known to form microfibrillar structures that contribute to wall strength. In some algae,  $\beta$ -1,4 mannans and  $\beta$ -1,3 xylans are known to form microfibrils, but these two molecules are considerably weaker than cellulose or are chemically unstable (Preston 1979). Chitin is a polymer of  $\beta$ -1,4-linked *N*-acetyl-glucosamine units whose functions in cytomorphogenesis are almost identical to those of cellulose (Blackwell 1982, Muzzarelli 1977). Cellulose and chitin are probably the only compounds that theoretically would have offered an advantage as structural components for land plants.

Although chitin is currently an abundant material in the exoskeletons of arthropods and in the cell walls of prokaryotes, some diatoms,

some unicellular algae, and most fungi (Herth and Schnepf 1982, Kendrick 1985, Muzzarelli 1977), cellulose is the predominant cell wall microfibrillar component in vascular land plants. Two properties of chitin may have been disadvantages for terrestrial plants. First, the tensile strength of chitin microfibrils is only 40 kg/mm<sup>2</sup>, half that of cellulose (Muzzarelli 1977). Second, and perhaps more important, chitin-walled organisms require an enormous allocation of reduced nitrogen for wall synthesis during growth.

The average nitrogen content of a woody plant, including all tissues, is approximately 0.34% dry weight (Kramer and Kozlowski 1979). If terrestrial plants were chitin-walled rather than cellulose-walled, then one nitrogen atom would have to be incorporated into every *N*-acetyl-glucosamine moiety entering the chitin microfibrils. Based on the number of moles of glucose molecules contained in 1 g of wood that is approx-

imately 50% cellulose (Cote 1977, Panshin and de Zeeuw 1980), one can determine the number of nitrogen atoms required to build the same quantity of chitin-walled wood. From this determination, the average nitrogen content of a woody plant would be increased 12-fold, to approximately 4%.

In most terrestrial environments, however, the availability of reduced nitrogen in assimilable form is the factor most limiting to plant growth (Kramer and Kozlowski 1979, Salisbury and Ross 1985, Schubert 1986). Consequently, terrestrial chitin-walled green plants would be smaller than cellulose-walled plants because of the channeling of nitrogen into chitin. Moreover, the reduction of nitrates and nitrites contained in the soil solution for metabolic uses requires some of the reducing power provided by the plant's photosynthetic activity. Therefore, the nitrogen metabolism in chitin-walled plants would significantly increase the demand for reducing power at the expense of plant growth.

The fitness of chitin-walled terrestrial plants would be considerably lower than that of cellulose-walled plants, because they would be inferior competitors for light and nutrients compared with cellulose-walled plants. The fact that modern chitin-walled organisms are restricted to nitrogen-rich environments (Muzzarelli 1977), such as those colonized by saprophytic and parasitic fungi, supports this hypothesis. It would be impossible to experimentally test this hypothesis because of the lack of chitin-walled terrestrial plants, but a comparison of the energy budget and the nitrogen requirements of a number of chitin-walled and cellulose-walled algae might be useful.

### Cellulose and chemical stability

In nature, cellulose is subject to two classes of selection pressure apart from that on cell wall structure. The first includes a broad array of well-armed pathogens with the ability to degrade cellulose through the action of cellulase. The second type of selection pressure involves such features of the abiotic environment as fluctuations in temperature.

Plant resistance to the pathogens has been achieved through an array of physiological, anatomical, and morphological defenses (Goodman et al. 1986). Persistence of cellulose in abiotic environments, however, is dependent on the strength of its chemical bonds. Microfibrils made of  $\beta$ -1,4 mannans and  $\beta$ -1,3 xylans such as those found in some algae are too chemically weak or unstable (Preston 1979) and, therefore, were not selected as a universal component of land plants. In cellulose microfibrils, hydrogen bonding between adjacent parallel cellulose chains increases their stability and provides the tensile strength of cellulose (Preston 1979).

Under conditions of fluctuating energy flows, as in the natural world, certain chemical bonds are favored because of their higher levels of thermodynamic stability (Morowitz 1968). Such chemical bonds, therefore, are likely to be retained in terrestrial environments with fluctuating energy flow. For example, single, double, and triple carbon-carbon bonds and carbon-oxygen bonds all require a greater amount of energy for their disruption than do other types of bonds, such as carbon-nitrogen and oxygen-oxygen bonds.

Morowitz (1968) notes that some of these most stable chemical bonds also favor the formation of chain-extending molecules, or polymers. Because molecules generated by stable chemical bonds tend to accumulate relative to less stable chemical bonds, there is an accumulation of the stable molecules through positive feedback. Therefore, the accumulation of cellulose in the biosphere may be the result of a sunlight-driven and gene-regulated cycle of positive feedback operating on the available molecular diversity and leading to the accumulation of long-chain molecules as a natural and perhaps inevitable consequence of selection for chemical stability.

The chemical stability of the cellulose molecule may have another significant effect in the biosphere. Because of their stability, cellulose and other wall materials act as a constant reservoir of energy and nutrients in the biosphere. Without the inherent

stability of cellulose, the biosphere would be subject to variations in atmospheric carbon dioxide greater than those normally encountered (excluding the contribution of industrial societies) (Colvin 1980, Stuiver 1978). Most important, the large-scale elimination of the greenhouse effect on this planet may depend on our capacity to increase the incorporation of CO<sub>2</sub> into cellulose through reforestation.

## Acknowledgments

Thanks to M. Chapple, R. L. Peterson, and S. Wetzel for reviewing the manuscript and to K. J. Niklas for useful comments.

## References cited

- Bartnicki-Garcia, S. 1984. Kingdoms with walls. Pages 1–18 in W. M. Dugger and S. Bartnicki-Garcia, eds. *Structure, Function, and Biosynthesis of Plant Cell Walls*. Proceedings of the Seventh Annual Symposium in Botany (12–14 January 1984). University of California, Riverside.
- Blackwell, J. 1982. The macromolecular organization of cellulose and chitin. Pages 403–428 in R. M. Brown, Jr., ed. *Cellulose and Other Polymer Systems: Biogenesis, Structure and Degradation*. Plenum Press, New York.
- Colvin, J. R. 1980. The biosynthesis of cellulose. Pages 544–570 in J. Preiss, ed. *The Biochemistry of Plants, a Comprehensive Treatise*. vol. 3. *Carbohydrates: Structure and Function*. Academic Press, New York.
- \_\_\_\_\_. 1982. Ultrastructure of the cell wall. Pages 2–28 in W. Tanner and T. A. Loewus, eds. *Plant Carbohydrates, Extracellular Carbohydrates*. *Encyclopedia of Plant Physiology*. Springer-Verlag, Berlin, FRG.
- Cote, W. A. 1977. Wood ultrastructure in relation to chemical composition. Pages 1–44 in F. A. Loewus and V. C. Runeckles, eds. *The Structure, Biosynthesis, and Degradation of Wood*. Plenum Press, New York.
- Delmer, D. P. 1987. Cellulose biosynthesis. *Annu. Rev. Plant Physiol.* 38: 259–290.
- Goodman, R. N., Z. Kiraly, and K. R. Wood. 1986. *The Biochemistry and Physiology of Plant Disease*. The University of Missouri Press, Columbia.
- Green, P. B. 1980. Organogenesis: a biophysical view. *Annu. Rev. Plant Physiol.* 31: 166–190.
- \_\_\_\_\_. 1984. Shifts in plant cell axiality: histogenic influences in cellulose orientation in the succulent, *Graptopetalum*. *Dev. Biol.* 103: 18–27.
- Greulach, V. A. 1973. *Plant Function and Structure*. MacMillan Publ., New York.
- Herth, W., and E. Schnepf. 1982. Chitin-fibril

- formation in algae. Pages 185–206, in R. M. Brown, Jr., ed. *Cellulose and Other Polymer Systems: Biogenesis, Structure and Degradation*. Plenum Press, New York.
- Horowitz, N. H. 1945. On the evolution of biochemical synthesis. *Proc. Natl. Acad. Sci.* 31: 153–157.
- Jensen, W. A., and F. B. Salisbury. 1982. *Botany*. Wadsworth Publ. Belmont, CA.
- Kendrick, B. 1985. *The Fifth Kingdom*. Mycology Publ., Waterloo, Ontario, Canada.
- Kramer, P. J., and T. T. Kozlowski. 1979. *Physiology of Woody Plants*. Academic Press, New York.
- Lieth, H., and R. H. Whittaker. 1975. *The Primary Production of the Biosphere*. Springer-Verlag, New York.
- Morowitz, H. J. 1968. *Energy Flow in the Biosphere*. Academic Press, New York.
- Muzzarelli, R. A. A. 1977. *Chitin*. Pergamon Press, New York.
- Panshin, A. J., and C. de Zeeuw. 1980. *Textbook of Wood Technology*. McGraw Hill, New York.
- Percival, E., and R. H. McDowell. 1981. Algal walls: composition and biosynthesis. Pages 277–316 in W. Tanner and J. A. Loewus, eds. *Plant Carbohydrates, Extracellular Carbohydrates*. *Encyclopedia of Plant Physiology*. Springer-Verlag, Berlin, FRG.
- Preston, R. D. 1974. *The Physical Biology of Plant Cell Walls*. Chapman and Hall, London.
- \_\_\_\_\_. 1979. Polysaccharide conformation and cell wall function. *Annu. Rev. Plant Physiol.* 30: 55–78.
- Salisbury, F. B., and C. W. Ross. 1985. *Plant Physiology*. Wadsworth Publ. Co., Belmont, CA.
- Schnepf, E. 1986. Cellular polarity. *Annu. Rev. Plant Physiol.* 37: 23–47.
- Schubert, K. R. 1986. Products of biological nitrogen fixation in higher plants: synthesis, transport and metabolism. *Annu. Rev. Plant Physiol.* 37: 539–574.
- Setterfield, G., and S. T. Bayley. 1961. Structure and physiology of cell walls. *Annu. Rev. Plant Physiol.* 12: 35–62.
- Stamm, A. J. 1964. *Wood and Cellulose Science*. The Ronald Press, New York.
- Stuiver, M. 1978. Atmospheric carbon dioxide and carbon reservoir changes. *Science* 199: 253–258.
- Swain, T. 1971. Biochemical evolution in plants. Pages 274–296 in E. Schoffeniels ed. *Biochemical Evolution and the Origin of Life*. North Holland Publ., Amsterdam, The Netherlands.
- Taiz, L. 1984. Plant cell expansion: regulation of cell wall mechanical properties. *Annu. Rev. Plant Physiol.* 5: 585–657.
- Vian, B. 1982. Organized microfibril assembly in higher plants. Pages 23–43 in R. M. Brown, Jr., ed. *Cellulose and Other Polymer Systems: Biogenesis, Structure and Degradation*. Plenum Press, New York.
- Woodwell, G. M., R. H. Whittaker, W. A. Reiners, G. E. Likens, C. C. Delwiche, and D. B. Botkin. 1978. The biota and the world carbon budget. *Science* 199: 141–146.