Biuletyn Ogrodów Botanicznych, **12**: 23–29, 2003

STOREYED STRUCTURE OF CAMBIUM AS AN ADAPTIVE STRATEGY TO ENVIRONMENTAL CONDITIONS IN TREES FORMING THE CANOPY AND THE EMERGENT LAYER OF THE TROPICAL RAIN FORESTS

Piętrowa struktura kambium jako strategia adaptacyjna do warunków środowiska u drzew tworzących sklepienie lasu i poziom drzew wynurzających się w deszczowym lesie tropikalnym

Paweł KOJS[1,3], Wiesław WŁOCH[1,2], Aleksandra RUSIN[1], Waldemar SZENDERA[1,2]

[1]*Botanical Garden – Centre for Biological Diversity Conservation of the Polish Academy of Sciences, ul. Prawdziwka 2, 02-973 Warszawa 76, Poland*
[2]*Faculty of Biology and Environmental Protection, Silesian University, ul. Jagiellońska 28, 40-032 Katowice, Poland*
[3]*Faculty of Ethnology and Educational Study, Silesian University Branch at Cieszyn, ul. Bielska 62, 43-400 Cieszyn, Poland*

STRESZCZENIE

W danym środowisku dominują organizmy najlepiej potrafiące optymalnie wykorzystać czynnik znajdujący się w minimum, określający warunki konkurencji. W deszczowych lasach tropikalnych czynnikiem znajdującym się w minimum w początkowym okresie wzrostu drzew jest światło. W walce o zasoby światła zwycięża osobnik najszybciej osiągający piętro sklepienia lasu. Wysokość drzew jest ograniczona wytrzymałością mechaniczną pnia, która zależy od jego struktury, ta zaś zależy od aktywności kambium. Dużą wytrzymałość mechaniczną pnia zapewnia włóknistość zapleciona drewna. Powstaje ona w wyniku cyklicznej zmiany orientacji inicjałów wrzecionowatych kambium i zachodzi szczególnie szybko w kambium piętrowym. Układ piętrowy jest znaczącym osiągnięciem ewolucyjnym, pozwalającym na szybką przebudowę układu komórek bez konieczności wydatkowania energii na intensywny wzrost intruzywny i częste, skośne podziały antyklinalne, co obserwuje się w przypadku kambium niepiętrowego.

ABSTRACT

In a given environment, organisms capable of optimizing the utilization of the resource available as a limiting factor, dominate. In tropical rainforests, during first few years of growth of trees light is a limiting factor in understorey strata. The individuals that reach the canopy first, win the struggle for light. However the height of trees is limited by the mechanical properties of the trunk which depend on its anatomical structure, especially the structure of wood which in turn depends on the structure and activity of vascular cambium. High mechanical strength is provided by the interlocked grain of wood. The formation of interlocked grain is based on a fast cyclical change in orientation of the fusiform cambial initials. Such a fast cell rearrangement is possible only in the storeyed cambium. It is hypothesized that the presence of the storied cambium has an adaptative value for the fast growing trees. It seems to be an important evolutional achievement which facilitates fast cell rearrangement in the cambium without excessive expenditure of energy on such events as intensive intrusive growth, frequent oblique anticlinal divisions and rapid eliminations of excessive fusiform initials which are characteristic of a non-storeyed cambium.

Key words: adaptation to environment, the canopy and emergent trees, storeyed cambium, interlocked grain, tropical rainforest

INTRODUCTION

Tropical rainforests constitute the biologically most diverse ecosystems on the Earth for over a million years. About 50–90% of the 300 thousand plant species inhabiting the Earth exist in the tropical rainforests which occupy only about 2% of Earth area, meaning thereby that a one hectare piece of land encompasses more than 600 tree species (Lawton 1978; Anonymous 1994).

Unfortunately, more than 310 000 km^2 area of tropical rainforests, equivalent to the total area of Poland, is being destroyed each year. It is estimated that if the rate of deforestation is not slowed down, only small patches of rainforests will survive in the protected areas of national parks by the year 2030. However, as seen in the case of *Swietenia macrophylla*, protection in the natural reserves and national parks may not essentially be effective.

In the tropical rainforests, the vegetation can be identified as forming four strata, namely the emergent layer, the canopy layer, the understorey and the forest floor. The highest stratum, i.e., the emergent layer, is made up of 35–70 m high trees, often with a trunk diameter of more than 2 m.

Young trees of these forests grow fast in order to attain the canopy height in a relatively short period of time. In comparison with trees of the temperate forests, their elongation growth is much faster than their radial growth (associated with the widening of the trunk). During the first stage of growth (up to the height of about 20 m) they may not produce branches, thus looking even taller than they really are. The crown of the tree begins to grow in the next stage, after the tree has reached the canopy layer and secured an access to light. Then the size of the crown increases, and the trunk widens.

Tall trees are likely to endure not only the pressure of their own crowns but also the weight of a large number of epiphytes and lianas growing upon them. These trees, growing in conditions of a high humidity and low light and on a relatively poor soil, initially form a shallow root system, insufficient for their support. The supportive function is performed by the root plate formed by the buttress roots that may gain a diameter of almost 10 m at the base of a trunk, and at times by the prop roots. During the fast growth of trees of the canopy and the emergent strata in the tropical rainforests, accumulation of the secondary phloem is slow, and this remains functional for several years. This situation allows for a greater investment of energy and matter on the xylem production. The longevity (about 300 years) of trees of these forest strata is also connected with the permeation of the wood with different exudates like tannins, resins, gums and toxins (fungicides and insecticides) (Hillis 1987).

The wood of these trees, like mahogany, palisander and ebony, normally belongs to the commercial timber type. This valuable resource is being exploited in an uncontrolled manner. Eradication of a few mighty emergent trees does, in fact, mean a total destruction of a large area of the forest.

This paper evaluates some anatomical and morphological features of the large tropical trees which may facilitate a fast elongation growth of trees under conditions of limited illumination.

RESULTS AND DISCUSSION

The environment is relatively stable in the tropical climatic conditions. The annual as well as the daily temperature amplitudes are not high; the precipitation is high and regular. The limiting factors in the tropical rainforests are light and, to some extent, the mineral nutrients like nitrogen. For trees of the high forest storeys (the emergent and the canopy layers), the most important task is to gain an access to light.

Many of the tree species in the higher vegetation strata of the tropical rainforests belong to the group *Leguminosae*. They are capable of fixing nitrogen in the root system (due to symbiosis with the nodule bacterium *Rhizobium*). This phenomenon may be of advantage to these trees, enabling them to grow fast in conditions of soil nitrogen deficit. However, it is to be noted that this feature is often accompanied by another one, i.e., the presence of storeyed structure of the cambium, which possibly plays a primary role in the growth of the tall trees.

The storeyed arrangement of cells in the cambium is an advanced, polyphyletic feature which has developed in many unrelated families of the dicotyledonous plants. This feature occurs also in families like *Ulmaceae* and *Lauraceae* that exhibit several primitive features (Metcalfe & Chalk 1965).

More than 80% of the individuals in the canopy and the emergent layers of a tropical rainforest belong only to a few families (Tabs 1 and 2). Interestingly, most of these possess the double storeyed arrangement of the cambial cells (i.e. storeyed arrangement of fusiform initials accompanied by a storeyed arrangement of rays) (Wagenführ & Scheiber 1974; Yunus et al. 1978; Carlquist 1988; Anonymous 1994).

The double-storeyed arrangement has the ability to bring about a fast reorientation of cambial cells in the successive layers, thus parvng the way for the formation of interlocked grain. Fracturing of a several cm thick disc of wood, obtained from the stem of trees having interlocked grain, such as *Entandrophragma cylindricum*, exhibits a wavy surface of the fracture, with a variable amplitude (Fig. 1) and a high frequency. The higher is the amplitude, the bigger is the angle between the long axis of the fusiform cells and the stem axis. The fusiform initials in the storeyed cambia are short. Reorientation of cells in such cambia occurs very fast with a minimal range of intrusive growth. This type of cell rearrangement

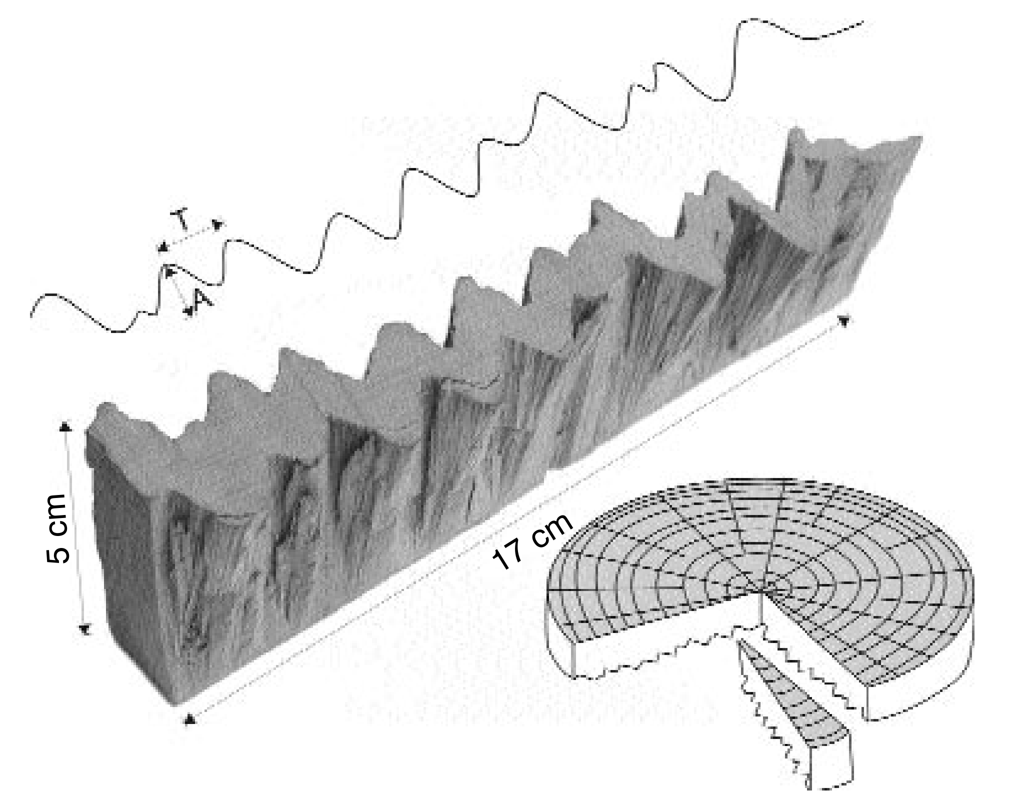

Fig. 1. Radial fracture of a wood disc cut of the stem of *Entandrophragma cylindricum*. The length of the fracture is 17 cm and height 5 cm. The lower surface of the fracture is wavy, with variable amplitude and wave frequency. Large amplitude corresponds to the large range of angles of cell inclination towards the stem axis, whereas a high frequency indicates a fast reorientation of cells in successive layers of the xylem
Ryc. 1. Przełup o długości 17 cm i wysokości 5 cm przez krążek drewna wycięty z pnia *Entandrophragma cylindricum* wykonany wzdłuż promienia. Na dolnej krawędzi przełupu widoczna jest falista linia o zmiennej amplitudzie i częstotliwości. Duża amplituda odzwierciedla duży zakres zmiany kąta komórek względem osi pnia, a wysoka częstotliwość wskazuje na szybką zmianę orientacji komórek w kolejnych warstwach ksylemu.

Table 1. Non-leguminous tall trees of the tropical rain forests, characterized by the storeyed structure of cambium, and having timber of a high commercial value. (Based on: Anonymous 1994, Carlquist 1988, Lawton 1978, Metcalfe and Chalk 1965, Richter and Dallwitz 2000, Wagenführ and Scheiber 1974, Watson and Dallwitz 1992, Włoch et al. 2002).
Tabela 1. Wysokie drzewa deszczowego lasu tropikalnego nie należące do roślin motylkowych, charakteryzujące się piętrową strukturą kambium i mające dużą wartość gospodarczą. (Na podstawie: Anonymous 1994, Carlquist 1988, Lawton 1978, Metcalfe and Chalk 1965, Richter and Dallwitz 2000, Wagenführ and Scheiber 1974, Watson and Dallwitz 1992, Włoch et al. 2002).

Family Rodzina	Genus/Species Rodzaj/Gatunek	Storeyed arrangement of cambial fusiform initials Piętrowy układ inicjałów wrzecionowatych kambium	Storeyed arrangement of rays Piętrowy układ promieni
Bignoniaceae	*Tabebuia obtusifolia* (Chamisso) Bureau	+	+
	Tabebuia rosea (Bert.) DC	+	+
Bombacaceae	*Ceiba pentandra* Gaertn.	+	
	Cavanillesia platanifolia H.B.K.	+	
Boraginaceae	*Cordia* spp.	+	
Burseraceae	*Aucoumea klaineana* Pierre	+	+
	Canarium schwenfurthii Engl.	+	+
Dipterocarpaceae	*Anisoptera cochinchinensis* Pierre	+	
	Hopea ferrea Pierre	+	+
	Parashorea macrophylla Wyatt-Smith ex P. Ashton	+	
	Shorea acuminate Dyer	+	
	Shorea atrinervosa Sym.	+	
	Shorea balangeran (Karth.) Burck	+	
	Shorea ovata Dyer ex Brandis	+	
Ebenaceae	*Diospyros virginiana* L.	+	+
Lauraceae	*Aspidostemon louvellii*	+	+
Meliaceae	*Entandrophragma cylindricum* (Sprague) Sprague	+	+
	Entandrophragma candollei Harms	+	+
	Khaya anthotheca Welw.	-, +	
	Khaya ivorensis A.Chev.	+	
	Swietenia macrophylla King	+	+
	Swietenia mahagoni (L.) Jacq.	+	
Simaroubaceae	*Simarouba amara* Aubl.	+	+
Sterculiaceae	*Cola* spp.	+	+
	Eriobroma oblonga (Mast.) Bod.	+	
	Heritiera utilis (Sprague) Sprague	+	+, -
	Mansonia altissima (A. Chev.) A. Chev.	+	+
	Nesogordonia papaverifera (A. Chev.) R. Capuron	+	+
	Pterospermum acerifolium Willd.	+	+
	Pterospermum canescens Roxb.	+	+
	Pterospermum elongatum Karth.	+	
	Pterospermum javanicum Jungh.	+	
	Pterygota macrocarpa K. Schum	+	
	Sterculia apetala (Jacq.) Karst.	+	
	Triplochiton scleroxylon K. Schum.	+	+, -
Tiliaceae	*Heliocarpus popayannensis* Hook. & Arn.	+	+, -
	Pentace spp.	+	+
Ulmaceae	*Holoptelea* spp.	+	+

Table 2. Tall leguminous trees of the tropical rain forests, characterized by the storeyed structure of the cambium and with timbers of high commercial value (Based on: Anonymous 1994, Carlquist 1988, Lawton 1978, Metcalfe and Chalk 1965, Richter and Dallwitz 2000, Wagenführ and Scheiber 1974, Watson and Dallwitz 1992, Włoch et al. 2002).
Tabela 2. Wysokie drzewa deszczowego lasu tropikalnego należące do roślin motylkowych, charakteryzujące się piętrową strukturą kambium i mające dużą wartość gospodarczą. (Na podstawie: Anonymous 1994, Carlquist 1988, Lawton 1978, Metcalfe and Chalk 1965, Richter and Dallwitz 2000, Wagenführ and Scheiber 1974, Watson and Dallwitz 1992, Włoch et al. 2002).

Family Rodzina	Genus/Species Rodzaj/Gatunek	Storeyed arrangement of cambial fusiform initials Piętrowy układ inicjałów wrzecionowatych kambium	Storeyed arrangement of rays Piętrowy układ promieni
Caesalpinaceae	*Afzelia africana* Smith ex Pers.	+	+
	Amphimas ferrugineus Pierre ex Pellegr.	+	+
	Apuleia leiocarpa (Vog.) Marbride	+	+
	Baikiaea plurijuga Harms	+	+
	Brachystegia spp.	+	+
	Caesalpinia brasiliensis L.	+	+
	Caesalpinia paraguariensis (D. Parodi) Burk.	+	+
	Daniellia ogea (Harms) Rolfe ex Holl.	+	+
	Daniellia oliverii Hutch. & Dalz	+	+
	Dialium guianense (Aubl.) Sandw.	+	+
	Dialium platysepalum Baker	+	+
	Dicorynia guianensis Armsh.	+	+
	Didelotia spp.	+	+
	Distemonanthus benthamianus Baillon	+	+
	Erythrophleum ivorense A. Chev	+	+
	Koompassia excelsa (Becc.) Taub	+	
	Koompassia malaccensis Maing.	+	+
	Swartzia fistuloides Harms	+	+
	Tetraberlinia bifoliolata Harms	+	+
Mimosaceae	*Cedrelinga catenaeformis* Ducke	+	
	Pterogyne nitens Tulasne	+	+
Papilionaceae	*Amburana cearensis* (Fr. Allem.) A. C. Smith	+	+
	Bowdichia nitida Benth.	+	+
	Castanospermum australe A. Cunn & C. Fraser	+	+
	Dalbergia latifolia Roxb.	+	+
	Dalbergia nigra Allem.	+	+
	Dipteryx odorata (Aubl.) Willd.	+	+
	Erythryna falcate Bernht.	+	+, -
	Hymenolobium excelsum Ducke	+	+
	Lonchocarpus sericeus (Poir.) DC	+	+
	Machaerum scleroxylon Tul.	+	+
	Millettia laurentii De Wild.	+	+
	Myroxylon spp.	+	+
	Pericopsis elata (Harms) von Meeuwen	+	+
	Platymiscium pinnatum (Jacq.) Dugand	+	+
	Pterocarpus indicus Willd.	+	+
	Pterocarpus soyauxii Taub.	+	+

leads to the formation of interlocked grain which improves the mechanical properties of the trunk (Kojs et al. 2002; Włoch et al. 2002; Kojs et al. 2003). In consequence, trees with storeyed cambium may reduce the increase in the trunk girth to the minimum, and grow faster in height in order to gain access to sun light.

In a given environment, only those organisms dominate which are able to exploit optimally the factors available in a minimum and determining the conditions of competition. In the tropical rain forests, light is a factor that becomes limiting due to the dense plant population. Individuals that reach the canopy win the struggle for light. The height of a tree is limited by the mechanical strength of its trunk depending on its structure which, in turn, is dependent on the cambial characteristics. The highest mechanical strength results from the interlocked grain of wood which is formed as a consequence of a periodical, intensive reorientation of the cambial initials visible especially in a storeyed cambium. The storeyed arrangement of the cambium is a significant evolutionary achievement, which allows for a very quick rearrangement of cells without any energy loss for an intensive intrusive growth and for frequent oblique, anticlinal divisions, as against the nonstoreyed cambia (Fig. 2).

CONCLUSIONS

In the canopy and the emergent layers of a tropical rainforest, over 80% individuals seem to possess storeyed arrangement of cambial cells. It seems that the storeyed cambium helps the tall trees to gain ecological success, facilitat-

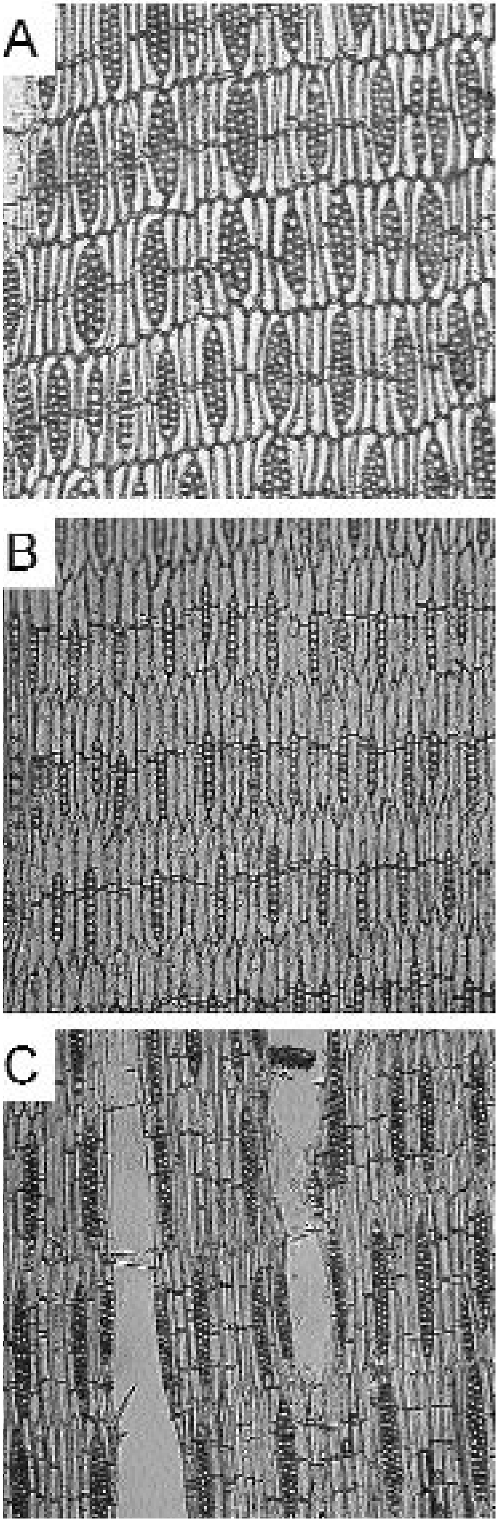

Fig. 2. Tangrential sections of wood in some tree species showing the storeyed arrangement of cambium. A – *Lonchocarpus sericeus* (Poir.) DC, B – *Pterocarpus soyauxii* Taub., C – *Nesogordonia papaverifera* (A. Chev.) R. Capuron

Ryc. 2. Przekroje styczne przez miękisz osiowy w drewnie wybranych gatunków drzew tropikalnych charakteryzujących się piętrową strukturą kambium. A – *Lonchocarpus sericeus* (Poir.) DC, B – *Pterocarpus soyauxii* Taub., C – *Nesogordonia papaverifera* (A. Chev.) R. Capuron.

ing them to grow in height fast under the severe competition for light resources, and providing them enormous mechanical strength through the development of interlocked grain of wood.

Acknowledgements We thanks Professor Muhammad Iqbal for helpful comments and careful linguistic correction of the manuscript.

REFERENCES
LITERATURA

Anonymous (1994) Die grosse farbige Enzyklopädie Urania Pflanzenreich. Urania – Verlagsgesellschaft G.m.b.H., Leipzig.

Carlquist S. (1988) Comparative wood anatomy. Springer Verlag, Berlin, New York. Anonymous (1994) Urania – Verlagsgesellschaft G.m.b.H., Leipzig.

Hillis W.E. (1987) Heartwood and Tree Exudates. Springer Verlag, Berlin, New York.

Kojs P., Włoch W., Rusin A., Szendera W., Duda J., Jura J., Rusin T., (2002) From nonfunctional to functional storied arrangement in the cambium. Models of storied arrangement. Biul. Ogr. Bot. 11: 93-104.

Kojs P., Włoch W., Rusin A. (2003) Rearrangement of cells in storied cambium connected with formation of the interlocked grain in xylem of *Lonchocarpus sericeus* (Poir.) DC. Trees.

Lawton R.M. (1978) The management and regeneration of some Nigerian high forest ecosystems. In: Tropical forest ecosystems. A state of knowledge report. Part XIV: Natural Resources Research Series, UNESCO/UNEP/FAO.

Metcalfe C.R., Chalk L. (1965) Anatomy of the dicotyledons. Vols 1, 2. Ed. 3. University Press, Oxford.

Richter H.G., Dallwitz M.J. (2000 onwards) Commercial timbers: description, illustration, identification and information retrieval (version: 4th May 2000). http://biodiversity.-uno.edu/delta

Wagenführ R., Scheiber Ch. (1974) Holzatlas. VEB Fachbuchverlag, Leipzig.

Watson L., Dallwitz M.J. (1992 onwards) The families of Flowering Plants (version: 14th December 2000). http://biodiversity.uno.edu/delta

Włoch W., Kojs P., Rusin A., Szendera W., Duda J., Rusin T. (2002) Comparative studies of the storeyed cambium of woody plants present in collections of botanical gardens in Poland. Biul. Ogr. Bot. 11: 85-91.

Yunus M., Yunus D., Iqbal M. (1978) On the cambial structure of some industrially important tropical trees. Flora 167: 159-163.