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2. The following changes of address have been brought to the knowledge of our office:

Prof. Dr. K.A. Chowdhury, Head of the Botany Dept. Muslim University, Aligarh, India

Dr. E. Schmidt, Inst. f. Holzforschung u. Holztechnik, Winzererstr. 45, München 13

Mr. W.N. Watkins, 4519 West Virginia Avenue, Bethesda 14, Maryland, USA

Mr. Michael A. Taras, Southeastern Forest Experiment Station, P.O.B. 2570, Asheville, N.C.

Professor Lawrence Leney, College of Forestry, University of Washington, Seattle 5, Washington

3. Mr. Michael V. Labern, Eastmalling Research State, Maidstone, Kent, England, has resigned membership of our Association.

4. Members who have not yet paid their membership fees for 1960 are invited to do so at their earliest convenience.

Edited by the Secretary Treasurer

Zurich, Switzerland

Office: Laboratorium für Holzforschung E.T.H., Universitätstrasse 2

EDITORIAL

Our Association has broadened its scope in the last years. Originally it was founded by botanists who had an interest in tree taxonomy and phylogeny. They helped to find out which types are ancient or derived in gymnosperms and which families are primitive among the angiosperms; they discovered the evolutionary trend in tracheids, vessels and sieve tubes, solved the enigma of cambial differentiation as far as it is a morphological problem, classified the tendencies of specialization in xylema and phloema or established the relationship between wood structure and ecological features. Although these lines of investigation open a large field of research, the number of scientists interested in such type of pure wood anatomy is relatively small.

On the other hand tree physiologists depend on a thorough knowledge of the histological structure of their objects so that they take a vived interest in our anatomical work. And modern wood technologists specialized in microtechnology have become a third group of fervent wood anatomists. Microtechnology intends to solve technological problems on a microscopical level by studying the properties and shortcomings of wood depending on its anatomical structure. Therefore, we have admitted to our Association a certain number of new members working on those lines.

At the end of 1959 the I.A.W.A. comprised 123 members. This number has risen to 137 in 1960 by the admission of 16 candidates and a loss of 2 members.

A. Frey-Wyssling
Secretary Treasurer

SCIENTIFIC REVIEW

Anticlinal Division and Cell Length in the Cambium of Conifers

by M.W. Bannan, Professor of Botany, University of Toronto, Toronto, Canada.

Introduction

The size of wood cells has been the subject of extensive investigation over a period of many decades. Attention has been given to varied aspects such as the influence of environmental factors on cell size, relationship to growth rates, trends of variation in different parts of the tree, and genetic control. Because the length of tracheids in conifers is largely determined by the size of the originating cambial cells, it might be expected that events in the perpetuation of the latter would have an important bearing on cell size. In conifers the multiplication of fusiform cambial cells is achieved by anticlinal division, mostly of the pseudotransverse type. A summary of the author's work on anticlinal divisions in conifers, and their effect on cell length, is presented in this review.

Types of Anticlinal Division

In the periods of most active growth periclinal divisions in the cambial area take place in a belt several cells wide. This zone of division comprises a uniseriate layer of initials and derived tissue mother cells on either side (Sanio (15), Mischke (14), Bannan (3)). During the vernal surge of activity most active division is among the redividing xylem mother cells, the rate of division here surpassing that in the initiating layer. As growth slackens through the summer, redivision of the xylem mother cells diminishes and the zone of periclinal division correspondingly narrows.

Anticlinal divisions are the means by which the multiplication of cambial cells required in circumferential expansion is brought about. These divisions are of two types, pseudotransverse and division to produce small segments off the side. In pseudotransverse division a more or less sigmoidal wall is laid down, usually near the centre of the dividing cambial cell (Klinken (11), Bailey (1)). Orientation and length of the partition vary from short and almost transverse to more than one-half the length of the original cell. Subsequently the two daughter cells elongate by tip growth to full size. In the case of division from the side the length of the segment so produced likewise varies greatly, but it seldom exceeds one-fourth the length of the mother cell.

When growth is slow and the zone of periclinal division is narrow, anticlinal divisions are almost entirely confined to the uniseriate tier of initials. As the growth rate increases, the proportion of anticlinal divisions takes place in xylem mother cells rather than in the initials rises. In Thuja occidentalis the proportion of extra-initial anticlinal divisions was only 0.3% of all anticlinal divisions in trees with rings under 1 mm. wide, but it increased to more than 1% in trees with rings exceeding 3 mm. (Bannan (5)). The most frequent occurrence of anticlinal divisions in xylem mother cells was observed in a tree of Cedrus deodara with rings up to 1 cm. wide where the proportion was 20% of all anticlinal divisions. The high degree of restriction of anticlinal divisions to the specific cambial cells which function as initials is significant.

Most of the anticlinal divisions in the cambium are of the pseudotransverse type, divisions to produce segments off the side making up only 2% of all

anticlinal divisions in the conifers studied. Pseudotransverse division is, of course, the means by which fusiform cambial cell multiplication takes place, although the proportion of newly formed initials that survives varies greatly with age and other factors. Segments cut from the side of fusiform initials usually become reduced to ray initials. Only in those cases where their length approximates one-half that of the mother cell are they likely to elongate and continue as fusiform initials.

Time of Anticlinal Division in the Growing Period

During the development of the earliest wood, when the annual rings are usually wide, anticlinal division of fusiform initials occurs at various times during the growing season. This distribution of multiplicative divisions through the period of radial accretion obviously facilitates continuous circumferential expansion of the cambium. In the later growth, when there is a steady decrease in the perimeter extension from year to year and the annual rings generally become narrower, pseudotransverse divisions tend to be more definitely an aestival phenomenon, occurring toward the end of the growing season or even after the cessation of periclinal division. Sometimes, however, deviation occurs from the usual aestival incidence of pseudotransverse division, particularly if the outer rings are wide. Thus in a stem of Cedrus deodara with rings 1 cm. wide 30% of the pseudotransverse divisions of fusiform initials took place during the production of the first half of the rings, 30% during the development of the third quarter, and 40% in the final quarter. In a bole of Picea glauca 3 dm. in diameter, with the outermost ring 7 mm. wide, a somewhat different distribution of anticlinal divisions was noted. Here 70% of the divisions occurred during the deposition of the third quarter of the ring and 30% in the final quarter. By way of contrast, in a stem of Thuja occidentalis 2.5 dm. in diameter with a peripheral ring 3.3 mm. wide anticlinal divisions were strictly aestival, all occurring during the development of the final eighth of the ring.

Frequency of Pseudotransverse Divisions

During the development of the inner wood pseudotransverse divisions follow one another in relatively rapid sequence, but with increasing age the rate of multiplicative division declines in relation to the production of xylem. Thus in a 60-years old stem of Thuja occidentalis the frequency of pseudotransverse division dropped from 5 per cm. of xylem accretion at 1 cm. from the pith to an average of one division per cm. at distances of 11 - 13 cm. from the pith (Bannan (7)). Mean cell length at pseudotransverse division increased from 1.64 mm. to 2.91 mm. During the production of the first few annual rings, when there is rapid circumferential expansion, pseudotransverse divisions occur in close sequence, the ratio of survival of newly formed cambial cells is high, an continuous increase in mean cell length follows. Accommodation of the cambium to perimeter growth is thus facilitated. With increasing age and diminishing rate of circumferential expansion the frequency of anticlinal divisions declines, the survival rate of new formed cambial initials falls off, and increase in cell length slackens.

In some old trees there is a gradual decline in the rate of pseudotransverse division and slow increase in cell length through to the final growth. More often stabilization is achieved with minor fluctuation in frequency of anticlinal division and cell length. Such variations in cell size have been noted by Bailey and Faull (2), Bisset, Dadswell and Wardrop (9),

Harlow (10), Lee and Smith (12), and Liang (13). The extent to which the frequency of pseudotransverse division is maintained through the successive yearly increments may be illustrated by reference to Thuja occidentalis. In a study of 128 trees growing at similar rates but differing in size, the frequency of pseudotransverse division was 2.3, 2.1, 2.3 and 2.5 per cm. of xylem increment in the periphery of boles 1.5-2, 2.5, 3, and 4-5 dm. in diameter. During the final growth of 8 trees of Thuja plicata ranging in diameter from 10 - 18 dm. the frequency of anticlinal division averaged 2.2 per cm. In 8 boles of Sequoia sempervirens with diameter of 12 - 18 dm. mean frequency of pseudotransverse division was 2.3 per cm., and in 7 stems of S. gigantea 24 - 80 dm. in diameter average frequency was 2.9 per cm. of peripheral xylem accretion.

Through the middle to late growth the frequency of pseudotransverse divisions apparently is not related to ring width (Bannan (6)). Study of the peripheral growth of more than a hundred boles of Thuja occidentalis which were of similar diameter (2.5 - 3 dm.) but differed in growth rates revealed an average frequency of 2.0 divisions per cm. of xylem production when the rings were 0.3 - 1.0 mm. wide and an identical mean rate of 2.0 divisions per cm. when the rings exceeded 3.0 mm. Mean cell length, however, was significantly different, being 3.02 mm. in the slowly growing trees and 2.57 mm. in the vigorous specimens. Although pseudotransverse divisions were found to occur at mean rates of 1.5 - 3 per cm. of xylem production in most species studied, considerable variation was noted in the samplings from different trees. The occurrence of relatively high rates at points around the bole in some trees, and low rates in others of similar size and growth rate would seem to indicate the existence of inherent differences in the basic rate of anticlinal division. Differences in rate of division of a strictly local nature may also develop within the tree. Sometimes these are related to irregularities in growth, as for instance in fluted stems where the frequency of division is higher and the ratio of survival of newly formed initials is lower in the grooves than in the adjoining convex portions of the bole (Bannan (4)). Here compression may be a factor in the altered cambial behaviour in the grooves. At other times variations in rate of division occur in different sectors which are not related to other anatomical manifestations. Sometimes certain sectors of the cambium appear to be in a state of expansion whereas neighbouring areas are contracting as a consequence of high cambial cell mortality.

Preliminary investigations have revealed the presence of generic and specific differences in the basic rate of pseudotransverse division. Among the Pinaceae, Abies (A. balsamea and A. concolor) and Pseudotsuga tend to have lower frequencies of division than Tsuga (T. canadensis). In the Cupressaceae Thuja (T. occidentalis and T. plicata) and Libocedrus (L. decurrens) have less frequent anticlinal divisions than Cupressus (C. arizonica and C. glabra) or Juniperus (J. occidentalis, J. utahensis and J. virginiana). Within the genus Cupressus differences occur between the coastal C. pygmaea and the inland C. arizonica and C. glabra. On the whole xeric species have higher rates of pseudotransverse division, and shorter cells than mesic species. However, this anticipated inverse relationship between frequency of multiplicative division and cell length does not always hold. For instance, the rate of anticlinal division is appreciably higher in Tsuga canadensis than in Abies balsamea but the cambial cells are of similar length. The evidence indicates the existence of inherent specific differences in both rate of anticlinal division and cell length. It is probable that both these

features of the cambium are under some degree of genetic control. It is also manifest from interspecific comparisons that considerable independence exists between the rate of multiplicative division and cell length.

Frequency of Pseudotransverse Division, Cell Length and Cambial Cell

Survival

While high rates of pseudotransverse division usually result in a decrease in mean cell length, the cell shortening is not as much as might be expected. For example, comparison of trees of Thuja occidentalis with above average and under average rates of pseudotransverse division showed that a two and one-half fold increase in frequency of division brought about an overall reduction in cell length of only 10 per cent. The limited effect of high rates of anticlinal division on cell length is due to the operation of factors which prevent drastic reduction in cell length. Accelerated pseudotransverse divisions in the cambium are usually accompanied by faster rates of cell elongation between divisions so that the recently formed cambial cells soon become longer. Additionally, the shortest of the fusiform initials newly formed in pseudotransverse division are generally eliminated in the intracambial competition and only the longest cells survive.

In the perimeter growth of the cambium a repetitive process of cell multiplication by pseudotransverse division and intervening cell elongation is involved. In this cycle of division and enlargement cells become more prone to anticlinal division after elongation has occurred. In other words, the longest cells are most apt to divide. Many exceptions occur, however. Sometimes long cambial initials continue from year to year with little or no additional elongation and pseudotransverse divisions are very infrequent. Such fusiform initials produce radial files of tracheids with tips lying at the same level across successive annual rings, a phenomenon which is observable in strictly radial sections. Meanwhile shorter initials nearby may undergo pseudotransverse divisions in relatively rapid sequence. The frequency of anticlinal division often varies markedly in different families of fusiform initials. Another circumstance that is of frequent occurrence is the succession of a pseudotransverse division by a second such division so that the fusiform initial is quartered. When this happens the mortality of the derivatives is high, because short fusiform initials do not usually continue as such. Rather, they become reduced to ray initials or pass off into maturation. If newly formed short fusiform initials are favourably situated with respect to rays, the chance of survival is increased and they may eventually elongate to full size. Fate of fusiform initials in the severe intracambial competition is determined in part by the extent of ray contacts (Bannan and Bayly (8)). Presumably the rays are the source of required nutrients. Both ray contacts and cell length are critical factors in the continued functioning of fusiform initials in conifers.

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Recent Work on Lignified Cell Walls

On the Nature of Lignin Incrustation

There is an old controversy whether lignin is adsorbed by the cell wall in an orientated manner or whether it is incrustated in an amorphous way. From the fact that lignification does not sensibly change the birefringence of the wall, lignin was declared to be incorporated as amorphous material (1). Later LANGE (2) found that woody membranes show UV-dichroism due to lignin, and this was considered in favour of an orientated adsorption. In the electron microscope pictures of the incrustated lignin were produced (3), but no clue concerning its state of aggregation could be obtained. Only recently has this problem been solved by two doctoral theses at the Swiss Federal Institute of Technology.

H.P. FREY (4) has shown that the anisotropy of UV absorption is not intrinsic but only form dichroism due to the nature of the cell wall as a rodlet composite body with a texture of parallel submicroscopic cellulose microfibrils surrounded by the incorporated lignin. Form anisotropy is characterized by its variability depending on the refractive index of the mounting liquid with which the composite object is imbibed. For studies in UV the choice of such liquids is small, because as a rule the compounds with high refraction are aromatic and, therefore, highly UV absorbing.

For this reason this study was completed by examining the fluorescence effects of lignin. If lignified fibres are hit by short-wave light, they display a conspicuous blue difluorescence. This effect, too, has been considered as a proof of orientated lignin adsorption. But Helen HEN-GARTNER could demonstrate in her thesis (5), that here again there is only a form effect and no intrinsic difluorescence. With different series of imbibition liquids (ethanol / α -bromonaphtalene; water / Clerici solution) the fluorescence anisotropy could be reduced and finally almost completely abolished. For this investigation the difficulty consisted in finding fluids completely exempt from fluorescence.

The demonstration that UV dichroism and difluorescence of woody cell walls are mere form effects is conclusive proof of the amorphous state of incrustated lignin. This result is the more remarkable as the lignin molecule itself displays anisotropic effects in solution. But seemingly the lack of any orientation compensates that anisotropy and produces statistical isotropy in the cell wall lignin.

Lignin Distribution in the Cell Wall

In cross-sections of spruce wood UV absorption curves, obtained with monochromatic mercury light 280 m μ across the cell wall along a line from one cell lumen to the next, display a high maximum in the region of the middle layer (i.e. middle lamella and primary walls) and symmetrical slopes extending into the adjacent secondary walls. (see (6) p. 173). From this finding LANGE (7) concluded the content of lignin to be highest in the middle lamella, decreasing on both sides towards the cell lumina; this means that the outer part of the secondary wall may contain a considerably higher amount of lignin than its inner part.

These considerations neglected the influence of diffraction and the high numerical aperture of the high objectives used (4). As seen in the dark-field microscope, light scattering is much stronger in the middle layer than in the secondary wall, with the result of a loss of light intensity in the middle layer and a corresponding gain in the adjacent parts of the secondary wall. The high aperture of the objective produces a similar effect, because the oblique light beams furnish no adequate illumination for microphotometry. As a matter of fact this method needs bundles of rigorously parallel light, so that a beam passes only through the middle layer or only through the secondary wall; but oblique beams entering the object in the neighbourhood of the phase boundary between middle layer and secondary wall traverse adjacent parts of both wall layers so that no clear cut measurement is possible.

Using fluorescence photometry instead of UV photometry, these errors can be avoided or diminished and their extent can be calculated in the UV absorption measurements. Combining these two procedures Prof. RUCH and Miss HENGARTNER (8) can show that both methods yield the same result, viz. that the lignin content does not sensibly vary within the secondary wall and that the amount of lignin is about twice as high in the middle layer as in the secondary wall. This is in accordance with the size of available submicroscopic interfibrillar space in wall layers with a dispersed (primary wall) or a parallel (secondary wall) texture of their cellulosic microfibrils. By using the interference microscope which allows the masses involved to be determined, the relative figures obtained can be converted into absolute lignin concentrations. The following contents are thus found for jute fibres (8):

middle layer 7,3 % ± 1,1 % lignin by weight
 secondary wall 3,4 % ± 0,5 % lignin by weight.

A. Frey-Wyssling

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Book Reviews

Festschrift Albert Frey-Wyssling
 Edited as : Beiheft zu den Zeitschriften des Schweizerischen Forstvereins No. 30 (1960) 300 pages Sw.Fr. 15.--

available from: Geschäftsstelle des Schweizerischen Forstvereins, Englischviertelstrasse 32, Zurich 7/32.

Professor Dr. A. Frey-Wyssling, our Secretary Treasurer, recently had his sixtieth birthday. On this occasion he was presented with a book published in his honour by his closest collaborators, containing 25 original contributions on morphology, genetics and physiology. This publication is eloquent evidence of his variegated scientific work.

Index of contributions:

Morphology and genetics: BOSSHARD, H.H.: Fluoreszenzmikroskopische Untersuchungen in Spanplatten. BUCHER, H. : Ueber morphologische Untersuchungen in der Holzchemie und die Diffusion von Flüssigkeiten in Fichtenholz. CHRISTEN, H.R. : Gyropaigne Skuja, eine bemerkenswerte Gattung der farblosen Eugleninen. KOBEL, F. : Die Entstehung neuer Blütenfarben und Blütenzeichnungen bei Primula malacoides

Franchet. MEIER, H. : Ueber die Feinstruktur der Markstrahltracheiden von Pinus silvestris L. MUEHLETHALER, K.: Die Feinstruktur der Zellulosemikrofibrillen. NICOLAI, E. : Untersuchungen über Zellwandstrukturen bei Algen. RUCH, F. und HENGARTNER, H. : Quantitative Bestimmung der Ligninverteilung in der pflanzlichen Zellwand. RUTISHAUSER, A. : Fragmentchromosomen bei Crepis capillaris. SCHOCH-BODMER, H. : Spitzenwachstum und Tüpfelverteilung bei sekundären Fasern von Sparmannia. VOGEL, A. : Zur Feinstruktur der Drüsen von Pinguicula. WAELCHLI, O. : Mikroskopischer Nachweis von mikrobiologischen Schäden bei Baumwolle. Plant physiology: ARTHO, A.J.: Evaluation of Certain Characteristics of Connecticut Shade Tobacco. BONNER, J. : The Mechanical Analysis of Auxin-Induced Growth. EICHENBERGER, E. : Ueber das Wachstum eines Säulenkaktus Cereus horridus. HUTER, R. : De différents moyens utilisés pour éviter la formation ou pour empêcher le développement des bourgeons axillaires de la plante de tabac après l'écimage. KESSLER, G. : Chemische Struktur und enzymatische Synthese der Kallase. LEIB-UNDGUT, H. und HELLER, H. : Photoperiodische Reaktion, Lichtbedarf und Austreiben von Jungpflanzen der Tanne. MATILE, P. : Ueber die Beeinflussung der Atmung nicht assimilierender Pflanzenteile durch das Licht. MOOR, H. : Reaktionsweisen der Pflanzen auf Kälteeinflüsse. NEUKOM, H. und DEUEL, H. : Ueber den Abbau von Pektinstoffen bei alkalischer Reaktion. THIMANN, K.V. and GRUEN, H.E. : The Growth and Curvature of Phycomyces Sporangiohores. WALTZ, P. : Nornikotin bei Inlandtabaken. WANNER, W. : Phosphatverteilung und Transport in keimendem Mais. ZIMMERMANN, M.H. : Longitudinal and Tangential Movement within the Sieve-Tube System of White Ash (Fraxinus americana L.).

H.H.F

Symposium on treated Wood for Marine Use -- STP 275

70 + v pages, Hard Cover, 6 x 9", \$ 2.50

A major problem in harbor development and especially in maintenance is the prevention of marine borers from seriously shortening the life of wood piling. These voracious wood-boring organisms attack and destroy millions of dollars worth of wood piling annually. The seriousness of the problem varies in different parts of the world and in different harbors, depending in the salinity of the water.

Treatment with creosote and other coal-tar solutions has long been considered the most effective means of marine borer protection. Even this type of treatment has not been fully effective. Consequently, research continues in the attempt to solve this costly problem.

ASTM Committee D-7 on Wood, in recognition of the problem, has sponsored this symposium on the subject of wood and treatments of wood for marine use. The volume is well illustrated and contains numerous references.

A.L. Batik

Zurich, February 1961

Edition 200 copies

Edited by the Secretary Treasurer

Zurich, Switzerland

Office: Laboratorium für Holzforschung E.T.H.,

Universitätstrasse 2

EDITORIAL

Our News Bulletin has become a respectable publication which is read not only by the members of our Association, but also subscribed to by libraries, experimental stations, establishments and plants of wood industry. As a consequence we thought it advisable to separate communications on our domestic affairs from the more scientific section. This is done by a mimeographed leaflet which members of the Association will find enclosed in this number. The procedure has been started with the last 1961/1 number of the bulletin, and since no objections have been raised by any of our members, we intend to continue this new pattern.

Besides wood technology, wood chemistry becomes increasingly interested in micro-morphological problems. SPERLING AND EASTERWOOD (Applied Polymer Science 6.25; 1960) show that the troubles of haze and bad filterability in solutions of wood cellulose acetate is not only due to impurities of fibre rests, but above all to a nearly monodisperse fraction of spherical or potato-shaped particles with about 0,3 µ diameter in dispersion (light scattering) or 0,1 µ dry (electron microscopy). They comprise about 1 % of the total mass and contain hemicelluloses, principally xylan and mannan. This morphological and chemical behaviour recalls certain properties of the warts which coat the tertiary membrane in certain Gymnosperm tracheids and Angiosperm wood fibres. In a letter to your Secretary Treasurer, the authors ask for the wood anatomist's comment on this question. Tempting as an identification of the involved particles (which cellulose chemists call "gels") with cell wall warts may be, especially since the wood pulp used was from pine whose tracheids are richly dotted with submicroscopic inside excrescences, there is a serious difficulty for such an interpretation: Unexpectedly, a cellulose acetate solution of linters contains the same "gel fraction" of submicroscopic insoluble particles as wood cellulose! Therefore, I wrote to Dr. SPERLING (The Buckeye Cellulose Corporation, Memphis, Tenn. U.S.A.):

"I am astonished that cotton linters produce a result similar to pine pulp; because there are no warts in cotton hairs. I never looked at linters which are short cotton hairs of only some mm, instead of some cm length. But I cannot imagine that warts lacking in cotton hairs would occur in linters!

"As to recent publications on warts of woody fibres I would mention: WARDROP, A.B., LIESE, W. and DAVIES, G.W.: The Nature of the Wart Structure in Conifer Tracheids, Holzforschung 13.115 (1959).

"These authors have isolated warts mechanically. They find globular bodies which absorb UV and display a staining reaction of the lignin (e.g. phloroglucin/HCl). For their study they have chosen tracheids of Actinostrobus with large warts visible in the light microscope. It would be of interest to know whether your particles contain residues of lignin. Further you should examine their UV absorption spectrum which could give some information on the nature of their compounds.